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JAMES COOK UNIVERSITY AUSTRALIA

Spatial variability and covariability of chlorophyll
and zooplankton on the Great Barrier Reef.

Thesis submitted by
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for the degree of Doctor of Philosophy in
the Department of Marine Biology at
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Finally, I am indebted to my supervisors, Dr. Miles Furnas and Dr. John Collins for their advice and encouragement throughout this project.

ABSTRACT

The work described in this thesis has two objectives: to quantify the spatial variability of phytoplankton biomass, zooplankton biomass and zooplankton community structure over spatial scales from 10-1000 km in relation to the large-scale structure of the Great Barrier Reef, and to quantify the covariability of zooplankton biomass and community structure with phytoplankton biomass in Great Barrier Reef shelf waters.

Near-surface chlorophyll concentrations and zooplankton assemblages were concurrently surveyed between 14° and 22.5°S on the Great Barrier Reef, Queensland, between Jan 1987 and Feb 1989 using underway continuous sampling techniques. Chlorophyll concentrations, ranging from 0.08 to 1.57 ug l^{-1}, were highest near the coast and lowest in the Coral Sea, with little difference between the inner and outer parts of the shelf. Mean concentrations of chlorophyll increased with latitude, from 0.31 ug l^{-1} between 9.5°-16.5°S to 0.76 ug l^{-1} between 20°-21°S. Chlorophyll concentrations on the outer shelf were higher in the wet season than in the dry season, a change attributed to seasonal differences in nutrient supply.

The spatial variability of chlorophyll was characterised using two techniques; the chlorophyll coefficient of variation which characterised the magnitude of chlorophyll spatial variability in discrete intervals, and time series analysis which characterised the distribution of variability across a continuum of spatial scales. The chlorophyll coefficient of variation characterised the extent of spatial variability over the length scales 15 m to 8000 m. Close to individual reefs small but sharp changes in chlorophyll concentration were commonly observed. The localized reef-associated increases in chlorophyll spatial variability appear to result from the movement of chlorophyll enriched water off reefs. The high chlorophyll variability close to the coast was attributed to a steepening of the onshore-offshore chlorophyll gradient in shallow waters.

Time series analysis techniques characterized the distribution of spatial variability of chlorophyll over a continuous range of spatial scales; from 0.5-10 km. The distribution of chlorophyll and temperature spatial variability over these scales did not differ regionally. This large-scale uniformity of the distribution of chlorophyll spatial variability stands in contrast to the marked regional differences in reef structure and density, features thought to affect water movement and thence chlorophyll spatial variability.

Zooplankton samples, integrated over 8 km subtransects, were collected concurrently with chlorophyll measurements. Both zooplankton biomass and overall abundance decreased offshore, but neither changed significantly with latitude or with season. Copepod abundances were positively correlated with chlorophyll concentration at both small (8, 16 and 32 km) and regional (100-200 km) scales. Zooplankton biomass exhibited the same cross-shelf trend as chlorophyll concentration, but was not well correlated with chlorophyll concentration at small or regional scales.

Individual taxa differed in their cross-shelf patterns of abundance, but at the sampling scale (8 km), none were significantly correlated with chlorophyll or its spatial variability. At the regional scale (100-200 km) there was good correspondence between mean abundances of most herbivorous zooplankton and the mean chlorophyll concentration.

Zooplankton taxa fell into three distinct cross-shelf communities; inshore, outer shelf, and shelf edge. These communities tended to be restricted to particular geographic regions, the Great Barrier Reef lagoon, the reef matrix and the East Australian Current respectively, and were latitudinally coherent. The inshore community was dominated by small herbivorous copepods, the outer shelf community by omnivorous copepods and the shelf edge community by small carnivorous copepods. The abundance of the inshore community, largely small herbivorous copepods, paralleled the cross-shelf gradient of surface chlorophyll concentration, suggesting a causal link. This inference was reinforced by the atypical situation in the Pompey zone. There, the highest chlorophyll concentrations were found on the outer shelf, and were matched by high densities of the normally inshore herbivorous zooplankton. The factors controlling the other two communities were not clear.

Local relationships between chlorophyll concentration and zooplankton were investigated more directly using observations made after a cyclonic disturbance of inshore waters. Chlorophyll concentrations changed little during the two week post-cyclone sampling period, and were similar to concentrations in inshore samples taken at other times. Conversely zooplankton standing crop and abundance increased significantly within two weeks post-cyclone, although no change in community structure occurred. The zooplankton changes suggested that zooplankton abundance was food limited in inshore waters.

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DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary eduction. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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Chapter 1. Spatial variability and covariability of chlorophyll and zooplankton on the Great Barrier Reef.

INTRODUCTION

The distribution of plankton in the oceans is known to be spatially variable (reviewed by Fasham 1978a). With the use of appropriate sampling (Cassie 1959, Herman 1988) and statistical techniques (Platt and Denman 1975a), it has become apparent that phytoplankton and zooplankton patchiness occurs over a wide range of spatial scales (Haury **et al.** 1978). Spatial patchiness of organisms has ecological implications; both advantages and disadvantages may accrue to individuals from a particular degree of aggregation (e.g. reduction in predation, increase in competition: Longhurst 1981, Hamner 1988). Some zooplankton appear to be adapted to feed upon phytoplankton at a particular degree of spatial variability (Dagg 1977, Borchers and Hutchings 1986), and phytoplankton may differ in their ability to grow under different regimes of nutrient variability (Sommer 1985).

Consequently phytoplankton and zooplankton populations present in a region may represent a response not only to the physical, chemical and biological conditions, but also to the spatial variability of those conditions. The characterization of the plankton populations and their spatial variability, together with physical and chemical conditions in the same region, provides a foundation for understanding their biogeography. At a more pragmatic level, a further consequence of plankton spatial variability is that plankton found in a sample may differ from the plankton in nearby samples. The quantification of the spatial variability of plankton in an area can lead to more effective and representative sampling in that area.

By definition, plankton are passively moved with the water in which they live. Their spatial variability therefore tends to reflect that of the spatial variability of water movement (Horne and Platt 1984). Water movement is variable over a large range of spatial scales, from molecular diffusion to ocean currents, and influences plankton spatial variability over most of those scales (Mackas **et al.** 1985). In open waters, eddies at the scale 50-100 km appear to be largely generated by meandering and horizontal shear of large scale structures (Mackas et al. 1985). Eddies at any particular spatial scale exist for only a limited time before they are twisted and distorted into smaller eddies and finally dissipated as heat (Harris 1986). This evolution of eddies in open water gives rise to a characteristic range of eddy sizes, with more variability across large scales than across smaller scales (Platt and Denman 1975b).

Accompanying conservative tracers such as temperature and phytoplankton, follow the same distribution of spatial variability.

Although the observed spatial distribution of plankton is influenced by water movement, it can also be modified by biological activity. Different sorts of biological processes, e.g. physiological adaptations, behavioural responses, population growth and change in community structure, take different times to occur, and can be arranged in a hierarchy based on the time scales they occur over (reviewed by Mackas **et al.** 1985). As the temporal persistence of eddies is related to their spatial scale, i.e. larger features persist longer than smaller ones (Harris 1986), only rapid biological adaptations will be associated with small scale chemical or biological variability. Behavioural responses and physiological adaptations occur more quickly than population growth, and will tend to be the most important biological influences on the plankton spatial variability at small spatial scales (below approximately 100 m)(Harris 1980). Examples of this are the small scale patchiness of zooplankton that result from swarming behaviour (Hamner and Carleton 1979), and surface patchiness of plankton associated with Langmuir circulation (Powell **et al.** 1975, Riley 1976). Population growth takes longer and becomes the most important biological activity influencing the spatial variability of plankton at scales larger than 100 m (Mackas **et al.** 1985). At these larger scales, plankton spatial variability may arise as a result of spatial differences in growth rate in response to resource patchiness and in predation. Although resource patchiness may occur at smaller scales it may be too ephemeral to permit population growth (Harris 1980).

At spatial scales larger than approximately 10 km, eddies persist long enough for relative differences in plankton growth to effect changes in the community structure. This phenomenon can give rise to the development of distinct plankton flora and fauna over spatial separations greater than 10 km. For example, on the shelf off Vancouver Island, Canada, Mackas (1984) found that the correlation length of zooplankton community structure, a measure of the distance over which the community changed by a certain amount, ranged from 35 to 65 km. In the same region, the correlation length of zooplankton biomass was 20 to 35 km, indicating that community structure was changing over larger spatial scales than biomass.

The spatial variability of phytoplankton biomass on continental shelves can be strongly influenced by the physical processes that occur in such areas, e.g. enhanced vertical mixing (Walsh 1976, Kahru **et al.** 1981, Bowman **et al.** 1983), by river plumes (Mackas **et al.** 1980) and by fronts (Parsons **et al.** 1981, Cox **et al.** 1982,Wolanski and Hamner 1988).

These processes can generate phytoplankton biomass patchiness that is far more pronounced than that encountered in open oceans. Under such coastal conditions there is often a strong correlation between zooplankton and phytoplankton biomass over mesoscale distances (100's of metres to 10's of kilometres) (Pingree **et al.** 1975, Mackas **et al.** 1980). This cannot be taken to indicate that food availability is theprimary determinant of zooplankton spatial patchiness in coastal regions, as zooplankton are subject to the same physical processes as are phytoplankton. In tropical waters, the opposite appears to apply. In some tropical shelf waters, phytoplankton production appears to be underutilized by herbivores (Longhurst 1983, Walsh 1988). Contrastingly, in tropical open oceans, production and consumption are in a closer balance (Heinrich 1977). Huntley and Boyd (1984) suggested that the regions in different oceans where food limitation of zooplankton would occur could be identified by relating data on zooplankton feeding and respiration to known chlorophyll concentrations. Using this approach they concluded that, in both temperate and tropical seas, the growth of herbivorous zooplankton was likely to be food limited in oceanic waters but not in coastal waters.

Although the spatial variability of water movement affects both phytoplankton and zooplankton, it does not indicate that the places in which zooplankton are in greater abundance will necessarily coincide with those of phytoplankton, or vice versa. The covariance of zooplankton with phytoplankton depends on the biological interactions between the two communities, such as the extent of food limitation of herbivorous zooplankton and the impact of grazing on phytoplankton populations. The importance of these processes on zooplankton and phytoplankton populations will depend on the relative strength of food limitation and grazing compared to other processes affecting population size, e.g. nutrient limitation of phytoplankton growth.

The relationship between zooplankton biomass, zooplankton community structure, and phytoplankton biomass is made more complex by spatial and temporal fluctuations in phytoplankton biomass. Spatial (Wiens 1976) and temporal (Huston 1979) fluctuations of resources are conjectured to influence biomass or community structure as individual species track resource or environmental variability with different efficiency (Dagg 1977, Borchers and Hutchings 1986). Consequently, even though the mean levels of resources in two places may be similar, community structure may differ in response to differences in resource variability (Caswell 1978).

Despite the influence of physical processes on both phytoplankton and zooplankton spatial variability, it may be possible to make inferences about the influence of competition on zooplankton biomass and community structure. Under consistent resource limitation, biomass will be strongly linked to the level of resources

(Holling 1973, Schoener 1974), and the ranking of species will be spatially uniform (Wiens 1977, Harris 1983). Under conditions in which resource fluctuations or environmental variability is greater, biomass will be less closely related to resource levels (Wiens 1977), and the community structure will differ spatially, as in each region it will be determined by the prevailing and historical conditions (Hayward and McGowan 1979, McGowan and Walker 1979).

STUDY OBJECTIVES

The work described in this thesis had two objectives; 1) to quantify the spatial variability of epi-pelagic phytoplankton biomass, zooplankton biomass and zooplankton community structure in the open shelf and inter-reef waters of the Great Barrier Reef over spatial scales from 0.03-1000 km, and 2) to examine the covariability of phytoplankton biomass with zooplankton biomass and community structure.

The horizontal spatial variability of near-surface phytoplankton and zooplankton biomass and community structure were taken as estimates of their three dimensional spatial variability. In pelagic ecosystems vertical physical and chemical gradients are usually much more intense than horizontal ones due to the presence of a thermocline or nutricline, giving rise to pronounced vertical gradients of biological variables (Harris 1983). On the GBR shelf the water column is usually well mixed. This may be illustrated by reference to a previous oceanographic survey carried out in GBR waters. In a series of cruises during 1983, Furnas and Mitchell (1984) measured water temperature, nutrient and chlorophyll a concentrations through the water column at stations along a cross-shelf transect. The transect was sampled 20 times during the course of the year. Data from seven of these transects is presented here, from cruises in January, February, March, June, August, October and December (Fig. 1.1). The first three profiles, made during the summer months, show change in temperature and chlorophyll-a concentration (hereafter referred to as chlorophyll) with depth. These profiles probably result from intrusion of colder water from the Coral Sea onto the shelf, a phenomenon that primarily occurs during the summer months (Furnas and Mitchell 1986). Intrusions rarely extend inshore further than the reef matrix, and rarely come within 10 m of the surface (Andrews 1983, Furnas and Mitchell 1986). The water column over the rest of the shelf tends to be vertically uniform, with an absence of thermoclines or nutriclines (Andrews 1983, Furnas and Mitchell 1986). Transects later in the year showed little vertical structure (Fig 1.1), and overall the change in temperature and chlorophyll through the water column was not great.

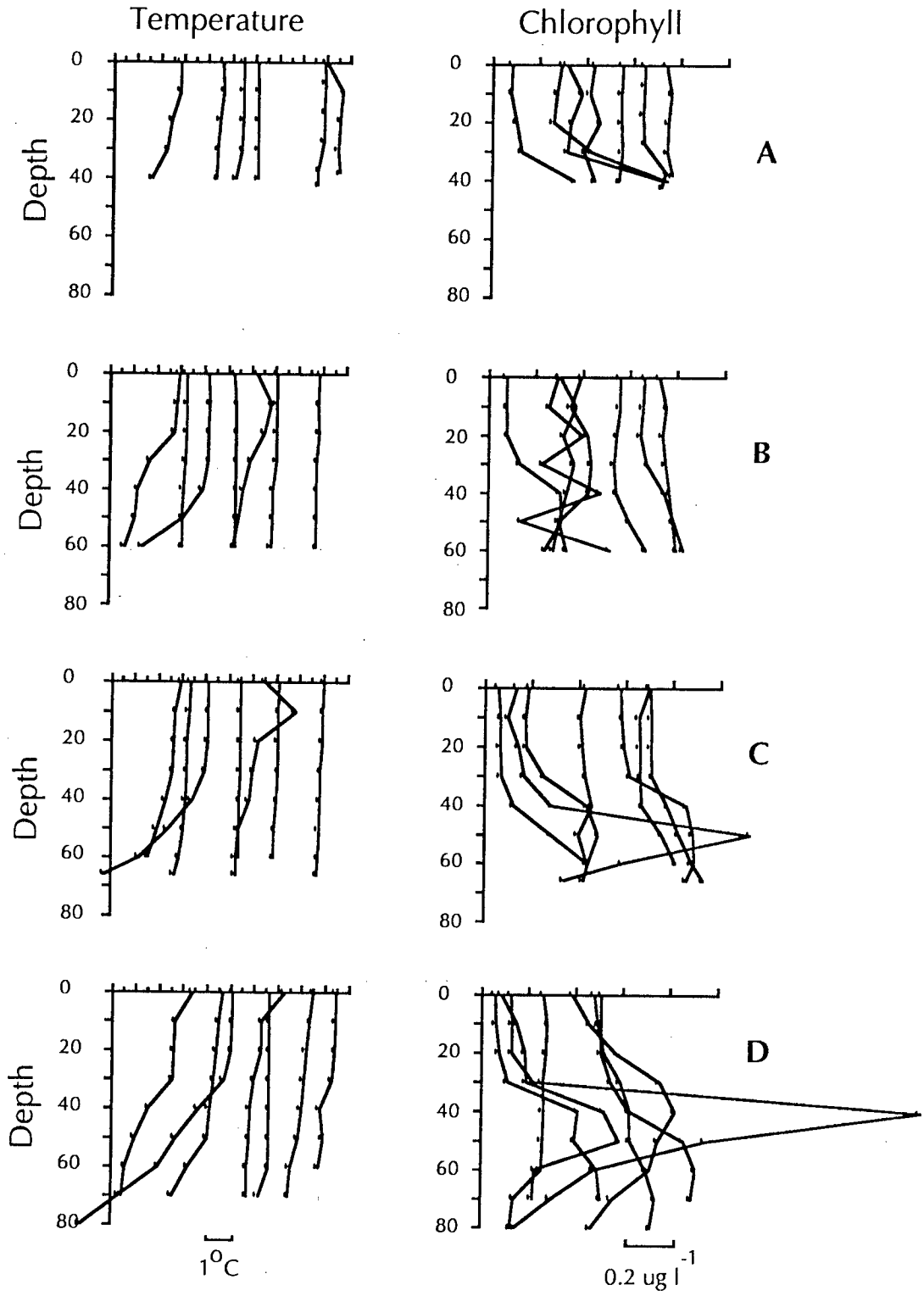


Figure 1.1 Vertical profiles of temperature and chlorophyll concentration at four cross-shelf stations in the central part of the GBR, sampled 7 times during 1983. Station A is close to the middle of the shelf, progressing to station D at the shelf edge. Change in these variables through the water column can be assessed by reference to the scale on the top axis of each plot (temperature: each tic = 0.5 ° C. chlorophyll: each tic = 0.2 ugl-1), or from the legend at the bottom. Data from Furnas and Mitchell (1984).

The extent of vertical changes in water temperature, chlorophyll and nitrate concentrations was summarized for all 20 cruises by taking the difference between top of the water column and bottom of the water column values for these variables at each station (Fig. 1.2). In more than 50% of stations (total 94) chlorphyll concentration differed by less than 0.3 ug l^{-1} top to bottom and temperature by less than 0.5 ^{o}C. Furthermore, these data probably give an inflated impression of the mean top to bottom difference in these variables for the whole GBR shelf, as 75% of these transects were made during the four months of the year in which intrusions are most likely, and the stations were located in the reef matrix, the place where intrusions occur. Data from other parts of the GBR shelf also show little vertical change in water column variables (Wolanski and Jones 1981, Mitchell **et al.** 1982, Wolanski **et al.** 1984). It can be concluded therefore that phytoplankton and zooplankton samples taken close to the surface would rarely be influenced by vertical structure in the water column, and would be representative samples of the epi-pelagic flora and fauna.

Measured concentrations of chlorophyll on the GBR shelf (Andrews and Gentien 1982, Revelante and Gilmartin 1982, Andrews 1983, Furnas and Mitchell 1986) are higher that those found in the oligotrophic central ocean provinces (Hayward and McGowan 1985, Dandonneau and Gohin 1984), but lower than those measured on tropical shelves such as the Peruvian shelf on which active upwelling occurs (Walsh **et al.** 1971, Guillen and DeRondan 1972). These low concentrations may arise because upwelling on the GBR shelf is weak (Andrews and Gentien 1982) and river inflows are relatively small compared to those on other tropical shelves (e.g. Walsh 1988). Chlorophyll concentrations on the GBR shelf therefore fall between those in ecosystems in which zooplankton biomass appears to be food limited (e.g. oceanic ecosystems, Heinrich 1977) and those in ecosystems in which zooplankton biomass is not well correlated with phytoplankton biomass (e.g. some tropical shelves, Longhurst 1983, Walsh 1988).

Spatial variability of plankton on the GBR shelf, and the degree of covariability of zooplankton with phytoplankton biomass were investigated by addressing the following questions:

1. What is the variability of phytoplankton biomass on the GBR shelf over spatial scales ranging from 30 m to 1200 km?
2. Does the spatial pattern of phytoplankton biomass vary in relation to the marked cross-shelf and latitudinal changes in reef density on the GBR shelf?
3. Do zooplankton form recurrent assemblages, and do these assemblages correspond to different parts of the GBR; e.g. reef matrix versus lagoon, open reef matrix versus dense reef matrix?

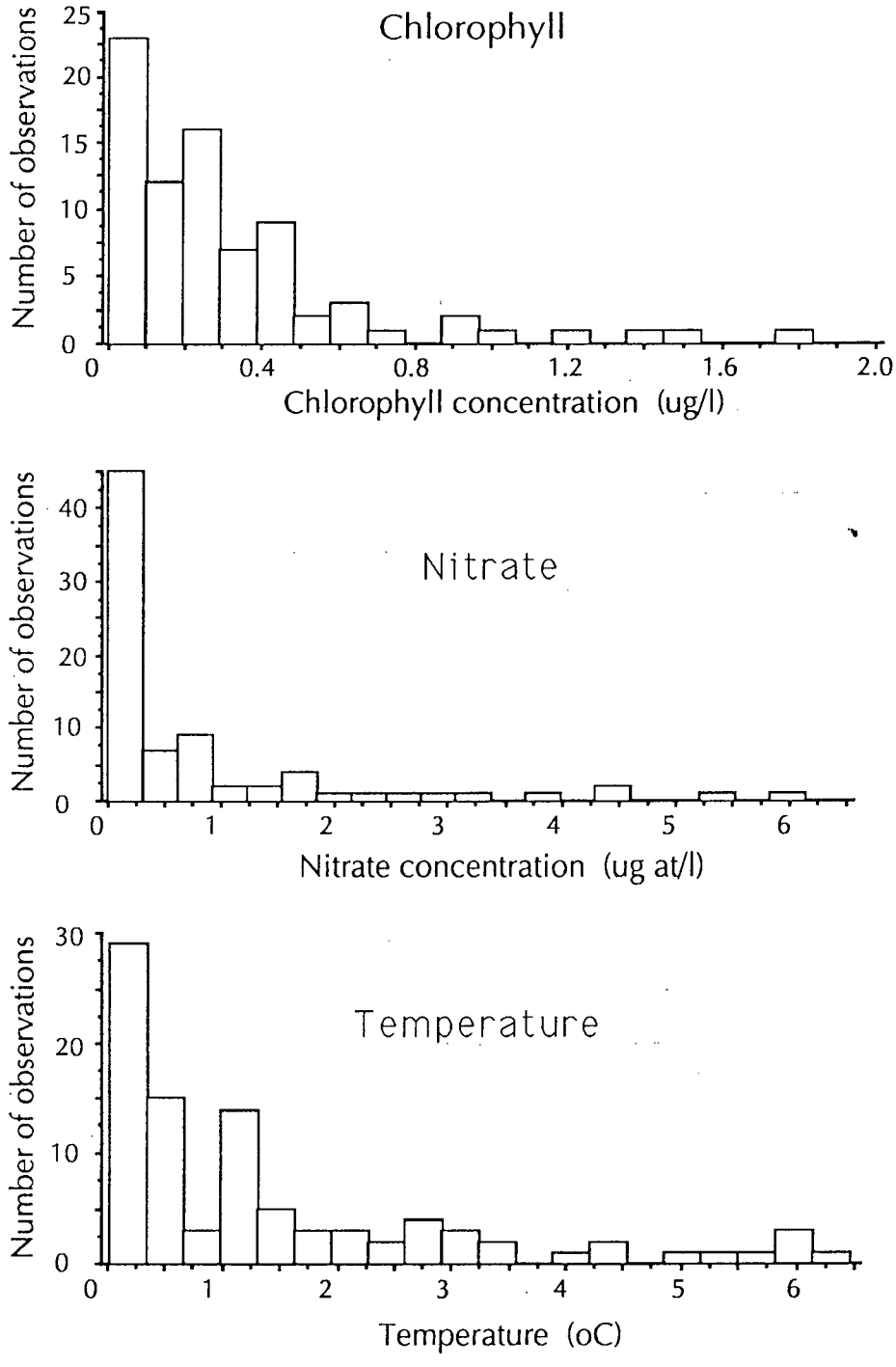


Figure 1.2 Histograms of the difference between top of the water column and bottom of the water column values for 94 stations occupied in the central region of the GBR, 1983. A. Temperature, ^{o}C. B. Chlorophyll, ugl^{-1}, and C. Nitrate, ug atl^{-1}. Data from Furnas and Mitchell (1984).

4. Are the patterns of zooplankton community structure and phytoplankton biomass similar, i.e. can the zooplankton community structure be related to phytoplankton biomass or its spatial variability?
5. Can the abrupt effects of a cyclone on inshore waters be used to assess the effects of changes in physical and chemical water variables on phytoplankton biomass, and ultimately on the zooplankton biomass and assemblage structure?

PHYTOPLANKTON IN THE GBR

The first studies of GBR phytoplankton were carried out during the Great Barrier Reef Expedition 1928-29 by Marshall (1933). Densities of phytoplankton were found to be much lower than in samples taken in temperate waters off Plymouth, Loch Striven (Scotland), and La Jolla (California), and exhibited much smaller seasonal changes in abundance (Marshall 1933). Diatoms were the most numerous group of phytoplankton counted, and their increases in abundance were correlated with periods of strong winds.

Subsequent work on GBR phytoplankton communities has confirmed Marshall's (1933) observations on the dynamics of net phytoplankton (Revelante and Gilmartin 1982, Revelante **et al.** 1982, Furnas and Mitchell 1986). Advances in microscopy and counting techniques reveal that nano- and picoplankton, primarily microflagellates, are more abundant than net phytoplankton and dominate biomass on most occasions (Furnas and Mitchell 1986).

Chlorophyll concentration, has been measured at a large number of stations on the GBR shelf, and in this study will be taken as a proxy of phytoplankton biomass. This assumption should be made with caution as the ratio of chlorophyll to total organic carbon in a phytoplankton cell can vary with such factors as temperature (Yoder 1979), species composition (Chan 1980), nutrient concentration and irradiance (Bannister and Laws 1980). However, under conditions of relatively constant temperature, nutrient supply and irradiance, such as occurs in clear nutrient-poor tropical surface waters, the assumption made here of an invariate chlorophyll to total carbon ratio seemed reasonable.

Phytoplankton biomass on the GBR, as measured by chlorophyll concentration, is low (Wolanski and Jones 1981a, Andrews and Gentien 1982, Mitchell 1982, Revelante and Gilmartin 1982, Revelante **et al.** 1982, Andrews 1983, Furnas and Mitchell 1986). Most chlorophyll measurements have been made in the GBR region between latitudes 18° and 20°S, and less is known of chlorophyll concentrations in regions further north or south.

The spatial variability of chlorophyll on the GBR shelf has not been specifically characterised, though a crude estimate can be made from the variation between stations and at discrete depths at each station. Comparisons of chlorophyll concentrations from stations across the shelf and from different depths in the water column (20 - 80 m), indicate that the horizontal and vertical variability is generally small, two to fivefold. Exceptions occur when bodies of Coral Sea water are intruded onto the continental shelf (Furnas and Mitchell 1986), when cyclones affect the shelf (Furnas 1989), and possibly following floods. Again, these observations are largely confined to the central section of the GBR between latitudes 18° and 20°S.

Chlorophyll concentrations on other tropical shelves without upwelling are also low (Newell 1973, Tranter and Leech 1987). Again, the horizontal spatial variability of phytoplankton biomass on tropical shelves has not been directly characterised but may be estimated over spatial scales of kilometres by comparisons between stations. Phytoplankton biomass on tropical shelves varies up to thirty fold on shelves with upwelling (Guillen and DeRondan 1972, Ilahude **et al.** 1990) but only twofold on shelves unaffected by upwelling or river outflows (Tranter and Leech 1987).

ZOOPLANKTON IN THE GBR

Zooplankton in waters of the GBR shelf were also first investigated during the 1928-29 Great Barrier Reef Expedition (Russell and Colman 1934, Farran 1936, 1949). They recorded that numerical abundances of zooplankton were similar to those in northern temperate shelf waters, and copepods comprised approximately the same proportion of the zooplankton on the GBR (71%) that they did in northern waters (Russell and Colman 1934). There was a summer increase in zooplankton numbers on the GBR shelf, but it was much smaller than that seen in samples taken from lightships on Northern European continental shelf (Russell and Colman 1934, Farran 1949). The species composition of zooplankton on the GBR shelf differed from that in European shelf waters, and the copepod species present on the GBR were smaller than those at higher latitudes (Russell and Colman 1934). Carnivorous zooplankton were twice as abundant in relative terms in GBR waters as in European shelf waters. Russell and Colman (1934) also noted that the GBR lacked the spring diatom bloom that commonly occurs in high latitude waters, and suggested that throughout the year the zooplankton populations were at the maximum that the phytoplankton could support.

Little further work was done zooplankton in the GBR until the 1970's. Since then there have been a number of studies dealing with demersal zooplankton and plankton close to reefs (Sale **et al.** 1976, Alldredge and King 1977, Hamner and

Carleton 1979, Hamner and Hauri 1981, Jacoby and Greenwood 1988), but relatively few studies on zooplankton in inter-reefal waters (Sammarco and Crenshaw 1984, Williams **et al.** 1988). These two latter studies confirmed that there is a cross-shelf change in zooplankton abundance and community structure. In both studies, cross-shelf changes were associated with changes in chlorophyll concentrations.

Spatial variability in the zooplankton biomass and assemblage structure on the GBR shelf is known to occur over distances ranging from a few metres (Hamner and Carleton 1979, Alldredge and Hamner 1980, Sale **et al.** 1976, Alldredge and King 1977) to tens of kilometres (Russell and Colman 1934, Sammarco and Crenshaw 1984, Williams **et al.** 1988). The studies focusing on spatial scales up to hundreds of metres have largely been done in the proximity of reefs or islands and zooplankton community change has been associated with differences in reef morphology or substratum (Sale **et al.** 1976, Alldredge and King 1977). Biomass and community structural changes in open waters have been attributed to changes in phytoplankton biomass (Sammarco and Crenshaw 1984) and season (Russell and Colman 1934, Sammarco and Crenshaw 1984, Williams **et al.** 1988). These three latter studies have all been based on discrete samples taken at only a small number of stations. Little is known of the spatial coherence of zooplankton community structure, or of changes in zooplankton biomass over scales of tens to hundreds of kilometres.

STUDY APPROACH

The Great Barrier Reef (GBR); which comprises over 2500 individual reefs and extends along the shelf for over 2000 km, is likely to be a major influence on the spatial variability of phytoplankton and zooplankton. Although the reef structure at a regional scale is complex, different parts of the GBR may be identified in which reef density and reef type have a degree of uniformity (Maxwell 1968, Pickard **et al.** 1977). Most of the reefs are located on the outer half of the continental shelf. This large scale structure is consistent along the length of the GBR even though the shelf width ranges from 23 to 260 km. The extent to which the reefs form a physical barrier to cross-shelf water movement also varies latitudinally from 10% to 90% (Pickard **et al.** 1977).

Chlorophyll spatial variability has been linked to the spatial variability of water turbulence (Platt and Denman 1975a, Wroblewski and O'Brien 1976), based on the assumption that phytoplankton act as passive particles (Platt and Denman 1975b). Much of the work on the spatial variability of water movement and the associated spatial variability of chlorophyll has been done in open oceans (e.g. Platt and Denman 1975a, Denman 1976, Fasham and Pugh 1976, Horwood 1978). The generation and

dissipation of water turbulence on continental shelves may be restricted by bathymetry and coastal topography, as enclosed water bodies like lakes can support eddies only as large as half their smallest linear dimension (Boyce 1974). Consequently water bodies that are physically bounded will have a restricted range of eddy sizes. The range of chlorophyll spatial variance should accordingly be modified in shelf waters (Harris 1983), or within the reef matrix, through its dependence on the spatial variance of horizontal water turbulence.

Within the reef matrix, the open ocean model of the orderly cascade of turbulence from large spatial scales to small (Harris 1986), and the associated cascade of plankton spatial variability, is unlikely to be appropriate. The circulation of water around reefs is complex (Hamner and Hauri 1981, Wolanski **et al.** 1984, Wolanski and Hamner 1988). Eddies and the associated plankton patchiness may be stretched out into long filaments by currents in the vicinity of reefs and islands (Wolanski **et al.** 1984, Wolanski 1988), or there may be an aggregation of plankton close to a reef as a result of the current pattern (Hamner and Hauri 1981, Hamner and Carleton 1979, Wolanski **et al.** 1989, Black **et al.** 1990). Reefs, as well as generating or disrupting plankton patchiness by their influence on the current patterns around them, may also have a more active influence on the plankton in their vicinity. Tidal flushing of reefs may move reef plankton into inter-reefal waters (Wolanski **et al.** 1989, Black **et al.** 1990), or reef predators may remove plankton from waters that move past or a reef (Hamner **et al.** 1988).

The effect of the GBR reef matrix on plankton patchiness may also vary latitudinally as the density of the reef matrix varies. For example, in the northern part of the GBR there is an almost complete barrier of reefs along the edge of the continental shelf, restricting tidal water movement onto the shelf to narrow openings. Strong currents flow through these openings, and eddies form on the inside of the reef barrier (Wolanski **et al.** 1988). In the central third of the GBR, reefs are more widely separated and the strong shelf edge tidal currents evident further north do not occur.

Between the matrix of reefs and shore, and extending the length of the GBR, is a region of relatively open water known as the GBR lagoon. In the northern part of the GBR the reef matrix is close to the the coast and the lagoon is narrow (9 to 25 km), widening in central and southern parts of the GBR (60 to 120 km, Maxwell 1968). Within the GBR lagoon water movement is less constrained than in the reef matrix and larger eddies and associated plankton patchiness is theoretically possible. However, water entering the GBR lagoon as a result of tidal water movement or long-term residual currents, must pass through the reef matrix, and the plankton patchiness in the lagoon may be affected by this history.

Taking these structural features of the GBR into consideration, three geographical regions, each with a distinct regime of horizontal water turbulence and therefore of plankton spatial variability, were expected; the reef matrix, the GBR lagoon and oceanic waters off the continental shelf.

In oceanic waters of the Coral Sea, chlorophyll spatial variability should be continuously distributed over a wide range of spatial scales, with a variance structure similar to that found in other oceanic regions (Platt and Denman 1975a, Harris 1986). Within the reef matrix, the spatial variability of horizontal mixing and chlorophyll will be constrained by the distances between reefs, reducing large scale chlorophyll variability in this region. Additionally, plankton patchiness within the reef matrix may be generated and dissipated by the currents around reefs, or by plankton being flushed off reefs or consumed on reefs. In the GBR lagoon plankton spatial variability is expected to be between that in open water and that in the reef matrix. Water movement and the scale of plankton patchiness may be constrained by coastal features, and may carry spatial features resulting from the passage of lagoon water through the reef matrix.

The third question addressed in this paper is the extent to which zooplankton community structure and zooplankton biomass are correlated with the chlorophyll concentration. Ideally the influence of chlorophyll concentration on zooplankton community structure is most satisfactorily addressed by an experimental situation in which the effect of different factors, alone and together, can be held constant, and the extent of their influence assessed. Such a project is beyond the scope of this work. Even in simple communities with relatively few species there may be a daunting array of potential interactions (Lehman 1988). Processes such as competition and disturbance may take many generations for their full effects to be realized. Also, in an ecosystem such as the pelagic waters of the GBR which is as yet poorly described, detailed knowledge of system processes from one place cannot be reliably generalized.

An alternative approach adopted for this study was to assess the importance of different factors acting on the zooplankton community by observation of differences in zooplankton community structure and biomass in relation to regional differences in the chlorophyll concentration, and other environmental variables. This approach can be limited by the confounding of environmental variables, several of which may be statitistically related to the variable of interest. Disentangling true cause and effect relationships from a wealth of statistical correlations can be difficult. Nevertheless such an approach can give indications of the different factors acting on zooplankton communities, and has been applied widely in work on marine plankton communities (Peterson **et al.** 1979, Hayward and McGowan 1979, Mackas and Sefton 1982).

Chlorophyll concentration was used as proxy for the food available to zooplankton. This involves making two assumptions, firstly that the chlorophyll concentration is a reliable indicator of phytoplankton biomass, and secondly that phytoplankton biomass is a reliable indicator of the food available to zooplankton. The first of these assumptions has already been discussed. The second assumption is also a simplification of the real situation as not all zooplankton are nominally herbivorous. Additionally, the food of "herbivorous" zooplankton may include organic detritus (Richman **et al.** 1975, Roman **et al.** 1988) and other zooplankton (Landry 1981). Despite these caveats, equating chlorophyll concentration with food available to zooplankton is a useful approach as major constituents of the zooplankton often correlate with the chlorophyll concentration (Durbin **et al.** 1983, Kiorboe **et al.** 1985). As herbivorous zooplankton may respond not only to the absolute amount of phytoplankton biomass but also to the variability of that amount (Dagg 1977), a comprehensive description of the chlorophyll concentration on the GBR shelf requires quantification of both the absolute concentration and its spatial and temporal variability.

The different chlorophyll regimes presumed to arise in the three cross-shelf regions of the GBR shelf provide a natural experiment to investigate the covariability of zooplankton abundances and community structure with chlorophyll. Correlation of the anticipated cross-shelf differences in both chlorophyll concentration and its spatial variability will give an indication of their influence on zooplankton biomass and community structure.

A more direct assessment of the association between chlorophyll concentration, zooplankton biomass and community structure was made using observations of inshore plankton after a cyclonic storm. The passage of the cyclone produced abrupt changes in water column nutrients, salinity and turbidity with ramifications for phytoplankton and zooplankton communities. Changes in chlorophyll concentration, and zooplankton biomass and abundance were traced in the period following the cyclone to assess the importance of food limitation of zooplankton in inshore GBR waters.

Chapter 2. Spatial variability of near-surface chlorophyll concentrations in waters of the Great Barrier Reef: cross-shelf, latitudinal and seasonal differences.

INTRODUCTION

Phytoplankton biomass in tropical oceans is usually lower than that found in equivalent temperate oceanic regions (Longhurst and Pauly 1987). On continental shelves, however, there is less of a tropical - temperate dichotomy as upwelling ((Walsh **et al.** 1971, Guillen and DeRondan 1972, Ilahude **et al.** 1990) and river outflows (Ryther **et al.** 1967, Zeitzschel 1978, Pati 1980) result in higher phytoplankton biomass. Tropical continental shelves and shelves around islands on which upwelling does not occur and river outflows are small may be characterised by very low concentrations of phytoplankton biomass (chlorophyll: 0.1-0.5 ug l^{-1})(Kidd and Sander 1981, Bienfang **et al.** 1984, Tranter and Leech 1987).

Pelagic food webs support the planktonic life stages of many reef species (Longhurst 1985). Low phytoplankton biomass can therefore adversely affect survival and recruitment of both pelagic and reef species through food limitation of herbivorous zooplankton (Lasker 1975, Bigford 1978). Both the spatial and temporal means and variances of phytoplankton biomass need to be quantified, as zooplankton species may be adapted to both a particular food concentration and its variability (as measured by chlorophyll concentration)(Mullin and Brooks 1976, Dagg 1977, Borchers and Hutchings 1986).

Distinct cross and long-shelf gradients in chlorophyll concentration are well known features in coastal upwelling zones (Walsh **et al.** 1980, Ilahude **et al.** 1990), but little work on spatial variability has been done in non-upwelling tropical shelf waters. Seasonal chlorophyll variability in tropical regions appears to depend on regional hydrological and climatological conditions with no overall pattern (Sournia 1969).

In this study the concentration and spatial variability of surface chlorophyll in shelf waters of the Great Barrier Reef (GBR) are quantified, and their relation to large-scale differences in bathymetry and GBR structure assessed.

The reef matrix of the GBR is the dominant geographical feature of the tropical north east shelf of Australia, comprised of 2500 reefs and extending along the shelf for more than 2000 km (9°S to 24°S; Fig. 2.1). Chlorophyll concentrations have been measured at a number of stations in GBR shelf waters and are generally low (Andrews and Gentien 1982, Revelante and Gilmartin 1982, Revelante **et al.** 1982, Andrews 1983, Furnas and Mitchell 1986). Indications of the horizontal spatial

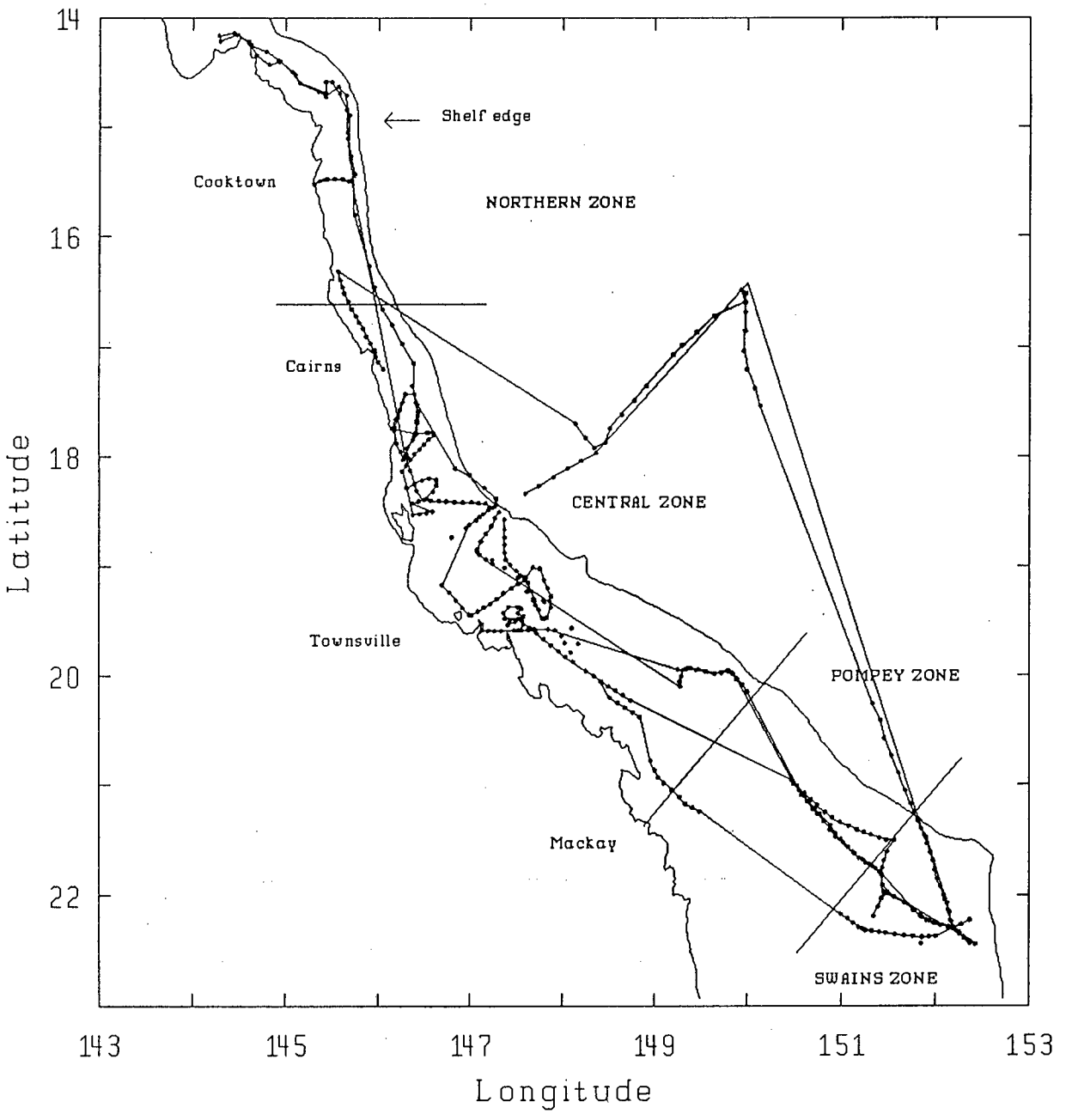


Figure 2.1. The Great Barrier Reef shelf and transects surveyed in this study (solid lines). Centres of subtransects indicated by (•). Divisions between the four latitudinal zones are indicated.

variability of phytoplankton biomass on the GBR shelf can be inferred from the variation of chlorophyll between stations. At a range of length scales extending up to the width of the continental shelf (80 km), chlorophyll concentrations appear to vary only five-fold.

Water movements on the GBR shelf can be complex. Islands and reefs generate rapid local flows (Wolanski **et al.** 1986), and wakes (Wolanski **et al.** 1984, Wolanski 1987) in which planktonic material would be rapidly swept downcurrent (Wolanski **et al.** 1989) or maintained in the vicinity for some time (Hamner and Hauri 1981, Black et al. 1990). Water within reef lagoons will be flushed to a varying extent by tidal forces (Wolanski and Pickard 1983). Coastal features can produce similar acceleration and stalling of water movement (Wolanski and Ridd 1990). Such currents through the GBR reef matrix may contribute to spatial differences in chlorophyll concentration (Wolanski **et al.** 1984). Consequently, water temperature was recorded as a water mass tracer to assist interpretation of the mechanisms affecting spatial variability of phytoplankton biomass.

Two spatial scales were chosen over which to quantify near-surface chlorophyll variability; 20-1200 km (mesoscale), and 0.015-8 km (small scale). These distance scales were suggested by the physical structure of the GBR shelf, comprising a reef free inner shelf, and a reef rich outer shelf, with also latitudinal changes in reef density and type. Differences in the chlorophyll mean and variance associated with such geographical changes could be resolved by examining mesoscale change. Small scale chlorophyll variability could identify variability associated with features of a smaller size, e.g. individual reefs or the coastline.

The importance of chlorophyll spatial variability to higher trophic levels will depend on the period that the chlorophyll variability persists. If chlorophyll variability at a particular scale persists long enough, a distinctive zooplankton community structure may arise that is adapted to those particular conditions (Wiens 1977, Mackas 1984). On the GBR, distinct hydrological regimes are anticipated in the structurally different parts of the GBR, giving rise to distinct regimes of chlorophyll variability with effects on zooplankton biomass and community structure. Small scale chlorophyll variability should be more ephemeral (Platt and Denman 1975a) with smaller reverberations up the food web (Harris 1980).

METHODS

Sampling

Near-surface chlorophyll fluorescence, and water temperatures were sampled continuously along research vessel transects run between January 1987 and February

Table 2.1

Details of cruises on which chlorophyll fluorescence measurements were made.

Cruise	Date	Zones surveyed	No. of subtransects
COT	12-11 Jan '87	Central	28
COT2	8-17 Jan '87	Central	53
COT3	8-12 May '87	Central	30
COT3A	23 May - 3 Jun '87	Central,Pompey,Swains	59
COT4	9-26 Oct '87	Northern,Central	74
COT5	9-21 Feb '88	Central,Pompey,Swains	71
WILL88	3-13 May '88	Northern,Central,Pompey, Swains	72
COT6	14-19 Feb '89	Northern,Central	30

1989 in shelf waters of the Great Barrier Reef and the Western Coral Sea (Fig. 2.1). Seawater was sampled by pumping (Mono pump - 120 l min^{-1}) through a pipe clamped to the side of vessel with the intake 2 m below the surface and 1 m away from the ship's hull (Fig. 2.2). Water coming from the pump was debubbled and passed through a Turner Designs (model 10-005R) fluorometer with a flow-through sample cell for measurement of *in vivo* chlorophyll fluorescence. The hose delay time for chlorophyll measurements was 22.2 seconds. Only data from transects run in the daytime (2 hours post-sunrise to 2 hours pre-sunset) are used as a lack of navigation markers within the reef matrix precluded operations at night. Temperature was measured with a thermistor (Glass bead, type FS 23D, ITT, response time 400 msec) mounted on the intake hose upstream of the pump.

The thermistor was calibrated against a Hewlett Packard 2804A quartz thermometer, and had a temperature resolution of 0.07 C °. Analogue outputs from the fluorometer and thermistor were digitized and averaged over three second intervals with a JED STD-800 datalogger (JED Microprocessors, Vic.), and recorded together with a time record on a microcomputer.

Discrete water samples (100 ml) were taken from the fluorometer outflow at half hourly intervals to calibrate fluorescence against extracted chlorophyll concentration. These samples were filtered through Whatman GF filters and stored frozen for a maximum of two weeks prior to analysis. The extracted chlorophyll analysis followed the fluorometric procedure in Parsons **et al.** (1984). Chlorophyll - *in vivo* fluorescence calibrations were calculated for each cruise or for groups of transects within a cruise if different areas of the GBR were surveyed (Fig. 2.3). Correlation coefficients for calibrations ranged from 0.46 to 0.97 (Table 2.2). Standard errors for the calibrations ranged from 0.036 to 0.210 ug l^{-1} chlorophyll with a mean of 0.116 ug l^{-1}.

Although *in vivo* fluorescence was used as a proxy for chlorophyll concentration, the ratio of chorophyll concentration to *in vivo* fluorescence (R) may vary markedly with factors such as nutrient starvation (Kiefer 1973), ambient light (Harris 1978) and species composition (Strickland 1968). The effect of ambient light on *in vivo* fluorescence was evaluated by examining the fluorescence trace from an 18 hour transect made overnight (Fig. 2.4). No systematic change associated with diel irradiance was observed, nor was there a relationship between chlorophyll concentration and the time of day samples were taken (Fig. 2.4). The effects of other environmental and physiological factors on the value of R could not be assessed within the ambit of this work.

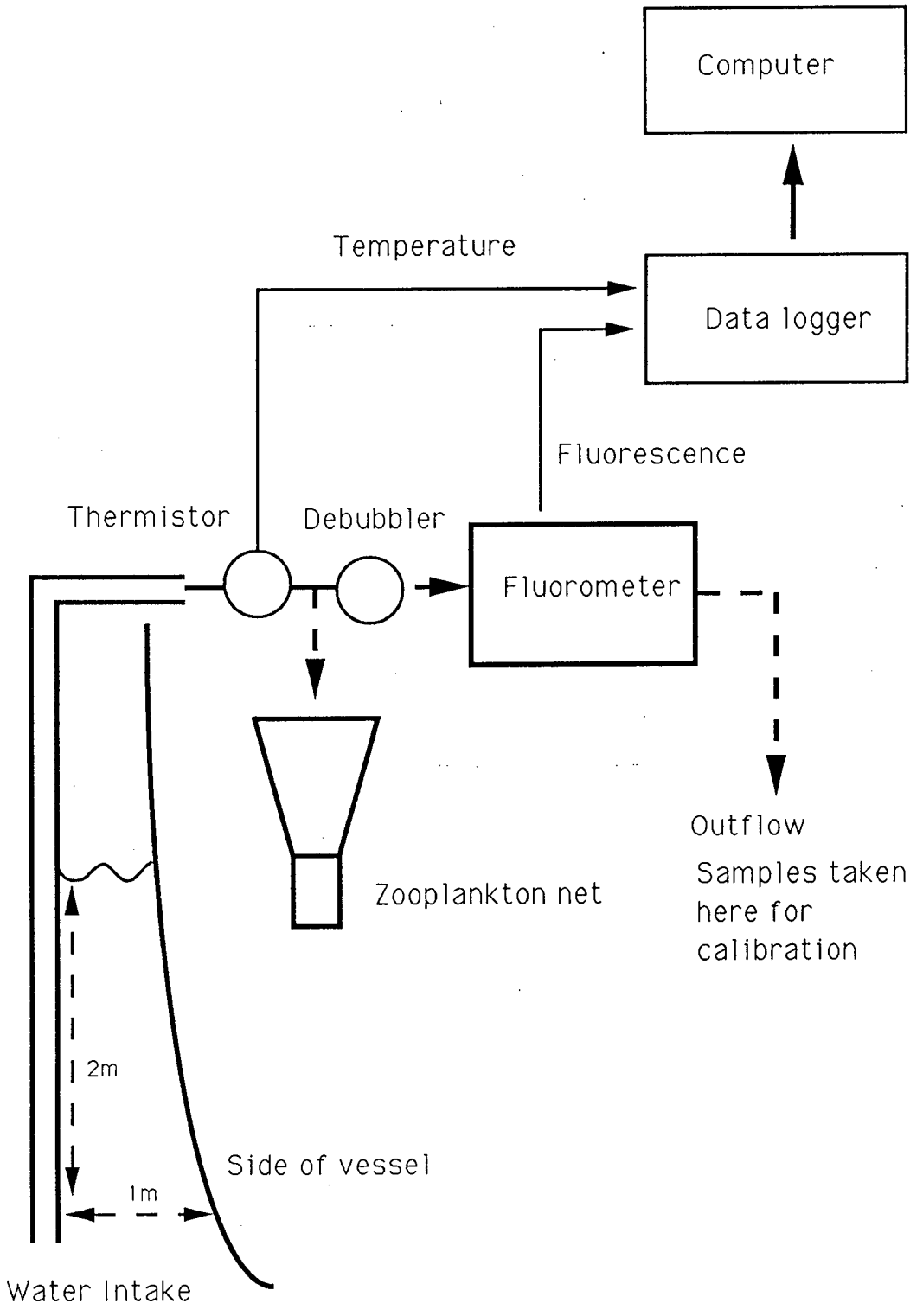


Figure 2.2. Schematic diagram of the underway pumping system, sampling and datalogging equipment.

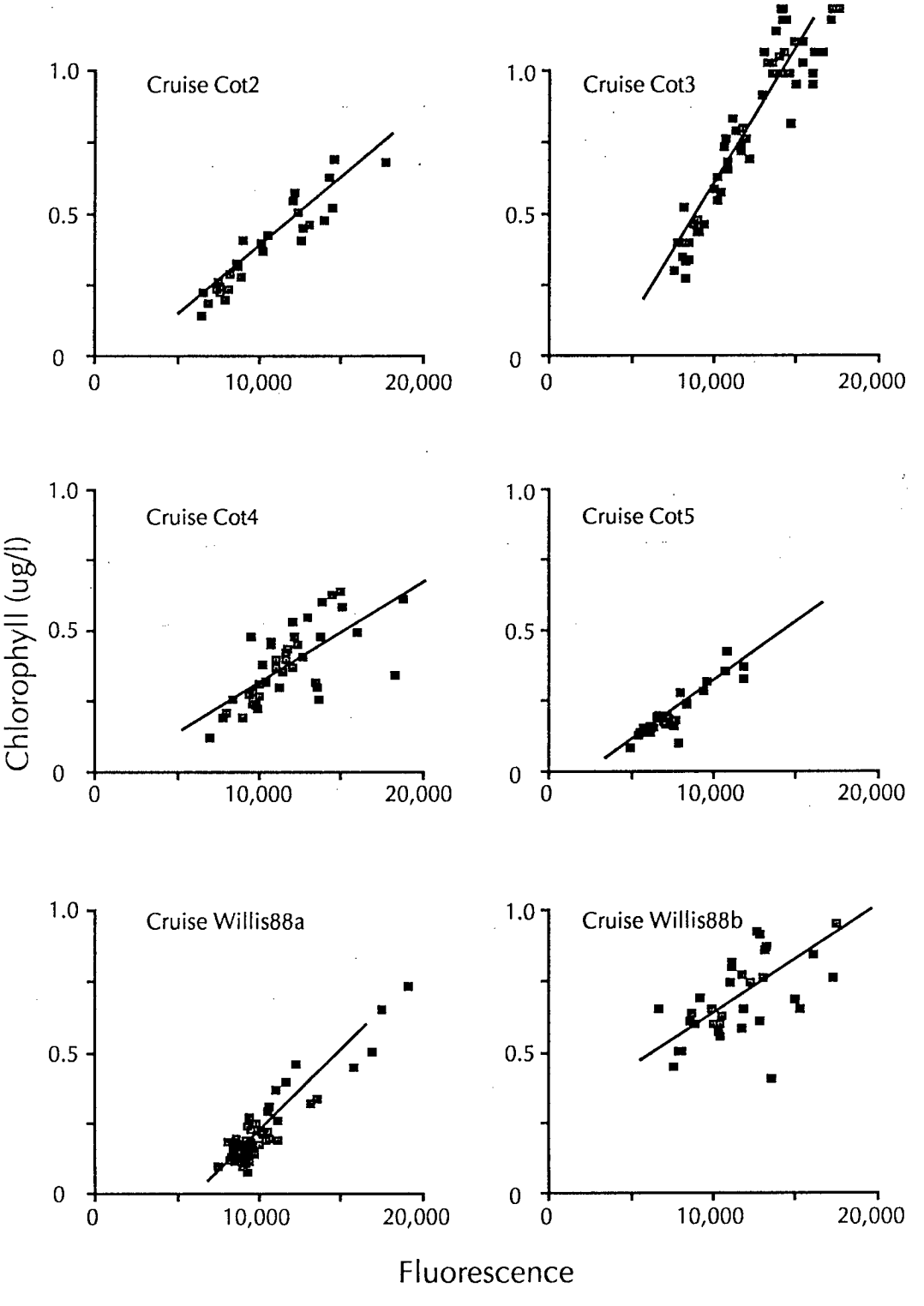


Figure 2.3. Representative chlorophyll - fluorescence calibrations for the transects surveyed.

Table 2.2

Details of the calibrations used to calculate chlorophyll concentration from in vivo chlorophyll fluorescence. The standard error of the estimate (ug l^{-1} chl) was used as a measure of the resolution of the calibration.

Cruise	Calibration	r	n	SE of estimate	Slope
COT1	1	0.46	69	0.170	0.0000464
COT2	2	0.84	42	0.210	0.0000511
COT2	3	0.67	16	0.130	0.0000388
COT2	4	0.75	45	0.180	0.0000614
COT2	5	0.79	50	0.180	0.0000639
COT2	6	0.66	28	0.200	0.0000339
COT3	7	0.92	42	0.053	0.0000342
COT3	8	0.63	27	0.132	0.0000258
COT3	9	0.82	28	0.069	0.0000327
COT3	10	0.97	27	0.098	0.0000352
COT3A	11	0.91	20	0.091	0.0000560
COT3A	12	0.72	33	0.102	0.0000359
COT3A	13	0.57	39	0.164	0.0000172
COT3A	14	0.92	33	0.086	0.0000439
COT3A	15	0.89	36	0.044	0.0000267
COT4	16	0.94	28	0.178	0.0000310
COT4	17	0.94	58	0.036	0.0000487
COT4	18	0.91	29	0.036	0.0000413
COT4	19	0.86	42	0.098	0.0000601
COT5	20	0.70	15	0.114	0.0000551
COT5	21	0.73	16	0.103	0.0000279
COT5	22	0.94	32	0.092	0.0000511
WILL88	23	0.74	18	0.178	0.0000415
WILL88	24	0.93	57	0.112	0.0000481
WILL88	25	0.82	29	0.187	0.0000417
WILL88	26	0.95	73	0.052	0.0000567
WILL88	27	0.74	35	0.120	0.0000381
COT6	28	0.78	19	0.079	0.0000929
COT6	29	0.84	31	0.066	0.0001159
Mean		0.80	35	0.116	0.0000467
Minimum		0.46	15	0.036	0.0000172
Maximum		0.97	73	0.210	0.0001159

r = correlation coeff.n = number in sample, SE = standard error

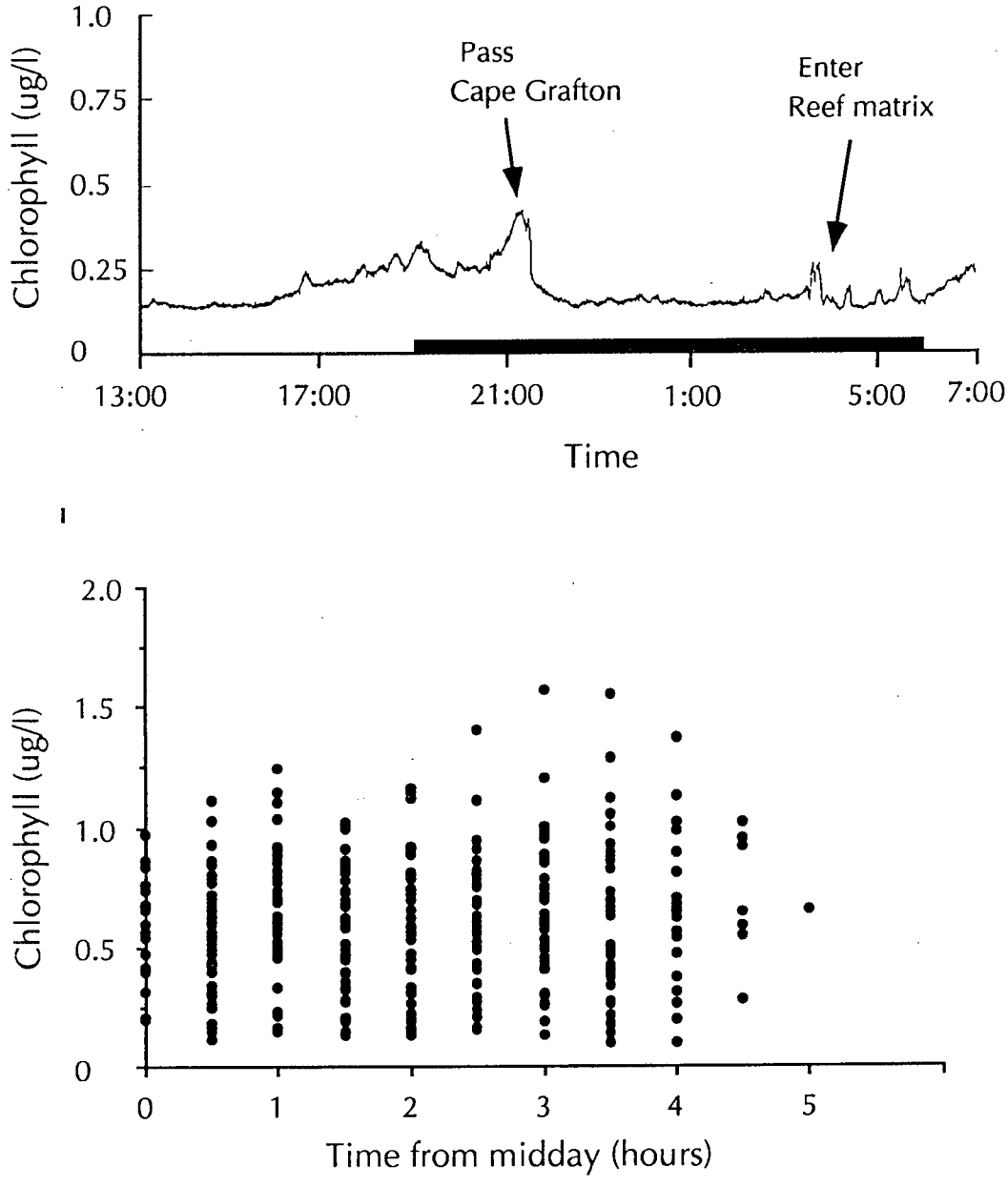


Figure 2.4 **Above.** Chlorophyll concentration along a transect extending over 18 hours. Hours of darkness indicated by thickened horizontal axis (the nightime portion of this transect were not used in subsequent analysis). **Below.** Mean chlorophyll concentration in subtransects plotted against the time from midday to the mid-point of the subtransect. Correlation coefficient not significant.

Application of a calibration based on samples from one area to *in vivo* fluorescence from another could lead to bias in the calculated chlorophyll concentrations. Consequently, separate chlorophyll calibrations were made for each cruise and for different regions within a cruise if possible. This procedure may decrease the precision of the calibration as samples with different R values may be incorporated in one calibration, but avoids the bias that could be generated by applying the calibration from one cruise or region to another. The variability in the value of R within a calibration can be assessed by the scatter in the calibration (Fig 2.3)(assuming constant analytical error), and of the variability of R between calibrations by the slopes of the regressions (Table 2.2). There were differences at both these levels, particularly in the regression slopes, but no systematic pattern could be discerned.

Ship positions, recorded at hourly intervals and at each course change were determined by radar fixes while on the shelf and from SATNAV position fixes in the Coral Sea. The cruise track and the mid-point of each subtransect were calculated from these fixes (Fig. 2.1). Water depths, taken from the ship's echo sounder along transects were recorded at course changes or at hourly intervals. The mean water depth of each subtransect was estimated by linear interpolation. As the shelf between reefs is relatively flat or smoothly sloping (Maxwell 1968) this procedure was regarded as adequate. Water depth was used as an indication of the distance offshore of a sample, as in most parts of the shelf there is a regular increase in depth with distance offshore (Maxwell 1968). Linear distance was not used as it was biased by differences in shelf width when comparing samples from the north of the GBR with ones from the south.

Data analysis

For the purpose of analysis, the GBR shelf was divided into four latitudinal **zones** based on the extent to which the reef matrix occludes cross-shelf water movement (Pickard **et al.** 1977); hereafter defined as the northern, central, Pompey and Swains zones (Fig. 2.1). In the northern zone (14°-16.5°S) reefs extend along 90% of its latitudinal extent, with passages between reefs occupying only 10% of this distance. The central zone (16.5°-22.5°S) has reefs along 10%, the Pompey zone (20°-21°S) along 90% and the Swains zone (21°-22.5°S) along 10%. Each zone was further divided into four cross-shelf **bands**; inshore (0-20 m deep), the inner shelf (20-40 m), the outer shelf (40-80 m) and the Coral Sea (oceanic waters outside of the reef barrier). These cross-shelf divisions were chosen to distinguish inshore waters, in which resuspension of sediment by waves may be important (inshore band), the GBR

lagoon, lying between the inshore band and the reef matrix (inner shelf band), and an outer shelf band containing the majority of reefs. As the shelf is narrower and shallower in the northern zone (Maxwell 1968), a slightly different definition of bands was used; inshore (waters 0-20 m deep), the inner shelf (20-30 m), and the outer shelf (30-80 m). Two **seasons** were defined; a nominal dry season during which south east tradewinds dominate (April to November), and a nominal wet season (December to March), characterized primarily by a shift in the wind direction to the north and usually by an increase in rainfall (Pickard **et al.** 1977).

Transects of surface fluorescence and temperature data were divided into 8 km long subtransects to correspond with zooplankton samples taken over this distance by the same pumping system. Reliable estimates of the zooplankton community composition (chapter four) required a minimum of 3 m^3 of water to be filtered. At the normal ship speed (5 m sec^{-1}), the vessel travelled eight kilometres in the time taken for this quantity of water to be pumped on board. Means and coefficients of variation (CV) of chlorophyll concentration in each 8 km subtransect were calculated to make latitudinal, cross-shelf and seasonal comparisons of concentration and spatial variability. The 8 km CV's are an estimator of spatial variability up to the length of subtransects. Although CV's characterised only part of the chlorophyll spatial variability, they permitted correlations to be drawn between chlorophyll variability and local differences in topography and bathymetry. Chlorophyll spatial variability across the full continuum of spatial scales contained in transect lengths is examined by times series analysis in chapter three.

Hypotheses regarding cross-shelf and latitudinal differences in near-surface chlorophyll concentration and 8 km CV's were tested by two factor, fixed effects analyses of variance (ANOVA). The two factors were cross-shelf band (inner shelf, outer shelf and Coral Sea) and latitudinal zone (northern, central, Pompey and Swains). There were not enough subtransects in the inshore bands of all zones to include this band as a level in the cross-shelf factor (Fig. 2.5). Seasonal differences (dry, wet) in chlorophyll concentration and chlorophyll CV were tested by two factor fixed effect ANOVA's (season, band: inshore, inner shelf, outer shelf, Coral Sea) using subtransects from the more intensively sampled central zone. Although there were numerous subtransects from the northern, Pompey and Swains zones, they came from only three cruises to each of these areas (Table 2.1), whereas the central zone was sampled on eight occasions (Table 2.1). As these were fixed ANOVA's, each significant factor and interaction term was statistically independent, and its significance could be assessed in relation to the error mean square (Sokal and Rohlf 1981). *A posteriori* comparisons of means were performed using the Tukey test, with

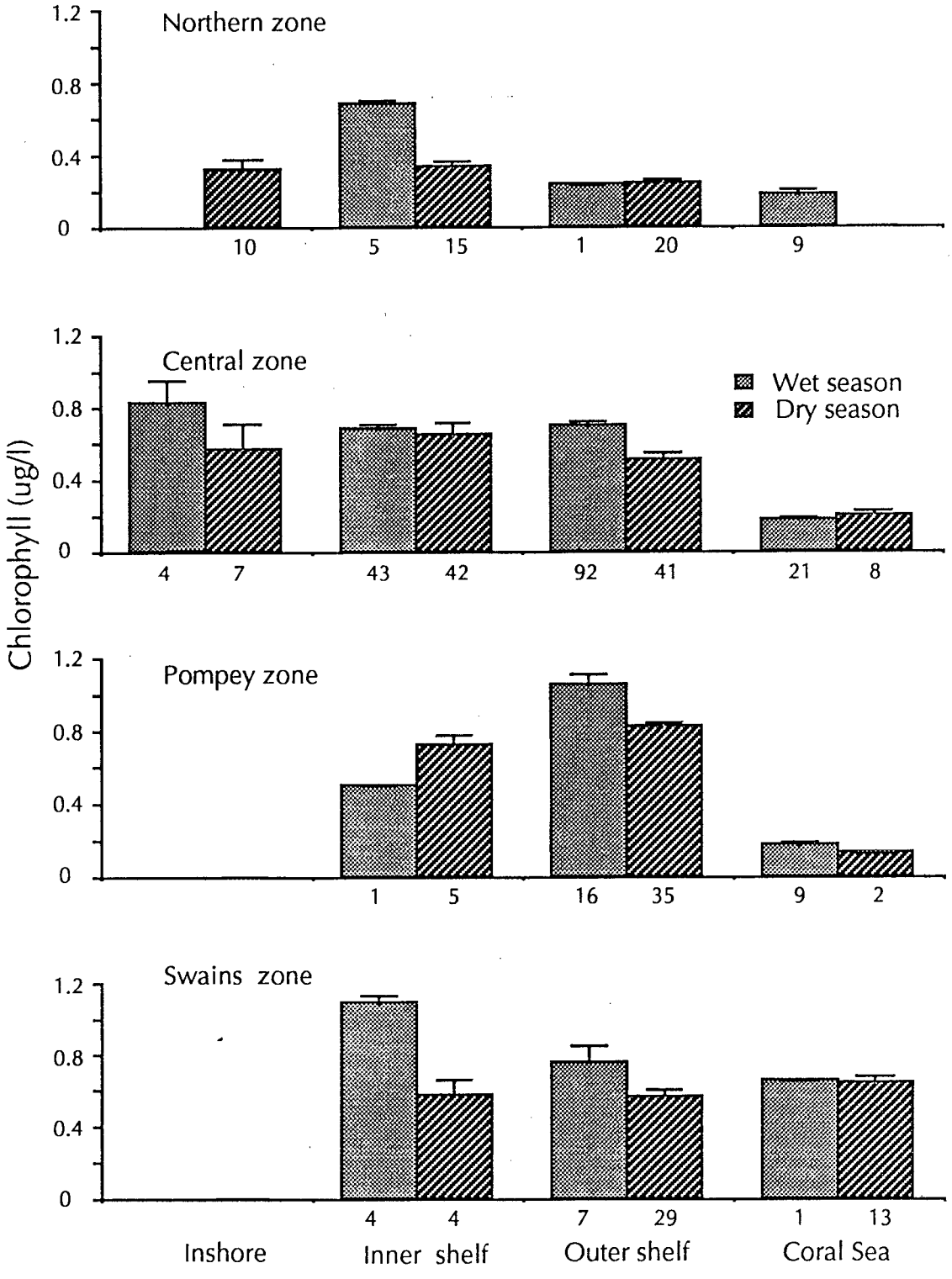


Figure 2.5. Mean chlorophyll concentrations in cross-shelf bands and long-shelf zones, and over the two defined seasons. Error bars represent one standard error of the mean value. Numbers below columns indicate the number of subtransects in each group.

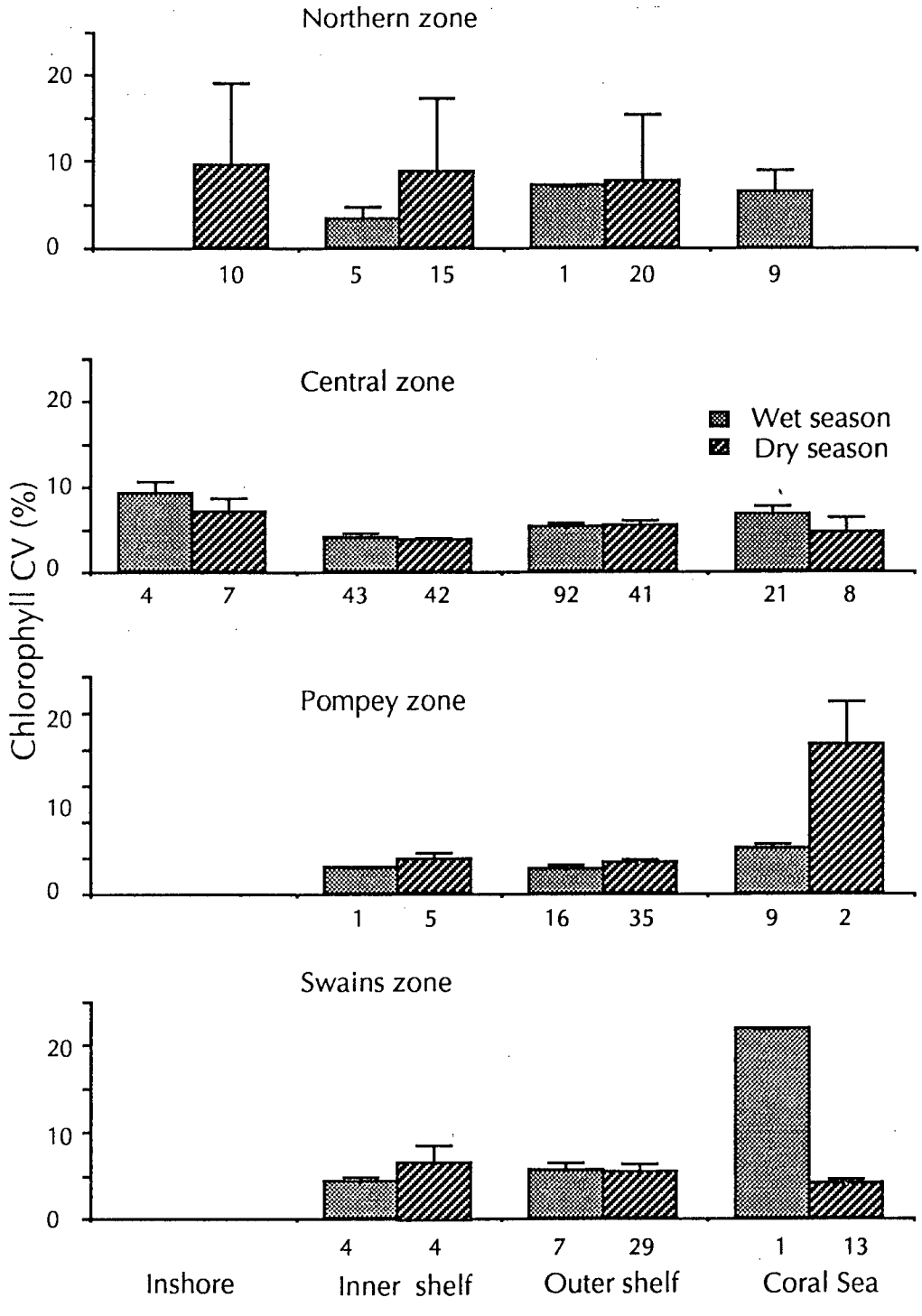


Figure 2.6. Mean chlorophyll coefficients of variation in cross-shelf bands and long-shelf zones, and over the two defined seasons. Error bars represent one standard error of the mean value. Numbers below columns indicate the number of subtransects in each group.

corrections for unequal sample sizes (Zar 1984). Variables were tested for heterogeneity of variance (Cochran's C test) prior to analysis, and log transformed if heteroscedasticity was present.

The concentration and variability of chlorophyll in each subtransect was also related to the mean depth of the water column (as a measure of distance offshore), and to the distance between the centre of the subtransect and the nearest reef.

RESULTS

Cross-shelf chlorophyll concentration

Mean near-surface chlorophyll concentrations for subtransects ranged from 0.20 ug l^{-1} in the Coral Sea to 1.57 ug l^{-1} in GBR shelf waters (Table 2.3). Absolute surface concentrations were similar to those found in previous studies (Andrews and Gentien 1982, Revelante and Gilmartin 1982, Revelante **et al.** 1982, Andrews 1983, Furnas and Mitchell 1986).

Most cross-shelf transects had a consistent chlorophyll gradient characterised by relatively high concentrations near the coast and low concentrations in the Coral Sea (Fig. 2.8). This structure was observed in transects in the central zone, but less distinctive in a transect in the northern zone (Fig. 2.8). Analysis of variance confirmed that mean subtransect chlorophyll concentrations differed significantly cross-shelf, though the significant interaction term indicated that this cross-shelf gradient did not occur in all zones (Table 2.4). The exception to the cross-shelf pattern was in the Pompey zone where outer shelf surface chlorophyll concentrations were higher than those on the inner shelf (Fig. 2.5). Overall, the mean Coral Sea surface chlorophyll concentration (0.20 ug l^{-1}) was significantly lower than that on the inner (0.64) and outer shelf (0.65). There was no difference between mean chlorophyll concentrations in the inner and outer shelf bands even when data from the Pompey zone was excluded (Table 2.4).

Long-shelf and seasonal chlorophyll concentrations

The mean of surface chlorophyll concentrations increased significantly from north to south (Table 2.3, Fig. 2.5). This long-shelf gradient in chlorophyll concentration occurred over much greater distances than cross-shelf differences, the part of the shelf sampled varied in width from 23-260 km, but extended north-south 1300 km . Individual long-shelf transects did not show any consistent structure such as that seen in cross-shelf transects (Fig. 2.8), though they often showed abrupt local changes in chlorophyll concentration close to individual reefs (Fig. 2.9).

Table 2.3

Summary statistics of surface chlorophyll spatial variability at three different scales; 1) across the length and breadth of the GBR shelf, 2) within latitudinal zones, cross-shelf bands and seasons (i.e. between subtransects), and 3) within subtransects.

1. Length and Breadth of GBR shelf:

Chlorophyll mean	0.59
Chlorophyll range	0.08 - 1.57

2. Within latitudinal zones and cross-shelf bands:

Cross-shelf band	Inshore	Inner shelf	Outer shelf	Coral Sea
Chlorophyll mean	0.48	0.63	0.65	0.19
Chlorophyll range	0.15-1.25	0.14-1.39	0.10-1.57	0.08-0.55

Latitudinal zone	Northern	Central	Pompey	Swains
Chlorophyll mean	0.31	0.60	0.76	0.65
Chlorophyll range	0.08-0.75	0.08-1.40	0.11-1.57	0.33-1.16

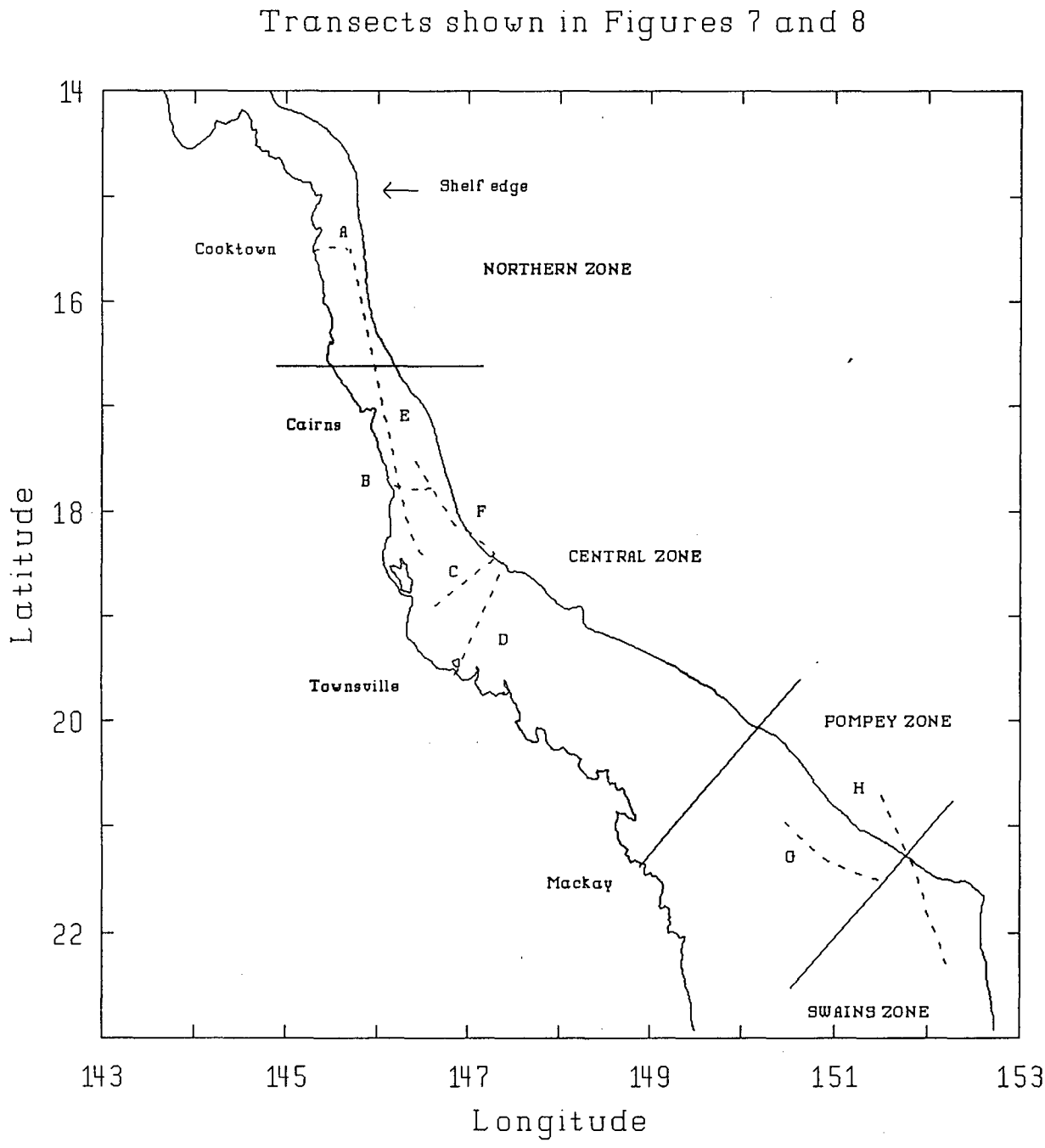
Season	Wet (Dec-Apr)	Dry (May-Nov)
Chlorophyll mean	0.63	0.55
Chlorophyll range	0.08-1.57	0.10-1.39

3. Within subtransects:

Cross-shelf band	Inshore	Inner shelf	Outer shelf	Coral Sea
Mean chlorophyll CV	0.17	0.09	0.11	0.14
Range of CV's	0.04-0.83	0.02-0.49	0.01-0.39	0.04-0.54

Latitudinal zone	Northern	Central	Pompey	Swains
Mean chlorophyll CV	0.15	0.10	0.10	0.11
Range of CV's	0.04-0.83	0.02-0.49	0.01-0.53	0.04-0.44

Season	Wet (Dec-Apr)	Dry (May-Nov)
Mean chlorophyll CV	0.11	0.11
Range of CV's	0.02-0.54	0.01-0.83



2.7. Location of transects depicted in Figures 2.8 and 2.9.

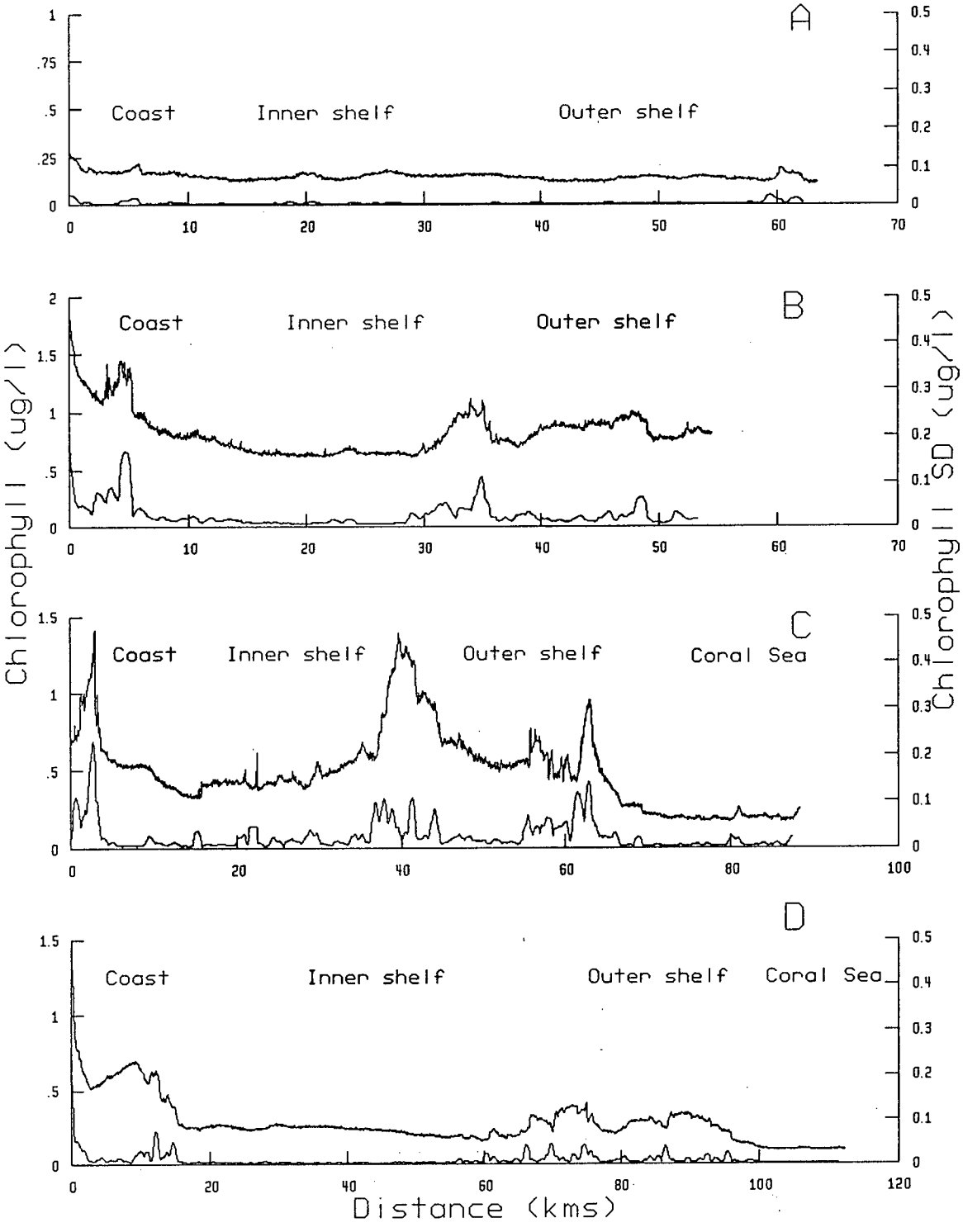


Figure 2.8. Representative cross-shelf transects of chlorophyll concentration and the running standard deviation of the chlorophyll concentration. Bottom trace in each plot is the running standard deviation. The letter above each transect identifies it on Figure 2.7.

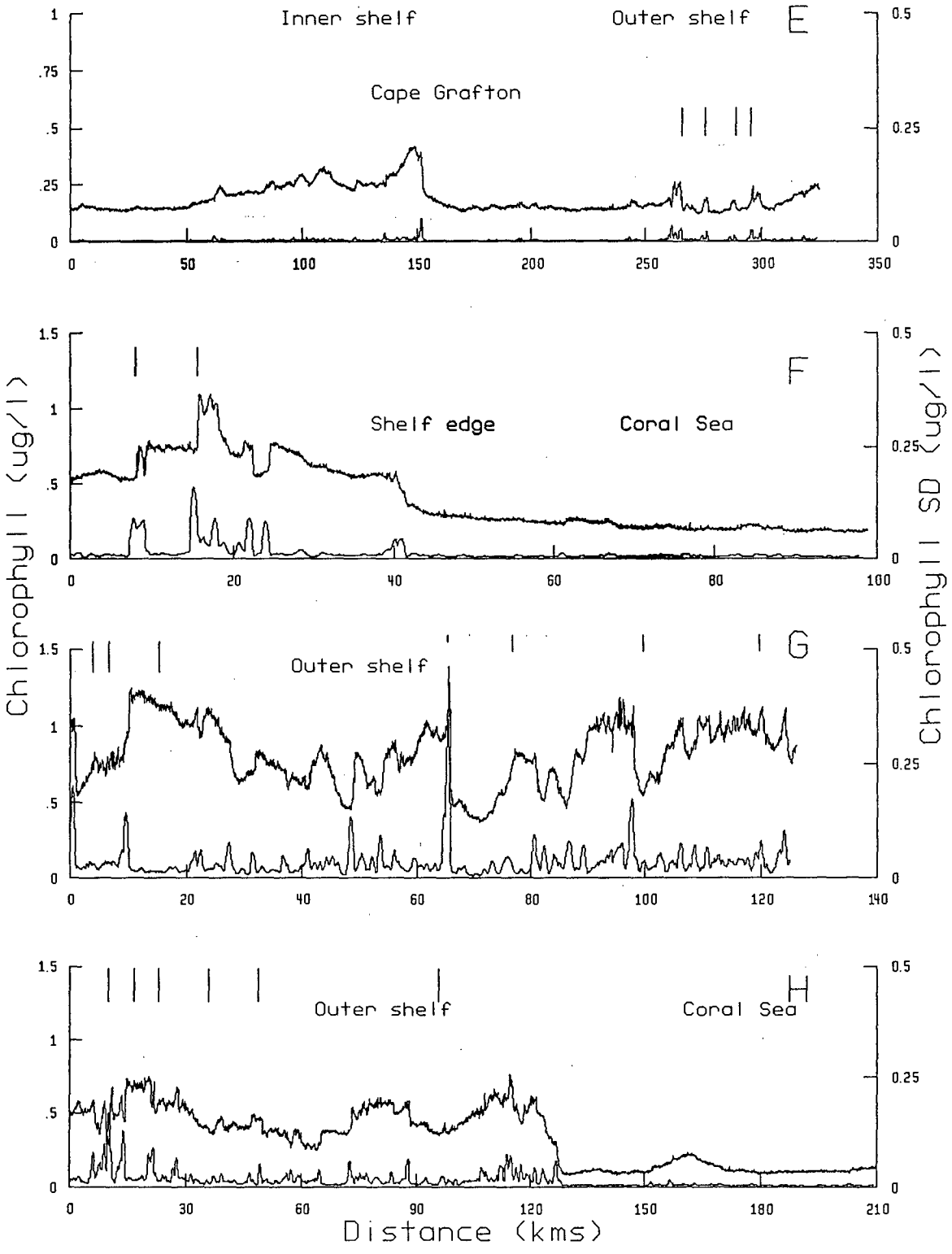


Figure 2.9. Representative long-shelf transects of chlorophyll concentration and the running standard deviation of the chlorophyll concentration. Bottom trace in each plot is the running standard deviation. Vertical marks above plot indicate close approach to an individual reef. The letter above each transect identifies it on Figure 2.7.

Table 2.4

Analysis of variance of chlorophyll concentration. A) Factors were cross-shelf band (inner shelf, outer shelf and Coral Sea), and latitudinal zone (northern, central, Pompey and Swains). B) Factors were cross-shelf band (inner shelf, outer shelf and Coral Sea), and season (wet and dry). In this second ANOVA only subtransects from the central zone were used. Data untransformed: Cochran's C = 0.163, $p < 0.05$. Underline between means in Tukey test indicates no significant difference between means ($p < 0.05$). NS = not significant.

A. Chlorophyll concentration

Factor	DF	Mean square	F-ratio	Probability
Latitudinal zone	3	0.855	17.845	< 0.01
Cross-shelf band	2	1.419	29.618	< 0.01
Zone * Band	6	0.395	8.254	< 0.01
Error	411	0.048		

Tukey tests:

Latitudinal zones

	northern	central	Swains	Pompey
Chl. mean (ug l^{-1})	0.31	0.60	0.65	0.76
		———		

Cross-shelf bands

	inner shelf	outer shelf	Coral Sea
Chl. mean (ug l^{-1})	0.67	0.62	0.17
	———	———	

B. Chlorophyll concentration: Central zone only

Factor	DF	Mean square	F-ratio	Probability
Cross-shelf band	3	1.470	25.302	< 0.01
Season	1	0.310	5.329	< 0.05
Band * Season	3	0.153	2.627	NS
Error	250	0.058		

Tukey tests:

Cross-shelf bands

	inner	outer	inshore	Coral Sea
Chl. mean (ug l^{-1})	0.63	0.65	0.59	0.19
	———	———		

Chlorophyll concentrations in the central zone were significantly higher in the wet season (Tables 2.3, 2.4). This trend was apparent in the data from the other zones (Fig. 2.5) although there was an inadequate number of subtransects to confirm this difference statistically.

Comparisons between the surface chlorophyll concentrations in the four cross-shelf bands and four long-shelf zones gives a measure of mesoscale spatial variability across the width and length of the shelf (Table 2.3). The overall range of measured chlorophyll concentrations throughout the GBR was small (0.08-1.57 ug l^{-1}). There was little difference between the ranges and means of chlorophyll concentrations within a zone or band, and that of the shelf as a whole, indicating that the spatial variability of chlorophyll did not increase as the size of the area surveyed increased from that of a band or zone to that of the whole GBR shelf (Table 2.3).

Small scale chlorophyll variability

Examination of chlorophyll concentrations along individual transects revealed that variability in chlorophyll concentration was higher in the inshore and outer shelf bands than in the inner shelf (GBR lagoon) and Coral Sea bands (Fig. 2.8). One way of quantifying and presenting this variability is to calculate running variances for data along transects (Cruzado 1971). A running variance is analogous to a running mean, and similarly requires specification of the number of points (n) over which each variance will be calculated. If n is small, only very local variability in chlorophyll concentration will be represented. If n is very large, local variability in chlorophyll concentrations will be blurred across much of the transect. Running variances of chlorophyll concentrations from 7 points (= 100 m) to 667 points (= 10 km) were plotted. A 67 point (= 1 km) running variance was chosen as it most clearly resolved localized differences in variance.

Running variances calculated for cross-shelf transects also indicate that chlorophyll variability was higher in inshore and outer shelf bands than elsewhere (Fig. 2.8). Running variances of chlorophyll concentration often increased close to individual reefs (Fig. 2.8). The CV's for chlorophyll concentrations calculated for each 8 km subtransect provide a measure of chlorophyll variability, allowing variability in different cross-shelf bands and latitudinal zones to be compared. Although the CV's are an objective measure of variability, they only incorporate chlorophyll variability on length scales up to 8 km. Differences in chlorophyll concentrations over greater spatial separations will not affect the CV.

Coefficients of variation were highest inshore and in the Coral Sea bands (Fig. 2.6), but these differences were not statistically significant (Table 2.5). The

Table 2.5

Analysis of variance on 8 km chlorophyll coefficients of variation. A) Factors were cross-shelf band (inner shelf, outer shelf and Coral Sea), and latitudinal zone (northern, central, Pompey and Swains). B) Factors were cross-shelf band (inner shelf, outer shelf and Coral Sea), and season (wet and dry). In the second ANOVA, only subtransects from the central zone were used. Data untransformed: Cochran's $C = 0.169$, $p < 0.01$. Underline between means in Tukey test indicates no significant difference between means ($p < 0.05$). NS = not significant.

A. Chlorophyll CV

Factor	DF	Mean square	F-ratio	Probability
Latitudinal zone	3	0.018	3.057	< 0.05
Cross-shelf band	2	0.012	2.088	NS
Zone * Band	6	0.015	2.680	< 0.05
Error	411	0.006		

Tukey tests:

	Latitudinal zones			
	Pompey	Central	Swains	Northern
Chl. CV (%)	9.8	10.1	10.8	15.2

B. Chlorophyll CV: Central zone only

Factor	DF	Mean square	F-ratio	Probability
Cross-shelf band	3	0.031	5.603	< 0.01
Season	1	0.013	2.425	NS
Band * Season	3	0.004	0.778	NS
Error	250	0.006		

Tukey tests:

	Cross-shelf bands			
	Inner	Outer	Coral Sea	Inshore
Chl. CV (%)	7.8	10.5	12.8	15.8

localised higher chlorophyll variance near reefs (Fig. 2.8) did not significantly increase the mean outer shelf CV (Fig. 2.6). The apparent high variability in Coral Sea subtransects was not visually apparent (Figs. 2.8, 2.9) and most likely is an artifact arising from the very low absolute chlorophyll concentrations in oceanic waters. Because the chlorophyll concentrations in the Coral Sea were close to the limit of detection, the background instrumental noise level in these subtransects was relatively higher than for other bands. Consequently, although all measurements of chlorophyll variability contain an instrumental noise component, relative noise levels in the Coral Sea were more exaggerated. The instrument used in this study was not sensitive enough to arrive at an unbiased measure of chlorophyll variability in the Coral Sea.

Chlorophyll variability in the northern zone was significantly greater than in the other three latitudinal zones (Fig. 2.6, Table 2.5). There was also a significant cross-shelf - long-shelf interaction (Table 2.6), indicating that cross-shelf differences in CV's changed latitudinally. This interaction term arose largely as a result of the high Coral Sea CV's in the Pompey and Swains zones, based on a small number of subtransects (Fig. 2.6).

Using only subtransects from the well sampled central zone, analysis of variance confirmed that the inshore chlorophyll CV's were significantly larger than those in other bands, and that the chlorophyll CV did not differ significantly between seasons (Table 2.5). The lack of a significant difference between inner and outer shelf bands ran counter to a visual interpretation of transect data from the central zone in which chlorophyll variability appeared to be higher in the matrix of reefs (Fig. 2.8).

Surface chlorophyll variability showed no clear relationship to water depth (an analog of distance offshore, Fig. 2.10), although chlorophyll CV's from the reef matrix (depths 40 m to 80 m) were slightly greater than those from the GBR lagoon (inner shelf band: 20 m to 40 m). As chlorophyll variability appeared to increase close to individual reefs (Fig. 2.9), the chlorophyll CV of inner and outer shelf subtransects was plotted against the proximity of the midpoint of individual subtransects to the nearest reef (Fig. 2.10). CV's of subtransects within 15 km of reefs were higher than that of subtransects further away (Fig. 2.10). Only inner and outer shelf subtransects were considered to avoid confusion with coastal processes.

The higher variability of surface chlorophyll in the vicinity of reefs (Fig. 2.10) clearly suggests that water masses with different chlorophyll concentration were mixing. Two processes might be responsible. Reefs may cause localized upwelling of the colder, chlorophyll enriched water that intermittently intrudes onto the outer shelf (Andrews and Furnas 1986) through interactions with tidal currents (Wolanski and Hamner 1988). Such processes would be characterised by lower surface

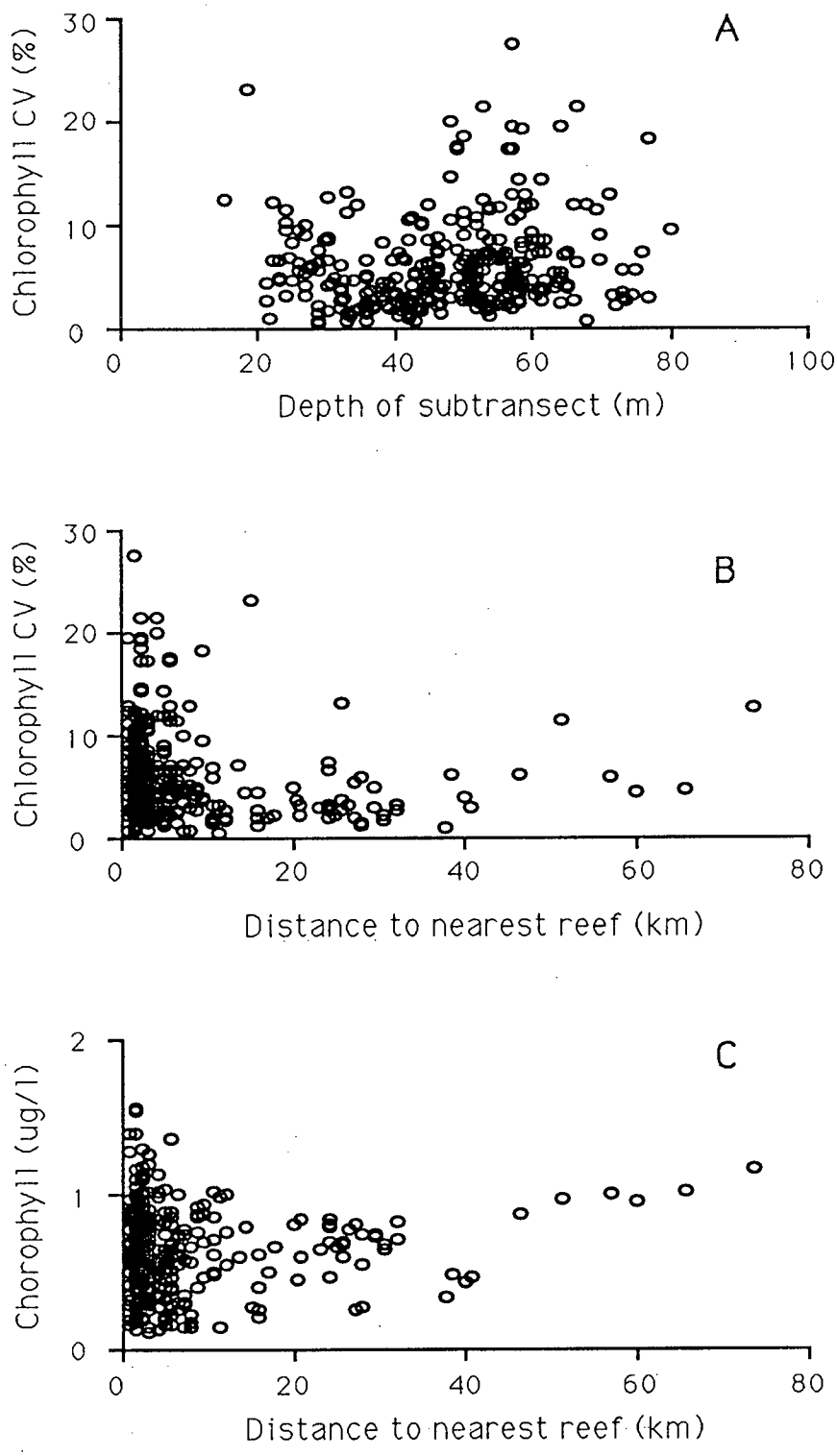


Figure 2.10. **A.** Chlorophyll coefficients of variation as a function of mean subtransect depth. **B.** Chlorophyll coefficients of variation as a function of proximity to individual reefs. **C.** Chlorophyll concentration as a function of proximity to individual reefs.

temperatures in conjunction with high chlorophyll concentrations. Alternatively, water may be exported from shallow reef flats or out of reef lagoons by tides or wind (Wolanski and Pickard 1983, Pickard 1986). This water usually is characterised by higher temperature (Potts and Swart 1984) and higher chlorophyll concentration (Furnas **et al.** 1990).

To evaluate the relative importance of these mechanisms, subtransects from the December to March period, during which water in reef lagoons and on reef flats is warmer than oceanic water (Potts and Swart 1984, Wolanski and Hamner 1988, Andrews **et al.** 1984) were examined. This is also the time of year in which intrusions of cold, chlorophyll enriched water occur most frequently (Andrews and Furnas 1986). As temperature decreased significantly with latitude ($r = -0.94$), a latitudinal trend was removed by the linear least squares method (Sokal and Rohlf 1981).

Water in subtransects less than 15 km from reefs was significantly warmer and had higher CV's ($p < 0.05$) than in subtransects further away (Figs. 2.10, 2.11). These results suggest that surface water temperature and higher near-reef chlorophyll variability in the vicinity of reefs could more reasonably be attributed to the mixing of water exported from reefs than to the mixing of upwelled water.
There was no clear relationship between temperature and chlorophyll variability within these wet season subtransects (Fig. 2.11). The scatter in this relationship may result because, even though significant changes to both water temperature and chlorophyll concentration may occur within the confines of individual reefs, they operate over different spatial and temporal scales. Reef water temperature varies diurnally and with water depth (Potts and Swart 1984), and chlorophyll concentrations within reef lagoons can be more variable that between different lagoons (Furnas **et al.** 1990).

Mean surface chlorophyll concentrations also appeared to be influenced by reef proximity. Within 10 km of reefs, chlorophyll concentrations in many subtransects were either higher or lower than those in subtransects further away (Fig. 2.10c). This signified that chlorophyll variability was higher in the vicinity of individual reefs both at the spatial scale resolved by the chlorophyll CV (< 8 km, Fig. 2.10b), and at a slightly larger scale, as indicated by the chlorophyll means (Fig. 2.10c). The high chlorophyll variability of inshore subtransects (Fig. 2.6) was a consequence of the steep gradients in chlorophyll concentration near the coast (Fig. 2.8).

The CV's for northern zone subtransects were significantly greater than those of the other three zones (Table 2.5). The high spatial variability of chlorophyll in the northern zone largely resulted from a group of transects run immediately behind the

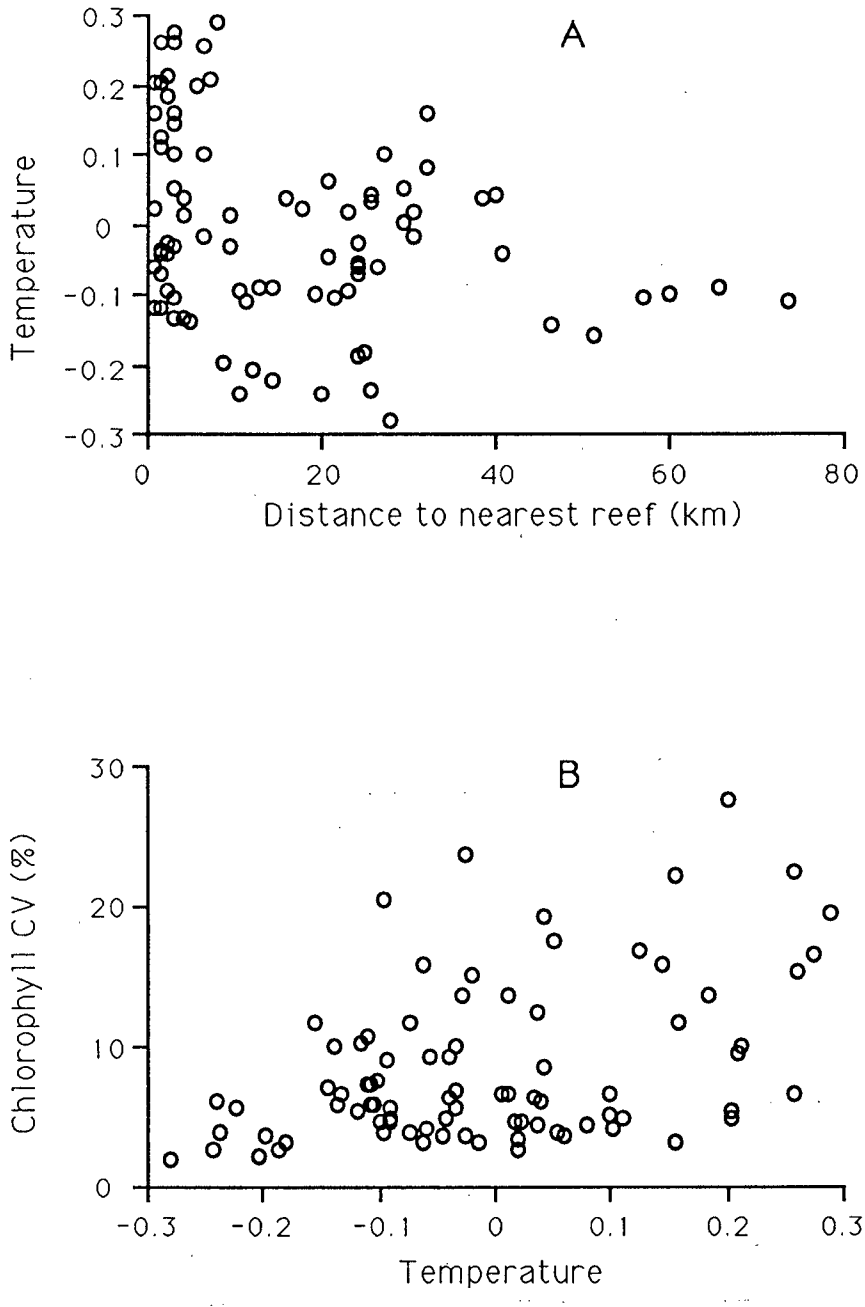


Figure 2.11. **A.** Mean subtransect temperature in relation to the proximity of nearest individual reef. **B.** Chlorophyll coefficients of variation in relation to temperature. Only wet season subtransects were used, and subtransects less than 15 km from the coast were excluded. A latitudinal temperature trend has been removed from temperature measurements.

Ribbon Reefs which comprise a shelf edge barrier along much of the length of this zone. Transects run close behind this barrier intersected plumes of chlorophyll enriched water opposite gaps in the barrier. When subtransects passing through chlorophyll plumes were removed from the analysis, there were no significant between zone differences in chlorophyll variability. The chlorophyll CV did not differ with season (Fig. 2.6), nor did it vary seasonally within any band (Fig. 2.6).

DISCUSSION

Regional and seasonal changes in chlorophyll concentration

The GBR shelf, together with the shelves to the north and north-west of Australia, differ from many other tropical shelves in that they are unaffected by the large scale upwellings found on western continental margins or by large river outflows (Longhurst and Pauly 1987). Chlorophyll concentrations on the north west shelf of Australia are similar to those on the GBR shelf (water column maxima 0.22-1.07 ug l^{-1}, Tranter and Leech 1987), but those in the Arafura sea and in the Gulf of Carpentaria are slightly higher (water column maxima 0.70-2.34 ug l^{-1}, Newell 1973, Hallegraef and Jeffrey 1984, Ilahude **et al.** 1990). The north west shelf of Australia has similarities to the GBR shelf in that nutrient rich sub-thermocline water is forced onto the shelf during the wet season in a 'vestigial upwelling' (Tranter and Leech 1987) similar to that on the GBR shelf (Andrews and Furnas 1986). Unlike the situation on the GBR shelf, this intrusion appears to persist throughout the wet season as it is primarily current driven. The seasonal range of chlorophyll concentrations on the north west shelf is larger than that found on the GBR shelf, most likely as a result of the more persistent nature of intrusions. The higher chlorophyll concentrations found seasonally in the Arafura Sea have been attributed to upwelling in the Banda Sea (Hallegraef and Jeffrey 1984) and local coastal upwelling in the Arafura Sea itself (Ilahude **et al.** 1990). In the Gulf of Carpentaria the higher chlorophyll concentrations have been attributed to strong tidal mixing (Forbes 1984).

Surface chlorophyll concentrations on the GBR shelf and the north west shelf are higher than mean concentrations in offshore Indian Ocean waters (0.17 ug l^{-1}, Humphrey and Kerr 1969) and in the Coral Sea (0.20 ug l^{-1}, this study), but do not approach the concentrations found on tropical shelves on which major upwellings occur (2.5-10 ug l^{-1} Peru, Walsh **et al.** 1971; 5-11 ug l^{-1} Senegal, Gallardo 1981).

The very low chlorophyll concentrations in the Coral Sea are of a similar magnitude to those in surface waters of other non-upwelling tropical oceanic regions (Dandonneau and Gorhin 1984, Herbland and Voituriez 1979). The conditions that give rise to such low concentrations elsewhere; a nutrient poor surface mixed layer

above a permanent thermocline (Herbland and Voituriez 1979), also prevail in the Coral Sea (Andrews 1983).

Furnas and Mitchell (1986) have suggested that the low dissolved inorganic nitrogen concentrations on the GBR shelf, and low dissolved inorganic nitrogen to dissolved inorganic phosphorus ratios indicate that phytoplankton biomass is nitrogen limited. Consequently processes by which 'new' nitrogen (Dugdale and Goering 1967) is introduced to GBR shelf waters should result in an increase in phytoplankton biomass, and regional differences in such processes should be echoed by regional differences in chlorophyll concentration.

On the outer shelf 'new' nutrients are intermittently introduced by intrusions of nutrient rich sub-thermocline water from the Coral Sea particularly during the wet season (Andrews and Furnas 1986). Water in intrusions has higher chlorophyll concentrations than shelf water (Furnas and Mitchell 1986). The fate of intruded water is unknown; it may be withdrawn off the shelf when the conditions forcing the intrusion dissipate, or be mixed into the water column increasing surface chlorophyll concentrations (Andrews and Furnas 1986). On the inner shelf and inshore bands, high DIN levels can result of wind driven sediment resuspension (Walker and O'Donnell 1981, Ullman and Sandstrom 1987) and terrestrial runoff (Wolanski and Van Senden 1983). Terrestrial runoff may be discounted as an influence on central zone chlorophyll concentrations over the period of this study as no major floods occurred during the sampling period.

Mean surface chlorophyll concentrations in inner and outer shelf bands were not significantly different, despite the strucural differences between these regions (reef matrix compared to open GBR lagoon) and the possible effect of shelf edge intrusions. The lack of high surface chlorophyll values suggests an absence of persistent or intense nutrient upwelling.

Surface chlorophyll concentrations in the outer shelf band were higher during the wet season (Dec. to March), when intrusions occur most frequently (Andrews and Furnas 1986). Furnas and Mitchell (1986) also recorded a wet season increase in chlorophyll concentration on the outer shelf, and Revelante and Gilmartin (1982) found that phytoplankton biomass increased two to threefold in the central zone of the GBR during the wet season. In contrast, Marshall (1933) found no seasonal change in phytoplankton numbers.

Distinctly higher wet season chlorophyll concentrations were found on the inner shelf in both the northern and Swains zones (Fig. 2.5), but different processes appear to be responsible. The shelf is narrow in the northern zone and the hinterland is wet with a regular seasonal increase in river discharge (Queensland Water Resources

Records 1988). Terrestrial runoff will consequently have a more marked seasonal enriching effect on the inner shelf band in this zone. In contrast the shelf is over 200 km wide in the Swains zone and the subtransects classified as 'inner shelf' were all from the Capricorn channel which has closer affinities to Coral Sea water than to water on inner shelf zones further north. The higher wet season chlorophyll concentrations on the inner shelf band of the Swains zone (Fig. 2.5) may be the result of a seasonal intrusions of high nutrient water, as in the central zone.

Latitudinal changes in chlorophyll concentration

Latitudinal differences in surface chlorophyll concentrations may be the consequence of two phenomena; latitudinal changes in the overall chlorophyll concentration of surface waters, and latitudinal differences in the hydrodynamic processes that influence chlorophyll concentration indirectly. Dandonneau and Gorhin (1984) found that chlorophyll concentrations in oceanic waters east of Australia increased with latitude (14°S to 32°S), primarily as a result of a more pronounced vertical winter mixing at higher latitudes. Similar latitudinal changes in the mean depth of the thermocline and associated nutricline might be expected in Coral Sea waters off the GBR shelf, but have not been demonstrated. Additionally, if shelf edge intrusions occur in the Pompey and Swains zones, a shallower nutricline such as Dandonneau and Gorhin (1984) found, could enhance on-shelf movement of nutrient enriched water, particularly during the wet season.

Latitudinal differences in another shelf edge hydrodynamic processes may also contribute to the latitudinal differences in chlorophyll concentration. In the northern and Pompey zones, the reef matrix creates a more complete barrier to on-shelf water movement than the other zones, resulting in strong tidal currents between shelf edge reefs (Maxwell 1968, Wolanski **et al.** 1988). During spring tides, shelf edge tidal currents in the northern zone are postulated to be strong enough to entrain nutrient enriched sub-thermocline water as they move onto the shelf (Wolanski **et al.** 1988). This nutrient-enriched water is believed to promote growth of the calcareous alga Halimeda in reef matrix waters (Wolanski **et al.** 1988), and could also result in higher concentrations of phytoplankton biomass in the outer shelf band.

Spatial variability in chlorophyll concentration

Mesoscale chlorophyll variability (between different cross-shelf bands or latitudinal zones) on the GBR shelf is smaller, both spatially and seasonally, than that recorded on temperate and other tropical shelves. On the narrow Californian shelf, chlorophyll varies across the shelf by a factor of 20 (Hayward and Venrick 1982) and

seasonally by a factor of two (Smith and Eppley 1982). Surface chlorophyll concentrations off the Peruvian coast vary spatially 30-fold (Guillen and DeRondan 1972) as a result of the sharp nutrient gradients within the upwelling zone. On the north west shelf of Australia, a tropical shelf more similar to the GBR shelf in that it is unaffected by major upwelling or river outflows, depth averaged chlorophyll varied both seasonally and cross-shelf by a factor of two (Tranter and Leech 1987).

Small scale (< 8 km) spatial variability of chlorophyll was also low (Table 2.3). Within subtransects, chlorophyll concentrations varied by a factor of only 1.5, similar to the small scale variation in the North Pacific gyre (Hayward **et al.** 1983). Although on a regional basis small scale variability was not significantly higher on the outer shelf or in the inshore band than in other regions (Table 2.3), local variability was noticeably higher near individual reefs and coastal features (Figs. 2.8, 2.9). Changes in the chlorophyll concentration near reefs were often marked, but limited to the close vicinity of the reef. Reef effects on small scale spatial variability of chlorophyll were not apparent as a feature of the reef matrix as a whole.

The relative regional constancy of the surface chlorophyll concentration over the GBR shelf may have implications for the pelagic community structure. The spatially consistent zooplankton community structure found in the central North Pacific gyre is believed to be a consequence of the temporally and spatially invariant nature of the phytoplankton biomass (McGowan and Walker 1979). Places where the chlorophyll spatial variability was locally higher, close to the coast and to reefs, would also effect the zooplankton community. Zooplankters capable of responding behaviourally or physiologically to a more variable food supply may be advantaged in such places (Dagg 1977).

A comparison of the phytoplankton biomass on the GBR shelf with those at which zooplankton production has been found to be limited can provide an indication of the significance of GBR phytoplankton biomass for zooplankton survival and growth. Most studies on food limitation of copepod production, the most numerous group of zooplankton on the GBR shelf, have been in temperate waters. Egg production of *Paracalanus parvus* off California was food limited at chlorophyll concentrations up to 3 ug l^{-1} (Checkley 1980). Egg production of *Acartia tonsa* in Narragansett Bay was food limited at chlorophyll concentrations up to 20 ug l^{-1}, with negligible egg production below 1 ug l^{-1} (Durbin **et al.** 1983), and similarly egg production of *Temora longicornis* in Long Island Sound was nil at concentrations less than 2 ug l^{-1} (Peterson 1985). The chlorophyll concentrations below which egg production ceases in these species are still higher than concentrations in most places on the GBR shelf. *Paracalanus* spp., *Acartia* spp. and *Temora* spp. on the GBR shelf

must sustain egg production at much lower chlorophyll concentrations than temperate species of the same genus. These comparisons tell us more of the adaptability of copepod species than the ecological significance of GBR chlorophyll concentrations.

The food requirements of only one zooplankter found in GBR waters, an echinoid larva, has been investigated in detail. Lucas (1982) suggested that crown-of-thorns starfish larvae, which feed upon phytoplankton, required a minimum chlorophyll concentration of 0.4 ug l-1 for survival. This estimate has subsequently been revised downwards by Olson (1987), who found that starfish larvae raised in situ in natural seawater could survive and develop at chlorophyll concentrations of 0.2-0.3 ug l^{-1}. These concentrations are close to mean chlorophyll concentrations on the GBR shelf, so higher concentrations of chlorophyll, such as those associated with individual reefs, may be of importance to this species.

SUMMARY

Surface chlorophyll concentrations in waters on the NE Queensland shelf were higher than those in adjacent tropical oceanic waters of the Coral Sea though not as high as on tropical continental shelves on which upwelling occurs. Over the 1200 km section of the GBR shelf sampled, the surface chlorophyll concentration ranged only up to 1.57 ug l^{-1}, and in most cross-shelf and long-shelf regions ranged over less than an order of magnitude.

There was a consistent pattern in cross-shelf chlorophyll concentration; highest inshore and lowest in the Coral Sea with little difference in mean chlorophyll concentration between the GBR lagoon and outer shelf reef matrix. High inshore concentrations are likely due to wind driven resuspension of sediment and runoff, and low Coral Sea concentrations to low nutrient concentrations in the surface mixed layer. Mean chlorophyll concentrations increased with latitude but the processes underlying this change were not resolved.

Surface chlorophyll concentrations on the outer shelf were higher during the wet season (Dec. to March) than the dry season (April to Nov.). The high wet season concentrations appeared to be the result of the more frequent intrusions of enriched water across the shelf break during this season.

Close to individual reefs there were commonly small but sharp changes in chlorophyll concentration. Such changes were the result of water export from reefs rather than reef induced upwelling of bottom water. This phenomenon resulted in higher levels of small-scale surface chlorophyll variability in the proximity of individual reefs, but was not extensive enough to result in a higher small-scale chlorophyll variability over the outer shelf band as a whole.

Chapter 3. The horizontal spatial variability of chlorophyll on the Great Barrier Reef: spectral analysis.

INTRODUCTION

Spatial pattern in phytoplankton biomass results from interactions between physical mixing processes and the net growth rates of phytoplankton communities, as individual phytoplankton cells have limited control over their physical location. Physical processes appear to be the primary determinant of phytoplankton spatial variability over mesoscale distances (10-1000 km) (Platt and Denman 1975a, Powell **et al.** 1975, Leigh-Abbott **et al.** 1978), with phytoplankton growth and zooplankton grazing upon phytoplankton modifying the spatial pattern of phytoplankton abundance imposed by physical processes (Wroblewski and O'Brien 1976).

The effects of physical and biological processes on phytoplankton spatial variability have been formalized in models in which processes that reduce concentrations of phytoplankton biomass (physical turbulence and zooplankton grazing), are counteracted by phytoplankton growth (Wroblewski and O'Brien 1976, Platt and Denman 1980). Within spatial models, phytoplankton are assumed to behave as passive particles. Hence, the spatial variability of chlorophyll, used as a proxy for phytoplankton biomass, should be similar to the variability of physical variables dispersed by water turbulence (Denman **et al.** 1977). Differences between the spatial variability of chlorophyll and that of water temperature, a convenient passive property, indicate the extent that other processes, including growth and grazing, influence chlorophyll spatial variance (Denman **et al.** 1977, Platt and Denman 1980).

Time series analysis techniques, which can quantify variability across a continuum of spatial scales, have been used to describe chlorophyll spatial variability. Most descriptions of chlorophyll spatial variability using time series analysis have been confined to temperate oceanic (Platt and Denman 1975a, Horwood 1978, Gower **et al.** 1980), temperate shelf waters (Campbell and Esaias 1985), and tropical oceanic waters (Fasham and Pugh (1976). As yet, time series analysis techniques have not been used to describe chlorophyll spatial variability on a tropical continental shelf or on a shelf as bathymetrically complex as the GBR shelf.

The nature of the horizontal spatial variability of chlorophyll in surface waters of the Great Barrier Reef (GBR) shelf and Coral Sea are investigated by time series analysis in this section. This analysis served two purposes. First, the spatial variability of chlorophyll is characterized for different geographical provinces of the GBR shelf. This extends the description of surface chlorophyll spatial variability in the

previous chapter in which variability was quantified at three spatial scales; across the whole GBR shelf (1200 km), within cross-shelf or latitudinal regions (20 to 300 km), and within discrete 8 km subtransects. Secondly, differences in chlorophyll spatial variability identified by time series analysis were related to regional differences in bathymetry and reef density. Geographical differences in chlorophyll spatial variability, in conjunction with a comparison between chlorophyll and temperature spatial variability, enabled inferences to be made about the processes that affect spatial variability in near-surface chlorophyll concentrations.

DATA COLLECTION AND ANALYSIS

Surface chlorophyll fluorescence and temperature were sampled concurrently at 15 m intervals along 43 underway transects (Fig. 2.1). Strictly speaking, the transect data are records of both the spatial and temporal changes in the variables along each transect, as transects could not be sampled instantaneously. If, however, the transect sampling was completed in a time much shorter than that over which the variable was changing, Taylor's frozen field hypothesis states that the series can be used to describe the spatial structure of the variable (Tritton 1977). Ship speed was 5 m sec^{-1}, 10-100 times current speeds on the GBR (0.1-0.2 m sec^{-1} central GBR, Andrews 1983, Wolanski and Pickard 1985). Under such conditions one may reasonably invoke Taylor's hypothesis and regard the transect data as representing spatial differences in chlorophyll and temperature (Walsh 1988).

Spectral analysis, the technique used here to characterize the chlorophyll variability, has been widely employed to characterize spatial variability in planktonic ecosystems (Denman 1976, Denman and Platt 1976, Fasham 1978b, Fasham and Pugh 1978, Gower **et al.** 1980, Weber **et al.** 1986). This technique partitions the total variance of a property into variance associated with different wavelengths. The end product of spectral analysis, the power spectrum, is a plot of the variance of a property against wavelength. Chlorophyll and temperature power spectra were calculated to compare the spatial variability of chlorophyll and temperature in different regions.

Cross-spectral analysis was then used to compare the shapes of chlorophyll and temperature power spectra (Chatfield 1984). The output from cross-spectral analysis, the coherence, is analogous to a correlation coefficient between the two variables at a particular wavelength. The coherence spectrum is a measure of the correlation between two variables over a range of wavelengths. Coherences significantly greater than zero, indicating a significant association between chlorophyll and temperature at a particular wavelength, were tested by their departure from the theoretical distribution of coherence values (Koopmans 1974).

Transects were divided into smaller segments if they crossed boundaries between cross-shelf bands or latitudinal zones. Only segments longer than 40 km were used. Cross-shelf bands and latitudinal zones to which segments were assigned have been described in chapter two (Fig. 2.1). Prior to spectral analysis, segments were detrended (linear least squares method, Chatfield 1984) to remove diel fluctuations and spatial trends of longer wavelength than the segments. Power spectra and cross spectra were then calculated with the IMSL subroutines (IMSL 1984). Power spectra were computed using the Blackman-Tukey method and smoothed with a Hamming window of 5 km (Chatfield 1984), providing resolution of wavelengths from 30 m to 10 km.

RESULTS

Spectral analysis - shape of spectra

Chlorophyll power spectra were log transformed and plotted against log wavelength as recommended by Denman (1976). Most transformed chlorophyll spectra decreased in a linear fashion (Fig. 3.1a), indicating that surface chlorophyll concentrations were more variable across larger spatial scales than across smaller scales. Eight of the 46 chlorophyll spectra became asymptotic to the x-axis at short wavelengths (Fig. 3.1b) at a spectral value of about -4.5 to -5, which corresponds to a chlorophyll concentrations standard deviation of 0.05 and 0.1 ug l^{-1} respectively. The precision of chlorophyll values calculated from fluorescence, based on the standard error of the estimate of the calibration equation, ranged from 0.04 to 0.21 ug l^{-1} (mean 0.12 ug l^{-1}). Consequently, the flattening of these eight spectra suggests that chlorophyll variability on these transects was smaller than instrument error over short distances (< 0.5 km). There was no obvious explanation for the occurrence and low spatial variability of these eight spectra. They were not confined to any one cross-shelf band, latitudinal zone, or particular cruise.

Should a preponderance of chlorophyll spatial variability occur at a particular length scale, e.g. the mean distance between reefs within a zone, this feature would be represented on the power spectrum by a peak at the corresponding wavelength. None of the chlorophyll power spectra exhibited peaks, indicating that the spatial variability in each segment was distributed regularly across a range of spatial scales (Fig. 3.1). Most temperature spectra also decreased in a linear fashion with wavelength, becoming asymptotic at a spectral value that corresponded to a mean temperature deviation of 0.05 C° (Fig. 3.2).

The resolution of temperature measurements in this study was calculated to be 0.07 C°, indicating that the spectra were flattening at the level similar to instrument

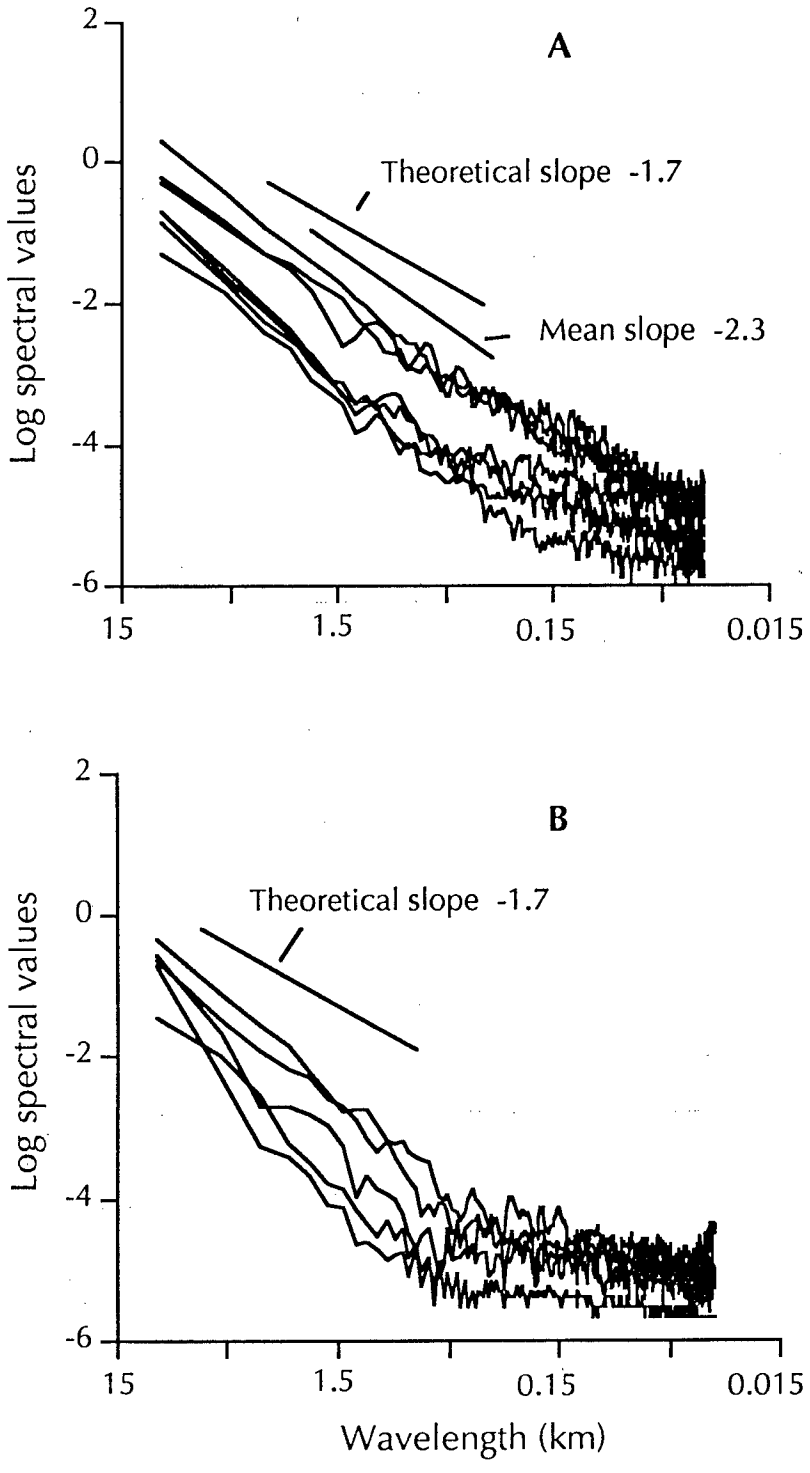


Figure 3.1. Representative chlorophyll power spectra; A - chlorophyll power spectra, B - chlorophyll spectra with an inverse inflexion. The mean slope of chlorophyll spectra is marked, as is the theoretical slope (-1.7) of water turbulence.

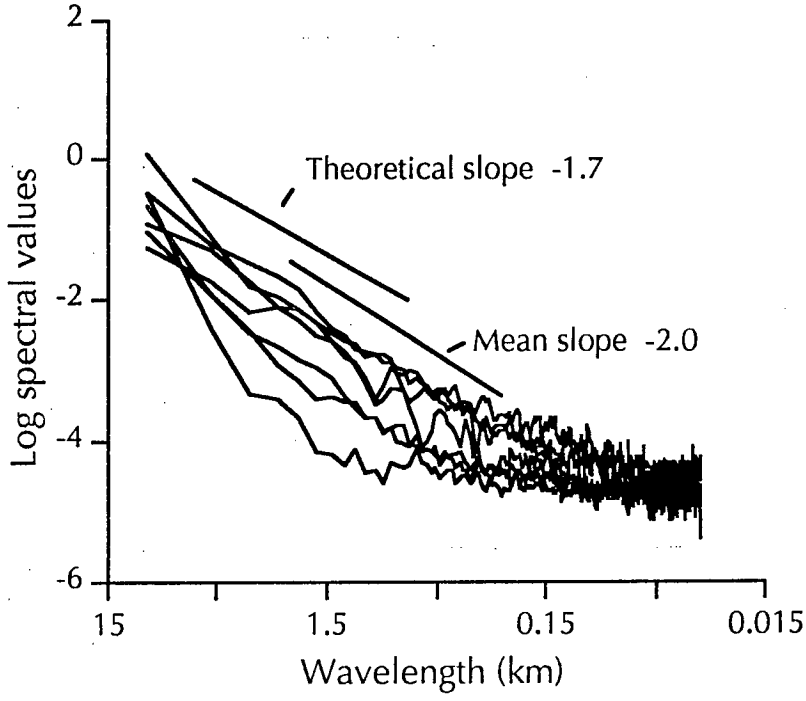


Figure 3.2. Representative temperature power spectra. The mean slope of temperature spectra is marked, as is the theoretical slope (-1.7) of water turbulence.

noise. The wavelength at which the temperature signal was lost in noise ranged between 100 m and 450 m, much longer than the smallest spatial scale over which variability could be resolved (30 m). As with chlorophyll, the spatial variability of temperature was distributed regularly across the range of spatial scales (Fig. 3.2).

Much of the horizontal spatial variability of chlorophyll is thought to derive from water turbulence (Platt and Denman 1975b). It is of interest to remove this effect from the chlorophyll spectra to estimate the chlorophyll variability presumed to derive from biological activity. To do this, normalized chlorophyll spectra ($f_{chl}(w)$) were multiplied by the coherency spectra (C(w)) to estimate the proportion of the chlorophyll spectra that was similar to temperature spectra. These were subtracted from the chlorophyll spectra to give residual chlorophyll spectra (Resid $f_{chl}(w)$)(Chatfield 1984).

$$\text{Resid } f_{chl}(w) = f_{chl}(w) - [f_{chl}(w) * C(w)]$$

Residual spectra were calculated for each segment. Almost all were identical to the chlorophyll spectra (Fig. 3.3). There were no significant peaks in the residual spectra and like the chlorophyll spectra they decreased linearly with log wavelength (Fig. 3.3). This similarity was unsurprising as the modification of the chlorophyll spectrum to derive the residual spectra was a function of the cross spectral coherence, which was low (Fig. 3.6).

Spectral analysis - slopes of spectra

Slopes of spectra are a measure of the distribution of spatial variability over wavelength and were used to compare the distribution of variability of chlorophyll and temperature across the range of length scales. Only the portion of the spectra above a wavelength of 450 m was considered to minimize the confounding effect of instrumental noise at shorter wavelengths. Above this wavelength, spectra were almost linear: mean r-squared value of linear fits to temperature spectra above 450 m was 91.7% (range 62.4 to 98.9) and of chlorophyll 96.2% (range 83.1 to 99.7). Consequently spectral slopes could be used as a precise estimate of the distribution of spatial variance over wavelength.

Slopes of chlorophyll spectra ranged from -1.66 to -3.06 (mean -2.25), and of temperature spectra from -0.82 to -2.64 (mean -1.98; Fig. 3.4). Neither the mean chlorophyll nor mean temperature spectral slope was significantly different from the theoretically predicted slope of -1.7. The slopes of chlorophyll and temperature

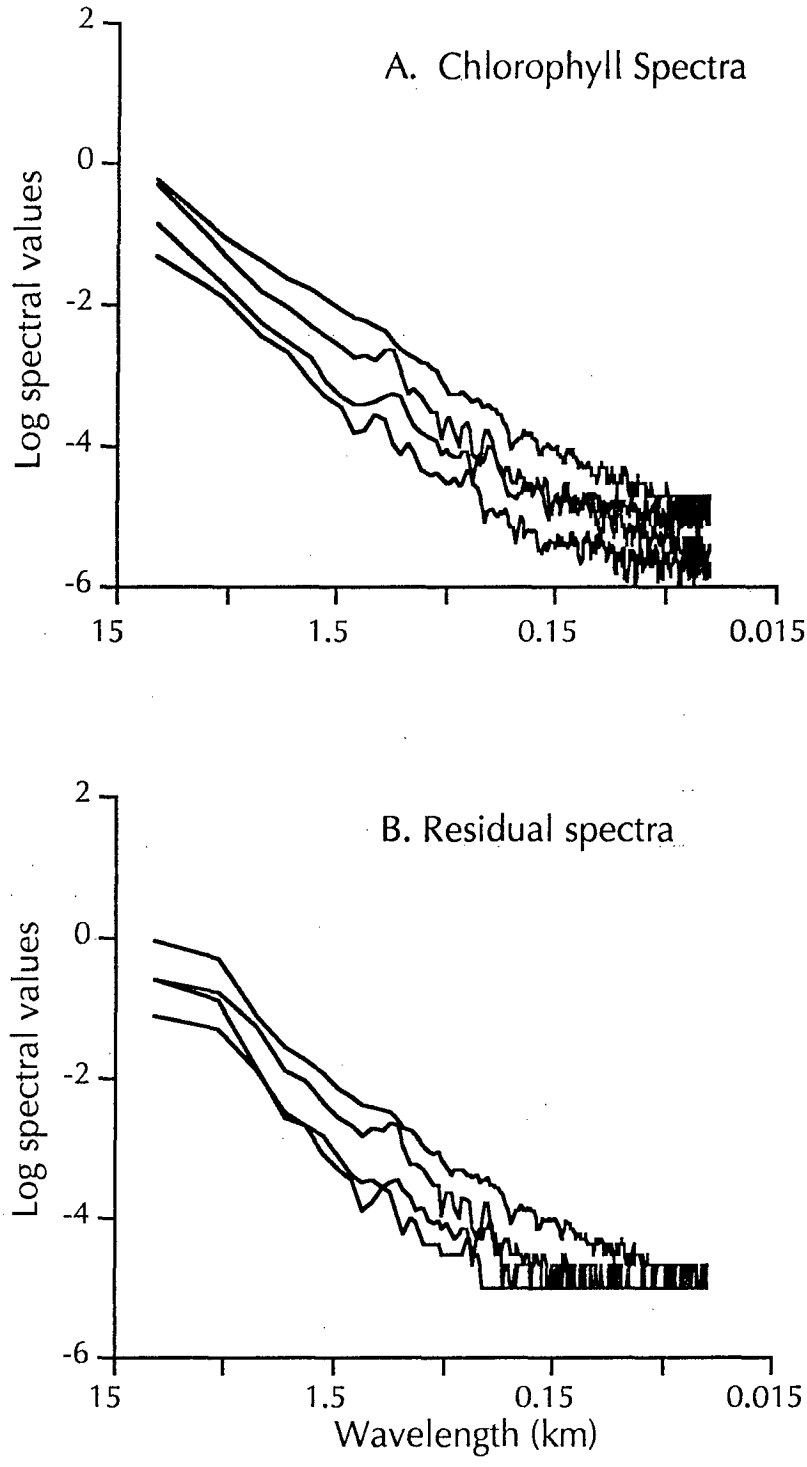


Figure 3.3. Chlorophyll power spectra; A - chlorophyll spectra, and B - chlorophyll spectra from the same segments after removal of the variance attributed to turbulence.

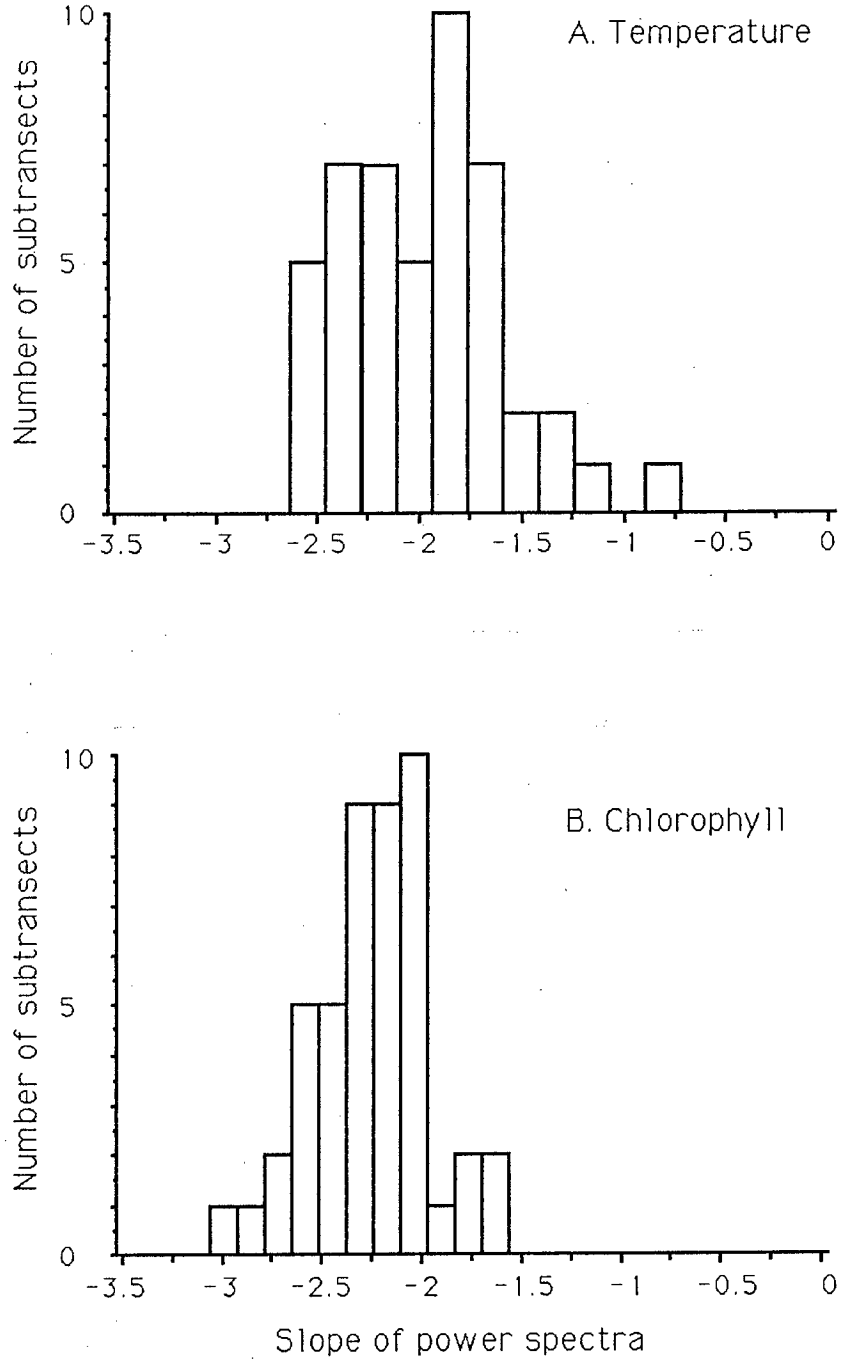


Figure 3.4. Frequency histogram of spectral slopes; A - Temperature, B - Chlorophyll.

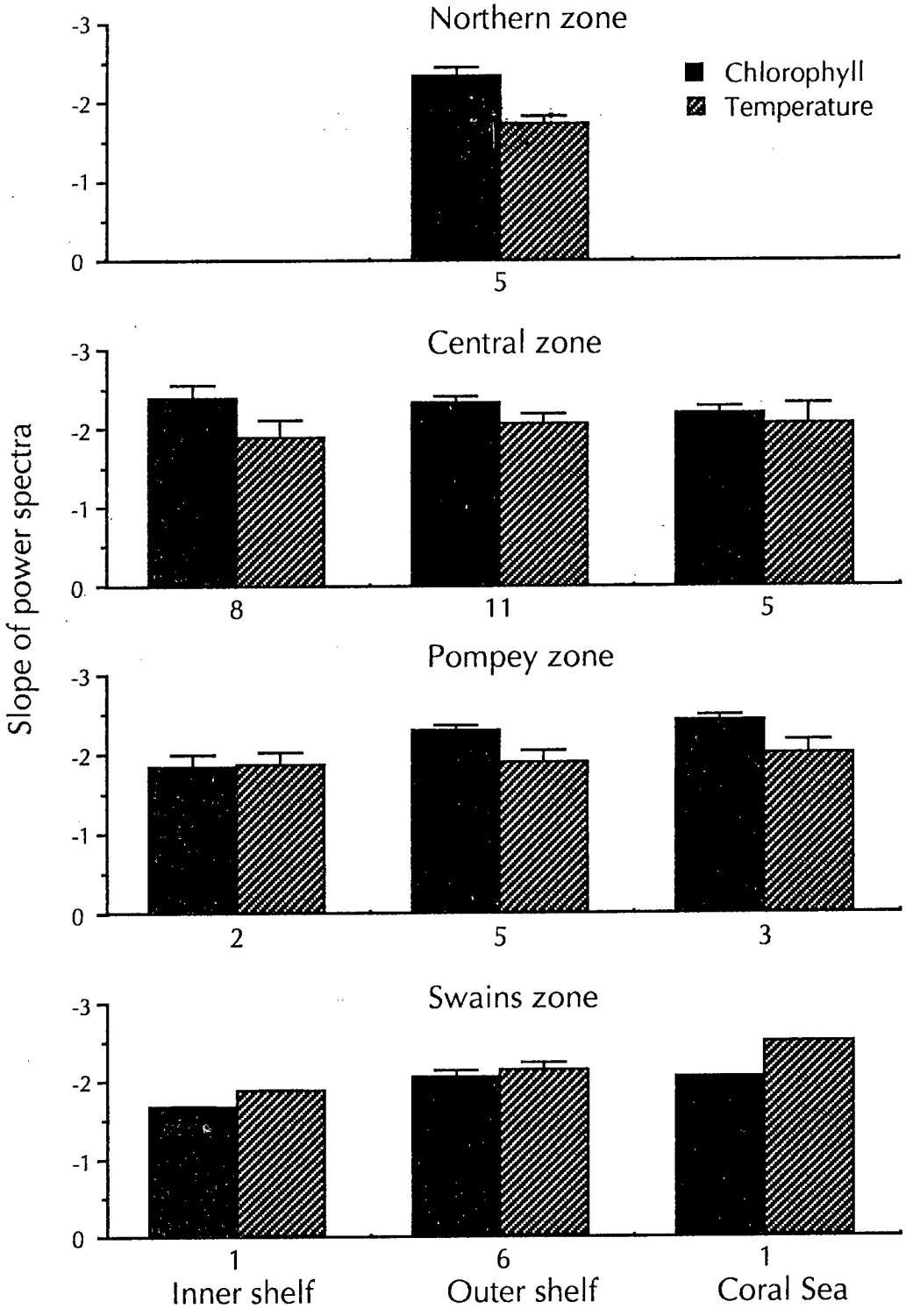


Figure 3.5. Slopes of spectra of segments from each cross-shelf band within each latitudinal zone. Numbers below the axis are the number of segments within each category. Error bars indicate one standard error.

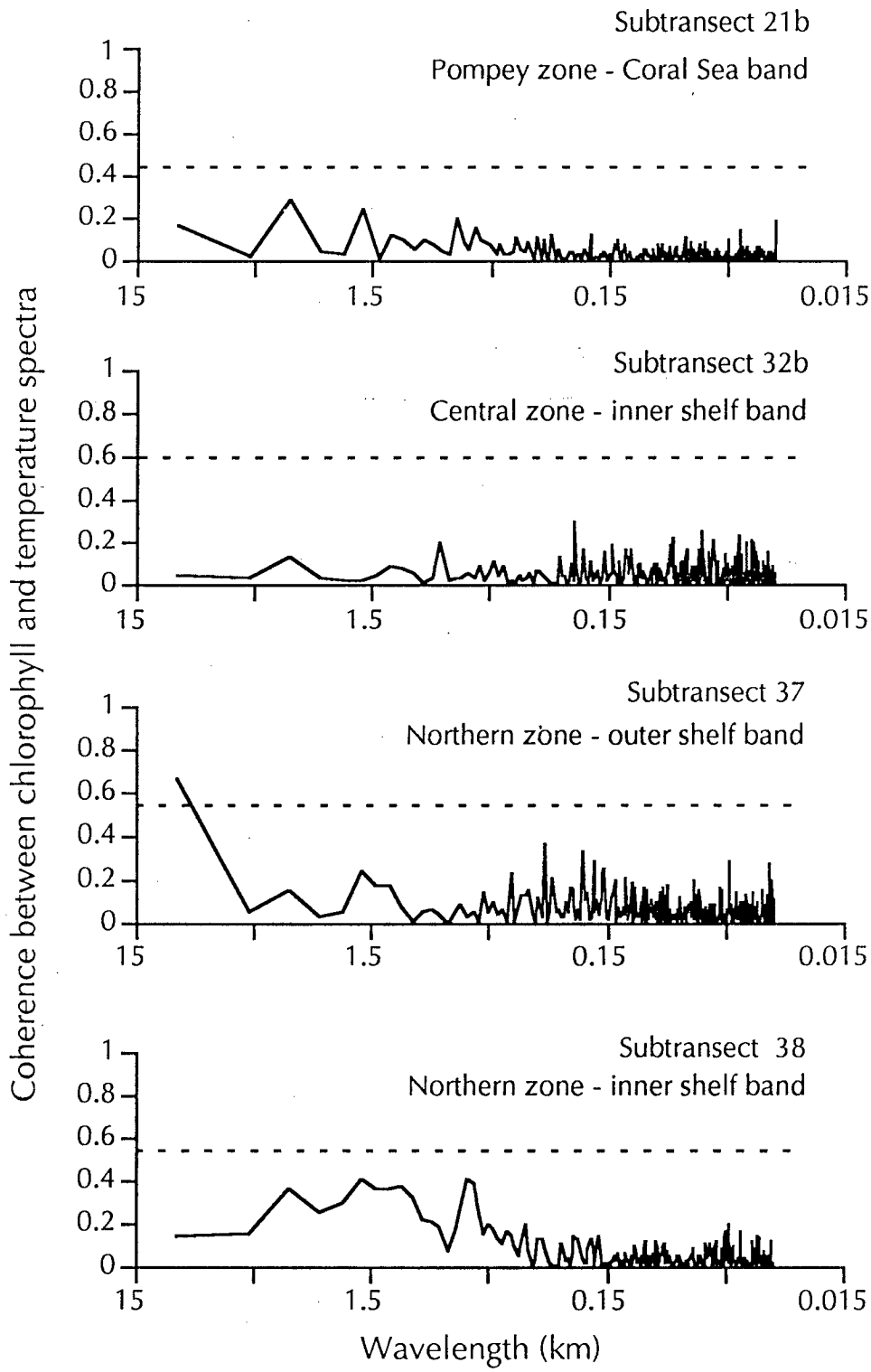


Figure 3.6. Representative chlorophyll - temperature coherence spectra from different latitudinal zones and cross-shelf bands. Dashed line indicates boundary for coherence values significantly larger than zero ($p < 0.05$).

spectra did not differ significantly, nor did chlorophyll or temperature slopes differ between cross-shelf bands or latitudinal zones (Table 3.1). Consequently the wavelength-dependent distribution of spatial variability for both chlorophyll and temperature was the same for all three cross-shelf bands and latitudinal zones. Spectral analysis revealed that, over the spatial scales between 0.45 and 10 km, chlorophyll and temperature spatial variability did not differ, nor did they differ in different parts of the GBR shelf at this length scale.

Cross spectral analysis

Chlorophyll and temperature were not significantly coherent along any of the segments (Fig. 3.6). Some coherence spectra contained several significant coherence values (Fig. 3.6), but with the type one error level set in the significance test at 5%, one could expect one in twenty of the coherence values to be significant by chance. Examination of the phase spectra of transects with significant coherence values showed no systematic relationship of phase with wavelength, suggesting that such values had occurred by chance. The absence of significant coherence between chlorophyll and temperature indicated that, even though the distribution of variability across spatial scales was similar for both chlorophyll and temperature, patches of higher (or lower) chlorophyll were not regularly associated with patches in which the water temperature was higher (or lower).

DISCUSSION

Spectral analysis - shape of spectra

The shapes of chlorophyll spectra have been used to infer the nature of the mechanisms generating the observed chlorophyll spatial variability (Platt and Denman 1975b, Denman and Platt 1976, Fasham and Pugh 1976). The basis for this interpretation is that phytoplankton, as shown by chlorophyll, are assumed to act as passive particles in the water column (Platt and Denman 1975b). Biological activity that may affect the spatial variability of phytoplankton, e.g. growth and grazing, can then be inferred by comparisons of chlorophyll spectra with those of temperature, a passive tracer of the horizontal mixing of water (Walsh 1988). Over length scales of 5-100 km the power spectra of horizontal mixing (and its proxy, temperature) is predicted to display a loglinear relationship with wavelength with slopes of -1.7 to -3 (Fasham and Pugh 1976, Deschamps **et al.** 1981). Differences between slopes of chlorophyll and temperature power spectra are attributed to phytoplankton growth or grazing mortality. The critical length scales at which growth begins to dominate over diffusive forces will depend on local net growth rates and turbulence. In oceanic

Table 3.1

Analyses of variance of slopes of power spectra with a three way fixed model ANOVA. Factors were variable (chlorophyll, temperature), band (inner shelf, outer shelf and Coral Sea), and zone (central, Pompey and Swains).

Data untransformed, Cochran's C = 0.237, $p < 0.05$.

Factor	DF	Mean square	F ratio	Probability
Variable	1	0.123	0.96	NS
Band	2	0.253	1.97	NS
Zone	2	0.113	0.89	NS
Variable * Band	2	0.036	0.28	NS
Variable * Zone	2	0.266	2.08	NS
Band * Zone	4	0.099	0.78	NS
Var * Band * Zone	4	0.092	0.72	NS
Error	66	0.128		

DF = degrees of freedom, NS = not significant

waters off the eastern Canadian coast the critical length scale has been calculated to be 1 km (Denman and Platt 1976). At wavelengths larger than that of the critical length scale, chlorophyll power spectra will diverge from those of temperature.

Power spectra of chlorophyll and temperature measurements have not provided unequivocal support for these models. Denman (1976) found that the slopes of his chlorophyll spectra had inflexions, diverging from temperature slopes above a wavelength of about 1 km, the predicted critical wavelength (Denman and Platt 1976). Chlorophyll spectra from the tropical eastern Atlantic also had inflexions (Fasham and Pugh 1976) but others from the Bay of Biscay (Fasham and Pugh 1976), the North Sea (Horwood 1978), and North American shelf waters (Lekan and Wilson 1978, Campbell and Esaias 1985) did not.

Although chlorophyll and temperature power spectra from the GBR had slopes close to the predicted value for pure turbulent dispersion, -1.7 (Fasham and Pugh 1976)(Figs. 3.1, 3.2, 3.4), none of the chlorophyll spectra had inflexions. If values for the turbulent energy dissipation rate and phytoplankton growth used in the Denman-Platt (Denman and Platt 1976) model apply to the GBR, then the critical wavelength on the GBR would be about 1 km and an inflexion would be expected at this wavelength. Even if these values for the model parameters are inappropriate to the GBR shelf, the predicted critical patch size would change little as it is a function of the square root of these parameters. The absence of inflexions in any of the 46 chlorophyll spectra, even those from the Coral Sea, casts doubt on the validity of the Denman-Platt model for the spatial distribution of phytoplankton for GBR waters.

An examination of one assumption underlying the Denman-Platt model suggests one reason why it may not be appropriate for GBR shelf waters. The range of spatial scales investigated is presumed to be an inertial subrange, i.e. water turbulence is generated at scales larger than the observed spatial scales, and dissipated at smaller scales. Such an assumption which is probably invalid on the shelf where water motion is influenced by reefs and coastal bathymetry (Wolanski **et al.** 1984, Wolanski 1987).

A further assumption the Denman-Platt model makes is that the phytoplankton biomass is in equilibrium with environmental conditions, neither increasing nor decreasing over time (Fasham 1978a). This assumption may be untenable for many ecosystems. Accordingly, Fasham (1978a) modified the growth term in the Denman-Platt model from exponential to logistic, in order to model more realistically limiting factors such as herbivore grazing and nutrient depletion. Taking a homogeneous distribution of chlorophyll variance across wavelength as starting conditions, Fasham (1978a) followed the development of chlorophyll spatial heterogeneity under different

simulated growth regimes. When net phytoplankton growth was positive, chlorophyll spectra were steeper than those of temperature, and when net growth was negative, chlorophyll spectra developed inflexions at larger length scales. When the net growth rate of phytoplankton was close to zero, chlorophyll spectral slopes were similar to those of temperature. Fasham's model could therefore explain the spectra both with and without inflexions that had been observed. However, because of the variety of spectral shapes predicted by Fasham's model under different conditions of phytoplankton growth, without independent measurements of the growth rate in areas in which transects were made, the validity of this model for GBR waters could not be determined.

Spectral analysis - slopes of spectra

Horizontal chlorophyll variability over mesoscale distances (450 m to 10 km), as shown by the chlorophyll spectral slopes, did not differ cross-shelf or latitudinally (Table 3.1), despite marked cross-shelf and latitudinal differences in reef density and type (Pickard **et al.** 1977). Not only are absolute chlorophyll concentrations and spatial variability on the GBR shelf low (chapter two), but the spatial variability is distributed in a similar fashion in different structural provinces of the reef. Spectral analysis could not identify the higher chlorophyll spatial variability near reefs (Figs. 2.9, 2.10). Such uniformity suggests that while features such as reef density and the attendant complex water circulation around reefs may affect phytoplankton patchiness close to individual reefs, they do not generate shelf scale differences in chlorophyll spatial heterogeneity. Power spectra provide estimates of the overall chlorophyll variability at each spatial scale (Ripley 1978), so the approach used in chapter two is better suited to quantify spatial variability distributed irregularly at a particular scale, such as around reefs.

Comparison of surface chlorophyll variability on the GBR shelf with that elsewhere is hampered because few studies of chlorophyll spatial variability quantify variability at specific spatial scales. Abbott and Zion (1987) recorded chlorophyll coefficients of variation in 16 km^2 blocks off the California coast ranging from 0.47 to 1.16 (this study 1 km 0.15, 5 km 0.31). Kahru **et al.** (1981) found chlorophyll concentration varied about two-fold over 10 km separation of stations in the Baltic Sea. Comparison with these studies suggests that, at these scales, chlorophyll spatial variability on the GBR shelf is lower than that in other shelf waters.

Cross spectral analysis

With the similarity between computed temperature and chlorophyll spectra, it would seem intuitive that the two variables be coherent. However cross spectral analysis is most effective at identifying relationships between variables that are related linearly. With monotonic but non-linear relationships between variables, cross spectral analysis is less sensitive in detecting relationships (Star and Cullen 1981). The absence of significant coherence between chorophyll and temperature spectra may indicate that different processes were responsible for the spatial variability of chlorophyll and temperature (Richerson et al. 1978). Chlorophyll variability on the GBR appears to be related to movement of water away from individual reefs, coastal resuspension of nutrients and terrestrial inputs. Temperature variability will be largely dependent on differential heating and cooling of waters. These processes would not be expected to be spatially or temporally synchronized.

Denman (1976) and Fasham and Pugh (1976) found significant coherence between chlorophyll and temperature spectra. Both suggested that this coherence may have arisen because their water intake had passed through a series of internal waves, intersecting water with very different chlorophyll and temperature properties. Using data acquired by remote sensing and relatively unaffected by internal waves, Campbell and Esaias (1985) found that chlorophyll and temperature spectra had similar slopes yet were not significantly coherent.

The biological significance of a lack of coherence is that temperature gradients, small that they are, cannot be used by herbivores to locate denser patches of food. Both the chlorophyll and the temperature environments are patchy, but the chlorophyll patchiness is not organized in relation to temperature patchiness.

SUMMARY

Spectral analysis was used to characterize chlorophyll and temperature spatial variability across scales from 0.5 to 10 km. Over these spatial scales chlorophyll and temperature spatial variability did not differ, nor did the apparent spatial variability of either variable differ regionally. Within this range of spatial scales horizontal spatial variability of chlorophyll was similar in all cross-shelf and latitudinal regions of the GBR, despite the marked differences in bathymetric and reef matrix structure between these regions.

The chlorophyll spectra produced resembled those predicted by Fasham's (1978a) model of phytoplankton spatial variability more closely than those predicted by the Denman-Platt model (Denman and Platt 1976) even though GBR shelf conditions fell outside those for which these models were formulated. Temperature

spectra were also similar to those predicted by turbulence theory, again despite violation of model assumptions. The coincidence of chlorophyll spectral slopes with those of model predictions cannot then be taken as a confirmation of the validity of the Fasham model or of rejection of the Denman-Platt model.

Chapter 4. Near-surface zooplankton standing crop and community structure on the Great Barrier Reef shelf: relationships to phytoplankton biomass.

INTRODUCTION

The identification of spatial patterns of zooplankton biomass and community structure in the ocean has received much attention from biological oceanographers (e.g. Hayward and McGowan 1979, Mackas **et al.** 1980, Collins and Williams 1982, Colebrook and Robinson 1986). Two of the ways in which community structure can be characterized are; by the relative abundance of species and by the diversity of species. Although obviously interrelated, these elements can vary over different spatial and temporal scales. Within small spatial domains, for instance, the abundance of individual species tends to be more variable than do assemblages (Mackas 1984). By measuring physical and other biological attributes of the ecosystem in conjunction with community structure, hypotheses may emerge about the processes that have given rise to that community structure.

The processes that determine the spatial pattern of abundance of individual zooplankton species can, in part, be investigated by comparing their distribution with those of biological, physical or chemical variables. Similarities and differences in such patterns, together with a knowledge of the biology of the species, can be used to infer processes or constraints influencing individual species (McGowan 1971). Zooplankton species differ physiologically or behaviourally, so their population sizes may be controlled by different factors.

A complimentary approach to investigate spatial differences in species composition involves looking at collective changes in abundance of all the species in the community, so that the effects of biological interactions on community structure, e.g. mutualism, competition, are then implicitly included (McGowan 1971). Differences in relative abundance of zooplankton species can then be compared with differences in physical and chemical variables, or in other trophic levels, to identify factors causing change in the community structure. This approach has been widely employed in investigations of the community structure of planktonic systems (Tranter 1977, Star and Mullin 1981, Collins and Williams 1982, Mackas and Sefton 1982).

The processes that determine the diversity of species in a community, i.e. the absolute number of species in a region and their relative abundance, are still unresolved (May 1988). Species diversity has been attributed to resource limitation (Schoener 1983), predation (Paine 1966, Mitchell 1986) and environmental variability (Huston 1979). There are marked changes in zooplankton diversity across large scales (Raymont 1983), particularly with change in latitude, but the reasons underlying

such changes are not known. In the North Pacific central gyre, zooplankton species diversity could not be related to phytoplankton biomass or its variability, and may have been determined by fish predation (McGowan and Walker 1979, Hayward and McGowan 1979).

The shelf scale community structure of epi-pelagic zooplankton on the GBR shelf is described in this chapter in terms of species composition and species diversity. Shelf-scale characteristics of the zooplankton community on the GBR shelf have not been described. The GBR shelf differs from many others studied to date in the tropics in that no major upwelling occurs, nor are there large inputs of nutrients from riverine sources. Seasonal changes in river inputs (Wolanski and Van Senden 1983), the prevailing winds (Pickard et al. 1977) and in the frequency of shelf edge intrusions of nutrient rich water (Andrews and Furnas 1986) occur, but they are minor in comparison to seasonal changes recorded on other shelves, e.g. the west coast of India (Devassy and Goes 1988) and equatorial West Africa (Postel 1985). The GBR shelf is also distinctive in its physical structure, an extensive matrix of reefs on the shelf edge paralleling more open water close to the coast.

In this study, the epi-pelagic zooplankton community structure is described at both local and regional scales. A sampling programme was undertaken in which surface zooplankton and chlorophyll concentrations were sampled, and water temperature measured in each of the regions across and along the GBR shelf, over several seasons. The nature of zooplankton community structure at local and regional scales was related to the complex reef structure, and also to chlorophyll concentration and its spatial variability (Chapters 2 and 3). As the regional distribution of mean surface chlorophyll concentrations differed from that of reef structure, it was possible to evaluate their respective influence on the zooplankton community.

The first part of this chapter describes the distribution of epi-pelagic zooplankton biomass and of the most numerous zooplankton taxa in relation to GBR shelf structure, and their correlation with concurrently measured physical and biological variables. In the second section, pattern analysis techniques are used to examine similarities between samples based on their community structure. Similarly constituted groups of samples were then considered in relation to physical and biological characteristics of the GBR shelf that may have been responsible for determining such groupings. The third section describes regional and seasonal differences in zooplankton species diversity.

SAMPLING

Near-surface zooplankton samples were collected with a pumping system while underway. The pump intake was located 2 m below the surface and 1 m from the ship's hull (Fig. 2.2). The pump output not going to the fluorometer (85% of flow) was directed through a flowmeter (General Oceanics) and then a 200 um net. The flowmeter was calibrated by pumping a known volume of water and calculating a regression between water volume and flowmeter reading ($R^2 = 0.99$, $n = 40$). Based on zooplankton abundances measured in previous studies (Sammarco and Crenshaw 1984, Williams **et al.** 1988), a minimum of 3 cubic metres of seawater was estimated to be required to accumulate sufficient animals to characterise the zooplankton assemblage reliably. The pumping system (Mono displacement type, Type CP1600) delivered 100 l min^{-1}, so a sample was integrated over thirty minutes, which at normal ship speed (5 m sec^{-1}) represented a distance of eight kilometres. Each zooplankton sample thus nominally consisted of the animals in a cylinder of water eight km long and 32 mm across. An advantage of pump sampling is that it may characterize the zooplankton assemblage more reliably than net sampling. Wiebe (1971) demonstrated that a sampling strategy in which a long thin cylinder of water was sampled provided a more precise measure of zooplankton abundance than sampling the same volume of water in several short net tows. A possible limitation of pump sampling may arise from avoidance of the pump intake by zooplankton. Comparison of net samples with pumped samples in other studies indicate that for underway sampling this effect is negligible, the composition and biomass of zooplankton samples taken simultaneously with nets and using a pump did not differ (Pillar 1984, Moehlenberg 1987, Boltovskoy and Mazzoni 1988). In this study avoidance of the intake orifice by meso-zooplankton did not appear to be significant as large, more agile zooplankton like fish larvae were captured. Damage to organisms by the displacement type pump used was small, copepods and larger zooplankton such as chaetognaths and salps usually passed through to the net intact and alive.

Zooplankton samples were only collected during daylight hours, between 2 hours post-sunrise and 2 hours pre-sunset, to avoid confounding spatial differences in zooplankton community structure with diel changes produced by vertical migration. The assumption that diel changes to the epi-pelagic zooplankton were eliminated by this sampling regime was tested by examining sets of zooplankton samples taken during one day and within one cross-shelf band (Fig. 4.1). Diel changes in biomass within the daytime sampling period were not apparent, nor was zooplankton biomass in samples related to the time of day samples were taken (Fig. 4.2, correlation coefficient not significant).

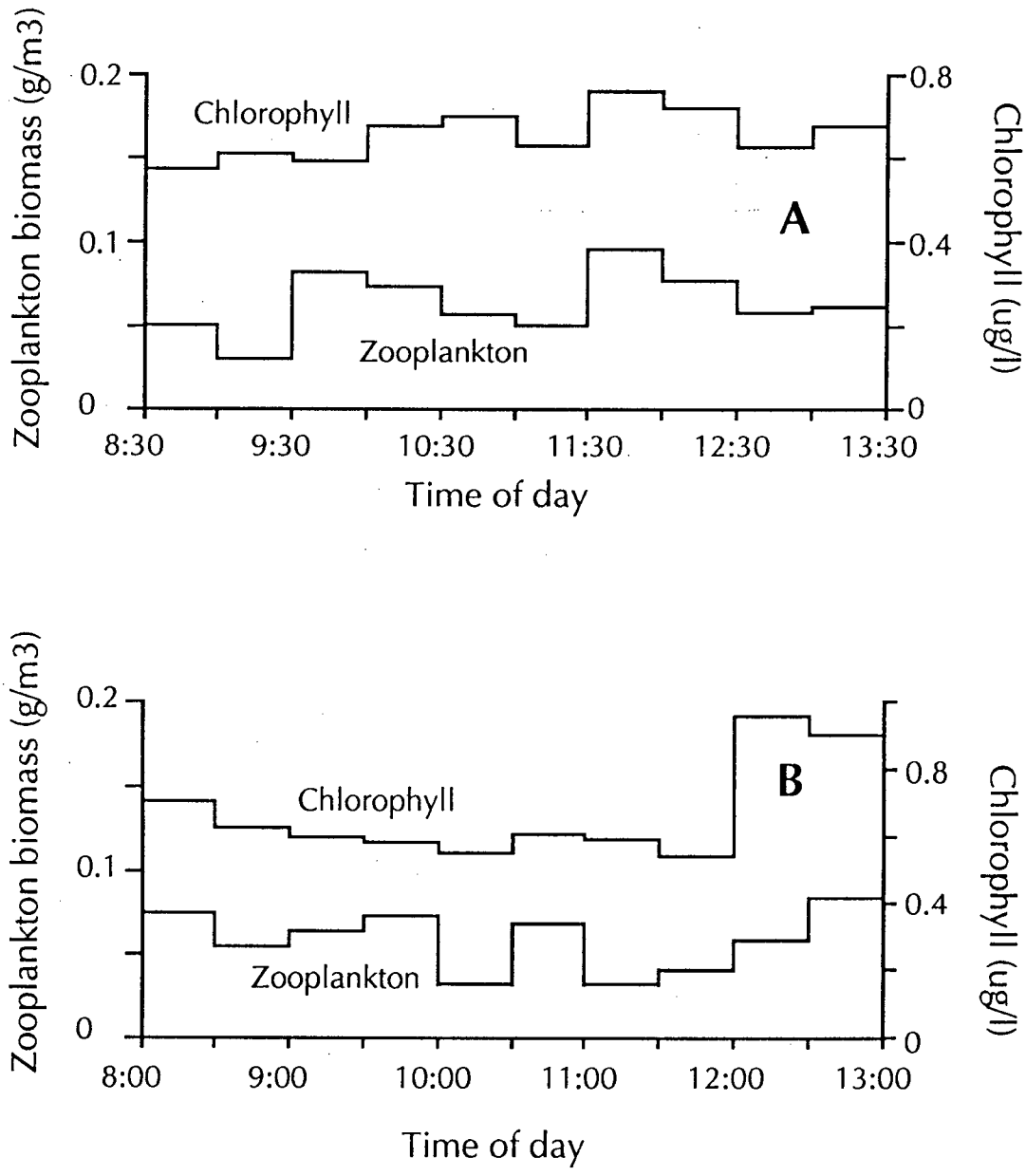


Figure 4.1. Zooplankton biomass along two transects. **A.** Inner shelf. **B.** Outer shelf. No diel change in biomass is apparent.

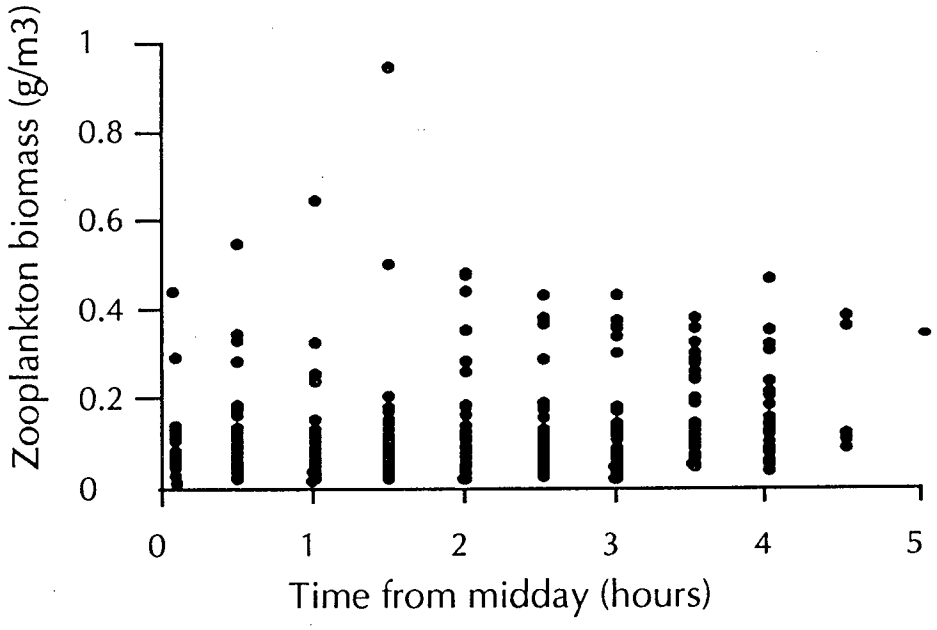
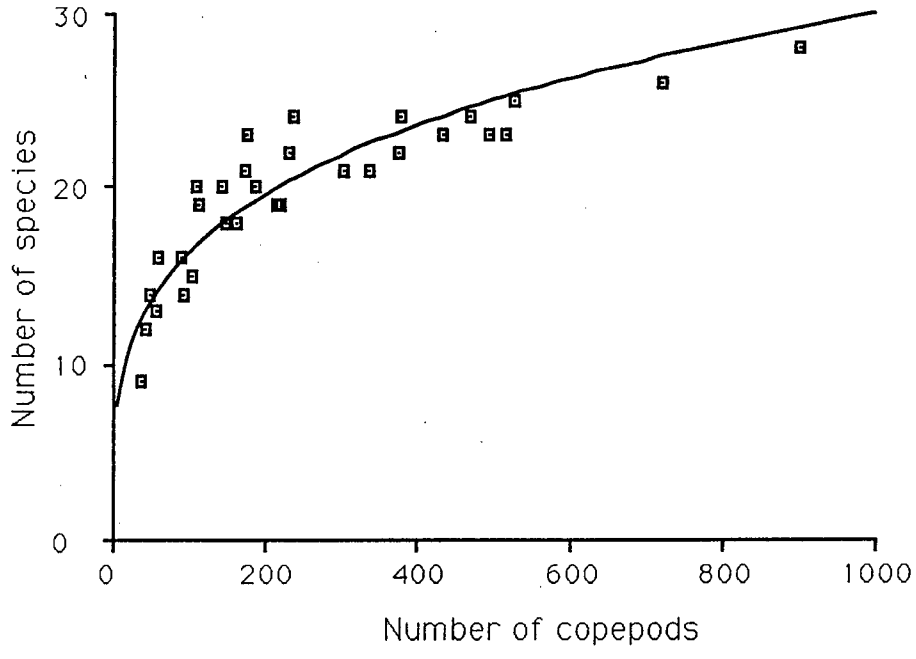


Figure 4.2. Zooplankton biomass in samples plotted against the time from midday of the midpoint of each sample subtransect. Correlation between biomass and time of day not significant.

Zooplankton wet weight was chosen as the measure of biomass as it is a relatively precise, non-destructive technique (Beers 1976). Samples were weighed at least one month after preservation to allow preserved weight to stabilise (Omori 1978). The entire sample was filtered under vacuum (< 20 Kpa) onto a preweighed piece of 53 um netting and reweighed.

Species rarefaction curves were generated for copepods (the numerically dominant group) to allow estimation of the number of organisms that needed to be counted in a sample to give an accurate estimate of the structure of the copepod assemblage. With samples from the GBR shelf, a rarefaction curve showed an inflexion at around 200 animals with 80-90% of species present (Fig. 4.3). Samples were therefore split with a Folsom splitter (McEwen **et al.** 1954) until the subsample contained approximately 300 copepods (6.25 - 100% of sample). Copepods in the subsample were identified to genus or species if practicable. Other zooplankters were identified to various levels of taxonomic resolution (Tables 4.1, 4.2). Authorities for identification of zooplankton were; copepods (Dahl 1912; Sewell 1929; Rose 1933; Farran 1936, 1948; Vervoort 1951, 1952, 1963; Grice 1962; Kasturirangan 1963; Mori 1964; Owre and Foyo 1967; Frost and Fleminger 1968; Wells 1970; Corral 1972; Bradford and Jillett 1974; Isaac 1975; Greenwood 1976, 1977, 1978, 1979; Bradford 1978; Bradford et al. 1983; Malt 1983; Robinson 1983; Nishida 1985), other taxa (Dakin and Colefax 1940; Fraser 1947a, 1947b,1957; Poulsen 1969a, 1969b; Van der Spoel 1972; Della Croce 1974).

The reproducibility of the pump sampling technique was assessed by comparison of a replicated set of surface zooplankton samples from the same body of water. A drogued buoy was deployed in inshore waters off Low Isles (16.1°S) and six samples were collected using the pump sampling system while re-traversing an 8 km north - south track centred on the drogue. Zooplankton in the samples were identified and counted, and the rank order of all zooplankton taxa, and of copepod taxa in these samples was compared by calculating the Kendall Tau correlation coefficient between samples. The use of a ranking procedure for this procedure is appropriate as it gives every sample equal weight and eliminates bias resulting from outsized samples (Fager 1957). These correlations were all significant ($p < 0.05$) after adjusting the experimentwise significance level by the Dunn-Sidak technique (Sokal and Rohlf 1981), indicating that the sampling procedure provided reproducible samples of the surface zooplankton assemblage (Table 4.3). To provide a measure of the reproducibility of the zooplankton abundance estimates, these same six samples were divided into two groups of three (12 possible combinations) and tested for differences in mean abundance. None of the comparisons showed a significant



4.3. Species rarefaction curve used to estimate the number of animals required to be counted in each sample to characterise the community composition.

Table 4.1

Summarization of zooplankton occurrence. Mean and maximum abundance are in number m^{-3}. Ubiquity of taxa are expressed as the percentage of samples in which they occur. h = herbivore, o = omnivore, c = carnivore.

	Mean	Max	% of samples	Trophic category
Copepods	240.8	1795	100	
Appendicularians	27.6	295	93.0	h
Chaetognaths	12.6	196	93.8	c
Echinoid larvae	3.5	232	35.5	h
Polychaete larvae	2.5	96	61.1	o
Pteropods	2.1	24	58.2	h
Salps	1.5	44	33.2	h
Fish eggs	1.4	39	59.5	
Decapod larvae	1.4	62.5	62.9	o
Brachyuran larvae	1.3	57.3	66.0	o
Mollusc larvae	0.9	67.6	34.8	h
Fish larvae	0.9	29.1	55.9	c
Siphonophores	0.9	0.3	51.8	c
Cladocera (*Evadne* sp.)	0.6	29.1	22.2	c
Ostracods	0.3	0.3	16.5	o
Luciferids	0.2	13.4	10.1	o
Stomatopod larvae	0.1	8.4	8.2	c
Total zooplankton	301.3	1908.4		

Table 4.2

Summarization of copepod occurrence. Mean and maximum abundance are in number m^{-3}. Ubiquity of taxa are expressed as the percentage of samples in which they occur. h = herbivore, o = omnivore, c = carnivore.

	Mean	Max	% of samples	Trophic category
Paracalanus spp.	47.2	1154	86.1	h
Acartia australis	29.1	955	88.4	o
Oithona spp.	23.2	348	95.9	o
Centropages orsinii	20.6	591	65.2	o
Corycaeus (D) spp.	17.7	251	97.9	c
Microsetella rosea	15.2	403	87.6	h
Oithona rigida	7.2	129	83.2	o
Acrocalanus gracilis	6.7	167	61.6	h
Canthocalanus pauper	6.7	189	45.6	h
Macrosetella gracilis	6.3	176	71.6	h
Corycaeus lubbocki	5.9	113	87.6	c
Oithona plumifera	5.7	104	74.0	o
Acrocalanus gibber	5.4	180	47.2	h
Undinula vulgaris	5.2	108	65.2	h
Farranula spp. (male)	5.2	75	76.5	c
Euterpina acutifrons	4.1	104	58.8	h
Corycaeus pacifica	4.0	104	73.5	c
Calanopia elliptica	3.1	33	63.7	c
Eucalanus subcrassus	1.7	49	39.9	h
Farranula concinnus (female)	1.5	30	52.3	c
Clausocalanus spp.	1.2	57	24.2	h
Clytemnestra scutellata	1.1	89	21.4	h
Farranula gibbulus (female)	1.1	19	47.4	c
Oncaea medea	1.0	17	56.7	c
Acartia pacifica	0.9	37	12.1	o
Oncaea conifera	0.9	20	28.6	c
Corycaeus speciosus	0.8	39	27.8	c
Temora turbinata	0.6	102	7.0	o
Centropages furcatus	0.5	281	7.0	o
Labidocera minuta	0.	523	24.2	c
Tortanus barbatus	0.5	33	14.2	c
Acartia negligens	0.3	5	27.6	c
Oncaea venusta	0.3	5	26.5	c

Table 4.2 continued

Summarization of copepod occurrence. Mean and maximum abundance are in number m^{-3}. Ubiquity of taxa are expressed as the percentage of samples in which they occur. h = herbivore, o = omnivore, c = carnivore.

	Mean	Max	% of samples	Trophic category
Calocalanus pavo	0.2	4	22.4	h
Labidocera acuta	0.2	15	12.1	c
Temora stylifera	0.2	11	11.1	o
Candacia pachydactyla	0.1	15	7.7	c
Sapphirrina spp.	0.1	2	11.9	c
Labidocera laevidentata	0.09	6	9.0	c
Sapphirella tropica	0.06	4	5.7	h
Acrocalanus monachus	0.04	2	4.9	h
Centropages elongatus	0.03	1	7.5	o
Rhincalanus cornutus	0.03	6	1.6	h
Candacia pectinata	0.02	3	2.6	c
Eucalanus mucronatus	0.02	2	2.3	h
Mecynocera clausi	0.02	1	3.4	h
Candacia catula	0.02	5	0.77	c
Metis jousseaumi	0.009	2	1.0	h
Thaumaleus thompsoni	0.008	1	1.3	
Candacia truncata	0.007	0.7	1.6	c
Temora discaudata	0.006	1	0.52	o
Pontellina plumata	0.004	0.5	1.6	c
Corycaeus longistylis	0.004	1	0.77	c
Candacia ethiopica	0.004	0.7	0.77	c
Eucalanus attenuata	0.004	0.6	0.77	h
Pseudodiaptomus aurivilli		0.004	0.7	0.52h
Aetideus giesbrechti	0.003	0.5	0.77	h
Calocalanus pavoninus	0.003	0.5	0.77	h
Centropages gracilis	0.002	0.5	0.52	o
Scolecethrix bradyi	0.001	0.4	0.52	o
Lucicutia flavicornis	0.001	0.3	0.26	o
Haloptilus longicornis	0.001	0.3	0.26	c
Neocalanus gracilis	0.001	0.3	0.26	h
Labidocera detruncata	0.001	0.3	0.26	c
Total copepods	240.8	1795		

Table 4.3

Abundances (animals m^{-3}) of the ten most numerous zooplankton taxa in the six repeat sampled transects. Taxa in each sample in rank order of abundance.

Sample	1	Sample	2	Sample	3
Para. spp.	95	*Oit.* spp.	39	*M. gracilis*	40
M. rosea	62	*M. gracilis*	21	*Oit.* spp.	29
Cor. (D) spp.	45	*M. rosea*	18	Chaet.	18
Oit. spp.	42	*A. gibber*	17	*A. gibber*	17
Pteropods	39	*Para.* spp.	14	*Cor.* (D) spp.	15
Chaet.	34	*Cor.* (D) spp.	9	Pteropods	14
M. gracilis	33	*O. plumifera*	8	*Para.* spp.	12
A. gibber	26	Chaet.	6	*O. rigida*	10
Append.	12	Pteropods	5	*L. minuta*	7
A. gracilis	10	*C. pauper*	5	*C. pauper*	6

Sample	4	Sample	5	Sample	6
M. gracilis	25	Chaet.	27	Chaet.	29
Chaet.	23	*M. gracilis*	25	*Oit.* spp.	23
C. pauper	18	*C. pauper*	19	*M. gracilis*	20
A. gibber	12	*Oit.* spp.	10	*C. pauper*	18
Oit. spp.	12	*A. gibber*	9	*A. gibber*	15
Gastro. larvae	9	*O. rigida*	9	*O. rigida*	13
A. gracilis	8	*A. gracilis*	7	Brachy. larvae	11
Para. spp.	7	*L. minuta*	7	*L. minuta*	8
L. minuta	6	*Cor.* (D) spp.	6	*A. pacifica*	8
A. pacifica	6	*Para.* spp.	5	*Cor.* (D) spp.	8

Abbreviations: *Para.* = *Paracalanus, Oit.* = *Oithona, M. gracilis* = *Macrosetella gracilis, M. rosea* = *Microsetella rosea, Cor (D)* = *Corycaeus (Ditrichocorycaeus), A. gibber* = *Acrocalanus gibber, O. plumifera* = *Oithona plumifera, O. rigida* = *Oithona rigida, L. minuta* = *Labidocera minuta, C. pauper* = *Canthocalanus pauper, A. pacifica* = *Acartia pacifica,* Chaet. = chaetognaths, Gastro. = gastropod, Brachy. = brachyuran.

difference in mean zooplankton abundance (t tests, $p < 0.01$), indicating that this sampling procedure provided reproducible samples of surface zooplankton abundance.

STATISTICAL ANALYSIS

Analysis of variance

Samples were assigned to previously defined cross-shelf bands and latitudinal zones to assess regional differences in variables such as zooplankton standing crop and numerical abundance. The significance of differences between mean values was then determined by two factor fixed effects analyses of variance (ANOVA) in which the factors were cross-shelf band (inner shelf, outer shelf and Coral Sea) and latitudinal zone (northern, central, Pompey and Swains). There were insufficient inshore subtransects in each zone to include this band as a level in the cross shelf factor. The significance of seasonal differences (dry or wet season) was determined by two factor fixed effect ANOVAs (season, band: inshore, inner shelf, outer shelf, Coral Sea) using subtransects from the central zone only. *A posteriori* comparisons of means were performed using the Tukey test with a correction for unequal sample sizes (Zar 1984). Variables were tested for heterogeneity of variance prior to analysis (Cochran's C test) and log transformed to reduce the correlation of the variance with the mean if required. If data transformation was required, the Cochran's test reported with the ANOVA table was that made after transformation.

Pattern analysis

Pattern analysis techniques were employed to discern spatial changes in the composition of the epi-pelagic zooplankton community, as it is very difficult to objectively perceive relationships in large data sets by a simple examination (Clifford and Stephenson 1975). The basic postulate of pattern analysis is that each sampling site constitutes a sample of the available habitats to which species have responded in different ways (Gauch 1983). Areas with similar zooplankton communities are therefore assumed to have arisen in response to similar environmental or ecological features.

A logarithmic transformation ($\log_{10}(x+1)$) was applied to the numerical abundance data to compress the ranges of abundance values so that both quantitative and qualitative information could have an influence on the ordination (Gauch 1983).

Rare taxa were excluded from the pattern analysis as their presence in a sample is more a matter of chance than an indication of ecological conditions. Inclusion of

rare taxa may also be deleterious to subsequent ordination as their presence may obscure the analysis of the rest of the taxa (Gauch 1983). In this study, taxa that occurred in less than 2% of samples (10 samples) were excluded from the pattern analysis. Large zooplankton were also excluded from pattern analysis as large mobile plankton are likely to be under-represented in pumped samples (Aron 1957).

The Bray-Curtis distance measure (Bray and Curtis 1957) was used to estimate the similarity between samples. This measure has been widely used in ecological studies (Gauch 1983) and compares well with other measures of similarity (Faith **et al.** 1987).

Ordination was chosen as the most appropriate pattern analysis technique. Ordination makes the assumption that the composition of samples extends over a continuum and that discontinuities indicate boundaries between groupings of samples. Classification techniques on the other hand are based on the assumption that samples come from different groups, and will assign samples to groups even if they occupy a continuum (Gauch 1983). Ordination was regarded as the most appropriate approach for plankton where distributions tend to be continuous rather than discrete (Raymont 1983). Following ordination, ecological interpretation of the patterns was aided by overlaying environmental measurements taken in conjunction with the samples.

Multidimensional scaling (MDS) was used as the ordination technique. This technique differs from the well used principal components and principal coordinates analysis in that it assumes only that distance measures are monotonically related to ecological dissimilarity. This assumption is more conservative than the assumption of linearity made in principal components and principal coordinates analysis.

Multidimensional scaling has been used for analysis of ecological patterns in marine systems by a number of authors (Smale 1987, Collins and Williams 1982, Potter **et al.** 1986). Field **et al.** (1982) suggested that MDS is the most suitable ordination procedure for marine ecology because of its more conservative assumption that distance measures be only monotonically related to ecological distances. Comparisons between ordination techniques using trial data sets indicated that MDS reproduced known relationships between samples more reliably than principal components or principal coordinates analysis (Faith **et al.** 1987, Jackson **et al.** 1989).

With MDS, the dimensionality of the ordination must be chosen before analysis (usually 2 or 3 dimensions). The success of the ordination is judged by the "stress"; a measure of the distortion required to compress the information in the data into the chosen number of dimensions. The lower the stress, the more accurately the ordination represents the information in the data; a stress below 0.15 indicates a fair ordination, and below 0.05 a very good one (Kruskal 1964).

Diversity

A "neutral" model developed by Caswell (1976) was used to characterise diversity. This approach uses a modified Shannon index of diversity to characterise the extent of biological influence on species diversity. With this approach the effect of sample size on the measure of diversity is largely removed (Caswell 1976). In the model, a hypothetical species distribution is generated by repeatedly replacing the community with a random sample taken from the previous "generation", each individual of which can be replaced by an individual from a new species (Caswell 1976). This procedure results in a distribution of species compositions that is independent of interspecific biotic interactions and of differential responses to the environment (i.e. neither predation nor competition occur), hence the descriptor "neutral". From this distribution a theoretical diversity (E(H')) is produced, and a deviation statistic V is calculated by subtracting the theoretical diversity from the calculated Shannon index of diversity (H'), and dividing by the standard deviation of the theoretical diversity (SD(H')).

$$V = [H' - E(H')]/ SD(H')$$

When V=0 the sample is regarded as deriving from a "neutral" species assemblage, when V is positive the assemblage is more diverse and when V is negative less diverse. This approach has been used successfully to quantify the impact of disturbance on the diversity of benthic organisms (Rainer 1981, Lambshead 1986, Lambshead and Platt 1988).

RESULTS

Zooplankton biomass

Surface zooplankton biomass (wet weight) ranged between 5 and 935 mg m^{-3} (mean 107 mg m^{-3}). Biomass was significantly higher in the inshore band (303 mg m^{-3}, Table 4.4, did not differ between inner and outer shelf, and was lowest in the Coral Sea (59 mg m^{-3}, Fig. 4.5). There was no significant latitudinal variation in biomass, but there was a wet season increase in biomass inshore as a result of higher wet season abundances of meroplankton (Table 4.3, Fig. 4.4). This effect produced the significant interaction term in the ANOVA (Table 4.3).

In parts of the GBR shelf where steep gradients in the surface chlorophyll concentration occurred, e.g. the inshore band, zooplankton biomass showed a similar gradient (Fig. 4.6). Elsewhere biomass was poorly correlated with chlorophyll

Table 4.4

Analyses of variance of zooplankton wet weight (mg m^{-3}) with two way fixed effects model ANOVA. Factors are zone (northern, central, Pompey and Swains) and band (inner shelf, outer shelf and Coral Sea). Underline between means in Tukey test indicates no significant difference between means ($p < 0.05$).

All four zones - A

Data log(x+1) transformed, Cochran's C = 0.449, $p < 0.05$.

Factor	DF	Mean square	F ratio	Probability
Zone	3	0.001	0.505	NS
Band	2	0.004	3.13	< 0.05
Zone * Band	6	0.001	0.46	NS
Error	356	0.001		

Central zone only - B

Data log(x+1) transformed, Cochran's C = 0.287, $p < 0.05$.

Factor	DF	Mean square	F ratio	Probability
Band	3	0.012	9.08	< 0.01
Season	1	0.002	1.87	NS
Band * Season	3	0.017	13.22	< 0.01
Error	211	0.001		

Tukey tests:

	Inshore	Inner	Outer	Coral Sea
Wet weight (mg m^{-3}) (geometric mean)	303.2	129.8	86.4	59.3

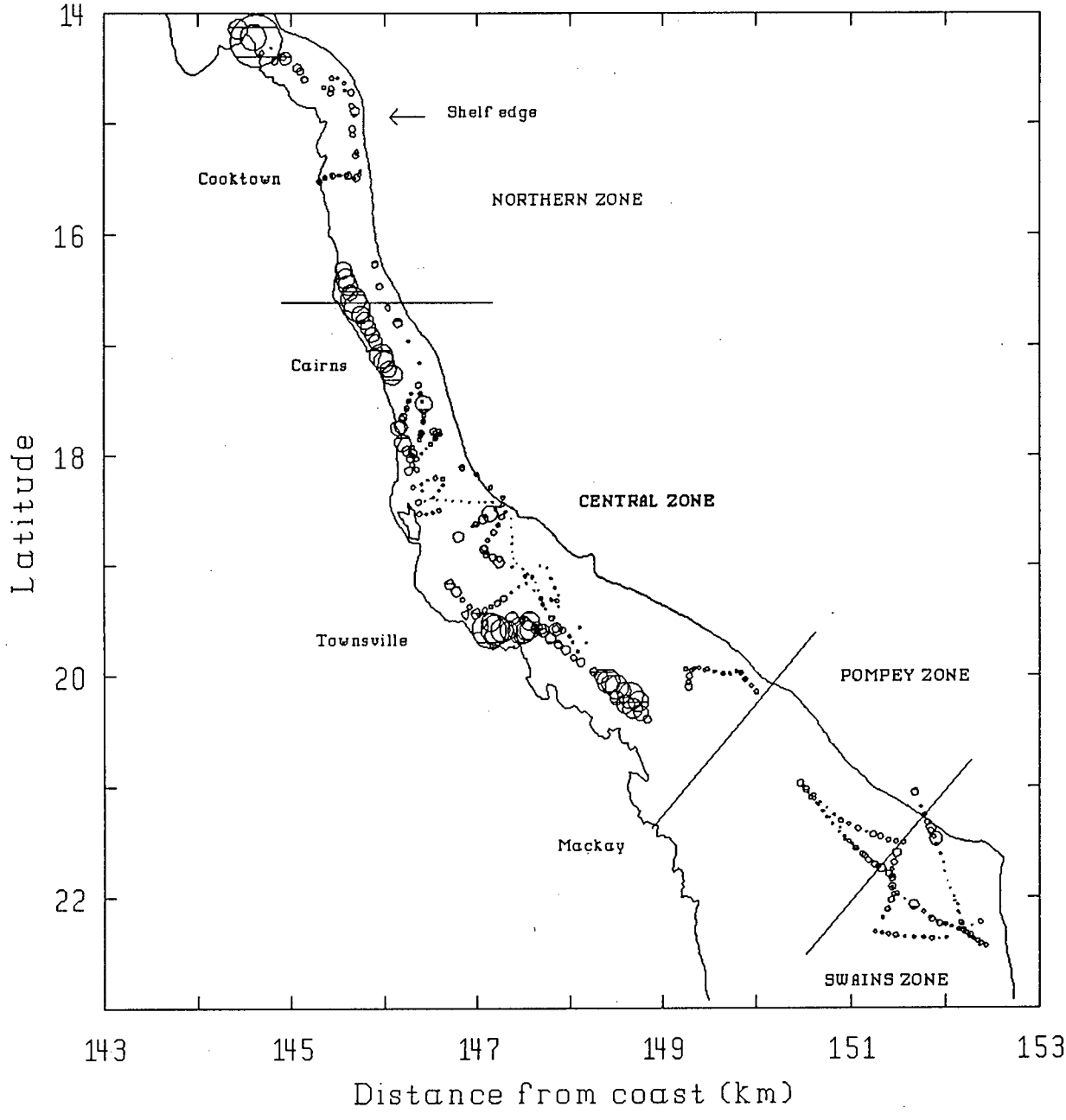


Figure 4.4. Map of the GBR shelf showing zooplankton wet weight in surface samples. Each circle represents one sample, with the diameter of the circle proportional to the zooplankton wet weight.

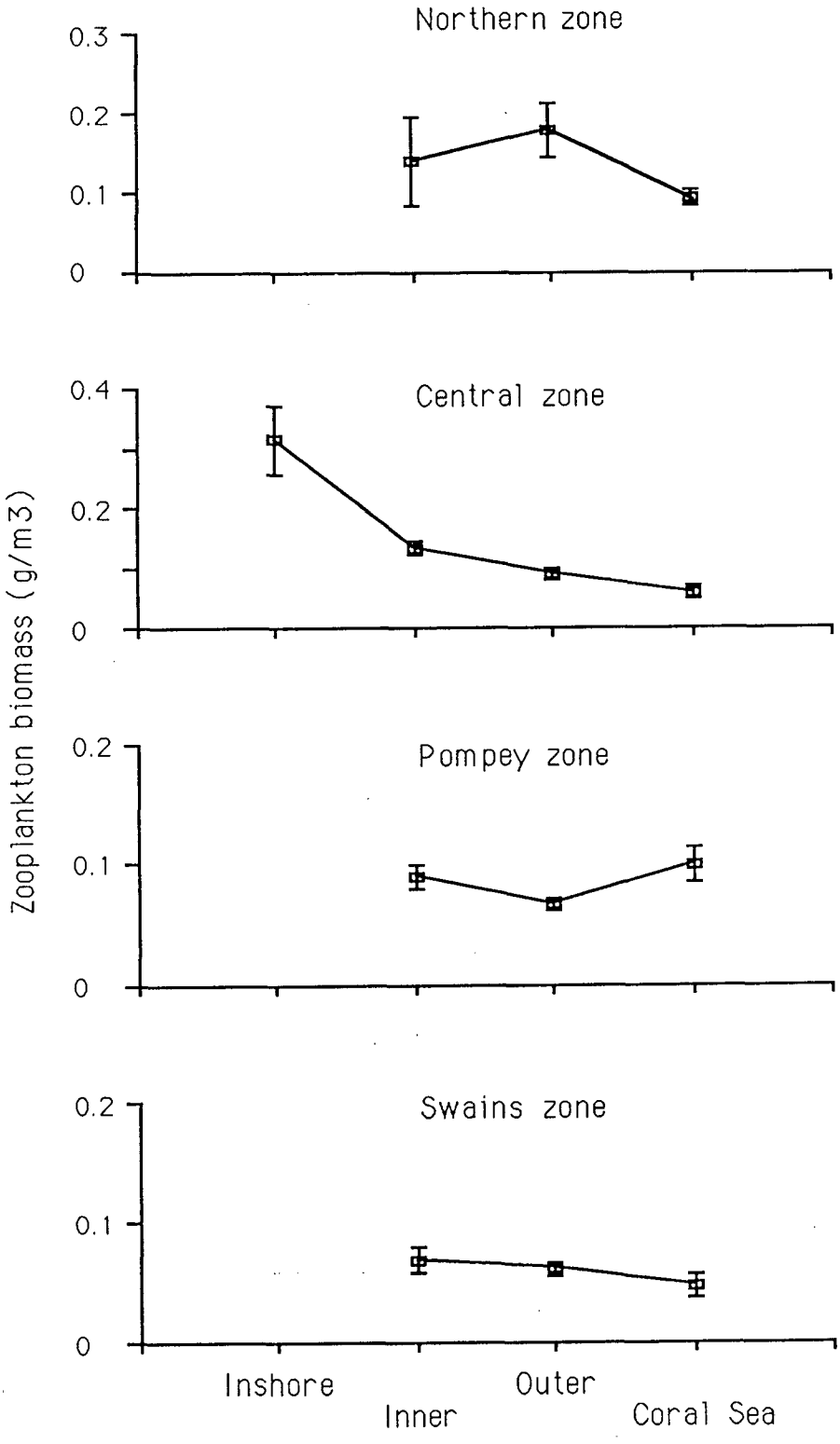


Figure 4.5. Cross-shelf changes in mean zooplankton biomass (wet wt. - mg m^{-3}) in latitudinal zones. Error bars are one standard error. There were no samples from the inshore band in the Northern, Pompey or Swains zones.

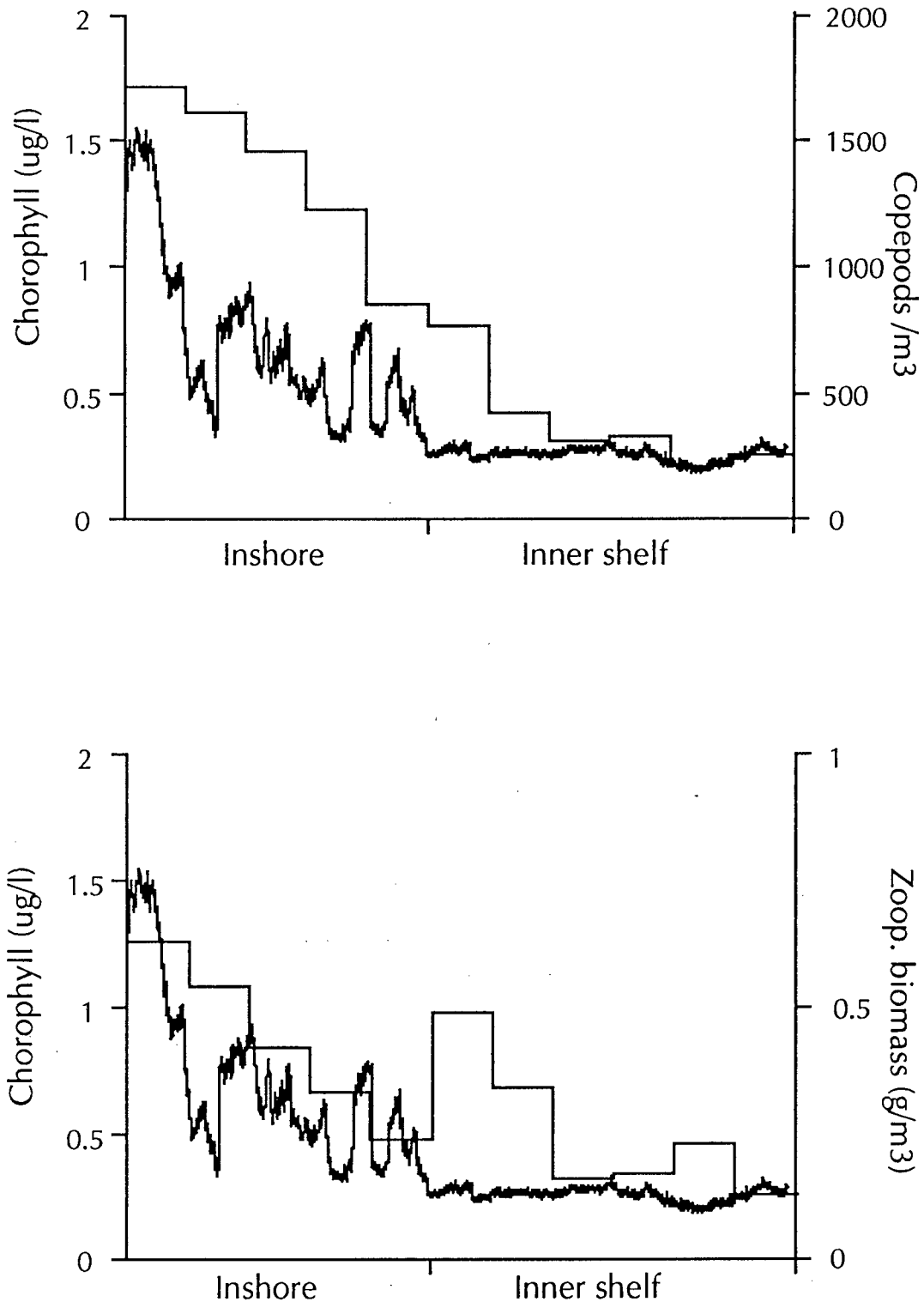


Figure 4.6. Surface chlorophyll concentrations along long-shelf transect 17 from 10 a.m. to 4 p.m. showing **A)** zooplankton biomass, and **B)** copepod abundances along the transect.

concentration. Correlations were calculated between the zooplankton biomass in samples and the mean chlorophyll concentration taken over the same 8 km subtransects, and in consecutive samples aggregated in pairs (representing mean chlorophyll and zooplankton biomass over 16 km) and in groups of four subtransects (32 km) (Table 4.5). In the inshore band chlorophyll concentration and zooplankton biomass were significantly ($p < 0.01$) correlated at the 8 km and 16 km scale (although the latter correlation comprised only 6 data pairs as a result of the limited number of inshore samples). In the inner and outer shelf bands chlorophyll concentration and zooplankton biomass were not significantly correlated at any of these three levels of spatial aggregation. Zooplankton biomass was not significantly correlated with chlorophyll subtransect variability at any of the three spatial scales (Table 4.5).

There are two other analyses of zooplankton biomass distribution on the GBR shelf with which the results of the present study may be compared. Sammarco and Crenshaw (1984) described the zooplankton fauna from three inshore stations sampled by Ikeda **et al.** (1980) over two years, and Williams **et al.** (1988) took five sets of samples along a cross-shelf transect over three months.

Nets with similar mesh size were used in all three studies (Sammarco and Crenshaw 1984 - 205 um; Williams **et al.** 1988 - 235 um, this study - 200 um), though zooplankton were sampled by vertical net tows in the two earlier studies. Sammarco and Crenshaw (1984) reported zooplankton wet weights from sites in the central GBR of comparable magnitude (80 - 300 mg m^{-3}). As in this study, they found zooplankton biomass to be higher inshore than on the inner shelf, and significantly higher in the wet season. In contrast, Williams **et al.** (1988) found that zooplankton dry weight in central GBR samples was higher on the outer shelf than on the inner shelf.

Copepods

Zooplankton assemblages were numerically dominated by copepods which ranged between 25% to 100% of individuals counted (mean 79%). Copepod abundances ranged from 1 to 1795 m^{-3} with a mean of 240.8 m^{-3} (Fig. 4.7). Copepod abundances declined significantly with increasing distance from the coast (Table 4.6), ranging from 543 copepods m^{-3} in the inshore band to 73 m^{-3} in the Coral Sea. Abundances of copepods did not vary significantly between the latitudinal zones or between season (Table 4.6).

Previous zooplankton studies in the central zone of the GBR shelf showed a similar cross-shelf gradient in copepod abundances (Sammarco and Crenshaw 1984,

Table 4.5

Correlations of zooplankton biomass and copepod abundance with chlorophyll concentration and subtransect chlorophyll coefficient of variation at three levels of spatial aggregation: values from the same subtransect (8 km), mean value from two adjacent subtransects (16 km), and mean value from four adjacent subtransects (32 km). The probabilities are the significance of the correlation coefficient. NS = not significant.

Chlorophyll mean

	Copepod abundance			Zooplankton biomass		
	Inshore	Inner	Outer	Inshore	Inner	Outer
8km	< 0.01	<0.01	<0.05	<0.01	NS	NS
16km	<0.01	<0.01	NS	<0.01	NS	NS
32km	--	<0.01	NS	--	NS	NS

Chlorophyll subtransect variability

	Copepod abundance			Zooplankton biomass		
	Inshore	Inner	Outer	Inshore	Inner	Outer
8km	NS	<0.05	<0.05	NS	NS	NS
16km	NS	<0.05	NS	NS	NS	NS
32km	--	<0.05	NS	--	NS	NS

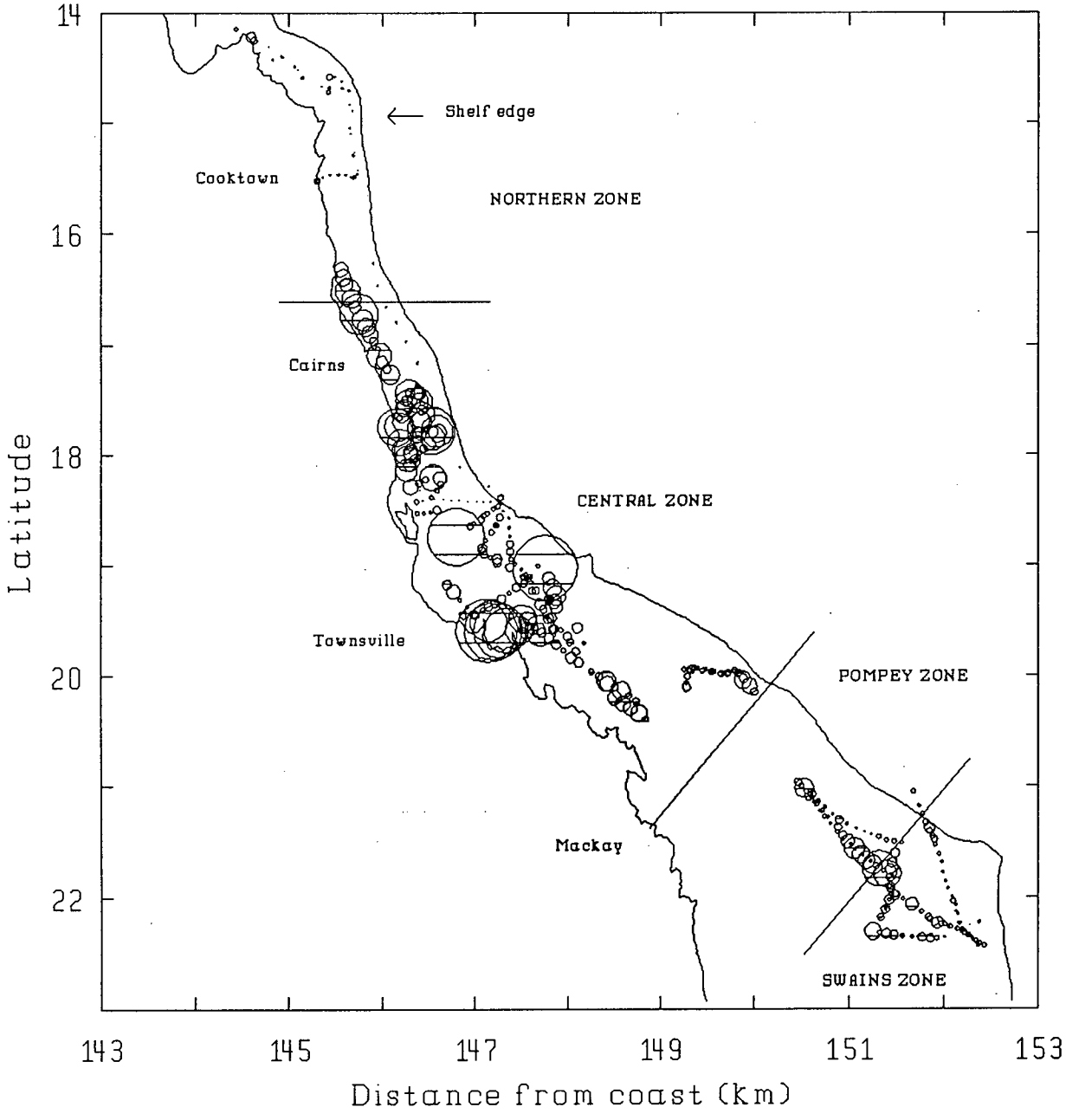


Figure 4.7. Map of the GBR shelf showing copepod abundances in individual samples. Circles represents individual samples, with the diameter of the circle proportional to the copepod density (no. m^{-3}).

Table 4.6

Analyses of variance of abundances of copepods (organisms m^{-3}) by two way fixed effects model ANOVA, A) Factors are zone (northern, central, Pompey and Swains) and band (inner shelf, outer shelf and Coral Sea). B) Factors are band (inshore, inner shelf, outer shelf and Coral Sea) and season (wet, dry). Underline between means in Tukey test indicates no significant difference between means ($p < 0.05$).

All four zones - A

Data log(x+1) transformed, Cochran's C = 0.248, P < 0.05.

Factor	DF	Mean square	F ratio	Probability
Zone	3	0.053	0.286	NS
Band	2	0.425	2.29	NS
Zone * Band	6	0.206	1.11	NS
Error	360	0.185		

Central zone only - B

Data log(x+1) transformed, Cochran's C = 0.263, P < 0.05.

Factor	DF	Mean square	F ratio	Probability
Band	3	1.212	5.98	< 0.01
Season	1	0.141	0.69	NS
Band * Season	3	0.249	1.23	NS
Error	215	0.197		

Tukey tests:

	Inshore	Inner	Outer	Coral Sea
Copepod densities (geometric mean)	543.3	272.9	130.3	73.3

Williams **et al.** 1988). Williams **et al.** (1988) found copepod densities of a similar magnitude; 100-600 m^{-3} on the shelf and < 50 m^{-3} in the Coral Sea. Sammarco and Crenshaw (1984) recorded much lower abundances at the three inner shelf stations they sampled; 25-100 m^{-3}. Sammarco and Crenshaw (1984) found higher densities of copepods in the wet season at their most inshore station, but abundances differed little between their two stations on the inner shelf, or with season. A more rigorous comparison of abundance between these two studies and the present study is not strictly appropriate because of sampling technique differences previously mentioned.

Copepod abundances followed the same large scale trends as chlorophyll concentration when compared over long transects (Fig. 4.6) or over the whole shelf (Figs. 4.4, 4.7). The correlation between copepod abundance and chlorophyll concentration was calculated at three scales of aggregation, taking data from same 8 km subtransect, from the mean value of consecutive pairs of subtransects (16 km) and groups of four subtransects (32 km). In the inshore and inner shelf bands, copepod abundance was significantly correlated with chlorophyll concentration and chlorophyll variability at all spatial scales where statistical comparisons could be made (no 32 km scale comparison possible in the inshore band as a result of limited samples; Table 4.5). In the outer shelf band, copepod abundance was significantly correlated with chlorophyll concentration and chlorophyll variability at the 8 km scale, but not at larger spatial scales (Table 4.5). These results suggested a correspondence between copepod abundance and chlorophyll concentration across a range of scales in the open waters of the inner shelf, but in the reef matrix where chlorophyll concentration was 'patchy' at small scales (8 km), abundances were linked to chlorophyll concentrations only at this small scale.

Calanoid copepods were the most numerous order of copepods, comprising 49.6% of all copepods counted. Cyclopoids comprised 39.2% of copepods and harpacticoids 11.4%. These proportions changed both across and along the shelf. Close to the coast, calanoid and cyclopoid copepods comprised 69% and 20% respectively of the copepod fauna, changing to 42% and 51%, respectively, in the Coral Sea where cyclopoid copepods were the most abundant group (Fig. 4.8). Latitudinal changes in proportions of copepod orders were also evident. Calanoid copepods comprised 45% of all copepods in northern zone samples, rising to 58% in Pompey zone samples and dropping to 40% in Swains zone samples (Fig. 4.8).

The distribution and abundance of copepod families provides a clearer picture of regional differences in the structure of the copepod assemblage. The most numerous copepod families present were the Corycaeidae (20.5% of all copepods counted), the Paracalanidae (16.8%), the Acartiidae (15.9%), the Oithonidae (15.7%), the

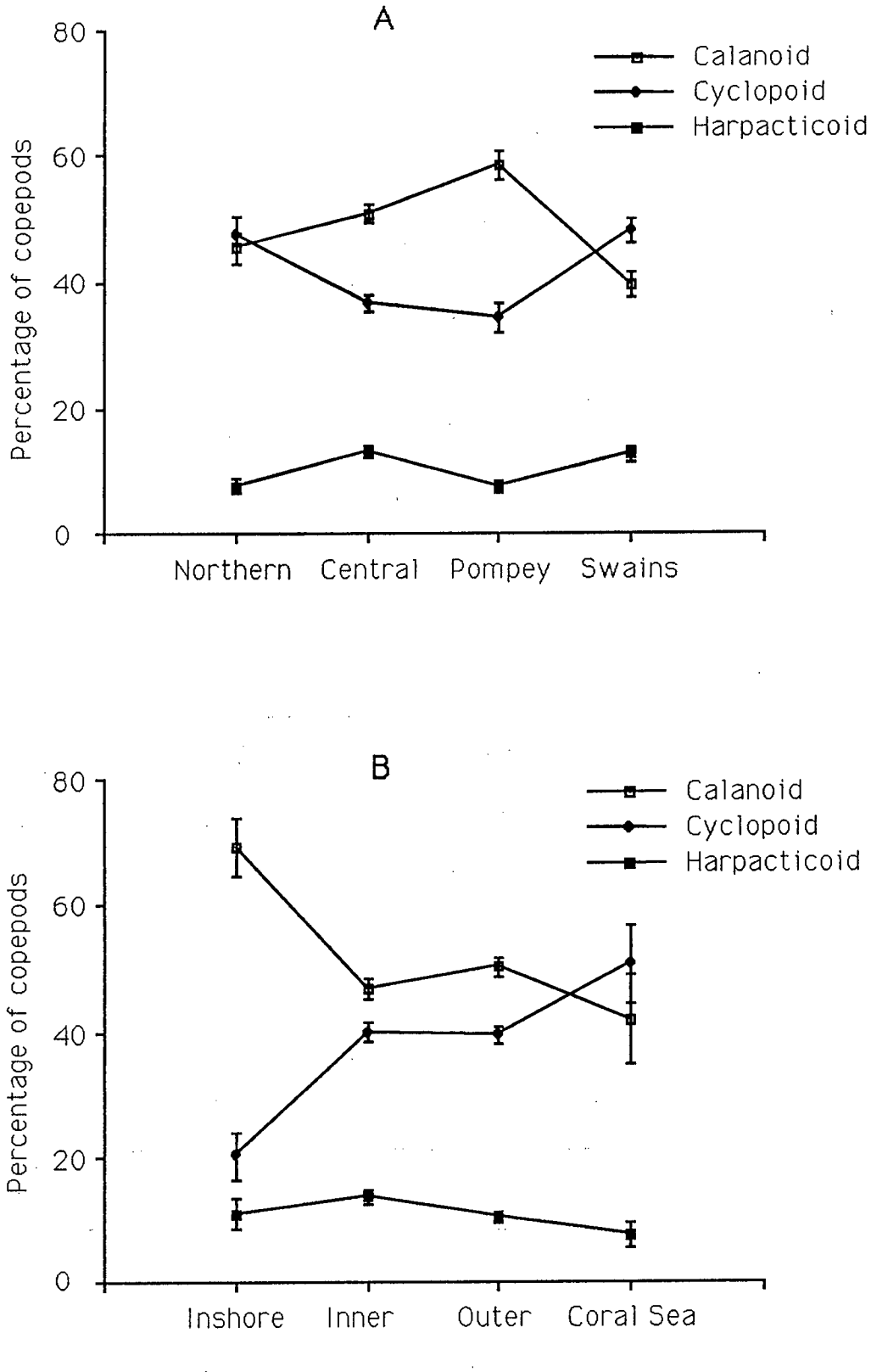


Figure 4.8. Mean proportions of calanoid, cyclopoid and harpacticoid copepods in **A**) Latitudinal zones, and **B**) Cross-shelf bands. Error bars are one standard error.

Harpacticoidae (11.2%), the Centropagidae (6.4%) and the Calanidae (4.4%). Although the most abundant individual species were calanoid copepods (Table 4.2), the most numerous family was the cyclopoid family Corycaeidae.

Corycaeidae

The Corycaeidae were represented on the GBR shelf by a number of species from two genera, *Farranula* and *Corycaeus*. *Corycaeus* spp. of the subgenus *Ditrichocorycaeus* were the most numerous group in this genus, but with the exception of *Corycaeus lubbocki* were not distinguished. Abundances of *Corycaeus* (D) spp. changed little across the shelf and between the shelf and Coral Sea. This contrasts to most other copepods whose abundances decreased in the Coral Sea. *Corycaeus lubbocki* and *C. pacifica* were also distributed evenly across the shelf, but whereas the abundance of *C. lubbocki* changed little with latitude or season, *C. pacifica* was most abundant in the central zone and in the wet season.

Farranula spp. were ubiquitous, occurring in 77% of samples. Only female *Farranula* were identified to species as the males of the two species present cannot be separated with assurance (Tanaka 1957). Both species were more abundant in mid-shelf samples than inshore, and with the cross-shelf decrease in abundance of many other taxa, *Farranula* spp. comprised a high proportion of the copepods in samples from the Coral Sea. Both *Farranula* species were common along the shelf in both wet and dry seasons. *Farranula* spp. were not as abundant on the GBR shelf as in other regions. *F. carinata* was the second most numerous copepod in collections from the Caribbean (Michel and Foyo 1976), and was the most numerous surface copepod in the Eastern Gulf of Mexico (Hopkins 1982).

Paracalanidae

Paracalanus spp. (comprising *P. aculeatus* and *P. indicus* which were not distinguished) was the most numerous copepod taxon. Cross-shelf members of this genus were most numerous close to the coast. *Acrocalanus gibber*,also numerous, had a similar distribution to that of *Paracalanus spp.* whereas the morphologically similar *A. gracilis*, was evenly distributed across the shelf, and was significantly ($p < 0.01$) more abundant in the wet season. Both Williams **et al.** (1988) and Farran (1936) found *Paracalanus* spp. and *Acrocalanus* spp. to be among the most numerous of copepods on the GBR shelf. *Paracalanus* spp. are also very abundant on other tropical shelves particularly in inshore samples, yet *Acrocalanus* spp. are uncommon (West Africa - Thiriot 1978; New Caledonia - Binet 1985).

Acartiidae

Three species of Acartia were found, each with a distinctive distribution. *Acartia australis*, the most numerous acartiid and the second most numerous copepod, was most abundant in the outer shelf band (Fig. 4.9), particularly in the proximity of individual reefs. This species comprised as much as 79% of the copepods in some outer shelf samples. Williams **et al.** (1988) also found *A. australis* to be abundant with highest concentrations in the outer shelf band. In contrast, Farran (1936) found *A. australis* to be neither numerous nor ubiquitous.

Acartia pacifica was never very numerous and was most abundant in the coastal and inner shelf bands. Farran (1936) found *A. pacifica* to be ubiquitous on the GBR shelf, and Greenwood (1981) found it to be common in samples from Moreton Bay, Queensland (27° S), where its abundance appeared to be limited by temperature.

Acartia negligens was the least numerous *Acartia* spp., occurring only in samples from the Coral Sea and the outer shelf band. *A. negligens* is one of the few oceanic members of the genus *Acartia* (Tranter 1977), yet in Farran's (1936) collections from the GBR shelf this species occurred across the shelf and was the most numerous *Acartia* spp..

Oithonidae

Oithonids were assigned to one of two taxonomic categories, *Oithona plumifera, O. rigida* or a mixed group of *Oithona* spp. *Oithona* spp. were evenly distributed across, but not along the shelf; they were more abundant in the central zone and in the Pompey zone. They were also significantly ($p < 0.01$) more numerous in the wet season. *Oithona* is a characteristic zooplankton genus in tropical regions (Deevey 1971). On the GBR shelf *Oithona* spp. was the third most numerous copepod taxon.

Oithona plumifera was ubiquitous but not numerous. This is in contrast with Farran's (1936) records in which it was the second most abundant copepod, and with Michel and Foyo's (1976) collections in the Caribbean in which it was the most abundant. Both *O. plumifera* and the more abundant *O. rigida* were evenly distributed across the GBR shelf. Similar to *Oithona spp., O. rigida* was almost twice as abundant in the wet season ($p < 0.01$), but *O. plumifera* showed no seasonal change in abundance.

Harpacticoidae

Three harpacticoid copepods were abundant in samples; *Macrosetella gracilis*, *Euterpina acutifrons* and *Microsetella rosea*, each with a distinct pattern of distribution. *Macrosetella gracilis* was most numerous in outer shelf waters and in the central zone of the GBR. The samples in which this species was most abundant were almost all collected during the cruise COT5 (Feb. 1988)(Table 2.1). As *M. gracilis* was not abundant in samples collected on other cruises, this increase in abundance appeared to be an episodic event rather than a seasonal phenomenon.

Euterpina acutifrons, a common tropical neritic species (Raymont 1983), was highest in abundance close to the coast. However, Farran (1936) found only small numbers of both this species and of *M. gracilis*.

Microsetella rosea, another common tropical copepod (Michel and Foyo 1976), was the most abundant harpacticoid copepod in GBR shelf waters (Table 4.2). It was most numerous in inner shelf waters (Fig. 4.9). The abundance of neither this species, nor *E. acutifrons* was significantly correlated with the chlorophyll concentration.

Centropagidae

Centropages orsinii and *C. furcatus* were the two most abundant and ubiquitous species of *Centropages* (Table 4.2). *C. orsinii* exhibited a cross-shelf distribution similar to *Acartia australis* with greatest numbers in the outer shelf band, especially in samples close to individual reefs. Together, *C. orsinii* and *Acartia australis* comprised up to 87% of copepods enumerated in some outer shelf samples. *C. orsinii* was more abundant in the wet season than the dry season ($p < 0.01$), and appeared to be restricted latitudinally, occurring only in small numbers in samples outside the central zone even in the wet season.

Centropages furcatus was most abundant in inshore samples. This distribution was also observed in other studies (Moreton Bay - Greenwood 1982, New Caledonia - Binet 1985). The relative abundance of these two species of *Centropages* is the reverse of that recorded by Farran (1936), who found *C. furcatus* to be the most numerous species of *Centropages*.

Calanidae

Although this family comprised only 4.4% of total copepod abundance, it contained two species that were relatively abundant in inshore waters, *Canthocalanus pauper* and *Undinula vulgaris*. *Canthocalanus pauper* occurred chiefly in inshore waters, sometimes comprising more than half of the copepods in individual samples.

Undinula vulgaris was less abundant but more widespread (present in 65% of samples), with slightly higher abundances on the inner shelf. Both these species have occurred commonly in previous samples taken on the GBR shelf (Farran 1936, Sale **et al.** 1976), and on other tropical shelves (Binet 1977, Moore and Sander 1979, Binet 1985).

Non-copepod zooplankton

Chaetognaths and appendicularians were the most abundant and ubiquitous of the non-copepod zooplanktres (Table 4.1). Their dominances accord with previous zooplankton surveys on the GBR shelf (Russell and Colman 1934, Sammarco and Crenshaw 1984). As recorded on other tropical shelves (reviewed by Longhurst 1985), many of the non-copepod zooplankton were meroplanktonic larvae; including larvae of gastropods, polychaetes, echinoids and decapods. Non-copepod zooplankton were significantly less abundant in the Coral Sea samples, but did not differ in abundance latitudinally (Table 4.7).

There were distinct seasonalities in the shelf-scale abundances of meroplankton larvae. Decapod, brachyuran, polychaete and mollusc larvae were significantly more abundant in the wet season ($p < 0.01$). Echinoderm larvae were more abundant in the dry season ($p < 0.05$), while appendicularians and pteropods showed no seasonal changes in abundance.

Most non-copepod zooplankton taxa were most abundant inshore and least abundant in Coral Sea samples. This trend was reversed in the Pompey zone where abundances were higher on the outer than the inner shelf. Another individual exception was the distribution of echinoid larvae, where abundances peaked in samples taken on the outer half of the shelf. Samples with the highest echinoid abundances were not those taken in the immediate vicinity of reefs, suggesting that these larvae may have been from species that live on the sea floor between reefs, rather than species on reefs.

The rank ordered abundances of non-copepod zooplankton on the GBR shelf are similar to other tropical shelves, where copepods, chaetognaths and appendicularians are usually the three most numerous groups (Raymont 1983, Longhurst 1985).

Functional categories

Zooplankton were assigned to trophic categories to permit comparison of the functional structure of the zooplankton community on different parts of the GBR shelf. Assignment to functional category was based on literature description of mouthparts and of gut contents (Timonin 1971, Itoh 1970, Marshall 1973, Longhurst

Table 4.7

Analyses of variance of abundances of non-copepod zooplankton (organisms m^{-3}) by two way fixed effects model ANOVA, A) Factors are zone (northern, central, Pompey and Swains) and band (inner shelf, outer shelf and Coral Sea). B) Factors are band (inshore, inner shelf, outer shelf and Coral Sea) and season (wet, dry). Underlined means in Tukey test indicates no significant difference between means ($p < 0.05$).

All four zones - A

Data log(x+1) transformed, Cochran's C = 0.249, P < 0.05.

Factor	DF	Mean square	F ratio	Probability
Zone	3	0.052	0.275	NS
Band	2	0.622	3.31	< 0.05
Zone * Band	6	0.467	2.48	< 0.05
Error	360	0.188		

Central zone only - B

Data log(x+1) transformed, Cochran's C = 0.348, P < 0.05.

Factor	DF	Mean square	F ratio	Probability
Band	3	2.086	9.98	< 0.01
Season	1	1.658	7.93	< 0.01
Band * Season	3	0.413	1.98	NS
Error	215	0.197		

Tukey tests:

	Inshore	Inner	Outer	Coral Sea
Zooplankton densities (geometric mean)	108.9	70.0	29.3	5.1

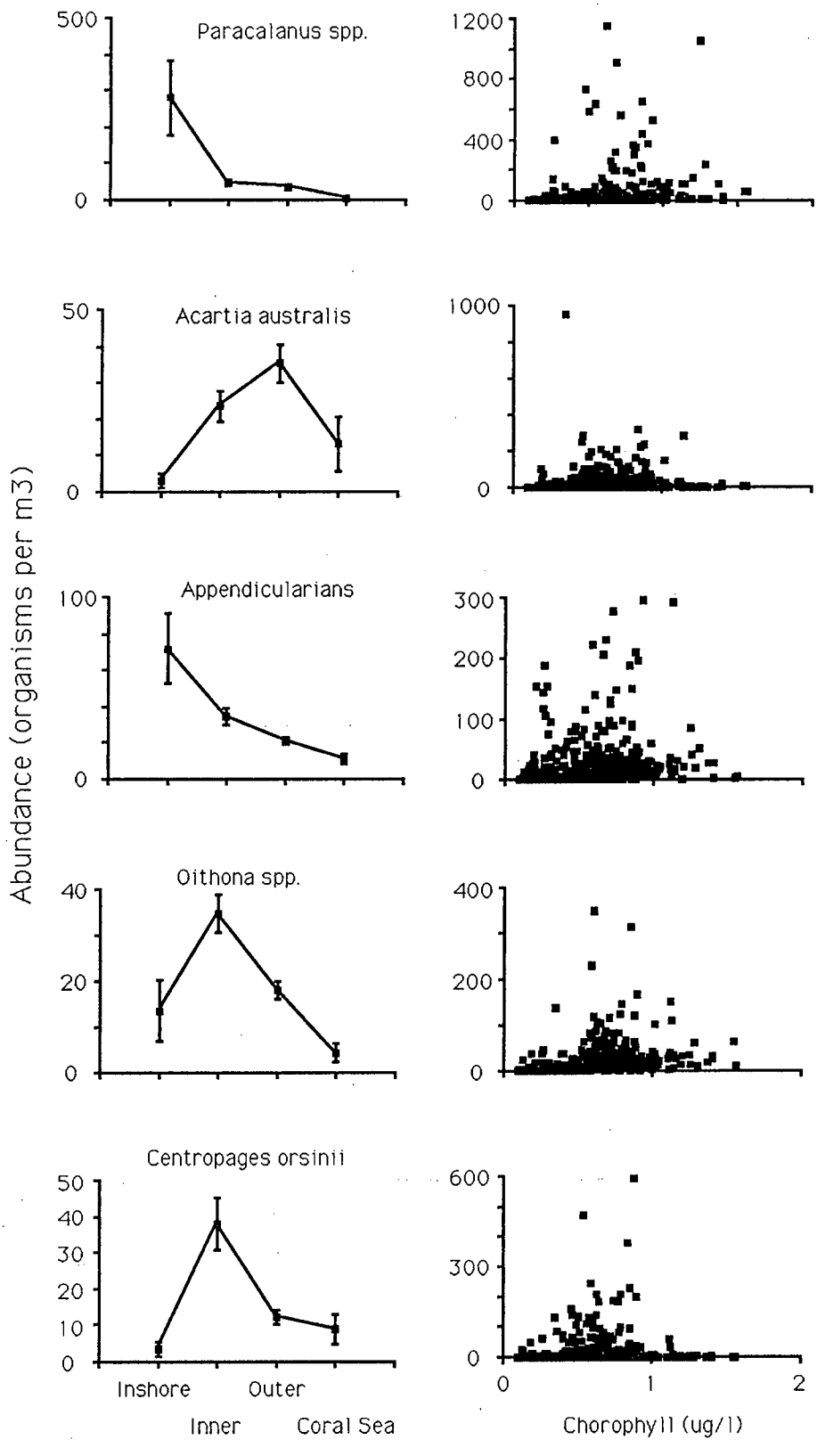


Figure 4.9. Cross-shelf changes in mean abundance of the five most numerous taxa. Abundances of taxa are plotted against the chlorophyll concentration taken along the same 8 km subtransect. Error bars are one standard error.

1985; Tables 4.1, 4.2). These assignments must be taken only as approximations of the trophic status of taxa, as species may be capable of changing their feeding behaviour (Lonsdale **et al.** 1979, Landry 1981).

Overall, omnivores were the most numerous category on the GBR shelf (42%), followed by herbivores (33%) and carnivores (25%). There were marked cross-shelf and latitudinal changes in the proportions of these three categories (Fig. 4.10). Herbivores were the most abundant group inshore, largely because of the abundance of small herbivorous copepods and of appendicularians. Omnivores were the most numerous category in the inner and outer shelf bands, reflecting the dominance of the copepods *Acartia australis* and *Centropages orsinii* (Fig. 4.10). Carnivores were the most numerous group in Coral Sea samples as a consequence of the relatively high numbers of Corycaeidae.

Omnivores were the most numerous group in all latitudinal zones except the northern zone. Within the northern zone, herbivores numerically dominated the zooplankton (Fig. 4.10), a result of the relatively greater numbers of *Paracalanus* spp., and relatively lower numbers of *Acartia australis* and *Centropages orsinii* in this zone.

Ordination of samples

An ordination of all samples in three dimensions (stress = 0.15) revealed no clear sample groupings. Environmental variables were correlated with ordination vectors to assess their importance as gradients along which zooplankton samples were distributed. The two variables with the highest correlation (i.e. environmental gradients along which the samples were best separated) were chlorophyll concentration ($r = 0.47$) and cross-shelf position (water depth) ($r = 0.35$). Individual ordinations were carried out for each long-shelf zone to investigate the differences in zooplankton community structure relative to the cross-shelf position and proximity to reefs of samples in more detail, and on the mean and variability of chlorophyll taken along the same subtransects.

Northern zone samples could be separated into four groups based on a visual examination of the ordination plot (Fig. 4.11). Group A was comprised solely of samples taken in the wet season. The three remaining groups were distinguished on the basis of their distance offshore and their association with the reef matrix. Group D were predominantly inshore samples, group B mid-shelf samples collected close to reefs, and group C outer shelf samples collected further away from reefs (Table 4.8). The mean chlorophyll concentration was higher in group A samples (0.68 ug l^{-1}) than in the other three groups (0.27-0.30 ug l^{-1}; Table 4.8). One-way ANOVA's for each

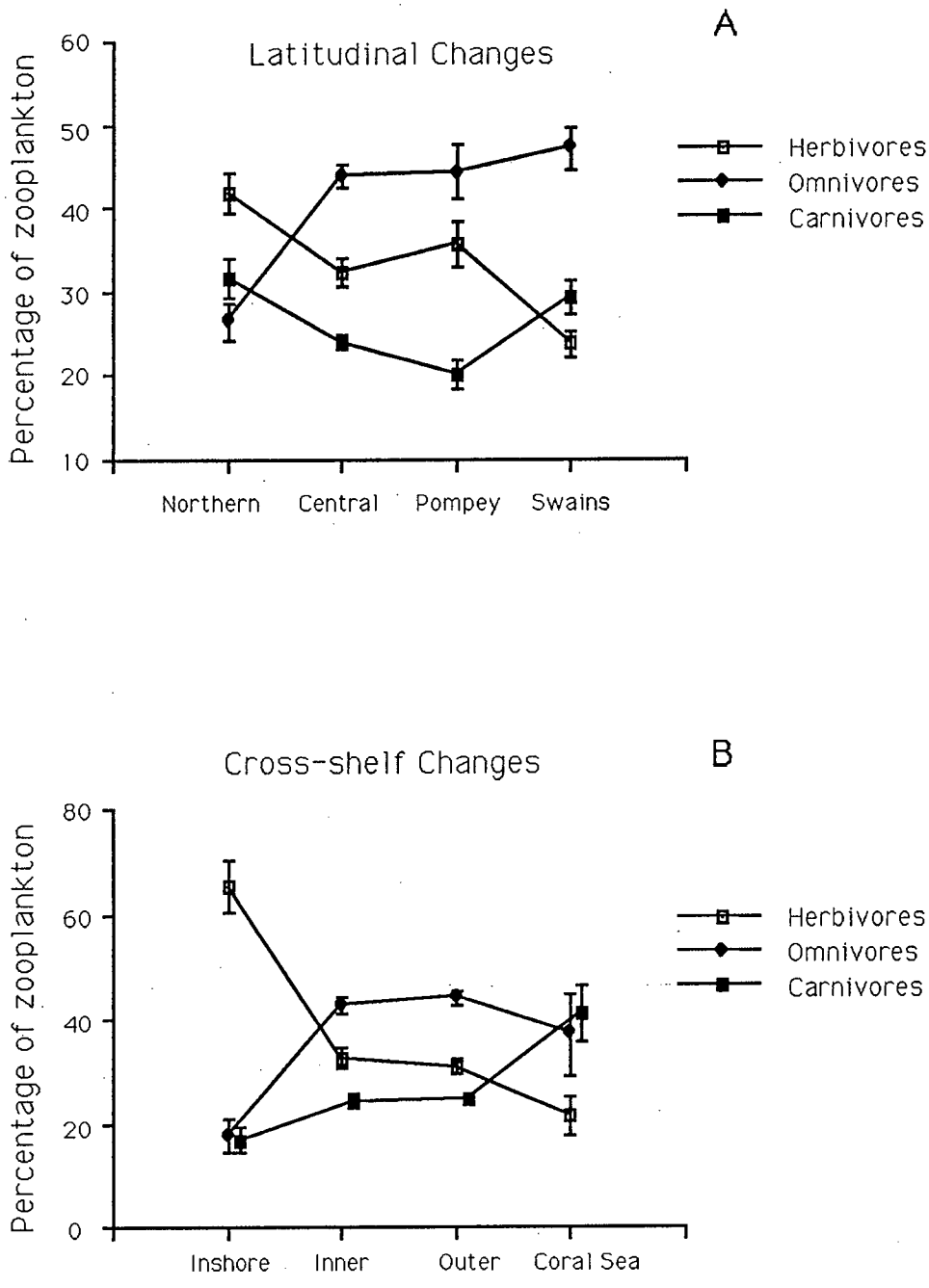


Figure 4.10. Mean proportions of herbivores, omnivores and carnivores in **A)** Latitudinal zones, and **B)** Cross-shelf bands. Error bars are one standard error.

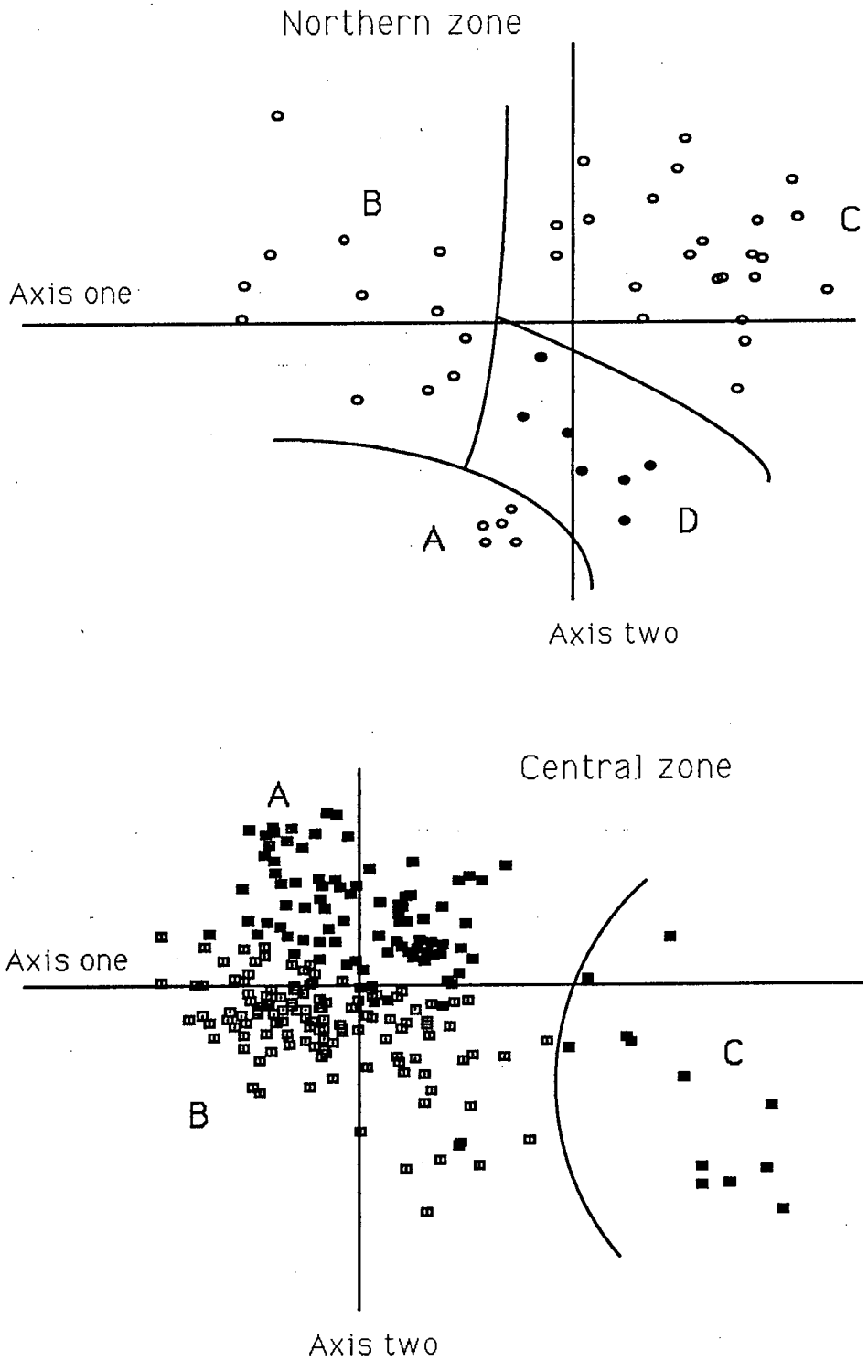


Figure 4.11 Ordination of samples from the Northern and Central zones. Samples identified as belonging to a group and referred to in the text are indicated by a letter.

Table 4.8

Summarization of the four groups of northern zone samples identified by the ordination. Abbreviations: dist. off. = distance offshore, reef prox. = reef proximity, Chl. = chlorophyll concentration, cope. = copepods, non cope. = non-copepod zooplankton, * = group means significantly different at $p < 0.05$, ** at $p < 0.01$.

Variable	Group A	Group B	Group C	Group D
Dist. off. (km)	14.0	19.1	34.9	4.9 **
Water depth (m)	26.6	29.5	33.3	16.5 **
Reef prox. (km)	7.2	2.4	5.0	5.0 **
Chl. (ug l^{-1})	0.68	0.27	0.27	0.30 **
Chl CV (%)	1.3	8.6	15.4	3.2
Cope. (no. m^{-3})	182.2	413.5	235.4	95.0
Non cope. (")	40.5	47.9	41.2	102.3
Herbivores %	55.9	36.4	38.8	53.6 *
Omnivores %	30.8	41.8	19.5	20.5 **
Carnivores %	13.3	21.8	41.7	25.9
Distribution of zooplankton with ten highest Cramer scores across the four groups (no. m^{-3}). Ranked in order of their Cramer score.				
Paracalanus spp.	224.4	0.56	0.07	12.8
Acr. gibber	24.4	0.19	0.18	10.0
Canth. pauper	14.2	0.56	0.10	19.9
Cal. elliptica	6.5	0.56	0.08	7.5
Chaetognaths	17.0	0.34	0.54	5.1
Cen. furcatus	4.7	0.03	-	2.3
Oit. plumifera	35.4	0.73	0.75	1.6
Acar. pacifica	13.8	0.10	-	2.1
Echinoid larvae	3.5	0.11	-	0.07
Cor. (D) spp.	14.5	1.4	1.1	13.9
Distribution of the five most abundant zooplankton in the northern zone (no. m^{-3}). Ranked in order of overall abundance.				
Paracalanus spp.	224.4	0.56	0.07	12.8
Appendicularians	10.0	6.4	23.0	30.0
Oith. spp.	47.8	6.0	2.7	3.5
Canth. pauper	14.2	0.56	0.10	19.9
Cor. (D) spp.	14.5	1.4	1.1	13.9

Taxa abbreviations: *Acr.* = *Acrocalanus, Canth.* = *Canthocalanus, Cal.* = *Calanopia, Cen.* = *Centropages, Oit.* = *Oithona, Acar.* = *Acartia, Cor.* = *Corycaeus.*

of the environmental variables with group as the factor showed that the four groups of zooplankton samples were differentiated with regard to offshore distance, water depth, reef proximity, and mean chlorophyll (Table 4.8).

Zooplankton taxa contributing most to the discrimination of individual groups were determined by calculating Cramer scores for each taxon. The Cramer score is the between-group sum of squares divided by the total sum of squares; the greater the Cramer score, the more that taxon differs in abundance between groups (Belbin **et al.** 1984). Abundances of taxa with the highest Cramer scores are presented in Table 4.8. Groups A and to a lesser extent D, the most inshore groups, were characterized by the high abundances of *Paracalanus* spp., *Acrocalanus gibber* and *Centropages furcatus*. Group B was characterized by higher densities of outer shelf taxa, e.g. *Farranula* spp. and *Acrocalanus gracilis*.

The ordination of central zone samples did not separate samples into obvious groups (Fig. 4.11). Consequently, samples were divided into three groups using a classification procedure (unweighted pair group averages algorithm, Belbin 1987) to investigate the changes in the zooplankton community and associated environmental gradients. The three groups identified represent an objective grouping of samples into the middle and two end-points of the continuum in samples.

The means of all measured environmental variables, excepting distance offshore and chlorophyll variability, differed significantly between the zooplankton groups (Table 4.9). Environmental variables with the most marked differences between groups were mid-transect water depth, reef proximity and chlorophyll concentration. Group A samples were chiefly from shallow waters far from reefs characterised by the highest chlorophyll concentration (Table 4.9). Group B samples were collected from waters close to reefs and with high chlorophyll concentrations. Group C samples were from deeper waters further offshore, and from waters with the lowest chlorophyll concentration (Table 4.9). Zooplankton taxa exhibiting the greatest change between these three groups, as assessed by their Cramer scores, are given in Table 4.9.

Small herbivorous copepods such as *Paracalanus* spp. and *Canthocalanus pauper* were most numerous in the inner shelf group A assemblage. Group B, which came from parts of the reef matrix with high chlorophyll concentrations, was characterized by higher abundances of *Centropages orsinii* (Table 4.9) and *Acartia australis*. Group C, which came from parts of the reef matrix in which chlorophyll concentration was lower, had low numbers of most zooplankton taxa.

These cross-shelf changes in zooplankton community structure in the central section may be compared with the distribution identified by Williams **et al.** (1988).

Table 4.9

Summarization of the groups of samples identified by the classification of Central zone samples. Abbreviations: dist. off. = distance offshore, reef prox. = reef proximity, Chl. = chlorophyll concentration, cope. = copepods, non cope. = non-copepod zooplankton, * = group means significantly different at $p < 0.05$, ** at $p < 0.01$.

Variable	Group A	Group B	Group C
Dist. off. (km)	70.5	77.0	82.6
Water depth (m)	15.3	19.5	58.7 **
Reef Prox. (km)	11.2	3.7	3.9 **
Chl. (ug l^{-1})	0.67	0.62	0.16 **
Chl CV (%)	8.9	10.1	13.3
Cope. (no. m-3)	223.8	328.6	123.8 **
Non cope. (")	40.2	90.4	32.6 **
Herbivores %	51.7	19.0	14.0 **
Omnivores %	31.1	54.2	39.3 **
Carnivores %	17.2	26.8	46.7 **

Distribution of zooplankton with ten highest Cramer scores across the three groups (no. m^{-3}). Ranked in order of their Cramer score.

Onc. conifera	2.6	0.22	-
Paracalanus spp.	121.7	9.8	0.47
Acr. gibber	15.0	3.2	-
Canth. pauper	19.3	3.1	-
Oit. plumifera	11.3	3.9	1.3
Pteropods	4.2	1.0	0.03
Acar. pacifica	2.7	0.03	0.09
Ostracods	0.67	0.02	-
Euc. subcrassus	3.7	1.0	0.02
Cen. orsinii	4.5	61.5	0.02

Distribution of the five most abundant zooplankton in the central zone (no. m^{-3}). Ranked in order of overall abundance.

Paracalanus spp.	121.7	9.8	0.47
Appendicularians	47.5	35.4	1.1
Cen. orsinii	4.5	61.5	0.02
Acar. australis	3.4	44.6	18.9
Oit. spp.	24.3	33.1	1.5

Taxa abbreviations: *Onc. = Oncaea, Acr. = Acrocalanus, Canth. = Canthocalanus, Oit. = Oithona, Acar. = Acartia, Euc. = Eucalanus, Cen. = Centropages.*

They identified six zooplankton assemblages along their cross-shelf transect. Furthest inshore were *Paracalanus* spp. and *Paracalanus* spp. plus *Canthocalanus pauper* dominated assemblages. An assemblage dominated by *Acartia australis* occurred in the reef matrix on many occasions, and three zooplankton assemblages with low densities occurred in the Coral Sea extending sometimes into the reef matrix. These assemblages bear similarities to those identified in the central zone in this study; a *Paracalanus* spp. rich zone inshore and an *Acartia australis* dominated zone in the reef matrix.

Samples from the Pompey zone fell into three groups plus one outlier (Fig. 4.12). Groups of zooplankton samples could be characterised by their distance offshore (as indicated by water depth), the concurrent surface chlorophyll concentration and chlorophyll variability (Table 4.10). The distance offshore measurement of samples in this and the Swains zone is biased by the increasing width of the shelf, and was not used. Group A samples were collected close behind the dense outer reef barrier. They had the highest zooplankton abundance in the Pompey zone and came from water masses with the highest surface chlorophyll concentrations (Table 4.10). *Paracalanus* spp. numerically dominated zooplankton in this group (Table 4.10). In other latitudinal zones, this taxon was most abundant inshore. Group B samples were also collected in the reef matrix, but from shallower water depths (closer to the coast) than group A (Table 4.10). These samples had higher abundances of *Acartia australis* and *Centropages orsinii*, the taxa that usually numerically dominate in reef matrix assemblages. Group D samples all came from the Coral Sea. They were distinguished by higher relative abundances of Corycaeidae and some of the small herbivorous calanoids; *Acrocalanus gracilis* and *Clausocalanus* spp. (Table 4.10). Carnivores comprised almost half the zooplankton in this group.

Samples from the Swains zone were divided into two groups with one outlier (Fig. 4.12). The two groups differed significantly with respect to their distance offshore (water depth), absolute abundance of zooplankton and mean chlorophyll concentration (Table 4.11). Samples in group A were from the southern part of the Swains zone, with mean chlorophyll concentrations lower than those of group B samples coming from the north of the Swains (Table 4.11). Omnivores (predominately *Acartia australis* and *Centropages orsinii*) numerically dominated the zooplankton assemblage of group A (Table 4.11). Group B was dominated by carnivores, primarily Corycaeidae and *Oncaea* spp.

The sample groups from the four latitudinal zones have a number of common features. *Paracalanus* spp. and other herbivorous copepods were the most abundant

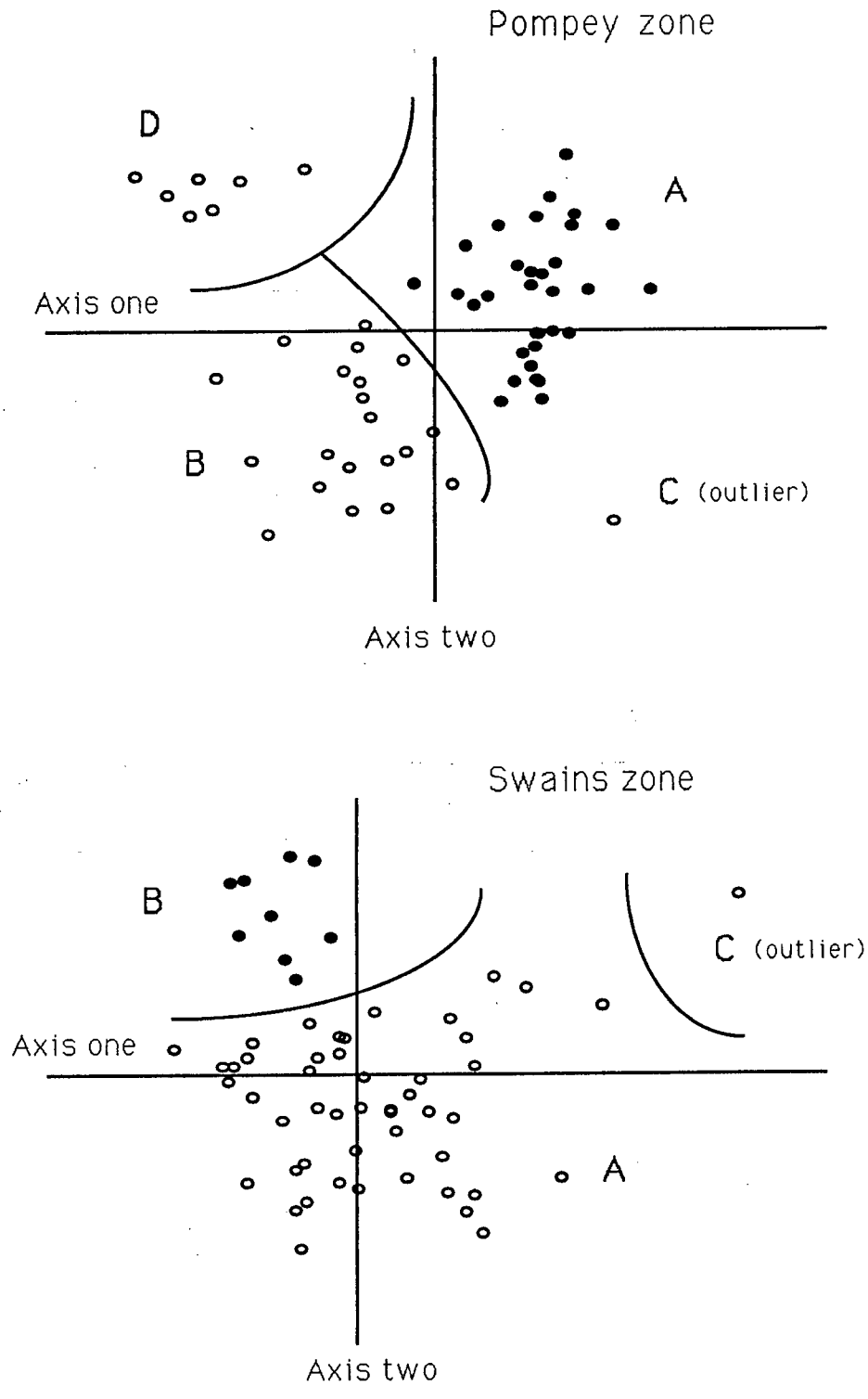


Figure 4.12 Ordination of samples from the Pompey and Swains zones. Samples identified as belonging to a group and referred to in the text are indicated by a letter.

Table 4.10

Summarization of the four groups of samples identified by the ordination of the Pompey zone samples. Abbreviations: reef prox. = reef proximity, Chl. = chlorophyll concentration, cope. = copepods, non cope. = non-copepod zooplankton, N.A. = not applicable, * = group means significantly different at $p < 0.05$, ** at $p < 0.01$.

Variable	Group A	Group B	Group C	Group D
Water depth (m)	61.0	49.2	38.0	N.A. **
Reef Prox. (km)	5.4	4.1	1.9	N.A.
Chl. (ug l^{-1})	0.96	0.76	0.50	0.18 **
Chl CV (%)	5.9	13.1	7.5	20.8 **
Cope. (no. m^{-3})	130.8	103.0	110.5	85.5
Non cope. (")	31.0	38.1	2.8	20.3
Herbivores %	46.4	20.7	22.1	31.4 **
Omnivores %	32.0	70.7	52.9	23.1 **
Carnivores %	21.6	8.6	25.0	45.5 **
Distribution of zooplankton with ten highest Cramer scores across the four groups (no. m^{-3}). Ranked in order of their Cramer score.				
Acar. australis	8.1	77.7	8.2	0.81
Paracalanus spp.	47.2	3.2	1.3	1.0
Euc. subcrassus	2.1	0.12	-	0.06
Cal. elliptica	5.6	0.67	1.3	0.24
Cor. (D) spp.	16.9	4.2	7.4	5.5
Acr. gibber	1.3	0.10	-	-
Fish eggs	0.15	0.78	-	0.20
Micro. rosea	8.2	1.9	2.3	9.2
Cen. orsinii	0.50	3.5	-	2.6
Pteropods	1.4	0.23	0.26	0.23
Distribution of the five most abundant zooplankton in the Pompey zone (no. m^{-3}). Ranked in order of overall abundance.				
Paracalanus spp.	47.2	3.2	1.3	1.0
Acartia australis	19.8	88.1	8.2	1.1
Oithona spp.	26.3	19.3	-	4.6
Appendicularians	16.1	5.3	6.4	6.2
Cor. (D) spp.	16.9	4.2	7.4	5.5

Taxa abbreviations: *Acar. = Acartia, Euc. = Eucalanus, Cal. = Calanopia, Cor. = Corycaeus, Acr. = Acrocalanus, Micro. = Microsetella, Cen. = Centropages.*

Table 4.11

Summarization of the three groups of samples identified by the ordination of Swains zone samples. Abbreviations: reef prox. = reef proximity, Chl. = chlorophyll concentration, cope. = copepods, non cope. = non-copepod zooplankton, * = group means significantly different at $p < 0.05$, ** at $p < 0.01$. (Group C excluded from comparisons).

Variable	Group A	Group B	Group C
Water depth (m)	58.0	89.2	47.0
Reef Prox. (km)	5.9	5.0	3.7
Chl. (ug l^{-1})	0.69	0.43	0.51 **
Chl CV (%)	10.7	10.9	15.8
Cope. (no. m-3)	181.7	101.4	253.3
Non cope. (")	62.8	20.3	85.3
Herbivores %	25.0	17.7	13.9
Omnivores %	50.3	27.1	75.0 **
Carnivores %	24.7	55.2	11.1 **
Distribution of zooplankton with ten highest Cramer scores across the three groups (no. m^{-3}). Ranked in order of their Cramer score.			
Far. concinnus	0.25	2.9	-
Clausocalanus spp.	0.05	1.24	-
Far. spp. (male)	1.7	13.3	-
Oncaea media	0.38	3.18	0.22
*Oncaea venusta*0.111.4-			
Cor. lubbocki	2.9	13.7	-
Oithona spp.	17.2	2.6	0.22
Cor. speciosus	0.13	0.97	-
Cor. (D) spp.12.83.90.66			
*Cal. elliptica*3.30.32-			
Distribution of the five most abundant zooplankton in the Swains zone (no. m^{-3}). Ranked in order of overall abundance.			
Acartia australis	35.5	6.0	2.9
Oithona spp.	17.2	2.6	0.22
Appendicularians	16.5	7.9	-
Cor. (D) spp.	12.8	3.9	0.66
Paracalsnus spp.	15.0	3.6	0.2

Taxa abbreviations: *Far.* = *Farranula, Cor.* = *Corycaeus, Cal.* = *Calanopia.*

category in the zooplankton community in the inshore and inner shelf bands. *Acartia australis, Centropages orsinii* and a range of *Oithona* spp. dominated the community in the outer shelf band in three of the four latitudinal zones. Corycaeidae were the most numerous group in the zooplankton community on the outer edge of the shelf and in the Coral Sea in all zones, less through an increase in their abundance than through a decrease in the abundance of other taxa.

Zooplankton sample groups were associated with differences in the chlorophyll concentration in all four zones. Chlorophyll variability, i.e. the chlorophyll coefficient of variation in each 8 km subtransect, was associated with differences in the zooplankton community only in the Pompey zone. Differences in zooplankton community composition were also related to distance offshore in each of the zones, though this may have been a chance correlation as distance offshore (water depth) and chlorophyll concentration exhibited similar gradients.

The cross-shelf differences in zooplankton community structure in the Pompey zone were unlike the pattern found in the other three zones. As in other zones, *Acartia australis* and *Centropages orsinii* were most numerous in the Pompey zone reef matrix, and Corycaeidae most numerous close to the edge of the continental shelf. However, in the Pompey zone, the continental shelf edge assemblage was co-dominated by *Paracalanus* spp., which in other zones was only numerous inshore.

Seasonal changes in zooplankton community structure could not be discerned. Only in the northern zone was a seasonally coherent group (group A) differentiated. However, as group A samples were all collected on one cruise, the separation of this group is not clear evidence of a seasonal change in community structure.

Location of subtransects with respect to individual reefs did not appear to be consistently influencing the zooplankton assemblage. Significant associations between reef proximity and species composition only occurred in the northern and central zones. In the northern zone, samples closest to reefs were numerically dominated by herbivorous zooplankton. However, in the central zone the opposite was found, carnivorous zooplankton numerically dominated the samples close to reefs.

A final possibility considered is that the zooplankton assemblages identified were an artifact resulting from a surface expression of the diel vertical migration of zooplankton. Should this be the case, samples within a zone that fell a particular group would have all been collected at a similar time of day. To test this possibility, the time of collection fro samples in each group was recorded, and the mean calculated. For this exercise time of day was recorded as the number of hours from midday, rather than the actual time, as a diurnally symmetric migration could produce

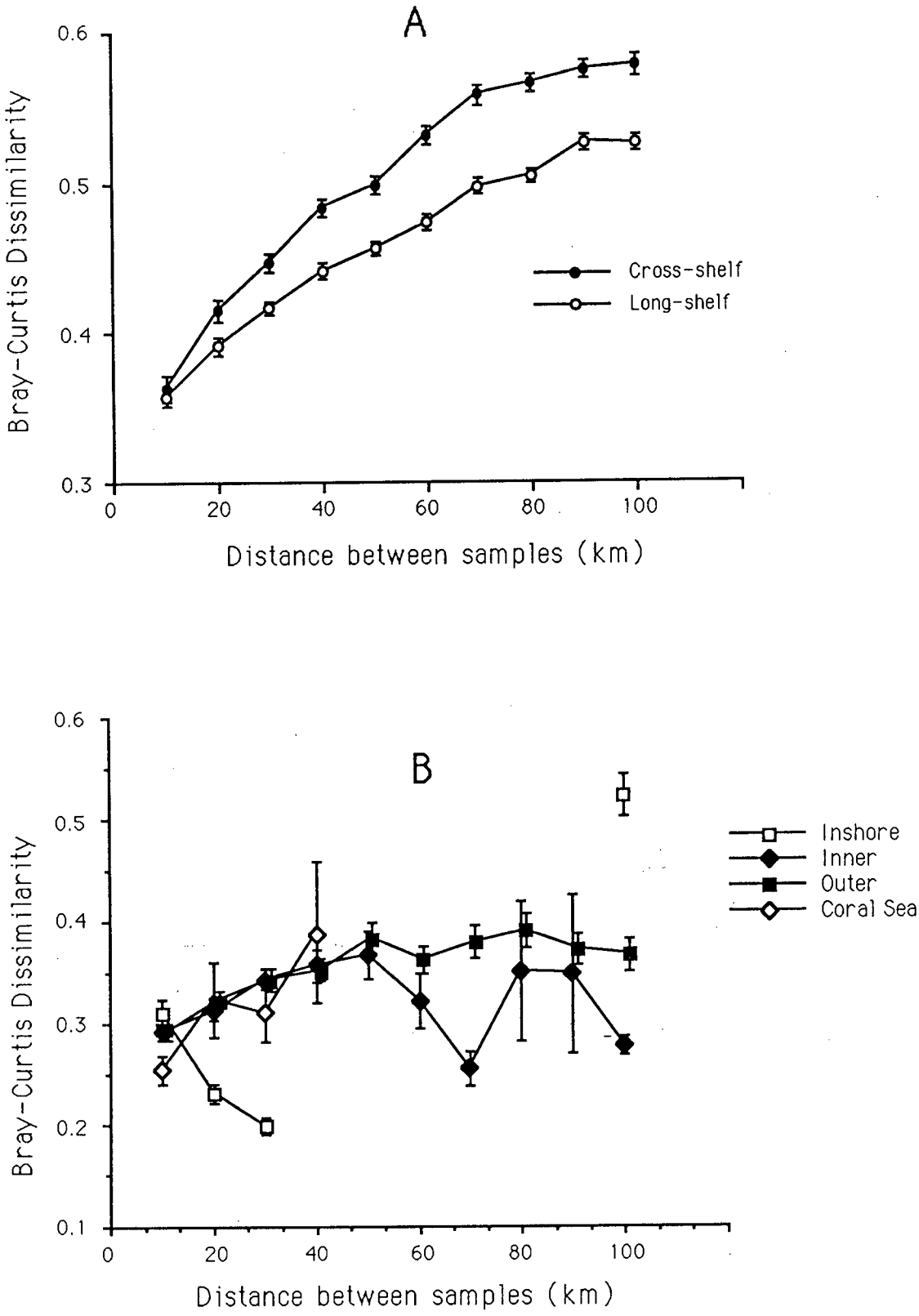
morning and afternoon surface assemblages which were more similar than to one at midday. The mean times of collection for groups within a zone were compared using analysis of variance. Only in the central zone was there a significant ($p < 0.05$) difference between groups in the mean time samples in groups were collected: the mean value for group A samples differed from that of group B samples by 0.6 hours. These results suggest that within the daytime sampling period, the zooplankton assemblage was not affected by diel vertical migration.

Spatial scales of zooplankton community structure

Variability in zooplankton community structure over distance was estimated by comparing the similarity of the zooplankton assemblage in samples separated by different distances. The Bray-Curtis measure was again used as the measure of similarity between samples. To avoid confounding spatial differences in the community structure with changes caused by advection, only samples collected on the same day were compared. This limited the range of spatial scales to 8 - 128 km, the distance the ship could travel in daylight hours, though in practice there were very few samples separated by more than 100 km. Similarities of samples separated by 10 km increments were grouped to calculate confidence intervals, e.g samples separated by 0 - 10 km, 10 -20 km and so on.

The cross-shelf or long-shelf orientation of comparisons was noted so that cross-shelf and long-shelf differences in the spatial scale of zooplankton change could be assessed. To do this, if a line joining the two samples compared was within 45° of a line normal to the coast, the comparison was regarded as cross-shelf, otherwise long-shelf. The dissimilarity between samples increased with distance for both cross-shelf and long-shelf comparisons (Fig. 4.13a). The greater the distance between samples, the greater the difference in their composition. This trend was more pronounced in the cross-shelf direction; for an equivalent dissimilarity, samples were about 1.4 times further apart in a long-shelf than a cross-shelf direction (Fig. 4.13a).

Samples were also compared only with others within the same cross-shelf band to avoid confounding within-band spatial heterogeneity with that between bands (Fig. 4.13b). As a result of the requirement that only samples collected on the same day be compared, the full range of distances could not be represented in the inshore and Coral Sea samples (Fig. 4.13b). These comparisons reveal a different picture to that in which all comparisons were used (Fig. 4.13a). Within cross-shelf bands, zooplankton assemblages changed little in composition over increasing distances (Fig. 4.13b). Together these results indicated that most spatial changes in the zooplankton community structure occurred between cross-shelf bands and not within them.



4.13. Dissimilarity of assemblages in samples separated by increasing distances for **A)** Cross and long-shelf pairs of samples, and **B)** Pairs of samples from within each of the four cross-shelf bands. Error bars are one standard error.

Regressions of sample dissimilarity against distance for each cross-shelf band revealed slight but significant increases in the inner and outer shelf bands ($p < 0.01$), and in the Coral Sea ($p < 0.05$), but not in the inshore band. This difference between the inner and outer shelf, and the other two bands, more likely reflects different numbers of samples rather than biological differences. Fewer samples were taken in the Coral Sea and inshore bands and hence there were fewer comparisons (18 and 18) than in the inner and outer shelf bands (527 and 915). This reduced the power of the regression significance tests in the former two bands, and may have led to the lower significance of the Coral Sea regression, and the non- significant inshore band regression.

Species diversity

Zooplankton species diversity was significantly lower in the Pompey zone than in the other three zones (Table 4.11). Within cross-shelf bands there was considerable variability in the species diversity (Fig. 4.14), but no significant cross-shelf differences in species diversity (Table 4.11). Wet season assemblages were significantly more diverse (V statistic = -0.064) than dry season assemblages (V statistic = -0.567).

Correlations between the V-statistic and environmental and biological variables were calculated to identify the conditions associated with change in the species diversity. Diversity was positively correlated with the abundance of nominally carnivorous zooplankton ($p < 0.01$), and negatively correlated with the abundance of nominal herbivores ($p < 0.01$). Diversity was also positively correlated with reef proximity in the central and Pompey zones ($p < 0.01$). Diversity was not correlated with the distance of samples from the coast, chlorophyll concentration or its variability within 8 km subtransects.

DISCUSSION

Abundance and biomass of zooplankton

Near-surface zooplankton biomass and abundance both decreased with increasing distance from shore, but neither changed significantly with latitude or season. Copepod abundances were correlated with chlorophyll concentration at three spatial scales (8, 16 and 32 km), in the inshore and inner shelf bands, and at the 8 km scale in the outer shelf. In the outer shelf band the correlation of copepod abundance with chlorophyll concentration and variability at just the 8 km scale appears to reflect the nature of chlorphyll variability in the reef matrix; particularly the more variable chlorophyll concentations close to individual reefs. Copepod abundances may have been correlated with chlorophyll concentrations close to reefs, but further from reefs

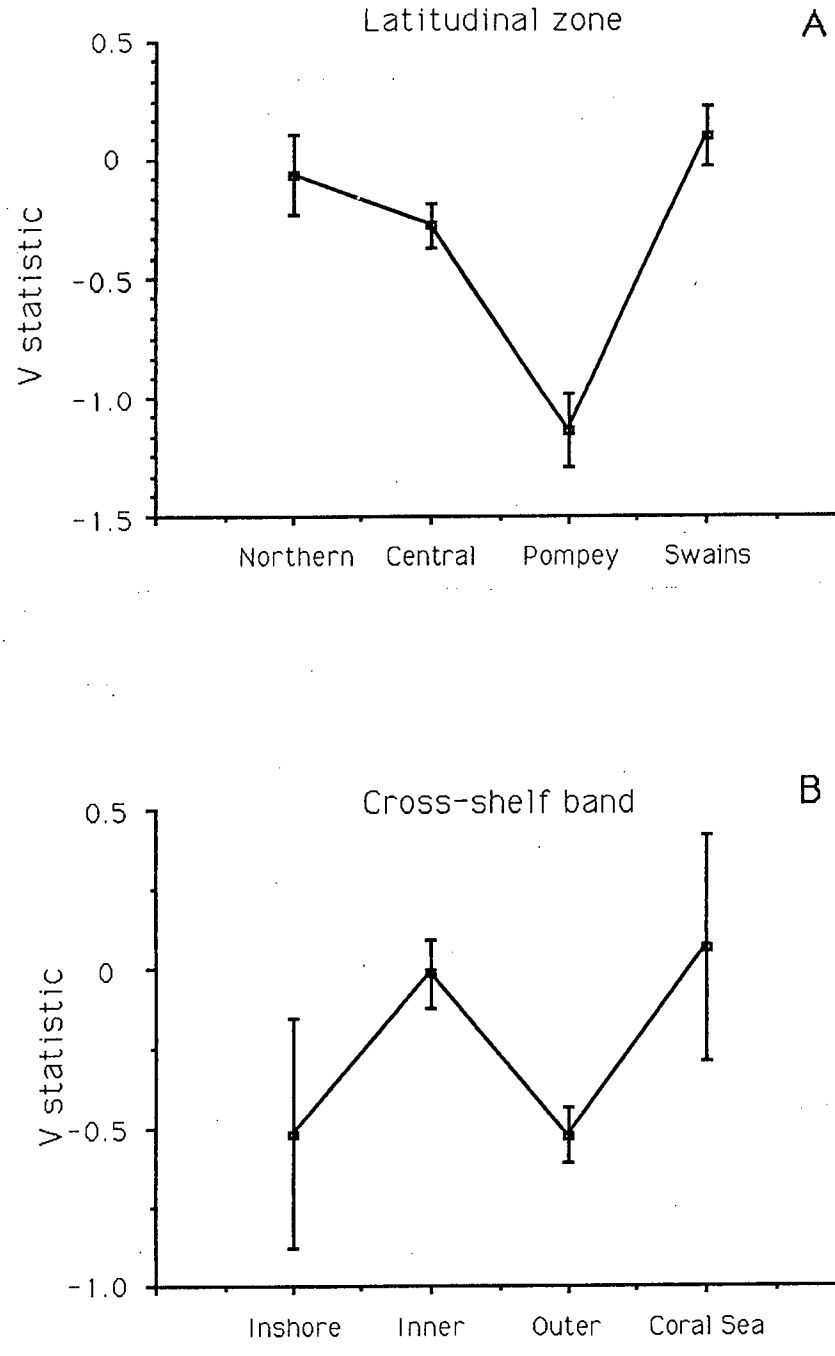


Figure 4.14. Mean species diversity in **A**) Latitudinal zones, and **B**) Cross-shelf bands. A V-statistic value greater that zero indicates that the assemblage is more diverse than that predicted by a neutral model, and a value less than zero indicates the assemblage is less diverse. Error bars are one standard error.

Table 4.12

Analyses of variance of the V statistic for zooplankton assemblages, an unbiased measure of species diversity, with two way fixed effects model ANOVAs; A) factors were zone (northern, central, Pompey and Swains) and band (inner shelf, outer shelf and Coral Sea), and B) factors were band (inshore, inner shelf, outer shelf and Coral Sea) and season (wet, dry). Underline between means in Tukey test indicates no significant difference between means ($p < 0.05$).

All four zones - A

Data not transformed, Cochran's C = 0.157, P < 0.05.

Factor	DF	Mean square	F ratio	Probability
Zone	3	6.96	4.93	< 0.01
Band	2	2.36	1.67	NS
Zone * Band	6	4.66	3.30	< 0.01
Error	350	1.41		

Tukey tests:

	Pompey	Central	Northern	Swains
V statistic (mean)	-1.14	-0.24	-0.16	0.01

Central zone only - B

Data not transformed, Cochran's C = 0.243, P < 0.05.

Factor	DF	Mean square	F ratio	Probability
Band	3	1.13	0.87	NS
Season	1	23.18	17.87	< 0.01
Band * Season	3	1.20	0.93	NS
Error	206	1.56		

(and at the 16 and 32 km spatial scales) the complex water circulation in the reef matrix and different generation times of phytoplankton (half a day, Furnas 1990) and copepods (1 - 2 weeks, Paffenhoffer and Harris 1979) may destroy this relationship.

Regional copepod abundances were broadly correlated with chlorophyll concentration, even in the Pompey zone where the normal cross-shelf chlorophyll gradient was reversed. The higher copepod abundances in Pompey zone outer shelf waters resulted from high densities of small herbivorous copepods (chiefly *Paracalanus* spp.) which were normally only abundant in inshore waters. These results suggest that copepod abundance was linked to chlorophyll concentration over a range of scales.

Zooplankton biomass was correlated with the chlorophyll concentration in inshore waters at small spatial scales (8 and 16 km), but not at a regional scale, suggesting that overall biomass was not strongly associated with the chlorophyll concentration. Such a lack of correlation was hardly surprising as the overall zooplankton biomass was sometimes strongly influenced by the presence of large or abundant micro-filter feeders (appendicularians) or carnivores (chaetognaths, siphonophores). The inshore biomass - chlorophyll correlations more probably indicate a similar change in relation to different inshore gradients than a limitation of zooplankton biomass by phytoplankton biomass.

Neither zooplankton biomass nor copepod abundance were significantly correlated with the degree of chlorophyll subtransect variability, nor were cross-shelf gradients in biomass copepod abundance similar to those of chlorophyll subtransect variability. It appears unlikely that either zooplankton biomass or copepod abundance were dependent on chlorophyll subtransect variability at either small (8, 16, and 32 km) or regional scales.

There was a significant seasonal change in the abundance of non-copepod zooplankton on the GBR shelf, primarily resulting from a seasonal increase in meroplankton, but no seasonal change in copepod abundance. The absence of significant seasonal variation in copepod abundance suggests that the seasonal change in the hydrological and meteorological processes affecting water column conditions are small. Sournia (1969) found no global seasonal change in the plankton in tropical waters comparable to that in temperate waters (Raymont 1983). Changes in zooplankton abundance and biomass on other tropical shelves were associated with local hydrological or meteorological processes (Sournia 1969). Where there is seasonal upwelling or monsoon associated river runoff, zooplankton biomass and abundance can exhibit strong seasonal changes (west coast of India - Murty 1987, Peru - Walsh **et al.** 1980). On tropical shelves without such influences, e.g. New

Caledonia (Binet 1985) and the GBR shelf, little seasonal change in zooplankton biomass or copepod abundance may occur.

Overall, copepod abundances and zooplankton biomass in GBR shelf waters are similar to those measured on other non-upwelling tropical shelves (Wickstead 1961, Calef and Grice 1967, Thiriot 1978) but are considerably lower than those on tropical (Gulf of Guinea - LeBorgne 1977, Peru - Walsh **et al.** 1971) and temperate shelves (Oregon - Peterson **et al.** 1979) on which upwelling occurs.

Dominant zooplankton taxa and their distribution

There were different cross-shelf patterns of abundance of the most numerous zooplankton taxa; some were most numerous inshore, others on the mid-shelf or at the shelf edge. While there were general compositional similarities to the fauna on other tropical shelves; e.g. the abundance of *Eucalanus subcrassus, Paracalanus* spp. and *Acrocalanus* spp. as in the Singapore and Malacca straits (Wickstead 1961, Sewell 1947), and of *Acartia, Corycaeus, Centropages* and *Oithona* spp. as off Jamaica (Grahame 1976) and New Caledonia (Binet 1984), comparisons with Farran's 1928-29 collection on the GBR (Farran 1936) reveals some interesting differences. *Acartia negligens, Centropages furcatus* and *Oithona plumifera*, species Farran found to be common, were uncommon in my samples, and conversely some species ubiquitous in this study; *Acartia australis* and *Centropages orsinii*, Farran recorded as rare. These differences cannot easily be attributed to latitudinal differences, for although Farran's collections were largely made in the vicinity of Low Isles (16°S), these species are widespread. Nor would these differences result from the different sizes of mesh used (Farran 430 um, this study 200 um) as the copepods compared are of a similar size. Instead these differences suggest that marked changes in the distribution and abundance of some of the numerically dominant copepods on the GBR shelf have occurred in the intervening half century. These changes in the copepod assemblage are large when viewed in the context of the apparent small physical and chemical variability of GBR waters, and the small seasonal variation in phytoplankton and zooplankton biomass.

The relative abundance of copepod orders changed distinctly cross-shelf; from a calanoid dominated fauna inshore to a higher proportion of cyclopoids in the outer shelf waters. The high proportions of cyclopoid and harpacticoid copepods on the GBR were similar to proportions in other tropical areas (reviewed by Raymont 1983), but the reason for this phenomenon is not clear. The distinct offshore decrease in calanoid abundance on the GBR shelf may arise from a gradient in environmental variability (Turner 1981), as both temperature and salinity are more variable close to

the coast (Wolanski **et al.** 1981). An alternative explanation, that these cross-shelf changes are attributable to different degrees of dietary specialization, is unlikely. Many calanoid copepods are opportunistic in their feeding habits (Paffenhofer and Knowles 1980) and cyclopoid copepods are possibly just as omnivorous (Turner 1981).

Association of individual taxon abundances with chlorophyll concentration and its variability was estimated at both sampling (8 km), and regional scales (200-400 km). No individual taxa were significantly correlated with chlorophyll concentration (Fig. 4.9), or its variability, at the sampling scale. Yet at the regional scale many taxa, primarily herbivores such as *Paracalanus* spp. and *Canthocalanus pauper*, showed the same cross-shelf pattern as that of chlorophyll. This apparent contradiction may arise through differences in the spatial scale over which correlations were sought. Zooplankton abundance is determined not only by food conditions at the time of sampling but also by conditions for some preceding time. Zooplankton and phytoplankton populations take different times to increase in size, which, together with advection, may result in peaks in zooplankton and phytoplankton biomass and abundance becoming spatially separated (Haury 1984). If this occurs, the correlation between zooplankton abundance and chlorophyll concentration may be reduced at small scales while it is still present at regional scales, as was the case on the GBR shelf.

Functional categories

The high proportions of carnivores and omnivores in the GBR zooplankton community are characteristic of tropical waters (Longhurst 1985). Such proportions have been attributed to the latitudinal changes in the type of food available to zooplankton. Food concentrations are generally lower but plankton are more diverse in tropical waters, resulting in a higher degree of omnivory than in temperate waters (Petipa 1978). Picoplankton and nanoplankton comprise a greater proportion of the phytoplankton biomass in tropical waters (Malone 1980) favouring small and gelatinous herbivores (Longhurst 1985), which in turn can be consumed by zooplanktonic carnivores (Longhurst 1985).

The abundance of herbivores across the shelf reflected that of the chlorophyll concentration, highest near the coast and decreasing offshore. Omnivores were more abundant in reef matrix and carnivores in the Coral Sea. The predominance of omnivores in the reef matrix may have been associated with a change in the food available to zooplankton in this region, e.g. detrital material washed off reefs, as changes in omnivore abundance did not correspond to changes in the chlorophyll

concentration. The cross-shelf distribution of carnivores followed neither cross-shelf changes in chlorophyll concentrations nor the cross-shelf abundances of non-carnivorous zooplankton.

Regional change in zooplankton community structure

Zooplankton taxa fell into three distinct cross-shelf assemblages; inner shelf, outer shelf, and shelf edge. The inner shelf assemblage was dominated by small herbivorous copepods, the outer shelf assemblage by omnivorous copepods and the shelf edge assemblage by small carnivorous copepods. These assemblages were coherent along the 1200 km section of the GBR shelf that was sampled. Within regions of the GBR which were comparatively homogeneous structurally, e.g. the reef matrix, zooplankton assemblages changed little over large spatial distances. When reef structure boundaries were crossed, e.g. in moving from the reef matrix to the inner shelf, assemblages changed relatively sharply.

There are distinct cross-shelf changes in the species composition of other taxa on the GBR shelf, including reef fish (Williams and Hatcher 1983), sponges (Wilkinson and Trott 1983), corals (Done 1983), and a mixture of benthic and pelagic fauna from trawls (Cannon et al. 1987, Watson and Goeden 1989), but not fish larvae (Leis and Goldman 1987, Williams **et al.** 1988). In general such differences in fauna are most marked with the transition from the GBR lagoon to the reef matrix region. Differences have been attributed or related to current dispersal of larvae (fish - Williams and Hatcher 1983), food supply (fish - Anderson **et al.** 1981, Williams and Hatcher 1983), depth and sediment type (trawled species - Cannon **et al.** 1987, Watson and Goeden 1989) and extent of sedimentation (sponges - Wilkinson and Trott 1983). However, as most of the groups mentioned above are sessile, benthic or demersal, it is not appropriate to generalize factors affecting their distribution to planktonic organisms.

The connection between the regional differences in the GBR reef structure, and associated changes in the zooplankton community may be by an "island mass effect" in which zooplankton communities in the vicinities of islands and reefs have a higher biomass (Le Borgne *et al.* 1985, Hernandez-Leo 1988). This effect can result from an enhanced vertical mixing close to an island bringing nutrients into surface waters (Simpson **et al.** 1982), export of zooplankton, or food available to zooplankton (phytoplankton or detritus) from reefs by tidal flushing (Le Borgne *et al.* 1985). On the GBR shelf, enhanced vertical mixing could be expected to have a relatively minor effect on the zooplankton community as a nutrient-enriched sub-thermocline layer occurs only infrequently (Andrews and Furnas 1986). In contrast, flushing of

chlorophyll off reefs occurs regularly (chapter 2, Furnas **et al.** 1990), and the correlation of copepod abundance in the reef matrix with chlorophyll concentration and variability at the 8 km spatial scale suggests that copepod abundance may be affected by this "island mass effect". Export of zooplankton themselves from reefs seems less likely as the reef zooplankton fauna is very different from that in open waters (Sale **et al.** 1976). Stronger similarities would be expected between reef and nearby open water zooplankton if the flushing of zooplankton off reefs were an important influence on the reef matrix zooplankton assemblage.

An element of the reasoning underlying the "island mass effect" is that zooplankton are food limited, and therefore local increases in phytoplankton biomass result in zooplankton population growth. This assumption could be tested through the relationship between zooplankton community structure and chlorophyll concentration. As GBR zooplankton assemblages extended over large regions, e.g. the reef matrix, correspondence with associated environmental variables could only be examined at this regional level. Although the cross-shelf changes in zooplankton community structure on the GBR shelf parallelled those of many of the cross-shelf gradients in environmental variables, there was a stronger relationship with chlorophyll. Change in the zooplankton community structure was associated with differences in the regional mean value of the chlorophyll concentration in each of the four latitudinal zones. Where the cross-shelf distribution of chlorophyll changed, e.g. in the Pompey zone, the zooplankton community structure followed this change. These correlations indicated that zooplankton community structure in an area is dependent on the level of phytoplankton biomass. Conversely, zooplankton community structure did not appear to be dependent on the spatial variability of the chlorophyll concentration, perhaps as a result of the small absolute magnitude of the variability both cross-shelf and long-shelf.

In two previous studies of GBR zooplankton, cross-shelf differences in zooplankton community structure were found to be related to cross-shelf differences in the chlorophyll concentration (Sammarco and Crenshaw 1984, Williams **et al.** 1988). When the cross-shelf gradient in chlorophyll changed in response to physical forcing, the zooplankton community also changed, e.g. inshore changes in community were synchronous with river discharge and the associated changes in water column nutrients (Sammarco and Crenshaw 1984), and reef matrix changes were associated with intrusions of nutrient enriched Coral Sea water (Williams **et al.** 1988). Similarly, off New Caledonia there is a transition from an inshore assemblage dominated by small herbivores to an outer shelf assemblage dominated by *Acartia*

australis , a change associated with a cross-shelf gradient in chlorophyll concentration (Binet 1984).

Overall, there was little seasonal change in the zooplankton assemblage. The absence of seasonal variability in zooplankton community structure reflects the absence of major seasonal changes in the hydrological conditions on the GBR. On tropical shelves where seasonal changes in the zooplankton community occur, such changes are often related to quite distinct changes in the hydrological regime. The zooplankton assemblage on the West African coast changes when conditions change from upwelling to non-upwelling (Thiriot 1978). Similarly, in the upwelling zone off the Peruvian coast changes in the zooplankton community are related to changes in the upwelling conditions (Timonin and Flint 1986).

Species diversity

The only distinctive feature in the spatial pattern of zooplankton diversity on the GBR is the low diversity in the outer shelf band of the Pompey zone. There were no significant cross-shelf changes in diversity in other zones.

Regional differences in species diversity have been attributed to many different ecosystem processes; increased competition (MacArthur and Wilson 1967), reduced competition (Connell 1978), stability (Tramer 1969) and spatial heterogeneity (Richerson et al. 1970), but the most comprehensive theory relates species diversity to the frequency of disturbance to a community (Huston 1979). Communities disturbed infrequently lose species through competitive exclusion, and those disturbed very frequently lose species unable to recover from population reductions. Communities with an intermediate level of disturbance will have the highest species diversity (Huston 1979). In this context disturbance is defined as a reduction of abundance through physical or chemical changes, or predation.

It is unlikely that physical and chemical variability in the Pompey zone would be severe enough to produce the species and density independent reductions of zooplankton populations required to modify diversity. Excluding the very shallow inshore waters, salinity (Pickard **et al.** 1977) and temperature (Andrews 1983) variation on the GBR shelf is relatively small. Chlorophyll concentration also is relatively invariate within a particular region (as measured by subtransect variability), and was not correlated to the diversity of samples over all zones, or within the Pompey zone. Predation upon the zooplankton, the second form of disturbance, was not measured. Little is known of pelagic fish populations on the GBR shelf, although in the Pompey region of the GBR shelf where zooplankton diversity was lowest, the reef fish assemblage was quite distinct from those further north (Williams 1983).

Zooplankton diversity was higher during the wet season in all cross-shelf bands of all latitudinal zones. This widespread seasonal increase in diversity resulted from an increase in the number of meroplanktonic species during the wet season.

The absence of significant cross-shelf changes in zooplankton diversity on the GBR shelf stands in contrast to other studies; fish communities on the GBR increased in 'evenness' towards the shelf edge (Williams and Hatcher 1983), and, in the Red Sea and Persian Gulf, zooplankton in neritic areas is less diverse than in oceanic waters (Kimor 1973). Neither of these authors ventured an explanation for such changes.

Although the cross-shelf differences in zooplankton diversity on the GBR were not statistically significant, they were qualitatively similar to cross-shelf differences in zooplankton diversity off New Caledonia; i.e. higher diversity on the inner shelf and oceanic waters, lower diversity inshore and on the outer shelf Binet (1985). Binet (1985) attributed the lower diversity of inshore and outer shelf zooplankton assemblages to stresses imposed by terrestrial runoff inshore, and water turbulence on reefs and predation by reef fish on the outer shelf. This explanation is not appropriate for the situation on the GBR. Zooplankton diversity on the GBR outer shelf was no higher in the northern and Swains zones in which the reefs are densest and water turbulence on reefs could be expected to be greatest.

Summary

Near-surface zooplankton biomass and abundance decreased with increasing distance from shore, but neither changed significantly with latitude or season. Copepod abundances were correlated with chlorophyll concentration at three spatial scales (8, 16 and 32 km) in the inshore and inner shelf bands and at the 8 km scale in the outer shelf. Regional copepod abundances followed the same trend even in the Pompey zone where the nearshore - offshore chlorophyll gradient was reversed. Zooplankton biomass was correlated with the chlorophyll concentration in inshore waters, but not at a regional scale suggesting that overall, biomass was not strongly associated with the chlorophyll concentration.

There were different cross-shelf patterns of abundance of the most numerous zooplankton taxa; some were most numerous inshore, others on the mid-shelf or at the shelf edge. However, there were no significant correlations between abundances of individual taxa and chlorophyll concentration or its spatial variability. When samples were aggregated to give regional means, there was a good correspondence between regional abundances of most herbivorous zooplankton and the regional chlorophyll concentration. Advection of zooplankton populations from the conditions under which they developed may have been responsible for the lack of correlation at

the (8 km) sampling scale. The proportions of copepods in the three major copepod orders; calanoids, cyclopoids and harpacticoids, resembled that on other tropical shelves, as did the proportions of herbivorous, omnivorous and carnivorous zooplankton.

Zooplankton taxa fell into three recognizable cross-shelf assemblages; inner shelf, outer shelf, and shelf edge. These assemblages were latitudinally coherent. The inshore assemblage was dominated by small herbivorous copepods, the outer shelf assemblage by omnivorous copepods and the shelf edge by small carnivorous copepods. As water on the GBR shelf is generally well mixed, it is unlikely that such cross-shelf changes were the result of the mixing of water masses with different zooplankton communities. Instead, zooplankton communities appeared to be composed of

taxa with similar adaptations to cross-shelf gradients in biological conditions.

Although there were cross-shelf gradients in a number of environmental variables, an atypical cross-shelf community structure in the Pompey zone paralleled an atypical gradient in the chlorophyll concentration, suggesting that food supply was determining the distribution of the community dominated by small herbivores. Factors influencing the distribution of omnivores and carnivores could not be ascertained.

Zooplankton diversity on the GBR shelf was significantly lower in the Pompey zone than in other zones, and higher during the wet season, but did not change significantly across the shelf. In other ecosystems changes in species diversity are best explained by the frequency and severity of population reductions by both predation and physical and chemical perturbation. On the GBR shelf physical and chemical variability was thought too small to produce the density-independent population reductions necessary to affect diversity. Changes in predation may have been responsible for the change in zooplankton diversity in the Pompey zone. The increase in zooplankton diversity in the wet season was caused by an increase in the number of meroplanktonic species, particularly crustacean, mollusc and polychaete larvae.

Chapter 5. Temporal changes in nearshore chlorophyll concentrations and the zooplankton community after a cyclonic disturbance.

INTRODUCTION

Many water column biological processes are influenced by physical forcing (Horne and Platt 1984). The temporal and spatial scales over which physical forcing occurs affect the types of biological responses (Haury **et al.** 1978, Silvert and Platt 1980). It is usually difficult to measure directly the relationship between physical events and biological responses because of the difficulty of following specific water masses and observing changes within them over time. As a consequence, coupling between physical and biological processes is often inferred from correlations of variables, particularly for processes encompassing long times and large spatial scales (Harris 1986). This approach was adopted in the work described in the previous chapter to examine the covariability between zooplankton and phytoplankton in GBR shelf waters.

Over shorter time periods and smaller spatial scales, biological responses to physical processes can sometimes be directly observed. Biological responses that occur within a few days to a few weeks may be able to be linked to physical forcing if the degree of confounding by advection is suitably reduced. If a physical event is short-lived and distinct, the association of biological changes with the physical event becomes more evident.

Cyclonic storms, the most energetic meteorological events that occur in tropical coastal regions, are characterised by very strong winds, heavy rainfall and floods in coastal rivers. The effect of cyclonic and other severe storms on phytoplankton and zooplankton communities has not been well documented. In Chesapeake Bay, phytoplankton biomass increased 3-10 fold following a cyclone (Zubkoff and Warinner 1977, Loftus and Seliger 1977). This increase was a result of an influx of floodwater with high concentrations of nutrients (Loftus and Seliger 1977). The effect of storms on phytoplankton biomass in continental shelf waters depends on the interaction of the winds with the local hydrography. Tropical storm Dennis produced changes in temperature and salinity off the coast of Georgia, but not in nutrient or chlorophyll concentrations (Zeeman 1985). In contrast, a winter storm in the Gulf of Mexico moved coastal, high chlorophyll waters offshore forcing the upwelling of low nutrient, low chlorophyll waters inshore (Dagg 1988). Cyclone Winifred produced up to tenfold increases in chlorophyll concentration and nutrients on the tropical shelf of north Australia (Furnas 1989).

The effects of cyclones and storms on zooplankton abundance is unclear. Under laboratory conditions, copepods are capable of responding to an increase in phytoplankton by increasing egg production within 24 hours (Dagg 1988, Durbin **et al.** 1983). Such experiments suggest that were phytoplankton biomass to increase following a cyclonic disturbance, there would be a corresponding increase in copepod abundance. However, this reasoning is base on the assumption that zooplankton are food limited. Observations made after cyclones or storms indicate that the effect on zooplankton may not be so unequivocal. Mullin **et al.** (1985) found that copepod nauplii were more abundant after passage of a storm on the California coast, yet the chlorophyll concentration had changed little. Although there were changes in the vertical stratification of the water column and in the vertical distribution of some zooplankters, there were not able to interpret the changes in zooplankton abundance (Mullin **et al.** 1984).

The effects of the passage of a cyclone on phytoplankton biomass and zooplankton biomass and abundance in inshore waters is described in this chapter. In February 1988, cyclone Charlie first made landfall near Cape Bowling Green, Queensland (Latitude 19{ 30' S, Fig. 5.1). An automated weather station on Cape Bowling Green recorded wind speeds up to 150 km hr^{-1} as the cyclone passed (Fig. 5.2). Torrential rains accompanied the passage of the cyclone and flow in the rivers near Cape Bowling Green increased by three orders of magnitude (Fig. 5.2). Fortuitously, water and plankton samples had been taken in the Cape Bowling Green area twenty days prior to the cyclone passage, providing data with which subsequent conditions in the water column could be compared. Over a two week period following the cyclone, five sites in Bowling Green Bay were sampled to monitor changes in the plankton.

After the passage of the cyclone, changes in plankton biomass and abundance and the covariability of zooplankton with phytoplankton, were investigated to resolve two general questions:

1. How might inshore phytoplankton biomass (as chlorophyll) change following a cyclone and how quickly?
2. Did zooplankton numerical abundance, biomass and community structure change after the passage of the cyclone?

METHODS

Wind speed and barometric pressure measurements were made at Cape Bowling Green by an automated weather station operated by the Australian Institute of Marine Science. Readings were taken every half hour. The anemometer was

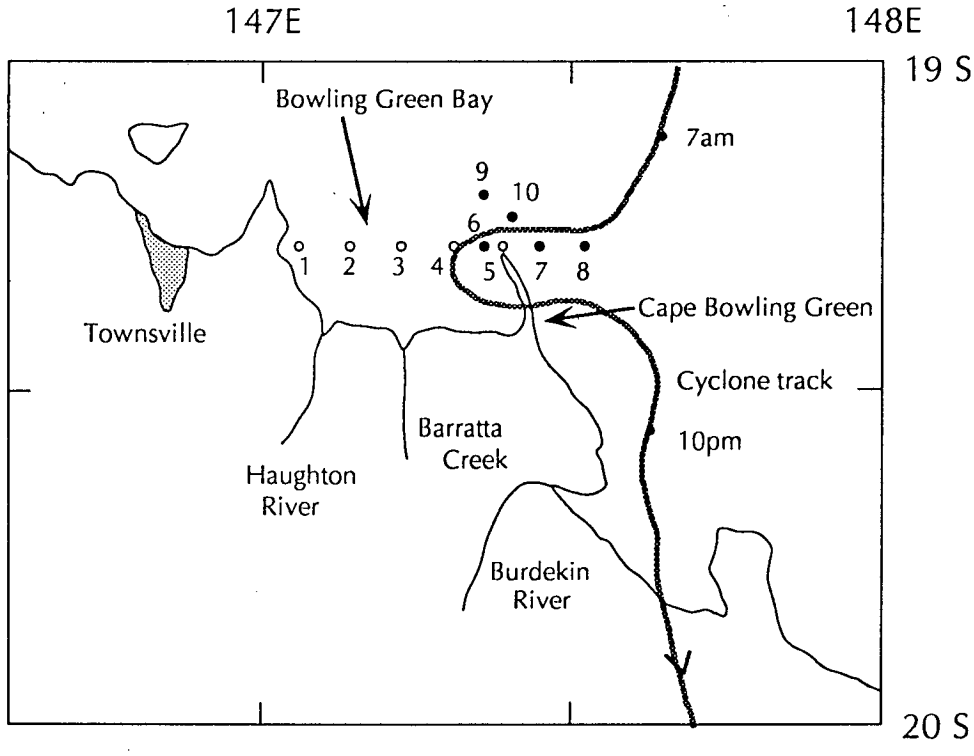


Figure 5.1. Map of the study area showing the cyclone track and pre- (6-10) and post-cyclone stations (1-5).

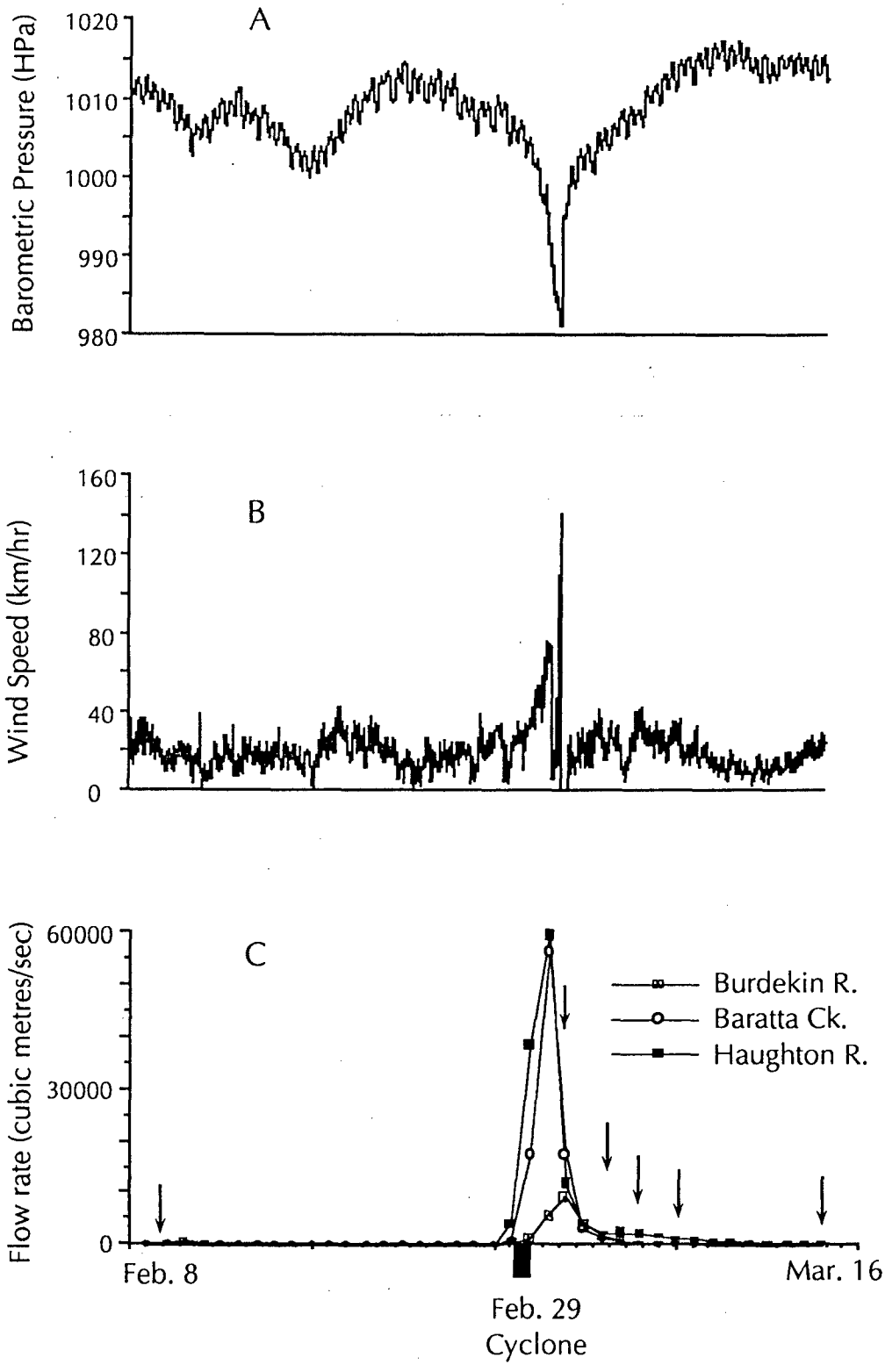


Figure 5.2. Weather conditions and river flow data during sampling period; **A.** barometric pressure, **B.** wind speed, and **C.** river flow rates. Passage of cyclone Charlie marked by a black bar. Arrows indicate days on which samples were taken.

damaged just after the eye of the cyclone crossed the Cape Bowling Green and no wind speed data was recorded over the subsequent ten hours. River discharge records were provided by the Queensland Water Resources Commission from automatic river height recorders.

Chlorophyll concentrations and zooplankton samples were obtained at five stations 20 days prior to the cyclone (Fig. 5.1). A five station transect across Bowling Green Bay was occupied 2, 4, 6, 8 and 16 days after the cyclone (Fig. 5.1). Station depths ranged from 9 m at site 1 to 24 m at site 9.

At each post-cyclone station (1-5) water was collected by Niskin bottle from three depths; surface, mid-water and near the bottom. Subsamples were taken for determination of chlorophyll concentration, dissolved inorganic nutrient concentrations (NO_3, NO_2, PO_4 and NH_4), salinity and suspended solids. Chlorophyll concentrations at the pre-cyclone stations were calculated from the *in vivo* fluorescence of water pumped through a flow-through fluorometer (Turner Designs 10-005R), as the intake was lowered to the bottom.

Suspended solids concentrations were measured only at the post-cyclone stations by filtering water samples (750 ml) from the top and bottom of the water column onto preweighed 47 mm Nuclepore filters (0.4 um pore size).

Water samples taken for nutrient analysis were filtered through precombusted Whatman GF/F filters and frozen in acid-washed scintillation vials. Nutrient analyses were carried out ashore on a multichannel segmented flow analyzer using the methods described in Ryle **et al.** (1981).

Zooplankton were sampled at both pre- and post-cyclone stations by vertical tows from the bottom using a 0.5 m flowmeter equipped net (200um mesh) and were preserved in a sodium tetraborate buffered 5% formalin-seawater solution. Two tows were made at each post-cyclone station. Zooplankton samples were repeatedly split with a Folsom splitter (McEwen **et al.** 1954) to obtain a subsample containing approximately 500 animals (3.125 - 100% of sample), which were identified and counted. With this sized mesh, copepodites and copepod nauplii were not collected quantitatively and were not included in the zooplankton counts. The mean zooplankton abundance, calculated from the replicate net tows at each station, was used for the statistical analyses. Most copepods were identified to species. Other taxa were identified to different degrees of taxonomic resolution (Tables 5.1, 5.2). Zooplankton wet weight was used as a measure of zooplankton biomass as it provides a precise estimate (Beers 1976), and is a non-destructive technique. The

Table 5.1

Zooplankton taxa in samples. Abundances are in animals m^{-3}. Trophic category indicated by c = carnivore, o = omnivore, h = herbivore. SD = Standard Deviation

	Mean	Max	SD	Trophic group
Total copepods	1320.4	3687	861.5	
Larvaceans	161.2	1280	213.3	h
Chaetognaths	93.3	477	76.8	c
Bivalve veligers	78.1	333	76.6	h
Gastropod veligers	62.8	239	42.3	h
Echinoid larvae	36.4	243	48.1	h
Brachyuran larvae	22.9	148	24.2	o
Decapod larvae	21.1	116	21.9	o
Pteropods	18.6	124	28.4	h
Siphonophores	16.3	94	17.3	c
Cladocera, *Penilia* sp.	12.6	104	21.8	c
Polychaete larvae	9.2	81	14.7	c
Coelenterate medusae	5.9	26	6.8	c
Luciferids	4.5	54	8.5	o
Ostracod, *Euconchoecia* sp.	3.6	34	6.0	o
Fish larvae	3.5	17	4.9	c
Phoronid larvae	3.4	27	4.8	h
Ostracod, *Pyrocypris* sp.	3.3	23	5.7	o
Amphipod larvae	2.2	15	3.4	o
Fish eggs	1.5	9	2.5	-
Salps	0.81	16	3.1	h
Cladocera, *Evadne* sp.	0.15	6	0.8	c
Stomatopod larvae	0.03	2	0.22	c

Table 5.2

Copepod taxa in samples. Abundances are in animals m^{-3}. Trophic category indicated by c = carnivore, o = omnivore, h = herbivore. SD = Standard Deviation

	Mean		Max	SD	Trophic group	
Copepod taxa						
Paracalanus indicus	562.1		1846	446.8	h	
Acrocalanus gibber	135.0		558	112.6	h	
Oncaea conifera	63.9		212	60.0	c	
Canthocalanus pauper	61.5		230	61.9	h	
Oithona australis	55.7		290	48.5	h	
Corycaeus lubbocki	51.2		172	46.3	c	
Euterpina acutifrons	46.5		320	62.6	h	
Centropages furcatus	42.6		211	43.9	o	
Acartia pacifica	39.2		287	50.6	o	
Corycaeus pacificus	38.5		174	37.6	c	
Calanopia elliptica		37.9		208	40.9	c
Eucalanus subcrassus	20.0		128	27.0	h	
Oithona plumifera		15.0		67	15.0	h
Paracalanus crassirostris	14.7		92	21.6	h	
Temora turbinata	13.8		144	23.0	o	
Oncaea media	11.0		59	14.0	c	
Oithona rigida	11.0		123	19.8	h	
Tortanus barbatus		10.3		46	11.2	c
Labidocera minuta		4.5		29	6.7	c
Undinula vulgaris	3.9		69	11.0	h	
Macrosetella gracilis	3.6		41	7.6	h	
Clytemnestra scutellata	3.1		44	7.0	h	
Centropages orsinii	2.9		24	5.0	o	
Candacia pectinata		2.9		52	8.3	c
Microsetella rosea		2.7		26	5.3	h
Labidocera acuta	1.3		18	3.7	c	
Acartia australis	1.1		18	3.0	o	
Acrocalanus gracilis	1.0		17	2.8	h	
Temora stylifera	0.53		6	1.5	o	
Sapphirina spp.	0.35		8	1.3	c	
Centropages elongatus	0.09		3	0.5	o	
Farranula spp. (male)	0.02		1	0.1	c	

entire preserved sample was filtered under vacuum (< 20 Kpa) onto a preweighed piece of 53 um netting and reweighed.

Data analysis

Temporal changes in chlorophyll concentration, zooplankton abundance and zooplankton biomass were analyzed using two factor mixed model analyses of variance (ANOVA) with time-after-cyclone the fixed factor and station the random factor. Tukey tests were used for subsequent comparisons between means (Zar 1984). As a single depth-averaged chlorophyll value was used for each post-cyclone station, an interaction term could not be calculated. Prior to analysis, variables were tested for heterogeneity of variance by Cochran's "C" test (Dixon and Massey 1969) and, where necessary, square root or log transformed to reduce heterogeneity of variance. The Cochran's C value reported in the ANOVA tables is that calculated after any data transformation had been carried out.

Similarities between samples based on the zooplankton collected were investigated by ordination of the samples. Raw zooplankton counts were log(x+1) transformed so that very numerous taxa did not dominate the results of the ordination (Gauch 1983). The Bray-Curtis measure (Bray and Curtis 1957) was used to calculate the similarity between pairs of samples, and metric multidimensional scaling used to order the samples (Faith **et al.** 1987).

RESULTS

In time series of observations at fixed stations, temporal changes in water column conditions can be confounded if advection moves a different water mass past the sampling site. Nothing definitive can be said of the current patterns over the sampling period as no current meters were deployed. Bounds on the distance water may have been advected during the sampling period can be estimated. Along this section of GBR the longshore current tends to be south, but is readily reversed by wind stress (Wolanski and Pickard 1985). Currents at a site 18 km east of Cape Bowling Green indicated a strong dependence upon wind stress. Current flow was to the southeast under the influence of northeast winds, reversing under the influence of southeast winds (Andrews and Furnas 1986). Progressive current vectors over a period of five days in which the wind was from the SE at 7 m sec^{-1} (mean post-cyclone winds, SE 5.5 m sec-1) indicated a net 19 km northwest movement of water (Andrews and Furnas 1986).

Water circulation within Bowling Green Bay has been modelled (Stephen Gay, unpublished data). For a southeast wind of 5 m sec^{-1} the longshore current is

balanced by the wind stress and water in the bay moves little over a nine day simulation (Stephen Gay, unpublished data). Together these data suggest that there would have been little advection of water out of Bowling Green Bay under the influence of the southeast wind that prevailed during the post-cyclone sampling period. However, it should be noted that if the northeast movement of water recorded by Andrews and Furnas (1986) at their mooring off Cape Bowling Green were to prevail within Bowling Green Bay, water would be advected northwest 61 km during the sampling period.

Excepting the day on which the cyclone occurred, wind speeds during the sampling period, 8/2/88 to 16/3/88, ranged from 0.1-13.2 m sec^{-1} (mean 5.5 m sec^{-1})(Fig. 5.2) and came from the southeast. Winds speeds in the 2 weeks following the cyclone ranged from 0.7-12.2 m sec^{-1} (mean 5.7 m sec^{-1}).

As phytoplankton biomass in GBR waters appear to be nutrient limited (Furnas and Mitchell 1986), it is worthwhile examining the effects of the passage of cyclone Charlie on concentrations of water column nutrients. Cyclones may affect the concentrations of dissolved nutrients in coastal waters by two processes; through resuspension of bottom sediments (Walker and O'Donnell 1981), and through enhanced river outflows of nutrient-rich water (Wolanski and Van Senden 1983). Their relative importance in Bowling Green Bay after the cyclone may be assessed using salinity as an indicator of flood waters.

Post-cyclone discharges of the three rivers nearest the study area; the Burdekin and Haughton Rivers and Baratta Creek, increased by three orders of magnitude over pre-cyclone flow rates (Fig. 5.2). Discharges from the Haughton River and Baratta Creek, which flow directly into Bowling Green Bay, peaked the day following the cyclone. Burdekin River discharge peaked two days after the cyclone (Fig. 5.2). Gauging stations on all three rivers are within 20 km of the sea and water passing these stations would reach the sea within a day. The Burdekin River mouth is 50 km south of Cape Bowling Green. Outflow was estimated to take five days to reach Bowling Green Bay based on a 0.1 m sec^{-1} northwards movement of Burdekin flood water (Wolanski 1982).

Surface salinity was low until day 6, rose on day 8 and decreased again by day 16 (Fig. 5.3). Near-bottom salinity varied less, with a decrease on day 5. There were large decreases in both surface and near-bottom salinities by day 16. Over a mean water column depth of 15 m, a reduction in near-bottom salinity similar to that seen at day 6 would be achieved if a 0.5 m thick surface layer of fresh water had been mixed through the water column. The reduction in salinity on day 16 could be accounted for by 1 m fresh water layer. These calculations suggest substantial fresh water inputs to

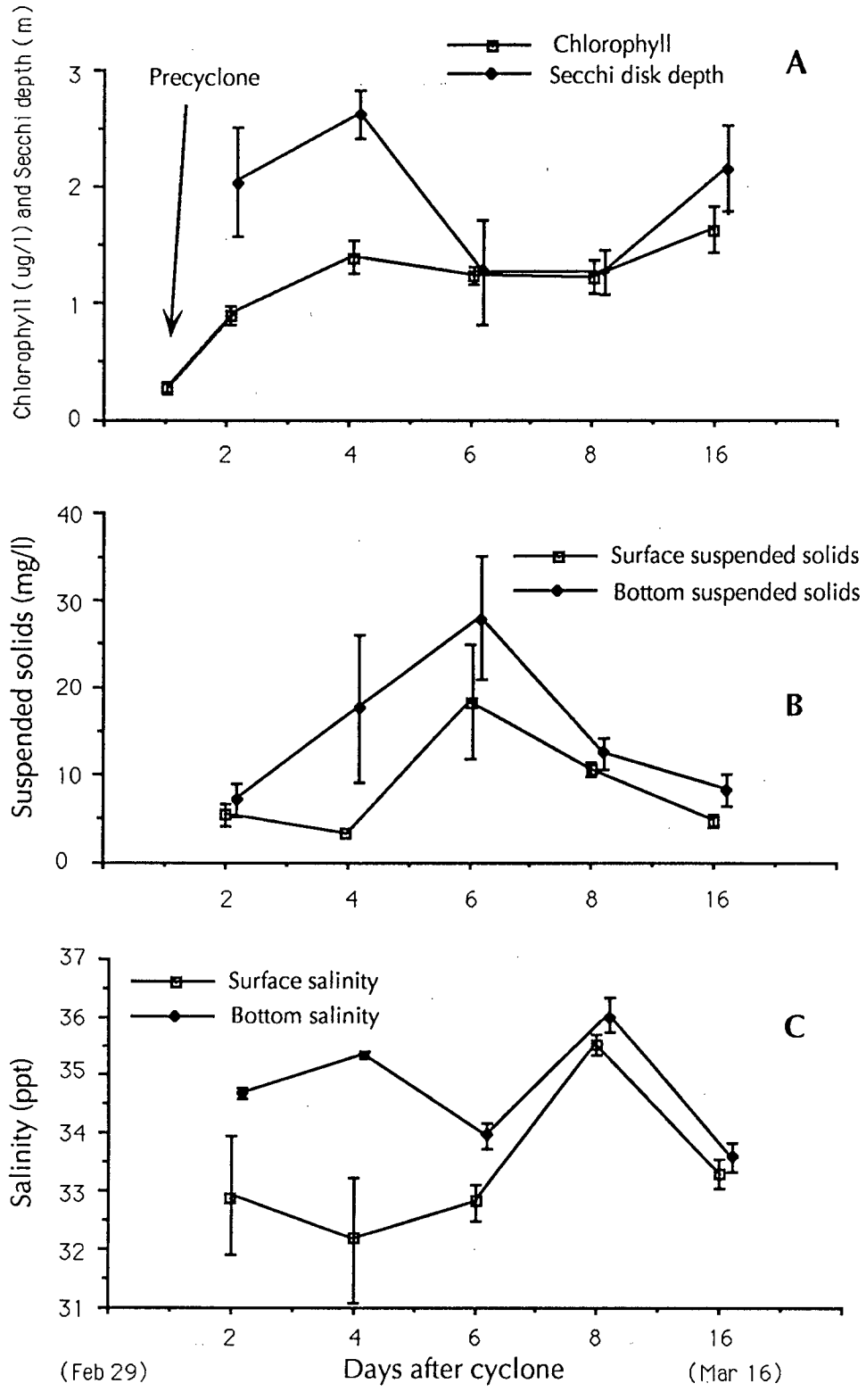


Figure 5.3. Physical and chemical water column variables. **A.** Secchi disk depths and chlorophyll concentrations, **B.** surface and near-bottom suspended solids concentrations, and **C.** surface and near-bottom salinity. Chlorophyll concentrations were measured pre- and post-cyclone, other variables only post-cyclone. Error bars are one standard error.

Bowling Green Bay occurred, which can be attributed to river outflows as little rain fell over the period day 4 to day 16.

Surface salinities were low initially, indicating that flood outflows had reached Bowling Green Bay before sampling commenced. By day 6 less saline surface waters were being mixed into the water column and by day 8 the whole water column was well mixed (Fig. 5.3). Both surface and near-bottom concentrations of suspended solids were low on day 2, suggesting that initial flood water did not have high concentrations of suspended solids. Suspended solids concentrations had increased by day 6 as flood water was mixed into the water column, then decreased.

Changes in dissolved nutrient concentrations over the sampling period are shown in Figure 5.4. These concentrations are relatively high compared to mean concentrations previously recorded at inshore stations; NO_3 - 0.26 uM, PO_4 - 0.2 uM (Walker and O'Donnell 1981), NO_3 - 0.5 uM, NH_4 - 0.48 uM, PO_4 - 0.29 uM (Revelante and Gilmartin 1982). Concentrations of all nutrients increased until day 6, then decreased (Fig. 5.4). The concentrations of all nutrients except NH_4 were higher at high levels of suspended solids (Fig. 5.5). Overall, nutrient concentrations were not correlated with salinity. However, using measurements made on days 2 and 4 only, i.e. the period in which there was a less saline surface layer, nutrient concentrations, excepting NH_4, were negatively correlated with surface salinity (Fig. 5.6). Over the days 6-16, when the water column was more homogeneous, nutrient concentrations showed no clear relationship with salinity (Fig. 5.6). These correlations suggest that nutrients in river discharges were the major source of water column nutrients in Bowling Green Bay following cyclone Charlie.

Pre- and post-cyclone chlorophyll concentrations are shown in Fig. 5.3. Chlorophyll concentrations fall within the range for inshore surface chlorophyll concentrations (Fig. 2.4: 0.15-1.25 ug l^{-1}), and for depth integrated chlorophyll at inshore stations (Walker 1981: 0.21-1.76 ug l^{-1}, Wolanski and Jones 1981a: 0.31-1.77 ug l^{-1}, Sammarco and Crenshaw 1984: 0.40 - 1.00 ug l^{-1}). Data from Wolanski and Jones (1981a) represent a series of observations from three stations in Bowling Green Bay 7 km north of my station 1, sampled at weekly intervals for 9 months. Chlorophyll concentrations were less than 0.7 ug l^{-1} on 50% of occasions. Initial post-cyclone chlorophyll concentrations were almost four times higher than pre-cyclone samples, but there was little change over the next two weeks despite high nutrient levels (Fig. 5.3, Table 5.3). Over this period the water transparency in the bay decreased until day 6, then transparency increased, with concurrent increases in the chlorophyll concentration, and decreases in nutrient levels. This chain of events

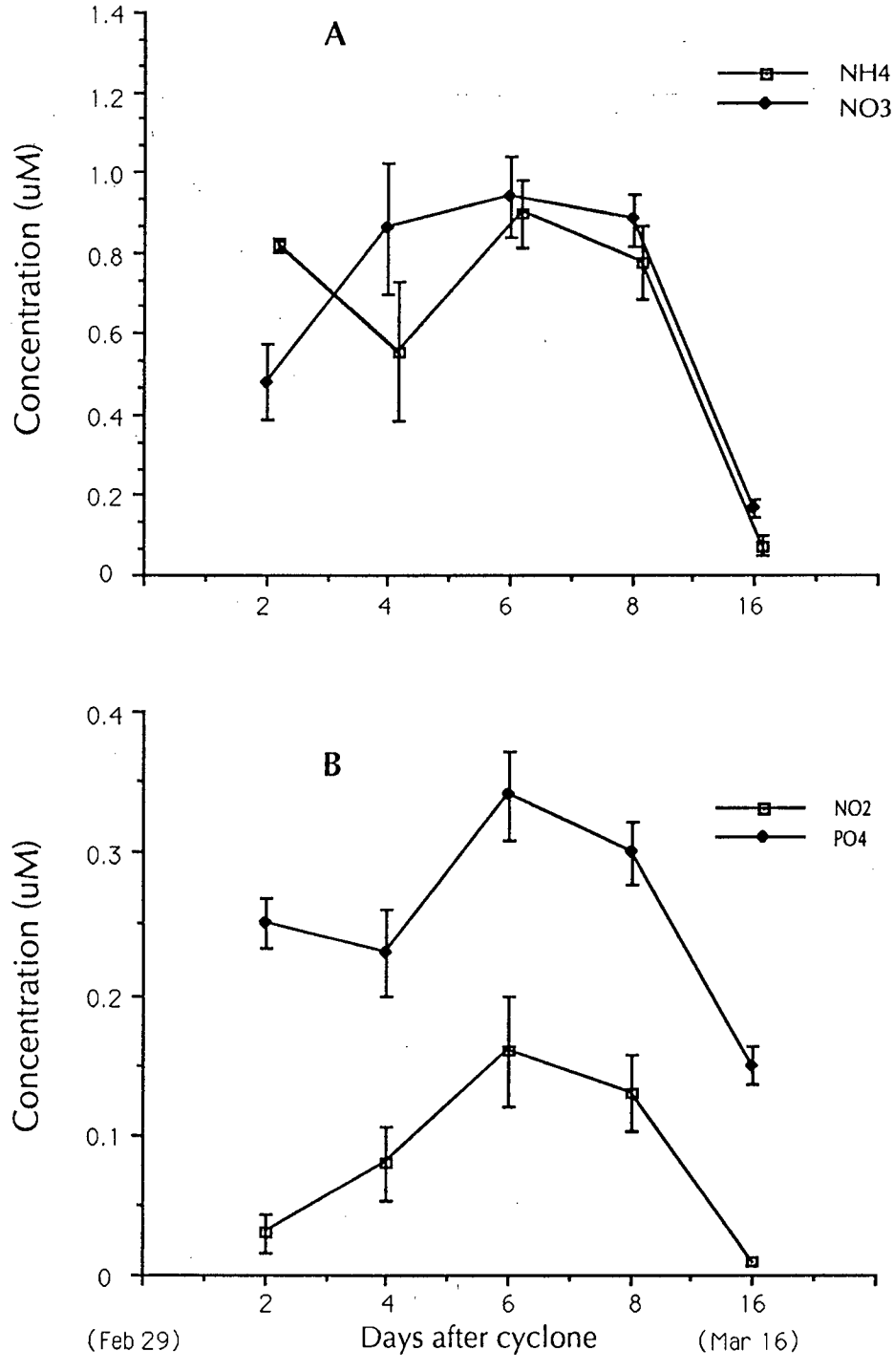


Figure 5.4. Water column nutrients in post-cyclone samples. A. Ammonia and nitrate, B. nitrite and phosphate. Concentrations are in micromolar. Error bars are one standard error.

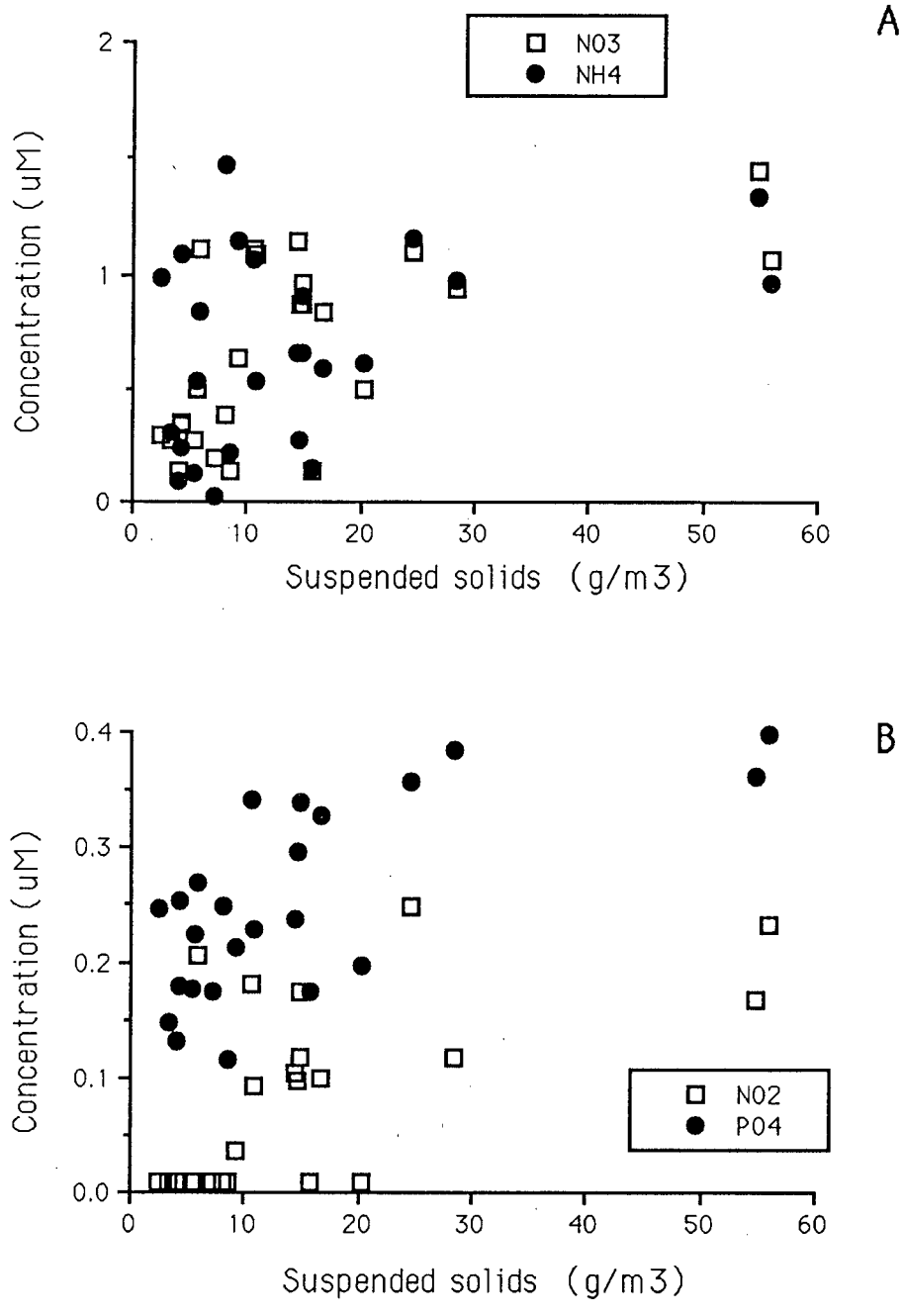


Figure 5.5. Plots of nutrient concentrations in the post-cyclone samples against near-bottom suspended solids concentration. **A**. NO_2 and NH_4, **B**. NO_2 and PO_4.

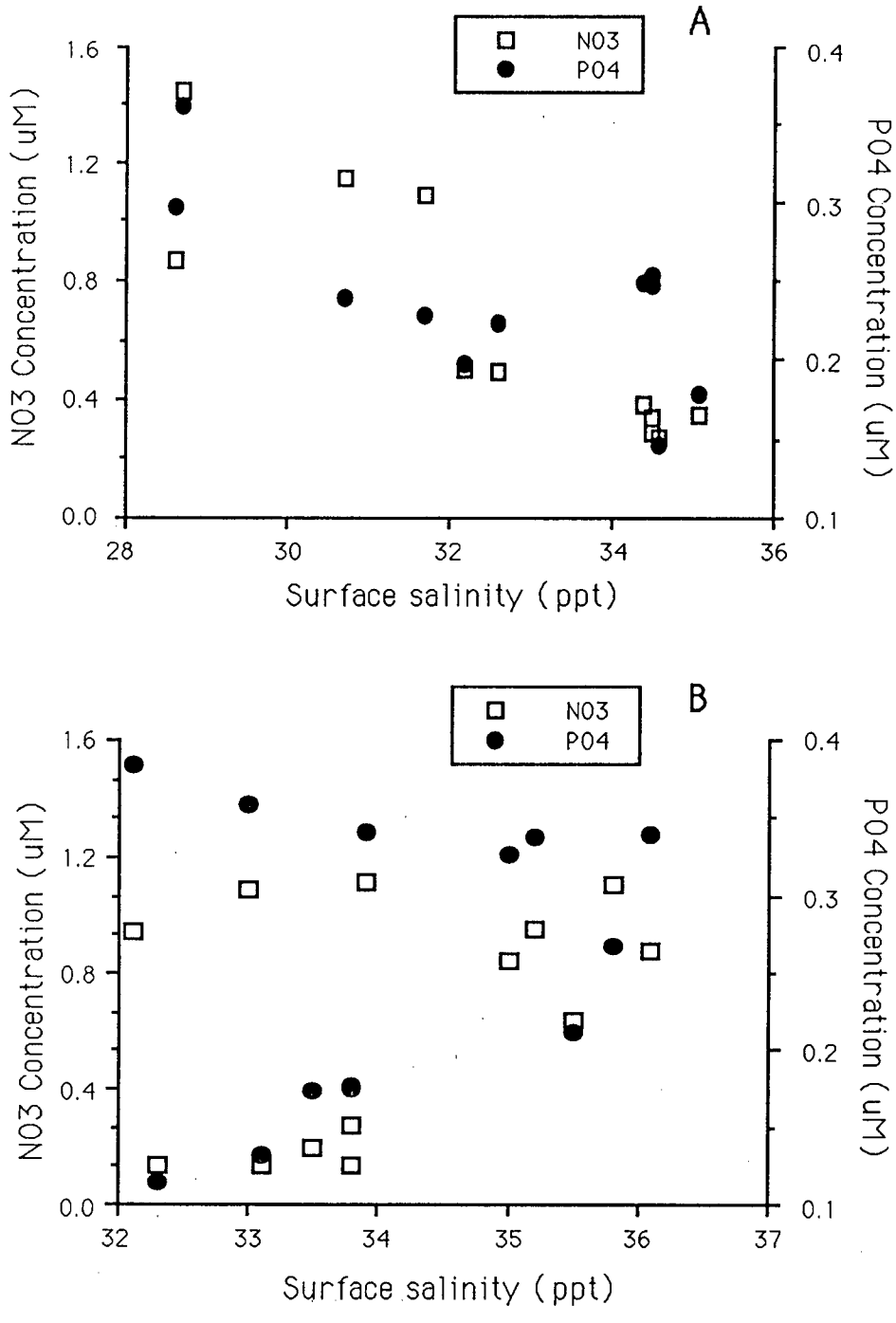


Figure 5.6. Plots of concentrations of NO_3 and PO_4 in post-cyclone samples against surface salinity. **A.** Samples taken on days 2 and 4. **B.** Samples taken on days 6-16.

Table 5.3

Analyses of variance on chlorophyll concentration (ug l^{-1}). The factors were: time-after-cyclone and station position (site). The first ANOVA was a two factor analysis and used only samples taken post-cyclone. The second ANOVA was one factor (time) and included both pre- and post-cyclone samples. There was no interaction term or test for homogeneity of variance in the two way ANOVA as there was only one observation per cell. The transformation appropriate for the one way ANOVA was applied also to the two way ANOVA. NS = not significant.

Chlorophyll concentration: Two factor, post-cyclone samples

	DF	Mean square	F ratio	Probability
Time	4	0.0744	4.86	< 0.01
Site	4	0.0068	0.45	NS
Error	16	0.0153		

Chlorophyll concentration: One factor, pre- and post-cyclone samples

	DF	Mean square	F ratio	Probability
Time	5	0.3958	26.3	< 0.01
Error	24	0.0151		

Data square root transformed, Cochran's C = 0.3397, P < 0.05

Contrasts between means by Tukey test:

	Pre-	Day 2	Day 8	Day 6	Day 4	Day 16
Mean	0.26	0.91	1.23	1.25	1.42	1.67

suggests that phytoplankton biomass had been nutrient limited up to day 2, then light limited from days 2 - 6. There was no significant difference in chlorophyll concentration between sites (Table 5.3).

Over 52 zooplankton taxa were encountered in samples (Tables 5.1, 5.2) with the ten most numerous taxa comprising around 70% of animals. The most common taxa were herbivores; the copepods *Paracalanus indicus* and *Acrocalanus gibber*, and larvaceans (Tables 5.1, 5.2). However carnivores; chaetognaths and the copepods *Oncaea conifera* and *Corycaeus* spp. were also relatively numerous. The species composition in these samples was similar to that of inshore samples described in chapter 4, i.e. a community numerically dominated by herbivores, primarily *Paracalanus* spp. One difference between the zooplankton in Bowling Green Bay samples and other inshore samples (chapter 4) was the abundance of *Oncaea conifera* and *Corycaeus lubbocki*. These species were common in inshore samples but were not as abundant as in Bowling Green Bay samples. Zooplankton abundance changed little over the first eight days after the cyclone, then increased twofold by day 16 (Fig. 5.7, Table 5.4). Zooplankton biomass changed in a similar manner. Biomass of zooplankton in samples up to day 8 did not differ from the zooplankton biomass in pre-cyclone samples, with biomass on day 16 four times higher (Fig. 5.7, Table 5.5).

An ordination of the samples by metric multidimensional scaling represented the affinity between samples in a two dimensional space (stress = 0.15). Stations fell into three groups (Fig. 5.8); comprised of pre-cyclone samples (groups A), most post-cyclone samples (group B) and three of the day 16 samples (group C) respectively. Within group B, samples on the same transect did not form distinct sub-groups (Fig. 5.8) indicating that temporal change in the zooplankton community from days 2 - 8 was small. Post-cyclone samples taken on the same station over the successive transects also did not group together, indicating that the zooplankton community was coherent within Bowling Green Bay (34 km), but changed over the time scale of the sampling (2 weeks).

Pre- (group A) and post-cyclone (group B) samples were primarily distinguished by absolute abundances of most taxa. Abundances of most taxa, including gastropod and bivalve veligers which reached a peak in abundance on day 8, were higher in group B. Group C, containing three of the day 16 samples, had the highest abundances of many taxa, particularly the more numerous copepods; *Paracalanus indicus, Acrocalanus gibber, Acartia pacifica, Oncaea conifera* and *Calanopia elliptica.*

As the pre-cyclone samples were from sites different from those sampled after the cyclone, it is important to determine which was responsible for the division of

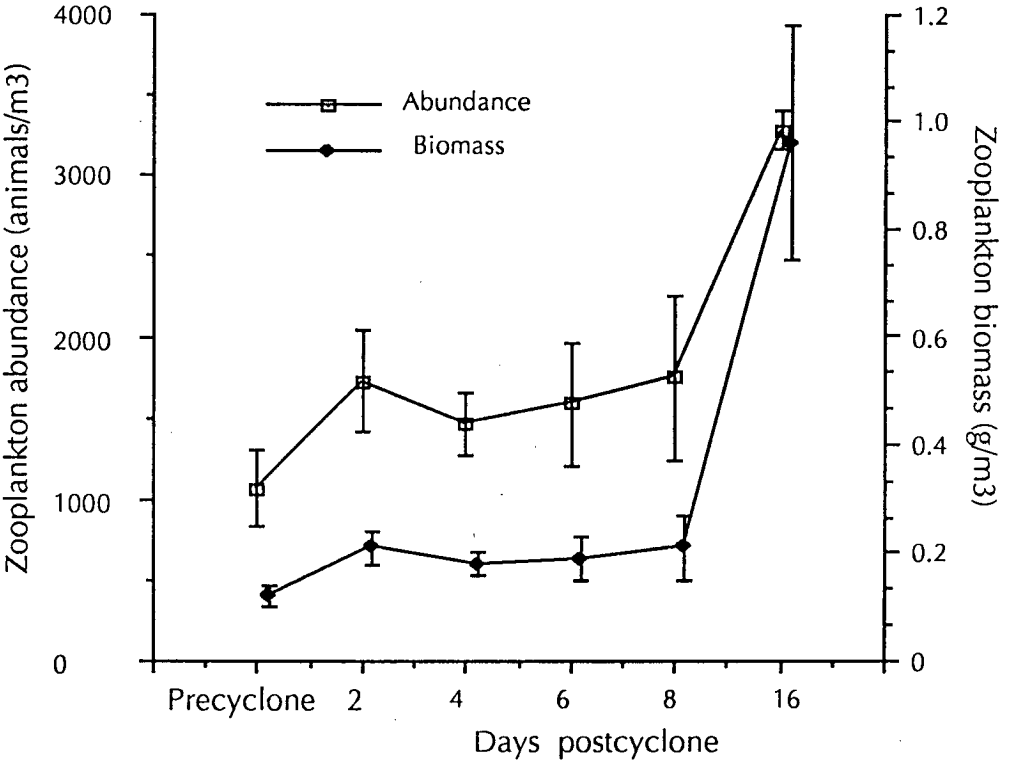


Figure 5.7. Zooplankton abundance and biomass in pre- and post-cyclone samples.

Table 5.4

Analyses of variance on zooplankton abundance (animals m^{-3}). The factors were: time-after-cyclone and station position (site). The first ANOVA was a two factor analysis and used only samples taken post-cyclone. The second ANOVA was one factor (time) and included both pre- and post-cyclone samples. NS = not significant.

Zooplankton Abundance: Two factor, post-cyclone samples
Data log(x+1) transformed, Cochran's Q = 0.686, P > 0.01.

	DF	Mean square	F ratio	Probability
Time	4	0.256	9.551	< 0.01
Site	4	0.010	0.360	NS
Time x Site	16	0.087	3.253	< 0.01
Error	26	0.027		

One factor, pre- and post-cyclone samples
Data untransformed, Cochran's C = 0.340, P < 0.05.

	DF	Mean square	F ratio	Probability
Time	5	5.111E+06	5.19	< 0.01
Error	49	9.847E+05		

Contrasts between means by Tukey test: Organisms m^{-3}

	Pre-	Day 2	Day 4	Day 6	Day 8	Day 16
Mean	1123	1737	1464	1589	1752	3285

Underline indicates no significant differences between means.

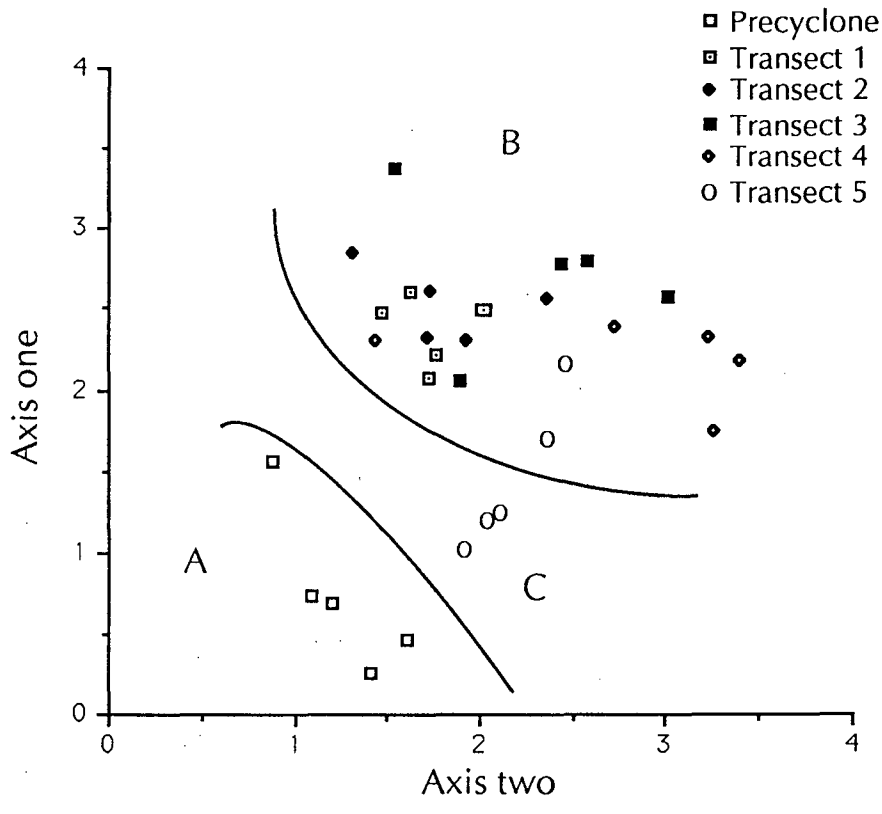


Figure 5.8. Plot of the two vectors from the ordination of samples. The three groups identified by letters are described in the text.

samples in the ordination. If the species composition of the pre-cyclone samples differed from post-cyclone samples, these samples may have come from a different habitat, and so the available pre-cyclone samples would provide a questionable baseline for post-cyclone changes. Taxa which had the greatest influence on the ordination, as indicated by their Cramer scores (Belbin **et al.** 1984), were present in all three sample groups, distinguishing sample groups by relative changes in abundance, not presence-absence. This suggested that all the samples came from a similar habitat, and that comparisons of pre- and post-cyclone samples provides a valid indication of cyclone induced change.

The rank order of zooplankton taxa from each sample was compared to that of all other samples by a Kendall concordance test to provide a further test of changes in community structure between the pre- and post-cyclone samples. There was no significant difference in rank order between samples ($p < 0.01$), confirming that there had not been major changes in the relative abundance of taxa.

Changes in the functional composition of the zooplankton community were explored by assigning taxa to one of three groups; herbivore, omnivore and carnivore, based on analysis of mouthparts and gut contents (Itoh 1970, Timonin 1971, Longhurst 1983; Tables 5.1, 5.2). Abundances of zooplankton belonging to each group were summed and plotted against time after cyclone (Fig. 5.9). All three groups showed an increase by day 16 (Fig. 5.9), and the ratio of carnivores to herbivores remained constant over the sampling period.

DISCUSSION

It is important to consider whether changes in Bowling Green Bay plankton reflect temporal changes in the plankton communities within the bay, or the advection of different communities into the sampling area. Both hydrodynamic modelling studies (Stephen Gay, unpublished data) and current meter data (Andrews and Furnas 1986) suggest that advection over the post-cyclone period may have ranged up to 60 km, potentially confounding temporal changes in plankton communities with spatial differences. On the other hand, the oceanographic effects of the cyclone extended over a much greater area than Bowling Green Bay, as the cyclone re-crossed the coast 80 km south of Cape Bowling Green (Fig. 5.1), and inshore plankton communities were likely to have been similarly affected throughout this region.

Chlorophyll concentration in samples taken 2-16 days following the cyclone differed little. Evidence for cyclone-caused changes in phytoplankton biomass arise largely from comparison of pre- and post-cyclone chlorophyll concentrations. Pre-cyclone concentrations were low compared to concentrations measured at inshore

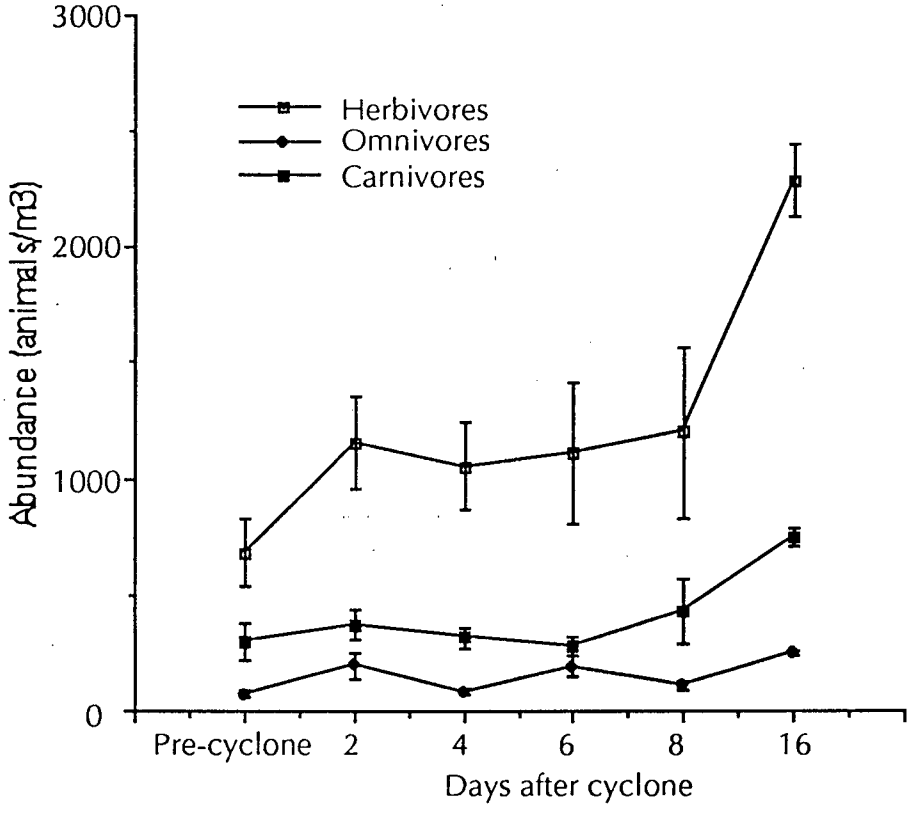


Figure 5.9. Abundance of the three functional groups of zooplankton over the sampling period. Error bars are one standard error.

stations on other occasions, e.g. 0.31-1.77 ug l^{-1} (Wolanski and Jones 1981), though still within that range. Post-cyclone chlorophyll concentrations were also within this range, indicating that, although the cyclone appeared to have affected chlorophyll concentrations, its effects were no greater than those of other coastal processes. The pre- to post-cyclone change in Bowling Green Bay chlorophyll concentrations was comparable to storm induced changes in inshore waters in temperate regions (Zubkoff and Warinner 1977, Loftus and Seliger 1977) and elsewhere on the Great Barrier Reef (Furnas 1989).

The increase in chlorophyll concentrations in Bowling Green Bay was associated with higher concentrations of dissolved nutrients, as found in other inshore areas after storms (Zubkoff and Warinner 1977). Nearshore changes in nutrients off South Carolina after tropical storm Dennis were linked to rainfall, and Zeeman (1985) concluded that river outflow was the source. Within Chesapeake Bay the large nutrient increases measured after tropical storm Agnes were also attributed to river outflows (Loftus and Seliger 1977).

On the GBR shelf, floods (Wolanski and Van Senden 1983) and resuspension of bottom sediment (Walker and O'Donnell 1981, Ullman and Sandstrom 1987) are thought to be important sources of nutrients in inshore waters. Results from this study suggest that river discharges were the most important source of nutrients in inshore waters after cyclone Charlie, but the evidence was not unequivocal.

Although the changes in zooplankton abundance and biomass after the cyclone were marked, it is useful to compare these levels with those from other inshore areas to evaluate the potential importance of the post-cyclone changes in the context of the normal inshore variability in zooplankton numbers and biomass. Data from other inshore stations is presented in Table 5.6.

Zooplankton biomass in the samples collected 16 days after the cyclone was higher than that in any of the other groups of samples, but only slightly higher than that measured in samples taken in Cleveland Bay, a bay adjacent to Bowling Green Bay (Ikeda **et al.** 1980). The mean copepod abundance in Cleveland Bay was higher than those recorded after the cyclone. These comparisons indicate that although there was a clear change in both zooplankton abundance and biomass in Bowling Green Bay after cyclone Charlie, these increases fell within the range of values that may occur in the absence of cyclones. The Cleveland Bay samples were taken over the period of a year, and high copepod abundances and biomass in samples were associated with lower salinity and increased river discharge from the nearby Burdekin River (Sammarco and Crenshaw 1984). This relationship was attributed by Sammarco and Crenshaw (1984) to a nutrient enrichment of inshore waters by river

Table 5.5

Analyses of variance on zooplankton biomass (wet weight m^{-3}). The factors were: time-after-cyclone and station position (site). The first ANOVA was a two factor analysis and used only samples taken post-cyclone. The second ANOVA was one factor (time) and included both pre- and post-cyclone samples. NS = not significant.

Zooplankton biomass: Two factor, post-cyclone samples

Data log(x+1) transformed, Cochran's C = 0.331, P < 0.05.

	DF	Mean square	F ratio	Probability
Time	4	0.0308	48.31	< 0.01
Site	4	0.0012	1.94	NS
Time x Site	16	0.0034	5.30	< 0.01
Error	26	0.0006		

One factor, pre- and post-cyclone samples

Data log(x+1) transformed, Cochran's C = 0.758, P < 0.05.

	DF	Mean square	F ratio	Probability
Time	5	0.02487	15.90	< 0.01
Error	49	0.00156		

Contrasts between means by Tukey test: Weight in g m^{-3}

	Pre-	Day 2	Day 4	Day 6	Day 8	Day 16
Mean	0.049	0.042	0.036	0.039	0.042	0.164

Underline indicates no significant differences between means.

Table 5.6

Comparison of the means and ranges of copepod abundances (no. m^{-3}) and wet weight (g m^{-3})measurements from four comparable coastal areas. Inshore samples (this study) were collected by pump sampling, all other samples were collected by vertical net tows. Samples were collected on similar size mesh (200 um this study, 205 um Ikeda **et al.** 1980). Wet weights determined in a similar manner in both studies.

	Copepods		
	Number	Mean	Range
Inshore (this study)	17	544.4	31 - 1706
Cyclone Charlie (Days 2 - 8)	40	1069.5	145 - 3687
Cyclone Charlie (Day 16)	10	2449.8	1641 - 3328
Cleveland Bay Ikeda **et al.** 1980, Stn. 1	44	2881.1	167 - 7697

	Wet Weight		
	Number	Mean	Range
Inshore (this study)	17	0.242	0.03 - 0.634
Cyclone Charlie (Days 2 - 8)	40	0.098	0.03 - 0.29
Cyclone Charlie (Day 16)	10	0.482	0.2 - 1.06
Cleveland Bay Ikeda **et al.** 1980, Stn. 1	44	0.301	0.001 - 1.622

discharge. As river discharges appear to have an important enriching effect on coastal GBR waters (Wolanski and Jones 1989b), it is not surprising that large river discharges, both as a result of cyclones and at other times, produce similar changes in the inshore zooplankton. No major flooding occurred during the period over which other inshore samples were collected (Table 5.6), which may explain their relatively low zooplankton biomass and copepod abundance.

The importance of the zooplankton changes in this study is that they illustrate the link between phytoplankton and zooplankton biomass and abundance in inshore waters. The increase in zooplankton abundance and biomass following the increase in chlorophyll concentration suggests that inshore herbivorous zooplankton are food limited. Laboratory studies have demonstrated that growth rates of zooplankton herbivores can be food limited (Mullin and Brooks 1976, Checkley 1980), but under field conditions the growth rates of copepods may be temperature dependent and food independent (McLaren 1978). Longhurst (1983) suggested that in the tropics there is a fundamental difference between oceanic and continental shelf waters in the extent to which zooplankton are food limited. On continental shelves phytoplankton production may be underutilized by herbivores (Longhurst 1983, Walsh 1988), whereas in oceanic ecosystems production and consumption are in a closer balance (Heinrich 1977, Joiris **et al.** 1982). The tropical shelves examined by Longhurst (1983) and Joiris **et al.** (1982) were both affected by upwelling or by large riverine exports of organic material, while the GBR shelf is not. In this regard, planktonic ecosystems on the GBR may have greater similarity to those in oceanic water than to other tropical shelves.

An alternative explanation for the increase in herbivorous zooplankton is that predator numbers were reduced by storm disturbance. Larger predators, including larval and adult fish, which can be a important predator on herbivorous copepods (Longhurst and Pauly 1987), were not collected quantitatively by the sampling techniques used here, so changes in their abundance are not known. Mullin **et al.** (1984) found that larval fish abundance decreased following a storm off California, even though copepod nauplii, a food source, increased. They attributed this change to starvation of the larval fish when previously concentrated copepod nauplii were dispersed throughout the water column by the storm. This scenario is not applicable to Bowling Green Bay as it is rarely stratified. It appears more likely that zooplankton increased in abundance after the cyclone because of an increase in the food available.

This natural experiment allows a first order estimation of the time the phytoplankton community in inshore GBR waters takes to respond to changed

conditions. Phytoplankton in tropical waters can rapidly increase with communities capable of doubling more than twice a day (Furnas 1990). Accordingly, the difference between pre-cyclone chlorophyll concentrations and those immediately after the cyclone indicate a rapid response to the higher nutrient levels. Chlorophyll concentrations increased only slightly over the subsequent two weeks despite continuing high concentrations of dissolved nutrients. Over this period the water was turbid, and phytoplankton biomass may have been light limited, prolonging the cyclone induced phytoplankton bloom until water clarity increased.

The response time of the zooplankton community to a change in conditions can also be estimated. The zooplankters that numerically dominated the inshore zooplankton increased significantly in abundance within the two week sampling period. Studies on individual tropical zooplankton species have shown that populations can increase rapidly (LeBorgne 1982; LeBorgne and Moll 1986), but little is known of how fast the zooplankton community as a whole can increase under natural conditions. Comparison can be drawn with enclosure experiments where chlorophyll concentrations may peak 2-4 days after nutrient enrichment, and herbivorous copepod numbers peak within 15-20 days (Mullin and Evans 1974, Harris **et al.** 1982, Alcaraz **et al.** 1988). Changes in phytoplankton and zooplankton in Bowling Green Bay are commensurate with these times, even though water temperatures in enclosure experiments were much lower (15-24°C) than in Bowling Green Bay (26-27°C).

It should be noted that although mean abundance of adult copepods in Bowling Green Bay increased twofold in two weeks after the cyclone, this does not necessarily indicate that this increase was generated by an increased egg production and growth through to adult copepods within this period. As a 200 um net was used, nauplii and copepodites were not collected quantitatively, and were not included in the counts of copepod abundance. Consequently, an increase in copepod abundance would be recorded if the percentage of copepodites surviving to become adults increased, change that could occur in days only , in contrast to one to two weeks for the growth from egg to adult for tropical copepods (Paffenhoffer and Harris 1979). The extent of observed increase in copepod abundance is therefore biologically possible. A similar argument can be applied to other zooplankton taxa.

The implications of these response times is that in the GBR zooplankton biomass can "track" (Harris 1986) phytoplankton biomass with time lags of 1-2 weeks, and that nutrient enrichment of inshore waters can produce a rapid ecosystem response, extending at least as far up the food web as the zooplankton.

The ordination analysis showed that little change occurred in zooplankton community structure over the sampling period. This is hardly surprising considering the processes that effect community change and the time scales they operate over. Community structure can be affected by competitive exclusion of taxa, by selective predation, or by differential ability of the zooplankton to survive changes in the physical or chemical environment, i.e. disturbance (Huston 1979, Sih **et al.** 1985). An increase in selective mortality by either an increase in predation or by disturbance could theoretically affect community structure in a relatively short time. Predation, at least in the mesozooplankton size category, did not change as carnivore numbers changed commensurately with those of herbivores. Disturbance mediated mortality also appeared to be unimportant at the community level as none of the numerically dominant zooplankters decreased in abundance after the cyclone. Competitive exclusion of taxa, the third major process affecting community structure, may take many generations to change community structure (Caswell 1978).

SUMMARY

Following the passage of cyclone Charlie there were significant changes in inshore water column conditions, zooplankton biomass and zooplankton abundance. Nutrient concentrations rose to levels 2-4 times higher than those measured at other nearby inshore stations. The changes in nutrient concentrations over the post-cyclone period appeared to be more the result of sediment resuspension than flood outflows of nutrient enriched water. Chlorophyll concentrations increased fourfold over pre-cyclone concentrations, though they remained within the range of concentrations measured at inshore stations unaffected by cyclones. Zooplankton abundance and biomass increased fourfold within two weeks of the passage of the cyclone, though this change also fell within the range of abundance and biomass recorded at other inshore stations.

Changes in the chlorophyll concentrations followed by changes in zooplankton abundance suggested that inshore zooplankton were food limited. The changes in plankton in Bowling Green Bay also give an indication of the time plankton take to respond to changed conditions. Chlorophyll concentrations changed within two days of the passage of the cyclone, and zooplankton abundances within two weeks. Cyclone initiated changes to the plankton may have long term ramifications in other parts of the ecosystem, as the recruitment of animals such as starfish larvae (Lucas 1982) and fish larvae (Lasker 1981, Kiorboe **et al.** 1988), can depend on plankton abundance. By influencing survival of larval or juvenile animals the planktonic changes effected by cyclones may have long-term consequences for the benthic and

pelagic fauna.

Chapter 6. Conclusion

This investigation sought to quantify the spatial variability of phytoplankton biomass, zooplankton biomass and zooplankton community structure in the GBR over a range of spatial scales, and to investigate the covariability of phytoplankton and zooplankton over these scales. It also sought to identify effects of the geographical structure of the GBR on plankton spatial variability. Here I wish to draw together the findings of this study using the questions detailed in chapter one as a framework.

1. What is the variability of phytoplankton biomass on the GBR shelf over spatial scales ranging from 30 m to 1200 km?
2. Does the spatial pattern of phytoplankton biomass vary in relation to the marked cross-shelf and latitudinal changes in reef density on the GBR shelf?
3. Do zooplankton form recurrent assemblages, and do these assemblages correspond to different parts of the GBR; e.g. reef matrix versus lagoon, open reef matrix versus dense reef matrix?
4. Are the patterns of zooplankton community structure and phytoplankton biomass similar, i.e. can the zooplankton community structure be related to phytoplankton biomass or its spatial variability?
5. Can the abrupt effects of a cyclone on inshore waters be used to assess the effects of changes in physical and chemical water variables on phytoplankton biomass, and ultimately on the zooplankton biomass and assemblage structure?

The spatial variability of surface chlorophyll was investigated using two approaches. Firstly, spatial variability in chlorophyll concentration was measured at two discrete length scales, local and regional, to allow comparisons of chlorophyll spatial variability in different parts of the GBR. Secondly, the distribution of the spatial variability of surface chlorophyll over a continuum of spatial scales was compared from one region to another.

Chlorophyll spatial variability was quantified and compared at the regional scale by regional differences in mean chlorophyll concentration, and a local scale by the chlorophyll coefficient of variation within 8 km subtransects. At the regional scale there was a consistent cross-shelf pattern; highest chlorophyll concentrations inshore and lowest in the Coral Sea with little difference in chlorophyll concentration between the GBR lagoon and outer shelf reef matrix. Cross-shelf gradients in chlorophyll concentration with a similar trend occur on other tropical (Walsh **et al.** 1980) and temperate (Joiris **et al.** 1982) shelves. However, the GBR shelf differs markedly

from all other continental shelves in the extent and number of islands and reefs that comprise its barrier reef. Around islands and reefs elsewhere nutrient and chlorophyll concentrations can be elevated in their vicinity; the "island mass effect". Yet on the GBR the numerous reefs appeared to have little affect on the chlorophyll concentration as the cross-shelf chlorophyll gradient did not differ from gradients on less structurally complex shelves.

Gilmartin and Revelante (1974) found higher nutrient and chlorophyll concentrations in inshore waters around the Hawaiian Islands, though stations with higher chlorophyll concentrations attributed to an "island mass effect" were mostly within 1 km of the coast. Similar effects have been observed in the Canary Islands (Hernandez-Leon 1988), Barbados (Sander 1981), Marion Island in the South Indian Ocean (El-Sayed **et al.** 1979), and the Scilly Islands (Simpson **et al.** 1982). In shallower waters the effect can be extensive. The Scilly Isles in the Celtic Sea produce elevated surface chlorophyll concentrations as far as 25 km from the islands, and change chlorophyll concentrations over an area 20 times that of the islands (Simpson **et al.** 1982). In contrast an "island mass effect" was not seen around Mare Is., New Caledonia (Le Borgne et al. 1985), or Mururoa atoll (Bourret et al. 1979)

This discrepancy can be partly resolved by the variety of causative mechanisms of the "island mass effect" which may not apply to all situations. Mechanisms include enhanced vertical mixing (Simpson **et al.** 1982), terrestrial run-off or seepage (Le Borgne **et al.** 1985), vertical mixing in island channels (Gilmartin and Revelante 1974), and eddies and upwelling on the leeward side of islands (Hernandez-Leon 1988).

Wakes and eddies have been recorded behind reefs and islands on the GBR shelf (Hamner and Hauri 1981, Wolanski **et al.** 1984), and can generate sufficient vertical mixing to scour sediment (Wolanski **et al.** 1984). As the wakes that have been observed on the GBR shelf can extend one to three times the size of the reef (Wolanski **et al.** 1984), where the reef matrix is dense much of the outer shelf may be covered by a complex of wakes from the many reefs.

However, the process that underlies the most of these "island mass effect" mechanisms is a vertical mixing of nutrient rich sub-thermocline waters by the modified currents around islands. On the GBR shelf stratified conditions with a nutrient rich sub-thermocline layer occur infrequently. Terrestrial run-off may produce an "island mass effect" on GBR islands, but not on the far more numerous reefs. The absence of a marked "island mass effect" on the GBR shelf can be attributed to the absence of the necessary water column conditions.

An alternative "island mass effect" mechanism is possible on the GBR shelf, when waters near reefs are enriched by nutrients or phytoplankton flushed from reef lagoons. Le Borgne **et al.** (1985) attributed the elevated chlorophyll concentrations off the New Caledonia barrier reef to this mechanism. There the off-reef chlorophyll gradient was small but was detectable at a distance of 18 km offshore. There were sharp changes in chlorophyll concentration close to individual reefs on the GBR and within subtransect variability was highest in these places, suggesting that phytoplankton or nutrients are being flushed out of individual reef lagoons by currents. This effect appeared to be quite localized, and even in those parts of the GBR where the reef matrix is composed of large and closely spaced reefs, e.g the northern zone, did not have a discernible effect on the regional chlorophyll concentration. However, in the Pompey zone, where reefs are both large and densely packed along the edge of the shelf, chlorophyll concentrations were higher in the reef matrix than on the inner shelf. The combination of very large reef surface areas, being swept by the strong tidal currents that occur in this zone (Maxwell 1968) may have influenced the chlorophyll concentrations in these outer shelf waters as a whole. Overall, the slight nature of the "island mass effect" on the GBR shelf is comparable with that reported by Le Borgne **et al.** (1985) off the New Caledonia barrier reef.

The second approach to quantifying chlorophyll spatial variability was to quantify variability over a continuum of spatial scales using spectral analysis. Spectral analysis characterised chlorophyll variability over spatial scales 0.5-10 km, and over these scales chlorophyll spatial variability showed a similar distribution in all cross-shelf and long-shelf regions of the GBR. Despite the considerable structural differences in the regions surveyed, from the reef matrix to the Coral Sea, the distribution of chlorophyll concentration across spatial scales changed only slightly. Two possibilities can be considered. First, that the horizontal spatial distribution of chlorophyll over the scales observed is not significantly affected by the presence of reefs and coastal features. This would seem unlikely as wakes and eddies have been documented around a number of reefs and islands on the GBR shelf (Hamner and Hauri 1977, Wolanski **et al.** 1984), and higher chlorophyll variability near reefs was detected in this study by other techniques. Alternatively, spectral analysis may be unsuited to detect the type of horizontal spatial structure in chlorophyll concentration that occurs on the GBR shelf. The changes in small-scale chlorophyll variability that occurred close to individual reefs was limited in its extent (<15 km from reef). The infrequent intersection of the higher areas of chlorophyll variability close to reefs appears to have precluded these features from affecting the chlorophyll spectra. Spectral analysis can be concluded to be a less appropriate technique for characterising

the chlorophyll spatial variability found on the GBR shelf than the techniques quantifying variability at discrete scales such as used in chapter two.

The distribution of zooplankton biomass and changes in community structure were characterised to allow comparisons between different parts of the GBR shelf, and with the distribution of the chlorophyll concentration. Zooplankton taxa fell into three assemblages, which were dominated by small herbivorous copepods, omnivorous copepods and small carnivorous copepods, respectively. The herbivorous copepod dominated assemblage occurred consistently in inshore waters, the omnivore assemblage in reef matrix waters, and the carnivore assemblage at the shelf edge. This cross-shelf pattern in zooplankton assemblages was found in three of the four latitudinal zones, but not in the Pompey zone in which the herbivore assemblage was abundant on the outer edge of the reef matrix. Paralleling the cross-shelf assemblage change were changes in zooplankton biomass and numerical abundance. Both were high in inshore waters, intermediate across the rest of the shelf, and low in Coral Sea waters. The similarity of zooplankton species composition in samples collected over different spatial separations indicated that the similarity of samples within each cross-shelf band changed little at separations up to 100 km. Differences in zooplankton species composition were more marked when comparing samples from different cross-shelf bands. Change in zooplankton community structure therefore corresponded to bathymetric features on the GBR shelf, and communities had cross-shelf dimensions of 10's of km, and long-shelf dimensions of 100's of km.

Water masses on the GBR shelf are generally well mixed therefore it is unlikely that such cross-shelf changes were the result of the mixing of water masses with different zooplankton communities. Furthermore, zooplankton community structure showed quite a different regional pattern to that of chlorophyll. Whereas both regional mean concentrations and regional subtransect variability of chlorophyll did not differ between the inner and outer shelf, zooplankton community structure was distinctly different. Such differences suggest that the GBR reef structure and in particular the reef matrix may have influenced zooplankton distributions.

The "island mass effect" discussed earlier in the context of nutrient and chlorophyll enrichment can also have repercussions at higher trophic levels with changes to zooplankton (Sander and Steven 1973, Roger 1986, Hernandez-Leon 1988). As a result of the longer generation times of zooplankton, changes to zooplankton communities may be apparent further downcurrent than those to phytoplankton, e.g. Peterson **et al.** (1979). Change in the zooplankton community may also persist longer than an ephemeral chlorophyll enrichment. In the Canary

Islands zooplankton biomass changes associated with an "island mass effect" lasted longer than the seasonal chlorophyll enrichment (Hernandez-Leon 1988). It is therefore possible that the localized variability in chlorophyll concentration around reefs as a result of flushing of reef waters into inter-reef areas might have a more spatially extensive effect on the zooplankton community. This possibility will depend on zooplankton generation times and and the distance they would be advected in this time. Studies of advection on the GBR shelf indicate that neutrally buoyant particles can be advected from reef to reef relatively quickly. Coral eggs released at Bowden Reef reached downcurrent reefs within a few days (Wolanski **et al.** 1989). Parslow and Gabric (1989) modelled diffusion and advection on the GBR shelf and found that a point release of material would expand to create a patch 20 km in diameter in 15-20 days. Taking 15 days as an estimate of copepod generation times in tropical waters (Paffenhoffer and Harris 1979), zooplankton could easily be advected to the next reef downcurrent (often < 20 km) within their lifetime. Zooplankon that grow in a chlorophyll enriched area close to a reef, could be advected to downcurrent reefs, effecting a change in zooplankton community that extended throughout the reef matrix. As long-term currents in both the reef matrix and the inner shelf run parallel to the north-south axis of the shelf (Williams **et al.** 1984, Wolanski and Pickard 1985), a reef matrix "island mass effect" on zooplankton will tend to be confined to the reef matrix.

An alternative mechanism whereby reefs on the outer shelf influence the zooplankton community is through the flushing of reef zooplankton out of reef lagoons and into the inter-reef shelf waters. If this is an important process, there should be greater similarities between reef zooplankton and reef matrix (outer shelf) zooplankton assemblages, than between reef matrix and inner shelf zooplankton. This was not the case, reef-associated zooplankton assemblages were quite distinct from both reef matrix and inner shelf zooplankton assemblages. In the reef lagoon surrounding Heron Is., Queensland, the surface copepod fauna differed markedly in composition from samples taken 300 m from the island; changing from a monstrilloid dominated assemblage on the reef to a calanoid dominated assemblage offshore (Sale et al. 1976). Similar differences between open-water and reef-associated zooplankton assemblages have been found on other reefs in the GBR (e. g. Davies Reef - Roman **et al.** 1990, Hamner **et al.** 1988). The reason why a distinct reef zooplankton fauna exists can help to explain why the reef matrix community is not composed of more zooplankton exported from reefs. The reef zooplankton community is comprised of a high proportion of demersal species (Alldredge and King 1977, Roman **et al.** 1990), as most open-water zooplankton advected onto reefs

are removed from the water column by intense predation (Hamner **et al.** 1988). Reef zooplankton species are believed to maintain their position and counter advective effects by schooling and migratory behaviour (Sale et al. 1976, Hamner and Carleton 1979). Although passive particles, for example coral spawn (Wolanski **et al.** 1989) and presumably phytoplankton, appear to be readily flushed away from reefs and advected downcurrent, behavioural responses of reefal zooplankton act to maintain their association with a the reef (Sale et al. 1976, Hamner and Carleton 1979). This leads to the conclusion that the export of zooplankton from reefs has less effect on inter-reef zooplankton communities than the export of nutrient or chlorophyll enriched water.

An additional factor that could affect the distinctive reef matrix zooplankton community is a change in the degree or nature of the predation on zooplankton in reef matrix waters. The assemblage of zooplanktivorous fish on reefs does change cross-shelf. Williams and Hatcher (1983) recorded a higher biomass of zooplanktivorous fish on a mid-shelf than an inner shelf reef. However, without knowledge of pelagic planktivore populations, and of the dynamics of the zooplankton - planktivore relationship, it is not possible to say whether regional differences in the zooplankton community are caused by differences in the zooplanktivore community.

Neither the zooplankton abundance nor biomass of zooplankton (wet weight) in individual samples was significantly correlated with mean chlorophyll concentrations on the same subtransect, indicating that at this scale (up to 8 km) zooplankton abundance was not strongly linked with phytoplankton biomass. Even assuming that zooplankton abundance or biomass was food limited, a correlation at this spatial scale is unlikely in view of the differences in the time zooplankton and phytoplankton take to grow. Phytoplankton may be scarce where zooplankton are abundant because they have all been eaten (Rose and Leggett 1990), or phytoplankton and zooplankton peaks in biomass may be separated in space as a result of advection (Haury 1984).

At a regional scale, zooplankton biomass and zooplankton community structure showed a geographic pattern similar to that of the chlorophyll concentration, i.e. distinct cross-shelf changes and less distinct latitudinal changes. However, other variables, including temperature and salinity, show a similar regional pattern. The importance of phytoplankton biomass as an influence on the zooplankton community structure was considered in light of the existence of an atypical cross-shelf gradient in the chlorophyll concentration in the Pompey zone. This gradient was paralleled by an atypical cross-shelf zooplankton community structure in the same zone, suggesting that food supply was determining the distribution of the zooplankton assemblage dominated by small herbivores.

The apparent association between chlorophyll concentration and zooplankton biomass and community structure, was investigated more directly by observing the effect of a relatively abrupt increase in water column nutrients on phytoplankton and zooplankton in inshore waters following the passage of a cyclone. Nutrient concentrations in inshore waters reached levels 2-4 times concentrations recorded at other times (Walker and O'Donnell 1981, Revelante and Gilmartin 1982), and chlorophyll concentrations increased fourfold over pre-cyclone concentrations. Zooplankton abundance and biomass increased fourfold within two weeks of the passage of the cyclone. These changes supported the conclusion made from the more widespread observations of zooplankton and chlorophyll, that the abundance of inshore zooplankton was food limited. These changes also indicated that the phytoplankton and zooplankton communities could respond to changed conditions rapidly; the phytoplankton in days only, and the zooplankton in less than two weeks.

Finally, the variability of surface chlorophyll and zooplankton at local and regional scales can provide indications of the extent to which they are representative of samples collected in an area. Chlorophyll concentrations were markedly higher close inshore but varied little over large-scale regions. Within both the inner and outer shelf bands, chlorophyll concentrations in samples were relatively similar over large distances, and could be taken to be representative of the region in which they were collected. There were two important exceptions to this generalization. In both the northern and Pompey zones elevated chlorophyll concentrations which appeared to be associated with tidal currents were found directly behind the reef barrier. Secondly, chlorophyll concentrations close (10 km) to individual reefs were more variable than elsewhere within the reef matrix. The sharp chlorophyll gradients in these places would require more spatially intensive sampling to characterize the chlorophyll concentration.

Estimates of zooplankton biomass and numerical abundance had regional homogeneity similar to that of the chlorophyll concentrations; high levels near the coast, but relatively invariate over the rest of the reef. Zooplankton were numerically more abundant on the outer shelf in the Pompey zone than in the outer shelf band in other zones, and within this region more intense gradients in biomass and abundance occurred. As with the chlorophyll concentrations, more intense sampling woud be required to characterize the zooplankton biomass and numerical abundance in this region. In the rest of the reef matrix, zooplankton biomass did not show an increase close to individual reefs similar to that of the chlorophyll concentration.

Zooplankton community structure also changes cross-shelf. There appeared to be distinctive inner shelf and outer shelf assemblages, but within these cross-shelf

bands the assemblage was similar in composition over large distances. However, on one transect across the outer half of the reef matrix, the zooplankton in samples were more similar to Coral Sea zooplankton. Williams **et al.** (1988) also recorded Coral Sea zooplankton in the reef matrix in conjunction with a shelf-edge intrusion. During intrusions the boundary between the epi-pelagic zooplankton of the Coral Sea and those of the outer shelf appears to move from the shelf-edge to within the reef matrix.

There was also a marked difference between the inner shelf assemblage and the assemblage found close inshore by the post-cyclone Charlie sampling. Although these assemblages could not be directly compared as the zooplankton samples were collected by different techniques, Sammarco and Crenshaw (1984) also reported the existence of a distinctive coastal assemblage which extended a varying distance into the inner shelf dependent on river discharge. The largest changes in zooplankton biomass and assemblage encountered on the GBR shelf occur in these two boundary regions, inshore - inner shelf and Coral Sea - outer shelf. Careful spatial and temporal sampling is required to charactize the zooplankton in these areas.

In conclusion, this work has characterised the chlorophyll concentration and zooplankton biomass and abundance on the GBR over a range of spatial scales. Despite considerable structural differences in the GBR, both cross-shelf and long-shelf, chlorophyll concentrations were relatively homogeneous. Localized increases in chlorophyll concentrations were observed near individual reefs, but this phenomenon did not influence chlorophyll concentrations in the reef matrix as a whole. In contrast, the zooplankton assemblage changed cross-shelf in a manner which corresponded more closely to the cross-shelf change in reef structure, with distinct differences between GBR lagoon and reef matrix zooplankton assemblages. The abundance of herbivorous zooplankton, most numerous in inshore waters, was correlated with the level of phytoplankton biomass at both small and regional scales suggesting that this component of the zooplankton was food limited. The distinct zooplankton assemblage in the reef matrix was attributed to an 'island mass effect' in which the localized changes in phytoplankton biomass close to individual reefs had an influence on the zooplankton assemblage that extended throughout the reef matrix as a result of longer zooplankton generation times. These differences in zooplankton assemblage may have ramifications for higher trophic levels in the GBR pelagic ecosystem. The ecological consequences of the spatial differences in the zooplankton asemblages to higher trophic levels will depend on the extent to which planktivores are food limited, and behavioural and nutritional differences in the zooplankton species comprising the different assemblages.

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Sample	21	22	34	35	36	37	56	57	58
Latitude	19.0	19.0	18.8	18.8	18.8	18.8	19.0	19.0	19.0
Longitude	147.9	147.8	147.6	147.6	147.6	147.5	147.7	147.7	147.8
Decapod larvae			1.9		1.0			0.4	0.5
Brachyuran larvae	3.6		0.5	1.2			0.3		0.5
Luciferids									
Stomatopod larvae									
Siphonophores		1.1	0.5		0.5				0.5
Chaetognaths	20.9	27.5	4.8	8.8	7.3	5.3	0.6	1.1	21.3
Appendicularians	10.0	14.8	50.2		41.5	27.1	4.8	23.6	28.8
Polychaete larvae	11.8	3.2	4.3	2.4	2.4	3.0	1.0	0.7	4.3
Pteropods				0.6		0.8			0.5
Salps									
Echinoid larvae			0.5					0.4	
Fish larvae	4.5	3.2	1.4	0.6	1.0	1.5	1.0	0.7	3.3
Fish eggs			3.3	1.8	1.5		2.5	2.5	0.5
Mollusc larvae		2.1	2.4	1.2		4.5	4.5	0.4	
Cladocera					0.5	0.8		0.4	
Ostracods									
Acrocalanus gracilis	30.9	18.0	1.0	2.9	1.0	0.8	3.2	9.1	41.6
A. monachus									
A. gibber									
Clausocalanus spp.			0.5		1.0	0.8	0.3		
Paracalanus spp.	1.8	3.2	6.2	4.7	7.3	3.0		0.4	2.8
Calocalanus pavo	0.9	1.1	1.0			1.5	0.3		
Canthocalanus pauper						0.8			
Centropages orsinii	185.5	59.3	4.8	5.3	2.9	3.0	8.0	2.2	12.3
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta	1.8		1.0	1.2		0.8		0.7	
Undinula vulgaris	0.9				0.5		0.3		1.4
Temora stylifera									
T. turbinata									
Calanopia elliptica						0.3			
Eucalanus subcrassus									
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	67.3	46.6	1.9	4.1	3.4	7.5	0.6	0.7	1.4
A. negligens			1.9		0.5	4.5		0.4	
Oithona rigida	0.9	2.1	2.4	10.6	6.8	1.5	1.0	1.1	1.9
O. plumifera	2.7		2.4			6.0	0.6		0.9
O. spp. 1.8	5.3	9.6	14.7	14.6	31.6	3.2	2.9	2.4	
Corycaeus pacifica	4.5	1.1	1.4		4.9	3.0	1.0	0.4	0.9
C. (D) spp.	20.9	43.4	25.3	41.8	33.2	27.1	16.2	18.5	19.4
C. speciosus	0.9	1.1				1.5			2.8
C. lubbocki	9.1	21.2	4.3	13.0	6.8	10.5	3.8	6.2	11.3
Farranula spp. (male)	14.5	21.2	3.8		16.6	6.0	7.0	6.2	51.0
F. gibbulus (female)	12.7	12.7	1.4	3.5	3.9	3.0		1.1	19.8
F. concinnus (female)	6.4	5.3	1.0	9.4	2.9		2.5	0.7	15.6
Onceae media			2.9	0.6	1.5	2.3	0.6	0.4	1.4
O. venusta			1.0			0.8			
O. conifera									
Sapphirina spp.									
Sapphirella tropica	1.8		0.5				0.3		0.9
Clytemnestra scutellata	1.8		1.4	1.2	0.5	1.5	1.0	1.1	5.7
Microsetella rosea	18.2	18.0	21.0	4.7	4.4	29.3	1.0	1.8	3.8
Macrosetella gracilis	13.6	11.6	1.4	10.6	6.3		0.6		1.4
Euterpina acutifrons					0.5		0.3		
Tortanus barbatus									
Mecynocera clausi									
Other copepods	0.9								
Total copepods	400.9	271.0	98.0	128.4	119.6	146.6	52.2	53.8	198.9
Total zooplankton	451.8	322.9	167.9	144.9	175.3	194.0	66.8	84.0	258.9
Mean chlorophyll	0.74	0.68	1.30	1.19	1.26	1.40	0.87	0.88	0.73
C. V. chlorophyll	0.11	0.08	0.14	0.04	0.09	0.07	0.04	0.05	0.08

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	59	60	64	67	68	69	70	75	76
Latitude	19.0	19.0	19.3	19.5	19.4	19.3	19.4	19.3	19.2
Longitude	147.8	147.8	148.0	148.1	148.0	148.1	148.2	147.9	147.8
Decapod larvae	0.5	0.3		0.6		0.5	1.4		0.6
Brachyuran larvae	0.5	0.3	1.9			1.0	2.1		1.9
Luciferids		0.6							
Stomatopod larvae				1.1			0.2	1.2	0.6
Siphonophores				0.6				0.6	0.6
Chaetognaths	10.8	9.7	28.4	19.9	10.1	9.4	5.2	29.0	30.4
Appendicularians	28.7	45.1	32.3	5.0	9.6	10.5	14.1	0.6	
Polychaete larvae	1.9	3.6	9.0	0.6	0.5	2.6	1.4	1.8	0.6
Pteropods		0.9	1.3		0.5		0.7		
Salps	0.3	3.2		0.5					
Echinoid larvae		2.1					0.7	3.0	
Fish larvae	3.4	1.2	0.6	1.1	1.0	0.5	4.5		
Fish eggs				1.7			0.7		
Mollusc larvae	1.9			1.1	3.9				
Cladocera	0.2		0.6		0.5	0.5	0.2		
Ostracods					1.0				
Acrocalanus gracilis	32.3	12.4	72.3	19.4	10.6	41.8	13.4	18.1	98.9
A. monachus									
A. gibber									
Clausocalanus spp.									
Paracalanus spp.	4.6	9.4	35.5		1.0	8.9	3.0	4.2	40.6
Calocalanus pavo		0.6	3.9		0.5	0.5	0.9	1.2	
Canthocalanus pauper			0.6						
Centropages orsinii	7.7	10.9	4.5	37.0	25.6	37.1	8.0	12.1	59.0
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta			1.1						
L. minuta	0.5				0.5	1.0	0.5	0.6	
Undinula vulgaris	3.4	4.2	5.8		0.5	11.0	0.7	1.8	7.6
Temora stylifera									
T. turbinata									
Calanopia elliptica						0.6			
Eucalanus subcrassus						1.2			
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	1.9	4.2	1.9	12.2	8.7	39.7	7.7	16.9	18.4
A. negligens	0.2						0.5		
Oithona rigida	0.7	2.1	1.9	3.3	2.4	5.2	4.5	1.2	
O. plumifera			2.6			2.6	0.7		
O. spp.	3.1	5.1	11.0	11.6	1.0	3.1	1.6	3.0	1.3
Corycaeus pacifica		0.3	5.2	2.2	1.9	2.1	2.3	7.2	4.4
C. (D) spp.	17.6	5.1	21.9	50.3	27.5	38.2	15.2	23.5	13.3
C. speciosus	0.2	0.6							
C. lubbocki	2.9	0.6		17.7	29.9	16.7	2.3	5.4	5.7
Farranula spp. (male)	9.9	3.6		32.1	48.2	36.6	4.2	7.2	5.7
F. gibbulus (female)	5.8	3.0		1.1	7.7	14.6	2.8		3.8
F. concinnus (female)	3.6	0.6		3.3	5.8	4.2	1.4	1.8	3.8
Onceae media			1.9	1.7	1.9	2.6	1.6	1.2	0.6
O. venusta	0.2						0.9		0.6
O. conifera									
Sapphirina spp.									
Sapphirella tropica	0.2	1.2		1.1	0.5				
Clytemnestra scutellata	1.2	3.9	0.6	1.7	0.5	0.5	1.2		0.6
Microsetella rosea	3.4	20.6	34.8	19.9	12.5	13.1	8.9	27.1	14.6
Macrosetella gracilis	1.7	4.5	14.8	2.2	2.9	6.8	3.5	2.4	1.9
Euterpina acutifrons			0.6	0.6		1.0			
Tortanus barbatus									
Mecynocera clausi									
Other copepods		0.3					0.23		
Total copepods	101.1	93.2	220.0	218.4	190.1	287.5	86.0	136.9	280.8
Total zooplankton	149.0	157.3	297.4	249.9	217.6	312.6	117.1	173.1	315.7
Mean chlorophyll	0.77	0.90	0.82	0.84	0.78	0.89	1.00	0.41	0.40
C. V. chlorophyll	0.13	0.19	0.07	0.06	0.06	0.31	0.20	0.10	0.11

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	77	78	80	81	82	83	88	89	92
Latitude	19.1	18.9	18.8	18.7	18.7	18.6	18.5	18.4	18.3
Longitude	147.7	147.6	147.5	147.4	147.2	147.1	146.8	147.0	147.1
Decapod larvae	0.7		0.3	0.6	5.3	0.7		1.3	
Brachyuran larvae	0.7		0.7	0.6			11.6	3.1	
Luciferids									
Stomatopod larvae					0.7		5.8	0.6	
Siphonophores					5.8				
Chaetognaths	31.2	7.7	6.0	20.8	35.5	10.6	151.3	13.8	6.2
Appendicularians			3.0	1.9	71.1	295.6	11.6		
Polychaete larvae	0.7		1.3	0.6	7.9	7.7	34.9	2.5	1.9
Pteropods						0.7	17.5		
Salps5.8									
Echinoid larvae					2.6	2.1	29.1		
Fish larvae		0.6	0.7		0.7	1.4	29.1	2.5	1.2
Fish eggs		0.6	1.7	1.3	2.6	1.4	5.8	0.6	13.0
Mollusc larvae	1.3								
Cladocera	7.3	1.3			0.7		29.1	2.5	
Ostracods									
Acrocalanus gracilis	105.0	26.8	34.5	83.1	54.6	13.4	58.2	9.4	10.5
A. monachus									
A. gibber									
Clausocalanus spp.									
Paracalanus spp.	8.0	2.6	3.7	3.9	11.2	8.4	209.5	10.6	9.3
Calocalanus pavo						0.6			
Canthocalanus pauper	2.0	0.6	1.0	0.6	2.6			0.6	
Centropages orsinii	87.0	61.2	11.7	7.8	82.2	33.8	226.9	43.8	8.0
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta	0.6	2.3	0.6						
L. minuta	0.7	0.6						0.6	
Undinula vulgaris	14.0	0.6	2.7	5.8	10.5	0.7			
Temora stylifera5.8									
T. turbinata									
Calanopia elliptica			0.3				11.6		
Eucalanus subcrassus						5.8			
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	8.6	2.6	9.7	31.8	67.1	52.1	221.1	45.1	63.6
A. negligens									
Oithona rigida	1.3	0.6	2.0	1.9	4.6	0.7	23.3	3.1	1.9
O. plumifera			0.7			0.7	104.7	5.6	
O. spp.	15.3	11.5	6.0	3.9	5.9	16.2	314.2		1.2
Corycaeus pacifica	10.6	1.3	2.0	4.5	3.3	13.4	104.7	15.6	6.2
C. (D) spp.	14.0	23.6	27.1	20.1	13.8	7.0	46.5	9.4	19.8
C. speciosus				1.3					
C. lubbocki	12.0	20.4	7.4	3.9	1.3		23.3		1.2
Farranula spp. (male)	15.9	23.0	6.0	20.8			11.6	1.3	13.6
F. gibbulus (female)	4.0	5.1	0.7	11.7	1.3		11.6	2.5	2.5
F. concinnus (female)		2.6	0.7	9.1	2.6		11.6		2.5
Onceae media	0.7		0.3	0.6		1.4			0.6
O. venusta					0.7				
O. conifera									
Sapphirina spp.									
Sapphirella tropica			0.3		0.7	0.7			
Clytemnestra scutellata	2.7	0.6	1.0	1.9	1.3	0.7	23.3	0.6	1.9
Microsetella rosea	6.6	3.8	2.7	2.6	9.9	14.1	128.0	14.4	8.0
Macrosetella gracilis	4.0		1.3	8.4	5.9	2.1	29.1	16.3	6.2
Euterpina acutifrons									
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	312.3	188.2	124.3	224.7	279.6	165.4	1570.9	179.7	156.8
Total zooplankton	354.1	198.4	138.0	250.6	406.6	485.7	1908.4	206.6	179.0
Mean chlorophyll	0.36	0.26	0.30	0.29	0.52	0.92	0.86	0.85	0.46
C. V. chlorophyll	0.13	0.21	0.36	0.16	0.34	0.23	0.13	0.25	0.26

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	94	114	115	116	117	118	119	120	121
Latitude	18.2	18.1	18.0	18.0	18.0	18.0	18.0	18.1	18.1
Longitude	147.3	146.3	146.4	146.5	146.6	146.6	146.6	146.6	146.5
Decapod larvae	1.0	12.1	0.8	0.6			0.7	0.7	0.4
Brachyuran larvae			0.4	0.6			1.4	2.0	1.5
Luciferids				0.6					
Stomatopod larvae		1.3							
Siphonophores							1.4	2.6	
Chaetognaths	12.9	69.8	10.9	14.3	75.8	20.9	5.6	11.2	8.1
Appendicularians		4.0	3.2	3.2	116.4	5.6	51.4	0.7	3.7
Polychaete larvae	1.0	8.1	6.1	2.6	10.8	20.9	9.9	7.3	6.2
Pteropods		2.7	0.4	0.6				14.5	0.4
Salps					1.4				
Echinoid larvae		6.7	0.4	1.3		4.2		0.7	
Fish larvae	1.3	1.3	1.2			2.8	2.1		0.4
Fish eggs		1.3	1.6	0.6	2.7	4.2	0.7	0.7	0.7
Mollusc larvae	1.0	5.4	1.6	1.3					0.7
Cladocera		10.7	1.6	0.6	2.7	1.4	0.7	2.0	2.2
Ostracods									
Acrocalanus gracilis	19.8	20.1	9.7	5.8	13.5	4.2	9.2	4.0	8.4
A. monachus									
A. gibber		2.7				1.4			
Clausocalanus spp.									
Paracalanus spp.	3.6	16.1	1.2	1.3			1.4	3.3	0.4
Calocalanus pavo	0.3		1.2	0.6					
Canthocalanus pauper	0.3								
Centropages orsinii	0.3	2.7	19.0	22.1	470.9	97.6	31.7	28.4	25.0
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta					0.7				
L. minuta				0.6		1.4			
Undinula vulgaris	7.3	2.7	2.4	3.2	8.1	2.8	0.7		0.7
Temora stylifera		5.4	1.2	0.6			0.7		
T. turbinata		1.3		0.6	2.7	1.4		0.7	
Calanopia elliptica	0.3	9.4	2.8	3.9	5.4		0.7		0.4
Eucalanus subcrassus		6.7		0.6					
E. mucronatus									
Candacia pachydactyla		1.3							
C. pectinata									
Acartia pacifica									
A. australis	1.7	13.4	1.6	7.8	10.8	44.6	19.7	5.3	4.4
A. negligens						0.7			
Oithona rigida	0.3	20.1	4.0	14.3	56.8	55.8	14.1	4.0	5.1
O. plumifera		13.4	6.1	1.3		2.8	4.2	0.7	
O. spp.	2.6	87.2	22.2	20.1	65.0	47.4	16.2	42.9	13.2
Corycaeus pacifica	1.3	21.5	3.2	7.8	10.8	7.0	4.9	4.0	6.2
C. (D) spp.	29.0	68.5	37.2	29.2	32.5	26.5	32.4	15.8	22.0
C. speciosus	1.0						1.4		
C. lubbocki	2.0	10.7	15.3	4.5	21.7	11.2	4.2	10.6	10.3
Farranula spp. (male)	44.6	13.4	12.1	5.2		5.6	4.2	3.3	8.1
F. gibbulus (female)	5.9		8.1	1.9		13.9	7.0	2.6	1.5
F. concinnus (female)	10.9	2.7	5.7	1.3				0.7	
Onceae media		2.7	2.8	0.6		2.8	1.4	0.7	1.5
O. venusta	1.3	1.3	1.6	0.6					0.4
O. conifera									
Sapphirina spp.			0.4						
Sapphirella tropica					2.7				
Clytemnestra scutellata	0.3		0.8	0.6		12.5	3.5	3.3	
Microsetella rosea	3.6	59.1	26.7	25.3	21.7	32.1	8.4	3.3	4.8
Macrosetella gracilis	2.0	2.7	1.6	1.3		1.4	3.5	2.0	1.1
Euterpina acutifrons		34.9	5.3	1.9		4.2	2.1	11.2	4.4
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	138.6	420.1	192.2	163.7	722.6	376.4	172.5	147.1	117.9
Total zooplankton	155.8	543.6	220.5	190.3	931.0	436.4	247.8	189.4	142.1
Mean chlorophyll	0.27	0.61	0.50	0.60	0.54	0.79	0.69	0.58	0.55
C. V. chlorophyll	0.18	0.09	0.03	0.11	0.06	0.16	0.06	0.07	0.02

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	154	155	156	157	158	159	160	161	162
Latitude	17.8	17.7	17.7	17.6	17.6	17.6	17.6	17.6	17.6
Longitude	146.4	146.5	146.5	146.6	146.6	146.6	146.5	146.5	146.4
Decapod larvae	1.2					2.8	7.2	2.5	0.9
Brachyuran larvae	0.4	0.9	1.9	2.0	3.2		7.2		6.1
Luciferids	0.8								
Stomatopod larvae						0.8			
Siphonophores		0.5	1.0			2.8			0.9
Chaetognaths	5.8	9.0	15.6	41.3	20.9	80.1	7.2	19.7	48.9
Appendicularians		0.9				187.8	211.6	149.6	231.5
Polychaete larvae	1.9	5.7	6.8	13.8	8.0	96.7	32.3	17.3	17.5
Pteropods	3.9	1.4		2.0	3.2				
Salps	0.5						1.6		
Echinoid larvae	0.8					2.8		1.6	
Fish larvae		0.5							
Fish eggs	2.3	1.4						1.6	0.9
Mollusc larvae	1.6	0.9				2.8	21.5		3.5
Cladocera	1.9	0.9	1.9	3.9		2.8	7.2	3.3	2.6
Ostracods									
Acrocalanus gracilis	4.3	4.7	1.9	17.7	17.7	22.1	39.4	18.1	23.6
A. monachus									
A. gibber	1.6						1.6		
Clausocalanus spp.									
Paracalanus spp.	1.2	1.4			4.8		10.8	9.0	7.0
Calocalanus pavo	0.8	0.9						0.8	
Canthocalanus pauper	1.9	2.8							
Centropages orsinii	17.9	63.5	183.1	208.5	181.9	375.7	591.7	93.7	80.4
C. furcatus						2.8		0.8	
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta						2.8	3.6		0.9
Undinula vulgaris	0.8			31.5	11.3		10.8	2.5	1.7
Temora stylifera	3.1				1.6			0.8	
T. turbinata									
Calanopia elliptica	8.5	1.4					3.6		
Eucalanus subcrassus	1.2	0.5						2.5	
E. mucronatus									
Candacia pachydactyla	0.4								
C. pectinata									
Acartia pacifica									
A. australis	2.7	13.3	22.4	92.4	114.3	314.9	236.7	33.7	3.5
A. negligens									
Oithona rigida	6.6	8.5	33.1	37.4	29.0	44.2	129.1	40.3	39.3
O. plumifera	3.5	2.4	1.0	2.0					
O. spp.	14.4	45.0	53.3	145.5	32.2	5.5	64.5	18.1	22.7
Corycaeus pacifica	1.9	4.7	10.7	7.9	16.1	16.6	50.2	15.6	28.0
C. (D) spp.	25.2	20.9	31.2	51.1	16.1	16.6	46.6	21.4	
C. speciosus						1.6			
C. lubbocki	0.8	0.5	1.0	3.9	1.6		14.3	1.6	1.7
Farranula spp. (male)	1.6	0.9	1.9		3.2	11.0	7.2	1.6	
F. gibbulus (female)	1.6		2.9	2.0			7.2		1.7
F. concinnus (female)		0.5	1.0			2.8			
Onceae media	0.4		1.0					1.6	
O. venusta	1.9								
O. conifera	1.2								
Sapphirina spp.	0.4					2.8			
Sapphirella tropica		1.9		2.0	4.8			0.8	
Clytemnestra scutellata	1.9	9.0	16.6	59.0	54.7	38.7	89.6	6.6	13.1
Microsetella rosea	28.3	12.3	1.9		1.6	11.0	10.8	3.3	7.9
Macrosetella gracilis	5.8	2.8	5.8		3.2	8.3		10.7	7.9
Euterpina acutifrons	5.0	4.3	8.8					0.8	
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	144.7	202.4	377.5	660.8	494.2	875.7	1316	287.7	239.4
Total zooplankton	165.3	225.1	404.8	723.7	529.6	1254	1610	485.8	552.2
Mean chlorophyll	0.67	0.71	0.64	0.79	0.78	0.84	0.88	0.86	0.68
C. V. chlorophyll	0.06	0.09	0.08	0.11	0.08	0.09	0.04	0.14	0.10

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	167	168	169	170	171	172	173	174	175
Latitude	17.5	17.5	17.4	17.3	17.2	17.2	17.3	17.4	17.5
Longitude	146.2	146.2	146.2	146.3	146.3	146.4	146.4	146.4	146.4
Decapod larvae	62.5	1.2	1.3						
Brachyuran larvae	57.3	3.0	3.8	6.4	1.3	2.5		1.3	1.2
Luciferids	5.2	0.6	3.8						
Stomatopod larvae		0.6							
Siphonophores	2.6	3.0		2.5		1.3	1.2		
Chaetognaths	101.5	19.3	46.5	57.2			12.1	26.9	28.9
Appendicularians	10.4	57.9	1.3	50.8	2.6	15.0		78.5	30.1
Polychaete larvae	13.0	6.0	8.8	7.6	6.5	3.8	6.1	12.1	10.8
Pteropods	2.6	2.4		1.3	1.3	1.3			
Salps	0.6								
Echinoid larvae	2.6		1.3						
Fish larvae	2.6	0.6	6.3	2.5					
Fish eggs			5.0	1.3		1.3			1.2
Mollusc larvae		2.4		3.8	1.3			0.7	2.4
Cladocera	7.8				1.3		2.4	0.7	6.0
Ostracods									
Acrocalanus gracilis	36.4	15.7	31.4	39.4	7.8	5.0	4.8	6.7	19.3
A. monachus						0.7			
A. gibber	96.3			1.3	3.9				
Clausocalanus spp.	20.80.7								
Paracalanus spp.	31.2	3.0	15.1	8.9	5.2	2.5	14.5	4.0	14.5
Calocalanus pavo		0.6							
Canthocalanus pauper	18.2	2.4	7.5		31.4		3.6		2.4
Centropages orsinii	57.3	16.9	45.3	207.0	241.7	129.1	95.7	65.1	62.7
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta			1.3						
L. minuta									
Undinula vulgaris		6.0		5.1		1.3		6.7	
Temora stylifera		2.4	8.8						
T. turbinata	46.8	1.8	3.8						1.2
Calanopia elliptica	26.0	3.0		2.5					1.2
Eucalanus subcrassus	26.0	0.6							
E. mucronatus		0.6							
Candacia pachydactyla	15.6								
C. pectinata									
Acartia pacifica		0.6							
A. australis	15.6	8.4	12.6	43.2	52.3	67.7	55.7	38.9	31.3
A. negligens									
Oithona rigida	88.5	3.0		64.8	82.3	51.4	58.2	16.8	85.6
O. plumifera	20.8	1.8							
O. spp.	150.9	27.7	89.3	67.3	228.6	82.7	349.0	65.8	107.3
Corycaeus pacifica	36.4	10.2	39.0	24.1	24.8		37.6	13.4	59.1
C. (D) spp.	187.4	24.1	46.5	39.4	35.3	32.6	42.4	42.3	47.0
C. speciosus									
C. lubbocki	62.5	1.2	3.8	7.6	5.2	2.5	9.7	1.3	14.5
Farranula spp. (male)			2.5		1.3		2.4		4.8
F. gibbulus (female)	2.4								
F. concinnus (female)						1.2	0.7	4.8	
Onceae media		3.6		1.3	1.3			0.7	
O. venusta									
O. conifera	10.4		1.3						
Sapphirina spp.			1.3						
Sapphirella tropica1.3									
Clytemnestra scutellata				6.4	5.2	1.3	8.5	2.0	2.4
Microsetella rosea	26.0	10.2	25.1	14.0	14.4	5.0	9.7	4.7	7.2
Macrosetella gracilis	7.8	7.8	62.9	25.4	7.8	8.8	3.6		3.6
Euterpina acutifrons	46.8	11.5	22.6	6.4	1.3	2.5	6.1	2.0	9.6
Tortanus barbatus									
Mecynocera clausi									
Other copepods				1.27					
Total copepods	1028	163.4	418.7	565.3	749.8	392.4	702.8	273.9	481.0
Total zooplankton	1296	261.0	496.7	698.6	764.2	417.4	724.6	394.1	561.8
Mean chlorophyll	1.12	0.79	0.69	0.63	0.59	0.58	0.61	0.67	0.63
C. V. chlorophyll	0.12	0.18	0.06	0.05	0.08	0.05	0.09	0.09	0.10

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	176	177	178	179	180	181	182	184	185
Latitude	17.6	17.6	17.7	17.8	17.8	17.7	17.7	17.5	17.4
Longitude	146.4	146.4	146.3	146.3	146.3	146.2	146.2	146.2	146.2
Decapod larvae			1.3	1.3		14.9	28.9	7.0	2.5
Brachyuran larvae	3.6		3.8	5.1	7.4	2.5	14.4	2.3	
Luciferids				1.3			9.0		
Stomatopod larvae									
Siphonophores			0.6		4.9	2.5			
Chaetognaths	31.3	32.2	50.8	81.0	196.7	168.3	193.0	68.0	43.3
Appendicularians	89.0	10.7	65.2	3.8	140.1	34.6	292.2		125.1
Polychaete larvae	1.2	10.7	8.2	15.2	4.9	12.4	12.6	25.8	5.0
Pteropods						2.5			2.5
Salps									
Echinoid larvae						1.8	9.4		
Fish larvae	1.2			1.3	4.9	2.5	1.8	2.3	3.7
Fish eggs		1.3		1.3				9.4	1.2
Mollusc larvae	2.4	1.3	0.6	1.3			10.8	14.1	
Cladocera	4.8		7.5		2.5		27.1	9.4	
Ostracods									
Acrocalanus gracilis	9.6	4.0	12.5	60.8	167.2	79.2	61.3	21.1	34.7
A. monachus									
A. gibber	2.4			8.9		84.1	3.6	86.8	2.5
Clausocalanus spp.						19.8			
Paracalanus spp.	7.2	16.1	20.7	10.1	59.0	61.9	104.6	4.7	18.6
Calocalanus pavo									
Canthocalanus pauper		2.7		27.9	9.8	175.7		18.8	6.2
Centropages orsinii	136.0	104.6	65.2	130.4	118.0	61.9	30.7	32.8	35.9
C. furcatus					4.9	2.5			
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta									
Undinula vulgaris	4.8		5.0		108.2		7.2		
Temora stylifera						2.3	11.1		
T. turbinata			0.6			2.5	102.8	68.0	
Calanopia elliptica			0.6			4.9	25.3		5.0
Eucalanus subcrassus					2.5	2.5		23.5	7.4
E. mucronatus							1.2		
Candacia pachydactyla						5.4	14.1	1.2	
C. pectinata									
Acartia pacifica									
A. australis	28.9	9.4	5.0	6.3	2.5		10.8	23.5	17.3
A. negligens	1.2						1.8		5.0
Oithona rigida	36.1	41.6	13.2	22.8	34.4	24.7	72.2	28.1	6.2
O. plumifera						9.4	8.7		
O. spp.	63.8	20.1	18.8	24.1	19.7	9.9	111.8	122.0	44.6
Corycaeus pacifica	7.2	14.7	11.3	10.1	12.3	32.2	10.8	18.8	19.8
C. (D) spp.	31.3	10.7	30.1	31.7	46.7	37.1	50.5	152.4	99.1
C. speciosus									
C. lubbocki	6.0		3.1	10.1	24.6	29.7	32.5	21.1	
Farranula spp. (male)	2.4	1.3	3.8	7.6	4.9	9.9	10.8		
F. gibbulus (female)		2.7	1.3	2.5					
F. concinnus (female)	2.4		0.6	5.1	4.9				
Onceae media	1.2	1.3	3.8	5.1	2.5	7.4			3.7
O. venusta									
O. conifera									
Sapphirina spp.						1.8			
Sapphirella tropica									
Clytemnestra scutellata	2.4		0.6				1.8		
Microsetella rosea	7.2	6.7		30.4	46.7	24.7	1.8	35.2	13.6
Macrosetella gracilis	3.6	1.3	5.0	12.7	14.8	4.9		18.8	7.4
Euterpina acutifrons		2.7	8.2	3.8	17.2	17.3	75.8	82.1	43.3
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	353.8	239.9	209.5	410.3	700.7	692.9	723.3	783.3	392.6
Total zooplankton	487.4	296.2	347.6	521.7	1062.1	932.9	1315.0	931.1	575.9
Mean chlorophyll	0.63	0.49	0.47	0.51	0.60	0.70	1.13	0.88	0.71
C. V. chlorophyll	0.17	0.04	0.05	0.10	0.06	0.15	0.22	0.03	0.08

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	186	187	188	189	190	193	194	197	199
Latitude	17.4	17.3	17.2	17.2	17.3	17.4	17.5	17.6	17.8
Longitude	146.2	146.3	146.3	146.4	146.4	146.4	146.4	146.4	146.3
Decapod larvae	1.2		1.3				7.3	1.2	
Brachyuran larvae	2.5	2.5	0.6		0.9			4.6	
Luciferids	3.7		0.6				5.5	2.3	
Stomatopod larvae	1.2								
Siphonophores		1.3	0.6	1.3	1.8	2.6	1.8	5.8	5.0
Chaetognaths	49.0	17.7	20.7	7.5	19.4	36.4	25.5	57.5	93.1
Appendicularians	1.2	32.3	0.6	40.1		197.5	5.5	277.3	
Polychaete larvae	9.8	2.5	11.3		5.5	7.8	21.8	13.8	7.6
Pteropods	3.7	0.6	0.6						
Salps	1.2	1.3		1.3	0.9		3.6	4.6	12.6
Echinoid larvae		0.6							
Fish larvae	1.2	1.3	1.9		0.9		1.8	3.5	
Fish eggs		0.6							
Mollusc larvae				6.3		67.6		2.3	
Cladocera		1.3	1.3		1.8	5.2	7.3	2.3	
Ostracods									
Acrocalanus gracilis	23.3	20.9	5.0	12.5	9.2	13.0	1.8	35.7	
A. monachus		2.5							
A. gibber	7.4	0.6	11.9		2.8	5.2	5.5	1.2	
Clausocalanus spp.									
Paracalanus spp.	14.7	5.7	6.3	2.5	4.6	5.2	16.4	3.5	15.1
Calocalanus pavo	1.2	1.9							
Canthocalanus pauper	7.4		3.8		1.8		7.3		5.0
Centropages orsinii	65.0	110.2	57.7	63.9	92.1	197.5	81.9	67.9	47.8
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta	1.2								
Undinula vulgaris		0.6				7.8	3.6	5.8	
Temora stylifera	1.2	1.3			0.9		1.8		5.0
T. turbinata	3.7		2.5					2.3	
Calanopia elliptica	1.2	0.6	0.6	1.3	3.7	2.6	7.3		
Eucalanus subcrassus	1.2	0.6							
E. mucronatus	1.21.2								
Candacia pachydactyla	2.5		1.3						
C. pectinata									
Acartia pacifica	1.2								
A. australis	12.3	8.2	14.4	57.7	78.3	132.5	49.2	42.6	17.6
A. negligens		0.6							
Oithona rigida	28.2	17.1	25.7	28.8	48.8	129.9	72.8	18.4	2.5
O. plumifera	8.6	1.3			1.8	2.6	3.6	4.6	
O. spp.	72.3	17.7	72.7	117.8	104.1	166.3	125.6	41.4	35.2
Corycaeus pacifica	22.1	12.7	14.4	11.3	43.3	13.0	49.2	15.0	32.7
C. (D) spp.	58.8	35.5	18.2	8.8	36.9	20.8	52.8	44.9	60.4
C. speciosus									
C. lubbocki	14.7	4.4	1.9		2.8	10.4	7.3	6.9	37.8
Farranula spp. (male)	14.7	0.6	1.3	1.3	0.9		18.2	6.9	
F. gibbulus (female)	2.5	1.9	1.9	2.5			10.9		
F. concinnus (female)						5.2			
Onceae media	3.7	1.3	0.6		0.9			2.3	
O. venusta									
O. conifera									
Sapphirina spp.	1.2						1.8	2.3	2.5
Sapphirella tropica									
Clytemnestra scutellata	1.2		2.5	2.5	2.8		18.2	3.5	2.5
Microsetella rosea	55.1	22.8	13.2	7.5	14.7		32.8	99.0	105.7
Macrosetella gracilis	20.8	21.5	12.5	3.8	5.5		5.5	16.1	27.7
Euterpina acutifrons	27.0	3.2	6.9	2.5	6.5	13.0	14.6	16.1	17.6
Tortanus barbatus									
Mecynocera clausi									
Other copepods	1.23								
Total copepods	473.0	291.3	275.2	324.7	462.6	724.9	588.1	439.6	417.9
Total zooplankton	546.6	353.4	314.7	381.1	493.9	1041.9	668.2	815.9	536.2
Mean chlorophyll	0.59	0.56	0.74	0.61	0.65	0.89	0.78	0.73	0.65
C. V. chlorophyll	0.04	0.06	0.11	0.10	0.09	0.11	0.13	0.07	0.03

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	224	225	226	227	228	229	230	231	235
Latitude	18.3	18.4	18.5	18.5	18.6	18.7	18.7	18.8	18.9
Longitude	147.4	147.4	147.4	147.4	147.4	147.4	147.4	147.5	147.6
Decapod larvae	0.3		1.1	1.5	2.3	1.5	1.5	0.7	0.5
Brachyuran larvae			0.7					0.7	0.5
Luciferids	0.4	1.1	0.2						
Stomatopod larvae	0.4								
Siphonophores						0.8		0.7	
Chaetognaths	0.3	0.4	1.1	1.2		0.8	1.9	0.4	1.4
Appendicularians	0.3	0.7	1.8	5.6	20.7	13.3	17.6	16.7	7.9
Polychaete larvae				0.4	2.3	0.4	2.6	0.7	0.5
Pteropods					0.8			0.8	0.7
Salps									
Echinoid larvae	0.3					1.1			0.2
Fish larvae				0.4			0.7		0.5
Fish eggs			0.4	0.7	0.8	1.5		1.5	0.5
Mollusc larvae				0.4	1.5		0.4		
Cladocera									
Ostracods									
Acrocalanus gracilis	1.0	1.5		0.7	2.3	0.4	0.7	1.9	1.2
A. monachus					1.5	0.4	0.4	0.7	
A. gibber				1.2	0.8		0.7		0.2
Clausocalanus spp.	0.3			0.4				0.4	
Paracalanus spp.	1.3	0.7		0.7	0.8		0.4	1.1	5.3
Calocalanus pavo	0.3	0.4	1.1	0.4	0.8	0.4		0.7	
Canthocalanus pauper									
Centropages orsinii	4.0	2.6	0.7	11.1	10.7	15.2	20.9	5.3	3.3
C. furcatus		0.5							
C. elongatus									
Labidocera laevigata	0.7		0.2						
L. acuta									
L. minuta									
Undinula vulgaris				6.3	9.2	12.9	10.1	7.4	
Temora stylifera									
T. turbinata									
Calanopia elliptica		0.4	0.4	5.1	6.9	3.0	2.2	4.1	0.2
Eucalanus subcrassus		0.7							
E. mucronatus									
Candacia pachydactyla									
C. pectinata				0.4					
Acartia pacifica				0.4	0.8				
A. australis	2.4	53.7	34.2	98.3	48.4	51.2	42.2	28.9	5.3
A. negligens	0.3	0.7	1.4						
Oithona rigida	2.4	2.6	2.1	5.9	16.1	5.3	3.0	3.3	0.5
O. plumifera	7.4	1.5	9.3	8.9	29.2	5.7	11.6	7.8	6.0
O. spp.	1.7	1.5	1.4	2.6	13.1	2.7	2.2	1.1	2.4
Corycaeus pacifica		0.7	0.4	1.5	3.8		2.6	1.1	0.7
C. (D) spp.	12.1	7.1	5.7	26.0	16.1	8.7	5.2	5.9	5.5
C. speciosus	1.0	1.9	1.1	1.9	5.4	1.5	3.0	0.7	1.9
C. lubbocki	5.7	3.7	3.2	9.7	10.7	2.7	0.4	1.5	1.0
Farranula spp. (male)	4.4	4.5	3.2	8.9	10.0	6.1	2.2	2.2	2.6
F. gibbulus (female)	2.7	0.4	1.8	4.1	5.4	0.8		2.2	
F. concinnus (female)	3.7	0.4	1.4	2.2	6.9	2.3	2.2	1.1	
Onceae media	0.7	1.1	0.4				0.4	1.1	1.2
O. venusta		1.5		1.2	1.5	1.5			1.2
O. conifera		0.4	0.2						
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	0.7	0.7	1.1		3.8	1.1	1.1	0.4	1.2
Macrosetella gracilis		0.4				0.4			
Euterpina acutifrons			0.4		0.8				
Tortanus barbatus									
Mecynocera clausi									
Other copepods				0.4					
Total copepods	52.2	88.3	69.0	197.9	205.0	122.2	112.3	79.0	41.3
Total zooplankton	53.6	89.5	74.0	208.0	233.5	141.6	137.7	102.3	54.2
Mean chlorophyll	0.30	0.42	0.49	0.48	0.52	0.56	0.58	0.70	0.60
C. V. chlorophyll	0.07	0.17	0.08	0.05	0.04	0.05	0.04	0.10	0.03

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	236	237	238	239	242	243	244	245	246
Latitude	18.9	19.0	19.1	19.2	19.2	19.1	19.0	18.9	18.8
Longitude	147.7	147.7	147.7	147.8	147.8	147.9	147.9	147.8	147.8
Decapod larvae	1.4	0.7	2.0	1.0	0.6	0.7		1.3	1.9
Brachyuran larvae	0.7	0.3	2.0	0.3	0.6				
Luciferids									
Stomatopod larvae									
Siphonophores	0.7	0.3		0.3	0.6				1.3
Chaetognaths	2.0	4.4	4.0	1.4	3.1	6.2	1.3	2.5	3.2
Appendicularians	20.4	8.8	17.2	4.8	28.3	11.8	7.8	7.5	21.8
Polychaete larvae	0.7	0.7	0.7						
Pteropods	2.0	1.0		0.3					
Salps	0.3								
Echinoid larvae	0.7	1.0		1.7	1.3				
Fish larvae		0.7	2.0	1.4					0.6
Fish eggs	0.7		1.3	0.7	1.3	1.4	1.3	2.5	2.6
Mollusc larvae	1.4	1.0	0.7	1.0	1.9				
Cladocera									
Ostracods									
Acrocalanus gracilis	4.1	1.4	2.0	0.7		1.4		2.5	
A. monachus									
A. gibber			4.6						
Clausocalanus spp.		1.9							
Paracalanus spp.	8.8	5.4	7.3	4.8	4.4	4.1		5.0	5.8
Calocalanus pavo					0.6		1.3		
Canthocalanus pauper									
Centropages orsinii	22.4	12.2	49.0	25.6	101.7	135.5	157.0	136.8	73.6
C. furcatus									
C. elongatus									
Labidocera laevigata		0.3				0.7			
L. acuta	0.3								
L. minuta		0.3		0.3					
Undinula vulgaris	7.5	11.8	29.1	6.6	6.3	21.4	7.8		6.4
Temora stylifera	0.7	0.3							
T. turbinata									
Calanopia elliptica	0.7	1.4		1.0	0.6	1.4			
Eucalanus subcrassus	2.0	1.4	2.6	0.7					
E. mucronatus		0.7	0.7	0.3					
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	77.6	35.5	89.4	73.3	114.9	169.4	250.4	281.1	117.8
A. negligens									
Oithona rigida	0.7	0.7	1.3	1.4	3.1	4.1	15.6	15.1	5.8
O. plumifera	12.9	1.4	7.9	1.7	0.6	2.1			7.0
O. spp.	19.7	0.3	5.3	5.9	29.5	12.4	23.4	26.3	38.4
Corycaeus pacifica	0.7	1.4	2.0	0.7	0.6	1.4			0.6
C. (D) spp.	15.6	4.4	4.6	2.1	3.1	6.2	9.1	2.5	20.5
C. speciosus	3.4	2.0	2.6	0.3	1.3				1.3
C. lubbocki	6.1				0.6	2.1	23.4		15.4
Farranula spp. (male)	10.9				1.3	0.7	33.7	15.1	28.2
F. gibbulus (female)						0.7	2.6		1.3
F. concinnus (female)	1.4						7.8	7.5	10.2
Onceae media	1.4	0.7	0.7			0.7			1.3
O. venusta		0.3		0.3		0.7			0.6
O. conifera									
Sapphirina spp.		0.6							
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	4.1	0.3			0.6	0.7			
Macrosetella gracilis	0.7	0.7	0.7						
Euterpina acutifrons					1.3	0.7			
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	201.4	83.2	209.9	125.8	270.7	366.4	531.9	491.8	336.6
Total zooplankton	232.0	102.5	239.7	139.0	308.3	386.5	542.3	505.6	368.0
Mean chlorophyll	0.63	0.58	0.49	0.50	0.60	0.51	0.46	0.46	0.41
C. V. chlorophyll	0.05	0.10	0.03	0.04	0.12	0.13	0.03	0.04	0.18

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	247	248	254	255	256	257	258	259	260
Latitude	18.7	18.7	18.8	18.9	18.9	19.0	19.0	19.1	19.1
Longitude	147.8	147.7	147.6	147.5	147.5	147.4	147.3	147.2	147.2
Decapod larvae		0.5	2.2	0.5	1.5		0.4		
Brachyuran larvae			0.5			0.7		2.7	1.3
Luciferids0.4									
Stomatopod larvae									
Siphonophores	10.3	0.5		0.5	0.7	2.0	2.9	0.7	
Chaetognaths	3.4	0.5	1.1	1.1	17.6	5.3	15.0	6.8	14.5
Appendicularians	30.9	6.9		56.0	36.6	5.3	24.2	37.2	29.7
Polychaete larvae		1.0	1.6	1.1	2.9	1.3	2.2		
Pteropods			0.5	3.3	14.7	4.0	20.5	18.3	
Salps				0.7					
Echinoid larvae			0.5		2.2		0.7	3.4	
Fish larvae	3.4				0.7		0.7		0.7
Fish eggs				1.6	2.9	0.7	1.5	2.0	
Mollusc larvae			5.4	1.1	1.5		3.7		
Cladocera									
Ostracods									
Acrocalanus gracilis	6.9	1.0	4.3	6.6	10.2	0.7	1.5	16.2	28.4
A. monachus							1.1		
A. gibber			0.5	2.7	5.1	2.6	53.1	19.6	21.8
Clausocalanus spp.			8.1	5.5					0.7
Paracalanus spp.	27.5	0.5	1.6	10.4	14.6	1.3	16.1	16.2	60.8
Calocalanus pavo			1.1	1.1					
Canthocalanus pauper									
Centropages orsinii	130.7	10.4	11.9	12.6		19.0	8.1	2.0	0.7
C. furcatus				0.5					
C. elongatus					0.7				
Labidocera laevigata			1.1					0.7	
L. acuta				0.7		1.8	1.4	15.9	
L. minuta	1.4								
Undinula vulgaris		0.5	9.7	12.1	45.4	31.5	76.1	74.4	51.6
Temora stylifera			0.5	0.5					
T. turbinata				0.5					
Calanopia elliptica			14.1	2.7	8.8	2.0	4.8	15.6	2.6
Eucalanus subcrassus			0.5	5.5	5.1		5.9		
E. mucronatus						2.0			
Candacia pachydactyla									
C. pectinata							0.4		
Acartia pacifica									
A. australis	956.0	51.1	11.9	24.7	35.1	23.0	12.4	8.1	2.0
A. negligens			2.2	0.5					
Oithona rigida	13.8	3.0	1.1	3.3	3.7	2.6	2.6	2.7	1.3
O. plumifera	13.8	1.5		14.3	13.9	8.5	4.0	2.0	2.0
O. spp.	137.6	1.5	2.7	10.4	11.7	15.8	6.6	3.4	0.7
Corycaeus pacifica	10.3		1.1	3.3	0.7	1.3		2.7	1.3
C. (D) spp.	251.0	12.4	17.3	20.9	35.9	2.6	14.3	12.2	4.6
C. speciosus	24.1	1.0	4.8	3.3	22.0	2.6	3.3	18.3	2.0
C. lubbocki	113.5	11.9	18.4	9.9	1.5	3.9	2.2		
Farranula spp. (male)	75.7	7.9	4.3	15.4	2.9	2.6			
F. gibbulus (female)			2.2	2.2		1.3			
F. concinnus (female)	30.9	4.0	3.2	3.3	0.7				
Onceae media		0.5	1.6	1.6		0.7	1.5		0.7
O. venusta	3.4		4.3		2.2			1.4	
O. conifera	10.1								
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea			0.5		0.7		0.7		
Macrosetella gracilis			0.5		5.9	1.3	10.3	11.5	17.2
Euterpina acutifrons				0.5	2.2	0.7	6.6	6.1	
Tortanus barbatus									
Mecynocera clausi									
Other copepods		0.5							
Total copepods	1795	107.2	129.8	174.7	229.7	126.1	233.4	226.0	214.1
Total zooplankton	1843	116.6	141.7	240.0	311.7	145.3	305.5	297.1	260.4
Mean chlorophyll	0.35	0.41	0.59	0.56	0.55	0.46	0.48	0.55	0.47
C. V. chlorophyll	0.07	0.22	0.05	0.04	0.03	0.08	0.14	0.11	0.05

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	261	262	264	265	266	267	268	269	270
Latitude	19.1	19.1	19.2	19.3	19.3	19.3	19.3	19.3	19.3
Longitude	147.1	147.0	147.1	147.1	147.2	147.3	147.3	147.7	147.5
Decapod larvae	1.4	3.5		5.7				2.7	5.3
Brachyuran larvae		27.3	5.6	11.3	10.8		2.6	2.7	2.7
Luciferids					5.4			5.4	2.7
Stomatopod larvae									
Siphonophores	0.7								
Chaetognaths	21.0	11.2	39.2	73.5	21.6	32.6	31.4	13.4	37.4
Appendicularians	27.3	25.9	16.8	84.8	53.9	21.7	78.6	16.1	34.7
Polychaete larvae	0.7	4.2			5.4				
Pteropods	4.9	2.8	2.8			10.9		5.4	
Salps					5.4	2.6	2.7	2.7	
Echinoid larvae	0.7		16.8	11.3	5.4		2.6		
Fish larvae				5.7					10.7
Fish eggs		0.7					2.6		2.7
Mollusc larvae									
Cladocera									
Ostracods									
Acrocalanus gracilis	7.0	29.4	14.0	5.7			7.9		
A. monachus									
A. gibber	38.4	16.1	75.6	180.9	118.6	113.9	136.3	18.8	80.2
Clausocalanus spp.									
Paracalanus spp.	11.9	102.0	632.8	1051.2	1154.0	906.1	728.5	584.3	400.9
Calocalanus pavo									
Canthocalanus pauper			89.6	163.9	102.5	189.9	115.3	112.6	48.1
Centropages orsinii						5.4			
C. furcatus		0.7	2.8	28.3			2.6		
C. elongatus									
Labidocera laevigata									
L. acuta	1.4					2.7	2.7		
L. minuta	4.9	3.5							
Undinula vulgaris	28.0	11.2	22.4	11.3	37.7	43.4	55.0	21.4	88.2
Temora stylifera									
T. turbinata									
Calanopia elliptica	9.8	10.5	33.6	11.3	27.0	27.1	13.1	5.4	13.4
Eucalanus subcrassus			5.6	5.7	5.4	5.4	2.6		10.7
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica		4.2	5.6	5.7			10.5	2.7	10.7
A. australis									
A. negligens									
Oithona rigida	0.7	0.72.7							
O. plumifera		5.6	5.6	33.9	37.7	21.7	26.2	16.1	42.8
O. spp.	4.2	3.5		33.9	5.4		5.2		2.7
Corycaeus pacifica	6.3	2.1	8.4	17.0	5.4	16.3	2.6	2.7	2.7
C. (D) spp.	11.9	2.1	84.0	45.2	43.1	54.3	44.5	40.2	
C. speciosus	1.4	0.7	19.6	39.6	16.2	10.9	23.6	13.4	8.0
C. lubbocki			5.6			5.4			
Farranula spp. (male)		2.7							
F. gibbulus (female)									
F. concinnus (female)									
Onceae media		3.5	2.8		5.4			2.7	2.7
O. venusta									
O. conifera			19.6	17.0	16.2	10.9		8.0	
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea			5.6	28.3	5.4	5.4		5.4	
Macrosetella gracilis	23.1	7.7	8.4	11.3	10.8	10.9	31.4	5.4	16.0
Euterpina acutifrons	0.7	0.7		17.0	16.2	21.7	13.1	5.4	32.1
Tortanus barbatus			2.8	11.3			2.6	5.4	
Mecynocera clausi									
Other copepods		0.7				0.7			5.43
Total copepods	149.7	204.1	1041	1706	1607	1448	1218	846.9	767.1
Total zooplankton	206.4	279.5	1122	1899	1709	1519	1339	895.1	866.0
Mean chlorophyll	0.53	0.92	0.54	1.25	0.62	0.68	0.47	0.50	0.27
C. V. chlorophyll	0.12	0.24	0.12	0.18	0.24	0.16	0.25	0.30	0.08

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	280	281	282	283	284	285	286	287	288
Latitude	19.6	19.7	19.6	19.6	19.7	19.7	20.6	20.7	20.7
Longitude	149.6	149.6	149.7	149.8	149.8	149.9	150.5	150.6	150.6
Decapod larvae	0.7	2.7	1.4	0.5	1.2	1.5	3.5	1.4	0.3
Brachyuran larvae	0.7	1.3	1.1		0.6		1.4	0.7	1.0
Luciferids									
Stomatopod larvae									
Siphonophores					0.6				
Chaetognaths	3.4	4.7	1.8	3.3	3.6	10.2	5.5	3.4	6.4
Appendicularians	40.8	29.6	11.8	7.1	10.1	42.2	8.3	8.2	25.8
Polychaete larvae		1.3	0.4	0.5	0.6			0.7	
Pteropods		2.0		0.5					0.7
Salps	0.3	0.7	0.4						
Echinoid larvae									
Fish larvae			0.4	0.5		1.5	0.7		
Fish eggs	0.7	0.7	1.1	3.3				1.4	0.3
Mollusc larvae									
Cladocera									
Ostracods			1.1	2.2	1.2		1.4	0.7	1.3
Acrocalanus gracilis	0.3		0.7	0.5			0.7	0.7	
A. monachus									
A. gibber	0.3		0.7		0.6	4.4	0.7		0.7
Clausocalanus spp.				2.2					
Paracalanus spp.	25.0	76.1	119.1	88.7	123.7	371.2	79.0	37.0	32.5
Calocalanus pavo	0.3		0.4						
Canthocalanus pauper	0.7				2.4	1.5			3.7
Centropages orsinii		0.7	0.4						
C. furcatus									
C. elongatus				0.5					
Labidocera laevigata									
L. acuta									
L. minuta									
Undinula vulgaris	1.0	0.7	2.5	2.2	4.8		2.1	0.7	1.3
Temora stylifera									
T. turbinata									
Calanopia elliptica	1.4	0.7	2.5	1.6	3.6	2.9		1.4	5.0
Eucalanus subcrassus			0.7	1.1	2.4		5.5	2.1	5.0
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	3.8	4.0	0.7	1.6	1.2	5.8	3.5	2.1	7.4
A. negligens	0.3	1.3		1.6	1.2	1.5	0.7	0.7	0.7
Oithona rigida	2.1	6.7	6.1	7.1	1.8	1.5		1.4	2.3
O. plumifera	6.9	6.7	2.5	7.1	1.8	1.5	4.9	2.1	1.0
O. spp.	23.3	53.9	13.6	9.3	5.9	26.2	13.2	23.3	6.0
Corycaeus pacifica	1.0		1.4	0.5	0.6	2.9	2.1	0.7	0.7
C. (D) spp.	16.8	16.8	14.3	13.6	18.4	32.0	29.1	32.9	38.2
C. speciosus	1.0		0.7	0.5					0.3
C. lubbocki			3.2	0.5		1.5			0.3
Farranula spp. (male)	4.1	4.7	5.0	8.2	0.6	1.5	2.1	2.7	0.7
F. gibbulus (female)	1.0	1.3	2.2	1.6		2.9			
F. concinnus (female)	1.7	2.0	2.5	2.2				0.7	0.3
Onceae media	2.4	0.7	3.9	5.4	1.8	4.4	0.7	2.1	1.7
O. venusta	1.7		1.8	1.1			1.4	0.7	0.3
O. conifera				0.5					
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	5.8	2.7	2.9	4.4	1.2	2.9	2.8	4.1	1.3
Macrosetella gracilis									
Euterpina acutifrons					0.6	1.5	0.7	8.2	
Tortanus barbatus						2.9	0.7	0.7	0.7
Mecynocera clausi			1.1						
Other copepods			0.4		0.6				0.3
Total copepods	101.1	179.1	187.9	162.2	172.5	465.8	149.0	123.4	109.5
Total zooplankton	147.8	222.2	207.3	180.2	190.3	521.1	169.8	139.9	145.3
Mean chlorophyll	0.55	0.61	0.60	0.54	0.96	0.90	0.82	0.83	0.87
C. V. chlorophyll	0.08	0.07	0.06	0.09	0.07	0.03	0.01	0.03	0.06

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	289	290	291	293	294	295	296	297	298
Latitude	20.8	20.8	20.9	21.0	21.0	21.1	21.1	21.2	21.2
Longitude	150.7	150.7	150.8	150.9	150.9	151.0	151.1	151.1	151.2
Decapod larvae	2.6	0.3	0.3	0.7	0.7		2.7	1.4	1.4
Brachyuran larvae	1.3	1.0	0.3	0.7		1.4			1.4
Luciferids									
Stomatopod larvae									
Siphonophores		0.3	0.3	0.7			2.7	4.1	2.7
Chaetognaths	0.7	1.4	1.4	3.4	2.0	9.9	8.0	8.2	13.6
Appendicularians	15.7	7.0	11.4	17.5	40.8	31.1	90.8	9.5	10.8
Polychaete larvae			0.7		0.7	1.4		1.4	1.4
Pteropods	0.7					2.8			1.4
Salps									
Echinoid larvae					0.7				
Fish larvae	0.7	0.3					1.3	1.4	
Fish eggs	1.3	0.7							
Mollusc larvae									
Cladocera									
Ostracods					2.0				5.4
Acrocalanus gracilis			0.3						1.4
A. monachus									
A. gibber	3.9	0.3	0.3	2.0	1.4				4.1
Clausocalanus spp.									
Paracalanus spp.	26.2	18.4	44.1	91.5	118.3	223.0	435.4	348.9	329.4
Calocalanus pavo		0.7	0.3	0.7					
Canthocalanus pauper	4.6		0.3		2.7	4.2	17.4	21.8	12.2
Centropages orsinii			0.3			1.4		1.4	5.4
C. furcatus									
C. elongatus		1.4							
Labidocera laevigata	2.7								
L. acuta									
L. minuta									
Undinula vulgaris	2.0	0.3	1.0	0.7	2.0	2.8	15.0	36.8	23.0
Temora stylifera									
T. turbinata									
Calanopia elliptica	6.6	4.9	1.4	6.1	10.2	18.3	10.7	4.1	13.6
Eucalanus subcrassus	3.3	2.1	1.0	0.7	3.4	1.4	1.3	2.7	4.1
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	7.9	9.0	6.9	21.5	10.2	28.2	5.3	2.7	2.7
A. negligens							1.3		
Oithona rigida	0.7	5.6	1.4	4.7	3.4	18.3	9.3	9.5	10.8
O. plumifera	3.9	1.4	1.0	2.0	1.4	4.2		1.4	5.4
O. spp.	44.6	20.9	9.0	33.0	23.1	24.0	21.4	9.5	12.2
Corycaeus pacifica	1.3	2.1	0.7				4.0		1.4
C. (D) spp.	26.9	18.4	10.3	20.2	17.0	18.3	30.7	30.0	29.8
C. speciosus	0.7						1.3		
C. lubbocki	2.0	5.2	2.1	4.0	6.8	1.4	5.3	2.7	1.4
Farranula spp. (male)	2.6	7.6	6.2	3.4	3.4	5.6	1.3		1.4
F. gibbulus (female)	0.7	1.4	0.7	1.3				1.4	
F. concinnus (female)	0.7	0.7					1.3		
Onceae media		1.4	0.7	0.7			1.3		
O. venusta	1.3	1.0		0.7	0.7	1.4			
O. conifera	0.7	0.3	0.3		1.4				1.4
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	2.6	5.6	3.4	2.0	3.4	7.1			5.4
Macrosetella gracilis									
Euterpina acutifrons	4.6	2.8	1.7	0.7	4.1	2.8			1.4
Tortanus barbatus		0.3		0.7	0.7	1.4	1.3		1.4
Mecynocera clausi									
Other copepods					0.7				
Total copepods	147.4	110.2	93.7	195.8	212.8	362.7	562.6	475.6	467.6
Total zooplankton	170.4	121.3	108.2	218.6	259.7	409.3	668.1	501.5	505.6
Mean chlorophyll	0.86	0.89	0.86	0.81	0.86	0.85	0.86	0.81	0.81
C. V. chlorophyll	0.08	0.04	0.07	0.04	0.05	0.03	0.03	0.05	0.06

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	299	300	301	302	303	304	305	306	307
Latitude	21.3	21.3	21.4	21.7	21.7	21.8	21.8	21.8	21.8
Longitude	151.3	151.3	151.4	151.8	151.8	151.9	152.0	152.1	152.2
Decapod larvae	4.2	2.8	5.3		1.4			0.7	
Brachyuran larvae	1.4		7.9	2.9		1.4		0.3	0.4
Luciferids									
Stomatopod larvae									
Siphonophores	1.4	8.3		0.7		0.7		0.3	
Chaetognaths	5.6	5.5	18.4	2.2	4.9	2.1	5.7	1.7	2.2
Appendicularians	28.2	44.4	23.6	40.3	25.6	11.5	7.8	6.3	7.5
Polychaete larvae	1.4	2.8		0.7	0.7		0.7		
Pteropods		2.8	5.3	0.7		0.7	1.4	1.7	0.7
Salps									
Echinoid larvae						0.7			0.7
Fish larvae			2.6						0.7
Fish eggs					1.4			0.3	0.4
Mollusc larvae									
Cladocera									
Ostracods		8.3	2.6	0.7		0.7			
Acrocalanus gracilis	2.8				2.8				
A. monachus									
A. gibber	1.4		5.3	1.4		2.1	0.7		
Clausocalanus spp.									
Paracalanus spp.	298.6	652.1	527.7	21.6	53.4	27.9	12.8	7.7	3.6
Calocalanus pavo					0.7	0.7			
Canthocalanus pauper	22.5	8.3	28.9	0.7	2.8	3.6	0.7		
Centropages orsinii	9.9	16.6							
C. furcatus									
C. elongatus									
Labidocera laevigata			2.6		0.7			0.7	0.7
L. acuta									
L. minuta									
Undinula vulgaris	33.8	55.5	28.9		1.4				0.4
Temora stylifera									
T. turbinata									
Calanopia elliptica	22.5	30.5	13.1	5.8	9.7	10.7	8.5	7.0	4.7
Eucalanus subcrassus	4.2		5.3	2.9		2.9			
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis			13.1	5.8	2.8	4.3	7.8	5.6	14.0
A. negligens		5.5		2.2	2.1	3.6		1.7	
Oithona rigida	23.9	99.9	34.1	4.3	7.6	9.3	2.1	3.1	2.9
O. plumifera	1.4			12.9	16.6	19.3	11.4	6.6	4.3
O. spp.	35.2	44.4	31.5	2.2	20.8	37.9	14.2	0.7	9.3
Corycaeus pacifica	4.2	2.8	5.3	2.2	1.4	1.4	3.6		0.7
C. (D) spp.	28.2	27.7	23.6	26.6	37.4	42.2	20.6	16.0	22.3
C. speciosus			2.6	1.4	0.7		1.4	0.3	
C. lubbocki	2.8		10.5	1.4	7.6	5.0	5.7	6.6	8.6
Farranula spp. (male)		2.8		7.2	7.0	7.9	4.3	4.2	7.2
F. gibbulus (female)				2.2	0.7	3.6	0.7		0.4
F. concinnus (female)				2.2	1.4	0.7		0.3	0.4
Onceae media	1.4	2.8		2.9	4.2	0.7	2.8	1.0	0.4
O. venusta					1.4	1.4		0.3	
O. conifera				6.5		2.1	0.7	2.8	1.4
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	4.2	11.1	5.3	6.5	9.0	17.2	24.9	5.6	4.7
Macrosetella gracilis									
Euterpina acutifrons	4.2				2.8		8.5		2.9
Tortanus barbatus		2.8		0.7	0.7	2.1			
Mecynocera clausi									
Other copepods	1.4			0.7					
Total copepods	501.4	960.1	737.8	118.6	194.8	204.7	131.6	70.4	88.8
Total zooplankton	543.7	1035.0	803.4	166.8	228.8	222.6	147.3	81.9	101.3
Mean chlorophyll	0.81	0.86	0.93	0.66	0.50	0.53	0.52	0.45	0.45
C. V. chlorophyll	0.06	0.05	0.06	0.05	0.13	0.12	0.11	0.07	0.07

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	308	309	310	311	312	313	314	315	316
Latitude	21.9	21.9	22.0	21.8	21.8	21.7	21.6	21.6	21.5
Longitude	152.3	152.3	152.4	152.2	152.2	152.2	152.1	152.1	152.1
Decapod larvae	0.7	0.7	0.3	0.7	0.4	0.7			
Brachyuran larvae	0.3	0.7	0.3	1.1	0.4		0.4	0.4	
Luciferids			0.3						
Stomatopod larvae									
Siphonophores			2.1	1.1	1.1		1.5	0.4	
Chaetognaths	2.7	2.5	1.3	3.2	5.4	0.4	0.7	0.4	0.4
Appendicularians	6.4	7.6	2.6	9.7	6.9	11.8	14.8	8.1	5.9
Polychaete larvae		0.4	0.5	0.4	1.1		0.4		
Pteropods	1.0	3.3	3.1	1.4	1.5	0.4	0.4		0.4
Salps									
Echinoid larvae			0.3				0.4	0.4	
Fish larvae	0.3						0.4	0.4	
Fish eggs		0.7	1.0				1.9	3.3	1.1
Mollusc larvae									
Cladocera									
Ostracods									
Acrocalanus gracilis				0.7	1.1				
A. monachus	0.4								
A. gibber		0.4		0.4	0.7				
Clausocalanus spp.		0.4		0.4	0.4	0.4	0.4	0.4	
Paracalanus spp.	5.8	14.9	13.6	17.6	12.3	5.0	3.7	0.4	1.1
Calocalanus pavo	0.7								
Canthocalanus pauper			0.5	1.4	0.7	0.7	0.4	0.4	
Centropages orsinii						0.7			
C. furcatus									
C. elongatus									
Labidocera laevigata	0.7	0.7	1.0				0.4		
L. acuta									
L. minuta									
Undinula vulgaris		0.4	1.3	1.4	0.7	0.7	0.4		
Temora stylifera		0.4							
T. turbinata									
Calanopia elliptica	4.8	1.8	2.9	8.6	5.4	1.1		0.4	
Eucalanus subcrassus				0.7	1.5				
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica				0.4					
A. australis	7.8	12.7	7.6	0.7	1.5	3.2	4.1	5.6	3.7
A. negligens		0.7	0.5	1.1	1.1	1.4	0.4		
Oithona rigida	2.0	5.1	3.4	2.2	1.5	0.7	1.1		
O. plumifera	2.0	2.2	1.3	6.8	10.2	9.3	8.1	4.1	1.9
O. spp.	8.8	5.1	5.2	3.2	5.8	4.6	3.3	0.4	1.1
Corycaeus pacifica	0.7	1.1	2.6	3.6	1.1	0.7	0.7		0.4
C. (D) spp.	12.9	15.7	16.4	19.4	16.3	6.4	5.2	2.2	3.0
C. speciosus	0.3				0.7	0.4	3.3		0.4
C. lubbocki	5.8	2.2	2.3	16.2	13.4	10.3	18.1	10.4	11.5
Farranula spp. (male)	4.4	1.8	1.3	2.9	5.8	5.0	17.4	12.2	9.3
F. gibbulus (female)		0.7	0.5	1.1	1.5			1.5	0.4
F. concinnus (female)	0.3	0.7	0.3		0.4	0.4	0.7	2.2	1.9
Onceae media	0.3	0.4	0.8	0.4	3.3	2.1	1.9	4.1	7.0
O. venusta				0.4	1.5	0.4	0.7		1.5
O. conifera	1.0		1.6	6.8	0.7	0.4			
Sapphirina spp.		0.4							
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	3.4	5.1	3.4	19.4	16.7	5.0	5.6	4.1	7.4
Macrosetella gracilis		0.4	0.3	0.4					
Euterpina acutifrons	1.0	2.9	1.3	1.8	0.7	0.4		0.4	0.4
Tortanus barbatus		0.4		0.4					
Mecynocera clausi									
Other copepods				0.4					
Total copepods	62.1	75.4	68.0	117.7	104.8	59.2	75.9	49.6	51.5
Total zooplankton	73.6	91.4	79.8	135.3	121.5	72.4	96.7	63.0	59.3
Mean chlorophyll	0.47	0.57	0.44	0.62	0.51	0.41	0.41	0.34	0.33
C. V. chlorophyll	0.09	0.17	0.21	0.12	0.15	0.07	0.10	0.12	0.14

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	317	318	319	320	321	322	323	359	360
Latitude	21.4	21.3	21.3	21.2	21.1	21.0	21.0	18.2	18.2
Longitude	152.0	152.0	152.0	151.9	151.9	151.9	151.9	147.2	147.2
Decapod larvae				0.4			1.1		
Brachyuran larvae		0.4	0.4	1.5	0.7	0.4			
Luciferids									
Stomatopod larvae									
Siphonophores	0.4	0.7	0.4	0.4	0.7	0.7	2.2		
Chaetognaths			2.2	1.9	1.5	3.7	5.6		
Appendicularians	7.0	1.5	0.7	15.2	6.3	10.4	12.3	0.5	0.9
Polychaete larvae		0.4		0.7		2.2	2.2		
Pteropods			0.7	0.7			1.1		
Salps									
Echinoid larvae		0.7							
Fish larvae									
Fish eggs	0.7		0.7	1.9	1.9	0.4			0.9
Mollusc larvae									
Cladocera									
Ostracods									
Acrocalanus gracilis			0.7	1.1	0.7	3.0	13.4		0.2
A. monachus									
A. gibber									
Clausocalanus spp.	1.5	1.5	0.7	3.3	1.9	15.6	33.5		1.9
Paracalanus spp.	7.4	3.7	2.6	3.0	5.2	1.5	4.5	1.4	0.2
Calocalanus pavo	0.7	0.7	0.4	1.5	0.4	1.1	4.5	0.2	
Canthocalanus pauper	0.4	1.1	0.4				5.6		
Centropages orsinii				3.7	2.2	19.6	25.7	0.2	
C. furcatus									
C. elongatus			0.4			0.4	1.1		
Labidocera laevigata							1.1		
L. acuta	1.1								
L. minuta									
Undinula vulgaris			0.4			4.1	23.4		1.6
Temora stylifera	0.4	0.4							
T. turbinata									
Calanopia elliptica	1.1	0.4							0.9
Eucalanus subcrassus	0.4							0.2	
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	7.4	4.4	4.8	2.2	18.1	0.7	1.1		0.5
A. negligens	0.4	0.4		2.2		2.2	3.3	0.5	0.2
Oithona rigida	0.4	0.4	0.4	1.1	3.3		2.2	0.9	0.7
O. plumifera	5.2	4.1	4.8	7.0	1.9	3.3	2.2	4.9	3.3
O. spp.	1.1	0.4	1.9	2.6	15.2	3.0	25.7	0.5	1.9
Corycaeus pacifica	0.4	0.7		0.4		0.4			
C. (D) spp.	1.5	3.3	3.7	4.1	3.0	4.8	15.6	2.6	4.4
C. speciosus	1.1	0.7	1.5	1.5	1.5	0.4	2.2		
C. lubbocki	11.9	17.4	12.6	14.4	19.3	18.1	15.6		0.9
Farranula spp. (male)	7.0	11.1	17.4	18.9	22.6	37.0	33.5	3.5	3.3
F. gibbulus (female)	0.7	2.2	5.2	5.9	3.3	1.9	2.2	0.2	0.7
F. concinnus (female)	2.2	3.3	4.4	9.6	6.3	17.4	13.4	1.2	2.8
Onceae media	4.8	3.0	0.4	5.6	0.7	0.4	2.2	0.5	0.7
O. venusta	1.1	2.6	5.2	5.2	2.6	1.9	4.5		
O. conifera									
Sapphirina spp.	0.4								
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	5.9	0.7	6.7	10.7	2.2	2.2	45.7	0.7	0.9
Macrosetella gracilis									
Euterpina acutifrons		0.4							
Tortanus barbatus					0.4				
Mecynocera clausi			1.9					0.2	
Other copepods			0.4					0.2	
Total copepods	63.3	63.0	74.4	104.1	110.4	138.9	283.4	17.6	25.3
Total zooplankton	71.5	66.7	79.6	126.7	121.5	156.7	307.9	18.0	27.1
Mean chlorophyll	0.49	0.54	0.40	0.44	0.55	0.13	0.13	0.10	0.10
C. V. chlorophyll	0.15	0.08	0.07	0.11	0.14	0.53	0.30	0.02	0.07

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	361	362	363	364	365	366	367	368	369
Latitude	18.2	18.2	18.2	18.2	18.2	18.2	18.2	18.2	18.1
Longitude	147.1	147.0	146.9	146.8	146.7	146.7	146.6	146.5	146.4
Decapod larvae			0.2						
Brachyuran larvae		0.2				0.2	0.2		
Luciferids									
Stomatopod larvae									
Siphonophores	0.2								
Chaetognaths	0.2						0.2	0.2	0.6
Appendicularians	0.9	0.1							
Polychaete larvae							0.2		0.2
Pteropods	0.2								
Salps	0.2								
Echinoid larvae									
Fish larvae	0.2	0.3							
Fish eggs	2.6	0.5					0.5		1.5
Mollusc larvae									
Cladocera									
Ostracods									
Acrocalanus gracilis	0.2								
A. monachus									
A. gibber									
Clausocalanus spp.	2.8	0.1							
Paracalanus spp.		0.1							
Calocalanus pavo									
Canthocalanus pauper									
Centropages orsinii									
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta									
Undinula vulgaris		0.6							
Temora stylifera									
T. turbinata									
Calanopia elliptica		0.1							
Eucalanus subcrassus									
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica		0.1							
A. australis		0.2	0.5	0.2		0.2	0.5		0.1
A. negligens	1.2	0.8							
Oithona rigida	0.5					0.2			0.2
O. plumifera	6.8	0.5	0.2			0.2	0.7		0.2
O. spp.	1.9	0.2						0.4	0.4
Corycaeus pacifica							0.7		
C. (D) spp.	2.8						0.2	0.2	0.5
C. speciosus									
C. lubbocki	0.9	0.2	0.7	0.9	0.5	3.0	1.1	0.9	3.8
Farranula spp. (male)	1.6	0.2		0.7		0.2		0.4	1.7
F. gibbulus (female)		0.1							
F. concinnus (female)	0.9	0.1							
Onceae media	0.70.2	0.1							
O. venusta									
O. conifera									
Sapphirina spp.		0.1							
Sapphirella tropica									
Clytemnestra scutellata					0.3	0.5			
Microsetella rosea	0.7								
Macrosetella gracilis				0.2		1.8	0.2	1.3	2.9
Euterpina acutifrons									
Tortanus barbatus									
Mecynocera clausi	0.5								
Other copepods									0.1
Total copepods	21.2	1.4	1.4	2.0	0.8	6.2	3.4	3.4	12.2
Total zooplankton	25.4	2.1	1.6	2.0	0.8	6.4	4.5	4.1	15.0
Mean chlorophyll	0.14	0.21	0.22	0.19	0.22	0.17	0.21	0.15	0.15
C. V. chlorophyll	0.16	0.34	0.13	0.09	0.19	0.19	0.12	0.11	0.05

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	370	371	377	378	379	380	381	382	383
Latitude	17.9	17.8	15.4	15.4	15.4	15.4	15.4	15.4	15.4
Longitude	146.3	146.3	145.7	145.6	145.5	145.4	145.4	145.3	145.3
Decapod larvae	0.1	0.2	0.8	0.2		0.2	0.5	0.6	
Brachyuran larvae	0.1	0.2	1.6	2.5	0.7		1.2		2.0
Luciferids									
Stomatopod larvae				0.5		0.2	0.2		
Siphonophores	0.1			0.2	0.2	0.2	0.2	0.6	1.3
Chaetognaths	6.1	1.3	0.4	0.5	0.5	1.8	1.4	2.6	15.9
Appendicularians	5.3	7.2	1.6	0.5	26.6	22.9	17.5	20.5	40.5
Polychaete larvae	0.1	0.8		0.2	1.6	0.4	0.5		
Pteropods		0.2	0.8	0.2	1.9	0.9	0.5	1.3	2.0
Salps	0.2		3.2	1.6	0.2				
Echinoid larvae					0.2	0.2	0.5		
Fish larvae	1.4	1.8	1.6	0.5		0.2	0.9	0.6	2.0
Fish eggs	1.4		4.5	0.9	0.2	3.8	2.3	1.3	4.6
Mollusc larvae									
Cladocera	0.1		0.4						0.7
Ostracods									
Acrocalanus gracilis	0.1		0.8						
A. monachus									
A. gibber	0.2		14.7		0.2	0.2	1.6	12.8	19.2
Clausocalanus spp.			14.3	0.9	0.5	1.3	0.2	9.0	
Paracalanus spp.	2.9	1.5	0.4		0.2	0.4	1.8	8.3	9.3
Calocalanus pavo			0.4						
Canthocalanus pauper			0.4	0.2		0.4	15.9	32.0	81.6
Centropages orsinii			0.4			0.7	0.2		
C. furcatus	0.1						0.5	0.6	2.0
C. elongatus			0.8						
Labidocera laevigata									
L. acuta			0.2		1.6	3.2		0.7	
L. minuta	0.2								
Undinula vulgaris	16.2	5.0	2.0	0.2		9.8	3.0		
Temora stylifera									
T. turbinata									
Calanopia elliptica	0.1					0.4	0.7	16.0	9.3
Eucalanus subcrassus						0.2	0.5	0.6	
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica	1.0	4.0							
A. australis			11.0	14.1	8.6	0.9	0.2		
A. negligens	0.2	0.9			0.5	0.2			
Oithona rigida	0.3	0.6	0.8			1.1	1.2		1.3
O. plumifera	0.4	0.2	1.2	1.4	4.2	1.6	2.1	1.9	
O. spp.	0.5	0.1	5.7	6.5	37.8	8.5	3.5	4.5	1.3
Corycaeus pacifica	0.2	0.3				0.7	0.5		2.0
C. (D) spp.	0.8	0.4	0.4	0.7	0.2	1.6	4.6	12.1	7.3
C. speciosus			1.2	0.2					
C. lubbocki	1.9	0.2	2.5	0.2	1.6	3.6	0.9	5.1	2.0
Farranula spp. (male)	1.3		13.9	3.0	0.2	0.4	0.2		
F. gibbulus (female)	0.2			0.2					
F. concinnus (female)	0.8	0.2	3.7	0.5	0.5	0.2	0.2		2.0
Onceae media	0.2			0.2	0.5			1.3	
O. venusta			0.8						
O. conifera			0.8	0.2			0.2		
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata					0.2				
Microsetella rosea	0.1	0.1	4.5	0.7	0.9	0.4	0.2		
Macrosetella gracilis	3.7	1.3	2.0	0.5	0.2	0.4	6.9	3.2	11.3
Euterpina acutifrons		0.1				0.4	1.6	9.6	14.6
Tortanus barbatus							0.5		
Mecynocera clausi				0.2					
Other copepods			0.4	0.2					
Total copepods	31.3	11.0	83.0	30.0	56.5	35.2	50.2	117.0	167.8
Total zooplankton	46.0	23.0	94.9	39.5	90.1	66.3	75.8	144.5	236.8
Mean chlorophyll	0.14	0.15	0.20	0.17	0.19	0.17	0.17	0.21	0.19
C. V. chlorophyll	0.03	0.06	0.08	0.07	0.04	0.09	0.09	0.08	0.13

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	384	385	386	387	388	403	404	405	406
Latitude	15.4	15.4	15.4	15.4	15.4	15.4	15.2	15.0	14.8
Longitude	145.4	145.4	145.5	145.6	145.7	145.7	145.7	145.7	145.7
Decapod larvae				0.6	1.5		0.2	0.2	
Brachyuran larvae	0.7			0.6	1.2		0.3	0.9	0.5
Luciferids				0.2					
Stomatopod larvae									
Siphonophores		0.2			0.2		0.2		
Chaetognaths	0.4	0.5		0.4	0.5	0.2	0.2	0.6	
Appendicularians	13.2	7.4	1.9	1.4	2.1	1.6	3.2	41.9	4.0
Polychaete larvae			0.2		0.9	0.7	0.5	0.4	
Pteropods	0.4				0.3		0.2	0.4	
Salps	0.2	0.2	1.9	3.7					
Echinoid larvae	0.2								
Fish larvae		0.2		0.2	0.9	0.1	2.1	0.9	0.8
Fish eggs	2.0	0.5	0.2		3.6	1.1	0.8	4.0	2.2
Mollusc larvae									
Cladocera	0.2			0.4	0.5	0.2			
Ostracods									
Acrocalanus gracilis					1.1				
A. monachus									
A. gibber	0.9				0.2				
Clausocalanus spp.				1.0	9.3	1.4	2.0	10.7	2.5
Paracalanus spp.	0.9	0.2			0.2				
Calocalanus pavo									
Canthocalanus pauper	4.7	0.9							
Centropages orsinii		0.5	0.9						
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta	2.2				0.3				
L. minuta									
Undinula vulgaris	1.6	0.2	0.4	0.8					
Temora stylifera									
T. turbinata									
Calanopia elliptica	1.3	0.5	0.2						
Eucalanus subcrassus									
E. mucronatus									
Candacia pachydactyla					0.8		0.2	0.2	0.4
C. pectinata									
Acartia pacifica	2.2				0.2				
A. australis			1.3	1.0				1.8	0.4
A. negligens				0.2			0.3	0.4	
Oithona rigida		0.2						0.4	
O. plumifera					0.2	0.5	0.6		
O. spp.	0.4	0.2	0.6	1.2	0.2	0.1		0.4	
Corycaeus pacifica	0.7				0.3				
C. (D) spp.	2.0	0.7	1.3	0.8	1.8	0.2		1.5	1.0
C. speciosus				0.2					
C. lubbocki	0.7	0.5	0.2	0.2		0.4	0.2	1.5	1.2
Farranula spp. (male)	0.9	0.2		1.7	24.9	8.1	3.8	8.6	3.1
F. gibbulus (female)					0.5			0.2	
F. concinnus (female)		0.2		0.2	12.3	2.2	1.1	3.5	1.6
Onceae media			0.4		0.9	0.7	0.2	1.7	0.5
O. venusta					0.9	0.5		1.1	
O. conifera	0.2				0.2				
Sapphirina spp.					1.2		0.2	0.2	
Sapphirella tropica				0.2					
Clytemnestra scutellata						0.1			
Microsetella rosea	0.2		0.2	0.2	0.2	1.0	0.4		
Macrosetella gracilis	10.5	0.2	0.6	1.2	1.7	0.1		0.2	
Euterpina acutifrons	2.5	0.2		0.2	0.2				
Tortanus barbatus									
Mecynocera clausi	0.2								
Other copepods				0.2	0.2	0.1	0.2		
Total copepods	31.9	4.7	6.2	9.3	57.0	15.3	9.0	32.2	10.5
Total zooplankton	49.3	13.8	10.4	17.0	68.7	19.3	16.6	81.4	18.0
Mean chlorophyll	0.15	0.15	0.16	0.13	0.14	0.12	0.15	0.32	0.23
C. V. chlorophyll	0.10	0.09	0.04	0.07	0.10	0.20	0.35	0.17	0.27

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	407	408	409	410	412	413	414	415	416
Latitude	14.7	14.6	14.6	14.6	14.6	14.5	14.4	14.3	14.2
Longitude	145.6	145.5	145.4	145.4	145.1	145.1	144.9	144.8	144.6
Decapod larvae	0.2	0.6	0.6	5.4	0.3	0.5			1.0
Brachyuran larvae		0.4		1.5	0.8	1.2	0.6	0.1	1.9
Luciferids		0.1							
Stomatopod larvae				0.3					
Siphonophores					1.8		0.1	0.1	3.9
Chaetognaths	0.4	0.3	1.1	1.5	1.1	0.5	0.1		4.8
Appendicularians	16.7	5.5	11.9	154.1	12.4	2.8	1.0		41.4
Polychaete larvae	1.7	1.1	1.1	2.7	0.8			0.1	1.0
Pteropods	0.2		1.1	2.1	1.6		0.1		
Salps				0.5	3.2	2.1		44.3	
Echinoid larvae						0.2	0.1		
Fish larvae	1.3	1.8	3.4	5.7	0.5	1.4	0.9	0.5	
Fish eggs	2.4	0.5	2.8	12.0	9.5	6.7	0.9	1.2	2.9
Mollusc larvae						2.8	2.1	1.0	
Cladocera	0.4		0.6	1.2					
Ostracods	0.7	0.2							
Acrocalanus gracilis	0.2			0.6	0.5				1.9
A. monachus	0.1								
A. gibber		18.3							
Clausocalanus spp.	16.7	13.7	57.6	8.4	6.8	0.2	0.2		1.9
Paracalanus spp.						3.7		0.4	29.8
Calocalanus pavo									
Canthocalanus pauper				0.6			0.5		19.3
Centropages orsinii				0.6					
C. furcatus		5.8							
C. elongatus	0.2	0.1							
Labidocera laevigata				1.2					
L. acuta					0.9	0.1			
L. minuta		1.9							
Undinula vulgaris				8.7	2.6	0.9	1.8		5.8
Temora stylifera									
T. turbinata									
Calanopia elliptica				0.9		0.7	0.9		13.5
Eucalanus subcrassus									
E. mucronatus									
Candacia pachydactyla	1.9	0.4	4.5		0.5		0.1		
C. pectinata									
Acartia pacifica									
A. australis	2.1	0.6	4.5	4.8	1.8	7.4	11.9	0.5	5.8
A. negligens					0.5		0.1		
Oithona rigida	0.6	0.1		0.3		6.2	1.3		6.7
O. plumifera	0.2			1.8	3.9	1.4	0.1		1.0
O. spp.	0.4		2.3	16.5	18.7	4.9	2.4		2.9
Corycaeus pacifica		3.9							
C. (D) spp.	1.3	0.1	7.9	2.4	3.4	1.4	0.9	0.2	27.0
C. speciosus		0.1							
C. lubbocki	1.7	0.5	1.1	0.9	5.5	2.3	2.9	1.2	21.2
Farranula spp. (male)	13.2	8.2	54.2	3.9	11.8	1.4	0.8	0.1	1.0
F. gibbulus (female)			1.1	0.6	0.8		0.1		
F. concinnus (female)	4.1	3.4	25.4	1.8	4.7	0.5	0.5	0.2	
Onceae media	4.9	1.1	7.9	2.1	3.4		0.2		1.0
O. venusta		0.3	1.1		0.3				
O. conifera									
Sapphirina spp.	0.4	0.3	2.3	0.3	0.3	0.2			
Sapphirella tropica									
Clytemnestra scutellata	0.2			0.3					
Microsetella rosea			0.6	2.7	1.1		0.1		
Macrosetella gracilis			2.3	1.2		0.2		0.7	17.3
Euterpina acutifrons						0.5			5.8
Tortanus barbatus									
Mecynocera clausi					0.5				
Other copepods				0.3	0.3				
Total copepods	47.9	28.9	172.7	60.7	66.8	32.9	25.0	3.3	191.6
Total zooplankton	71.2	39.2	195.2	247.1	96.0	52.1	33.7	6.5	292.6
Mean chlorophyll	0.17	0.19	0.18	0.28	0.26	0.39	0.42	0.26	0.39
C. V. chlorophyll	0.13	0.14	0.28	0.83	0.16	0.16	0.29	0.26	0.16

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	420	421	422	423	424	425	426	427
Latitude	14.1	14.2	14.3	14.4	14.4	14.5	14.6	14.6
Longitude	144.4	144.6	144.7	144.8	144.9	145.1	145.1	145.3
Decapod larvae	1.5	3.9		0.2				
Brachyuran larvae		5.9	0.1	0.7	1.0	0.2	0.1	0.6
Luciferids								
Stomatopod larvae								
Siphonophores	1.0	2.0	0.3	0.4	0.7			0.4
Chaetognaths	3.6	12.8	0.2	0.4		0.1	0.3	0.1
Appendicularians	8.2	52.2	1.8	2.2	2.2	1.3	1.3	4.0
Polychaete larvae						0.3	0.6	0.7
Pteropods		1.0		0.4	1.2	0.1		0.1
Salps	29.2	1.0	4.3	6.0	6.7	2.6	0.6	
Echinoid larvae			0.1		0.2			
Fish larvae	1.5	1.0		1.3	2.2	0.1	0.1	
Fish eggs	1.0	5.9	0.1	2.2	6.5	4.1	6.4	1.9
Mollusc larvae	0.5		1.3	1.8	3.1	0.6	0.2	
Cladocera					0.2	0.1		
Ostracods	0.5	1.0			0.2			
Acrocalanus gracilis		1.0			0.2	0.1	0.2	0.1
A. monachus	0.1	0.3						
A. gibber	7.2	14.8	0.1	0.7	0.5			0.1
Clausocalanus spp.	1.0		0.1	0.2	0.2	1.3	6.8	2.2
Paracalanus spp.	17.9	42.3	0.3	6.6		1.6		
Calocalanus pavo							0.1	
Canthocalanus pauper	2.6	24.6	0.1	5.3	1.0	0.1		0.1
Centropages orsinii						0.1		
C. furcatus	0.5	15.8			0.5			
C. elongatus	0.5					0.1	0.2	0.3
Labidocera laevigata								
L. acuta							0.5	
L. minuta	1.0	4.9	0.3	0.2			0.1	
Undinula vulgaris		2.0	1.4	3.8	0.7	0.5		
Temora stylifera								
T. turbinata	0.5	2.0		0.2	0.2			
Calanopia elliptica	4.1	15.8	0.7	1.5	2.6	0.3		
Eucalanus subcrassus	1.5	4.9						
E. mucronatus								
Candacia pachydactyla	2.2							
C. pectinata								
Acartia pacifica	4.1	36.4						
A. australis			3.2	16.4	6.5	0.9	0.1	1.0
A. negligens	0.5		0.1		0.2		1.4	0.9
Oithona rigida		5.9	0.9	4.0	2.9	0.7		0.1
O. plumifera	3.6	3.0	0.1	1.3	2.4	0.1	0.8	0.7
O. spp.	5.6	3.0	0.7	3.1	5.7	0.5	0.2	0.6
Corycaeus pacifica	2.6	3.9		0.7	0.5		0.1	
C. (D) spp.	16.9	34.5	0.7	5.1	7.7	1.5	0.7	0.6
C. speciosus								
C. lubbocki	15.3	29.5	0.6	2.7	4.3	1.6	0.9	0.4
Farranula spp. (male)					0.7	5.8	15.7	1.8
F. gibbulus (female)						0.3	0.5	0.4
F. concinnus (female)	1.5				0.2	1.3	14.5	1.2
Onceae media						0.3	0.7	0.6
O. venusta	1.4	0.1						
O. conifera	1.5			0.4	1.0			
Sapphirina spp.						0.1		
Sapphirella tropica								
Clytemnestra scutellata								
Microsetella rosea	2.6	3.0			0.2		0.9	0.1
Macrosetella gracilis	9.7	18.7	0.3	0.4	2.9	0.2	1.5	0.9
Euterpina acutifrons	2.0	9.8		0.7	2.6	0.1		
Tortanus barbatus	3.6	1.0			0.2			
Mecynocera clausi	0.2	0.6						
Other copepods								
Total copepods	103.3	275.7	9.7	53.4	43.8	17.5	49.1	12.7
Total zooplankton	150.4	362.3	18.1	69.1	68.0	27.1	58.8	20.7
Mean chlorophyll	0.42	0.41	0.33	0.41	0.50	0.33	0.26	0.31
C. V. chlorophyll	0.12	0.08	0.11	0.20	0.20	0.14	0.10	0.21

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	428	429	430	431	433	434	435	469	470
Latitude	14.7	14.6	14.7	14.8	15.0	15.2	15.4	16.1	16.3
Longitude	145.4	145.6	145.6	145.7	145.7	145.7	145.7	145.9	146.0
Decapod larvae	5.1	0.3	0.2	0.2	0.2	1.4	0.4	1.6	0.4
Brachyuran larvae	0.7	1.6	2.0	1.1	0.5	0.9	0.5	1.2	0.3
Luciferids	0.7	0.1					0.1		
Stomatopod larvae							0.1		
Siphonophores	2.9		0.2		0.2	0.2	0.3		
Chaetognaths	2.2	0.7	0.8	0.7	0.3	0.7	1.4	0.1	0.4
Appendicularians	224.0	1.6	6.7	1.6	14.4	16.1	7.8	7.8	3.5
Polychaete larvae	0.7	0.3	0.2			0.2	0.5	0.3	0.3
Pteropods	1.5	0.1					0.1	0.3	
Salps	0.7	0.1							
Echinoid larvae									
Fish larvae	1.5		1.4	2.1	1.0	1.6	0.5		0.1
Fish eggs	37.3	1.0	4.7	5.3	3.6	9.9	4.4	11.6	16.4
Mollusc larvae	5.9	0.3				0.5			
Cladocera			1.0	0.1	0.5	0.7	1.8	2.0	1.1
Ostracods		0.1	0.2						
Acrocalanus gracilis	2.2	0.3	0.4	0.8	1.1	2.1		1.3	0.4
A. monachus								0.3	
A. gibber	1.5								
Clausocalanus spp.	3.7	4.4	9.4	2.2	3.9	10.8	8.8	8.0	3.3
Paracalanus spp.	2.9							0.3	
Calocalanus pavo		0.1	0.2						
Canthocalanus pauper	0.7		0.2						
Centropages orsinii	3.7			0.2				0.5	3.0
C. furcatus									
C. elongatus		0.3	0.4	0.1	0.2	0.2	0.3		0.2
Labidocera laevigata	2.2								
L. acuta									
L. minuta							0.1		
Undinula vulgaris	6.6		0.2	0.1		0.5	0.9	0.1	
Temora stylifera									
T. turbinata									
Calanopia elliptica	0.7								0.1
Eucalanus subcrassus									
E. mucronatus						0.2			
Candacia pachydactyla		0.3	0.4	0.4	0.3	1.1	0.6		
C. pectinata									
Acartia pacifica									
A. australis	34.4	0.7	3.9	6.1	1.3	0.5	7.3	6.6	18.3
A. negligens	2.2					0.7	1.1	0.7	
Oithona rigida	1.5	1.0	1.0	1.0	0.3		0.6	0.7	0.6
O. plumifera	11.7	0.6	0.8		1.0	0.7	3.7	1.6	0.3
O. spp.	7.3	1.1	3.9	0.7	1.3	2.3	1.0	0.5	0.9
Corycaeus pacifica	0.7							0.3	
C. (D) spp.	5.9	1.7	1.4		0.5	1.4	1.0	0.9	0.2
C. speciosus							0.3	0.7	
C. lubbocki	0.7	1.4	4.1	0.7	1.0	3.4	0.6	6.1	6.0
Farranula spp. (male)	4.4	4.9	7.5	3.7		13.8	7.7	5.7	1.5
F. gibbulus (female)	0.7	0.1		0.2	0.3		0.1	0.5	0.3
F. concinnus (female)	7.3	5.6	7.5	1.7	5.7	3.4	4.9	2.2	1.1
Onceae media		3.3	3.1		1.5	5.1	1.9	2.4	0.8
O. venusta		1.6	1.0	0.1	0.3	1.6	0.6	0.7	0.3
O. conifera									
Sapphirina spp.	0.7				0.2	0.2	0.8		
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	4.4	0.3	0.2	0.1	1.5	0.9	2.5	0.5	0.2
Macrosetella gracilis	0.7	0.7	0.4	0.4	1.1	0.2	1.1	0.1	0.1
Euterpina acutifrons	2.2						0.1		
Tortanus barbatus									
Mecynocera clausi							0.5		
Other copepods	1.46			0.1	0.8		0.9		
Total copepods	109.1	28.4	46.0	18.6	21.4	49.1	46.1	40.7	37.7
Total zooplankton	392.3	34.7	63.3	29.7	42.0	81.3	64.0	65.7	60.4
Mean chlorophyll	0.59	0.27	0.32	0.40	0.33	0.30	0.27	0.48	0.35
C. V. chlorophyll	0.21	0.08	0.19	0.10	0.33	0.16	0.11	0.14	0.21

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	471	472	473	474	475	476	477	478	479
Latitude	16.5	16.6	16.8	17.0	17.2	17.3	17.9	17.9	18.1
Longitude	146.0	146.1	146.3	146.4	146.4	146.4	146.8	147.0	147.2
Decapod larvae				0.1	0.7	7.1	0.1	0.1	
Brachyuran larvae			0.1	0.1		1.5		0.5	
Luciferids									
Stomatopod larvae									
Siphonophores					0.2				
Chaetognaths			0.1	0.1		2.0	0.1	0.3	
Appendicularians	1.0	2.1	1.5	2.6	2.5	10.1	3.2	0.1	0.5
Polychaete larvae				0.1		0.5	0.1	0.1	
Pteropods						3.0	0.2		
Salps					3.5				
Echinoid larvae	0.1					0.5			
Fish larvae	0.1	0.4	0.1	0.3	0.5	4.1	0.2	0.2	
Fish eggs	4.2	39.0	5.5	2.0	5.0	10.6	1.4	0.9	0.2
Mollusc larvae									
Cladocera		0.5	4.3	1.0	0.7			0.1	
Ostracods									
Acrocalanus gracilis		0.3		0.1		2.0	0.1		
A. monachus									
A. gibber									
Clausocalanus spp.	0.2	0.8	0.2	0.8	0.7	3.5		0.2	0.1
Paracalanus spp.						4.1	6.8	0.1	
Calocalanus pavo									
Canthocalanus pauper									
Centropages orsinii	1.4	5.9	4.8	10.4	7.1	16.7	2.7	0.8	8.7
C. furcatus									
C. elongatus		0.1	0.1	0.2	0.2				
Labidocera laevigata					0.5				
L. acuta							0.3		
L. minuta									
Undinula vulgaris				0.2		2.0	0.3	1.3	0.8
Temora stylifera					0.5	0.5			
T. turbinata									
Calanopia elliptica					0.2		3.0	1.3	0.5
Eucalanus subcrassus									
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	9.3	33.1	10.8	34.8	33.1	46.6	14.3	19.7	22.0
A. negligens						0.5			
Oithona rigida	0.2	0.5	0.2	0.7	0.7	1.0	1.2	0.8	0.8
O. plumifera	0.4				1.1	8.1	0.1		
O. spp.	0.3	1.4		1.0	8.5	9.6	2.1	1.3	0.5
Corycaeus pacifica						0.5	0.6	0.2	
C. (D) spp.	0.5	0.3	1.0	0.5	0.7	3.5	0.6	0.9	0.1
C. speciosus	0.1			0.1	0.7	1.5	0.2		0.6
C. lubbocki	7.2	2.4	5.0	1.0	3.7	3.5	1.0	1.0	0.6
Farranula spp. (male)	1.7	1.5	4.2	3.6	4.3	3.0	1.5	1.3	0.3
F. gibbulus (female)			0.1			1.0			
F. concinnus (female)	0.3	1.9	3.0	0.8	0.9	2.5	0.3	0.1	0.3
Onceae media	1.3	0.5	0.2		1.1	2.0	0.3	0.1	
O. venusta	0.3	0.1	0.5		0.5		0.3		
O. conifera							0.2		
Sapphirina spp.									
Sapphirella tropica				0.1	0.2				
Clytemnestra scutellata	0.2	0.4	1.1	0.5	0.5	0.5			0.1
Microsetella rosea		0.2	0.1		0.7	1.5	0.7	0.8	
Macrosetella gracilis			0.2	0.3	0.5	1.5	0.9	0.5	
Euterpina acutifrons									
Tortanus barbatus									
Mecynocera clausi									
Other copepods					0.1	0.5			
Total copepods	23.5	49.5	31.7	55.2	66.2	116.1	37.4	30.7	35.4
Total zooplankton	28.9	91.5	43.3	61.6	75.8	159.1	42.7	33.2	36.0
Mean chlorophyll	0.36	0.31	0.25	0.28	0.29	0.50	0.37	0.24	0.20
C. V. chlorophyll	0.16	0.13	0.10	0.18	0.07	0.29	0.33	0.08	0.06

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	480	481	482	483	484	485	486	487	488
Latitude	18.1	18.2	18.2	18.3	18.3	18.4	18.9	19.0	19.0
Longitude	147.3	147.3	147.2	147.1	147.1	147.0	146.7	146.8	146.8
Decapod larvae		0.3				0.9		0.9	0.4
Brachyuran larvae		0.2						2.7	
Luciferids		0.2							
Stomatopod larvae	0.4								
Siphonophores						0.5			
Chaetognaths	0.9	0.2	2.5	0.4	1.1		18.3	14.3	18.0
Appendicularians					2.1	0.5	49.4	51.0	94.7
Polychaete larvae			0.6		0.5				
Pteropods	0.4		0.3				12.8	18.8	11.0
Salps			42.8	41.5	20.4	7.3	0.9	1.3	
Echinoid larvae						0.5			
Fish larvae	0.4		0.3	0.4	1.1	0.5	2.7	0.9	3.5
Fish eggs			0.8	1.7	3.7	0.5		2.7	
Mollusc larvae									
Cladocera	3.9		0.6						
Ostracods									
Acrocalanus gracilis	0.4		0.3				1.8	2.7	0.4
A. monachus									
A. gibber								16.1	6.1
Clausocalanus spp.	0.9	0.8	1.4	1.3					
Paracalanus spp.	0.4		11.8	0.8	4.3	5.4	59.4	93.1	15.3
Calocalanus pavo									
Canthocalanus pauper							129.9	112.8	41.6
Centropages orsinii	49.6	11.6	10.7	12.6	10.1	8.6			
C. furcatus									
C. elongatus									
Labidocera laevigata			0.3						
L. acuta	0.2		0.8				3.6		
L. minuta									
Undinula vulgaris	2.2	2.3	12.1	1.3	0.5		31.1	23.3	5.3
Temora stylifera									
T. turbinata									
Calanopia elliptica	0.4	0.8	3.9	0.8	0.5	1.4		0.9	
Eucalanus subcrassus							0.9	0.9	
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	98.7	44.4	75.1	78.4	121.9	88.3	0.9	13.4	
A. negligens									
Oithona rigida	2.2	1.0	3.3	1.7	2.1				1.8
O. plumifera							0.9	0.9	
O. spp.	2.6	1.0	0.8	6.7	17.0	5.9		6.3	0.4
Corycaeus pacifica				0.4	1.6	0.5	1.8	2.7	0.4
C. (D) spp.	0.9	1.2	1.9	3.8	10.1	2.7	6.4	6.3	1.3
C. speciosus							0.9		0.4
C. lubbocki	6.1	2.0	2.5	2.9	2.1	3.6		1.8	0.4
Farranula spp. (male)	7.9	1.5	2.8	2.1	3.7	2.3	0.9		
F. gibbulus (female)			0.3		0.5		0.9		
F. concinnus (female)	3.5	0.5		1.7	0.5	0.9			
Onceae media				1.3		0.5	6.4		4.4
O. venusta									
O. conifera									
Sapphirina spp.	0.4	0.2							
Sapphirella tropica									
Clytemnestra scutellata		0.2			2.1				
Microsetella rosea	0.9	0.3	0.3	1.3	1.6			1.8	0.4
Macrosetella gracilis			1.4	3.4	10.6	4.5	2.7	2.7	0.4
Euterpina acutifrons						0.5	21.0	104.7	20.6
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	177.3	68.1	128.8	121.2	189.5	125.0	266.1	393.9	99.5
Total zooplankton	183.0	68.9	133.8	166.5	239.5	148.6	356.7	486.1	228.8
Mean chlorophyll	0.18	0.20	0.20	0.47	0.56	0.66	0.38	0.34	0.31
C. V. chlorophyll	0.03	0.09	0.06	0.39	0.12	0.18	0.03	0.03	0.05

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	489	490	493	499	520	522	524	525	526
Latitude	19.1	19.1	19.3	19.2	19.2	19.2	19.2	19.3	19.3
Longitude	146.9	147.0	147.5	147.4	147.5	147.5	147.6	147.6	147.7
Decapod larvae	0.4		5.0	7.9		3.0	1.9		1.9
Brachyuran larvae		0.9	2.2		0.4	3.0			0.9
Luciferids						3.0		0.8	
Stomatopod larvae				0.5					
Siphonophores	0.4		0.7		1.2				2.8
Chaetognaths	20.4	10.7	2.9	5.9	1.6		3.9	4.2	7.5
Appendicularians	74.5	20.4	20.8	2.5	8.2	206.5	131.8	88.2	147.6
Polychaete larvae	0.4		2.9	1.5	0.8		1.9	2.5	2.8
Pteropods		6.2	1.4	2.5	0.8	6.1	5.8	9.3	6.6
Salps		0.7		1.2		1.9	11.0	4.7	
Echinoid larvae			5.7	14.8	22.1	9.1	17.4	5.1	8.5
Fish larvae	0.9	1.8	1.4	0.5	0.4		1.9		
Fish eggs			2.2	0.5	0.4	9.1	5.8	1.7	2.8
Mollusc larvae			0.7		2.1				1.9
Cladocera			1.4					0.8	1.9
Ostracods							1.9		
Acrocalanus gracilis		3.6	2.2	2.0	2.9	18.2	13.6	5.9	16.9
A. monachus									
A. gibber	3.8	3.6	7.9	3.5			1.9		0.9
Clausocalanus spp.				0.5					
Paracalanus spp.	18.7	18.7	2.9	12.8	1.6	33.4	15.5	5.1	24.4
Calocalanus pavo			0.7	1.0	0.4		1.9		0.9
Canthocalanus pauper	55.4	119.1		0.5		3.0			
Centropages orsinii						3.0	1.9	0.8	6.6
C. furcatus			5.0	1.0					
C. elongatus									
Labidocera laevigata						6.1			
L. acuta	0.9	1.8							
L. minuta		0.9	2.2				3.9		1.9
Undinula vulgaris	4.7	8.0							
Temora stylifera						3.0			
T. turbinata			0.7						
Calanopia elliptica			7.9	1.0	1.2	3.0	5.8	1.7	1.9
Eucalanus subcrassus	0.4		8.6	1.5			3.9		
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica		0.9					3.9		
A. australis			3.6	3.5	0.8		1.9	1.7	2.8
A. negligens			0.7	1.0			1.9		
Oithona rigida			8.6	3.0	10.3	45.6	27.1	10.2	8.5
O. plumifera			9.3	6.4	2.5	3.0			
O. spp.	1.8	9.3	5.9	12.3	63.8	25.2	6.8	6.6	
Corycaeus pacifica			5.7		4.5	9.1		9.3	3.8
C. (D) spp.	2.6	7.1	15.8	10.9	6.2	60.7	19.4	11.9	17.9
C. speciosus									
C. lubbocki			38.1	8.4	4.5	15.2	21.3	11.9	10.3
Farranula spp. (male)				0.5			1.9		1.9
F. gibbulus (female)	0.9								
F. concinnus (female)			5.0		0.4				
Onceae media		0.9		3.0					
O. venusta									
O. conifera	0.9	0.9		1.0	0.4				
Sapphirina spp.			2.2		0.4		1.9		
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	0.4		34.5	12.8	23.0	403.9	323.8	117.1	134.4
Macrosetella gracilis	0.4	1.8	2.9	2.0	2.5	6.1	5.8	5.9	5.6
Euterpina acutifrons		63.1	6.5	4.9	12.7	82.0	23.3	4.2	5.6
Tortanus barbatus			1.4						
Mecynocera clausi									
Other copepods			1.44						
Total copepods	88.2	231.9	180.3	86.8	86.5	759.3	506.0	192.6	251.9
Total zooplankton	185.3	271.9	228.4	123.3	125.9	999.2	680.5	316.5	441.8
Mean chlorophyll	0.29	0.30	0.55	0.65	0.67	0.66	0.71	0.70	0.75
C. V. chlorophyll	0.07	0.06	0.07	0.11	0.06	0.03	0.03	0.04	0.02

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	527	528	529	530	531	533	534	535	536
Latitude	19.4	19.4	19.5	19.5	19.5	19.6	19.7	19.7	19.8
Longitude	147.8	147.9	148.0	148.0	148.1	148.3	148.3	148.4	148.5
Decapod larvae	0.9		0.4			0.8	3.4	4.2	0.8
Brachyuran larvae	0.9	2.1	0.4			0.8			1.7
Luciferids									
Stomatopod larvae						0.8		8.4	0.8
Siphonophores		5.2	0.4		0.8				
Chaetognaths	13.1	5.2	3.8	10.6	15.1	4.1	14.3	61.0	11.0
Appendicularians	64.4	98.3	38.9	23.9	36.8	87.9	67.5	29.4	18.6
Polychaete larvae	2.6	3.1	0.8	3.5	6.7	5.7	5.1	8.4	4.2
Pteropods	7.8	7.2	2.1		0.8	2.5		4.2	4.2
Salps	7.0	8.3	6.3	3.5	3.3	2.5	4.2		0.8
Echinoid larvae	21.8	35.2	4.6	25.7	19.2	115.8	70.8	54.7	64.4
Fish larvae0.8									
Fish eggs	7.0	1.0	4.2	1.8	1.7		0.8	2.1	0.8
Mollusc larvae	0.9			1.8	0.8	4.9			
Cladocera							6.7		0.8
Ostracods	0.9							2.1	
Acrocalanus gracilis	14.8	11.4	13.1	18.6	17.6	1.6	7.6	16.8	
A. monachus	0.9								
A. gibber							3.4	2.1	2.5
Clausocalanus spp.									
Paracalanus spp.	5.2	5.2	2.1	2.7	6.7		13.5	27.3	10.2
Calocalanus pavo	1.7	2.1			0.8	0.8	0.8	2.1	1.7
Canthocalanus pauper		1.0		1.8	1.7	0.8	3.4	6.3	1.7
Centropages orsinii	21.8	15.5	5.9	22.2	17.6	10.7	4.2		3.4
C. furcatus							1.7	10.5	0.8
C. elongatus									
Labidocera laevigata									
L. acuta		0.4							
L. minuta					1.7	0.8		2.1	
Undinula vulgaris	0.9		3.8	8.0	14.2	1.6			
Temora stylifera							0.8	2.1	
T. turbinata									
Calanopia elliptica		1.0					1.7	2.1	0.8
Eucalanus subcrassus						1.6	3.4	10.5	0.8
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica								6.3	3.4
A. australis		4.1	1.3	21.3	36.8	1.6	13.5	10.5	3.4
A. negligens	1.7					3.3	0.8		
Oithona rigida	10.4	9.3	1.7	2.7	7.5	4.9	5.1		3.4
O. plumifera	0.9	3.1	1.3	0.9	0.8	5.7	8.4	25.2	11.9
O. spp.	25.2	11.4	4.2	19.5	14.2	9.0	10.1	67.3	21.2
Corycaeus pacifica	3.5	3.1	3.8	8.9	6.7	4.9	0.8	2.1	1.7
C. (D) spp.	22.6	23.8	13.1	24.8	23.4	18.1	23.6	33.6	28.8
C. speciosus	0.9	1.0			0.8	0.8			
C. lubbocki		15.5	7.2	19.5	10.9	4.9	5.1		8.5
Farranula spp. (male)	6.1	1.0	4.2	6.2			0.8		1.7
F. gibbulus (female)	1.7	4.1	2.1	4.4	2.5		0.8	2.1	
F. concinnus (female)	1.7	2.1	0.4	1.8	1.7				1.7
Onceae media	0.9			1.8	2.5	2.5	3.4	8.4	
O. venusta	0.9		0.8		0.8				
O. conifera								6.3	
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	128.8	103.5	47.3	84.2	53.5	47.6	83.5	227.0	51.7
Macrosetella gracilis	23.5	29.0	24.1	44.3	30.9	26.3	11.8	44.1	28.0
Euterpina acutifrons	3.5	7.2	0.8	1.8		1.6	1.7	12.6	0.8
Tortanus barbatus							1.7	4.2	
Mecynocera clausi									
Other copepods									
Total copepods	277.6	254.5	137.8	295.3	253.3	149.5	209.9	527.6	188.1
Total zooplankton	404.6	420.0	199.9	366.2	338.6	375.4	382.8	702.1	297.4
Mean chlorophyll	0.82	0.79	0.77	0.76	0.72	0.85	0.81	0.82	0.76
C. V. chlorophyll	0.06	0.06	0.02	0.04	0.03	0.04	0.07	0.03	0.04

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	537	538	539	542	543	544	545	546	547
Latitude	19.8	19.8	19.9	20.6	20.6	20.7	20.7	20.8	20.9
Longitude	148.6	148.7	148.7	150.5	150.5	150.6	150.7	150.7	150.8
Decapod larvae	1.6	1.7		0.8	1.0				
Brachyuran larvae				0.8		1.0	1.3	0.4	0.2
Luciferids									
Stomatopod larvae	3.3	6.1	5.0						0.5
Siphonophores	3.3			0.8					0.7
Chaetognaths	9.8	17.3	9.0	6.2	3.8	4.9	1.3	2.2	1.2
Appendicularians	89.6	32.1	34.1	45.9	15.3	8.3	0.8	4.7	10.7
Polychaete larvae	8.1	0.9	7.0	3.9		0.5			
Pteropods	1.6	1.7	5.0		3.8				
Salps	3.3	3.5	4.0						
Echinoid larvae	151.5	150.7	232.8	10.1	5.7				
Fish larvae		0.9	1.0	3.9	1.9	1.0	0.8	1.3	0.5
Fish eggs	3.3					0.5	0.8	0.9	1.2
Mollusc larvae		4.3		0.8	3.8			0.4	1.0
Cladocera			1.0						
Ostracods					3.8				
Acrocalanus gracilis	1.6	0.9	1.0	3.9	7.7	1.9			0.2
A. monachus									
A. gibber	1.6					0.5			
Clausocalanus spp.				1.6	1.0			0.4	
Paracalanus spp.	22.8	22.5	25.1	7.0	27.8	3.4	3.3	0.4	0.7
Calocalanus pavo			2.0						
Canthocalanus pauper		2.6	2.0		3.8				
Centropages orsinii	1.6	0.9		13.2	6.7	7.3	11.3	6.5	10.9
C. furcatus		1.7	1.0	3.1	1.9	1.0			0.2
C. elongatus								0.4	
Labidocera laevigata									
L. acuta									
L. minuta		0.9		0.8					
Undinula vulgaris			1.0	23.3	1.0	0.5	0.4		0.2
Temora stylifera									
T. turbinata									
Calanopia elliptica					4.8	1.5	0.4		
Eucalanus subcrassus	4.9	2.6	8.0	0.8	2.9				
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica			1.0						
A. australis	13.0	12.1	8.0	77.8	285.4	148.5	61.9	47.8	33.8
A. negligens	1.6	0.9							
Oithona rigida		0.9		1.6	3.8		1.7	0.4	1.0
O. plumifera	45.6	30.3	22.1		1.0		0.4		0.5
O. spp.	24.4	7.8	8.0	15.6	35.4	38.5	8.8	6.9	2.0
Corycaeus pacifica		2.6	3.0	5.4	1.9		0.4	0.4	0.2
C. (D) spp.	31.0	17.3	11.0	17.1	23.9	2.9	3.3	0.9	1.0
C. speciosus									
C. lubbocki	4.9	3.5	4.0	3.1	9.6	1.0	0.8	1.3	0.2
Farranula spp. (male)	1.6	1.7	1.0		1.0	1.0	0.4	0.9	0.2
F. gibbulus (female)	1.6	1.7						0.4	
F. concinnus (female)									
Onceae media	1.6	1.7			1.0				
O. venusta									
O. conifera	4.9	2.6	5.0	0.8					
Sapphirina spp.	1.6		1.0						
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	174.3	25.1	32.1	15.6	32.6	5.8	2.5	3.9	4.0
Macrosetella gracilis	140.1	26.9	52.2	21.0	58.4	6.3	9.2	9.5	2.2
Euterpina acutifrons	6.5	1.7	2.0	1.6	4.8	2.4	0.4		0.2
Tortanus barbatus		2.6							
Mecynocera clausi									
Other copepods									
Total copepods	485.5	168.9	190.7	213.2	516.2	222.4	105.4	80.1	57.9
Total zooplankton	760.9	388.1	489.8	286.3	555.4	238.5	110.4	90.0	74.0
Mean chlorophyll	0.73	0.68	0.65	0.75	1.14	1.02	0.74	0.67	0.67
C. V. chlorophyll	0.07	0.03	0.03	0.15	0.06	0.05	0.10	0.07	0.19

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	548	549	550	551	552	553	554	555	556
Latitude	20.9	20.9	21.0	21.0	21.0	21.0	21.1	21.1	21.1
Longitude	150.9	151.0	151.1	151.2	151.2	151.3	151.4	151.5	151.6
Decapod larvae			0.3		0.2	0.5	1.1	0.4	1.1
Brachyuran larvae	0.7	0.4		0.2	2.2	1.9	2.1	1.2	3.3
Luciferids									
Stomatopod larvae									
Siphonophores	2.0	0.9	2.0	0.2	0.7		1.6	0.4	0.4
Chaetognaths	2.0	1.7	1.7		0.4		1.6	2.9	0.7
Appendicularians	18.0	45.4	35.3	16.1	26.5	52.2	22.0	58.3	23.4
Polychaete larvae			7.4	0.2		0.9	0.5	0.8	
Pteropods		0.4	0.7					0.8	0.4
Salps							0.4	0.4	
Echinoid larvae			1.0						
Fish larvae	0.7	1.3	1.3	1.3	2.0	0.9	1.1	0.8	1.9
Fish eggs	2.7	0.4	1.3		1.8	1.9	1.6	1.2	
Mollusc larvae	1.3	0.4	1.0	0.4	1.1				1.9
Cladocera	0.4								
Ostracods						0.5			
Acrocalanus gracilis			0.7	0.7	0.2	0.5	1.6	1.6	1.1
A. monachus									
A. gibber			0.3			0.5			
Clausocalanus spp.									
Paracalanus spp.	1.3	3.1	2.0	0.2	0.9	3.7	3.8	7.0	2.2
Calocalanus pavo					0.2				
Canthocalanus pauper		0.4				0.5		0.8	
Centropages orsinii	57.8	6.5	6.0	2.2	1.1	1.4	0.5		1.5
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta	1.3	0.4		0.2					
Undinula vulgaris			7.1	0.9			0.5	0.8	0.7
Temora stylifera									
T. turbinata									
Calanopia elliptica								1.6	
Eucalanus subcrassus									
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	133.6	53.3	28.9	26.3	27.7	65.7	62.3	42.3	73.7
A. negligens									
Oithona rigida	4.7	1.3	0.7	0.7	0.7	0.9	0.5	0.8	0.4
O. plumifera						0.9	0.5	2.9	
O. spp.	4.0	12.7	4.7	1.7	4.3	23.3	18.3	26.3	
Corycaeus pacifica	0.7	0.9	0.3			0.5	0.5	2.1	0.4
C. (D) spp.	2.7	0.9	0.7	0.7	1.8	2.3	5.9	6.2	4.1
C. speciosus									
C. lubbocki	2.0	1.3	0.7	0.2	1.6	0.9	2.1	2.1	1.5
Farranula spp. (male)	0.7		1.0		0.9	0.9	3.2	0.8	0.7
F. gibbulus (female)					0.2		0.5	2.1	0.4
F. concinnus (female)				0.2	0.4				0.7
Onceae media							0.5	0.4	
O. venusta									
O. conifera				0.2		0.5		0.4	
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	1.3	1.3	1.3	0.7	1.8	3.3	11.8	23.8	8.9
Macrosetella gracilis	7.3	7.9	2.0	1.3	7.9	9.3	9.1	2.1	5.2
Euterpina acutifrons		0.4	0.7	0.2		0.5	0.5		
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	217.4	90.4	57.1	36.3	49.7	115.5	122.4	123.9	101.6
Total zooplankton	244.6	141.5	109.2	54.8	84.8	174.2	154.1	191.2	135.4
Mean chlorophyll	0.71	0.91	0.47	0.69	0.77	0.89	0.86	0.99	0.92
C. V. chlorophyll	0.17	0.12	0.28	0.15	0.22	0.22	0.14	0.05	0.10

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	559	560	561	562	563	564	565	566	567
Latitude	21.2	21.3	21.3	21.4	21.5	21.5	21.6	21.7	21.7
Longitude	151.5	151.5	151.4	151.4	151.4	151.5	151.4	151.4	151.3
Decapod larvae	2.0			0.9	0.9	0.6			
Brachyuran larvae				0.9			1.6	0.4	0.4
Luciferids									
Stomatopod larvae									
Siphonophores				4.4	3.5	4.6	2.7	8.7	4.6
Chaetognaths	3.3		0.9	1.8	12.4	2.3	7.0	4.8	1.5
Appendicularians	33.5	33.1	8.9	18.6	20.3	16.1	22.0	22.9	12.5
Polychaete larvae			0.9		2.6	2.9	0.5	1.7	0.7
Pteropods	0.7					1.2			
Salps	1.3	0.9		0.9	0.9	1.2	18.3	11.7	1.5
Echinoid larvae			0.9					2.2	4.8
Fish larvae	3.3	3.6	3.5		0.9		0.5	0.9	0.2
Fish eggs	0.7	0.9		0.9	0.9	1.2			0.2
Mollusc larvae	0.7				0.9	1.2		0.4	
Cladocera									
Ostracods									
Acrocalanus gracilis	2.7	3.6		2.7	1.8			1.3	
A. monachus									
A. gibber					0.9				
Clausocalanus spp.	3.3	0.9							
Paracalanus spp.	6.0		3.5	8.9	12.4	6.9	11.3	8.2	1.8
Calocalanus pavo									
Canthocalanus pauper	0.7								
Centropages orsinii	3.3		1.8	1.8	1.8	1.7	2.2	3.9	0.9
C. furcatus					0.9				
C. elongatus									
Labidocera laevigata							1.1		0.2
L. acuta									
L. minuta				1.8				0.4	
Undinula vulgaris	0.7			0.9	2.6	0.6		1.7	1.1
Temora stylifera	0.7								
T. turbinata									
Calanopia elliptica	4.0	2.7	2.7	1.8	1.8	0.6	1.6	0.9	0.4
Eucalanus subcrassus	0.7						0.5		
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	138.7	172.0	206.4	142.0	144.8	75.5	24.7	18.6	9.5
A. negligens									
Oithona rigida	2.0	6.3	0.9	2.7	0.9	1.7	1.1	0.4	
O. plumifera	3.3		0.9		1.8	0.6	2.7	0.9	0.7
O. spp.	34.8	29.6	41.6	23.1	62.7	26.5	17.7	11.7	13.9
Corycaeus pacifica	2.0	4.5	3.5	1.8	4.4		1.1	0.9	1.3
C. (D) spp.	12.1	10.8	9.7	8.9	10.6	2.9	7.5	3.9	1.8
C. speciosus									
C. lubbocki	7.4	17.9	6.2	4.4		0.6	0.5		0.9
Farranula spp. (male)	4.0		2.7			0.6	0.5		
F. gibbulus (female)			0.9						
F. concinnus (female)		0.9	0.9						
Onceae media	1.3				0.9				
O. venusta									
O. conifera									
Sapphirina spp.						0.6	1.1	0.9	
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	14.1	9.0	4.4	12.4	9.7	6.3	4.3	3.5	3.1
Macrosetella gracilis	2.7	2.7	0.9	0.9	1.8	1.2	1.6	2.2	1.3
Euterpina acutifrons		0.9		0.9			1.1		
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	244.5	261.6	287.0	214.8	259.7	126.2	80.6	59.3	36.8
Total zooplankton	290.1	300.1	302.0	243.2	302.9	157.3	133.3	113.0	63.4
Mean chlorophyll	0.86	0.66	0.59	0.70	0.71	0.74	1.02	0.96	0.70
C. V. chlorophyll	0.10	0.07	0.06	0.16		0.12	0.07	0.20	0.14

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	568	569	570	571	572	573	574	575	576
Latitude	21.7	21.7	21.6	21.5	21.6	21.6	21.7	21.7	21.8
Longitude	151.3	151.4	151.4	151.5	151.6	151.7	151.8	151.9	151.9
Decapod larvae	0.5			1.1					0.8
Brachyuran larvae	1.4		0.8	4.3	0.8				
Luciferids									
Stomatopod larvae									
Siphonophores	2.7	0.9	2.5	3.2	0.4			0.4	
Chaetognaths	5.0	4.6	4.2	5.4	6.2		0.5	1.8	4.1
Appendicularians	5.0	6.4	8.4	37.5	20.1	16.0	0.5	10.6	14.8
Polychaete larvae	0.5	0.9	1.7	7.5	2.1	1.1			
Pteropods	0.9			1.1	0.8			0.4	3.3
Salps	0.5	3.7	8.4	1.1	4.9				0.8
Echinoid larvae	0.9	0.9		1.1	0.4				
Fish larvae	0.5			1.1	0.4				0.8
Fish eggs	0.9			2.1		2.3	1.8	0.4	
Mollusc larvae					0.4				
Cladocera									
Ostracods									
Acrocalanus gracilis		0.9		1.1		1.1	0.5	0.4	
A. monachus									
A. gibber	0.5								
Clausocalanus spp.									
Paracalanus spp.	5.0	1.8	4.2	28.9	5.7	5.7	1.4	1.3	8.2
Calocalanus pavo						1.1			1.6
Canthocalanus pauper	0.5				0.4				
Centropages orsinii	11.0	8.2		1.1	2.1	2.3	1.8	3.5	3.3
C. furcatus	0.5			1.1					
C. elongatus									
Labidocera laevigata	0.9	0.9			0.8				0.8
L. acuta									
L. minuta									
Undinula vulgaris	0.9		0.8						
Temora stylifera					0.4				
T. turbinata									
Calanopia elliptica	1.4	3.7		12.9	3.7	8.0	0.9	0.4	6.6
Eucalanus subcrassus	1.4				0.8				
E. mucronatus									
Candacia pachydactyla									
C. pectinata					0.4				
Acartia pacifica									
A. australis	67.6	102.3	164.7	108.2	29.1	180.6	68.4	100.3	197.0
A. negligens									
Oithona rigida	2.7	0.9	1.7	2.1	0.8	3.4	1.8	0.4	1.6
O. plumifera	1.8	0.9	0.8	9.6	1.6	1.1	0.9	0.4	1.6
O. spp.	53.4	84.0	55.2	52.5	23.8	88.0	18.5	24.3	46.0
Corycaeus pacifica	1.4	4.6	3.3	5.4	0.8	5.7		0.9	3.3
C. (D) spp.	11.0	16.4	10.9	23.6	7.4	13.7	2.3	4.0	11.5
C. speciosus						1.1			
C. lubbocki	4.6			3.2	2.1	6.9	8.8	8.4	7.4
Farranula spp. (male)	0.5		0.8			6.9	1.8	6.2	12.3
F. gibbulus (female)					0.4	1.1		0.4	
F. concinnus (female)				1.1	0.4			0.9	
Onceae media						1.1	0.5	0.4	
O. venusta								0.4	
O. conifera				1.1		1.1			0.8
Sapphirina spp.	0.5								
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	6.8	7.3	7.5	8.6	4.5	14.9	2.3	8.8	15.6
Macrosetella gracilis	2.3	5.5	1.7	2.1	0.8	1.1			2.5
Euterpina acutifrons	1.8	0.9	1.7				0.5		
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	176.2	238.3	253.3	262.4	86.2	345.3	110.5	161.7	320.1
Total zooplankton	194.9	255.6	279.2	327.7	122.7	364.7	113.3	175.4	344.8
Mean chlorophyll	0.72	0.73	0.82	0.89	0.79	0.62	0.57	0.52	0.52
C. V. chlorophyll	0.14	0.24	0.07	0.10	0.07	0.09	0.05	0.04	0.17

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	577	578	579	580	581	582	583	584	585
Latitude	21.8	21.8	21.8	21.8	21.9	21.9	21.9	21.9	21.9
Longitude	152.0	152.2	152.3	152.4	152.0	151.9	151.9	151.8	151.7
Decapod larvae				0.6			1.0		0.8
Brachyuran larvae		0.2		0.3					0.4
Luciferids									
Stomatopod larvae									
Siphonophores				0.3			3.9	0.8	0.8
Chaetognaths	1.3	0.8		0.3	1.0	2.8	3.0	7.4	3.4
Appendicularians	7.0	3.9		10.8	19.6	10.8	48.3	29.6	14.3
Polychaete larvae		0.2		0.6			1.0	1.6	0.8
Pteropods	0.9	0.8	0.9	0.3	2.0	4.6	3.9	2.5	1.3
Salps	0.2			1.5					
Echinoid larvae	0.4			0.3	1.5	0.6	2.0	4.9	0.4
Fish larvae	0.4			0.6			2.0		
Fish eggs	3.5	0.2				0.6	2.0	0.8	0.4
Mollusc larvae		0.2		0.3	0.5	1.7			
Cladocera									
Ostracods									
Acrocalanus gracilis	1.8			0.3			2.0	6.6	
A. monachus									
A. gibber	1.3					0.6	1.0	0.8	
Clausocalanus spp.									
Paracalanus spp.	5.7		0.2	1.8	2.0	14.2	38.5	24.7	12.2
Calocalanus pavo									
Canthocalanus pauper									
Centropages orsinii	0.4	0.2			0.5	2.3	9.9	18.9	7.1
C. furcatus							3.0		
C. elongatus									
Labidocera laevigata	0.4				0.5	0.6	1.0		0.4
L. acuta									
L. minuta									
Undinula vulgaris	0.4						1.0	2.5	
Temora stylifera									
T. turbinata									
Calanopia elliptica	3.1			0.6	2.5	4.0	3.0	7.4	1.3
Eucalanus subcrassus	0.9			0.6		1.1	4.9	9.9	1.7
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica									
A. australis	25.0	15.6	2.9	27.7	5.5	10.8	45.4	44.4	35.7
A. negligens	1.8	0.2			0.5	1.1	2.0	0.8	
Oithona rigida	2.6	0.8		0.3	1.0	1.1		2.5	0.8
O. plumifera	9.2	1.7		3.4		14.8	13.8	11.5	6.3
O. spp.	15.8	5.0	0.2	9.6	13.6	17.1	42.4	36.2	13.9
Corycaeus pacifica	4.4			0.3	1.5	0.6		4.1	
C. (D) spp.	13.6	1.0	0.7	6.8	7.6	10.2	12.8	20.6	6.7
C. speciosus				0.3					
C. lubbocki	2.2	0.4		2.5	2.5	2.3	6.9	1.6	2.9
Farranula spp. (male)	4.4	0.2		0.9	2.5	0.6	4.9	4.9	1.3
F. gibbulus (female)	0.9			0.3			4.9	1.6	0.4
F. concinnus (female)	0.9					0.6		0.8	
Onceae media			0.2	0.3			1.0	0.8	
O. venusta						0.6			
O. conifera					0.5				
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata	0.4								
Microsetella rosea	18.0	2.5	2.4	21.3	8.6	40.4	22.7	27.1	6.3
Macrosetella gracilis	0.4		0.4	1.8		1.7	2.0	2.5	0.4
Euterpina acutifrons	1.3				1.0		1.0		1.7
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	114.7	27.6	7.0	78.9	50.4	124.6	223.8	230.2	99.5
Total zooplankton	128.3	34.2	7.9	93.4	76.5	145.6	290.9	277.9	122.2
Mean chlorophyll	0.68	0.43	0.51	0.49	0.57	0.61	0.59	0.68	0.70
C. V. chlorophyll	0.17	0.05	0.16	0.05	0.10	0.05	0.06	0.07	0.06

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	586	587	588	589	590	613	614	615	616
Latitude	21.9	21.9	21.9	21.9	21.9	20.0	20.0	19.9	19.9
Longitude	151.6	151.5	151.4	151.3	151.3	148.8	148.8	148.7	148.6
Decapod larvae	1.9	2.0	2.8	0.5	1.5	0.8		3.0	
Brachyuran larvae	0.9		0.9				1.8		
Luciferids									
Stomatopod larvae									
Siphonophores	3.2	4.9	2.8	3.7	4.6	1.6			
Chaetognaths	5.1	17.7	17.9	9.7	9.2	17.0	33.8	21.3	41.1
Appendicularians	9.3	6.9	20.8	7.4	12.2	97.8	83.7	45.6	78.8
Polychaete larvae	0.5			0.5	1.5	2.4	1.8	1.5	
Pteropods	0.9	3.9	4.7	1.4	16.8		1.8		
Salps		0.9	1.8					1.7	
Echinoid larvae	1.4	2.0	4.7	0.5	4.6	8.9	7.1	9.1	1.7
Fish larvae	0.5	1.0	3.8	1.4			1.8		1.7
Fish eggs	1.4	2.0	1.9		1.5		1.8	1.5	
Mollusc larvae								1.5	
Cladocera									
Ostracods					3.1				
Acrocalanus gracilis	1.4	2.9	2.8	0.5		6.5	37.4	53.2	53.1
A. monachus									
A. gibber			2.8	1.8	9.2	3.2		1.5	10.3
Clausocalanus spp.									
Paracalanus spp.	14.3	31.4	47.2	14.7	84.1	12.1	44.5	56.3	17.1
Calocalanus pavo									
Canthocalanus pauper			0.9		6.1	3.2	1.8	1.5	13.7
Centropages orsinii	4.6	5.9	3.8	3.2	4.6	17.0	51.6	53.2	49.7
C. furcatus	0.9	1.0	8.5	1.4	3.1	3.2	1.8	3.0	
C. elongatus									
Labidocera laevigata	1.4			0.5					1.7
L. acuta					1.6		1.5	1.7	
L. minuta		1.0				6.5	23.2	12.2	3.4
Undinula vulgaris	1.4	1.0	1.9	0.5	1.5	8.1		39.6	42.8
Temora stylifera	0.5								
T. turbinata									
Calanopia elliptica	0.5		0.9	0.5	1.5	3.2			
Eucalanus subcrassus	5.1	22.6	9.4	3.2	18.3	0.8		3.0	1.7
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica						0.8	7.1	9.1	15.4
A. australis	34.2	36.3	62.3	15.2	55.0	8.1	8.9	7.6	8.6
A. negligens	0.5								
Oithona rigida	0.9	1.0			4.6	12.9	42.7	27.4	24.0
O. plumifera	5.1	8.8	9.4	7.4	22.9	2.4	1.8		3.4
O. spp.	18.0	18.7	11.3	28.0	76.4	10.5	14.2	10.6	12.0
Corycaeus pacifica		2.9	3.8		3.1			1.5	
C. (D) spp.	14.8	46.2	51.0	21.1	81.0	14.6	17.8	19.8	10.3
C. speciosus			0.9						
C. lubbocki	3.7	6.9	9.4	1.8			7.1	4.6	6.9
Farranula spp. (male)	1.4	1.0					5.3		5.1
F. gibbulus (female)				0.5				1.5	1.7
F. concinnus (female)						0.8			
Onceae media	0.5							1.5	
O. venusta									
O. conifera		3.9	0.9	0.9			1.8	3.0	
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata								1.5	
Microsetella rosea	6.0	38.3	20.8	14.7	56.6	10.5	7.1	4.6	8.6
Macrosetella gracilis	2.8	3.9	9.4	3.7	18.3	27.5	176.3	51.7	121.6
Euterpina acutifrons	0.9	4.9	0.9	4.1	9.2	4.0	3.6	1.5	
Tortanus barbatus		2.0		0.5					
Mecynocera clausi									
Other copepods									
Total copepods	118.9	238.6	258.7	123.6	455.5	157.6	454.1	371.2	412.8
Total zooplankton	143.8	278.9	320.1	150.3	510.5	286.2	587.7	454.8	537.8
Mean chlorophyll	0.63	0.76	0.72	0.62	0.68	0.70	0.54	0.49	0.44
C. V. chlorophyll	0.09	0.05	0.07	0.06	0.04	0.19	0.09	0.13	0.09

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	617	618	741	742	743	744	745	746	747
Latitude	19.9	19.7	18.3	18.3	18.4	18.4	18.5	18.6	18.6
Longitude	148.5	148.4	147.3	147.3	147.2	147.2	147.1	147.1	147.1
Decapod larvae	1.8	6.0		0.6		0.5	1.0		0.5
Brachyuran larvae	3.6	2.0		0.6		0.5	3.1		1.0
Luciferids		2.0							
Stomatopod larvae									
Siphonophores		2.0		1.8	1.6	1.1		2.1	
Chaetognaths	41.3	31.8	2.5	12.5	7.3	8.1	3.6	10.3	11.9
Appendicularians	62.0	87.5	15.5	36.3	41.2	41.0	25.1	27.9	45.7
Polychaete larvae	3.6	6.0		0.6	1.0	0.5	0.5		2.1
Pteropods		4.0	3.2	2.4	1.0	3.2		3.1	5.2
Salps	2.0	0.4	0.6	0.5					
Echinoid larvae	5.4	11.9		0.6	0.5	0.5			0.5
Fish larvae				0.6		1.6	0.5	3.1	
Fish eggs			0.4			0.5	0.5		1.0
Mollusc larvae			0.4		2.1				1.6
Cladocera									
Ostracods							0.5		1.6
Acrocalanus gracilis	14.4	39.8	0.4	12.5	7.3		0.5		2.6
A. monachus									
A. gibber	44.9	13.9	1.4	1.2			0.5		2.6
Clausocalanus spp.									
Paracalanus spp.	35.9	31.8	5.6	13.7	17.2	3.8	6.7	1.0	6.2
Calocalanus pavo				1.2	1.0				
Canthocalanus pauper	5.4	19.9	1.8	1.8	0.5	1.1	1.0	1.0	3.6
Centropages orsinii	21.6	8.0	1.1	3.0	2.1	7.0	3.6	12.4	6.8
C. furcatus	5.4	6.0							
C. elongatus					1.0				
Labidocera laevigata									
L. acuta	1.8	2.0				1.1			0.5
L. minuta	14.4	11.9	0.7	2.4		1.1	1.0		2.6
Undinula vulgaris	18.0	9.9	0.4	1.8	0.5	1.1		1.0	2.1
Temora stylifera					0.5				
T. turbinata									
Calanopia elliptica	1.8		0.4			1.1	0.5		
Eucalanus subcrassus	5.4	49.7	0.4	0.6					1.0
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica	23.4								
A. australis		6.0	4.6	10.1	25.0	90.6	56.9	209.0	69.1
A. negligens					0.5				
Oithona rigida	19.8	6.0	0.7		3.1	2.2	0.5	2.1	
O. plumifera			10.6	3.0	1.6	0.5	4.1		1.0
O. spp.	12.6	6.0	4.2	8.9	18.2	12.9	12.3	16.6	21.3
Corycaeus pacifica	7.2	2.0		1.8	0.5	1.1	0.5		0.5
C. (D) spp.	25.2	9.9	4.2	16.7	6.3	4.9	5.1	5.2	6.8
C. speciosus									
C. lubbocki	5.4	2.0	2.5	18.4	8.9	9.2	2.1	1.0	5.2
Farranula spp. (male)	1.8		2.1	29.7	22.9	6.5	4.1	7.2	5.2
F. gibbulus (female)			0.4	5.9	3.1	1.1	0.5	2.1	
F. concinnus (female)		2.0		7.7	5.7	1.1	1.0	1.0	1.0
Onceae media		2.0	1.4	1.2			1.0	1.0	0.5
O. venusta				0.6					0.5
O. conifera	1.8	2.0			0.5				0.5
Sapphirina spp.						0.5			
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	25.2	33.8	3.5	26.2	13.0	3.8	2.1	1.0	45.7
Macrosetella gracilis	97.0	127.3		6.5	1.6	5.9			2.6
Euterpina acutifrons	1.8	11.9				1.6	4.6	1.0	7.8
Tortanus barbatus									
Mecynocera clausi									
Other copepods									
Total copepods	389.8	403.8	46.2	174.9	141.3	158.0	108.7	262.8	195.8
Total zooplankton	507.5	558.9	68.4	231.4	196.5	215.6	143.6	309.4	267.0
Mean chlorophyll	0.42	0.47	0.34	0.31	0.31	0.56	0.84	0.70	0.46
C. V. chlorophyll	0.10	0.06	0.12	0.11	0.23	0.16	0.10	0.31	0.23

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	748	749	750	751	752	753	754	755	756
Latitude	18.7	18.7	19.8	19.7	19.7	19.6	19.6	19.6	19.6
Longitude	147.2	147.2	149.3	149.3	149.3	149.3	149.4	149.5	149.6
Decapod larvae	0.9	5.3	1.1	1.5	6.1	1.1	1.6	0.5	1.0
Brachyuran larvae	0.4	0.9	7.4	1.0	2.2	0.6	1.6	1.0	1.0
Luciferids									
Stomatopod larvae		0.9							
Siphonophores	0.4	0.9	3.2	2.4	5.0	4.5	1.6		1.0
Chaetognaths	4.8	9.8	15.8	6.3	14.5	5.1	6.5	3.1	3.8
Appendicularians	19.8	48.1	27.4	19.5	13.4	15.3	16.2	10.3	17.1
Polychaete larvae		4.5			1.1	0.6			
Pteropods	2.6	2.7	1.1	0.5	2.2	1.1	2.2	1.0	0.5
Salps	0.4								
Echinoid larvae		1.8		0.5		1.1			
Fish larvae	0.4	1.8		0.5	1.1	1.7		0.5	0.5
Fish eggs	0.5								
Mollusc larvae	0.4		2.1		0.6	0.6	0.5	1.0	
Cladocera									
Ostracods			1.1	1.0	0.6	1.1	0.5		
Acrocalanus gracilis		0.9		1.0	1.1	4.0			
A. monachus									
A. gibber	0.9	1.8	3.2	6.3	7.2	1.7	0.5	1.5	0.5
Clausocalanus spp.									
Paracalanus spp.	3.1	30.3	87.5	48.3	70.2	49.8	51.2	55.9	110.8
Calocalanus pavo					0.6				
Canthocalanus pauper	2.2	4.5	6.3	3.9	5.6	0.6	0.5	0.5	
Centropages orsinii	4.4	3.6		0.5					
C. furcatus			1.1		0.6	0.6			
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta	2.2	3.6		1.5	0.6		1.6	0.5	
Undinula vulgaris	2.2	4.5	2.1		0.6	0.6			0.5
Temora stylifera									
T. turbinata									
Calanopia elliptica	0.4	1.8	10.5	2.4	3.3	2.8	3.2	2.1	1.9
Eucalanus subcrassus			7.4	3.4	8.4	2.8	1.1		2.4
E. mucronatus									
Candacia pachydactyla									
C. pectinata			3.2		0.6				
Acartia pacifica						0.6			
A. australis	47.5	105.2	4.2	1.9	6.7	4.0	3.8	3.6	5.2
A. negligens	0.4				0.6				
Oithona rigida	0.4	0.9	2.1	1.0	1.7	1.7	3.8	8.2	6.2
O. plumifera	2.6	6.2	6.3	1.5	1.7	1.1	4.3	6.2	2.9
O. spp.	36.9	46.4	30.6	21.0	27.3	28.3	25.9	26.2	14.7
Corycaeus pacifica	0.4	0.9	2.1		1.1		1.1		1.4
C. (D) spp.	0.9	7.1	17.9	7.3		16.4	14.0	5.6	9.0
C. speciosus	0.4								
C. lubbocki	1.8	9.8		0.5	2.8	5.7	9.7	9.7	10.9
Farranula spp. (male)	1.8	8.0	1.1		0.6	2.8	4.3	8.2	4.8
F. gibbulus (female)		1.8		0.5			1.1	1.5	0.5
F. concinnus (female)	0.4	0.9			0.6	1.1	0.5	1.5	2.4
Onceae media			1.1	0.5	1.1			1.0	1.4
O. venusta							1.1	1.0	
O. conifera				0.5	0.6			0.5	
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata	0.5								
Microsetella rosea	4.0	9.8	28.5	5.8	14.5	9.1	8.6	7.2	7.6
Macrosetella gracilis	2.2	7.1	2.1	0.5	0.6	2.3		0.5	1.4
Euterpina acutifrons		0.9	1.1	0.5	1.7	1.7	1.1	0.5	0.5
Tortanus barbatus			1.1		0.6		1.6	0.5	
Mecynocera clausi									
Other copepods					0.6	0.6			
Total copepods	115.2	255.9	218.1	108.7	160.0	137.6	137.5	142.1	185.5
Total zooplankton	145.6	332.6	277.1	141.8	206.8	170.4	168.3	159.5	210.8
Mean chlorophyll	0.39	0.63	0.99	1.05	1.00	0.91	0.92	1.01	1.04
C. V. chlorophyll	0.10	0.14	0.08	0.06	0.07	0.07	0.09	0.09	0.09

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	757	758	759	760	761	762	763	764	765
Latitude	19.6	19.6	19.6	19.6	19.7	19.7	19.8	20.7	20.8
Longitude	149.6	149.7	149.8	149.8	149.9	149.9	150.0	150.6	150.6
Decapod larvae	2.1	0.5	0.9	1.9	3.2	5.3	2.7	1.7	1.2
Brachyuran larvae	1.6	1.9	1.3	2.3		2.7	0.9	1.7	0.6
Luciferids0.3									
Stomatopod larvae	1.0								
Siphonophores	1.6	0.5	0.3	1.4	2.1	1.3	1.8	0.8	0.3
Chaetognaths	3.6	3.9	3.1	9.3	7.4	8.0	8.9	17.4	6.0
Appendicularians	14.0	8.7	12.6	13.0	21.0	18.7	25.8	18.2	6.9
Polychaete larvae			0.3		1.1				
Pteropods	0.5	0.5	0.9	0.9			0.9	10.8	2.7
Salps				1.1					
Echinoid larvae									
Fish larvae	0.5				1.1			0.8	
Fish eggs		0.5	0.3		1.1				0.3
Mollusc larvae	2.1	0.5		0.5		1.3		2.5	1.2
Cladocera									
Ostracods	0.5			0.5		1.3	0.9	4.1	0.9
Acrocalanus gracilis								0.8	0.3
A. monachus	0.5		0.3						
A. gibber		1.0	0.3	0.9		5.3	2.7	9.1	2.7
Clausocalanus spp.									
Paracalanus spp.	48.2	85.2	62.2	104.3	147.3	232.2	104.2	91.9	32.5
Calocalanus pavo									
Canthocalanus pauper	0.5		0.3	1.4	4.2	9.3	4.5	1.7	1.2
Centropages orsinii				0.9	1.1			2.5	
C. furcatus						1.3			0.3
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta									
Undinula vulgaris		1.0		6.0	4.2	2.7	1.8	4.1	1.2
Temora stylifera									
T. turbinata									
Calanopia elliptica	3.1	0.5	0.9	2.3	1.1			9.1	6.6
Eucalanus subcrassus	1.0	1.0		1.9	5.3	2.7	0.9	11.6	3.0
E. mucronatus									
Candacia pachydactyla									
C. pectinata									
Acartia pacifica			0.3						
A. australis	1.6	2.4	1.3	2.8	1.1	4.0	2.7	7.5	3.9
A. negligens	2.1	1.5		0.5	1.1	1.3	2.7	0.8	0.6
Oithona rigida	4.7	1.5	2.2	1.9	5.3	10.7	5.3	4.1	1.8
O. plumifera	1.6	2.9	6.0	3.7	1.1	2.7	6.2	9.1	2.1
O. spp.	32.1	17.9	9.1	4.2	32.6	61.4	18.7	26.5	5.1
Corycaeus pacifica	0.5	0.5	0.3		1.1	1.3	0.9	1.7	
C. (D) spp.	6.7	10.6	6.6	11.6	12.6	17.4	19.6	25.7	18.1
C. speciosus							0.9		0.3
C. lubbocki	6.7	9.7	2.8	6.0		6.7	4.5	8.3	5.7
Farranula spp. (male)	3.6	4.4	2.2	1.4	2.1	5.3	4.5	1.7	2.1
F. gibbulus (female)	0.5		0.6			2.7			0.3
F. concinnus (female)		0.5	0.6	0.9		4.0	0.9		0.3
Onceae media		1.5	0.9	1.4	3.2	4.0	3.6		
O. venusta			0.6	0.5					
O. conifera	0.5	0.5	0.3	0.5			0.9		0.9
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	5.7	6.8	7.2	9.7	14.7	24.0	12.5	9.1	2.7
Macrosetella gracilis	1.0	1.0	0.9	0.9		4.0	4.5		
Euterpina acutifrons	0.5	0.5				1.3	0.9		
Tortanus barbatus					2.1				
Mecynocera clausi									
Other copepods									
Total copepods	121.3	150.5	106.2	163.7	237.8	404.4	203.1	225.2	91.9
Total zooplankton	148.7	167.5	126.0	193.3	275.7	443.1	245.0	283.1	112.3
Mean chlorophyll	0.93	0.97	1.03	1.15	1.20	1.29	1.37	1.02	1.00
C. V. chlorophyll	0.08	0.06	0.06	0.06	0.05	0.07	0.04	0.07	0.03

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	766	767	768	769	770	771	772	773	774
Latitude	20.8	20.9	20.9	21.0	21.1	21.1	21.1	21.2	21.3
Longitude	150.7	150.8	150.8	150.9	150.9	151.0	151.1	151.1	151.2
Decapod larvae		0.5			0.3			0.5	
Brachyuran larvae	0.6			0.8		0.3	0.3	0.2	0.5
Luciferids									
Stomatopod larvae									
Siphonophores		0.5	1.3	4.3	2.0	1.0	1.5	1.7	0.7
Chaetognaths	2.4	3.8	3.3	2.7	5.9	1.5	5.0	2.4	2.1
Appendicularians	7.4	10.5	11.2	19.9	11.2	8.6	7.3	5.1	5.0
Polychaete larvae								0.2	
Pteropods	3.0	9.6	4.3	13.6	7.9	10.7	7.9	10.9	3.1
Salps	0.3	0.5		0.3			0.6		
Echinoid larvae				0.3			0.6	0.2	0.2
Fish larvae				0.3		0.8	0.9	0.7	0.2
Fish eggs			0.5				0.3	0.5	
Mollusc larvae		1.9		1.1	1.4	0.3	0.9		
Cladocera									
Ostracods	0.3		0.5		0.3		0.3		
Acrocalanus gracilis	0.3	1.4		0.3	0.3				0.2
A. monachus									
A. gibber	0.9	1.4	2.0	1.6	2.2	1.0	0.9	0.5	0.5
Clausocalanus spp.									
Paracalanus spp.	27.6	28.3	18.5	23.7	9.0	6.1	9.1	3.6	6.4
Calocalanus pavo					0.3		0.3		
Canthocalanus pauper	1.2	0.5	0.5	0.5		0.3		0.2	
Centropages orsinii			0.5					1.2	0.2
C. furcatus		1.0		0.3					
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta							0.3	0.2	0.5
Undinula vulgaris		0.5	1.0	0.8	0.8		0.6	0.2	
Temora stylifera									
T. turbinata									
Calanopia elliptica	1.2	4.8	3.8	3.2	2.0	4.6	1.8	1.7	4.8
Eucalanus subcrassus	2.4	1.4	2.5	2.1	2.5	0.5	0.9	0.2	0.5
E. mucronatus									
Candacia pachydactyla									
C. pectinata						0.3	0.3		
Acartia pacifica									
A. australis	5.9	9.1	9.4	12.5	16.3	12.5	16.4	22.8	23.8
A. negligens	0.3						0.6	0.2	
Oithona rigida	0.3	0.5	0.8	0.3	0.3	0.8			0.2
O. plumifera	0.9		3.0	1.3	0.3	1.8	0.6	0.5	0.5
O. spp.	8.0	21.6	11.4	26.1	10.1	36.4	17.9	23.8	21.4
Corycaeus pacifica	0.9	1.0	0.3	0.3	0.6	0.8	1.2	0.7	0.7
C. (D) spp.	15.7	18.7	11.7	14.1	8.7	6.4	8.5	4.1	7.4
C. speciosus				0.3		0.3			
C. lubbocki	3.9	3.8	3.0	2.7	2.5	1.3	1.2	1.7	4.3
Farranula spp. (male)	1.8	1.4		1.1	1.7	0.3	0.3	0.5	0.5
F. gibbulus (female)			0.5	0.3			0.9		
F. concinnus (female)								0.2	
Onceae media					0.6			0.2	0.2
O. venusta									
O. conifera	0.6	1.0	0.8	0.3					0.5
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata	0.3		0.3						
Microsetella rosea	1.5	1.9	1.3	1.6	2.0	3.1	1.2	1.9	3.6
Macrosetella gracilis	0.3								
Euterpina acutifrons	0.6	0.5	0.8	0.5		0.8	0.6	0.2	2.1
Tortanus barbatus			0.3						
Mecynocera clausi									
Other copepods									
Total copepods	74.5	98.8	72.1	93.6	60.1	76.8	63.4	65.0	78.3
Total zooplankton	88.5	126.1	93.1	136.7	89.0	99.9	88.9	87.5	90.2
Mean chlorophyll	1.00	0.95	0.93	0.91	0.88	0.84	0.84	0.86	0.92
C. V. chlorophyll	0.03	0.04	0.05	0.05	0.05	0.03	0.06	0.05	0.16

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	784	785	786	787	788	789	790	791	792
Latitude	22.0	22.0	21.9	21.9	21.8	21.8	21.7	21.6	21.1
Longitude	152.4	152.4	152.3	152.3	152.2	152.2	152.1	152.1	151.9
Decapod larvae			1.0		0.5	0.3	0.2		1.9
Brachyuran larvae	1.1	1.6	2.0	1.5	2.1	0.3	0.5	0.3	5.7
Luciferids									
Stomatopod larvae									
Siphonophores	1.1	1.1	0.5	0.5	1.0	1.6		0.5	3.8
Chaetognaths	1.6	1.6	3.5	0.5	1.0	0.3	1.0	1.8	2.8
Appendicularians	30.5	34.1	24.2	14.7	8.4	6.6	7.5	4.9	81.9
Polychaete larvae								0.5	
Pteropods	3.2	1.6	5.9	5.9	2.6	0.3	0.2	0.5	
Salps	2.1	1.1		2.0	1.6				3.8
Echinoid larvae									
Fish larvae						0.5	0.5		1.9
Fish eggs	1.6		0.5	1.0	3.1			0.3	1.9
Mollusc larvae	0.5	1.1	1.5	4.4	4.7	1.1	3.5	2.1	
Cladocera									
Ostracods									
Acrocalanus gracilis					0.5			66.0	8.5
A. monachus									
A. gibber	1.6	2.7	0.5		0.5			0.8	0.9
Clausocalanus spp.		0.5						1.0	8.5
Paracalanus spp.	6.9	8.1	5.9	5.4	10.4	1.3	1.7	10.1	15.1
Calocalanus pavo	0.5						0.2	0.5	4.7
Canthocalanus pauper					0.5	0.8		0.3	
Centropages orsinii		1.6	1.0	3.9	2.6		0.5		1.9
C. furcatus									
C. elongatus									
Labidocera laevigata									
L. acuta									
L. minuta	6.9	7.0	7.9	3.9	3.1	0.3	0.2	0.3	
Undinula vulgaris	0.5		0.5	0.5				0.8	9.4
Temora stylifera						0.3		0.3	0.9
T. turbinata									
Calanopia elliptica	6.9	3.8	10.4	5.4	5.2	1.3	0.2	3.9	0.9
Eucalanus subcrassus	1.6		0.5						0.9
E. mucronatus									
Candacia pachydactyla									
C. pectinata									0.9
Acartia pacifica		0.5							
A. australis	7.5	34.6	21.7	28.9	23.0	8.2	5.0	6.5	2.8
A. negligens								0.8	3.8
Oithona rigida		2.7	5.4	1.0	3.1			2.1	1.9
O. plumifera	2.1	2.2	2.5			2.7	0.5	5.2	17.9
O. spp.	26.7	31.9	26.7	43.5	61.1		12.7	10.9	8.5
Corycaeus pacifica	1.6	1.1	2.0	0.5	0.5				0.9
C. (D) spp.	12.8	9.2	8.4	5.9	10.4	6.4	6.2	6.7	13.2
C. speciosus									0.9
C. lubbocki	3.2	4.3	1.0	2.4	1.6	0.3	1.7	1.6	14.1
Farranula spp. (male)	1.1	1.6	1.5	1.5	1.6	0.3		0.8	26.4
F. gibbulus (female)	0.5	0.5					0.2	0.3	2.8
F. concinnus (female)			0.5		0.5		0.2	0.5	5.7
Onceae media	0.5						0.2	1.6	11.3
O. venusta					0.5	0.5		0.5	
O. conifera				0.5				0.3	0.9
Sapphirina spp.									
Sapphirella tropica					0.5				
Clytemnestra scutellata									
Microsetella rosea	27.3	10.8	4.9	6.4	9.4	10.4	9.0	21.0	34.8
Macrosetella gracilis		6.5	3.0	2.9	1.0	0.5	1.5	1.3	1.9
Euterpina acutifrons	4.8		6.4	5.4	6.3	1.6	2.0	1.6	
Tortanus barbatus									
Mecynocera clausi								0.5	
Other copepods							0.3	0.3	
Total copepods	113.3	129.8	110.7	117.8	142.5	34.8	42.3	145.3	200.6
Total zooplankton	155.0	172.0	149.7	148.2	167.6	45.7	55.7	156.2	304.2
Mean chlorophyll	1.16	1.11	1.10	1.00	0.74	0.50	0.49	0.41	0.66
C. V. chlorophyll	0.09	0.06	0.08	0.12	0.11	0.08	0.09	0.12	0.44

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	793	794	795	796	797	831	832	833	834
Latitude	21.0	20.9	20.9	20.8	20.7	16.2	16.3	16.3	16.4
Longitude	151.8	151.8	151.8	151.7	151.7	145.6	145.6	145.6	145.6
Decapod larvae	0.5			0.2		3.1	6.2	2.1	12.4
Brachyuran larvae	3.7	0.9		0.2	0.4	3.1		2.1	6.2
Luciferids							2.1		
Stomatopod larvae									3.1
Siphonophores	0.5	1.9	0.5					2.1	3.1
Chaetognaths	2.8	3.7	6.0	2.6	3.1	4.6	14.4	14.4	71.2
Appendicularians	20.9	23.3	12.1	6.3	28.9	4.6	4.1	2.1	24.8
Polychaete larvae	0.5	0.5	0.5						
Pteropods	0.5	0.5					8.3	12.4	9.3
Salps	1.4	1.4	1.4	0.9	1.3		2.1		
Echinoid larvae						7.7		4.1	12.4
Fish larvae				0.2					3.1
Fish eggs	0.9	0.5							
Mollusc larvae		0.5	0.5				2.1		
Cladocera									
Ostracods						1.5		10.3	3.1
Acrocalanus gracilis	6.0	1.9	1.4		4.5				
A. monachus									
A. gibber						23.2	28.9	18.6	18.6
Clausocalanus spp.	19.0	26.1	23.7	11.7	7.6				
Paracalanus spp.	3.7	0.5		0.5		215.1	196.0	198.1	318.9
Calocalanus pavo	0.9	0.9	1.4	1.2	0.4				
Canthocalanus pauper		0.5				15.5	14.4	4.1	27.9
Centropages orsinii	0.9		0.9	2.6			2.1		3.1
C. furcatus						4.6	2.1	4.1	12.4
C. elongatus			0.9	0.2	0.9				
Labidocera laevigata									
L. acuta				0.4	1.5		2.1		
L. minuta					1.3	3.1			
Undinula vulgaris	0.5	1.9		0.9	26.7		8.3	6.2	6.2
Temora stylifera				0.2					
T. turbinata									
Calanopia elliptica		0.9			1.3	6.2	8.3	2.1	9.3
Eucalanus subcrassus	0.5					3.1	2.1	4.1	
E. mucronatus									
Candacia pachydactyla	0.9		0.5						
C. pectinata									
Acartia pacifica						26.3	12.4	6.2	27.9
A. australis	1.4		0.5		4.0	1.5			
A. negligens	2.8	3.7	4.6	1.6	0.9				
Oithona rigida	2.8	0.9	0.5	1.4	3.1				3.1
O. plumifera	8.3	12.6		8.9	3.1	41.8	41.3	22.7	34.1
O. spp.	1.4		0.7	1.3	10.8	53.6	39.2	71.2	
Corycaeus pacifica	0.5	0.9				3.1		2.1	
C. (D) spp.	5.6	3.7	5.1	4.0	4.5	4.6	14.4	18.6	15.5
C. speciosus	0.9	0.5	1.4	0.5					
C. lubbocki	11.1	7.9	7.9	6.1	20.9	9.3	2.1	4.1	6.2
Farranula spp. (male)	28.3	32.2	20.0	26.4	29.8		2.1		
F. gibbulus (female)	3.7	1.9	6.0	0.9	0.4				
F. concinnus (female)	8.3	10.3	7.4	8.0	10.2				
Onceae media	3.7	5.6	3.7	0.9	1.3				
O. venusta		1.4	2.8	0.5	0.4	1.5			
O. conifera	0.5			0.2		4.6	2.1	6.2	15.5
Sapphirina spp.									
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	22.2	26.1	7.9	8.2	2.7	4.6	37.1	12.4	96.0
Macrosetella gracilis		2.8		0.9	0.4	6.2	8.3	10.3	12.4
Euterpina acutifrons		0.5				4.6	8.3	2.1	12.4
Tortanus barbatus						15.5	6.2	2.1	9.3
Mecynocera clausi									
Other copepods	0.5			0.2					
Total copepods	132.6	145.2	96.7	86.4	126.5	391.6	443.6	363.2	690.4
Total zooplankton	164.1	178.3	117.6	96.9	160.3	416.3	482.8	412.7	839.0
Mean chlorophyll	0.27	0.20	0.21	0.15	0.20	0.67	0.67	0.75	0.68
C. V. chlorophyll	0.14	0.10	0.17	0.09	0.13	0.05	0.07	0.06	0.06

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	835	836	837	838	839	840	841	843	844
Latitude	16.4	16.5	16.6	16.6	16.7	16.7	16.8	16.9	17.0
Longitude	145.7	145.7	145.8	145.8	145.8	145.9	145.9	146.0	146.0
Decapod larvae		3.1	8.3	2.1	6.2				4.1
Brachyuran larvae	2.1	1.0	4.1	4.1	2.1	2.1	3.1	8.3	3.1
Luciferids						4.1			2.1
Stomatopod larvae									
Siphonophores	2.1					2.1			
Chaetognaths	18.6	13.4	66.0	39.2	12.4	43.3	13.4	49.5	35.1
Appendicularians	14.4	7.2	53.6	14.4	6.2	14.4	3.1	14.4	12.4
Polychaete larvae			4.1			2.1		2.1	2.1
Pteropods	24.8	12.4	12.4	10.3	22.7	14.4	1.0	16.5	16.5
Salps					2.1		12.4	15.5	
Echinoid larvae	2.1	2.1	4.1	14.4	6.2	6.2	2.1	6.2	
Fish larvae	2.1				2.1			2.1	5.2
Fish eggs			4.1						
Mollusc larvae	2.1		4.1	2.1	4.1	6.2			
Cladocera									
Ostracods	6.2	2.1	4.1	4.1		4.1		6.2	6.2
Acrocalanus gracilis					2.1				
A. monachus									
A. gibber	37.1	23.7	49.5	45.4	28.9	16.5	19.6	35.1	6.2
Clausocalanus spp.									
Paracalanus spp.	212.5	148.6	557.1	196.0	210.5	222.9	99.0	365.2	179.5
Calocalanus pavo									
Canthocalanus pauper	20.6	12.4	41.3	22.7	31.0	28.9	12.4	35.1	9.3
Centropages orsinii	2.1			4.1	4.1			2.1	
C. furcatus	4.1	1.0	20.6	4.1	8.3	4.1		14.4	3.1
C. elongatus									
Labidocera laevigata									
L. acuta	2.1	1.0		4.1					
L. minuta			12.4	2.1	4.1		1.0	2.1	
Undinula vulgaris	4.1	3.1	20.6	10.3	12.4	4.1		6.2	
Temora stylifera									
T. turbinata									
Calanopia elliptica	10.3	3.1	4.1	26.8	16.5	6.2	9.3	10.3	1.0
Eucalanus subcrassus	6.2	1.0		2.1	4.1	8.3	7.2		1.0
E. mucronatus									
Candacia pachydactyla									
C. pectinata							2.1		
Acartia pacifica	8.3	7.2	37.1	16.5	10.3	12.4	9.3	24.8	5.2
A. australis	2.1	3.1		4.1	4.1				
A. negligens									
Oithona rigida	2.1			8.3				2.1	
O. plumifera	41.3	22.7	66.0	64.0	39.2	41.3	7.2	10.3	14.4
O. spp.	64.0	23.7	115.6	39.2	24.8	22.7	3.1	45.4	25.8
Corycaeus pacifica	2.1	1.0	4.1	4.1	6.2	4.1	5.2	10.3	2.1
C. (D) spp.	31.0	28.9	24.8	33.0	43.3	31.0	27.9	41.3	7.2
C. speciosus			4.1						
C. lubbocki	8.3	8.3		8.3	6.2	37.1	16.5	8.3	
Farranula spp. (male)				2.1	6.2			2.1	
F. gibbulus (female)				4.1	2.1			2.1	
F. concinnus (female)									
Onceae media	2.1							2.1	
O. venusta									
O. conifera		3.1	20.6	6.2	4.1	4.1	4.1	16.5	10.3
Sapphirina spp.									2.1
Sapphirella tropica									
Clytemnestra scutellata									
Microsetella rosea	49.5	25.8	70.2	53.6	28.9	4.1	4.1	20.6	45.4
Macrosetella gracilis	4.1	5.2	12.4	10.3	4.1	6.2	6.2	14.4	5.2
Euterpina acutifrons	8.3	3.1	8.3	4.1	2.1	6.2	1.0	6.2	2.1
Tortanus barbatus	10.3	2.1	33.0	8.3	4.1	8.3	4.1	16.5	14.4
Mecynocera clausi									
Other copepods									
Total copepods	522.1	326.0	1068	575.7	503.5	460.1	235.2	676.8	319.8
Total zooplankton	596.3	367.3	1233	666.5	565.4	561.3	257.9	794.4	422.0
Mean chlorophyll	0.66	0.59	0.71	0.69	0.66	0.66	0.78	0.80	0.79
C. V. chlorophyll	0.09	0.08	0.04	0.05	0.07	0.07	0.05	0.09	0.08

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}

Sample	845	846
Latitude	17.0	17.1
Longitude	146.1	146.1
Decapod larvae	2.1	4.1
Brachyuran larvae	3.1	
Luciferids		
Stomatopod larvae		
Siphonophores	5.2	
Chaetognaths	39.2	59.8
Appendicularians	5.2	4.1
Polychaete larvae		2.1
Pteropods	5.2	16.5
Salps	6.2	
Echinoid larvae		8.3
Fish larvae	1.0	6.2
Fish eggs		
Mollusc larvae	1.0	6.2
Cladocera		
Ostracods	4.1	6.2
Acrocalanus gracilis		
A. monachus		
A. gibber	20.6	18.6
Clausocalanus spp.		
Paracalanus spp.	107.3	257.9
Calocalanus pavo		
Canthocalanus pauper	9.3	12.4
Centropages orsinii	2.1	2.1
C. furcatus		
C. elongatus		
Labidocera laevigata		
L. acuta		
L. minuta	2.1	
Undinula vulgaris	6.2	
Temora stylifera		
T. turbinata		
Calanopia elliptica		6.2
Eucalanus subcrassus	1.0	4.1
E. mucronatus		
Candacia pachydactyla		
C. pectinata		
Acartia pacifica	9.3	8.3
A. australis	1.0	2.1
A. negligens		
Oithona rigida	3.1	
O. plumifera	15.5	55.7
O. spp.	16.5	35.1
Corycaeus pacifica	4.1	2.1
C. (D) spp.	10.3	10.3
C. speciosus		2.1
C. lubbocki	3.1	10.3
Farranula spp. (male)		
F. gibbulus (female)		
F. concinnus (female)		
Onceae media		
O. venusta		
O. conifera	5.2	12.4
Sapphirina spp.		2.1
Sapphirella tropica		
Clytemnestra scutellata		
Microsetella rosea	13.4	76.3
Macrosetella gracilis	15.5	2.1
Euterpina acutifrons	1.0	
Tortanus barbatus	5.2	4.1
Mecynocera clausi		
Other copepods		
Total copepods	246.6	520.0
Total zooplankton	318.8	633.5
Mean chlorophyll	0.64	0.65
C. V. chlorophyll	0.49	0.02

Abundances are in animals m^{-3}, chlorophyll is in ug l^{-1}