

3.3.6 Physical/biological interactions

The two studies carried out by Chang & Bradford (1985) and Bradford & Chang (1987) indicated the importance of depth of mixing and water column stability, among other factors, to phytoplankton growth off WCSI, especially in winter. The large freshwater inflow causes stratification of the upper water layers, and is related to high phytoplankton biomass composed mainly of diatoms in winter and dinoflagellates in summer. On the other hand nutrient-rich water that is newly upwelled or deeply mixed winter surface water can have low concentrations of phytoplankton. The complex interactions of all the factors leading to the observed biomass and primary production are difficult to untangle empirically. The relative importance of light, water column stability and nutrient renewal to phytoplankton productivity off WCSI was therefore investigated using one-dimensional models.

Models were constructed to demonstrate some of the main elements of physical and biological interactions off WCSI, using data obtained during field experiments. This work was approached in several ways. First, maximum primary production was estimated as a function of temperature and latitude (Vincent et al. 1989b). Second, a model of total phytoplankton growth was coupled with a model describing the seasonal cycles in temperature and nutrients over the continental slope (Hadfield & Sharples 1996). Third, a plankton-nutrient model was developed for a coastal system in which the water column is subject to large changes in mixed layer depth (Kumar et al. 1991; Hadfield et al. 1995).

As yet, we have not explored the consequences of food web interactions in the situation where there is a shallow mixed layer over the continental slope and lower than average nutrient input into the mixed layer in June and July. This is the situation that is deduced to have a very negative effect on the survival of hoki larvae when they first begin to feed (see Section 4).

Model 1. Temperature and irradiance

Vincent et al. (1989b) estimated potential primary production per unit area in the New Zealand region as a function of latitude. Their model included the effects of temperature and irradiance but excluded nutrient limitation and vertical mixing. According to the model, annual-average production rates decrease with increasing latitude and are strongly correlated with mean annual irradiance and to a lesser extent with mean annual temperature. The amplitude of the seasonal production cycle, increased with latitude. To the south, the seasonal cycle in production corresponded with the seasonal cycle in irradiance, but to the north, production followed the temperature cycle more closely.

This model suggests that the latitudinal range of New Zealand may exert a strong influence on the timing and magnitude of plankton production. Off WCSI, however, other variables act to locally reduce total production below the values calculated from this model. Low nutrient availability will substantially restrict the attainable biomass in the subtropical waters of the Tasman Sea and its adjacent coasts. In the deeply mixed region parallel to the shore over the WCSI slope there will be an interplay between light limitation through low average irradiance of the mixed layer, and changes in photo-adaptation which allows phytoplankton cells to grow under conditions of low average light. Complex interactions and feedbacks through the oceanic food web further regulate biomass and the availability of nutrients. Two modelling experiments were attempted to gain more insight into the controls that are superimposed upon light-temperature effects and the nature of food web interactions.

Model 2. Nutrients and mixing

Hadfield and Sharples (1996) modelled the seasonal cycles in phytoplankton biomass, and nutrient (N) concentration for a representative location over the continental slope near Hokitika. The model represents several physical and biological properties of the water column on a multi-level vertical grid, and was run for fifteen years (1980–1994) with surface forcing by local meteorological data. The physical component of the model reproduces the observed patterns of sea surface temperature variation very well. There is a realistic seasonal cycle, and anomalous periods, such as the cool summer of 1982–83 were reproduced in the model. This gives confidence that the model is representing vertical mixing realistically.

Plankton and nutrients in the water column model were represented simply. There is a single nutrient (dissolved inorganic nitrogen - DIN) and a single phytoplankton class, quantified in terms of its chlorophyll and nutrient content. The impact of zooplankton grazing on the phytoplankton was modelled as a simple biomass loss process. As biomass is destroyed in this process, a fixed fraction of the internal nutrient is released immediately to the DIN pool and the remainder is lost to the system. Nutrient replenishment in deep water is achieved through a term which forces DIN towards its background profile. The seasonal cycle in vertical mixing generates a well-defined seasonal cycle in the surface concentration of DIN, which is brought to the surface in June and depleted by the beginning of December. This is consistent with measurements (see Figure 3.2.2 in Section 3.2).

The model generates a distinct phytoplankton bloom in spring, with maximum surface chlorophyll *a* concentrations typically around 5 mg m^{-3} and maximum vertically integrated chlorophyll of around 200 mg m^{-2} . Satellite sea surface colour data (Murphy et al. 2001) indicate that maximum spring surface chlorophyll ranges from $0.4 - 0.8 \text{ mg m}^{-3}$ suggesting that the grazing term needs to be adjusted. The model typically produces a pronounced subsurface concentration of chlorophyll exceeding 1 mg m^{-3} . Although a subsurface maximum is evident in observed profiles in summer, the highest concentrations do not exceed 0.3 mg m^{-3} . The model's behaviour in this regard is affected by the grazing rate coefficient and Hadfield & Sharples (1996) concluded that to simulate summer observations the grazing coefficient needs to be quite high. In 1993, when field work nearest to the timing of the spring bloom was carried out, model output (Figure 3.3.6) shows that the mixed layer suddenly shoaled at the beginning of October, surface NO_3 began to decline rapidly, and chlorophyll *a* began to increase. Measurements of zooplankton grazing at that time, suggest that in spring, microzooplankton consumed about 40–60% of daily total primary production (James & Hall 1998) but mesozooplankton consumed a much smaller proportion of total daily primary production at (1–5%) (Bradford-Grieve et al. 1998). These results imply that phytoplankton biomass may have been accumulating, if the same level of zooplankton grazing continued throughout spring. The question of the magnitude of phytoplankton biomass accumulation during a spring bloom could probably be answered through analysis of remotely sensed ocean colour.

Model 3. Phytoplankton population structure and grazing

More than 50% of phytoplankton biomass and productivity off WCSI is associated with picoplankton (e.g. Vincent et al. 1989a; Hall & Vincent 1990) which is unusual in a coastal system with relatively high nutrient levels (Hall & Vincent 1990; Cushing 1989). In order to investigate the reasons for this, Kumar et al. (1991) developed a seven-component plankton-nutrient model in one-spatial dimension. The model incorporated three size classes of phytoplankton (<2, 2–20, 20–200 μm) and two size classes of zooplankton (<200, >200 μm) in a water column representing the surface mixed layer with constant vertical diffusivity and a permeable lower boundary layer. Initial conditions were taken from field data immediate after a winter mixing event and the model was integrated for 30 days (Kumar et al. 1991).

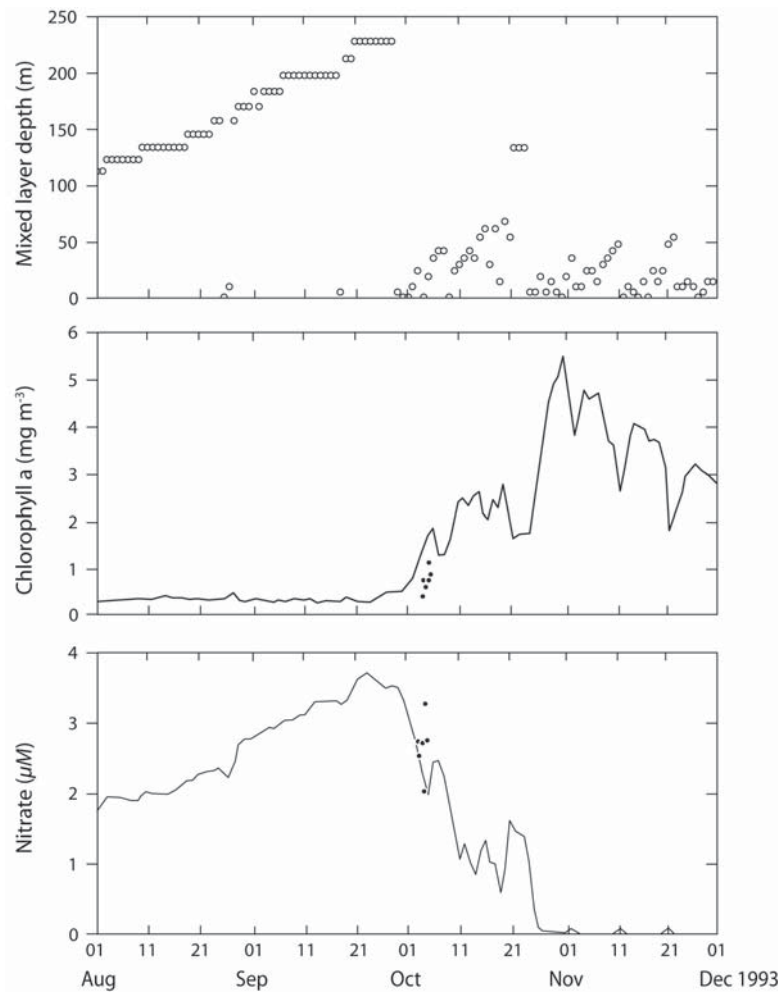


Figure 3.3.6: Modelled mixed layer depth, surface chlorophyll and nitrate concentrations August – November 1993. Filled dots on lower two panels are observations. Note that the grazing impact rate used in this model run gives unrealistically high chlorophyll concentrations. (after Hadfield & Sharples 1996)

The simulations demonstrated large changes in population size and structure of the plankton over the weeks following a simulated mixing event. Picoplankton achieved maximum concentrations within eight days of mixing (Figure 3.3.7). They were rapidly cropped by the rising microzooplankton populations and the phytoplankton community shifted towards dominance by nanoplankton (2–20 μm) after about 10 days. As pointed out by Kumar et al. (1991) the fraction of phytoplankton less than 2 μm off WCSI rarely drops below 20% of the total phytoplankton biomass, implying that the patterns simulated are continually being disrupted by other advective and mixing processes. This model (Kumar et al. 1991; Hadfield 1993) is not suitable for purposes other than for which it was intended (for events immediately after an upwelling/mixing event) because loss terms (sedimentation of phytoplankton and zooplankton and detrital material derived from zooplankton grazing) were not incorporated (Hadfield 1993). Nevertheless, this model demonstrates how quickly an injection of nutrients into the mixed layer might pass from phytoplankton to the rest of the food web on which hoki larvae depend.

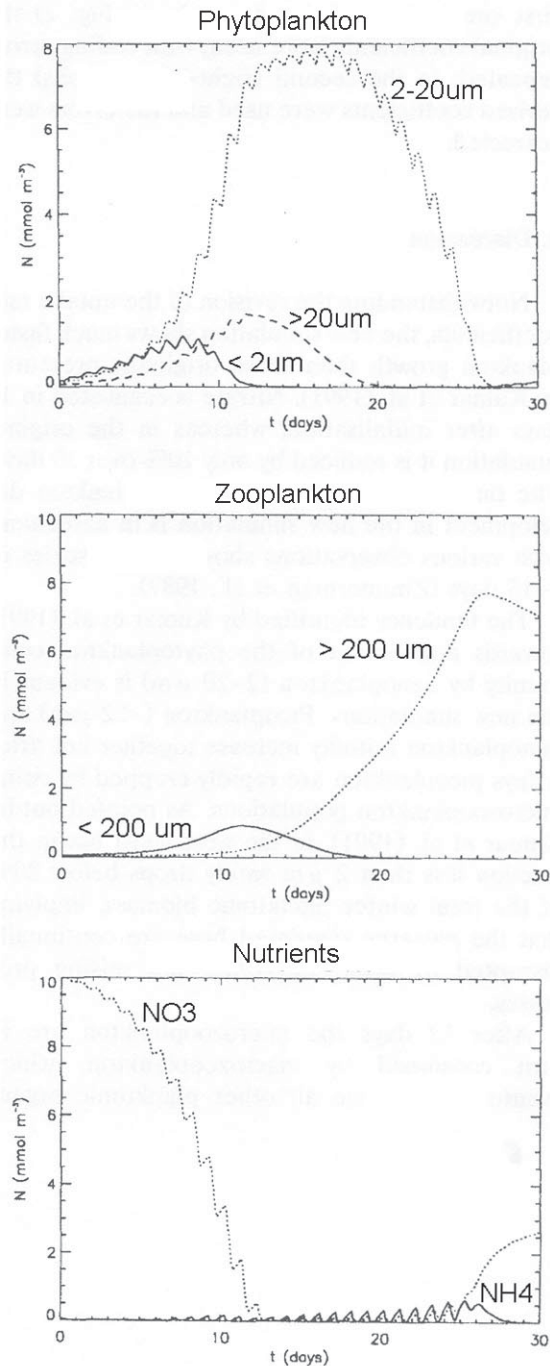


Figure 3.3.7: Model results in the mixed layer for three phytoplankton size fractions, two zooplankton size fractions and nitrate- and ammonia-nitrogen, for a 30 day period after a mixing event (after Hadfield et al. 1995). $\mu\text{m} = \mu\text{m}$

3.3.7 Summary

In offshore water, the phytoplankton cycle off WCSI can be generalised as follows: productivity is usually not light-limited and increases during winter as the progressive deepening of the mixed layer recharges the euphotic zone NO_3 . It is this winter increase in productivity over the slope that hoki appear to have evolved to exploit when they migrate to

the WCSI to spawn. At this time phytoplankton biomass accumulates slightly and “new” production is at its greatest. Nutrient limitation occurs in summer resulting in a dominance of phytoplankton populations by small cells, decreased production rate and decrease in rate of accumulation of phytoplankton. Nearshore, over the WCSI shelf, phytoplankton biomass and primary production are greater than offshore, but are much more variable because of intermittent upwelling and possible input of nutrients from river run off. The specific NO_3 uptake and ambient NO_3 during upwelling indicates that the WCSI coast lies towards the lower end of productive global upwelling regions.

Very small phytoplankton comprised a large proportion of total chlorophyll *a* off WCSI. In winter offshore waters, the less than 20 μm fraction was 78% of the integrated chlorophyll and 85% of the primary production and the 20–200 μm fraction made up 22% and 15% respectively. Nevertheless, under particular conditions, during the onset of winter mixing, the 20–200 μm size fraction can become a larger proportion of total chlorophyll *a* (32%) over the continental slope.

Light was the only parameter obviously related to integrated production per unit chlorophyll in winter and summer. One relationship was for locations with shallow mixed layers with most of the phytoplankton biomass, dominated by *Prorocentrum micans*, near the sea surface ($P^B = 3I - 0.54$) where 91% of the variance in P^B was explained by variance in light. The other relationship covered the general winter and summer populations ($P^B = 0.38I - 0.02$) where mixed layers were deeper and the vertical structure of phytoplankton did not have large vertical contrasts. Only 51% of the variance in P^B was explained by variance in light.

In winter $\text{NO}_3\text{-N}$ was the most important source of N available when more than 55% of mean total N-uptake ($\Sigma\rho\text{N}$) was accounted for by NO_3 . The 20–200 μm size fraction was dominant in the uptake of NO_3 that was light mediated. Uptake of N by the 2–20 μm size fraction was maintained at a level of about one third of $\Sigma\rho\text{N}$ in winter and was less sensitive to changes in the light environment. In winter offshore, NO_3 uptake by this size fraction was more or less the same at 100, 40, and 7% irradiance (Chang et al. 1992).

The complex interactions between phytoplankton assemblage composition, primary production, nutrients, light and vertical mixing can only be understood through the application of mathematical models combined with empirical data. Some progress has been made but further refinements are needed to be able to fully incorporate our understanding into three-dimensional, coupled, physical and biological models. As yet, we have not explored the consequences of food web interactions in the situation where there is a shallow mixed layer and lower than average nutrient input into the mixed layer in June and July, a situation that probably occurs in some years and would have a very negative effect on the survival of hoki larvae when they first begin to feed (see Section 4).

3.3.8 References

- Bradford, J.M. (1980). New Zealand region, chlorophyll *a*, surface and integrated. *N.Z. Oceanographic Institute Chart, Miscellaneous Series 42*.
- Bradford, J.M.; Chang, F.H. (1987). Standing stocks and productivity of phytoplankton off Westland, New Zealand, February 1982. *New Zealand Journal of Marine and Freshwater Research 21*: 71-90.
- Bradford-Grieve, J.M.; Chang, F.H.; Nodder, S.N.; Gall, M; Pickmere, S.; Richards, F. (1997). Size fractionated phytoplankton standing stocks and primary production during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. *New Zealand Journal of Marine and Freshwater Research 31*: 201-224.

- Bradford-Grieve, J.M.; Murdoch, R.C.; James, M.R.; Oliver, M.; Hall, J. (1996). Vertical distribution of zooplankton >39 μm in relation to the physical environment off the west coast of South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 30: 285-300.
- Bradford-Grieve J.; Murdoch, R.; Oliver, M.; James, M.; McLeod, J. (1998). Mesozooplankton biomass, composition, and potential grazing pressure on phytoplankton during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. *Deep-Sea Research I*, 45: 1709-1737.
- Chan, A.T. (1980). Comparative physiological study of marine diatoms and dinoflagellates in relation to irradiance and cell size. II. Relationship between photosynthesis, growth, and carbon/chlorophyll *a* ratio. *Journal of Phycology* 16: 428-432.
- Chang, F.H. (1983). Winter phytoplankton and microzooplankton populations off the coast of Westland, New Zealand, 1979. *New Zealand Journal of Marine and Freshwater Research* 17: 279-304.
- Chang, F.H. (1988). Distribution, abundance, and size composition of phytoplankton off Westland, New Zealand, February 1982. *New Zealand Journal of Marine and Freshwater Research* 22: 345-367.
- Chang, F.H.; Bradford, J.M. (1985). Standing stocks and productivity of phytoplankton off Westland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 19: 193-211.
- Chang, F.H.; Bradford-Grieve, J.M.; Vincent, W.F.; Woods, P.H. (1995). Nitrogen uptake by the summer size-fractionated phytoplankton assemblages in the Westland, New Zealand upwelling system. *New Zealand Journal of Marine and Freshwater Research* 29: 147-161.
- Chang, F.H.; Gall, M. (1998). Phytoplankton assemblages and photosynthetic pigments during winter and spring in the Subtropical Convergence region near New Zealand. *New Zealand Journal of Marine and Freshwater Research* 32: 515-530.
- Chang, F.H.; Vincent, W.F.; Woods, P.H. (1989). Nitrogen assimilation by three size fractions of the winter phytoplankton off Westland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 23: 491-505.
- Chang, F.H.; Vincent, W.F.; Woods, P.H. (1992). Nitrogen utilisation by size-fractionated phytoplankton assemblages associated with an upwelling event off Westland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 26: 287-301.
- Cushing, D. (1989). A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. *Journal of Plankton Research* 11: 1-15.
- Dugdale, R.C.; Goering, J.J. (1967). Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography* 12: 196-206.
- Dugdale, R.; Wilkerson, F. (1992). Nutrient limitation of new production in the sea. In: Falkowski, P.G.; Woodhead, A.D. ed. Primary productivity and biogeochemical cycles in the sea. New York, Plenum Press, pp. 107-122.
- Hadfield, M. (1993). Progress on modelling plankton population dynamics. *NIWA Biology Section report 1993/1*.
- Hadfield, M.; Kumar, S.K.; Vincent, W.F.; Austin, P.C.; Wake, G.C. (1995). Addendum to "Picoplankton and marine food chain dynamics in a variable mixed layer: a reaction-diffusion model". *Ecological Modelling* 82: 105-108.
- Hadfield, M.G.; Sharples, J. (1996). Modelling mixed layer depth and plankton biomass off the west coast of South Island, New Zealand. *Journal of Marine Systems* 8: 1-29.
- Hall, J.A.; Vincent, W.F. (1990). Vertical and horizontal structure in the picoplankton communities of a coastal upwelling system. *Marine Biology* 106: 465-471.
- James, M.R.; Hall, J.A. (1998). Microzooplankton grazing in different water masses associated with the Subtropical Convergence around the South Island, New Zealand. *Deep-Sea Research I*, 45: 1689-1707.
- Joergensen, N.O.G.; Kroer, N.; Coffin, R.B.; Hoch, M.P. (1999). Relations between bacterial nitrogen metabolism and growth efficiency in an estuarine and an open-water ecosystem. *Aquatic Microbial Ecology* 18: 247-261.
- Kumar, S.K.; Vincent, W.F.; Austin, P.C.; Wake, G.C. (1991). Picoplankton and marine food chain dynamics in a variable mixed-layer: a reaction-diffusion model. *Ecological Modelling* 57: 193-219.
- Longhurst, A. (1998). Ecological geography of the sea. London, Academic Press, 398 pp.
- Murdoch, R.C.; Quigley, B. (1994). A patch study of mortality, growth and feeding of the larvae of the southern gadoid *Macroronus novaezelandiae*. *Marine Biology* 121: 23-33.

- Murphy, R.J.; Pinkerton, M.H.; Richardson, K.M.; Bradford-Grieve, J.M.; Boyd, P.W. (2001). Phytoplankton distributions around New Zealand derived from SeaWiFS remotely-sensed ocean colour data. *New Zealand Journal of Marine and Freshwater Research* 35: 343-362.
- Siegel, D.A.; Doney, S.C.; Yoder, J.A. (2002). The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. *Science* 296(5568): 730-733.
- Vincent, W.F.; Chang, F.H.; Cole, A.; Downes, M.T.; James, M.R.; May, L.; Moore, M.; Woods, P.H. (1989a). Short-term changes in planktonic community structure and nitrogen transfers in a coastal upwelling system. *Estuarine, Coastal and Shelf Sciences* 29: 131-150.
- Vincent, W.F.; Wake, G.C.; Austin, P.C.; Bradford, J.M. (1989b). Modelling the upper limit to oceanic phytoplankton production as a function of latitude in the New Zealand Exclusive Economic Zone. *New Zealand Journal of Marine and Freshwater Research* 23: 401-410.

3.4 Microbial food web

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3.4.1 Introduction

Over the last 15–20 years, understanding of the marine food web has been modified considerably. The classical view of a short food web where phytoplankton are consumed by large zooplankton, which are in turn preyed on by larval and small fish, has been modified to incorporate what has been termed the microbial food web (e.g. Azam et al. 1983). This conceptual revision of the planktonic food web was stimulated by two major discoveries: (1) that very small, “picophytoplankton” (less than 2 μm) can be an important component of phytoplankton and (2) the role and importance of bacteria as remineralisers of dissolved organic substances released by phytoplankton and as a food source for the heterotrophic flagellates and ciliates.

The microbial food web includes bacteria, picophytoplankton (phytoplankton 0.2–2 μm) and microzooplankton that are defined as grazers 2–200 μm in size. They include nanoflagellates and ciliates. Picophytoplankton and bacterial cells are too small to be consumed directly by copepod crustaceans (e.g. Nival & Nival 1976) which dominate the mesozooplankton in the marine environment so that, if the organic material produced in the microbial food web is to be transferred to these large consumers, it must be repackaged into larger units.

Chang (1988) recognised the importance of the microbial food web of West Coast, South Island (WCSI) where the picophytoplankton were shown to contribute a significant proportion of the phytoplankton biomass, up to 90% of total chlorophyll (see also Hall & Vincent 1994). Subsequent studies began with an evaluation of the abundance and biomass of picophytoplankton, bacteria and microzooplankton. Research then progressed to investigations of feeding within the microbial food web. Based on our current knowledge of the ecology of hoki larvae off WCSI (e.g. Murdoch 1992; Bradford-Grieve et al. 1996) the microbial food web in the environment off the WCSI is clearly important to hoki larvae and their food supply.

In this section we review the current knowledge of the microbial food web (apart from Cyanobacteria which are dealt with in Section 3.3) and its role in the WCSI marine ecosystem. We show that the bulk of grazing on the phytoplankton is carried out by the microzooplankton. The activities of the microzooplankton repackage particles that are too small for the larger zooplankton to eat (bacteria, picophytoplankton, heterotrophic and autotrophic flagellates). Thus, production at the beginning of the food web becomes available, through larger microzooplankton, which is included in the food of larger zooplankton on which hoki larvae feed.

3.4.2 Components of the microbial food web

Heterotrophic bacteria

Heterotrophic bacteria are single-celled, ubiquitous organisms ranging in size from 0.1 to 1.0 μm and are dependent on organic material for their energy source. Bacteria play a key role in the microbial food web. They are major decomposers of organic matter, are food for microzooplankton and, thus, play an important role in energy and nutrient cycling (Pace 1996). Their metabolic activities link dissolved organic carbon to the higher trophic levels of the food web.

Early research on the composition of bacterial populations in New Zealand waters, including the Tasman Sea, was conducted using culturing techniques to assess bacteria numbers and population composition. Singleton and Skerman (1973) showed that all the species identified were gram-negative rods with the majority of cells either distributed singly or in pairs. They identified *Moraxella*, *Vibrio* and *Pseudomonas* as common forms over a wide range of depths. The luminous species *Vibrio fisheri*, *Photobacterium phosphoricum* were also isolated.

Bacterial numbers in the WCSI region ranged from 1.1 to 27×10^8 cells l^{-1} (MacKenzie & Gillespie 1984, Smith & Hall 1997). These numbers are similar to those reported in other low chlorophyll *a* waters. The horizontal spatial distribution of bacterial populations off WCSI was variable. In winter, high bacterial numbers were observed offshore (MacKenzie & Gillespie 1984, Smith & Hall 1997). In autumn 1992 and summer 1989, however, the highest numbers were observed at near shore stations (James & Hall 1995), whereas in spring, bacterial numbers were similar both at near shore and offshore stations. Nevertheless, there was no significant difference in integrated bacterial numbers between winter and spring for onshore and inshore stations in 1993 (Smith & Hall 1997). Vertical distribution in the water column is variable but numbers usually decreased with depth (Figure 3.4.1).

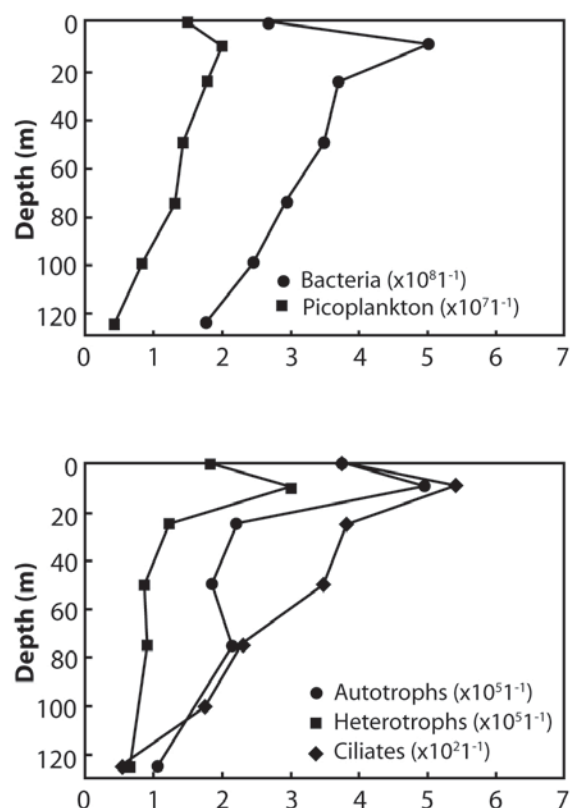


Figure 3.4.1: Profile of bacteria, picophytoplankton, flagellate and non-loricated ciliate numbers over the continental slope off Westland (from Hall et al. 1993). Note that greatest concentrations are found in the euphotic zone.

The relationship between bacterial numbers, chlorophyll *a* and primary production was variable. There may be no overall correlation between bacterial numbers and chlorophyll *a* in

autumn (MacKenzie & Gillespie 1984; NIWA Marine Biogeochemical Database), whereas significant relationships have been observed between bacteria and chlorophyll *a* and / or primary production by James et al. (1996) and Smith & Hall (1997). Oscillations between substrate and grazing control of bacterial numbers in this region may be the reason for these relationships.

Bacterial productivity ranged from 3 to 64% of primary production with a strong relationship between bacterial production and primary production in spring (Smith & Hall 1997). However, in winter there was no relationship with primary production suggesting that bacterial production was not controlled by the nutrient substrate during this period (Smith & Hall 1997). Productivity in the mixed layer ranged from 0.008 to 0.147 mg C m⁻³ h⁻¹ in winter and 0.11 to 0.23 mg C m⁻³ h⁻¹ in spring with highest productivity occurring in the surface waters (Smith & Hall 1997).

Doubling times for bacteria have been calculated during three studies in the region and ranged from 8–62 days (MacKenzie & Gillespie 1984, James & Wilkinson 1988; Smith & Hall 1997). This variability probably has a seasonal component as shown in 1993 with a mean doubling time of 17.4 days in winter and 5.4 days in spring (Smith & Hall 1997).

Nanoflagellates

Nanoflagellates are single celled organisms with one or more flagellae that are used for locomotion and food capture. They are ubiquitous in both marine and freshwater environments, occurring in coastal and oceanic regions from the tropics to the high polar regions. Nanoflagellate populations are recognised as providing a very important link in the microbial food web (e.g. Sanders & Wickham 1993) through their grazing on bacteria and picophytoplankton. This trophic link provides a pathway for the flow of energy from the very smallest organisms in the food web to the higher trophic levels (e.g. Hall et al. 1993). Nanoflagellates are not a single taxon but are a functional group where small size (2–20 µm) determines the functional role they perform in pelagic food webs. Within the group a range of taxa are represented: Choanoflagellida, Chrysomonadida, Helioflagellida, Euglenida, Kinetoplastida, Cryptomonadida and dinoflagellates.

The flagellate population is composed of three major functional groups. Heterotrophic nanoflagellates (HNF) are obligate heterotrophs and do not contain photosynthetic pigments but gain all their requirements for growth by grazing. Autotrophic nanoflagellates (ANF) are obligate autotrophs that gain all their requirements for growth from photosynthesis. Mixotrophic nanoflagellates (MNF) are capable of both photosynthesis and grazing. There is increasing evidence that many phytoflagellates in both marine and freshwater systems are capable of phagotrophy (e.g. Sanders et al. 1990). These organisms primarily come from the Chrysomonadida, Euglenida, Cryptomonadida and the Dinophyceae groups. The only way to identify these organisms as active mixotrophs is to observe feeding directly during grazing experiments.

Off WCSI, nanoflagellate numbers are greatest in the euphotic zone (Hall et al. 1993) (Figure 3.4.1). There is a significant difference between seasons with both HNF and ANF numbers being greater in spring than in winter (James & Hall 1998). Mean cell numbers of ANF and HNF at 10 m depth in winter were 0.35 and 0.17 x 10⁶ cells l⁻¹ and in spring 2.2 and 0.69 x 10⁶ cells l⁻¹, respectively. ANF tend to be smaller in size than the HNF, but there is a seasonal difference in cell size with a mean cell size, in winter, of 13.6 µm³ for ANF and 7.6 µm³ for HNF and, in spring, of 47.5 and 76 µm³ respectively.

The distribution of both HNF and ANF was closely related to the distribution of urea, NH₄, bacterial and picophytoplankton numbers (Safi & Hall 1999). The high ratio of ciliate : HNF

biomass, observed off WCSI during the spring, indicates the potentially high grazing pressure of ciliates on the nanoflagellate population.

Ciliated protozoa

Ciliated protozoa are single-celled microzooplankton ranging from 0.01 mm to over 1 mm and are characterized by fine, hair-like organelles that they use for locomotion and creating feeding currents. They have a range of feeding strategies including facultative autotrophy (*Myrionecta (Mesodinium) rubra*), bacterivory, herbivory and predation on other protozoa. Some species like *Askenasia* can be mixotrophic, bacterivorous, herbivorous or predatory depending on food availability.

Ciliates are cosmopolitan in their distribution, unlike higher organisms that have well defined geographic distributions. Endemism is the exception although this may reflect a general lack of taxonomic research on this group.

Numerically, the ciliate community off the west coast region was originally thought to be dominated by medium sized oligotrichs 20-50 μm , particularly *Strombidium*, *Halteria*, *Strobilidium*, *Lohmaniella* and *Urotricha* (Chang 1983, 1990; James 1989; James & Hall 1995). Subsequently, a close examination of samples collected with Niskin bottles found that ciliates less than or equal to 20 μm are a major constituent of neritic, shelf and slope waters off WCSI and can dominate the ciliate community particularly in offshore waters (James & Hall 1995). Earlier studies, using nets to concentrate microzooplankton, would not have included these small microzooplankton (James 1989). One species which is an important component of the community off WCSI is *Myrionecta (Mesodinium) rubra* (Chang 1983, 1990) which is a facultative autotroph relying on the products of photosynthesis of its symbiotic algal inclusions as its carbon source.

Tintinnids (loricate ciliates) are a more conspicuous component of the ciliate community because of their larger size and conspicuous lorica (or shell). The most diverse tintinnid fauna is generally found offshore and tends to be dominated by forms with hyaline loricas (*Eutintinnus*, *Salpingella*, *Proplectella* and *Undella*) or species such as *Dictyocysta fenestrata* that utilise coccoliths for lorica construction. *Dictyocysta* is one of the items in the diet of hoki larvae that is actively selected (Murdoch & Quigley 1994). Many of these genera are over 100 μm . Smaller taxa which have agglutinated lorica (*Tintinnopsis*, *Stenosomella bodonella*) are common in neritic waters close to freshwater inflows and shallow water, as would be expected of ciliates requiring mineral grains, silica or diatom frustules for lorica formation (Burns 1983; Chang 1990; James & Hall 1995).

Ciliate abundance and biomass off WCSI is similar for tropical and temperate waters elsewhere. Their numbers were greatest in the euphotic zone (Hall et al. 1993, Figure 3.4.1, 3.4.2). Ciliate abundances ranged from 114 to 19000 l^{-1} and biomass ranged from 0.05–1.92 $\mu\text{g C l}^{-1}$ in winter and 0.62 –15.37 $\mu\text{g C l}^{-1}$ in spring in the mixed layer (James & Hall 1995).

Total ciliate abundance off WCSI is greatest over the outer continental shelf in winter (James & Hall 1995) (Figure 3.4.2) and summer (Chang 1990). This has significance for first feeding hoki larvae in winter (Murdoch & Quigley 1994). While ciliate abundance tends to increase in spring, the community composition remained largely unchanged. Nevertheless, principal

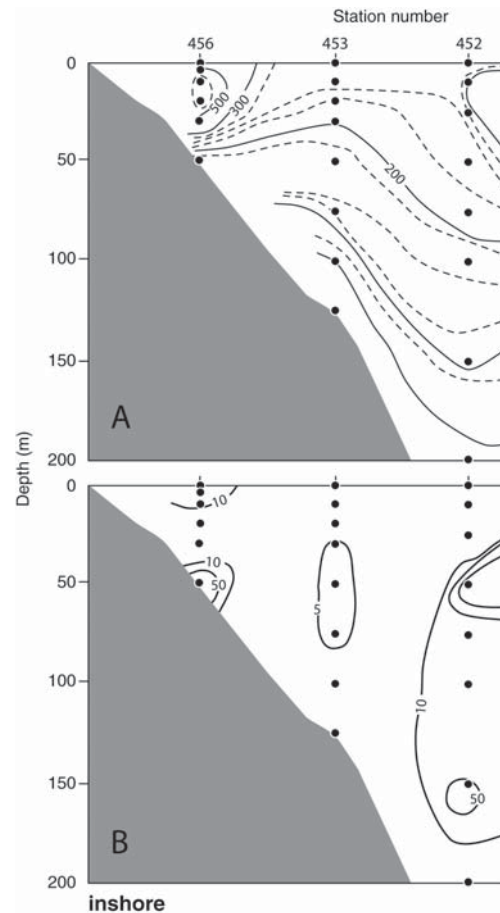


Figure 3.4.2: Vertical profiles of ciliate number off Westland, June/July 1990: (A) non-loricated ciliate abundance (no. l^{-1}) and (B) tintinnid abundance (no. l^{-1}) off Hokitika (from James & Hall 1995). Note that largest concentrations of ciliates occur inshore in water that has the greatest influence from freshwater inflow and seaward of the 200 m isobath.

component analysis on data from winter and spring in 1993 (James unpublished data) showed that there were distinct inshore and offshore groups of species in each season. Offshore waters were characterised by low tintinnid abundance and the large oligotrich *Laboea strobila* was relatively more abundant. These offshore waters were also characterised by high chlorophyll *a* concentrations and maximum abundance of picophytoplankton, flagellates and ciliates. The ciliate community was dominated by small species less than 25 μm that may have been responding to the greater numbers of small phytoplankton cells in these offshore waters.

The vertical distribution of ciliates depends on a number of factors including food availability, vertical diffusivity and mixed layer depth. James & Hall (1995) found consistently strong correlations between vertical profiles of ciliate abundance and both phytoplankton biomass (chlorophyll *a*) and picophytoplankton abundance. Correlation does not necessarily mean the relationship is causal but we know from grazing experiments that picophytoplankton (Hall et al. 1993) and nanophytoplankton (James & Hall 1998) are the major food sources for ciliates. Variations in the mixed layer depth and pycnocline have been found to have a major influence on the vertical distribution of ciliates. Nevertheless, profiles from several cruises in different seasons, have shown that peaks in the ciliate community are generally found in the surface 20 m and then abundance declines with depth (Figures 3.4.1, 3.4.2).

3.4.3 Microbial food web structure

The ratio of bacterial biomass to phytoplankton biomass can be used to evaluate the importance of the microbial food web in the pelagic ecosystem. Bacterial biomass was greater than phytoplankton biomass at 52% of the locations sampled in the region. The pattern of bacterial biomass domination was not related to NO_3 concentrations. There was also no trend in chlorophyll *a* at the sites where bacterial biomass dominated except that chlorophyll *a* concentrations were never greater than $0.5 \mu\text{g l}^{-1}$. The frequent dominance of bacterial biomass over phytoplankton biomass suggests that the microbial food web plays a significant role in the WCSI marine ecosystem even during periods of elevated nutrient concentrations (Hall & Vincent 1990). Changes in the bacterial: phytoplankton biomass ratio appear to be driven by the changes in phytoplankton biomass rather than changes in the bacterial biomass. This relationship, in turn, is associated with a high proportion (28 to 70 %; NIWA Marine Biogeochemical Database) of picophytoplankton in the phytoplankton population.

Microzooplankton play a pivotal role in the transfer of microbial biomass to higher trophic levels (e.g. Azam et al. 1983). Given that different groups of ciliates and flagellates have different food preferences and grazing rates, any change in the composition of the microzooplankton population is likely to result in changes in the food web structure. The ratio of heterotrophic flagellate : ciliate biomass off WCSI region is highly variable with ratios ranging from 0.3 to 17.8. This ratio lies between 5.6 to 17.8 in April, 0.5 to 1.6 in June, and 0.5 to 1.6 in October (NIWA Marine database). The lower ratio and higher proportion of ciliates in winter is probably advantageous to hoki larvae (Murdoch & Quigley 1994). These varying ratios between flagellate and ciliate biomass are likely to be a result of, not only their food supply, but also grazing pressure on flagellates and ciliates. To date, no experiments have been conducted to differentiate between population growth due to enhanced food supply and death rates through predation, although we know something about the grazing rates and the food of individual types of microzooplankton.

3.4.4 Grazing rates

80-194% of primary production was grazed by microzooplankton in winter and 20–64% in spring. A similarly large proportion of bacterial production was consumed in winter and spring: 92–154% and 79–250% respectively (James and Hall 1998, Table 1). It must be remembered that zooplankton larger than $200 \mu\text{m}$ were excluded from the dilution experiments and therefore, their grazing control of microzooplankton populations was absent. Nevertheless, these grazing rates indicate that microzooplankton grazing is capable of controlling phytoplankton and bacterial biomasses.

Group and species-specific grazing rates can be measured using fluorescently labeled tracers that can be observed within the predator. Fluorescently labeled beads and bacteria were used to evaluate the grazing preferences and impacts of microzooplankton on bacteria ($0.5 \mu\text{m}$) and picophytoplankton ($1.0 \mu\text{m}$) sized particles. Nanoflagellates are considered to be the primary grazers of bacteria (e.g. Sanders et al. 1989), with bacterial and heterotrophic flagellate populations often showing coupled oscillations (Bjoernsen 1988). The flagellates are also considered to be the major grazers of the picophytoplankton population (e.g. Hall et al. 1993).

Table 3.4.1: Comparison of grazing impact of microzooplankton on elements of the microbial food web standing stock and production at offshore locations off WCSI, 1993 (from James & Hall 1998, NIWA Marine database). When % of production removed is greater than 100% this implies that the biomass of the food source is declining.

Component	Integrated Biomass mg C m ⁻² 0-100 m	Production mg C m ⁻² d ⁻¹ 0-100 m	% Standing stock (Chl <i>a</i>) removed Percentage by microzooplank- ton grazing	% Production removed by Microzooplank- ton grazing
Total phytoplankton, Winter	1245	193	10-92	71-194
Total phytoplankton, Spring	1908	633	4-57	20-126
Picophytoplankton Winter	451	101	95	424
Picophytoplankton Spring	95	220	94	41
Ciliates Winter	51	-	-	-
Ciliates Summer	165	-	-	-
Heterotrophic flagellates, Winter	53	-	-	-
Heterotrophic flagellates, Spring	417	-	-	-
Bacteria Winter	1450	135	-	-
Bacteria Spring	2210	163	27-67	79-250

Experiments were conducted using the dilution method that measures grazing by the entire microzooplankton population (James & Hall 1998). Mean clearance rates, calculated for the total microzooplankton population, were 10 $\mu\text{l ind}^{-1}\text{h}^{-1}$ (James & Hall 1998). In winter 55–65% of the picophytoplankton standing stock was removed at both the inshore and offshore stations. In spring 60% of the picophytoplankton standing stock was removed offshore and 35% inshore. In spring, 60–65% of the standing stock of bacteria was removed on a daily basis (James & Hall 1998).

The MNF contributed a significant proportion of the nanoflagellate grazing pressure (Hall et al. 1993; Safi & Hall 1999). In June 1990, the MNF had clearance rates of 0.5 and 1.0 $\text{nl ind}^{-1}\text{h}^{-1}$ for 0.5 μm and 1.0 μm beads respectively. These compare to clearance rates of 1.8 and 0.9 $\text{nl ind}^{-1}\text{h}^{-1}$ respectively for the HNF. The MNF contributed 40% of the grazing pressure on the bacterial population and 30% on the picophytoplankton. Similar results were also recorded in April 1992 when MNF contributed 46% and 38% of the nanoflagellate grazing pressure on the bacterial and picophytoplankton population respectively (Hall et al. 1993). In June 1990, the MNF showed a significantly higher uptake of 0.5 μm compared to 1.0 μm fluorescently labeled beads (Hall et al. 1993). This may have been due to the smaller cell size of the MNF (Hall et al. 1993). The reason for the significant grazing pressure by the MNF is possibly related to a need to supplement their carbon supply because the mixed layer was deeper than the euphotic zone in June at all the stations sampled resulting in a decrease in

average light received and consequent reduction in photosynthetic activity by MNF (Hall et al. 1993).

Among ciliated protozoans, the choreotrichs are herbivorous and rely on pico- and nanophytoplankton rather than bacteria for food. This has been demonstrated off WCSI where choreotrich clearance rates, which dominate the ciliate community, ranged from 0.01–0.08 $\mu\text{l ind}^{-1}\text{h}^{-1}$ for bacteria sized fluorescent microspheres, 0.05–0.58 $\mu\text{l ind}^{-1}\text{h}^{-1}$ for labeled bacteria but 0.39–1.65 $\mu\text{l ind}^{-1}\text{h}^{-1}$ for picophytoplankton sized particles (James & Hall 1998). Larger taxa such as *Laboea* and tinnids had specific clearance rates up to 9.0 $\mu\text{l ind}^{-1}\text{h}^{-1}$. These results are consistent with the hypothesis that different ciliate taxa selectively ingest food according to size.

The dilution experiments also allowed the growth of the prey species to be estimated. In winter, the grazing on picophytoplankton was approximately balanced by growth. In spring, growth was higher than grazing offshore and growth was lower than grazing inshore although growth exceeded grazing on total phytoplankton at both locations suggesting that, at inshore stations, the microzooplankton may have been unable to graze on the larger species in the phytoplankton population (James & Hall 1998). The tight coupling between growth and grazing in winter suggests microzooplankton may play a pivotal role in the transfer of energy from primary producers in the upper water column.

3.4.5 Nutrients cycling

Microzooplankton are not only critical links in the food web but are also important as recyclers of nutrients. Microzooplankton produce very small faecal pellets that do not sink out of the surface mixed layer. Thus the action of bacteria in breaking down these waste products rapidly recycles nitrogen in forms such as ammonia that are immediately taken up by the phytoplankton.

Bacteria are important in nutrient cycles through several different processes. They not only remineralise dissolved organic exudates from photosynthesis but will affect the availability of nitrogen through nitrification processes that convert ammonia to nitrate and the reverse where bacteria act as denitrifying agents. There has not been any work undertaken on denitrification processes off WCSI but in western Cook Strait NH_4^+ oxidation by nitrifying bacteria accounted for about 30% of the total ammonia utilisation (bacteria and phytoplankton uptake) (Priscu & Downes 1985).

Zooplankton regenerate up to 70% of the particulate nitrogen they ingest as dissolved NH_4^+ . A study of the role of zooplankton in the nitrogen cycle in winter concluded that regeneration of NH_4^+ by zooplankton larger than 55 μm contributed on average only 12% of ammonia remineralisation and by inference 88% of potential remineralisation off WCSI must be by smaller cells (James 1989). Regeneration of N by organisms smaller than 20 μm (bacteria, nanoflagellates, ciliates) has not been determined for the region but regeneration rates measured for microzooplankton larger than 20 μm in summer 1989 (NIWA Database. data) were up to 20 times greater than for zooplankton larger than 55 μm .

3.4.6 Summary

The importance of the microbial food web in the WCSI pelagic ecosystem is highlighted by the large proportion of overall biomass contributed by bacterial and picophytoplankton populations. Bacterial biomass was greater than phytoplankton biomass at 52% of the stations

sampled. Picophytoplankton dominated the phytoplankton population at 50% of the stations sampled. These results imply that the microbial food web in this system will have a significant impact on the biomass of higher trophic levels such as zooplankton and fish larvae. The dominance of biomass by both bacteria and picophytoplankton occurred not only during low chlorophyll *a*, low nutrient conditions, but also in low chlorophyll *a*, high nutrient conditions. The primary grazers of the bacterial and picophytoplankton populations have been shown to be the microzooplankton (flagellates and ciliates). The growth of the bacterial and picophytoplankton populations is generally balanced by microzooplankton grazing. Mixotrophic nanoflagellates were shown to contribute significantly to total nanoflagellate grazing on both bacterial and picophytoplankton populations. Ciliates are likely to be the major grazers on picophytoplankton and small flagellates.

Tintinnid ciliates are a conspicuous component of the microzooplankton because of their large size and conspicuous shells. Large ciliates of the genus *Dictyocysta*, were actively selected for in the diet of hoki larvae in winter. The occurrence of *Dictyocysta* in the diet of hoki larvae is set in a background of greatest ciliate abundance in winter over the outer shelf and the fact that there are distinct inshore and offshore ciliate groups.

Over 80% of the recycled nitrogen off WCSI is potentially supplied by protozoans through excretion and production of faecal pellets. Because protozoans have faster metabolic and growth rates, compared with mesozooplankton, and produce small faecal pellets that do not export nutrients out of the euphotic zone, they play a very important role in maintaining primary production in surface waters particularly when nutrients become limiting.

The microbial food web is important to first feeding hoki larvae in winter because of the role of ciliated protozoa (and other microzooplankton) in repackaging very small, abundant bacteria, heterotrophic flagellates and picophytoplankton into particles large enough for small copepods to feed on. Small copepods of the genus *Calocalanus* are important food items for young larvae (see sections 2.2 and 3.5) in the deeply mixed water column over the slope. These small copepods are able to feed on both microzooplankton and phytoplankton that are large enough to be captured, thus acquiring the energy to reproduce.

3.4.7 References

- Azam, F.; Fenchel, T.; Field, J.G.; Gray, J.S.; Meyer-Reil, L.A.; Thinstad, F. (1983). The ecological role of water-column microbes in the sea. *Marine ecology progress series*. 10: 257-263.
- Bjoernsen, P.K. (1988). Grazing on bacterioplankton by heterotrophic flagellates: A test of methods. Proceedings of the third international workshop on the measurement of microbial activities in the carbon cycle in aquatic ecosystems. pp. 267-274, *Ergebnisse der Limnologie* no. 31.
- Bradford-Grieve, J.M.; Murdoch, R.C.; James, M.R.; Oliver, M.; Hall, J. (1996). Vertical distribution of zooplankton > 39 µm in relation to the physical environment off the west coast of South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 30: 285-300.
- Burns, D.A. (1983). The distribution and morphology of tintinnids (ciliate protozoans) from the coastal waters around New Zealand. *New Zealand Journal of Marine and Freshwater Research* 17:387-406.
- Chang, F.H. (1983). Winter phytoplankton and microzooplankton populations off Westland, New Zealand, 1979. *New Zealand Journal of Marine and Freshwater Research* 17: 279-304.
- Chang, F.H. (1988). Distribution, abundance, and size composition of phytoplankton off Westland, New Zealand, February 1982. *New Zealand Journal of Marine and Freshwater Research* 22: 345-367.
- Chang, F.H. (1990). Quantitative distribution of microzooplankton off Westland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 24: 187-195.
- Hall, J.A.; Barrett, D.P.; James, M.R. (1993). The importance of phytoflagellate, heterotrophic flagellate and ciliate grazing on bacteria and picophytoplankton sized prey in a coastal marine environment. *Journal of Plankton Research* 15: 1075-1086.

- Hall, J.A.; Vincent, W.F. (1990). Vertical and horizontal structure in the picoplankton communities of a coastal upwelling system. *Marine Biology* 106: 465-471.
- Hall, J.A.; Vincent, W.F. (1994). Vertical and horizontal structure of the picophytoplankton community in a stratified coastal system off New Zealand. *New Zealand Journal of Marine and Freshwater Research* 28: 299-308.
- James, M.R. (1989). The role of zooplankton in the nitrogen cycle off the west coast of the South Island, New Zealand, winter 1987. *New Zealand Journal of Marine and Freshwater Research* 23: 507-518.
- James, M.R.; Hall, J.A. (1995). Planktonic ciliated protozoa: their distribution and relationship to environmental variables in a marine coastal ecosystem. *Journal of Plankton Research* 17: 659-683.
- James, M.R.; Hall, J.A. (1998). Microzooplankton grazing in different water masses associated with the Subtropical Convergence around the South Island, New Zealand. *Deep-sea Research I*, 45: 1689-1707.
- James, M.R.; Hall, J.A.; Barrett, D.P. (1996). Grazing by protozoa in marine coastal and oceanic ecosystems off New Zealand. *New Zealand Journal of Marine and Freshwater Research* 30: 313-324.
- MacKenzie, A.L.; Gillespie, P.A. (1984). Bacterioplankton biomass and heterotrophic activity off Westland, New Zealand, June 1979. *New Zealand Journal of Marine and Freshwater Research* 18: 341-354.
- Murdoch, R.C. (1992). A review of the ecology of hoki *Macruronus novaezelandiae* (Hector), larvae in New Zealand waters. *Bureau of Rural Resources Proceedings* 15: 3-16.
- Murdoch, R. C.; Quigley, B. (1994). A patch study of mortality, growth and feeding of the larvae of the southern gadoid *Macruronus novaezelandiae*. *Marine Biology* 121: 23-33.
- Nival, P.; Nival, S. (1976). Particle retention efficiencies of an herbivorous copepod, *Acartia clausi* (adult and copepodite stages): effects on grazing. *Limnology and Oceanography* 21: 24-38.
- Pace, M.L. (1996). Heterotrophic microbial processes. In: Carpenter, SR; Kitchell, JF (eds). *The trophic cascade in lakes*. Cambridge University Press, New York, pp. 252-277.
- Priscu, J.C.; Downes, M.T. (1985). Nitrogen uptake, ammonium oxidation and nitrous oxide (N₂O) levels in the coastal waters of western Cook Strait, New Zealand. *Estuarine, Coastal and shelf sciences* 20: 529-542.
- Safi, K.A.; Hall, J.A. (1999). Mixotrophic and heterotrophic nanoflagellate grazing in the convergence zone east of New Zealand. *Aquatic Microbial Ecology* 20: 83-93.
- Sanders, R.W.; Porter, K.G.; Bennett, S.J.; DeBiase, A.E. (1989). Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community. *Limnology and Oceanography* 34: 673-687.
- Sanders, R.W.; Porter, K.G.; Caron, D.A. (1990). Relationship between phototrophy and phagotrophy in the mixotrophic chrysophyte *Poterioochromonas malhamensis*. *Microbial Ecology* 19: 97-109.
- Sanders, R.W.; Wickham, S.A. (1993). Planktonic protists and metazoan: population, food quality and population control. *Marine Microbial Food Webs* 7(2): 197-223.
- Singleton, R.J.; Skerman, T.M. (1973). A taxonomic study by computer analysis of marine bacteria from New Zealand waters. *Journal of the Royal Society of New Zealand* 3: 129-140.
- Smith, R.; Hall, J.A. (1997). Bacterial abundance and production in different water masses around South Island New Zealand. *New Zealand Journal of Marine and Freshwater Research* 31: 515-524.