Spawning fisheries and the productivity of the marine environment off the west coast of the South Island, New Zealand

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In this report we collate and review information and research about hoki and some other spawning fisheries off West Coast, South Island (WCSI). We also collate information on the ocean environment over the continental shelf (inshore) and the adjacent Tasman Sea (offshore). As well as recent work, the report includes previously unpublished work from research initiated during the West Coast Marine Ecosystem programme, 1979–1989.

Although the overall biological productivity of WCSI is moderate compared with other regions of the world, the region is noteworthy because it is adjacent to one of the more unproductive oceans – the Tasman Sea. This raises questions as to why hoki and other species spawn over the continental slope off WCSI and how local environmental variability impacts on the productivity of the region. Many of the species that spawn here migrate into the area to spawn and are absent for the rest of the year. Clearly the influence of the westerly wind flows on ocean currents and interactions between weather, ocean climate and the ecosystem on this coast combine to form a prime spawning location for several fish species. Not only is this location upstream from nursery and feeding grounds in the New Zealand region, but it also provides adequate food for newly hatched larvae and 0+ fish so they can achieve sufficient growth in their first year to reach the optimal size for surviving predation. Hoki form the largest fishery off the WCSI being 34% of the total New Zealand catch and spawn there in winter months. A number of other species are also caught here and form sizeable portions of the total New Zealand catch: hake (46%), frostfish (66%), albacore (most), barracouta (34%), giant stargazer (34%), red cod (18%), spiny dogfish (18%) and terakihi (21%) (Ministry of Fisheries 2011).

1. Hoki biology and fishery

Hoki is New Zealand's largest fishery, and is a major species ecologically and commercially on the WCSI. Hoki has a complex life history. Two stocks are recognised: a "western stock" which resides primarily on Campbell Plateau, southeast of New Zealand, and spawns off the WCSI; and an "eastern stock" which resides primarily on the Chatham Rise, and spawns in Cook Strait. Juvenile hoki of both stocks mix together on the Chatham Rise, and are believed to recruit to their respective home grounds at maturity (3–8 years). The Total Allowable Commercial Catch (TACC) for hoki throughout the New Zealand EEZ in 2010–11 was 120 000 t. Although this has increased from 90 000 t in 2007–08 and 2008–09, catch levels remain low compared with those of the late 1990s (up to 269 000 t in 1997–98). Most of the decline occurred in western stock fisheries and effort was reduced and shifted to the eastern areas. However, model assessments show that stocks have rebuilt and projections suggest that the biomass of the western stock is likely to continue to increase at the current catch levels. The major reason for the decline of the western stock is attributed to a period of poor recruitment from 1995–2001. Model estimates of western stock year-classes after 2001 are stronger, with five years of near or above average recruitment. The key factors driving hoki recruitment remain uncertain.

2. Hoki larval ecology

Off WCSI, hoki spawn above the continental slope in 400–600 m water in winter. Regions of high egg abundance are located primarily from the Hokitika Canyon area south to the Cook Canyon. At night aggregations of eggs form off the sea floor several hundred metres thick. Direct observations of spawning have shown that positively buoyant young eggs are found at about 300 m only in a 6–8 h period centred around 0200 h each day. The presence of distinct, daily cohorts of larvae in patches suggests that hoki have a synchronised, diel spawning periodicity. Areas of high larval abundance generally coincide with areas of high egg abundance, located primarily from the Hokitika Canyon area south to the Cook Canyon, but larval abundance is greatest closer to shore compared with egg abundance. Hoki larvae probably first feed at about 4.2 mm when the mouth has developed and the intestinal tract has opened. The diet of hoki larvae consists primarily of copepod adults and copepodites. The most actively selected prey species appear to be copepods of the genera *Calocalanus* and *Paracalanus* and the tintinnid *Dictyocysta.* Work on the range of variability in the density of preferred hoki food off WCSI in winter, indicates that starvation may be an important factor for larval survival. The abundance of preferred copepod prey of hoki may vary significantly over the continental slope in relation to the depth of mixing and nutrient concentrations. Numbers of copepod nauplii, and *Calocalanus* spp were 3–5 times greater when the waters over the slope have a mixed layer deeper than 75 m and nitrate-nitrogen concentrations are greater than 3 μM. Growing hoki larvae have been found at locations with these characteristics (high numbers of copepod nauplii and *Calocalanus*).

3. Other fish and fisheries

Besides hoki, other key WCSI fisheries include middle-depth species such as hake and ling and shallow water species such as barracouta. Catches of hoki and many other species off WCSI are highly seasonal. Many commercially caught species, including hake, ling, blue, silver and white warehou, gemfish, giant stargazer, hapuku, ribaldo and red cod, also spawn in the area in winter and spring and, like hoki, may have migrated there from other areas. Correlations between climate variables and recruitment have been observed although causal mechanisms are uncertain. The impact of large seasonal influxes of spawning fish during winter and spring months on trophic relationships into the area cannot be assessed from the information available. In at least four key species, a relatively high proportion (over 60%), do not feed during winter and spring. However, the eggs and larvae provide a source of prey for other small fish and zooplankton, and the spawning adults are probably prey for marine mammals and large fish such as tuna and sharks. Main prey for the four key species examined included crustaceans (particularly natant decapods and euphausiids), teleosts (particularly myctophids and hoki) and squid.

4. Physical environment

The WCSI is a very dynamic region. The Southern Alps mountain chain is exposed to prevailing westerly wind systems and results in high episodic freshwater input to the coastal region. The geography also results in high cloud cover, strong winds (5–20 day periodicity), with coastal upwelling accompanied by variability in the mixed layer depth. There is a 50–100 km wide surface band of coastal water affected by input from rivers. In winter, the mixed layer may reach a maximum of more than 150 m over the continental slope parallel to the coast, shoaling both inshore and offshore. This is a result of the interplay of the thermocline deepening towards the east associated with the large scale flow, together with the coastal band of fresh water. Inshore mixed layers are typically only a few tens of metres deep. Highly variable coastal flows are dominated by coastal-trapped waves (CTW), which are also important at time scales of 5–20 days. Upwelling along the WCSI coast occurs in sporadic events lasting 2–12 days, rarely reaching a discernible steady state. Recent analyses of the temperature field through the water column show strong interannual variability from the surface down to 800 m (the maximum depth of the measurements). In particular, the ocean warmed by 1.2° between 1996 and 2002. By inference, this warming could have an associated lowering of nutrients available to the plankton production system. Much of the underlying physics and biology have been studied but ongoing measurements to interpret interannual variability in both the physical environment and the biological systems have not been made.

5. Nutrients and light

Inshore WCSI waters generally have high attenuation coefficients (up to 0.29 m^{-1} in summer) and shallow euphotic depths compared with offshore waters. In both winter and summer, the euphotic zone ranges from depths of about 20 m inshore to about 75 m offshore. Differences in the average subsurface irradiance to which phytoplankton in the mixed layer are subjected are primarily due to differences in mixed layer depth. The mixed layer may exceed the depth at which vertically integrated primary production equals integrated respiration (the critical depth) in winter. Deep winter mixing and upwelling of deep water are key processes in recharging nutrient levels in surface waters. The mixed layer depth in winter is at a maximum over the continental slope and runs parallel to the coast. The orientation of the mixed layer depth is related to a tongue of warm water that is often observed to extend down the coast from the north. The depth of the mixed layer over the slope in summer is 15–50 m and lies within the euphotic zone (the depth to which light penetrates) that is about 50–80 m, that is light penetration extends beyond the mixed layer, which becomes nutrient-depleted. In winter the depth of the mixed layer has been measured at 130 m in June and may reach 100–300 m in August when the euphotic zone is 40–75 m. During winter, the progressive deepening of the mixed layer recharges the euphotic zone nitrate level, increasing it from less than 1 mmol m^{-3} to more than 3 mmol m^{-3}. Upwelling may elevate nitrate concentrations to more than 10 mmol m^{-3} although upwelled water does not always reach the euphotic zone as it can be capped by dilute surface water inshore. Based on limited observations, upwelling has never been seen to impact conditions over the continental slope in winter where hoki spawn. Deepening of the mixed layer over the slope is the physical process most likely to be influencing the prey environment of early stage hoki larvae. The impact of basin-scale oceanographic processes on WCSI ecosystems and the temporal and spatial relationships between nitrate and temperature below the seasonal thermocline may have relevance for the winter surface mixed layer and the food of hoki larvae, but remain unknown.

6. Phytoplankton and primary production

Offshore, phytoplankton productivity is low and not usually light-limited but increases during winter as progressive deepening of the mixed layer recharges nitrate in the euphotic zone. 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. The trajectories of the "critical depth" (the depth where integrated primary production equals total losses due to respiration) and the mixed layer depth show that the minimum in the critical depth in June (the month when the sun is lowest in the sky) and the maximum in the mixed layer depth (August-September) do not coincide over the slope, often leaving a window in July when the mixed layer is much shallower than the critical depth so that net phytoplankton growth may occur if sufficient nutrients are available. This window may be necessary for adequate concentrations of small copepods to develop in the habitat where hoki larvae first feed. In winter, phytoplankton biomass accumulates slightly and production based on uptake of nitrate (NO_3-N) peaks. Nitrogen is available in three forms. "New" nitrogen is in the form of NO_3 and regenerated nitrogen is in the form of ammonia (NH_4) and urea. Nutrient limitation in summer results in small cells dominating phytoplankton populations, decreased production rate based on regenerated (recycled) NH_4 and urea and a decrease in the rate of accumulation of phytoplankton. Phytoplankton biomass and levels of primary production off the WCSI are greater inshore than offshore, but are also more variable because of intermittent upwelling and additional inputs of nutrients from river run-off. The specific NO_3 uptake and ambient NO_3-N during upwelling indicates that the WCSI lies towards the lower end of productive global upwelling regions. Light is the only parameter correlated with integrated production per unit chlorophyll (P^B) in winter and summer. The scatter of data around this relationship in winter is partly contributed by the varying availability of light to phytoplankton in the photic zone, which is controlled by the depth of the surface mixed layer. In winter, NO_3-N is the most important source of nitrogen available, although the less than2 μm size fraction of phytoplankton is a major user of NH_4 in summer. As yet, the consequences of food web interactions with hoki larvae have not been explored 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.

7. Microbial food web

Bacterial and picophytoplankton biomass were greater than phytoplankton biomass at about 50% of the stations sampled in the WCSI region indicating the importance of the microbial food web in this system. Microzooplankton (flagellates and ciliates) are the primary grazers on bacterial and picophytoplankton populations. Tintinnid ciliates are a conspicuous component of the microzooplankton because of their large size and conspicuous shells. Tintinnids of the genus *Dictyocysta*, are particularly significant as they were actively selected by hoki larvae in winter. The presence of *Dictyocysta* in the diet of hoki larvae occurs when ciliate abundance is at its greatest over the outer shelf. Over 80% of the recycled nitrogen off the WCSI is potentially supplied by protozoans through excretion and production of faecal pellets. Because protozoans have faster metabolic and growth rates than mesozooplankton, and produce small, slow sinking 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 in the deeply mixed water column over the continental 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.

8. Zooplankton

Oceanic water further out in the Tasman Sea supports a relatively low biomass of larger zooplankton (25 mg m^{-3}) and has no distinct seasonal cycle. A larger, but more variable biomass of zooplankton (greater than 200 mg m^{-3}), with a winter minimum, is found over the WCSI continental shelf. Zooplankton species off the WCSI are typical of New Zealand near-surface coastal waters. Distinct WCSI zooplankton communities have been described for neritic, outer shelf / upper slope, and oceanic environments. A distinct outer shelf/ upper slope community probably occurs because of advection of warmer oceanic water from the north influenced by local deepening of the surface mixed-layer and entrainment of subsurface nutrients. Hoki eggs are spawned into the outer shelf / upper slope zooplankton community. As the mixed layer deepens in autumn, zooplankton species important in the diet of hoki larvae (*Calocalanus* spp., *Paracalanus indicus, Oithona similis*, *O. nana* and *Dictyocysta*) achieve their highest densities. The proportion of basic metabolic requirements of zooplankton met by the consumption of phytoplankton is usually very small (1–4%). The bulk of the food required to support basic metabolic needs, growth and reproduction of larger zooplankton is met by the consumption of microzooplankton and smaller zooplankton. A plankton-nutrient model suggested that immediately after an injection of nutrients into the water column, organic matter flows through the larger zooplankton in about 20 days. Field observations of the vertical distribution of small copepods *Calocalanus* spp., *Oithona similis* and *O. nana* in mixed layers of various depths corroborated the model results. That is, small copepods were recorded in concentrations 2–3 times greater in deep mixed layers (with greater amounts of entrained nutrient) compared with shallower, more nutrient limited, mixed layers.

9. Sediment and benthos

The benthos has a puzzling place in the WCSI shelf ecosystem. Benthic production seems to be low relative to planktonic energy input to the benthos. Possible explanations for this include efficient bacterial remineralisation of phytodetritus, its export off the shelf, and/or burial under sediment deposits. The continental shelf and upper slope off the WCSI are characterised by modern, terrigenous, fine-grained sediments. Inshore sediments tend to be coarser than outer shelf and upper slope sediment. Input of terrigenous sediment is high and the sedimentation rate for the shelf is estimated to average 1–2 mm y^{-1}. The carbonate content of sediments increases with water depth and towards the south. The effects of periodic upwelling on sediment geochemistry appear to be masked by high terrigenous input. For example, shelf sediments exhibit a near absence of siliceous organisms, sparse occurrence of benthic foraminifera, low organic contents and high C:N ratios. Anaerobic mineralisation of carbon and denitrification are likely to be important, at least on the inner shelf. Mean meiofaunal density (~ 80% nematodes) for the shelf and upper slope is 825 individuals per 10 cm^2. Benthic macrofauna of the shelf and upper slope largely comprises deposit feeders. Macrobenthic assemblages relate closely to bathymetry and sediment type, and include an inshore silty sand fauna, and mud bottom faunas at mid- to outer shelf and at upper slope depths. Mean macrobenthic biomass for inshore, mid-shelf to shelf break and upper slope zones is lower than that of the east coast (based on limited data), generally of the order of 50–150, 10–50, and 5–10 g wet wt m^{-2}, respectively. Rapid sedimentation and episodic upwelling may promote an abundance of opportunistic taxa and high temporal variability of benthic populations. Benthic energy flow is likely to occur primarily via the sediment micro- and meiobenthos and deposit-feeding macrobenthos.

10. Linking environmental variability and fish abundance

Initial correlations between environmental indicators and hoki year class strength led to a deeper examination of mechanisms that might be involved and further attempts to find predictors of year class strength. Preliminary results suggested that year-to-year variations in the year class strengths of hoki may be influenced by the timing of winter mixing and the pattern of its progression. It is reasonable to hypothesise that sufficient nitrate and other phytoplankton nutrients must be mixed into the upper water layers to allow the rate of primary production to increase and leave enough time before the hoki eggs are spawned for this additional primary productivity to flow through into the food of hoki (the "nitrate / larval survival hypothesis").

Further analysis, using revised estimates of YCS, an additional six years data, and including surface nitrate concentrations as a test of the nitrate / larval survival hypothesis, was used to investigate predictors of YCS in more detail, but failed to replicate the earlier results. No predictive power of practical significance was found in this analysis.

However, it is interesting to note that the relationship between YCS and nitrate changed with time from being significantly negative in the period 1980–1989 to significantly positive in the period 1989–2000. The period from 1990–1996 represents one of the more extensive periods of positive departures of the multivariate ENSO index since 1950. The significance of such an extended El Niño event on the behaviour of the ocean is not yet understood.

There are other reasons why the relationship between oceanographic processes and year class strength may be more complex than at first suspected. To evaluate these hypotheses, we need a greater understanding of the impact of ENSO events on the ocean and time series of data are required to verify model outputs.

11. Overall conclusions

A substantial body of research on the marine environment and the early life history of hoki off the West Coast South Island of New Zealand has been collated in this document. Hypotheses about which variables drive hoki recruitment have been presented, yet understanding of the underlying mechanisms and causal links between the West Coast marine environment and hoki year class survival remain elusive.

In our study, we have identified a lack of basic data and understanding about several aspects of hoki behaviour, stock structure and the oceanographic environment. We do not know the proportion of juvenile hoki on Chatham Rise that were spawned on WCSI. We lack verification that model estimated year class strength indices are indicative of the annual survival rates of larvae and juveniles. We lack basic data on the vertical distribution of young hoki larvae in relation to their physical environment. We do not know the minimum level of food that a first feeding larva needs in order to survive. We lack measured nitrate concentration profiles that are linked to an understanding of the oceanographic processes occurring in the Tasman Sea and further afield including ENSO events. We lack basic data on the links between mixed layer depth, phytoplankton growth, nutrients, light and small copepod growth with time and on the spatial and temporal variability in inshore / offshore transport in relation to the vertical and horizontal distribution of young fish. Finally, there is a need for novel approaches to modelling year class strength and larval survival that are capable of incorporating non-linear effects.

Any future examination of the predictive power of environmental data (e.g. temperature) should ideally include postulated mechanisms by which the identified environmental variable acts on year class strength. Schematic concepts need to be developed offering relatively well-understood, fairly well-defined frameworks for the identification and elaboration of important mechanistic linkages between climate variability and fishstock dynamics.

1. OVERVIEW

Authors: Mary Livingston, Janet Bradford-Grieve

Fisheries are ultimately linked to the underlying productivity of the region in which they occur, the intrinsic qualities of the fish populations being harvested, the environmental drivers of variability on fish populations, and the interaction of the fisheries management system with all of these. Investigating the biological mechanisms linking environmental variability to fish production systems requires the disentangling of the interactions between habitat, environmental adaptation and fitness (Claireaux and Lefrancois 2007). Since the number of environmental variables and regulatory processes is large, straightening out the environmental influences on fish performance is intractable unless the mechanistic analysis of the 'fish-milieu' system is preceded by an understanding of the properties of that system (Claireaux and Lefrancois 2007).

The largest fishery off the West Coast, South Island (WCSI) (Figure 1.1) is for hoki, a merluccid hake species found throughout New Zealand waters that dominates New Zealand's bottom fish communities in depths of 200–800 m. In 2009–10 the hoki catch off WCSI was 34% of the total New Zealand catch. Other important species caught off WCSI, and the percentage of the New Zealand catch they represent, are: hake (46%), frostfish (66%), albacore (most of troll fishery), barracouta (34%), giant stargazer (34%), red cod (18%), spiny dogfish (18%) and terakihi (21%) (Ministry of Fisheries 2011).

Hoki form New Zealand's largest fishery and is one the biggest export earners for the fishing industry. Hoki had an annual Total Allowable Commercial Catches (TACC) of 200–250,000 t from 1986 until 2003. An extended period from 1995 to 2001, however, saw poor recruitment, particularly in the western stock and substantial cuts to the TACC were necessary in 2004. Declines were also observed in populations of demersal fish such as red gurnard, red cod, tarakihi and a number of other species off the WCSI during this period. In recent years, however, the TACC has been increased to reflect the improved stock status of hoki (Ministry of Fisheries 2011).

The WCSI environment is important because it provides the spawning grounds for many species that reside elsewhere for most of the year. The link between the environment and larval survival for these species is likely to be important in determining year class strength and recruited biomass in the fisheries. Many migrant spawners may not be actively feeding on the WCSI, but may be important as food for other residents such as New Zealand fur seals and hake. The larval fish are an integral part of the WCSI ecosystem but may also be carried away or move to other areas as they mature.

The overall biological productivity of WCSI is moderate compared with other regions of the world, and it lies adjacent to one of the more unproductive oceans – the Tasman Sea. This raises questions about why hoki and other species have evolved to spawn on this coast and how environmental variability impacts vertebrates, plankton and benthos there. Amongst the answers must be the advantages of spawning "upstream" from the more productive waters of the Chatham Rise, the influence of the westerly flows in winds and ocean currents and interactions between weather, ocean climate and marine organisms on this coast.

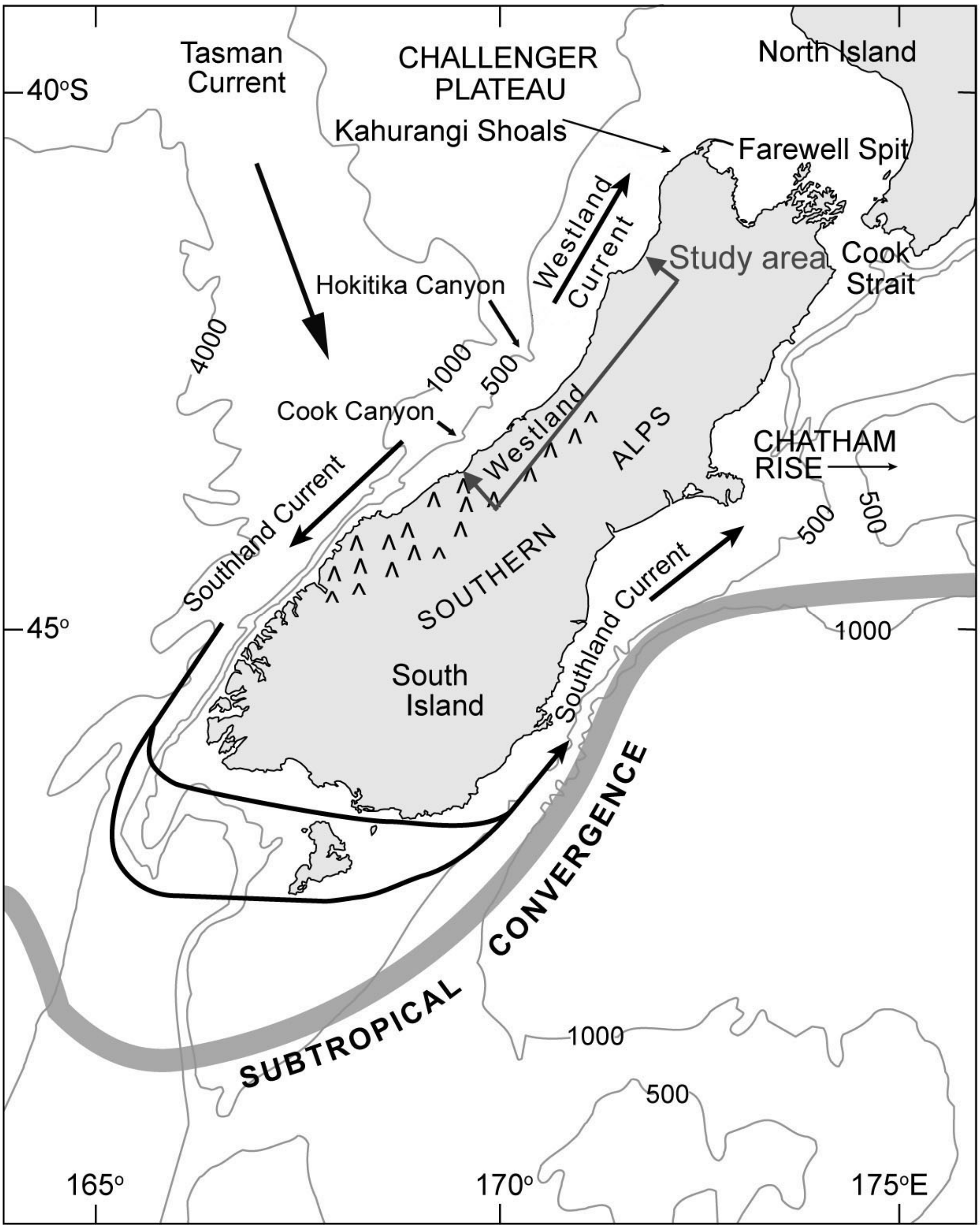

Figure 1.1: Bathymetric chart of South Island, New Zealand indicating the region of the West Coast South Island (WCSI) studied during the West Coast Ecosystem Programme and geographic names mentioned in the text. See also Figure 3.6.1 for a more detailed bathymetry.

In 1979, the New Zealand Oceanographic Institute, then a division of the Department of Scientific and Industrial Research (now incorporated into National Institute of Water and Atmospheric Research (NIWA)), began a collaborative, multidisciplinary study of WCSI − The Marine Environment of the West Coast that ran until 1989. This region was chosen because of its importance to fisheries and because of its "upstream" location relative to net flow around New Zealand. The goal of this programme was:

> "To understand the relationships between oceanic and biological variability off the west coast, South Island, as a contribution to basic understanding of a key New Zealand ecosystem. In particular, to identify effects of the chemical and physical environments on the marine food chain leading to improved assessments of resource sustainability and maintenance of the environment."

In 1993, new data were collected on ecosystem functioning processes off WCSI as part of the Foundation for Research Science and Technology Ocean Fronts Programme. Data on recent physical variability in the Tasman Sea are still being added through ongoing collaborations between Scripps Institution of Oceanography, CSIRO, and NIWA.

In this report, we collate and review relevant information and research about fisheries and the ocean environment off WCSI that is currently known. The report summarises the state of knowledge of selected aspects of fish and their fisheries as well as the physical and biological environment off the WCSI to explore the extent of interconnectedness. Fisheries are described in Section 2, as well as details of the life history of hoki, its biology, migrations and spawning. The development, diet, growth, survival and onshore / offshore transport of hoki larvae are then described. Section 2 is completed with a summary of other fish and their fisheries that occur off WCSI. Section 3 contains summaries of the physical WCSI marine environment, the nutrient and underwater light environment, phytoplankton and primary production, the microbial food web, zooplankton populations and processes and sediment and the benthos. Section 4 concludes the report with an evaluation of hypotheses about the impact of climate variability on the survival of hoki larvae and suggestions about future work.

Generalized symbolic constructs may be particularly important when addressing a complex adaptive system such as a marine ecosystem (Bakun 2010). Various examples have appeared in the climate–fisheries literature, each more or less effectively integrating hypothesized effects of several interacting environmental and/or biological processes in controlling the population dynamics of exploited fish species (e.g., match–mismatch, connectivity, school trap, loopholes, ocean triads, stable ocean hypothesis, several classes of nonlinear feedback loops as well as several prominent large-scale integrative climatic index series such as the Southern Oscillation Index, North Atlantic Oscillation and the Pacific Decadal Oscillation). Some of these are examined here, but a fully integrative approach has not been adopted.

We recognize that our understanding of hoki ecophysiology is limited, that our West Coast biophysical models are incomplete and likely to be simplistic and that more sophisticated approaches to simulated data modeling could be developed. Nevertheless, this report presents the first attempt to pull the existing information together and identify possible approaches to improving both our understanding of key processes driving fish recruitment off the West Coast South Island, and our ability to predict year class strength in the future.

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2. WEST COAST SOUTH ISLAND FISH AND FISHERIES

2.1 New Zealand hoki, *Macruronus novaezelandiae*

Authors: Mary E. Livingston, Richard L. O'Driscoll

2.1.1 Introduction

Hoki is a merluccid hake species found throughout New Zealand waters, also occurring in Australia and South America. It dominates bottom fish communities in depths of 200–800 m, particularly on the Chatham Rise and the Campbell Plateau to the east and south of the South Island (Bull et al. 2001, Francis et al. 2002). During winter hoki migrate to spawning grounds, primarily off Westland and in Cook Strait (Figure 2.1.1), dispersing east and south again in early spring. Two stocks of hoki are recognised based on morphometric and growth rate differences (Livingston & Schofield 1996, Horn & Sullivan 1996), and these have been assessed separately since 1989. The "western stock" resides primarily on the Campbell Plateau, south of New Zealand, and spawns on the west coast of the South Island (WCSI). The "eastern stock" home ground is the Chatham Rise, with most spawning occurring in Cook Strait. Juvenile hoki of both stocks mix together on the shallower areas of the Chatham Rise, and are believed to recruit to their respective stocks at maturity (Livingston et al. 1997). As New Zealand's largest fishery, with annual Total Allowable Commercial Catch (TACC) levels of 200 000–250 000 t from 1986 until 2003, hoki is one of New Zealand's biggest export earners for the Fishing Industry (www.seafood.co.nz). Recent years, however, have seen poor recruitment, particularly for the western stock, and there have been a series of reductions in the annual quota: to 180 000 t in 2003, to 100 000 t in 2004–05, and to 90 000 t in 2007–08 (Table 2.1.1). The TACC was increased to 110 000 in 2009–10 and to 120 000 t in 2010–11, reflecting the improved stock status of hoki (Ministry of Fisheries 2011).

Although empirical links between climate variables and hoki year class strength have been found (Bull & Livingston 2001, Livingston 2000), the underlying mechanisms that drive hoki recruitment are not known. Further, the effects of reduced biomass (perhaps reaching as low as 13% of unfished biomass in the case of the western stock, Francis (2004)) on spawning success are unknown. Here, we are seeking to review past studies that have been carried out off Westland and generate testable hypotheses on mechanisms that determine the survival rates of young hoki spawned off WCSI.

This chapter presents a brief overview of the commercial fishery and a summary of what is currently known about the biology and life-cycle of hoki. Studies which identify links between hoki year class strength and broad climatic signals, and those stages of the life-cycle which may be vulnerable to high mortality are also discussed.

2.1.2 The commercial fishery and status of hoki stocks

Historically, the main fishery for hoki has operated from mid-July to late August on spawning fish aggregated off WCSI (Figure 2.1.1). The spawning aggregations begin to concentrate in depths of 300–700 m over the continental slope around the Hokitika Canyon from late June, and further north off Westport later in the season. The head of Hokitika Canyon and the area immediately south lie inside a 25-mile restricted Fishing Zone where only small vessels (less than 46 m overall length) are allowed to fish. Until recently, this gave fish spawning inside the 25 mile zone some protection from disruption by the commercial fleet. In recent years, however, a number of smaller vessels have been working inside the 25 mile zone, reaching a peak in 2003–04, when 43% of the west coast catch came from inside the 25-mile zone (Ballara et al. 2008). The proportion of the catch from inside 25-miles has subsequently reduced, to 8% in 2009–10.

A second spawning fishery developed in Cook Strait after the discovery of spawning hoki there in 1986 (Murdoch et al. 1990, Livingston 1990). Like the west coast, the spawning season in Cook Strait also runs from late June to mid September, peaking in July and August. Small catches of spawning hoki are taken from other spawning grounds off the east coast South Island (ECSI) and late in the season at Puysegur Bank.

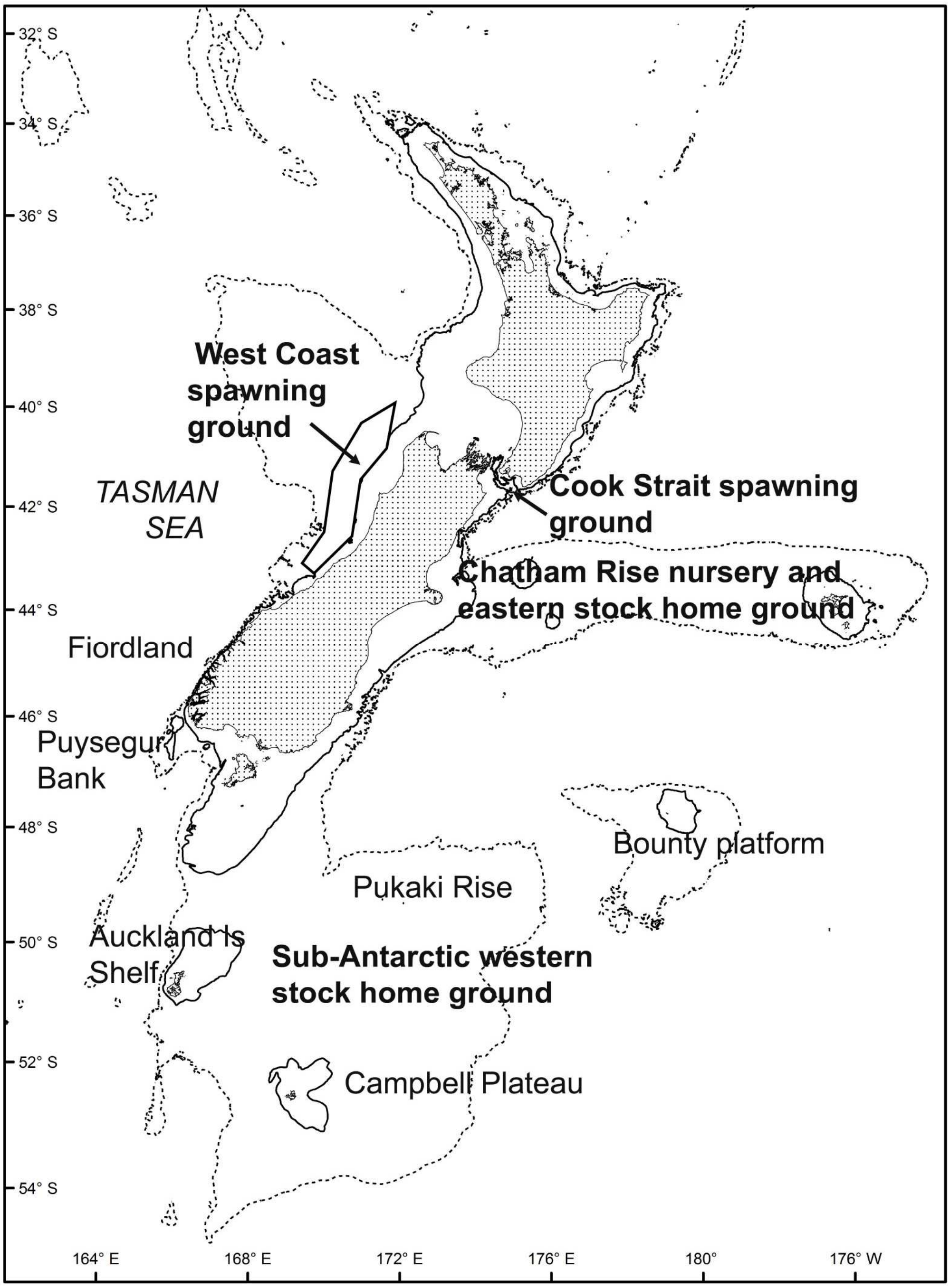

Figure 2.1.1: Spawning grounds and home grounds of western and eastern stocks of hoki.

Table 2.1.1: Estimated catch (t) of hoki by area, 1988–89 to 2009–10. Fishing year runs from 1 October to 30 September. – indicates catches less than 100 t. (Source: Ministry of Fisheries (2011)).

			Spawning					Non-spawning fisheries		TACC
Fishing Year	WCSI	Puysegur	Cook Strait	ECSI	Sub-Antarctic	Chatham and ECSI	ECNI	Unrep.	Total catch	
1988-89	188 000	3 500	7 000	–	5 000	5 000	–	–	208 500	250 000
1989-90	165 000	8 000	14 000	–	10 000	13 000	–	–	210 000	251 184
1990-91	154 000	4 000	26 500	1 000	18 000	11 500	–	–	215 000	201 897
1991-92	105 000	5 000	25 000	500	34 000	45 500	–	–	215 000	201 897
1992-93	98 000	2 000	21 000	–	26 000	43 000	2 000	3 000	195 000	202 155
1993-94	113 000	2 000	37 000	–	12 000	24 000	2 000	1 000	191 000	202 155
1994-95	80 000	1 000	40 000	–	13 000	39 000	1 000	–	174 000	220 350
1995-96	73 000	3 000	67 000	1 000	12 000	49 000	3 000	2 000	210 000	240 000
1996-97	91 000	5 000	61 000	1 500	25 000	56 500	5 000	1 000	246 000	250 000
1997-98	107 000	2 000	53 000	1 000	24 000	75 000	4 000	3 000	269 000	250 000
1998-99	90 100	3 000	46 500	2 100	24 300	75 600	2 600	–	244 500	250 000
1999-00	101 100	2 900	43 200	2 400	34 200	56 500	1 400	500	242 400	250 000
2000-01	100 600	6 900	36 600	2 400	30 400	50 500	2 100	100	229 900	250 000
2001-02	91 200	5 400	24 200	2 900	30 500	39 600	1 200	-	195 500	200 000
2002-03	73 900	6 000	36 700	7 100	20 100	39 200	900	-	184 700	200 000
2003-04	45 200	1 200	40 900	2 100	11 700	33 600	900	-	135 800	180 000
2004-05	33 100	5 500	24 800	3 300	6 200	30 700	500	100	104 400	100 000
2005-06	38 900	1 500	21 800	700	6 700	34 100	700	-	104 400	100 000
2006-07	33 100	400	20 100	1 000	7 700	37 900	700	-	101 000	100 000
2007-08	21 000	300	18 400	2 300	8 700	38 000	600	-	89 300	90 000
2008-09	20 600	200	17 500	1 100	9 800	39 000	600	-	88 800	90 000
2009-10	36 400	300	17 800	700	12 300	39 200	600	-	107 200	110 000

Table 2.1.2: Proportions of annual catch in spawning fisheries (West: WCSI, Puysegur); East: Cook Strait, east coast South Island) and non-spawning fisheries (West: Sub-Antarctic; East: Chatham Rise, east coast North Island). (Source: Ministry of Fisheries 2011).

	Spawning fisheries		Non-spawning fisheries	
Fishing Year	West	East	West	East
1988-89	92%	3%	2%	3%
1989-90	82%	7%	5%	6%
1990-91	74%	13%	8%	5%
1991-92	51%	12%	16%	21%
1992-93	51%	11%	14%	24%
1993-94	60%	19%	7%	14%
1994-95	47%	23%	7%	23%
1995-96	36%	33%	6%	25%
1996-97	39%	26%	10%	25%
1997-98	41%	20%	9%	30%
1998-99	38%	20%	10%	32%
1999-00	43%	19%	14%	24%
2000-01	47%	17%	13%	23%
2001-02	49%	14%	16%	21%
2002-03	43%	24%	11%	22%
2003-04	34%	32%	9%	25%
2004-05	37%	27%	6%	30%
2005-06	39%	21%	7%	33%
2006-07	33%	21%	8%	38%
2007-08	24%	23%	10%	43%
2008-09	23%	21%	11%	45%
2009-10	34%	17%	12%	37%

Outside the spawning season, other areas of substantial catch have been developed across the Chatham Rise and in the Sub-Antarctic since the early 1990s. The Chatham Rise fishery generally has similar catch levels over all months except for lower catches in July-September when hoki move to their spawning grounds. In the Sub-Antarctic, catches typically peak in April-June during the pre-spawning migration. Out-of-season (non-spawning) catches are taken from Cook Strait and the east coast of the North Island (ECNI), but these are small compared with other areas (Table 2.1.1).

The pattern of fishing has changed markedly since 1988–89 when over 90% of the total catch was taken in the WCSI spawning fishery. In the most recent fishing year (2009–10) just 34% of the catch came from the WCSI, and 17% came from Cook Strait (Tables 2.1.1 and 2.1.2). Chatham Rise and Sub-Antarctic catches have fluctuated over the years, but currently stand at around 37% and 11% of the annual catch respectively (Tables 2.1.1 and 2.1.2). Catches from other areas have remained at relatively low levels (Table 2.1.1). The catches by area do not necessarily reflect hoki abundance in each area. The hoki fleet has taken different initiatives to minimise exploitation of young hoki, and also to reduce effort on the western stock in recent years (Ministry of Fisheries 2011).

Other changes to commercial operations include the type of fishing. From 1986 to 1990 large surimi vessels using large nets dominated the catches from WCSI. However, since 1991, the surimi component of catches has decreased and processing to head and gut, or to fillet product has increased, as has “fresher” catch for shore processing. The hoki fishery now operates throughout the year, producing fillets from both spawning and non-spawning fisheries. More recently, the use of twin-trawl rigs (two nets deployed together from the same vessel giving increased effort) has been increasing in all hoki fisheries, except Cook Strait and inside the 25-mile restricted Fishing Zone off WCSI.

Off WCSI, most vessels use mid-water trawls, although in some parts of the fishing grounds, these trawls are used along the sea-bed, similar to a bottom trawl. The distribution of effort has changed over time. In the mid 1980s, effort was concentrated in Hokitika Canyon during the early part of the season, and the fleet would move north as younger fish appeared to spawn off Westport. As the western spawning stock has declined, hoki are not as widespread, and much of the recent effort has been focused in and around Hokitika Canyon (Dunn & Livingston 2004).

The status of both hoki stocks are assessed annually using research time series of abundance indices, proportions at age data from the commercial fisheries and trawl surveys, and estimates of biological parameters (e.g., Francis 2008). Five series of abundance indices are used in the stock assessment (Table 2.1.3). Trawl surveys of the Chatham Rise and Sub-Antarctic provide estimates of abundance of non-spawning hoki from the eastern and western stocks respectively. In addition, the Chatham Rise trawl survey provides an index of recruitment of young (age 1 and 2) hoki for both stocks. Acoustic surveys on the WCSI and in Cook Strait provide estimates of abundance of spawning hoki. Recent hoki stock assessments have been carried out using a Bayesian model developed in 2002 (Francis et al. 2003) and implemented in the general-purpose stock-assessment program CASAL (Bull et al. 2008).

The most recent assessment results (Ministry of Fisheries 2011) indicate that the western stock experienced an extended period of poor recruitment from 1995–2001 (Figure 2.1.2). Year-classes after 2001 are stronger, with five years in which recruitment is estimated to be near or above the long-term average. For the western stock, median estimate of current biomass is 41 $\%B_0$, (Figure 2.1.2), which is above the assumed value of B_{MSY} (25 $\%B_0$). Model projections suggest that the biomass of the western stock is likely to increase at current catch levels. For the eastern stock, the median estimate of current biomass is $53\%B_0$ (Figure 2.1.2), which is also above B_{MSY}. Recent recruitment (1995–2009) is estimated to be near the long-term average for this stock (Figure 2.1.2). Model projections suggest that the biomass of the eastern stock is likely to stay steady with current catches.

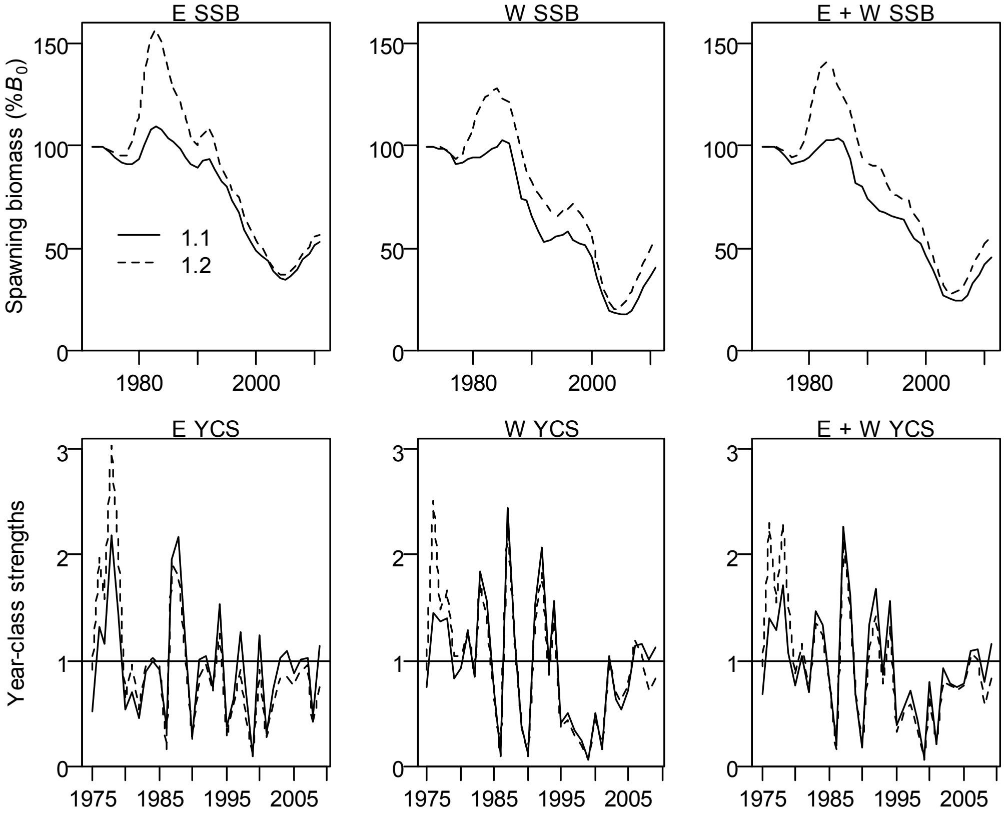

Figure 2.1.2: **Estimated spawning biomass trajectories (SSB, upper panels) and year-class strengths (YCS, lower panels) for the E (left panels), W (middle panels) and E + W stocks (right panels) from the base case model (Run 1.1) and one of the sensitivities (Run 1.2). Plotted values are medians of marginal posterior distributions. Years are fishing years (1990 - 1989-90). Source: Ministry of Fisheries 2011**

Table 2.1.3: Abundance indices ('000 t) used in the hoki stock assessment. Years are fishing years (1990 = 1989–90). – no data. From Ministry of Fisheries (2011). *, provisional estimate.

Year	Acoustic survey WCSI, winter	Trawl survey Sub-Antarctic, December	Trawl survey Sub-Antarctic, April	Trawl survey Chatham Rise, January	Acoustic survey Cook Strait, winter
1988	417	–	–	–	–
1989	249	–	–	–	–
1990	255	–	–	–	–
1991	340	–	–	–	180
1992	345	80	68	120	–
1993	550	87	–	186	583
1994	–	100	–	146	592
1995	–	–	–	120	427
1996	–	–	89	153	202
1997	654	–	–	158	295
1998	–	–	68	87	170
1999	–	–	–	109	243
2000	396	–	–	72	–
2001	–	56	–	60	220
2002	–	38	–	74	320
2003	–	40	–	53	225
2004	–	14	–	53	–
2005	–	18	–	85	132
2006	–	21	–	99	126
2007	–	14	–	70	216
2008	-	46	-	77	167
2009	-	47	-	144	315
2010	-	65	-	98	-
2011	-	-	-	94*	-

2.1.3 The biology and life-cycle of hoki

Hoki occur throughout New Zealand waters from 34° S to 54° S, from depths of 10 m to over 900 m, although their greatest abundance lies between 200 and 800 m, and is generally along or south of the Subtropical Front. Large hoki (greater than 80 cm total length) are generally found deeper than 400 m, while juveniles are more abundant in shallower water (Bull & Livingston 2000).

Inference about the life-cycle of hoki suggests that young hoki spawned off WCSI and in Cook Strait move to the Chatham Rise nursery grounds at age 1 to 2 years, and at some point between age 4 and 8 years, recruit to their adult distributions or stocks in deeper waters on the Chatham Rise (eastern stock) and south to the Campbell Plateau in the sub-Antarctic (western stock) where they continue to reside except for annual migrations to the spawning grounds (Table 2.1.4, Figure 2.1.3).

The planktonic eggs and larvae are widely dispersed north and south from the spawning centres with the result that 0+ and 1-year-old pelagic fish can be found in most coastal areas of the South Island and also parts of the North Island. Dense schools of 0+ hoki have been caught in Cook Strait (Kerstan & Sahrhage 1980) and off WCSI (Zeldis et al. 1998). They have been reported inshore in trawl surveys along the west coast of the South Island (Stevenson & Hanchet 2000a, Zeldis 1993), off Puysegur (Hurst & Bagley 1997, Patchell 1982), along the east coast of the South Island (Beentjes & Stevenson 2000a, 2000b), the east coast of the North Island (Bull & Livingston 2000, Stevenson & Hanchet 2000b) and at Mernoo Bank (Kuruwa 1985). Observers on board commercial vessels have also recorded the presence of 0+ hoki around much of the coastline of the South Island, and the southern part of the east coast North Island. The larvae and their distribution on the spawning grounds is described in more detail in Chapter 2.2 (this volume), but it seems that the larvae move inshore to

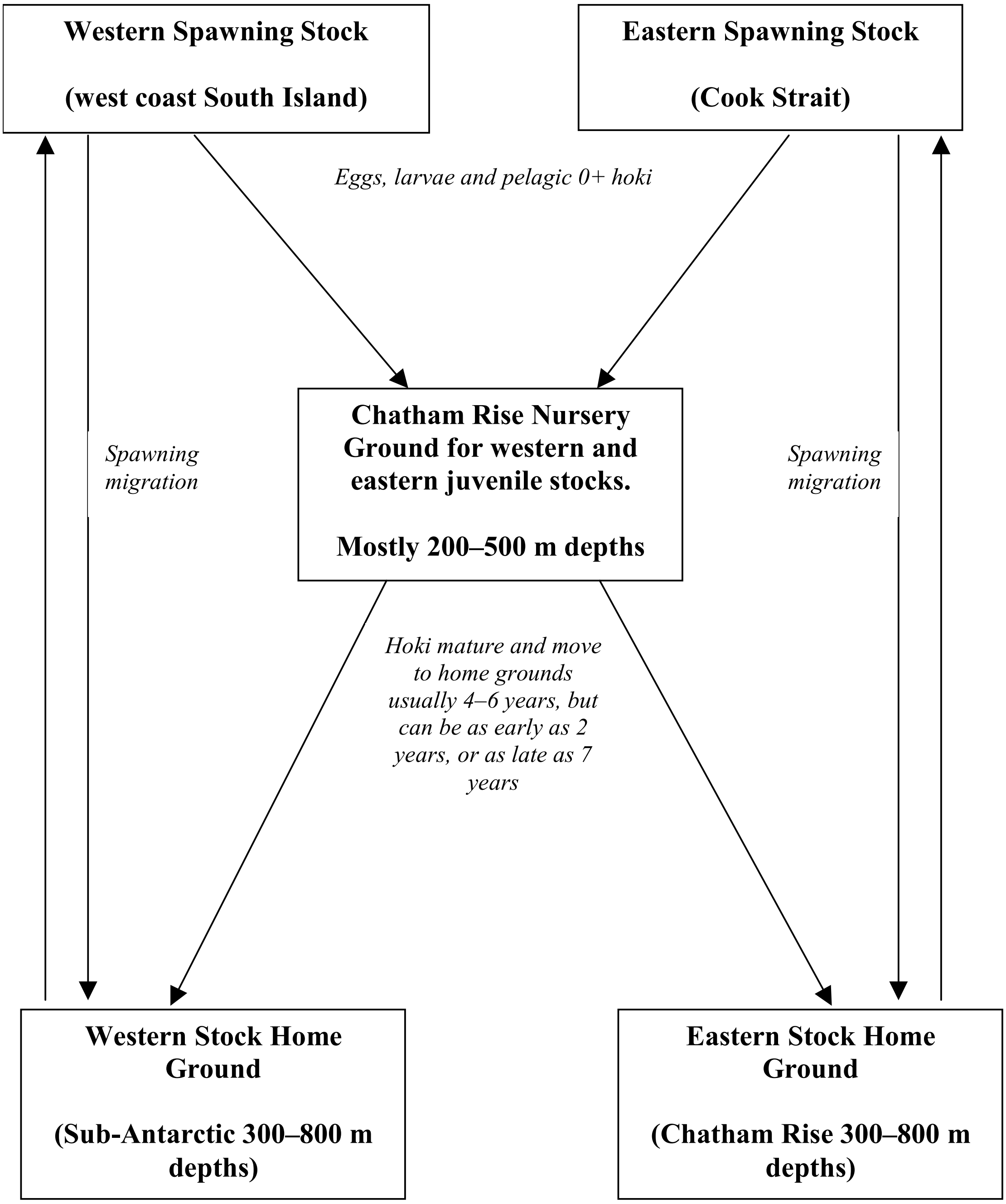

Figure 2.1.3: Current view of the life-cycle of hoki from Livingston (1990).

more productive feeding grounds both off WCSI (Murdoch 1992) and in Cook Strait (Murdoch et al. 1990). The major nursery ground for juvenile hoki aged 2–4 years is along the Chatham Rise, in depths of 200 to 500 m (Livingston & Stevens 2002), although a small proportion of two year olds are found at Puysegur in some years (O'Driscoll & Bagley 2001). Juvenile fish have not been found in any quantity on the Challenger Plateau in commercial or research catches (Bull & Livingston 2000).

Once hoki reach the age of 2 years, they become essentially demersal, and increasingly vulnerable to commercial trawl nets. There is evidence that they move into midwater at night to feed on mesopelagic fish layers that undergo diurnal migrations (Bull 2000).

The older fish (over 4 years) disperse to deeper water and are widely distributed on both the Sub-Antarctic and Chatham Rise. Analyses of trawl surveys (1991–2002) and commercial data suggests that a significant proportion of hoki move from the Chatham Rise to the Sub-Antarctic as they approach maturity, with most movement occurring between ages 3 and 7 years (Livingston et al. 2002). Based on a comparison of *Tangaroa* trawl survey data from the Chatham Rise and Sub-Antarctic, (assuming equal catchability between areas), 80% or more of hoki aged 1– 2 years occur on the Chatham Rise. Between ages 3 and 7, this drops to 60–80 %. By age 8, 35% or less of the fish are found on the Chatham Rise compared with 65% or more in the Sub-Antarctic (Livingston et al 2002). A study of the observed sex ratios of hoki in the two spawning and two non-spawning fisheries found that in all areas, the proportion of male hoki declines with age (Livingston et al., 2000). There is little information at present to determine the season of movement, the exact route followed, or the length of time required, or the cues for fish to move from the Chatham Rise to the Sub-Antarctic.

Table 2.1.4: Proposed migration paths at key stages of the hoki life cycle

Age	Biological development	Distribution	Proposed movements
0–3 months	Eggs hatch, larvae move inshore.	Near spawning grounds; WCSI, Cook Strait, Cloudy Bay.	Movement inshore from spawning grounds
3–18 months	Larvae develop into juvenile fish and extend range along shore. Pelagic lifestyle.	Found in coastal areas around South Island, especially Puysegur Bank. Also found on ECNI and at the Chatham Is. Depths less than 200 m.	Movement from WCSI south to Fiordland and Puysegur, and north towards Cape Farewell and Tasman Bay. Movement from Cook Strait south into Cloudy Bay and Kaikoura, and north to ECNI, and possibly also through Cook Strait to Tasman Bay.
18–24 months	Recruit to the sea floor and adopt a more demersal lifestyle.	Found in abundance on the Chatham Rise in 200–400 m depth. Also some occurrence at Puysegur. Low numbers found on WCSI and ECSI.	Movement towards Chatham Rise.
2–3 years	Mostly immature. Demersal lifestyle.	Highest abundance on Chatham Rise in 200–500 m depth.	No net movement
3–6 years	Increasing proportion of mature fish with age (varies between year classes).	Found in highest abundance in 300–600 m depth on Chatham Rise. Depending on year class, may become mature and move south to Sub-Antarctic.	Migration of western stock hoki south to the Sub-Antarctic. Hoki may commence spawning migrations.
7–15 years	Mature-size fish become fully recruited to western or eastern stock, and undergo spawning cycle.	Found in greatest abundance in Sub-Antarctic (western home ground) in 300–800 m depth, but also 400–800 m depth on Chatham Rise (eastern home ground).	A proportion of individuals undergo spawning migrations each year to the western and eastern spawning grounds, after which they return to the home grounds.

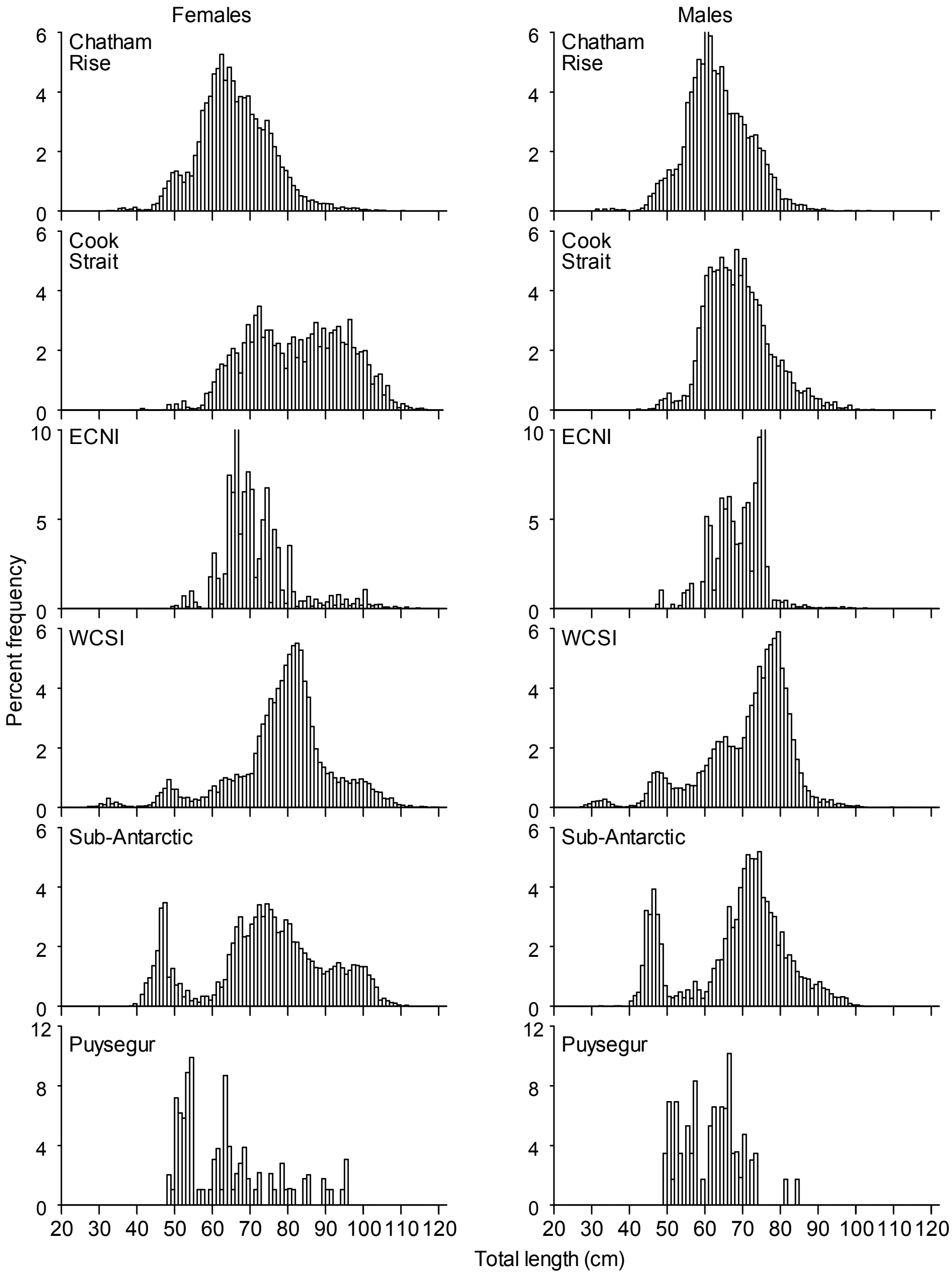

Figure 2.1.4: Comparison of length frequencies of hoki taken in commercial catches from different areas. Example is from the 2006–07 fishing year (Ballara et al. 2008).

Mature size hoki appear in the Cook Strait spawning fishery from about age 3 and in the WCSI fishery at from about age 4 (Ballara et al. 2008). Outside the spawning season, mature size hoki are found both on the Chatham Rise and in the Sub-Antarctic to the south. Larger hoki (over 7 years) are also found in low densities in mid-water at 650 m over hills and sea-mounts off the Chatham Rise and Campbell Plateau that are at depths of 900 m or greater (Dunn & Livingston 2004, Livingston et al. 2004). Tuna boats have also reported large-size hoki as bycatch over depths of 2000 m in the Bounty Trough (between the Chatham Rise and Pukaki Rise) and off the west coast South Island, but the age of these fish is unknown. The length frequency histograms from commercial catches around New Zealand are believed to reflect these movements (Figure 2.1.4).

Hoki spawn from late June to mid-September, releasing multiple batches of eggs over a series of spawning events (Langley 1993, Schofield & Livingston 1998). They have moderately high fecundity with an average sized female of 90 cm total length spawning over 1 million eggs in a season (Schofield & Livingston 1998).

Mature-size hoki migrate from their home grounds in the Sub-Antarctic and Chatham Rise to the main spawning grounds off WCSI and in Cook Strait in May and June. Evidence, from the effect of hoki bycatch on tuna boat position, suggests the seasonal movement of hoki from the corridor between the Stewart Snares Shelf and the Auckland Island Shelf in May, past Fiordland, and northwards to the west coast of the South Island through June and July (Bull & Livingston 2000). Smaller spawning grounds occur elsewhere, particularly off Puysegur Point and Banks Peninsula (Livingston 1990, O'Driscoll 2003).

The WCSI and Cook Strait spawning grounds are centered on submarine canyon features, i.e., the Hokitika Canyon off WCSI, and the middle arm of Cook Strait Canyon. Spawning also occurs on relatively flat ground north and south of Hokitika Canyon and in the Narrows Basin north of Cook Strait Canyon, but these sites are usually occupied by younger fish and are thought to be less optimal spawning locations than the canyons which are occupied by the larger more fecund fish. The courtship rituals and specific cues for spawning events are unknown. Gadiform courtship rituals range from intricate pairing of individual male and females to broadcast spawning of males and females in the general vicinity (Hislop 1984). Anecdotal observations by fishermen and analysis of gonad stage data collected by Observers from the commercial fleet (Langley 1993) suggest that dense prespawning schools disperse and reform a number of times throughout the spawning season. Numbers of running ripe female hoki peak at dawn suggesting that spawning occurs at this time (Zeldis 1993) and there have been unsubstantiated reports of paired fish moving up out of the school higher into the water column to mate.

Not all hoki within the adult size range spawn in a given year (Livingston et al. 1997). Winter surveys of both Chatham Rise and Sub-Antarctic have found significant numbers of large hoki with no gonad development, at times when spawning is occurring in other areas. Histological studies of female hoki in the Sub-Antarctic in May 1992 and 1993 estimated that 67% of hoki age 7 years and older in the Sub-Antarctic would spawn in winter 1992, and 82% in winter 1993 (Livingston et al. 1997). A similar study in April 1998 found that a much lower proportion (40%) of fish age 7 and older was developing to spawn (Livingston & Bull 2000). Unlike the 1992 and 1993 studies, the 1998 study was not preceded by a summer survey to allow estimation of the numbers of fish already departed from the Sub-Antarctic survey area. It was not clear whether the drop in proportion with developing gonads in 1998 was natural variation (driven for example by food availability on feeding grounds in autumn), part of a trend due changing population dynamics, or even a function of variability in lead time before gonad maturation (Livingston & Bull 2000).

Growth is fairly rapid with juveniles reaching about 27–35 cm TL at the end of the first year. There is considerable variability in growth rates in subsequent years and there has been a trend of increasing size at age in data from both the trawl surveys and the commercial catch since 1983 (Bull & Livingston 2000). In the past, hoki reached about 45, 55 and 60–65 cm TL at ages 2, 3, and 4 respectively. More recently, length modes have been centred at 45–50, 60–65, and 70–75 cm TL for ages 2, 3, and 4. Although smaller spawning fish are taken on the spawning grounds, males appear to mature mainly from 60–65 cm TL at 3–5 years, while females mature at 65–70 cm TL. From the age of maturity the growth of males and females differs. Males grow up to about 115 cm TL, while females grow to a maximum of 130 cm TL and up to 7 kg weight. Horn & Sullivan (1996) estimated growth parameters for the two stocks separately (Table 2.1.5). Fish from the eastern stock sampled in Cook Strait are smaller on average at all ages than fish from the WCSI. Maximum age is from 20–25 years, and the instantaneous rate of natural mortality in adults is about 0.25 to 0.3 per year.

Table 2.1.5: Estimates of biological parameters used for stock assessment. (M, natural mortality; weight = a (length)^b ; von Bertalanffy growth parameters: K, growth coefficient; L_∞, maximal length; T_0 hypothetical age at zero length)

	M	*a*	*b*	*K*	*T0*	*L∞*	Reference
Males	0.30						Sullivan & Coombs 1989
Females	0.25						Sullivan & Coombs 1989
Combined		0.00479	2.89				Francis 2004
Western males				0.261	-0.50	92.6	Horn & Sullivan 1996
Eastern males				0.232	-1.23	89.5	Horn & Sullivan 1996
Western females				0.213	-0.60	104.0	Horn & Sullivan 1996
Eastern females				0.161	-2.18	*101.8*	Horn & Sullivan 1996

2.1.4 Stock structure

The life-cycle and stock structure of hoki are difficult to model. Larvae spawned off WCSI and in Cook Strait appear to make their way to the Chatham Rise by age 2 years with juvenile hoki from both spawning stocks occurring together on the Chatham Rise. As hoki approach maturity they move to deeper water, and a proportion is believed to move south to Sub-Antarctic waters and become part of the western stock which resides there through most of the year except for the spawning season (Figure 2.1.3, Table 2.1.4). The eastern stock consists of those fish that do not move south. They are mostly found in deeper waters on the Chatham Rise and spawn in Cook Strait and ECSI.

Morphometric and ageing studies have found consistent differences between adult hoki taken from the two main dispersed areas (Chatham Rise and Southern Plateau), and from the two main spawning grounds in Cook Strait and WCSI (Livingston et al., 1992, Livingston & Schofield 1996, Horn & Sullivan 1996). These differences clearly demonstrate that there are two sub-populations of hoki. Whether or not they reflect genetic differences between the two sub-populations, or they are just the result of environmental differences between the Chatham Rise and Sub-Antarctic (the Chatham Rise lies under the influence of the Subtropical Front, and the Sub-Antarctic are in cold Sub-Antarctic waters), is not known. No genetic differences have been detected with selectively neutral markers (Smith et al. 1981, 1996), but a low exchange rate between stocks could reduce genetic differentiation.

In 2006 and 2007, the hoki stock assessment model had two variants that were associated with different stock structure hypotheses (Francis 2007, 2008). The original hypothesis (also used before 2006 and subsequently) assumes natal fidelity: a fish that was spawned in one area will grow up to spawn in the same area (i.e., a fish is 'eastern' or 'western' from birth). The alternative hypothesis does not assume natal fidelity, so fish spawned in one area can themselves spawn in another area (i.e., a fish becomes 'eastern' or 'western' when it matures). Under both hypotheses, once a fish has spawned it shows site fidelity – it cannot change spawning grounds. All model runs in 2011 assumed natal fidelity because of technical problems concerning the definition of unfished biomass without this assumption (Francis 2009). Two pilot studies appeared to provide weak support for the hypothesis of natal fidelity for the western and eastern spawning stocks. Smith et al. (2001) found significant differences in gill raker counts, and Hicks & Gilbert (2002) found significant differences in measurements of otolith zones, between samples of 3 year-old hoki from the 1997 year-class caught on the WCSI and in Cook Strait. However, when additional year-classes were sampled, differences were not always detected (Hicks et al. 2002).

The estimated poor recruitment in the western stock from 1995 to 2001 could therefore be a result of low larval survival off WCSI, which results in a low year class strength for the western stock (genetic model), or it could be that larval survival from spawning has been adequate, but hoki did not move off the Chatham Rise to join the western stock in the Sub-Antarctic because overall, population levels had declined to the point where there was little need to seek food elsewhere (environmental model). If this were true, hoki on the Chatham Rise would by default become part of the eastern stock. Under this scenario, larval survival off WCSI may be adequate, but recruitment to the adult western stock unit would remain low.

Table 2.1.6. Summary of life stages and key events in the life cycle of hoki (after Livingston 2000).

Age of hoki	*Key activity*	*Critical months*	*Geographic location*
0 to 4 months	hatching, feeding, avoiding predation, moving inshore.	July to October	WCSI, Cook Strait
4 months to 1 yr	Moving to appropriate coastal areas; attaining maximum size possible before onset of winter.	October to April	WCSI, Fiordland, Puysegur, Tasman Bay, Cook Strait
1-2 yrs	movement to Chatham Rise	unknown	east coast of the South Island, Kaikoura
3-6 years	feeding and growth to size or age of sexual maturity	October to April	Chatham Rise
First time spawning age (3-7yrs)	recruitment to adult grounds; migration to spawning grounds	recruitment period unknown; spawning migration in May-June	east coast South Island; Kaikoura, west edge of Stewart Snares Island Shelf
Adult hoki (from recruitment age on)	feeding and growth; development to spawn; migration to spawn	feeding in summer; gonad development March-April; migration May-June	Chatham Rise (eastern stock); Southern Plateau (western stock)

It is assumed that abundance surveys of the Chatham Rise provide pre-recruit indices of both stocks combined (because the stocks are mixed as juveniles), while surveys of the Sub-Antarctic provide indices of recruitment to the western stock only. The poor estimated recruitment seen in the western stock from 1995 to 2001 (Figure 2.1.2) was generated through the stock assessment model under these assumptions.

2.1.5 Year class strength and climate variation

In a paper exploring links between climate variables and hoki year class strength, Livingston (2000) summarized the key life events and critical months within the life-cycle of hoki that may render the fish particularly vulnerable to unfavorable oceanic and climatic conditions (Table 2.1.6).

A study of links between hoki recruitment and climate variation found a negative relationship between year class strength of the western stock and the Southern Oscillation Index, WCSI sea surface temperatures, and westerly or southwesterly flow over the South Island (Bull & Livingston 2001). The results support an earlier study that suggested that cooler conditions and negative SOI or 'El Nino' conditions favor western hoki recruitment (Livingston 2000). The results suggest that the conditions not only favor upwelling and therefore high productivity on the larval feeding grounds, but also transportation of larvae inshore to productive feeding grounds (Livingston 2000). The predictive power of the regression model developed by Bull & Livingston (2001) was not, however, particularly strong, and a recent study (Francis et al. 2006) using a more statistically robust method found that correlation of environmental variables with current western stock model estimates of year class strength is very low, and it was concluded that either the time series that Bull and Livingston (2001) used for their original study was too short to establish an empirical relationship (and was therefore spurious) or the variables were poor proxies for the driving mechanisms underlying recruitment. The relationship remains robust with the Chatham Rise indices of juvenile hoki from both stocks combined (Francis et al. 2006), but this result does not provide insight to larval survival close to the spawning grounds since the Chatham Rise juvenile population is considered to be both stocks combined.

Links between environmental variability and hoki abundance are further discussed in Section 4.

2.1.6 Summary

Hoki is New Zealand's largest finfishery, and is a major species ecologically and commercially on the WCSI. Hoki have a complex life history. Two stocks of hoki are recognised: a “western stock” which resides primarily on the Campbell Plateau, south of New Zealand, and spawns on the west coast of the South Island; and an “eastern stock” with a home ground on the Chatham Rise, with most spawning occurring in Cook Strait. Juvenile hoki of both stocks mix together on the Chatham Rise, and are believed to recruit to their respective stocks at maturity, which occurs at ages 3–8. The TACC for hoki throughout the New Zealand EEZ in 2010–11 is 120 000 t. This is much less than previous catch levels (up to 269 000 t in 1997–98), but has increased from a low of 90 000 t in 2007–08 and 2008–09, reflecting a positive change in the current status of the western stock estimated in recent stock assessments. The WCSI spawning fishery currently contributes about a third of the New Zealand hoki catch, a much lower proportion than in the past. However, model projections suggest that the biomass of the western stock is likely to increase with the current catches. The major reason for the decline of the western stock was a period of poor recruitment from 1995–2001. Year-classes after 2001 are stronger, with five years in which recruitment is estimated to be near or above the long-term average. The key factors driving hoki recruitment remain uncertain.

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2.2 Larval ecology of hoki

Authors: Janet M. Bradford-Grieve, Rob C. Murdoch

2.2.1 Introduction

Most adult hoki do not feed off the west coast of South Island as they migrate there only to spawn although they may be important as food for other residents such as fur seals and hake. On the other hand, larval hoki are an integral part of the WCSI ecosystem but may also be carried away or move to other areas as they mature. Nevertheless, plankton productivity and oceanography of this region appears to be very important to the survival and growth of hoki larvae and juveniles. It is beginning to emerge that environmental variability in the Tasman Sea may be one of the factors affecting recruitment of hoki to the fished population through the survival of larvae. Therefore, an understanding of the ecology of larval hoki off the west coast of South Island helps in hypothesis generation concerning mechanisms through which environmental variability might affect survival.

The west coast of South Island is considered to be the main spawning ground for hoki (Patchell 1982) although spawning also occurs in Cook Strait (Murdoch & Chapman 1989; Murdoch et al. 1990, Livingston 1990) and has also been recorded in Pegasus Canyon and Conway Trough (Livingston 1990) and Puysegur Bank areas (Annala et al. 2000). Off WCSI, adult hoki begin to aggregate in late June, spawn through July and August (Figure 2.2.1), and begin to disperse in September (see Zeldis et al. 1998 and references therein).

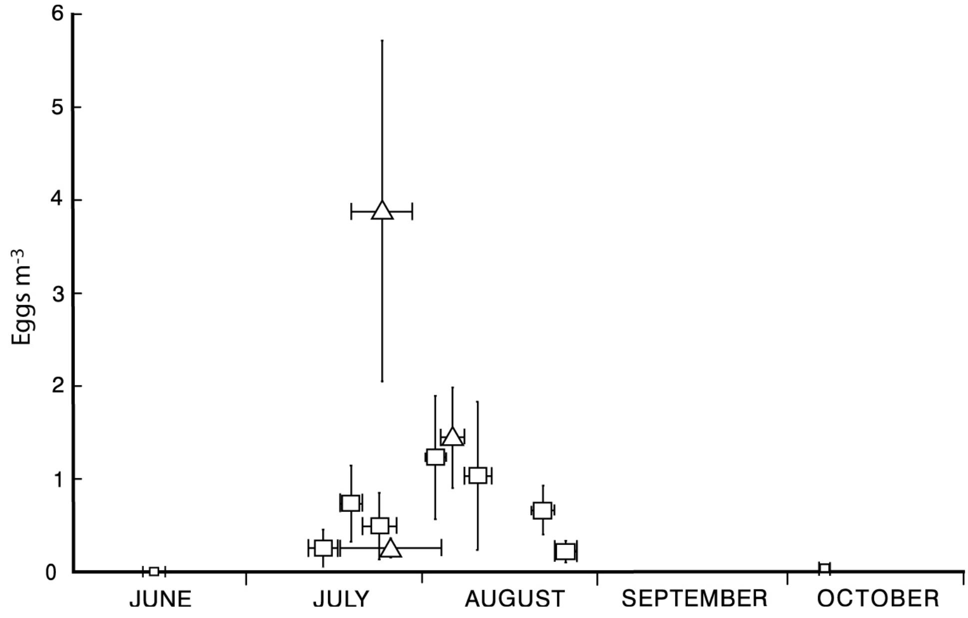

Figure 2.2.1: Mean ± 1 S.D. of density of hoki eggs in the upper 0-200 m for each survey by date as sampled by bongo net. Horizontal bars represent start and finish dates. Squares and triangles represent Ministry of Fisheries and NIWA surveys, respectively (Zeldis et al. 1998).

In this section we review our knowledge of spawning behaviour, larval diet and growth, the relationship between food and larval survival, and the role of onshore / offshore transport in maintaining larvae in an optimal environment for growth and survival.

2.2.2. Spawning and development

During daylight hours aggregations of spawning hoki off WCSI are closely associated with the sea floor on the continental slope in depths of 400–600 m water (Langley 1993). At night aggregations form off the sea floor in the water column and may be several hundred metres thick and be as shallow as 250 m. Direct observations of spawning have shown that positively buoyant young eggs are found only in a 6–8 h period centred around 0200 h each day, indicating that spawning occurs at this time (Zeldis 1993). Eggs are spawned at about 300 m depth (Langley 1993). The presence of distinct, daily cohorts of larvae suggests that hoki have a synchronised, diel spawning periodicity (Murdoch & Quigley 1994; Zeldis et al. 1998). Regions of high egg abundance are located primarily from the Hokitika Canyon area south to the Cook Canyon (Zeldis et al. 1998) (Figure 2.2.2).

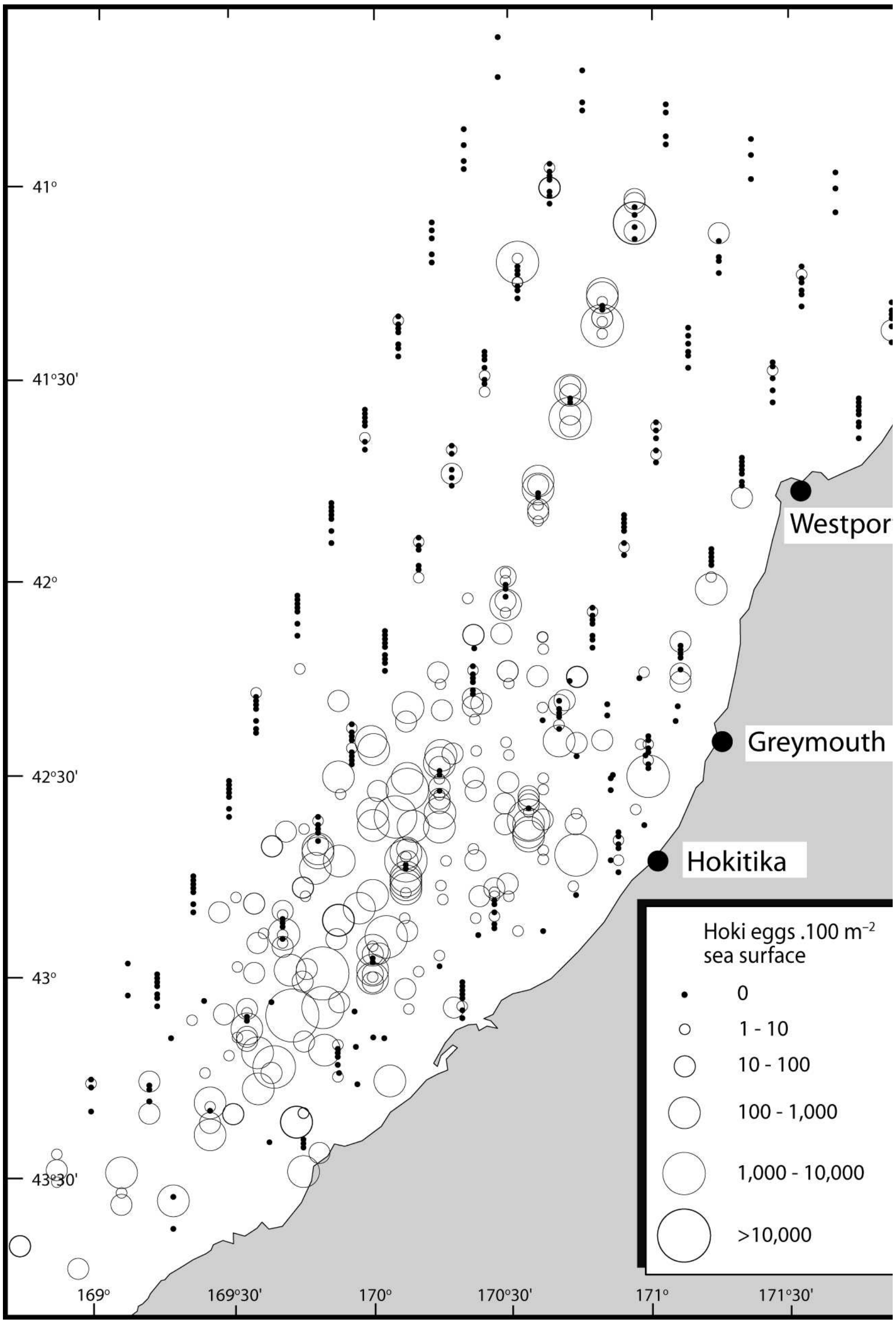

Figure 2.2.2: Distribution and abundance of hoki eggs from all surveys (Zeldis et al. 1998).

Hoki egg development takes 52–84 h after fertilisation depending on the temperature (Patchell et al. 1987). At hatching, the yolk-sac larva is about 2.2 mm long but has no mouth. In a 5-day old larva (4.2 mm) the yolk sac has almost been absorbed and the mouth is visible. High larval abundance was generally coincident with areas of high egg abundance in most surveys. However, analysis of across-shelf distribution of larvae indicates that larval abundance was greater closer to shore compared with egg abundance.

2.2.3. Diet

Hoki larvae probably first feed at about 3.2 – 3.9 mm (Murdoch 1990) when the mouth has developed and the intestinal tract has opened. Hoki are visual feeders and thus their gut fullness increases during the day to reach maximum fullness after sunset and decreases during the night to reach a minimum at dawn (Murdoch 1992) (Figure 2.2.3).

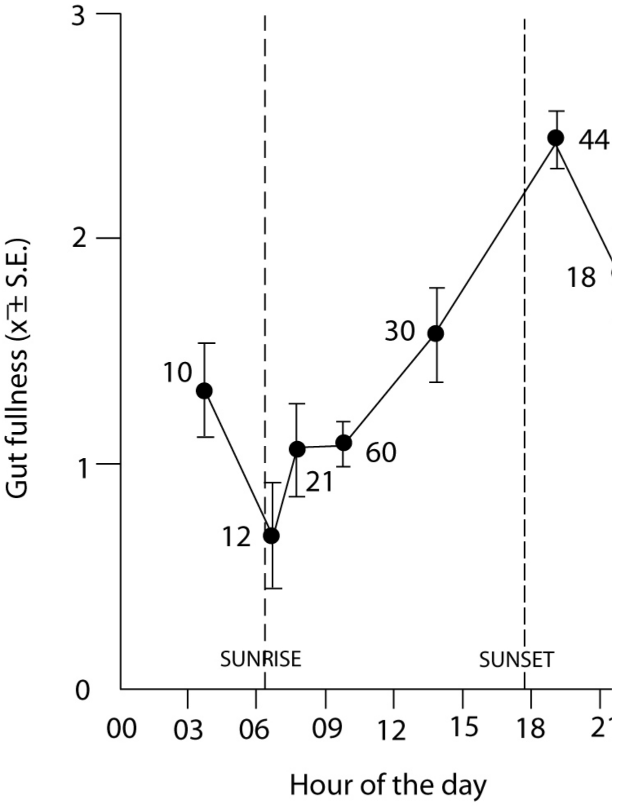

Figure 2.2.3: Diel variation in gut fullness (arbitrary units) of hoki larvae (number of observations listed besides each data point) collected from Cook Strait, September 1987 (Murdoch 1992).

The diet of hoki larvae consists primarily of copepod adults and copepodites but also includes a range of other taxa (Murdoch 1990). The maximum size of prey is similar for larvae in the range of 4–17 mm because the mouth width of a first-feeding larva is large at 0.4–0.5 mm. First feeding larvae feed on phytoplankton (coccolithophorids), tintinnids, and copepod nauplii, whereas older larvae consume copepod adults and copepodites almost exclusively (Figure 2.2.4). Other small, soft-bodied organisms such as naked dinoflagellates and non-loricate ciliates (which are abundant within the mixed layer: Chang 1983; James & Hall 1995) could not be visually detected in the gut using dissection techniques so any significance they may have in the diet of hoki larvae has not be assessed. Despite the numerical dominance of small prey types in the diet of small larvae they contributed only about 2% of the total prey volume consumed (Murdoch 1990). It is doubtful that such small prey items are nutritionally significant.

The presence of the often low numbers of *Calocalanus* in the diet of small larvae is probably essential if larval nutritional requirements are to be met.

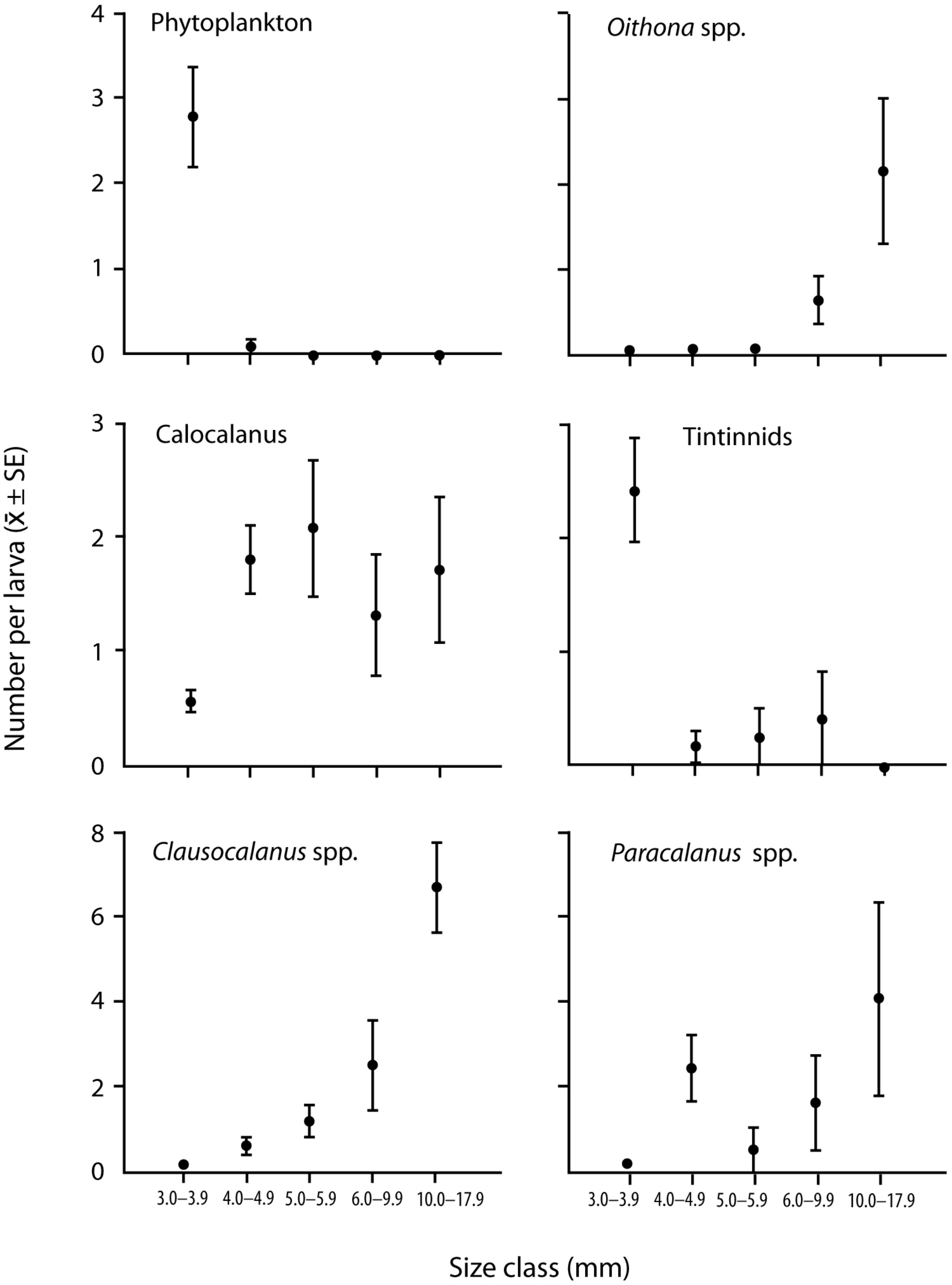

Figure 2.2.4: Mean number of selected prey types, approximately in order of increasing size, per hoki larva for the different size classes examined. The numbers of larvae for each size class were 130, 52, 19, 12, and 12 mm, respectively (Murdoch 1990).

A comparison of the different proportions of potential prey in the environment and the proportion in which species were found in the larval diet revealed the extent to which hoki larvae actively select their prey (Murdoch 1992) (Figure 2.2.5). Diatoms and thecate dinoflagellates were numerically dominant in the environment but were not recorded in the diet of hoki larvae. The most actively selected prey species were copepods of the genera *Calocalanus* and *Paracalanus* and the tintinnid *Dictyocysta*. *Calocalanus* (< 0.80 mm total length) was clearly the most important component of the diet of early stage larvae.

Murdoch (1992) considered size, visibility, swimming speed, and general morphology of potential prey to be the most likely factors to influence prey selectivity. The largest organisms consumed by larvae were all copepods. The length of copepods does not appear to be limiting since their width is well below the mouth width of the larvae. The low numbers of larger copepods (> 1.0 mm total length) such as *Clausocalanus* spp. in the diet of early-feeding larvae and their dominance in the diet of larger larvae, is presumed to be related to larval swimming ability. Similarly, the relatively low numbers of *Oithona* spp. in the diets of larvae < 4 mm, compared to larger larvae, suggests that the copepods' swimming and behaviour minimises predation by the small, less-experienced, slow-swimming hoki larvae. Conversely, the apparent vulnerability of *Calocalanus* to predation may indicate these copepods are not active swimmers all the time. *Calocalanus*, with its spread out, plumose setae, is commonly illustrated in textbooks to show the adaptation of some copepods for flotation when at rest (Figure 2.2.6).

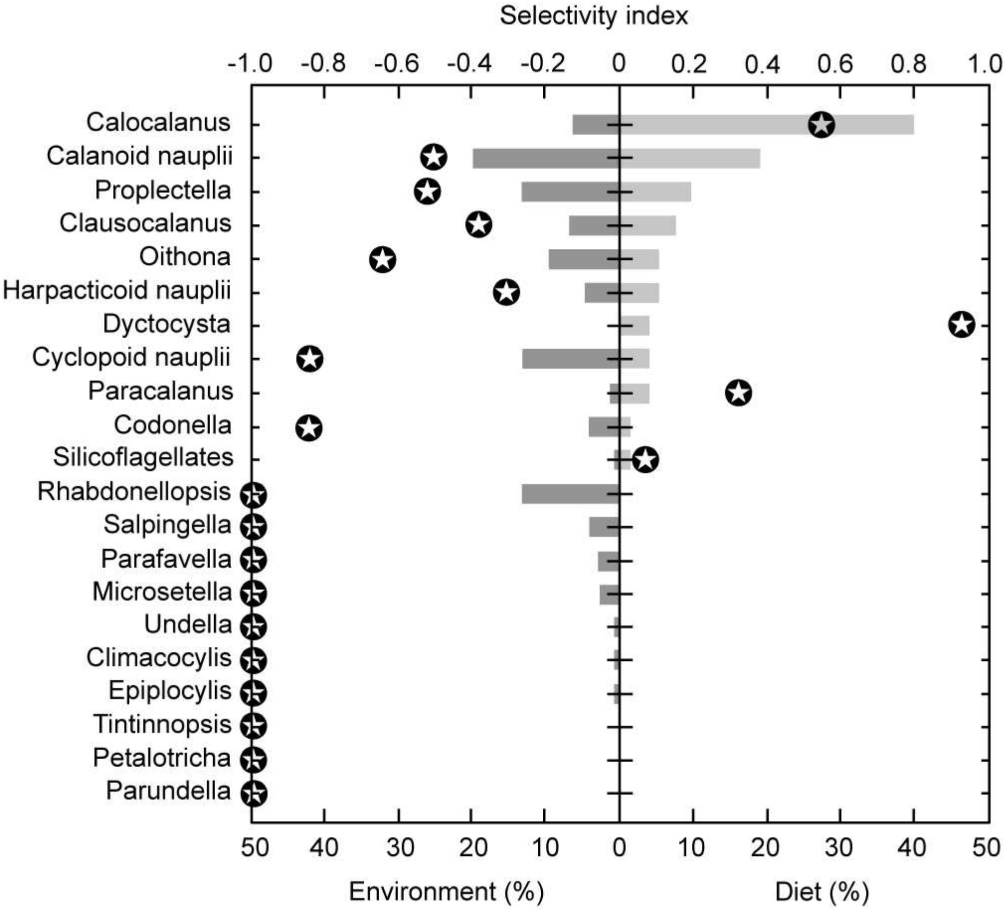

Figure 2.2.5: Percentages of different planktonic species in the environment (left) and diet (right) of hoki larvae. The value of the alpha Selectivity Index for each species is denoted by a star. Values greater than 0 represent positive selection, and values less than 0 represent negative selection and a 0 value indicates random feeding (Murdoch 1992).

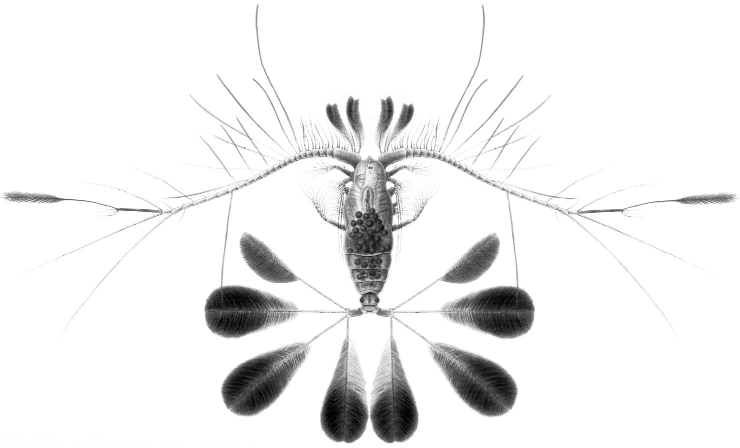

Figure 2.2.6: Morphology of the calanoid copepod genus *Calocalanus pavo* to show the features that apparently aid flotation when at rest (Giesbrecht 1892).

2.2.4 Growth

During July-August 1987 (a year that subsequently made a large contribution to adult recruitment (Sullivan et al. 1995)), growth and mortality of newly hatched larvae (2.0–4.5 mm) was estimated in a patch followed by a drogue (Murdoch & Quigley 1994). Modal analysis of size frequency distribution of the sampled larvae indicated the presence of up to six cohorts within the patch at any one sampling time. The mean standard lengths of each cohort were approximately 0.2 mm apart (Figure 2.2.7). Assuming larval growth is linear and is the same over the range of larvae examined, the mean growth rate of larvae was estimated to be 0.21 mm per day (c.f. 0.24 mm in Australian waters (Thresher et al. 1989)). This translates to a rather low daily weight specific growth rate of about 0.021 that is at the low end of the range for marine fish generally (Houde 1989).

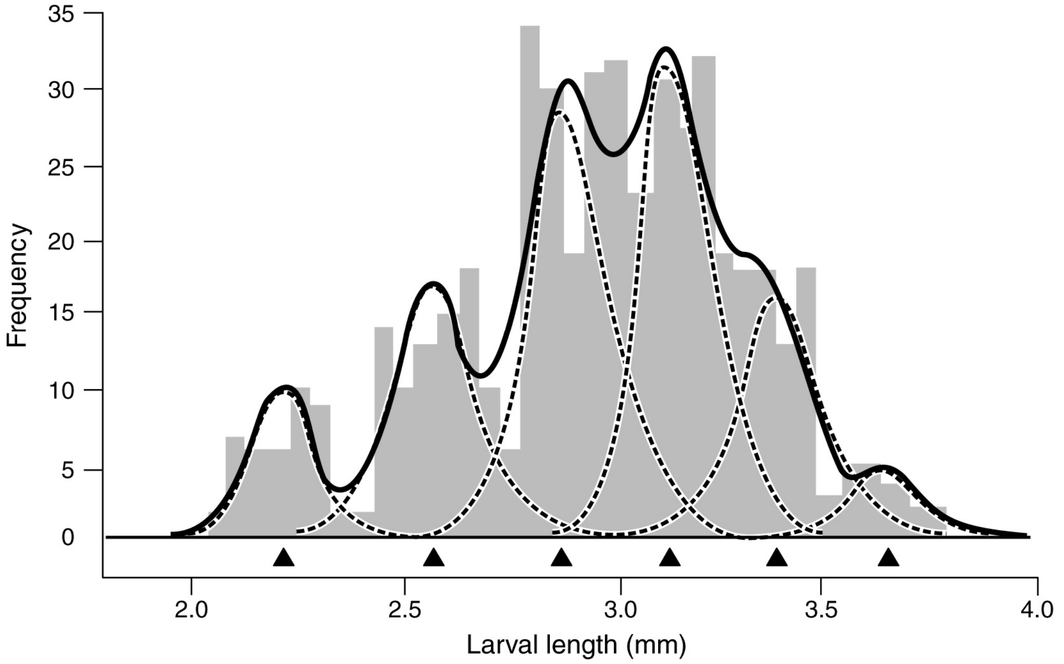

Figure 2.2.7: Histogram of size frequency distribution of hoki larvae from one sample collected within a patch. Results of a modal analysis are also shown, indicating the position of the normal distributions associated with each cohort (dotted lines), the estimated mean length of each cohort (triangles), and the modal estimate of the total sample distribution (solid line) (from Murdoch & Quigley 1994).

The total abundance of larvae within a patch showed an exponential decline over the sampling period. Daily mortality was relatively low, estimated over a 5 day period, at 0.19. This is likely to be an overestimate, as two general surveys of the patch showed that the patch of larvae had dispersed (Murdoch & Quigley 1994).

2.2.5 Food and larval survival

Murdoch (1992) summarised the general position of hoki in the spectrum of fish feeding ecology. He believed that hoki conform to the generalisations of Houde (1989) and others. Fish of temperate seas often have spawning confined in space and time. Daily mortality, growth and ingestion rates of these larvae tend to be low, and the duration of larval stages is long and potentially highly variable. In Australian waters hoki have a larval life of more than 65 days (Thresher et al. 1989).

Although Murdoch (1992) suggested that starvation was not an issue for hoki larvae, subsequent research on the range of variability in the density of preferred hoki food off WCSI in winter (Bradford-Grieve et al. 1996), indicates that starvation may be an important factor in larval survival. At locations over the continental slope where the mixed layers were more than 75 m deep and nitrate nitrogen concentrations were greater than 3 µM, copepod nauplii, and *Calocalanus* spp. were in concentrations of 10,000–16,000 m^{-3} and 288–577 m^{-3}, respectively. Whereas at slope stations with mixed layers less than 85 m and nitrate nitrogen less than 2 µM, copepod nauplii, and *Calocalanus* spp. were in concentrations of 3,000–6,000 m^{-3} and 53–86 m^{-3}, respectively. Therefore, depending on where and when hoki eggs are laid, the hatched larvae would find widely differing concentrations of their preferred food. In early August 1987, hoki were found in concentrations of up to 20 hoki m^{-3} at 70 m (Murdoch & Quigley 1994) where conditions had the first-mentioned characteristics (high numbers of copepod nauplii and *Calocalanus*). These conditions were clearly suitable for the survival and growth of hoki larvae in 1987.

2.2.6 Larval and juvenile habitats

Early stage larvae over the WCSI continental slope occur in the surface 75 m but greatest larval densities occurred below this depth (Murdoch & Quigley 1994) (Figure 2.2.8). Larvae greater than 5 mm length were found further inshore than larvae less than 5 mm (Zeldis et al. 1998).

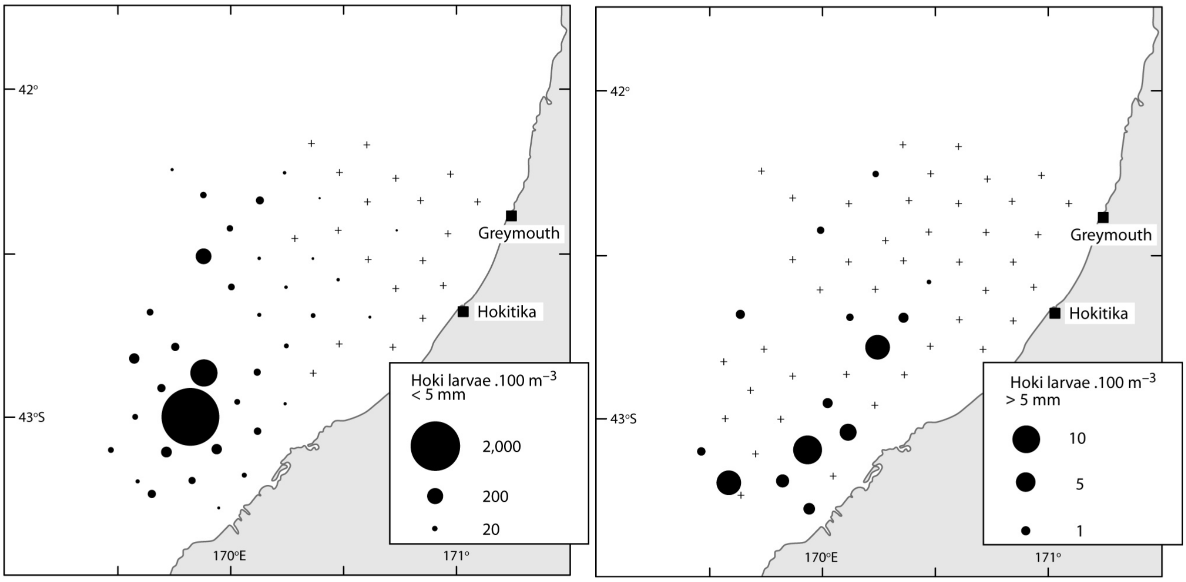

Figure 2.2.8: Abundance of hoki larvae less than 5 mm standard length (left panel) and greater than 5 mm standard length (right panel) off Westland, July 1987 (from Murdoch 1992).

At 29 mm total length, larvae have the appearance of juveniles but are still planktonic at 70 mm (Patchell et al. 1987) and appear in the diets of other fish. For example, hoki larvae and juveniles 42–137 mm were found in the diet of Chinook salmon off Canterbury in the summer of 1991/92 (James & Unwin 1996). The eventual habitat of juveniles appears to be the continental shelf where fish up to 1 year old (27–30 cm TL) are widespread in most coastal areas of the South Island and parts of the North Island (Annala et al. 2000).

Therefore, we deduced that it is important for hoki larvae to be transported inshore. Murdoch et al. (1990) present evidence from eastern Cook Strait that the vertical distribution of eggs and early stage larvae tends to promote their inshore transport in upwelling conditions. That is, there appears to be subsurface transport of larvae toward the shore in response to offshore surface water movement. The fact that the densest concentrations of larvae were found 75–190 m off WCSI (Figure 2.2.9) indicates that larvae would likewise be transported inshore there under upwelling conditions. Conversely, they would be vulnerable to eddies impinging on the continental slope (Cahill et al. 1991, Stanton & Moore 1992) and coastal jets (Moore & Murdoch 1993) that might carry them off shore.

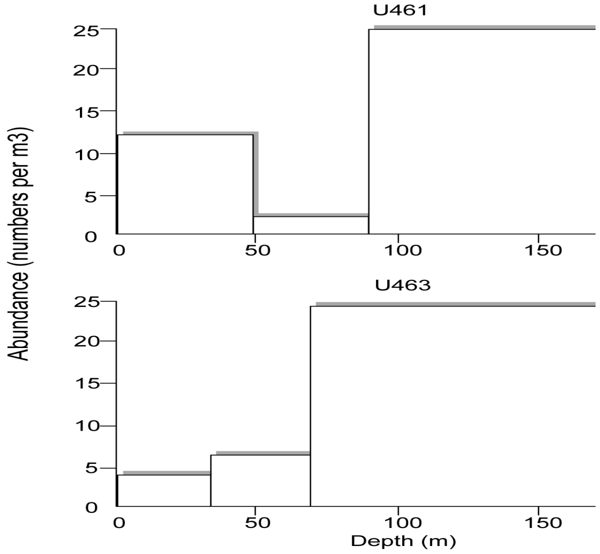

Figure 2.2.9: Vertical distribution of hoki larvae in the upper 200 m of the water column from two plankton net tow series off Westland (Murdoch & Quigley 1994).

2.2.7 Summary

Off WCSI, hoki spawn above the continental slope in 400–600 m water in winter. Regions of high egg abundance are located primarily from the Hokitika Canyon area south to the Cook Canyon. At night aggregations of fish form off the sea floor several hundred metres thick. Direct observations of spawning have shown that positively buoyant young eggs are found at about 300 m only in a 6–8 h period centred around 0200 h each day. The presence of distinct, daily cohorts of larvae in patches suggests that hoki have a synchronised, diel spawning periodicity. Areas of high larval abundance generally coincide with areas of high egg abundance, located primarily from the Hokitika Canyon area south to the Cook Canyon, but larval abundance is greatest closer to shore compared with egg abundance. Hoki larvae probably first feed at about 4.2 mm when the mouth has developed and the intestinal tract has opened. The diet of hoki larvae consists primarily of copepod adults and copepodites. The most actively selected prey species appear to be copepods of the genera *Calocalanus* and *Paracalanus* and the tintinnid *Dictyocysta.* Work on the range of variability in the density of preferred hoki food off WCSI in winter indicates that starvation may be an important factor for larval survival. The abundance of preferred copepod prey of hoki may vary significantly over the continental slope in relation to the depth of mixing and nutrient concentrations. Numbers of copepod nauplii, and *Calocalanus* spp were 3–5 times greater when the waters over the slope have a mixed layer greater than 75 m and nitrate-nitrogen concentrations are greater than 3 μM. Growing hoki larvae have been found at locations with these characteristics (high numbers of copepod nauplii and *Calocalanus*).

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2.3 Other fish and fisheries

Author: Rosemary Hurst

2.3.1 Introduction

In this section, information is summarized on the distribution, abundance, spawning and feeding of fish species other than hoki that are of commercial importance off West Coast South Island (WCSI). Hoki is by far the dominant species in commercial catches, but other species are locally or seasonally important. Some of these appear to exhibit similar seasonal patterns in abundance and catch to hoki, aggregating in spawning schools during the winter and spring. Others appear to be resident in the area over much of the year and may spawn at different times of year and in different depth ranges.

2.3.2 Main fisheries off WCSI

Reported catches of the key fish species for the last 20 years are shown in Table 2.3.1. "Key" is defined here as having an average catch of about 1000 tonnes or more per annum during at least one of the last two decades. All key species are managed by Quota Management Areas (QMA) which are derived from the Fishery Management Areas (FMAs, Figure 2.3.1). QMAs may vary by species and may include more than one of the 10 FMAs. For example, the hoki fishery is managed as a single QMA (HOK1), which encompasses most of the Exclusive Economic Zone (EEZ). Species caught on the WCSI often have a QMA that that extends north of Fishery Management Area 7 (FMA 7) to the west coast of the North Island (FMAs 8 and 9, see Figure 2.3.1). FMA 7 also includes Cook Strait and extends down to Kaikoura on the east coast of the South Island. Catches reported in Table 2.3.1 are therefore only indicative of the WCSI catch, unless WCSI is specifically stated. Where most of the catch for QMA 7 is taken from the WCSI, the area catch as a proportion of the total EEZ catch is given. If most of the catch is taken north of QMA 7, this proportion has not been calculated.

In the last 20 years, catches off WCSI have been dominated by hoki, averaging over 100,000 tonnes per year from 1986–87 to 1995–96. Even though catches have since declined, the decadal average up to 2005–06 was over 80,000 tonnes per year. The deepwater orange roughy fishery was also important in the first decade, at over 1000 tonnes per year, but has declined significantly in recent years. Catches for many of the other key species have been relatively consistent or increasing. These include hake, ling, silver warehou and frostfish in mid depths, and barracouta, red cod, tarakihi, blue warehou, spiny dogfish and stargazer in more inshore waters. The troll fishery for the pelagic albacore is important off WCSI whereas catches of other pelagic species such as jack mackerels, blue mackerel and trevally are higher in FMAs north of the WCSI area. There has been a substantial jig fishery for arrow squid off Farewell Spit in some years but reported catches are not separated from other areas around New Zealand and hence are not included in Table 2.3.1.

The WCSI fisheries for hoki, hake, frostfish and albacore are important on a national scale, making up more than 40% of the national total. All other species comprise 15–30% of national totals, except for the orange roughy fishery, which has been small scale (1–3%).

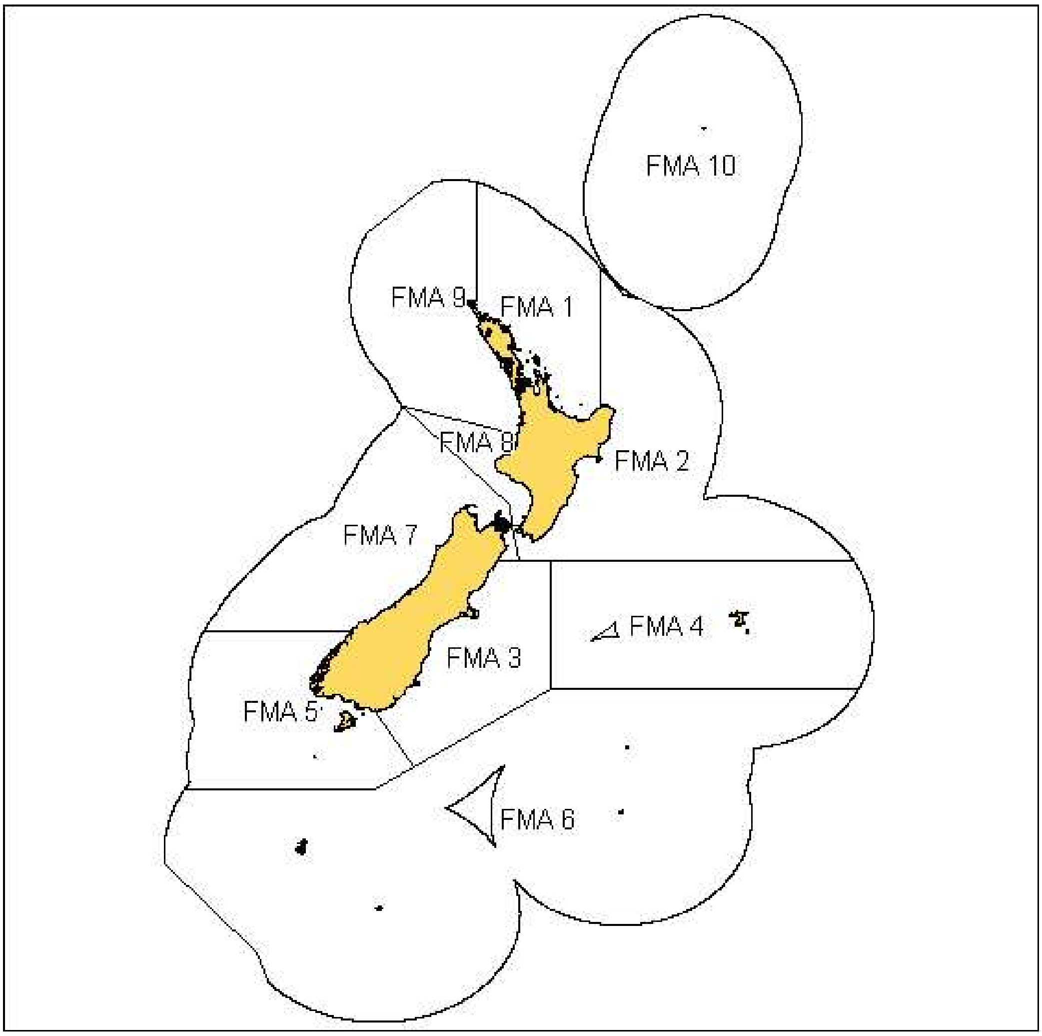

Figure 2.3.1: New Zealand Fishery Management Areas

Table 2.3.1: Average annual catch of key species (over about 1000 tonnes per year) for the last two decades off WCSI (in order of catch for the last decade). Catches are given by Quota Management Area (QMA) or for the WCSI only where this available. If QMA 7 includes FMA areas other than FMA 7, this is indicated in the Area column. Species with a high proportion of the catch from north of FMA 7 are in *italics* and the percentage of the EEZ catch has not been calculated. Source: Ministry of Fisheries 2006

Species (or species groups)	QMA	Area	Average catch 1986-87 to 1995-96 (t)	Average catch 1996-97 to 2005-06 (t)	QMA7/ WCSI catch as a % of total EEZ catch (t) 1986-87 to 1995-96	QMA7/ WCSI catch as a % of total EEZ catch (t) 1996-97 to 2005-06
Hoki	Part HOK1	WCSI[1]	131 800	81 050	63	40
Jack mackerels[2]	JMA7	FMA 7,8,9	19 881	20 511	Mostly FMA 8,9	Mostly FMA 8,9
Barracouta	BAR7	FMA 7,8,9	8 286	8 216	34	33
Hake	HAK7	FMA 7	5 857	7 723	60	59
Blue mackerel	EMA7	FMA 7,8,9	1 781	4 002	Mostly FMA 8,9	Mostly FMA 8,9
Ling	Part LIN7	WCSI[1]	2 301	2 908	18	15
Red cod	RCO7	FMA 7	2 180	2 217	22	27
Trevally	Part TRE7	FMA 7,8,9	1 820	2 021	Mostly FMA 8,9	Mostly FMA 8,9
Albacore[3]	ALB1	FMA 7	1 924	1 882	48	40

Frostfish	FRO7	FMA 7	2 116	1 658	68	63
Silver warehou	Part SWA1	WCSI[4]	1 775	1 532	22	15
Spiny dogfish	SPD7	FMA 7	1 076	1 245	21	15
Redbait[5]	Part RBT7	FMA 7		1 121		37
Tarakihi	TAR7	FMA 7	808	1 024	17	18
Blue warehou	WAR7	FMA 7	659	1 029	29	26
Stargazer[2]	STA7	FMA 7	696	985	24	30
Orange roughy	ORH7B	FMA 7B	1 193	185	3	1

Notes:
1. WCSI (bounded by 172° 41’ E, 39.6° S, 200 nm from coast, 45° S) catch from stock assessment estimated catch history, Ministry of Fisheries 2006; Ministry of Fisheries 2007, Ballara 2007.
2. Multiple species group.
3. Data for years 1989 to 2005. Albacore is currently outside the Quota Management System and is managed by the Western and Central Pacific Fisheries Commission.
4. Assumes 90% of SWA 1 catch is from off WCSI, based on data from 1989-90 to 2005-06, Figure 14, Middleton 2007
5. Data for years 2004-05 and 2005-06. (Source: Ministry of Fisheries, pers. comm.)

To a large extent the total catch of the fisheries reflect the relative abundance of species in the area, whether this is seasonal or year round. For inshore species there are some research survey data that allow comparison of abundance between the east coast of the South Island (ECSI) and WCSI. Surveys by *R.V. Kaharoa* from 1991–1996 used comparable survey design and fishing gear (i.e. same nets and codends) and took place in March-April (WCSI) and May/early June (ECSI) (Stevenson & Hanchet 2000, Beentjes & Stevenson 2000). Average biomass of key species recorded in these surveys is given in Table 2.3.2.

Species biomass estimates off WCSI are consistently lower than off the ECSI for all but two of the eleven inshore species: red gurnard and giant stargazer (Ministry of Fisheries 2006). However, inshore surveys do not necessarily estimate the maximum biomass for each species in the area even though the seasons of surveying are similar (see Table 2.3.2). Seasonal migrations to and from spawning grounds are likely to occur during autumn and early winter for those species that spawn in winter and early spring (*see* section 2.3 below). The ECSI is an important feeding ground for many species during summer and autumn but some species may have migrations away from ECSI by May/June. In contrast, many species migrating to spawn off WCSI in winter and spring and may not yet have areas arrived when surveys take place in May-June.

There are no time series of surveys in middle depths or deeper water using the same vessel and gear combinations that allow for the same type of comparisons between the WCSI and other areas.

Table 2.3.2: Average of mean biomass estimates from *R.V. Kaharoa* bottom trawl surveys that used the same trawl gear between 1992 and 1996. East coast South Island (ECSI), May-June, 4 surveys; WCSI, March-April, 3 surveys. Source: Ministry of Fisheries 2006

Species	**ECSI**	**WCSI**
Barracouta	13541	4085
Dark ghost shark	2430	623
Elephant fish	417	97
Giant stargazer	551	1401
Red cod	5125	3003
Red gurnard	334	572
Rough skate	313	207
Sea perch	2409	490
Smooth skate	489	332
Spiny dogfish	18609	6478
Tarakihi	2111	1406

2.3.3 Seasonality, spawning activity and the location of juvenile fish

Many of the fisheries off WCSI are seasonal, catching fish that migrate into the area to spawn or feed. Some of these species are thought to have migrated from waters south of New Zealand because of changes in the relative abundance of species caught in biomass surveys of Southland and the Sub-Antarctic during winter or spring months compared with summer. This includes hoki (Hurst & Schofield 1995), gemfish and barracouta (Hurst et al 1990, Hurst & Bagley 1997). Others may move in from more northern waters or just become more aggregated and more vulnerable to fishing gear during spawning.

Hurst et al (2000) and O'Driscoll et al (2003) summarised areas of importance for spawning, pupping or egg-laying and juvenile distribution of New Zealand fish, from research surveys and Ministry of Fisheries scientific observer records (Ministry of Fisheries *trawl* and *obs* databases). Species included were those for which fish size and gonad stage information had been collected. They produced a set of distribution maps of spawning fish and juveniles as well as graphs of spawning stages by month. A summary of these data is given in Table 2.3.3. Key data sources were the March-April inshore trawl survey time series and the Ministry of Fisheries observer data collected annually during winter/early spring. No data were available off the Fiordland coast. Observations of spawning reported were for females only and juveniles are defined as fish less than the 50% length at maturity.

Most observations of fish in spawning condition are off the WCSI during winter and early spring. Records of spawning activity include hoki, hake, ling, three species of warehou, gemfish, giant stargazer, hapuku, ribaldo and red cod. Barracouta and blue warehou have also been recorded spawning in Tasman Bay. Red gurnard spawns in autumn and spring. Warmer water species such as blue and jack mackerels spawn late spring and summer, with Murphy's mackerel also ripe in winter.

Records of the distribution of juvenile catch rates from research surveys are difficult to relate to the general observations on location of spawning. Juvenile fish of most species are recorded in low numbers, possibly due to the type of sampling gear which are designed to catch pre-recruits or recruits (i.e. research bottom trawl with 40–60 mm codends, commercial bottom or midwater gear with 100 mm mesh codends). Some species that spawn offshore in deeper water occasionally have moderate catch rates of juveniles extending into inshore waters off the WCSI in some surveys (hoki, hake). Others appear to have relatively higher catch rates of juveniles in Tasman Bay than off WCSI (barracouta, silver warehou, red gurnard).

Table 2.3.3: Fish species known to either occur as spawning, pupping or egg-laying adults or juveniles in FMA 7 (see Figure 2.3.1) and months of spawning. Location: Challenger, Challenger Plateau (western FMA 7); WC, west coast South Island; TB, Tasman Bay (northern FMA 7). Spawning (females only): R, ripe; RR, running ripe. Relative juvenile abundance denoted as low, moderate (mod) or high (from trawl survey data only). Note that species that were recorded as only spawning or occurring as juveniles in Tasman Bay are not included.

Main fishery	**Species**	**Spawning, pupping or egg-laying**		**Juvenile location**
		Location	**Period**	
Inshore	Blue mackerel	W, TB	R & spent Jan-Feb	
	Elephant fish	TB		WC: low
	Red gurnard	WC, TB	RR Mar-Apr, Oct	WC, TB: mod
	Rig			WC, TB: low
	Rough skate	WC, TB	Mature eggs Mar-Apr	WC, TB: low
	School shark			WC: mod-high, TB: low-mod
	Tarakihi	WC	RR Mar-Apr	WC, TB: low
Inshore & mid depths	Barracouta	WC, N, TB	RR Jul-Oct, Feb	WC: low; TB: mod
	Jack mackerel (*T. declivis*)	WC, TB	Peak RR Nov, extends Jan-Mar	
	Jack mackerel (*T. murphyi*)	WC, TB	RR Jan-Feb, R & spent Jul-Aug	
	Northern spiny dogfish			WC: low
	Sea perch			WC: low
	Smooth skate	WC, TB	Mature eggs Mar-Apr	WC: low
	Spiny dogfish			WC, TB : low
Mid depths	Alfonsino			WC: low-mod
	Blue warehou	WC, TB	RR Jul-Sep	WC, TB: low
	Bluenose	WC,	R Oct	
	Dark ghost shark			WC: low
	Frostfish	WC	R Mar-Apr, Jun-Aug	WC: low
	Giant stargazer	WC,	RR Jul- Aug	WC, TB: low
	Gemfish	WC,	R & spent, Jun-Sep	WC, TB: low
	Hapuku	WC	RR Jul	WC: low
	Hoki	WC,	R Jun-Sep	WC: low-high; TB: low
	Hake	WC,	R Jun-Oct	WC: low-high; TB: low
	Ling	WC,	RR Aug-Sep	WC: mod, TB: low
	Lookdown dory	WC	Spent Jun-Aug	WC: low
	Pale ghost shark			WC: low
	Ray's bream			WC: low
	Red cod	WC,	RR Jul-Sep	WC: TB: low-mod
	Ribaldo	WC	R Jul-Aug	WC: low
	Silver warehou	WC,	R Jul-Oct	WC: low; TB: mod
	Silverside			WC: low
	White warehou	WC,	R Jul-Sep	WC: low
Deep	Moonfish			WC
	Orange roughy	WC, Challenger Plateau	RR Jun-Aug	WC, Challenger: low

2.3.4 Links between climate and recruitment (e.g. gemfish, snapper)

Catches of the southern stock of New Zealand gemfish, *Rexea solandri,* reached a peak of nearly 7000 tonnes in the mid-1980s but declined dramatically to only 130 tonnes in the mid-1990s. Large fluctuations in recruitment to the fishery were observed over a 15 year period and these appeared to be related to the frequency of occurrence of southwesterly wind flow over New Zealand and to sea surface temperature variations during the winter spawning period (Renwick et al. 1998) off WCSI. Spawning success increased when local sea surface temperatures were higher than normal, and there was a lower than normal frequency of southwesterly flow patterns. The recruitment pattern observed for gemfish up to the mid-1990s was opposite to that observed for hoki (Figure 2.3.2).

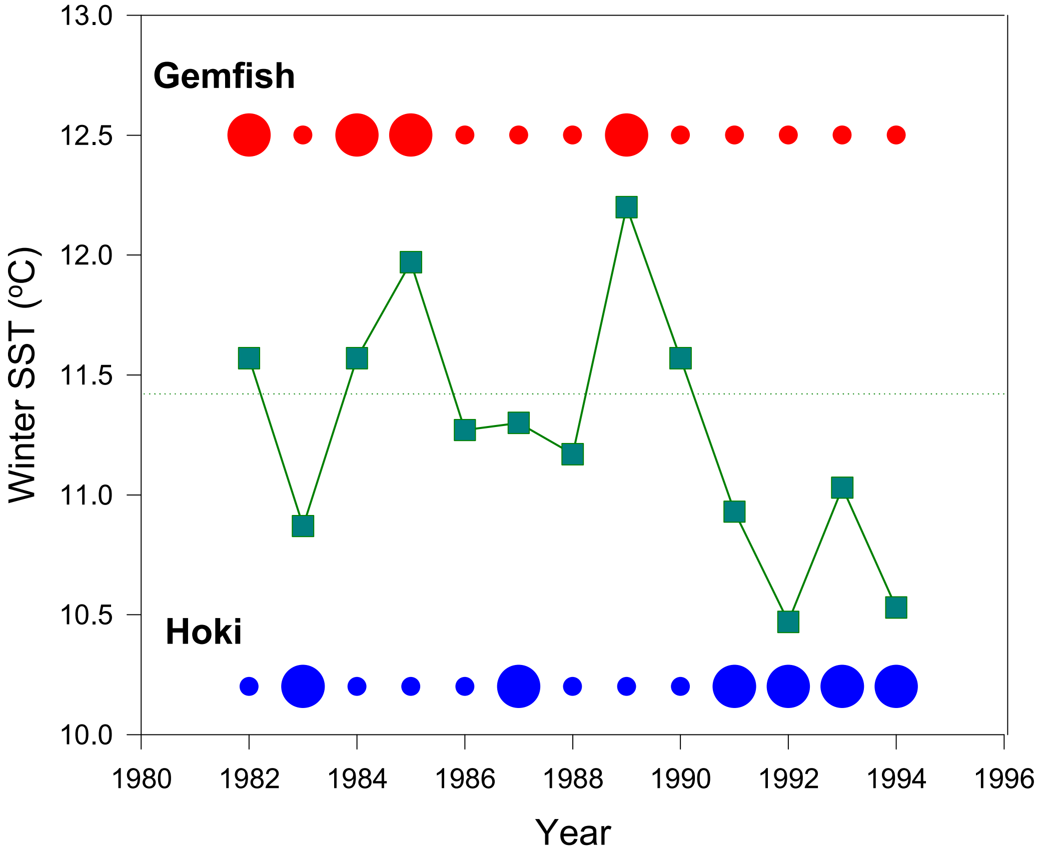

Figure 2.3.2: Patterns of gemfish (red circles) and hoki (blue circles) recruitment (circle size denotes strong or weak year class strength) and winter sea surface temperature (green).

Climate and recruitment relationships have also been determined for Tasman-Golden Bay snapper. Although slightly to the north of WCSI, snapper, like gemfish, also showed a positive relationship of year class strength to spring-summer temperatures (Gilbert & Taylor 2001). Fluctuations in landings of red cod also appear to be dependent on sea surface temperature, controlled largely by climatic variability, including El Niño and La Niña events A strong correlation between red cod landings on WCSI and predicted catches based on sea-surface temperatures in the area has been observed (Beentjes and Renwick 2001).

2.3.5 Feeding patterns

Stevens et al. (in press) summarised feeding information collected from research (bottom, midwater and prawn) trawls that were included in the Ministry of Fisheries research trawl database up to the year 2000. Of the 25 key species for which there were sufficient feeding data to be included in this report, only five (orange roughy, hoki, hake, ling and barracouta) contained enough records to allow a comparison of feeding patterns off WCSI with other areas. For these 5 species, it was also possible to analyse diet by fish size. Identification level varied amongst food types and data summaries are presented by major groupings such as teleosts, crustacean, cephalopod, etc. Lower levels of identification were often not made as these identifications were done macroscopically at sea.

For these five species from off WCSI the percentage of empty stomachs recorded was often high: orange roughy (72%); hoki (80%); hake (74%); ling (48%); and barracouta (61%). Crustaceans and teleosts were important in all five species diets. Teleosts were the major component in the diet for four of the five species: hake (all sizes), hoki (all sizes), ling (over 110 cm) and barracouta (under 60cm). For three species the importance of teleosts in the diet increased with fish size (ling, orange roughy, hake). Crustaceans were the major part of the diet for orange roughy of all sizes. The relative importance of crustaceans and teleosts and any trends by size were similar across all areas sampled for three species, ling, orange roughy and hake. For hoki, teleosts were slightly more important off WCSI than in other areas and, for barracouta, teleosts were more important off WCSI and the North Island than in other areas off the South Island and on the Chatham Rise. Prey types that were the most commonly recorded in the diet of these five key species off WCSI are given in Table 2.3.3:

Table 2.3.3: Prey species important in the diets of orange roughy, hoki, hake, ling, and barracouta off the west coast South Island (from Stevens et al 2000)

Species	**Prey Phylum**	**Prey species or group**
Orange roughy	Crustacea	natant decapods including *Pasiphaea* spp., *Sergestes* spp. and *Oplophorus novazeelandiae*
	Mollusca	Squid
	Teleosts	mesopelagics: Myctophidae, *Chauliodus sloani*
Hoki	Crustacea	natant decapods
	Teleosts	mesopelagics: Myctophidae
Hake	Crustacea	natant decapods
	Mollusca	Squid
	Teleosts	*Macruronus novaezelandiae*
Ling	Crustacea	*Munida gregaria*, *Metanephrops challengeri*
Barracouta	Crustacea	Euphausiacea
	Mollusca	Squid, *Nototodarus* spp.
	Teleosts	*Macruronus novaezelandiae*, *Capromimus abbreviatus*

2.3.6 Summary

Hoki is by far the most abundantly caught commercial fish species off WCSI, with catches over the last decade averaging 80,000 tonnes and exceeding the combined catch of other key species caught in the area. Of the other key species for which catch data from the WCSI area specifically are available, middle depth species such as hake and ling are the most important, along with the more inshore barracouta.

Catches of hoki and many other species off WCSI are highly seasonal. Hoki in particular is most abundant in winter and spring when fish aggregate for spawning. Many other species (including hake, ling, blue, silver and white warehou, gemfish, giant stargazer, hapuku, ribaldo and red cod) also spawn in the area at this time and some of them may also have migrated from other areas. The variability in resulting year class strength of gemfish is thought to be, in part at least, related to climate variability. Gemfish year class strength tends to be higher in spawning seasons that are warmer and have lower than normal frequency of south-westerly flow patterns. Snapper from Tasman-Golden Bay also appear to do better in warmer years.

The impact of large seasonal influxes of spawning fish during winter and spring months on trophic relationships off WCSI cannot be assessed from the information available. Records of feeding activity for species such as hoki, hake and barracouta suggest that a high proportion of fish (over 60%) are not actively feeding during the spawning season and that the proportion of fish not feeding are higher than for other areas. Main prey for the key species examined included crustaceans (particularly natant decapods and euphausiids), teleosts (particularly myctophids and hoki) and squid. However, data were generally insufficient to establish any seasonal trends in feeding and how this might relate to spawning activity. Also, there is no representation of the larval or early juvenile fish in the feeding records from bottom or midwater trawls so the critical trophic relationships in early life history stages cannot be determined from this data source.

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3. WEST COAST, SOUTH ISLAND ENVIRONMENT

Authors: Philip Sutton, Mike Moore

3.1 Physical environment

3.1.1. Introduction

The functioning of the West Coast, South Island (WCSI) ecosystem depends on its location on the globe, the geography of the New Zealand bathymetric platform and the physical oceanographic conditions (Bradford-Grieve et al. 2006). The WCSI region has a relatively narrow continental shelf that ranges from less than 25 km wide in the south broadening to approximately 100 km wide to the north and is flanked by the nearby Southern Alps. This region has the highest rainfall in NZ and very high riverine sediment discharges. It is exposed to prevailing westerly weather systems resulting in marked cloudiness, windiness, upwelling, and variability in mixed layer depth.

This section reviews what is known of the physical environment of the adjacent Tasman Sea (fronts, flows, water masses, meteorology) and the impact that these have on the west coast shelf region.

3.1.2. The Tasman Sea

Fronts

The physical oceanography of the West Coast must be interpreted in the context of the Tasman Sea. The interior of the Tasman Sea is bounded by two fronts: the Subtropical Front (a water mass front) to the south, and the Tasman Front (a dynamical front) to the north.

The Subtropical Front (STF) separates warm, salty subtropical water (STW) in the north from cold, less saline subantarctic water (SAW) to the south. Across the southern Tasman Sea, the STF can be identified by enhanced surface salinity gradients. Heath (1985) located the STF in the salinity range of 34.5–35, while Stanton & Ridgway (1988) defined the surface frontal location to be coincident with the 34.8 isohaline. The STF across the south Tasman is a zone up to several hundred kilometres wide between south of Tasmania and the latitude of Fiordland. Close to Fiordland, the STF dips southward, before turning northward off the east coast of the South Island. Very few surveys of the STF in the south-east Tasman exist. Stanton & Ridgway (1988) still give the best description of the front's spatial properties. Weak eastward zonal flows are associated with the STF in the south Tasman.

The Tasman Sea is bounded to the north by the Tasman Front. This front results from flows associated with the East Australian Current (EAC). The EAC is the western-boundary current of the wind-driven South Pacific subtropical gyre, carrying warm water down the east coast of Australia before separating from the Australian landmass at about 35°S. The EAC is highly variable, particularly in the separation region where large eddies are formed and spun off. The separated flow of the EAC across the northern Tasman Sea forms the Tasman Front. The Tasman Front is also highly variable with large meridional excursions and is influenced by the Lord Howe Rise and Norfolk Ridge systems (Ridgway & Dunne, 2003). As the Tasman Front approaches North Cape, a portion of the flow attaches to the east coast of Northland to form the East Auckland Current.

Flows

In the Tasman Sea interior the mean surface flow is a broad, weak eastward flow toward New Zealand. A northward tendency is associated with the flow of retroflected EAC water toward the north of New Zealand, although close to the west coast of the South Island there may be a southward flow, following the southern flank of the Challenger Plateau. The flow appears to extend between the surface and 500m; below 500m velocities are low. The flow along the southern margin of the

Challenger Plateau is important because it is believed to form mean coastal flows to the north and south: the Westland Current and Southland Currents respectively, separate somewhere around 42°S-43°S (Figure 3.1.1) (Heath 1982).

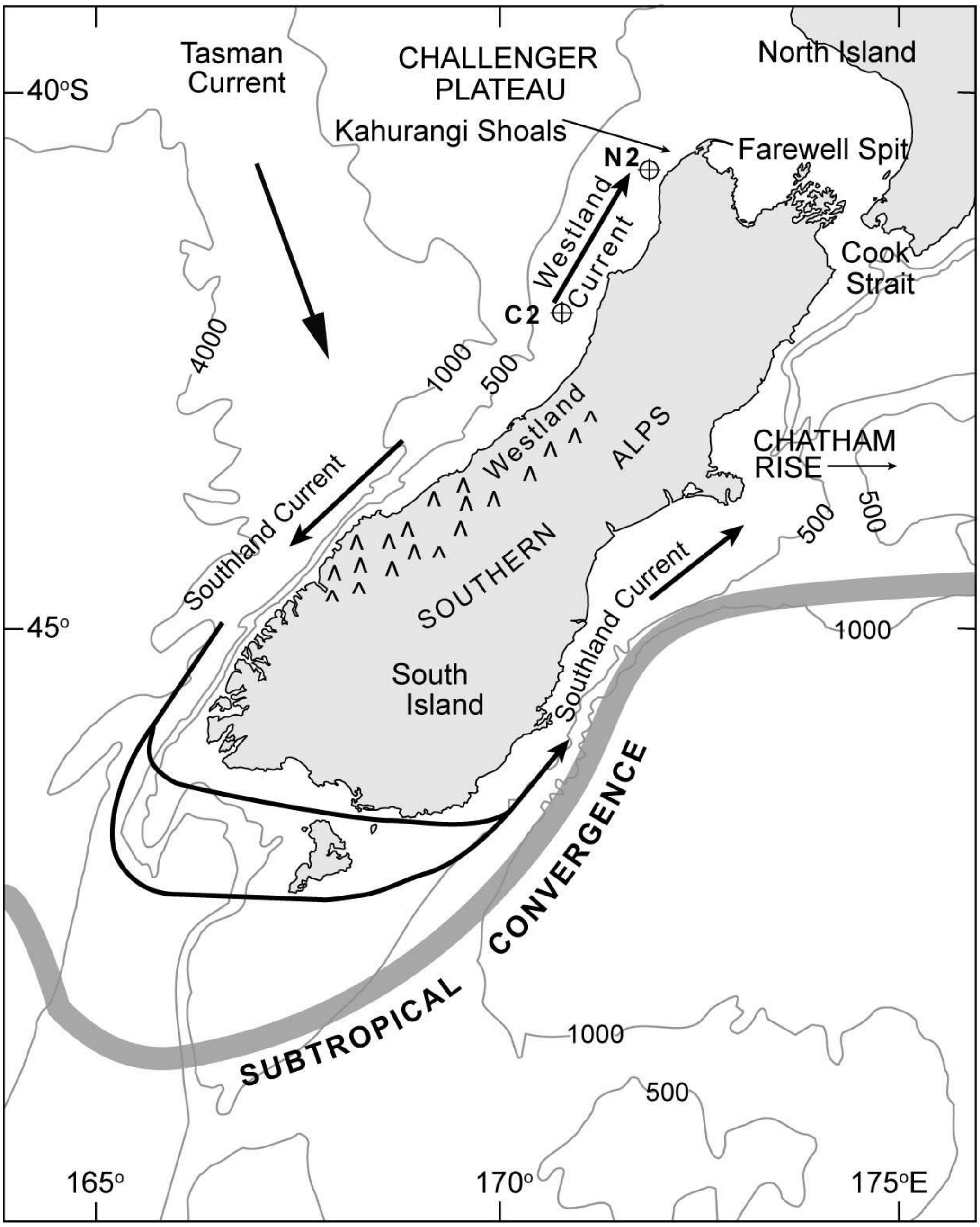

Figure 3.1.1: General Circulation features off Westland, bathymetry and location of current meter moorings (adapted from Moore & Murdoch 1993).

The impact of eddies shed into the Tasman at the retroflection of the EAC is uncertain. The warm-core eddies formed penetrate to a depth of about 500m and rotate anticyclonically. After they have been shed, they propagate into the Tasman Sea south of the Tasman Front, although Nilsson & Cresswell (1981) state that they can coalesce with the Tasman Front further east. These eddies are long-lived, with Nilsson & Cresswell (1981) tracking three of them for a period of two years. As the eddies aged they cooled and became capped with water indistinguishable from adjacent surface water (Nilsson & Cresswell 1981). Nevertheless, the original subsurface temperature structure (relatively warm and with low vertical temperature gradient) was retained for a year or two. The circulation speed actually increased as eddies aged, with speeds of 1 to 2 m s^{-1} observed. Winter thermal images show examples of warm-core eddies and suggest that eddies disperse in the Tasman more eastward than southward. Nilsson and Cresswell (1981) tracked an eddy as far south as Tasmania and as far east as 160°E before their field programme ended.

It is not clear whether EAC eddies propagate to the New Zealand west coast. There is evidence that eddies temporarily dominate coastal currents on the WCSI (Cahill et al. 1991, Stanton & Moore 1992). That such eddies are not a feature of observed sea surface temperatures (SST) in the vicinity of the WCSI may be because the surface temperature signal has been lost. Certainly, SST images are more suggestive of weak, meandering structures, similar to, but less distinct than, the Tasman Front meanders. Attempts have been made to observe eddy movements in the Tasman using satellite altimeter measurements of sea-surface height, but with inconclusive results (Laing, pers. comm.). A programme of *in situ* measurements would be necessary to define the offshore variability that sporadically impacts the coastal system.

Water masses

The surface water in the interior of the Tasman Sea is Subtropical Water (STW). It can be more precisely defined as Subtropical Lower Water (STLW) that is characterised by a shallow or surface salinity maximum formed by an excess of evaporation over precipitation in the centre of the South Pacific wind-driven gyre (Wyrtki 1962). While the salinity maximum is found at the surface in the centre of the subtropical gyre, in the Tasman Sea the surface water is fresher as a result of river water input from the coastal zone, and, to a lesser degree, precipitation over the Tasman Sea (and also, in the southern Tasman Sea, by interaction with fresher Subantarctic Water (SAW)). Thus in the Tasman Sea, the core of STLW, defined by the salinity maximum, occurs typically at 100–200m depth, i.e., below the winter mixed-layer.

At greater depths, (approximately 1000m) a salinity minimum identifies Antarctic Intermediate Water (AAIW). This water mass is thought to be formed by convection north of the Subantarctic Front (SAF) in the eastern Pacific (e.g., Hanawa and Talley, 2001). AAIW appears in all seas in contact with the Southern Ocean as a layer of low-salinity water, centred on about 1000 m depth in the Tasman Sea and southwest Pacific Ocean. The salinity minimum is most pronounced nearest its source: in the Tasman Sea the salinity minimum of AAIW is about 34.2 just north of the Subtropical Front (e.g. Chiswell 1995), while the salinity minimum weakens to the north. This indicates a general northward flow. However, there are sharp gradients in temperature and salinity at the salinity minimum, most notably in the northern Tasman Sea. Chiswell (1995), Tomczak & Godfrey (1994), McCartney (1977), Stanton (2002) and others ascribe this to the meeting of different bodies of AAIW that have followed different paths into the Tasman Sea.

Meteorology

New Zealand lies on the northern margin of a broad belt of westerly winds that encircle the Southern Hemisphere. The weather is dominated by an irregular succession of migrating anticyclones and intervening troughs that pass at 3–7 day intervals. Thus southern New Zealand is frequently under the influence of a fluctuating eastward flow, especially in spring, when the anticyclone tracks are found furthest north (Coulter 1975; Robertson 1966).

The flow over New Zealand is affected by the Southern Oscillation, with negative excursions of the Southern Oscillation Index being associated with anomalous southwesterly winds and cooler temperatures (Gordon 1986). The prevailing westerly winds flow over the Southern Alps and through Cook Strait; and surface winds can be affected up to a few hundred kilometres upwind of the topography (Neale & Thompson 1978; Revell 1993). The rainfall on the western side of the Southern Alps is very large (greater than 6,400 mm year^{-1}) (Tomlinson, 1992).

Wind measurements from a Met-Ocean Buoy indicate very good agreement between buoy winds and European Centre for Medium-range Weather Forecasts (ECMWF) winds (Stanton 1998). In fact, ECMWF winds were found to be a much better estimate of offshore conditions than any land-based measurements. The buoy measurements indicate that the wind speed exceeds 10 m s^{-1} 20% of the time and 15m s^{-1} 2.0% of the time. The winds are highly polarised with 79% of the variance accounted for by winds along a bearing of 64° (note that this gives a component of wind alongshore to the north). The wind component along the minor axis is skewed: strong winds directed towards the coast are quite common, but strong winds directed away from the coast are infrequent. Stanton (1998) analysed power spectra of winds along the major and minor axes and found that alongshore wind spectra have most of their variance at frequencies less than 0.2 day^{-1} but cross-shore winds have a pronounced peak at 0.2 day^{-1}. This represents the average cycle of weather systems across New Zealand (Robertson 1966).

3.1.3 The WCSI shelf region

Along the WCSI there is a 50–100 km wide band of coastal water typically affected by approximately 1% freshwater from large river flows, with a distinct thermohaline front separating it from offshore surface waters (Stanton 1976). As a result, inshore stations have the lowest surface salinity during all seasons. Surface mixed-layers are poorly defined in summer, but begin to appear in autumn and are well-developed in winter. Winter mixing extends to 200 m or more over the continental slope with a tendency to shoal inshore and offshore. Inshore stations have much shallower mixed layers of typically only a few tens of metres as a result of the freshwater.

The general eastward drift of Tasman water impacts the coast, resulting in the Southland and Westland Currents diverging from roughly the intersection of the slope of the Challenger Plateau and the WCSI coast (42°–44°S) (Heath 1982). If the flow followed topography, we would expect it to follow the southern path. Thus, given the trans-Tasman flow, we expect the Southland current to exist. Heath (1982) reviewed the early evidence for the mean flows and noted that they are weak relative to the variability. Later current meter measurements (Cahill et al. 1991) showed mean flows of about 4 cm/s northward and 5 cm/s southward in the northern and southern regions of the coast, with about 30–40 cm/s standard deviation in subtidal velocity. Whether the means in these 6 month measurements are statistically significant has not been addressed.

On theoretical grounds, Heath (1982) ascribed a mean northward Westland Current to be the effect of a prevailing northward alongshore component of wind. It has been common in the literature (e.g., Stanton 1976; Stanton & Moore, 1992) to discuss the variability as an enhancement or reversal of the Westland Current by the wind. Thus, the Westland Current can be regarded as a wind-driven flow with a northward bias due to the prevalence of winds from the southwest. Certainly, the Westland Current is at best a weak flow in a highly variable system.

3.1.3.1 Variability

Coastal-trapped waves

One of the major advances of the West Coast Ecosystem Programme was to gain a substantial degree of understanding of the subtidal variability of the coastal currents. The Tasman Boundary Experiment (TASBEX) found that the bulk of the alongshore flow variance within about 100 km of the coast can be explained by low mode, wind-forced, coastal-trapped waves (CTWs) (Stanton & Greig, 1991; Cahill et al. 1991).

TASBEX found that subtidal flows were dominated by CTWs with flow speeds of up to 30 cm/s, that is, much larger than the observed mean Westland or Southland Currents (with speeds of 4 cm/s and 5 cm/s respectively). Most of the subtidal energy was at time scales of about 5 to 20 days, associated with the "weather-band" wind variability (Cahill et al. 1991). These flows did not show any systematic variation over the 6 month measurement period. They were highly coherent along the mid and northern sections of the west coast of South Island, and were comprised of approximately equal amplitude mode 1 and 2 waves. Despite considerable changes in shelf profile from Wekakura Point to Jacksons Bay (Figure 3.1.1), most of the low-mode energy observed in the north was found to reach the south of the study region, though Cahill et al. (1991) speculated that some scattering into high modes may have occurred half way along the shelf at about 42°S, which was a region poorly sampled by the TASBEX moorings.

The nearly equal mode-1/mode-2 weighting is consistent with the theory of Buchwald and Kachoyan (1987) for CTW generation by volume-flux through a strait. Thus, variable flow through Cook Strait is considered to be the major forcing mechanism for CTWs on the WCSI shelf. Further support for this contention comes from Stanton and Greig (1991) who successfully modelled about 70% and 60% of the subtidal variance in alongshore currents at TASBEX sites "N2" and "C2" (Figure 3.1.1), using the theoretical phase delays and relative amplitudes of the mode-1 and mode-2 waves from the Buchwald and Kachoyan (1987) theory, combined with a simple model of the wind-driven flux through Cook Strait (Shirtcliffe et al. 1990).

This dynamic concept has become a connecting theme for a number of studies of biologically important processes. For example, the shelf to offshore exchange events (known as "coastal squirts") that occur in the Hokitika canyon region at 43°S may be forced by the southward cycle of CTWs (Moore and Murdoch, 1993). CTWs may also be important in generating upwelling. Off Westport, Chang et al. (1992) observed upwelling during the period 6–15 July 1988 when, from Moore & Murdoch's (1993) analysis, winds were not upwelling-favourable (though some uncertainty exists about the fine-scale structure in the marine winds). At this time, an upwelling favourable alongshelf flow existed as a result of the CTW field propagated from Cook Strait. It has been noted by Stanton (1971, 1976) that upwelling events off WCSI propagate with the coast on the left, which may be further evidence of the importance of CTWs in upwelling along the WCSI coast.

Because the CTW field is the dominant signal in the shelf currents up to 50–100km offshore at subtidal frequencies, the development of the Stanton and Greig (1991) hindcasting technique has enabled studies of other phenomena on the WCSI coast to test hypotheses about the importance of the large-scale shelf circulation, without the necessity for current measurements.

Off-shelf flows

There is a limited amount of knowledge about variability in off-shelf flows off WCSI. Some observations were made in 1982 showing non-seasonal temperature and salinity variations extending over the entire shelf between March and May (Heath & Ridgway 1985). Heath and Ridgway showed that widespread, surface, low-salinity water in March was replaced in May by saltier, warmer water.

Analysis of current meter observations from off WCSI and the southern flank of Challenger Plateau showed variable flows (Heath 1986) with an associated heat transport with a substantial inshore component. Stanton & Moore (1992) showed that low salinity surface waters can be displaced offshore by the circulation. They also suggested that the spreading of a riverine, brackish layer over the surface could be related to upwelling-favourable winds as, in downwelling situations, lower salinity water is likely to be confined close to the shore.

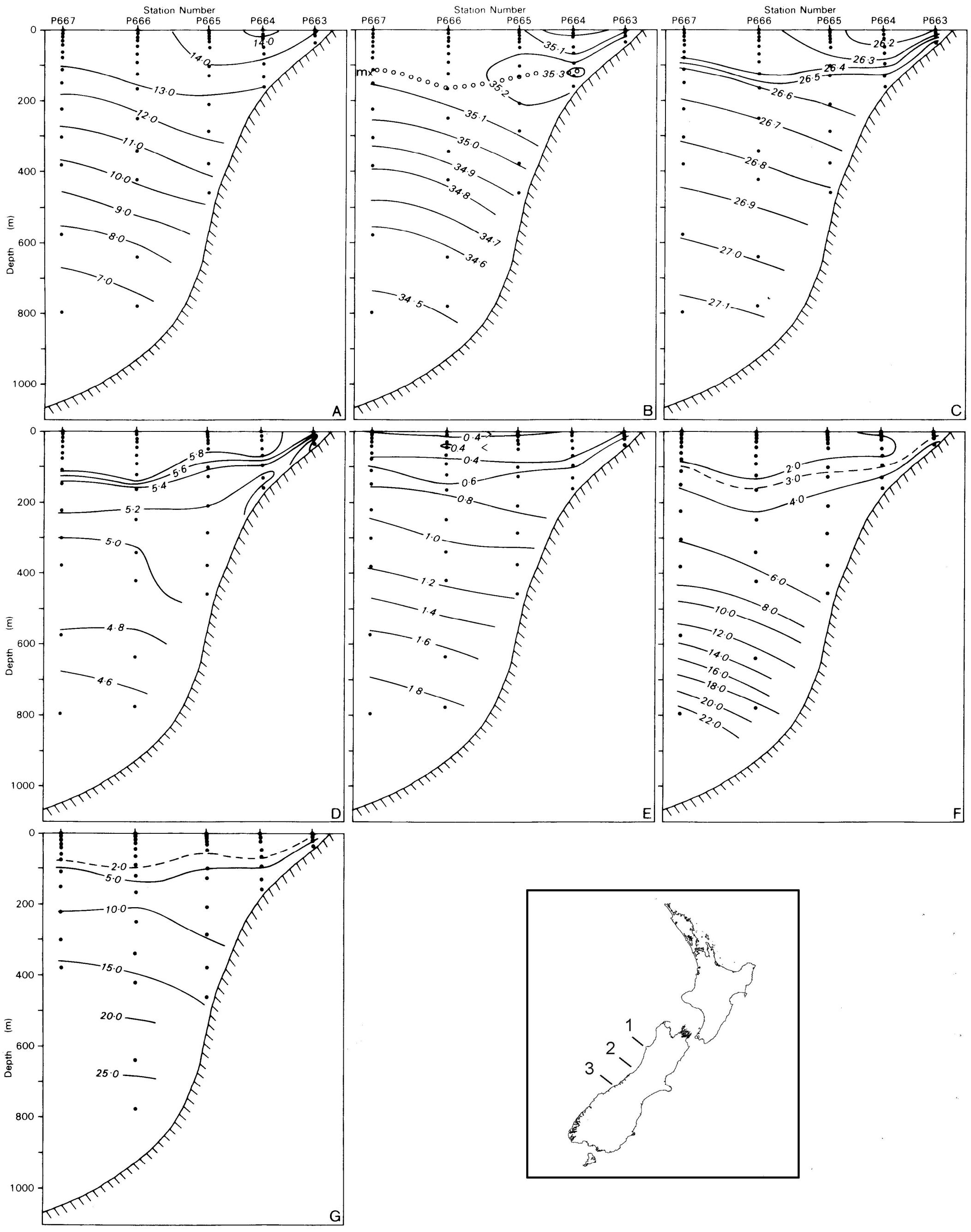

Figure 3.1.2: Winter vertical profiles of water properties along Transect 2. (A) temperature ^{0}C; (B) salinity PSU; (C) density g l^{-1}; (D) dissolved oxygen ml l^{-1}; (E) reactive phosphorus mmol m^{-3}; (F) reactive silicate mmol m^{-3}; (G) nitrate nitrogen mmol m^{-3} (Bradford 1983).

The CTW modes decay offshore decorrelating with the inshore flows at about 100 km offshore in the northern part of the TASBEX study region, and about 50 km in the south. Few current meter observations have been made in the offshore region and it is generally assumed to be a weak eastward mean flow impacted by eddies from the Tasman. Stanton & Moore (1992) interpreted a sudden breakdown in the correlation between wind and flow in one period during the TASBEX experiment as of an eddy impacting from the offshore region. In summary, the hydrodynamic of the offshore region is poorly understood, but it is believed to have significant impact on the shelf dynamics.

Tides

There has been no focused study of the tides on the WCSI. Studies have been based on measurements made for other primary purposes.

On the larger scale, WCSI tides are just a component of New Zealand tides, which are largely semi-diurnal with the principal lunar semi-diurnal tidal constituent (M2) significantly larger than the principal solar semi-diurnal tidal constituent (S2) (Heath 1977). The M2 tide is consistent with a progressive wave incident on NZ from the northeast trapped by the NZ bathymetric platform - the M2 wave travels anticlockwise around NZ with a commensurate variation in phase around the coast from 0° to 360° (Bye & Heath, 1975). The S2 tide has both a progressive wave component and a larger standing wave component resulting from a wave incident on NZ from the northwest (Heath 1984).

On WCSI the M2 tide amplitude varies from about 1.3 m in the north to about 0.7 m in the south, with an accompanying phase increase of about 70° (about 2.5 hrs). The corresponding variation in the S2 tidal amplitude is from 0.4 m in the north to 0.1m in the south, with a phase change of about 30°. The diurnal tides off WCSI are small with amplitudes of about 0.03 m (Heath 1977).

Only a few current meter measurements from the WCSI coast have been subjected to tide analysis (e.g. Heath 1984). Ship-borne acoustic doppler profile measurements from a near-fixed location over a ten hour period have allowed for vertical resolution of the tidal flows (Vennell & Moore, 1993). The current measurements are consistent with flows associated with a superposition of a progressive M2 tide and an internal (baroclinic) M2 tide. The S2 tidal flows are consistent with a substantially standing wave component on WCSI. Typical M2 tidal flows on the continental slope have amplitudes of about 5 cm/s - further inshore on the continental shelf the flows will be substantially faster. Heath (1984) found that the currents associated with the barotropic and baroclinic tides are about the same for the M2 tide but the internal (baroclinic) water speeds are larger than those of the barotropic component for the S2 tides. This result is consistent with Vennell & Moore's (1993) study, based on winter observations over the continental slope showing that the semi-diurnal tide is made up of a barotropic tide with a speed of about 10 cm s^{-1} and a 6.3 cm s^{-1} internal tide. The internal tide was consistent with a two-layered structure with the boundary between the layers being the bottom of the surface mixed layer.

3.1.3.2 Physical processes directly impacting primary productivity

Upwelling

Upwelling occurs along the WCSI coast north of Jacksons Bay, showing marked intensification at some locations such as Cape Foulwind and Cape Farewell. Upwelling has been shown to be important in maintaining primary productivity in WCSI waters (e.g., Chang & Bradford 1985; Bradford & Chang 1987; Chang et al. 1992).

Upwelling along WCSI occurs in sporadic events lasting several days, rarely reaching a discernible steady state. Upwelling favourable winds from the southwest quarter, are estimated to occur between 40% and 50% of the time (Stanton & Moore, 1992), and occur episodically in events lasting from 2–12 days, rather than in a distinct season as is found for example off California/Oregon. The limited duration of the upwelling conditions moderates the degree to which upwelling occurs. Upwelling estimates from TASBEX (Stanton & Moore, 1992) are in the lower part of the range compared with California/Oregon, Peru and Northwest Africa, where upwelling seasons can last for months.

Temperature, salinity and nutrient sections in upwelling conditions show subsurface contours sloping upwards towards the coast (e.g. Bradford 1983). The section in Figure 3.1.2 suggests that upwelling usually occurs from depths of about 100m.

Coastal Squirts

Interest in coastal squirts arose as a consequence of investigations into the life cycle of hoki (*Macruronus novaezelandiae*) by Murdoch (1990, 1992). The largest known New Zealand spawning aggregation occurs in Hokitika Canyon in July each year. Spawning lasts only a few weeks, during which commercial fishing is intense. High density CTD surveys made as a part of Murdoch's investigations (Moore & Murdoch, 1993) showed that during the 1987 winter, the southern flank of the canyon was briefly overlaid by a large tongue of low-salinity water flowing offshore (as established by tracking a drogued buoy). The size of the feature relative to the canyon, together with its impact on mixed layer depth and chlorophyll, made investigation of this feature essential to understanding the role of the physical environment on the ecology of the canyon. A subsequent survey in 1988 showed another similar feature, and satellite SST and sea surface chlorophyll (CZCS: Coastal Zone Colour Scanner) images show that similar events occur sporadically irrespective of season (though summer events are not visible in SST images because the inshore water is not clearly differentiated in temperature from the offshore water in summer) (Figure 3.1.3).

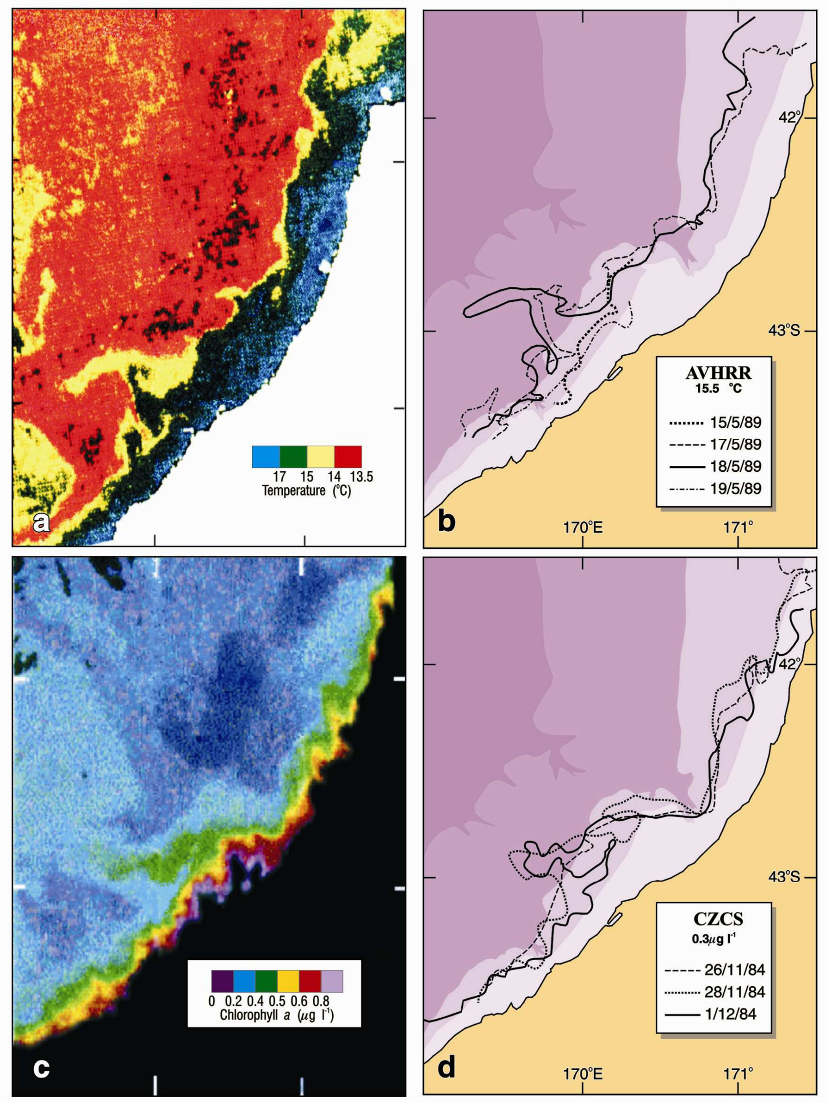

Figure 3.1.3: (A) Satellite AVHRR image from May 18, 1989. (B) Contours of the 15.5°C isotherm digitized from AVHRR images from May 15-19, 1989. (C) CZCS image of chlorophyll *a* from December 1, 1984, showing plumes off the Westland coast. (D) Contours of 0.3 mg m^{-3} chlorophyll *a* isoline digitized from CZCS from November 26 and 28, and December 1, 1984. 100 and 250 m isobaths indicated (from Moore & Murdoch 1993).

The impact of the squirts on primary productivity is as follows (Moore & Murdoch, 1993). A squirt carries inshore surface water offshore and mixes it into the offshore surface water. Initially this enhances the surface chlorophyll content because the inshore water is chlorophyll rich as a result of its nutrient content and shallow mixed layer. However, total water column chlorophyll subsequently reduces because the stability conferred by the freshwater in the shallow squirt prevents deep mixing in the offshore water and thus fewer phytoplankton are cycled into the euphotic zone.

Mixed Layer and upper ocean

More than 50 km off WCSI in the eastern Tasman Sea there is a well-defined seasonal cycle in SST and mixed layer depth. In a typical year the surface temperature in offshore waters varies between a minimum of 13 °C in early September and a maximum of 18 °C in February. The seasonal variation diminishes with depth to approximately zero at 200 m. The temperature maximum occurs in February at the surface, but is progressively later at greater depths until the seasonal cycle is reversed at 150 m (Rahmstorf 1992). As the seasonal surface warming occurs, a seasonal thermocline forms between 30 m and 80 m in September/October and breaks down in June. In summer the mixed layer depth is limited by the seasonal thermocline and fluctuates between 0 and 40 m, controlled by surface heating and wind mixing. The mixed layer grows by convection in winter and typically reaches 150 m deep or more by August/September. Mixed layer properties have been simulated successfully using one-dimensional numerical models forced at the surface by meteorological data generated from land stations (Rahmstorf 1992; Hadfield & Sharples, 1996) (Figure 3.1.4). The latter model simulated observed sea surface temperatures with a root mean square error of 0.6°C and appeared to reproduce the observed pattern of interannual variation, including the anomalously cool summer associated with the 1982/83 El Niño.

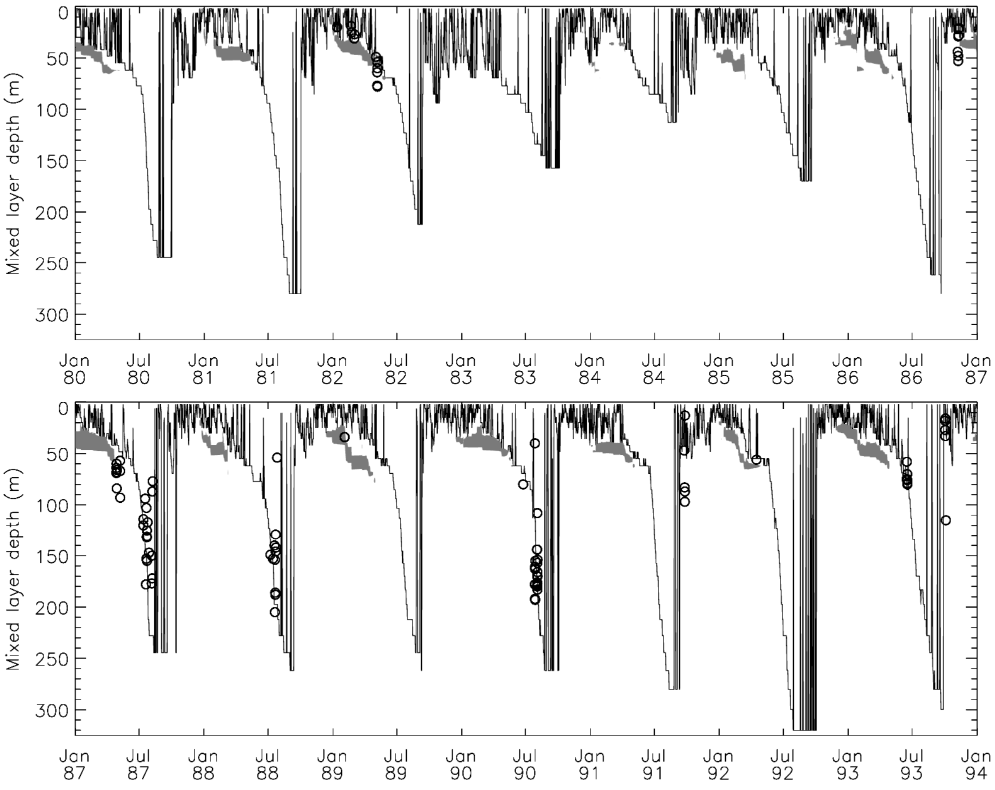

Figure 3.1.4: Modeled mixed layer depth compared with shipboard observations (o) (from Hadfield & Sharples 1996).

The shelf water along WCSI is modified by river outflow. Low salinity water comprising a mixture of offshore surface water and river water is found on the shelf throughout the year. The volume of freshwater varies by several orders of magnitude, making up ~1% of the shelf water volume, but affecting the salinity of 37% of the water over the shelf. The resulting relatively fresh water ($S<34.8$) forms a wedge ~50 m deep at the inshore end extending offshore to a maximum of ~50 km (e.g. Heath & Ridgway 1985). The density contrast at the base of this layer limits the mixed layer depth. The processes by which this water mixes with oceanic water are not well understood, but it appears that in winter a low-salinity layer moving out over oceanic water would take a few weeks to be mixed completely with the oceanic water (Hadfield, pers. comm.).

Studies of mixed layer development off the South Island west coast have used datasets spanning several years including, at a minimum, wind speed, temperature, humidity and solar radiation (and/or cloud cover). Hadfield (1995) presents a dataset for the years 1980–1994 based on land station data from Hokitika and Farewell Spit. Main features of the variations in temperature and mixed layer depth can be explained by the local meteorological forcing and vertical mixing, together with a persistent warming associated with the general southward flow (Rahmstorf 1992). Superimposed are short-term variations related to variable currents and associated heat transport, which can dominate temperature signals below the surface.

In winter, the mixed layer may reach a maximum over the continental slope parallel to the coast, shoaling both inshore and offshore (Bradford 1983; Heath & Ridgway 1985). This is a result of the interplay of the thermocline deepening towards the east associated with the large scale flow, together with the coastal band of fresh water (Figure 3.1.2).

There is considerable interannual variability in the upper ocean. Repeated measurements have been taken of the top 800 m of the ocean along a line between Sydney and Wellington, north of the region of interest. These data are collected from expendable bathythermographs (XBTs) dropped from container ships, and the section has been sampled approximately four times per year since 1991. This is part of a collaborative project between Scripps Institution of Oceanography, CSIRO and NIWA. The mean temperature versus time and depth for an eastern segment (167–168°E) of this section were analysed as in Sutton et al., 2005 and is shown in Figure 3.1.5. The seasons stand out clearly, with winter mixed layers extending to 100–150m and the seasonal thermocline forming and then eroding above this. A more subtle signal is the strong warming that occurred throughout the entire water column between 1996 and 2002 with a mean warming of ~1.2 ºC occurring through this time period. This warming is remarkable because it occurred almost barotropically- the average water depth is not much greater than 800 m in this area. This warm water propagated into the New Zealand region from an anomalous pool of warm water in the central Pacific at ~ 30°S (Bowen et al. 2006). The oceans continued to be warm both west and east of New Zealand through the 1998 to 2002 time period as a result of a spin-up of the entire South Pacific gyre (Roemmich et al. 2007).

This signal illustrates the possible importance of interannual variability to ecosystem functioning on this coast, and could have a strong impact on the productivity off WCSI. The changes in mixed layer behaviour are likely to indicate changes in nutrient levels as warmer water may be associated with lower nitrate levels (see Figure 3.1.2).

3.1.4 Summary

The interior of the Tasman Sea is dominated by a weak eastward flow. This eastward flow divides into the northward Westland Current and the southward Southland Current where the southern flank of Challenger Plateau intersects the coastline. The water in the Tasman Sea lies between two fronts: the Tasman front to the north and the Subtropical Front which intersects the WCSI coast off Fiordland.

Central Tasman water is STLW. There is a 50–100 km wide surface band of coastal water affected by ~1% freshwater resulting from river input. This freshwater affects mixed layer development, with mixed layers up to 200 m deep in winter offshore, while inshore mixed layers are typically only a few tens of metres deep.

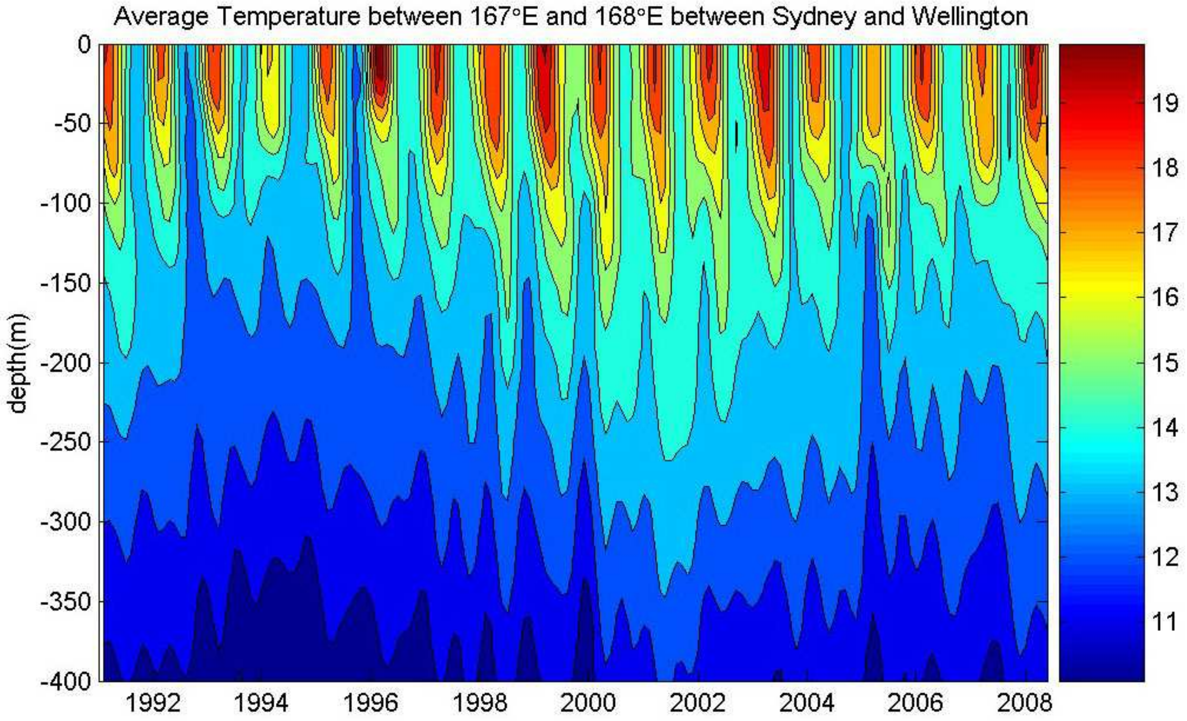

Figure 3.1.5: Interannual variability in temperature at 167-168°E between Sydney and Wellington, 1992-2008 (Source: Sutton et al. 2005).

The coastal flows are highly variable, with mean flows of about 4 cm/s northward in the Westland Current and 5 cm/s southward in the Southland Current but 30–40 cm/s standard deviation in subtidal velocity. This variability is dominated by coastal-trapped waves which are important at time scales of 5–20 days, i.e., similar to that of wind variability. CTWs sufficiently dominate the variability that accurate hindcasts of currents are possible given accurate wind fields.

CTWs also appear to be implicated in the occurrence of coastal squirts, where fresh surface water is directed offshore along the southern margin of Hokitika canyon. These coastal squirts have an important impact on stratification, and therefore on productivity.

Upwelling along the WCSI coast occurs in sporadic events lasting several days. A vigorous upwelling centre exists in the region of Cape Farewell and various mechanisms have been postulated. There are unexpected aspects to the relationship between wind and upwelling, with the upwelling system appearing to "ring" in response to sudden changes in wind.

Finally, recent analyses of the temperature field through the water column show strong interannual variability all the way down to 800 m (the maximum depth of the measurements). In particular, the ocean warmed by 1.2° between 1996 and 2002. By inference, this warming could have an associated lowering of nutrients available to the plankton production system.

In summary, the WCSI coast is a dynamically very active region. Much of the underlying physics and biology have been studied but ongoing measurements to interpret interannual variability in both the physical environment and also in the biological systems are missing.

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3.2 Nutrients and light

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3.2.1 Introduction

Primary production in the sea is mainly a function of the light and nutrient environment. The Tasman Sea is a special case of Longhurst's (1998) "westerlies domain" where production is generally not light limited but becomes nutrients limited in summer. Nevertheless, in the south east Tasman Sea, there are modifications to his general classification scheme such that the mixed layer depth may exceed the depth at which vertically integrated primary production equals integrated respiration (the critical depth) over the continental slope, parallel to the coast, and the sedimentation and phytoplankton regime can attenuate light penetration.

Here, we summarise what is known about the light and nutrient regime of the West Coast, South Island (WCSI) and discuss the physical and biological features of the region that may influence these drivers of biological production.

3.2.2 Light

As in other parts of the world, a major part of the variation in primary production per unit biomass is explained by variation in light (Bradford & Chang 1987). Therefore it is important to understand the nature of the light penetrating the sea surface and the factors that influence the depth of penetration into the water column in relation to the surface mixed layer. Surface irradiance (i.e. the amount of solar radiation impinging on the surface of the ocean), varies with latitude and season and decreases to varying degrees with increasing depth in the water column. The absorption of solar radiation as it passes through seawater (attenuation) is due to the water itself, dissolved yellow substance (usually dissolved material of biological origin that is resistant to bacterial degradation), phytoplankton (living, growing cells) and inanimate particulate matter (e.g. inorganic sediment, dead biological material). The attenuation coefficient for irradiance with depth is inversely related to the euphotic depth (Z_{eu}) (the depth at which irradiance is reduced to 1% of that at the water surface).

Seasonal changes in *surface irradiance* (i.e. the amount of solar radiation impinging on the surface of the ocean) can be calculated from theoretical clear sky irradiance and estimations of cloud cover (e.g. Straskraba 1980). The seasonal range of midday irradiance, modelled at 40°S and 50°S respectively, ranged from winter minima of approximately 250 and 600 μmol photons m^{-2} s^{-1} to summer maxima of 1132 and 1583 μmol photons m^{-2} s^{-1} (Vincent et al. 1989). At 40°S annual mean cloud cover is 66%, increasing to 73% at 45°S and cloud cover is significantly ($P<0.001$) inversely correlated with latitude (United States Navy 1979). Field measurements of surface irradiance off WCSI fit within these calculated values (Table 3.2.1).

Table 3.2.1: Summary of diffuse vertical attenuation coefficients (*K*) and range of incoming solar irradiance measured at West Coast sites: 1979 – 1993 and calculated by Vincent et al. (1989).

Date	Range of *K*	Irradiance (range) (μmol photon m^{-2} s^{-1})	Reference
9-26 June 1979	0.062-0.202	68-833 (average irradiance 1100 – 1500 h)	Chang & Bradford (1985)
18 Feb - 6 March 1982	0.060-0.288	117-1787 (average irradiance 1100 – 1500 h)	Bradford & Chang (1987)
6 July to 16 July 1988	0.056-0.852		NIWA unpublished data
16 to 28 May	0.139-0.159	277-888 (maximum midday	Howard-Williams *et al* (1995)

1989		irradiance)	
June/July 1990	0.129-0.239		NIWA unpublished data
June/July 1993	0.143		NIWA unpublished data
October 1993	0.083-0.142		NIWA unpublished data
40°S	Annual range	250-1132 (midday irradiance)	Vincent et al. (1989)
45°S	Annual range	600-1583 (midday irradiance)	Vincent et al. (1989)

In winter, average incoming irradiance between 1100 and 1500 h ranged from 68–883 μmol photons m^{-2} s^{-1} (Chang & Bradford 1985) and in summer, the range for the same period was 117–1787 μmol photons m^{-2} s^{-1} (Bradford & Chang 1987) (Table 3.2.1). Maximum midday irradiance in autumn, ranged from 277-888 μmol photons m^{-2} s^{-1} (Howard-Williams et al.1991).

Water clarity

Although the attenuation of Photosynthetically Active Radiation (PAR) with depth exhibits varying degrees of curvature (Howard-Williams & Vincent 1985; Kirk 1994), it may be approximated by an exponential decline with depth (Kirk 1994) (Table 3.2.1). The diffuse vertical *attenuation coefficient* (K) is defined as the rate of change of the logarithm of irradiance with depth. During autumn, values for the attenuation coefficient for downward irradiance (K_d) were very similar to the attenuation coefficient for scalar (coming from all directions) irradiance (K_o) in South Island waters in general (Howard-Williams et al. 1995) and as expected for waters of low reflectance (Kirk 1994). Off WCSI, inshore coastal waters generally had the highest attenuation coefficients, greater than 0.1 m^{-1} (K_o = 0.104 - 0.159 m^{-1}) (Howard-Williams et al. 1995) which are consistent with nearshore K values greater than 0.1 m^{-1} measured by Chang & Bradford (1985) and Bradford & Chang (1987) (Figure 3.2.1). Maximum values for K (0.22–0.29 m^{-1}) were recorded at coastal sites during summer (Bradford & Chang 1987).

In deeply mixed oceanic waters in winter, K was consistently low (less than 0.1 m^{-1}) (Chang & Bradford 1985). The highest extinction coefficients, and by definition the shallowest euphotic depths, have been consistently measured in the near surface waters close to the coast. In winter, Z_{eu} ranged from a minimum of 21 m at an inshore site off Greymouth to a maximum of 73 m at an offshore site (Chang & Bradford 1985). The same pattern was seen in summer with a range of 21–77 m (Bradford & Chang 1987; Howard-Williams et al. 1995).

The underwater light field is impacted by the varied biological communities together with suspended inorganic matter and dissolved organic matter from rivers and *in situ* water properties (Chang & Bradford 1985; Howard-Williams et al. 1995). Each of these components contributes, to differing degrees, to the attenuation of light and therefore to the euphotic zone depth. In winter, the proportion of PAR attenuation brought about by non-photosynthetic particles was significantly negatively correlated with salinity (Chang & Bradford 1985) and it was assumed that this was due, in general, to terrigenous sediment at inshore stations. In all water masses around the South Island significant correlations occurred between optical variables and chemical and biological variables. K_o can be predicted from chlorophyll *a* concentration, extinction coefficient at 440 nm (yellow substance), and particulate matter concentrations at 10 m (Howard-Williams et al. 1995).

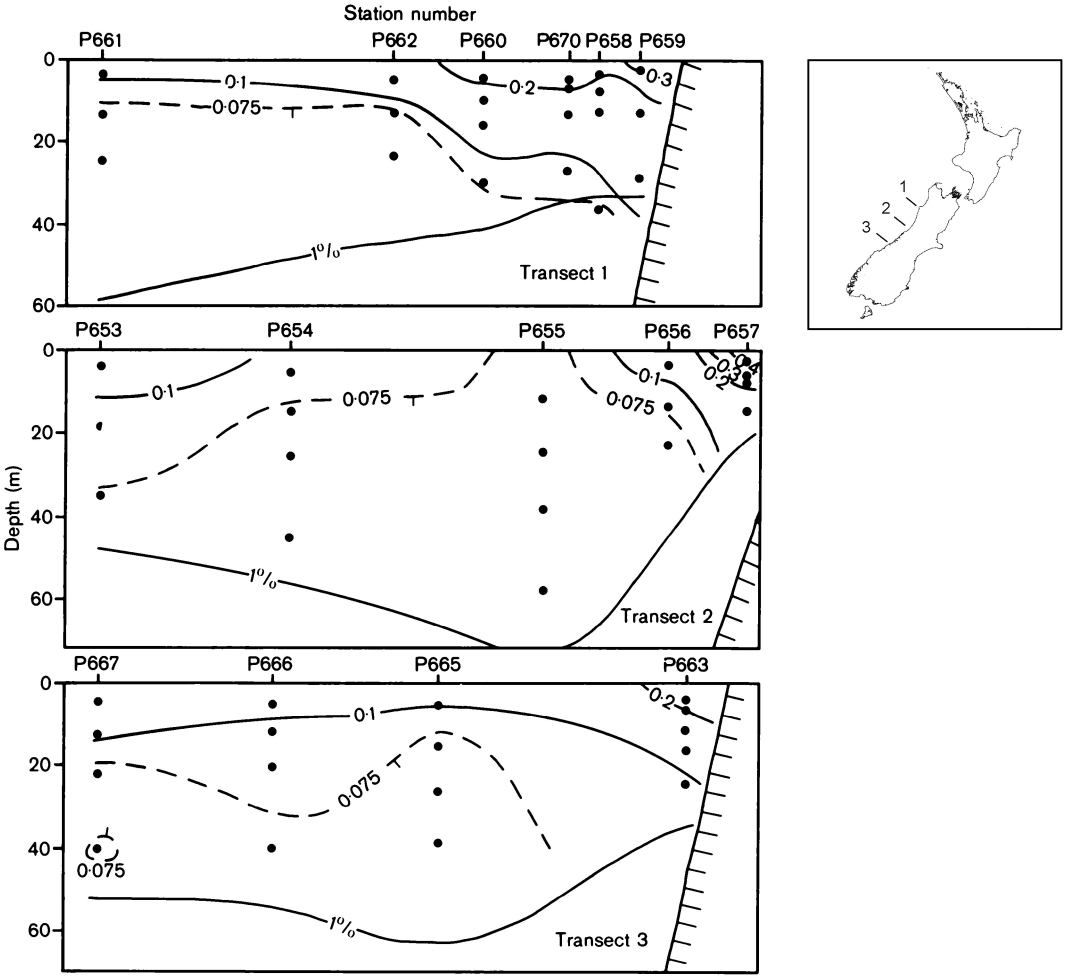

Figure 3.2.1: Vertical profiles of extinction coefficient and depth of the 1% light level along transects 1-3 (see inset) in June 1979 (Chang & Bradford 1985).

Yellow substance affects the spectral characteristics of waters by preferentially absorbing blue light. It can thus be regarded as a competitor with phytoplankton for blue light (Kirk 1976). In autumn, WCSI waters had higher concentrations of yellow substance than other waters off the South Island and blue light absorption by yellow substance in these waters reduced total light penetration of the water column as well as shifting the spectral distribution from blue towards green (Davies-Colley 1992; Howard-Williams *et al.* 1995). The range of values for the extinction coefficient at a wavelength of 440 nm, indicating yellow substance (*g*440) measured in marine waters off the WCSI (0.04–0.11 m^{-1}) covered the low end of the range reported by Bricaud et al. (1981) (Table 3.2.2). Yellow substance accounted for 45% (r^2=0.45) of the total variation in absorption of photosynthetically available radiation measured in May 1989 (Howard-Williams et al. 1991).

Table 3.2.2: Selected optical properties off the west coast, South Island, May 1989. Chl *a* – chlorophyll *a*, $\overline{E}_o$ – average quantum scalar light intensity for the mixed layer as percentage of subsurface irradiance, g_{400} – yellow substance, *K*d – attenuation coefficient for downward irradiance, *K*o – attenuation coefficient for scalar irradiance, PN – particulate matter, Zeu – euphotic zone depth (Howard-Williams *et al.*, 1995).

Location	Station	g_{400} (m^{-1})	Chl *a* (mg m^{-3})	PN (mg m^{-3})	*K*d (m^{-1})	*K*o (m^{-1})	Zeu (m)	$\overline{E}_o$ (%)
Greymouth	R391	0.04	0.71	0.97	0.137	0.158	25	18.1
Wanganui Bluff	R392	-	-	-	0.144	0.144	32	23.2
Fiordland	R393	0.08	0.53	1.07	0.140	0.139	33	28.8
Fiordland	R400	0.11	0.52	1.11	0.166	0.159	28	62.9
Fiordland	R401	0.05	0.32	0.58	0.084	-	55	11.2

Illumination of mixed layer and critical depth

The average irradiance, as a percentage of subsurface irradiance, that a circulating cell in the mixed layer is subject to ($\overline{E}_o$) can be calculated from surface irradiance, attenuation coefficients and the depth of the mixed layer (e.g. Howard-Williams et al. 1995). This measure provides an index of average mixed layer lighting. The mixed layer (Z_m) is defined from the first major density discontinuity detected from conductivity-temperature-depth profiles. The average lighting over the mixed layer can be estimated from the average quantum scalar irradiance for the mixed layer and $\overline{E}_o$ is approximated by $E_o(0)/(K_o Z_m)$ (Vincent 1983).

Differences in $\overline{E}_o$ are due primarily to differences in mixed layer depth. Relatively low values (less than 15%) were found in the deep mixed layers in the New Zealand region. Sites off WCSI ranged from 18% of subsurface irradiance off Hokitika to 63% in shallow mixed layers off Fiordland (Howard-Williams et al. 1995) (Table 3.2.2). It is noteworthy that the average irradiance that a circulating phytoplankton cell is subjected to was consistently higher in waters with the highest attenuation coefficients. Although $\overline{E}_o$ is an indicator of light availability in the mixed layer the strong non-linearity of production versus irradiance curves, precludes direct use of this index in models (McBride 1992).

Howard-Williams et al. (1995) noted that data collected in May 1989 reflect autumn-winter conditions and that the optical properties of waters around the South Island of New Zealand may be appreciably different in summer. In particular the parameter $\overline{E}_o$ may be less variable in summer when surface warming of the ocean results in a more-nearly uniform, shallow mixed layer depth as shown for February 1982 (Bradford & Chang 1987) compared to June 1979 (Bradford 1983).

When the mixed layer is greater than the depth of the photic zone, Sverdup's (1953) concept of "critical depth" is relevant: where total vertically integrated phytoplankton production equals total respiration. Off WCSI the critical depth may lie between 70 – 260 m in June. This calculation has been made using the formulation of Siegel et al. (2002), assuming a community compensation illumination of 1.3 mol photons m^{-2} d^{-1}, a diffuse attenuation coefficient (K) = 0.08 and the range of field measurements of illumination made in June (Chang & Bradford 1985). Therefore, it is highly likely that from time to time there will be no net phytoplankton growth when surface winter mixing is very deep.

3.2.3 Nutrients

The winter distribution of nitrate (and other nutrients) in the Tasman Sea is best shown by a transect from inshore to offshore (see Figure 3.1.2 in Section 3.1). The water column may be divided into three layers: a surface layer where nutrient concentrations are low and uniform with depth, a narrow layer where concentration changes rapidly with depth, and a layer where concentrations change more gradually with depth. In summer, surface layers are almost depleted of nutrients (Bradford & Chang 1987).

Nutrient concentrations, in conjunction with the depth of mixing and light, have a strong control, not only over the quantum of primary production, but on the structure of phytoplankton populations and indirectly on the timing and extent of grazing on this production. Concentrations of dissolved inorganic nutrients in the sunlit surface waters off WCSI, are influenced by several processes. Nearshore waters receive river water that contains some dissolved compounds that can contribute to phytoplankton growth. The seasonal cycle of surface cooling, heating and mixing renews nutrients in surface waters in late autumn and winter. Wind-driven upwelling of nutrient-rich waters from well below the sunlit layers potentially impact the structure and functioning of the ecosystem off WCSI. And finally, processes that affect the background distribution of subsurface nutrients may have far reaching effects on the WCSI ecosystem.

Freshwater sources

The closeness of the western slopes of the Southern Alps to the coast and the fact that WCSI is one of the wettest areas of the country (average rainfall is greater than 6400 mm y^{-1}) strongly influences river flow regimes there (Duncan 1992). This results in mean flows ranging from 89–425 m^3 s^{-1}. WCSI rivers are representative of New Zealand high altitude or less-developed catchments that drain major mountain ranges. These rivers are fairly low in dissolved reactive phosphorus (DRP), dissolved reactive silica (Si) and nitrate (NO_3) (0.13–0.19, 384–470, 3.93–4.28 mmol m^{-3} respectively) (Close & Davies-Colley 1990). Off the Buller River, Bradford (1983) noted that there was a good correlation between salinity and silicate implying that, if other nutrients were in adequate supply, river water may enhance diatom growth there. Nevertheless, it is possible that the freshwater input of nutrients is not very significant on this coast, given the degree of dilution (1% freshwater) that occurs (e.g. Stanton 1976; Hawke & Hunter 1992). Deep winter mixing and upwelling of deep waters are more likely to be the dominant processes enhancing nutrient flux into surface waters.

Seasonal mixing of surface waters

The mixed layer depth in winter is at a maximum parallel to the coast over the continental slope (Chang & Bradford 1985). It appears that this orientation may be related to the fact that there is often a tongue of warm water extending down the coast from the north (see Section 3.1 for more) (see Figure 3.1.2).

The seasonal pattern of mixed-layer depth is not known in great detail from field measurements but a model of its progression (Hadfield & Sharples 1996) agrees well with field measurements made over the continental slope (Figure 3.2.2).

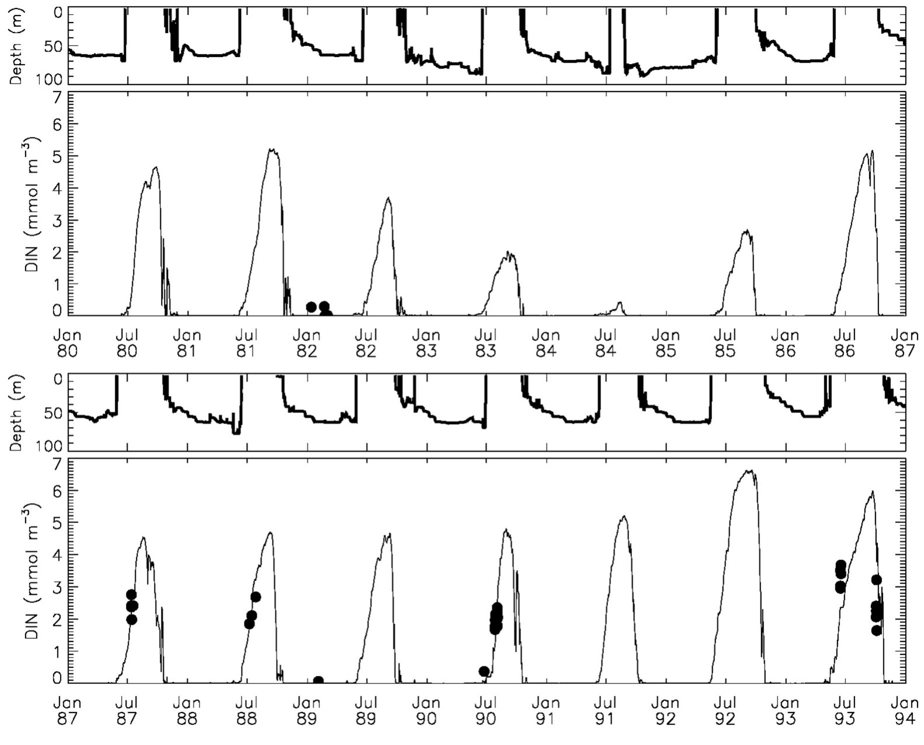

Figure 3.2.2: Modelled surface dissolved nitrate nitrogen (DIN) 1980-1994 compared with shipboard measurements (•). The upper panel in each series shows the depth at which the modeled concentrations equal 0.1 mmol m^{-3} (Hadfield & Sharples 1996).

The mixed layer depth in summer is 15–50 m deep and lies well within the euphotic zone that is about 50–80 m deep (Bradford & Chang 1987; Hadfield & Sharples 1996). In winter, the mixed layer can be very deep. It has been measured at 130 m in June and modeled to reach between 100 and 300 m in August, depending on the weather, in a setting where the euphotic zone is 40–75 m. During winter the progressive deepening of the mixed layer recharges the euphotic zone with dissolved inorganic nitrate and other nutrients. From limited data, nitrate nitrogen increases from less than 1 mmol m^{-3} (Chang & Bradford 1985) to 3 to more than 5 mmol m^{-3} (Bradford-Grieve et al. 1996) and could be as high as 7 mmol m^{-3} in some years (Hadfield & Sharples 1996).

Upwelling

Under intense upwelling, the supply of nutrients available to surface waters can be evaluated from the distribution of nitrate at 200 m depth at the edge of the continental shelf (Figure 3.2.3). Because New Zealand is located on the pole-ward boundary of the South Pacific gyre in the southwest Pacific Ocean nitrate concentrations at 200 m are low (4–10 mmol m^{-3}) (Ridgway et al. 2002) compared with many regions of the world (Conkright et al. 2002). The absolute concentrations of dissolved inorganic nutrients off WCSI depend on the properties of the South Pacific Central Water (SPCW) that has a typical mix of nutrients (Tomczak & Godfrey 1994). Nitrate and dissolved reactive silica are depleted by phytoplankton growth processes more or less together (Zentara & Kamykowski 1981) and iron is not limiting to phytoplankton growth (Boyd et al. 2004).

Field measurements of dissolved inorganic nutrient across the continental shelf and slope often show the impact of upwelling on near surface waters in cross-section. Upwelling is associated with an uplift of the isolines of nutrient concentrations against the continental slope in both winter (Bradford 1983; Chang & Bradford 1985) (see Figure 3.1.2 in Section 3.1) and summer (Bradford & Chang 1987). In some locations, nitrate was elevated to more than 10 mmol m^{-3} (Chang et al. 1989, 1992). Nevertheless, this uplift often did not reach the euphotic zone because a cap of low salinity water lay over the upwelled water at the surface inshore.

Upwelling has never been observed to impact conditions over the continental slope in winter where hoki spawn (Chang & Bradford 1985). It seems likely that the seasonal deepening of the mixed layer is potentially the most relevant physical process influencing the food environment of early stage hoki larvae.

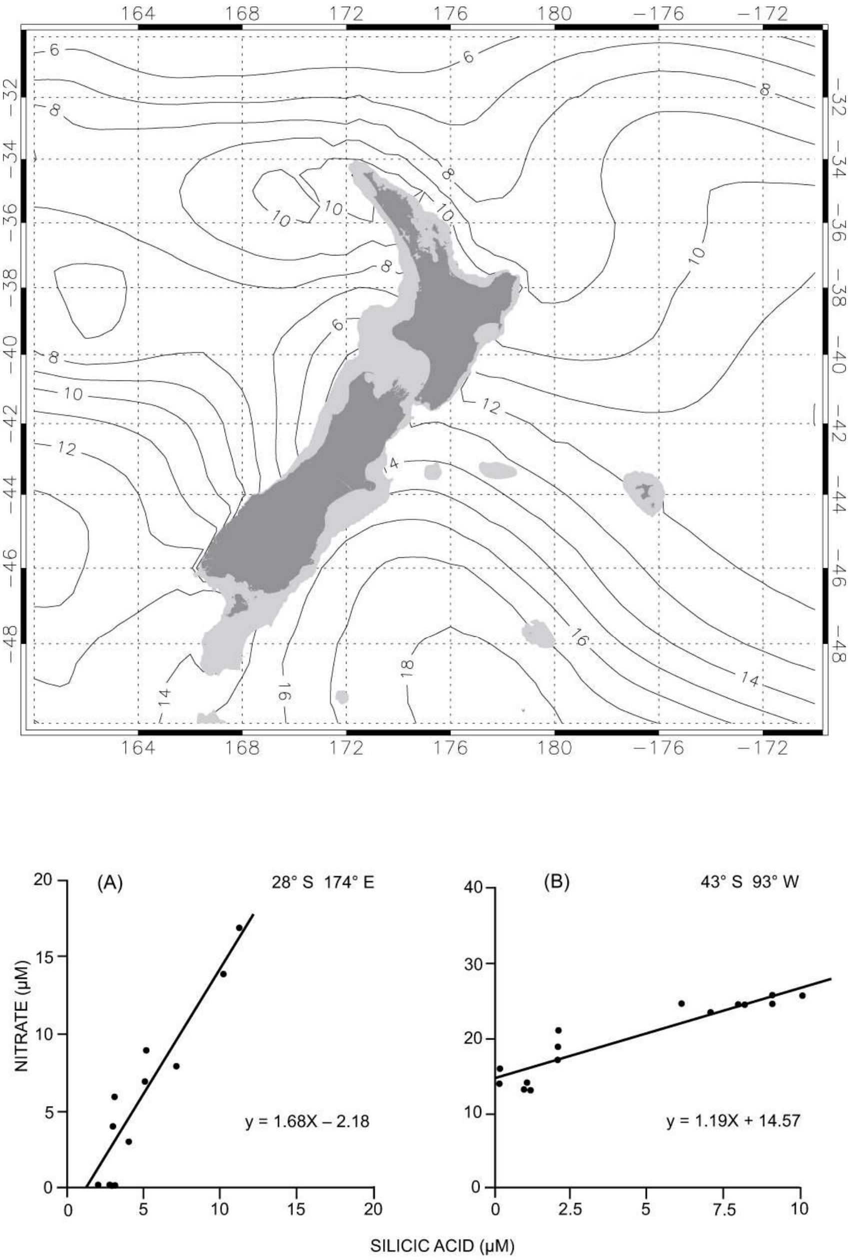

Figure 3.2.3: Upper panel: mean nitrate (mmol m^{-3}) at 200 m derived from a four-dimensional ocean interpolation system based on locally weighted least squares fitting (Ridgway et al, 2002). Lower Panel: scatter diagrams and regression lines of silicic acid vs nitrate concentration showing A, a near simultaneous decline of both silicic acid and nitrate to near zero values in South Pacific Central Water; B, the depletion of silicic acid when about 15 mmol m^{-3} nitrate remains in Subantarctic Surface Water (adapted from Zentara & Kamykowski 1981).

Between 1996 and 2002, water temperatures warmed off WCSI (Sutton et al. 2005) (see Section 3.1). This warming occurred at least down to 800 m and is probably a result of basin-scale oceanographic processes (Bowen et al. 2006). There is the possibility that this warming may have been accompanied by a lowering of nitrate concentrations. This proposition was examined using archived data.

The small amount of aggregated Tasman Sea data, sourced from several nations and stored by the National Oceanographic Data Center, are ambiguous about the relationship between temperature and nitrate between 250 and 800 m in the Tasman Sea west of New Zealand. Within data sets derived from individual countries, there is a negative correlation between temperature and nitrate (e.g. Figure 3.2.4 based on Australian data). Nevertheless, these data, collectively, suggest several unanswered questions about how conservative nitrate is relative to temperature in South Pacific Central Water below the seasonal thermocline and above Antarctic Intermediate Water, and about what processes, if any, could change the nitrate / temperature relationship geographically and / or with time.

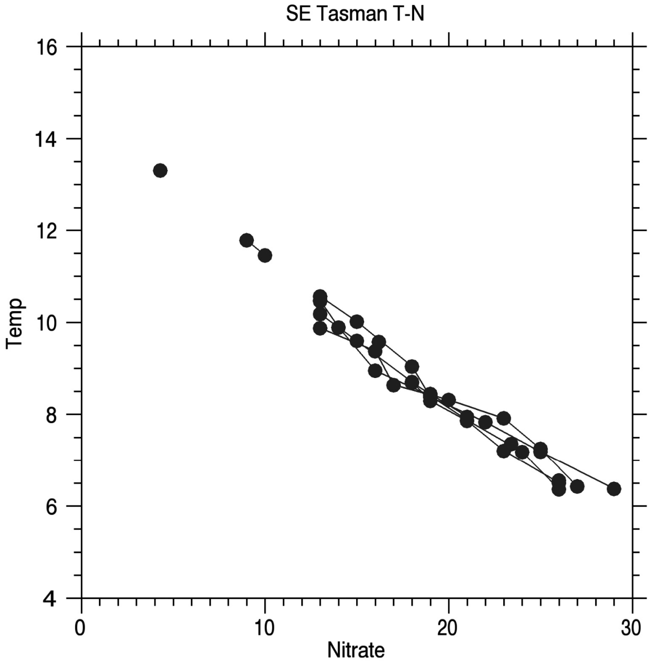

Figure 3.2.4: Temperature / nitrate relationship at Australian stations 250 – 800 m in Tasman Sea in general. Source is the National Oceanographic Data Center, US Department of Commerce, National Oceanographic and Atmospheric Administration (see Conkright et al. 2002).

Currently, we feel it is reasonable to assume that elevated temperatures in the Tasman Sea were accompanied by lowered nutrients, but ambiguity in historical data indicates that we should be cautious in using temperature as a proxy for nitrate in the sub-thermocline reservoir from which surface nutrient levels are recharged. These are obvious questions for future research.

3.2.4 Summary

Field measurements of surface solar irradiance off WCSI fit within calculated values assuming clear sky irradiance and expected cloud cover. Off WCSI, inshore coastal waters generally had the highest attenuation coefficients with K up to 0.29 m^{-1} in summer. The highest extinction coefficients, and by definition the shallowest euphotic depths, have been consistently measured in the near surface waters close to the coast. In winter, the depth of the euphotic zone ranged from a minimum of 21 m inshore to 73 m offshore. The same pattern was seen in summer with the depth of the euphotic zone 21–77 m. K_o can be predicted from chlorophyll *a* concentration, the extinction coefficient at 440 nm (yellow substance), and particulate matter concentrations at 10 m. Differences in the average irradiance, as a percent of subsurface irradiance, that a circulating cell in the mixed layer is subject to are due primarily to differences in mixed layer depth. Sites off WCSI ranged from 18% of subsurface irradiance off Hokitika to 63% in shallow mixed layers off Fiordland. It is noteworthy that the average irradiance that a circulating phytoplankton cell is subjected to was consistently higher in waters with the highest attenuation coefficients. The mixed layer may exceed the critical depth in winter.

Concentrations of dissolved inorganic nutrients in the sunlit surface waters off WCSI, are influenced river water, the seasonal cycle of surface mixing, and processes such as wind-driven upwelling of nutrient-rich waters. Freshwater input of nutrients is not very significant on this coast, given the degree of dilution (1% freshwater) that occurs. Deep winter mixing and upwelling of deep waters are more likely to be dominant in enhancing nutrient flux into surface waters. The mixed layer depth in winter is at a maximum parallel to the coast over the continental slope and appears to be related to the tongue of warm water that often extends down the coast from the north. The seasonal pattern of mixed-layer depth has been successfully modelled. The mixed layer depth in summer is 15–50 m and lies within the euphotic zone that is about 50–80 m. In winter the mixed layer has been measured at 130 m in June and modelled to reach 100–300 m in August, depending on the weather in a setting where the euphotic zone is 40–75 m. During winter, the progressive deepening of the mixed layer recharges the euphotic zone nitrate. From limited data nitrate nitrogen increases from less than 1 mmol m^{-3} to from 3 to more than 5 mmol m^{-3} and could be as high as 7 mmol m^{-3} in some years. Upwelling is associated with an uplift of the isolines of nutrient concentrations against the continental slope in both winter and summer and in some locations nitrate was elevated to more than 10 mmol m^{-3}. Sometimes this uplift does not reach the euphotic zone when a cap of dilute water lies over the upwelled water inshore. Upwelling has never been observed to impact conditions over the continental slope in winter where hoki spawn. It seems that the seasonal deepening of the mixed layer is likely to be the most relevant physical process influencing the food environment of early stage hoki larvae. In addition, there are questions about the impact of basin-scale oceanographic processes on WCSI coastal waters and the temporal and spatial relationships between nitrate and temperature below the seasonal thermocline and what this might mean for the winter surface mixed layer and the food of hoki larvae.

3.2.5 References

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3.3 Phytoplankton and primary production

Authors: Janet M. Bradford-Grieve, F. Hoe Chang

3.3.1 Introduction

In order to understand the components of phytoplankton production in the winter habitat of hoki larvae, off West Coast, South Island (WCSI), we first need to understand the seasonal and geographic variability of phytoplankton. In this chapter, the geographic area is divided into shelf waters (inshore) and waters beyond the shelf (offshore).

This chapter analyses the seasonal and spatial quantities of phytoplankton, its production, and the main factors that govern primary production off the WCSI placed in a Tasman Sea Province setting (Longhurst 1998). The original West Coast Ecosystem Programme focused on the hoki spawning ground and was aimed at understanding what was driving primary production, with emphasis on the winter period when hoki migrated to the region to breed. Although hoki larvae do not feed directly on phytoplankton (Murdoch & Quigley 1994) the items they feed on are directly or indirectly supported by phytoplankton. It is assumed that the composition of the phytoplankton populations, the structure of the food web and the environmental variables that support adequate primary production in winter, all impact on the survival of hoki larvae.

3.3.2 Phytoplankton assemblages

Phytoplankton populations off WCSI are best known in winter, spring and summer (Chang 1983, 1988; Chang & Gall 1998). Cyanobacteria (< 2 μm fraction) play a dominant role off WCSI. In winter, they make up about 50% of primary production and chlorophyll *a* and, in spring, 30% of primary production and 20% of chlorophyll *a* (Bradford-Grieve et al. 1997). In winter diatoms were generally most common in nearshore waters although they are generally not a dominant part of the phytoplankton (Chang 1983). Microflagellates were concentrated in the seaward part of the mixed coastal waters, landward of the 35 isohaline, and, although they were most abundant, their small size meant that they did not contribute as much to biomass as did dinoflagellates. Dinoflagellates (mostly non-thecate forms) were most plentiful offshore. In spring (Chang & Gall 1998), diatoms and microflagellates were more plentiful in terms of biomass than in winter and dinoflagellates least plentiful. In summer, dinoflagellates more completely dominated populations compared with winter (Chang 1988). In the water over the slope, the habitat of first feeding hoki larvae, phytoflagellates and dinoflagellates are quite plentiful whereas diatoms are variable (Chang 1983). Other attributes of phytoplankton populations: absolute biomass and the size of cells, appear to be more conspicuous characteristics of the hoki larva's environment.

3.3.3 Biomass

Chlorophyll is the most commonly used estimator of phytoplankton biomass, although the more labour-intensive method of cell counts, combined with cell volumes, have also been used (e.g. Chang & Bradford 1985; Bradford & Chang 1987). If chlorophyll is used as a proxy for biomass we have to take into account the variable ratio between carbon and chlorophyll. The ratio between phytoplankton carbon (C) and chlorophyll *a* (Chl) varied from less than 20 to more than100 in both winter (Figure 3.3.1F) and summer off WCSI. C:Chl ratios were less than 20 inshore in winter and at the bottom of the euphotic zone in both winter and summer, and were more than 80 offshore in winter and inshore in summer. The C:Chl ratio appears to be influenced by light adaptation, nutrient stress, physiological state, and species composition. Large C:Chl ratios reflected the dominance of a bloom of the dinoflagellate *Prorocentrum micans* inshore in summer (Chang 1988) (*P. micans* has a ratio of 120 at light saturation (Chan 1980)), and the generally higher proportion of dinoflagellates offshore in winter. At well-stratified stations in winter and summer, the C:Chl ratio decreased down the water column in a way that is consistent with low-light adaptation at the bottom of the photic zone and high light adaptation at the surface. In winter, where cold, high salinity, water had upwelled, the low C:Chl ratios are consistent with this water having upwelling from dimly-lit depths.

The greatest surface concentrations of chlorophyll *a* were generally found close to the coast in both winter and summer although the contrast was smaller in winter (Table 3.3.1; Figure 3.3.1E). The weighted average chlorophyll *a* in the euphotic zone had a similar pattern except that in winter a region of minimum concentrations was located over the slope parallel to the coast coincident with a maximum in the depth of the mixed layer. This region of minimum chlorophyll concentrations cannot be viewed simply as the dispersion of chlorophyll *a* down the deeply mixed water column. We note that the deeply mixed stations were dominated by dinoflagellates (Chang 1983) which have high C:Chl ratios. Thus the chlorophyll concentration, alone, in deeply mixed locations, dominated by dinoflagellates, in winter does not accurately reflect the phytoplankton biomass available to the prey of early stage hoki larvae.

The seasonal cycle of chlorophyll *a* offshore in the Tasman Sea usually reaches a minimum in summer and then increases in autumn (about May) with a slight dip in winter (July) before reaching a peak in spring (September October) (Figure 3.3.2) (see also Murphy et al. 2001). Over the shelf, nearer shore, based on limited data, the seasonal cycle is less clear. Usually, WCSI inshore water has higher chlorophyll *a* than offshore water but there is a great deal more variability there than in offshore waters. The high variability in inshore waters is probably due to periodic addition of nutrients from upwelling and possibly from freshwater runoff from the land.

Over the continental slope (Figure 3.3.2), there is less variability than in inshore waters and there is slightly more chlorophyll *a* in late winter and spring compared to summer and autumn and a small peak is evident in early winter (June). This small peak is probably important to hoki larvae. A study of the impact of mixed layers of various depths in June to July (Bradford-Grieve et al. 1996) shows that where mixing was greater than 150 m, nitrate was more than 3 µM although surface chlorophyll *a* remained relatively low (0.46–0.53 mg m^{-3}) apparently due to zooplankton grazing. There was clearly greatly increased secondary production because copepod nauplii and copepods of the genus *Calocalanus*, the food of hoki larvae, were in much larger concentrations than in shallow mixed layers.

Biomass measured as chlorophyll *a* can be broken down into the sizes of the cells involved. Chang (1988) recognised that very small phytoplankton (less than 5 µm) comprised a large proportion of total chlorophyll *a* off WCSI. In summer, in offshore water, the less than 5 µm size fraction was 40–90% of total chlorophyll *a,* whereas the 20–200 µm fraction was most plentiful inshore and represented 10–25% of total chlorophyll *a* (Chang 1988). On a later occasion, Bradford-Grieve et al. (1997), using a different range of size fractions, showed that, 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 (Table 3.3.2). 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 (Bradford-Grieve et al. 1996) where hoki larvae first feed.

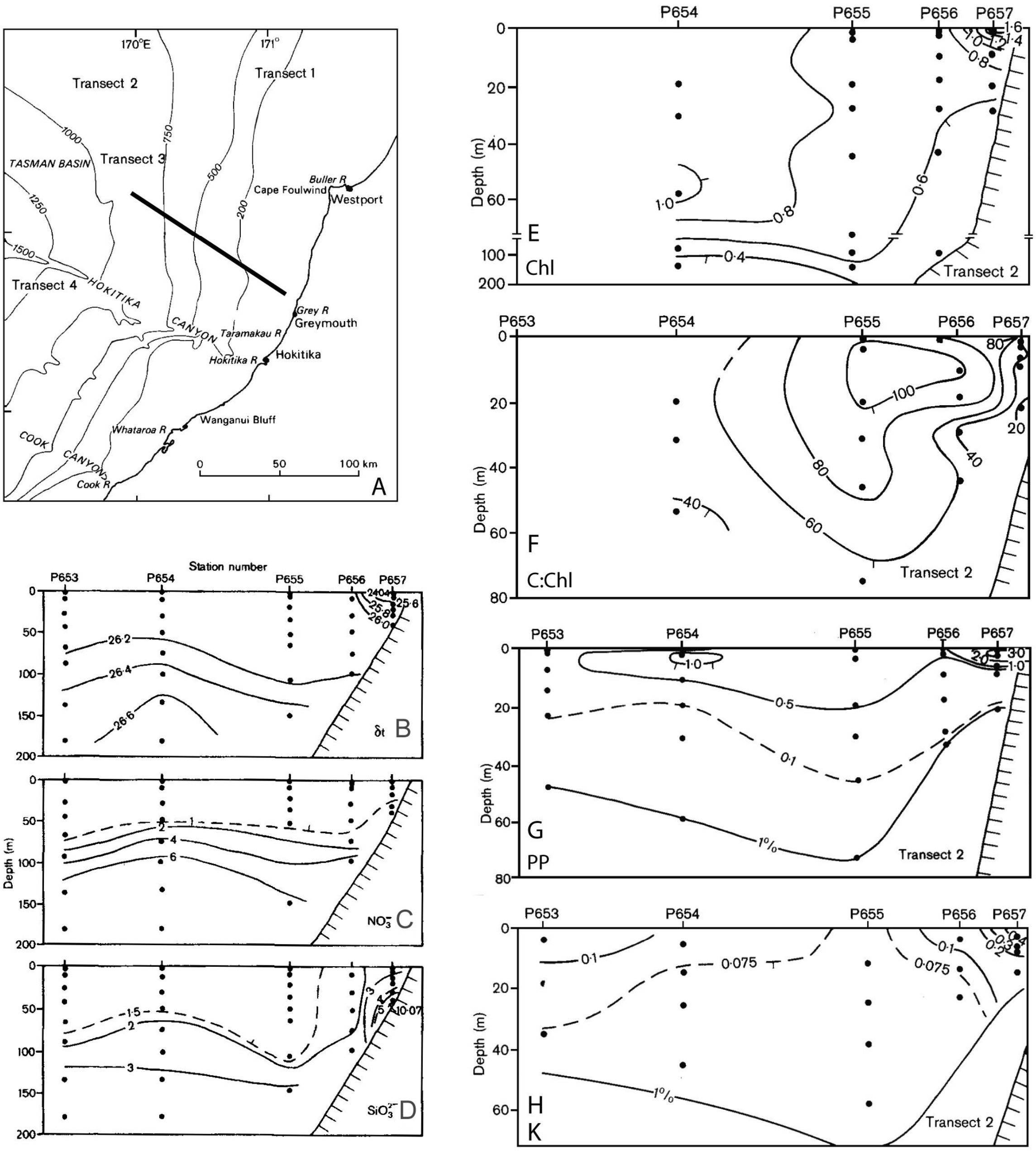

Figure 3.3.1: Water properties along a winter transect off Hokitika, Westland. (A), locality diagram; (B), density (g l^{-1}); (C), nitrate nitrogen (mmol m^{-3}); (D), reactive silicate (mmol m^{-3}); (E), chlorophyll *a* (mg m^{-3}); (F), carbon : chlorophyll ratio; (G), primary production (mg C mg Chla^{-1} h^{-1}); (H), extinction coefficient (m^{-1}) (Chang & Bradford 1985).

Table 3.3.1: Summary of phytoplankton and environmental parameters in winter and summer off WCSI (Chang & Bradford 1985; Bradford & Chang 1987). 1% light, depth where 1% of submarine surface irradiance is recorded (approximately the bottom of the euphotic zone); I_o, average photosynthetic irradiance; *K*, extinction coefficient for the euphotic zone; P^B, production per unit chlorophyll *a*; PC, phytoplankton carbon derived from cell volumes; Z_m, depth of mixing; μ, carbon-specific growth rates; Ψ, light utilisation index.

Season				PC	Chlorophyll *a*		C^{14} uptake					
Water type	1% light (m)	Z_m (m)	*K*	Integrated (mg m^{-2})	Surface (mg m^{-3})	Integrated (mg m^{-2})	Surface (mgC m^{-3} h^{-1})	Integrated (mgC m^{-2} h^{-1})	Daily (mgC m^{-2} d^{-1})	P^B max	μ max Doublings d^{-1}	Ψ (gC(gChl)$^{-1}$ E^{-1} m^2)
WINTER												
Inshore	21-33	1-40	0.135-0.202	720-1414	0.8-1.4	22-30	0.59-2.21	17.9-23.0	108-147	1.7-2.2	0.23-0.37	0.21-0.42
Upwelling	33	14	0.139	795	0.9	24	0.24	6.9	47	1.0	0.33	0.20
Offshore	34-73	10-130	0.062-0.112	1582-4473	0.6-1.3	29-52	0.07-0.67	5.3-21.3	55-152	0.7-1.8	0.07-0.57	0.11-0.71
SUMMER												
Inshore	21-51	3-18	0.090-0.219	2941-8818	1.7-8.8	15-84	5.43-35.73	87.5-317.5	662-4885	3.5-10.7	0.27-0.96	1.41-3.48
Upwelling	16	0	0.288	1180	2.4	30	4.42	24.2	270	1.9	0.45	1.89
Offshore	35-77	10-35	0.060-0.132	338-2054	0.3-1.3	19-32	0.14-1.91	143-64.2	110-401	1.4-5.6	0.48-1.85	0.12-0.74

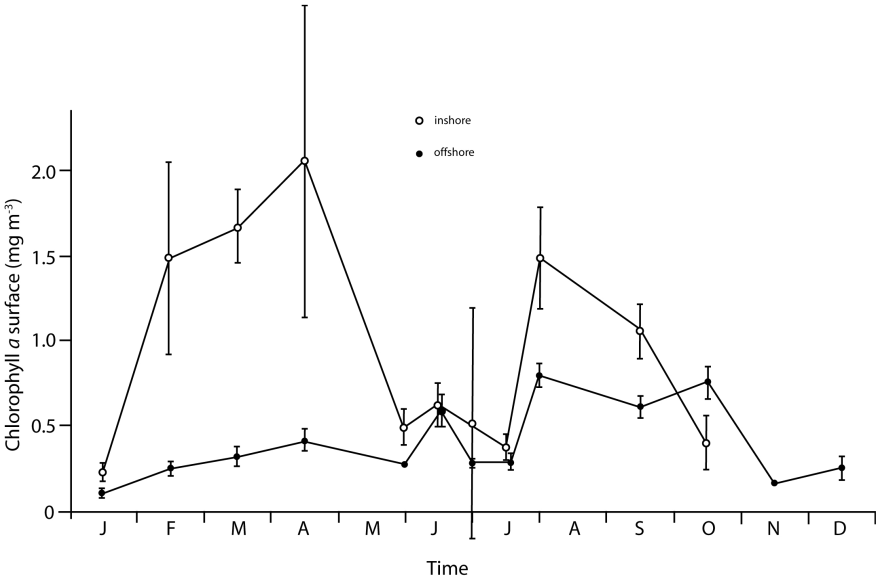

Figure 3.3.2: The annual cycle of chlorophyll *a* at the sea surface: comparison of inshore shelf and offshore water off WCSI constructed from all field data (Bradford 1980; Chang & Bradford 1985; Bradford & Chang 1987; Bradford et al. 1998; Chang & Gall 1998). All data are combined by month and expressed as a mean ± 1 S.E.

Table 3.3.2: Comparison of average total integrated water column (to 1% light) potential primary production and chlorophyll, and average percentage make-up of integrated potential primary production and chlorophyll biomass (to 1% light) by size fraction, winter and spring off WCSI (Bradford-Grieve et al. 1997).

		Potential primary production				**Chlorophyll *a***			
Location	**Season**	**Integrated total mg C m^{-2} d^{-1}**	**<2 μm**	**2-20 μm**	**20-200 μm**	**Integrated total mg m^{-2}**	**<2 μm**	**2-20 μm**	**20-200 μm**
Offshore	Winter	193	53%	32%	15%	18	42%	36%	22%
Offshore	Spring	633	36%	14%	50%	30	24%	30%	46%
Inshore	Winter	70	43%	34%	23%	9	44%	35%	21%
Inshore	Spring	237	15%	23%	62%	21	18%	28%	54%

3.3.4 Primary productivity

Primary production at the surface, in both winter and summer, followed trends similar to chlorophyll *a* and was generally greatest adjacent to the coast (Table 3.3.1; Figure 3.3.1G). In winter Bradford-Grieve et al. (1997) showed that the less than 2 µm fraction accounted for more than 50% of the total daily integrated winter primary production and about 40% in spring in offshore waters, but formed a smaller proportion in inshore waters (Table 3.3.2). The less than 2 plus the 2–20 µm fractions make up the bulk of winter and summer production, but in spring these two fractions make up about half of the integrated production (Chang 1988; Bradford-Grieve et al. 1997). Therefore, small cells in the phytoplankton populations make an important, if variable, contribution to primary production in this region and are particularly important in winter.

When production per unit chlorophyll *a* (P^B) is plotted against light it is clear that there is a variable response of phytoplankton to light down the water column (Figure 3.3.3). The initial slope (α) of the water column P^B *versus* light (I) curves was similar in the northern part of the

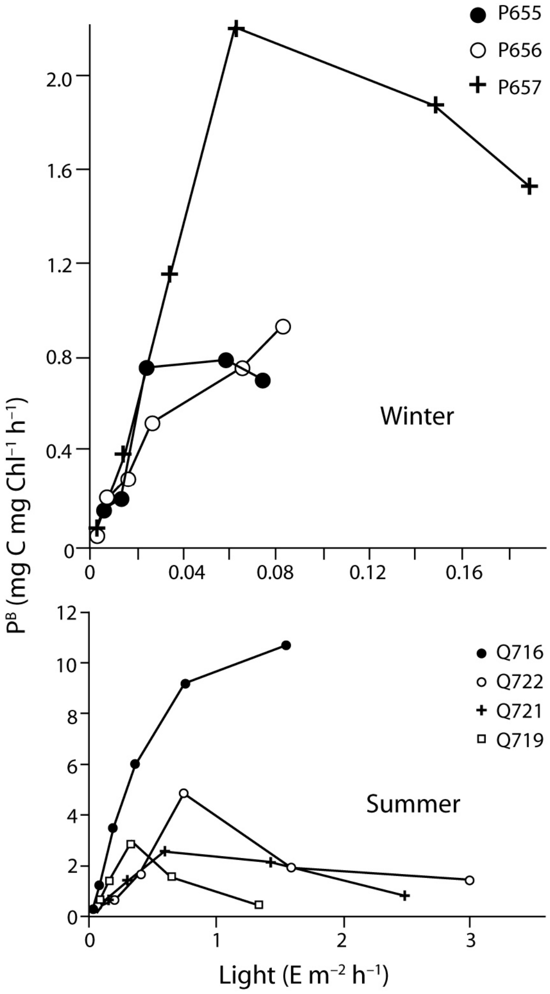

Figure 3.3.3: Production per unit chlorophyll (P^B) (mg C mg Chla^{-1} h^{-1}) plotted against light (I) (E m^{-2} h^{-1}) for each sampling depth for the a transect off Greymouth in winter and summer (from Chang & Bradford 1985; Bradford & Chang 1987).

study area but differed considerably among the sampling locations in regions to the south in both winter and summer. Photo-inhibition of photosynthesis was apparently observed over a variety of light intensities less than 0.04 μmol photon m^{-2} s^{-1} in winter and less than 0.30 μmol photon m^{-2} s^{-1} in summer, an order of magnitude difference.

Phytoplankton productivity as a function of biomass is regulated by various physical and biological parameters such as light, light history, physiological state, species composition, cell size, temperature, and nutrients. But most of the parameters known to regulate P^B did not have an obvious measured effect off WCSI, with the exception of light.

Light was the only parameter clearly related to P^B (Chang & Bradford 1985; Bradford & Chang 1987). Integrated water column P^B (production integrated over the euphotic zone divided by chlorophyll *a* integrated over the euphotic zone) plotted against the average measured irradiance between 1100 and 1500 h, showed two general trends (Figure 3.3.4). One relationship was for stations with shallow mixed layers, dominated by *Prorocentrum micans*, with most of the phytoplankton biomass 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 included the general winter and summer populations ($P^B = 0.38I - 0.02$) where the vertical structure of phytoplankton did not have large contrasts and only 51% of the variance in P^B was explained by variance in light.

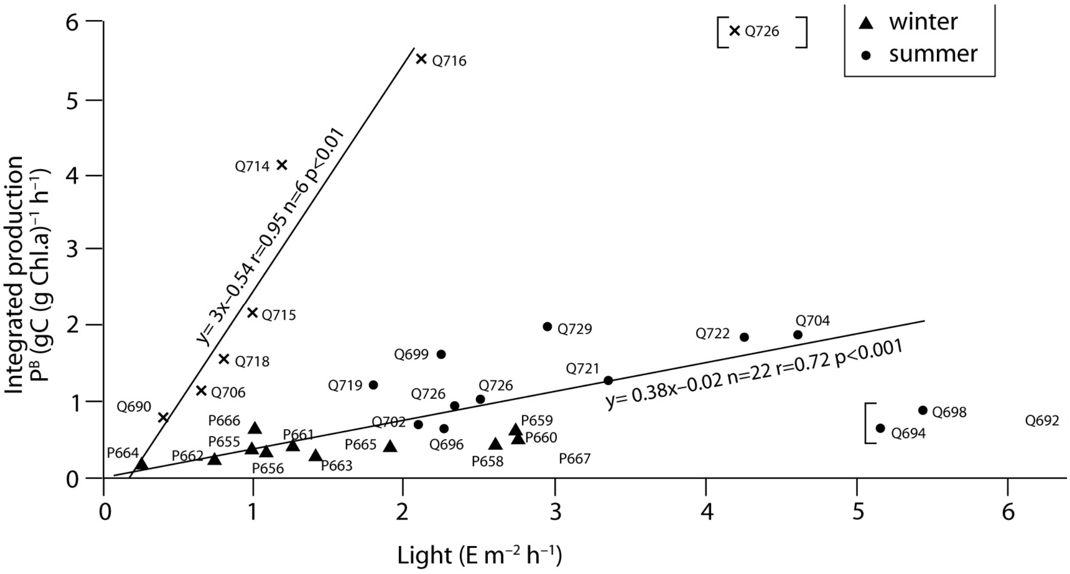

Figure 3.3.4: Production per unit chlorophyll a (P^B) integrated over the euphotic zone (gC (g Chl *a*)$^{-1}$ h^{-1}) plotted against incident solar irradiance (I) (E m^{-2} h^{-1}) (from Bradford & Chang 1987).

One of the factors contributing to the scatter around the relationship between P^B and light, illustrated in Figure 3.3.4, will be the fact that the availability of light to phytoplankton in the photic zone is controlled, on seasonal scales, by the depth of the surface mixed layer. The photic zone, the depth to which light penetrates oceanic water off WCSI in winter, is about 75 m (Chang & Bradford 1985). When the mixed layer is greater than the depth of the photic zone in winter, Sverdup's concept of "critical depth" is relevant: for net phytoplankton growth to occur the mixed layer depth has to be less than the critical depth where total vertically integrated phytoplankton production equals total losses due to respiration. At 42°S the critical depth may vary from 70 to 260 m in June, a range which depends on incident radiation, (calculated using the critical depth formulation $1/K \; Z_{CR}(1-e^{-kz_{CR}}) = I_c/I_o$, where the compensation depth $I_c = 0.6$ mol photons m^{-2} d^{-1} (*see* Siegel et al. 2002 for Sverdrup's value), $K = 0.07$ m^{-1} (see Chang & Bradford 1985 for June), and I_o is the flux of incident radiation. The trajectories of the critical depth and the mixed layer depth show that the minimum in the critical depth in June (the month when the sun is lowest in the sky) and the maximum in the mixed layer depth (August-September) do not coincide, often leaving a window in July when the mixed layer is much shallower than the critical depth so that net phytoplankton growth may occur if sufficient nutrients are available. This window may be necessary for adequate concentrations of small copepods to develop in the habitat where hoki larvae first feed.

Although light is the most obvious controller of primary production, as measured in the field, detailed experiments and modelling demonstrated the role of nutrients, physical water properties and grazing on primary productivity.

3.3.5 Nitrogen utilization

In coastal and ocean waters, nitrogen (N) has long been identified as the primary macro-nutrient limiting phytoplankton production. The role of N in governing primary production was evaluated in the winters of 1987 and 1988 and the summer of 1989 (Chang et al. 1989, 1992, 1995).

The concept of "new" and "regenerated" production, based on the assimilation of nitrate-nitrogen (NO_3) and ammonia-nitrogen (NH_4), respectively, was introduced by Dugdale and Goering (1967). "New" production is dependent on the new input of nutrients in the form of NO_3 from seasonal mixing, upwelling, terrestrial run off, and advection. Regeneration of N from the breakdown of organic matter and animal excretion into NH_4 and urea provides the balance of the N pool that supports primary production. ^{15}N-enriched stable isotopes of NO_3, NH_4, and urea were used to quantify "new" and "regenerated" production by the entire phytoplankton assemblage and by each size fraction (Chang et al. 1989, 1992, 1995), making the assumption that all NO_3 uptake is "new".

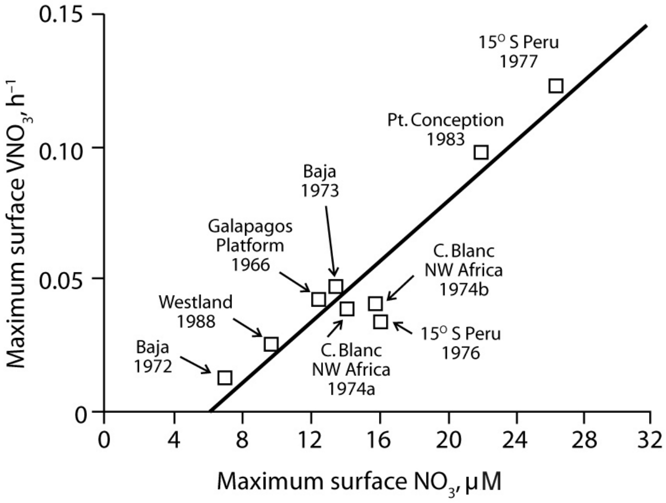

Figure 3.3.5: Regression of maximum surface nitrate uptake VNO_3 h^{-1} versus maximum surface nitrate (NO_3 µM) for coastal upwelling regions (Dugdale & Wilkerson 1992; Chang et al. 1992).

These investigations showed that in winter, NO_3 was the most important source of N available, off WCSI (Chang et al. 1989, 1992). At that time, ambient surface NO_3 concentrations were generally quite high, particularly in the winter of 1988, when upwelling was observed (greater than 10 µM). Specific NO_3 uptake (V_{NO3}) and the ambient surface NO_3 concentrations in the WCSI upwelling region are consistent with observations from other upwelling regions (Dugdale & Wilkerson 1992) (Figure 3.3.5). Upwelled NO_3 close to shore is important for older hoki larvae that have migrated shorewards to feed on the resulting enhanced secondary production. First feeding hoki larvae, in contrast, rely on the NO_3 that is entrained from below as the mixed layer deepens during autumn and winter over the slope.

In both winters studied, more than 55% of mean total N-uptake ($\Sigma\rho N$) was accounted for by NO_3. In summer, when ambient NO_3 concentrations were low, "new" production was also low, and accounted for about 19% of $\Sigma\rho N$ (Chang et al. 1995). At this time, in offshore waters, NH_4 and urea comprised more than 80% of $\Sigma\rho N$, showing that "regenerated" production was quantitatively more important than "new" production in summer. Most of the N is taken up by autotrophs, although some NH_4 and urea can be utilised by bacteria (Joergensen et al. 1999).

Nitrogen uptake by three size classes of phytoplankton had different characteristics. The 20–200 µm size fraction was dominant in the uptake of NO_3 (greater than10 µM) that had upwelled in the winter of 1988 (Table 3.3.3) (Chang et al. 1992). Most of this uptake was light-mediated. The bulk of "new" production in inshore waters was accounted for at high levels of irradiance. At lower irradiances this large size class responded less to high ambient NO_3 (Chang et al. 1992).

Uptake of N by the 2–20 µm size class was maintained at a level of about one third of $\Sigma\rho N$ in both winter and summer and was less sensitive to changes in the light environment. In winter, NO_3 uptake by this size class was more or less the same at 100, 40, and 7% irradiance offshore (Table 3.3.3) (Chang et al. 1992) showing that this size class takes up N in the dark as well as the light.

Uptake of N by the less than 2 µm size class, as a percentage of $\Sigma\rho N$, was greatest in summer (more than 52%), in offshore waters where NO_3 was almost completely depleted. They were the major users of "regenerated" N, accounting for more than 60% of $\Sigma\rho N$ in summer (Chang et al. 1989, 1992, 1995). In winter offshore waters, NH_4 uptake was not very light sensitive and was, on average, 25% of $\Sigma\rho N$ near the surface and 50% at 7% irradiance (Table 3.3.3) (Chang et al. 1992). In summer this size fraction was the least affected by the extremely low ambient nutrient concentrations.

All this work on nitrogen uptake shows that nitrogen is an important limiting factor where the form that nitrogen occurs in (NO_3, NH_4 or urea) interacts with the phytoplankton taxa present and available light. In N-depleted surface waters it is clear that phytoplankton populations were under nutrient stress in summer (Chang et al. 1995). Surprisingly, in winter, all three phytoplankton size classes showed a strong preference for NH_4 (Chang et al. 1989, 1992) despite this being the season when deeper mixing brings more NO_3 into surface waters.

Table 3.3.3: Winter mean absolute and percentage nitrogen uptake rates (ρ) (μmol m^{-3} h^{-1}) of NH_4^+, NO_3^-, and urea for the three size classes (< 200, < 20, < 2 μm), at three irradiances (Chang et al. 1992). % I_0, percentage of surface irradiance.

	ρNH_4^+			ρ NO_3^-			ρUrea		
%I_0	20-200 μm	<2-20 μm	< 2 μm	20-200 μm	<2-20 μm	< 2 μm	20-200 μm	<2-20 μm	< 2 μm
					Absolute				
Inshore									
100	0.70	0.28	0.16	6.74	1.99	1.56	0.22	0.23	0.07
40	0.39	1.19	0.50	0.51	0.47	0.22	0.08	0.27	0.08
7	0.43	0.18	0.08	0.98	0.43	0.13	0.29		0.12
Offshore									
100	0.21	0.41	0.21	0.68	0.23	1.06	0.08	0.04	0.13
40	0.17	0.22	0.23	0.95	0.83		0.20		0.10
7	0.16	0.12	0.29	0.37	1.05		0.44	0.08	0.10
					Percentage				
Inshore									
100	61	15	14	65	20	15	42	45	13
40	19	57	24	52	33	15	18	72	10
7	63	25	12	66	24	10	72		28
Offshore									
100	25	50	25	34	12	54	34	13	53
40	28	35	37	59	41		69		31
7	29	21	50	26	74		72	11	17

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 mg m^{-3} suggesting that the grazing term needs to be adjusted. The model typically produces a pronounced sub-surface 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).

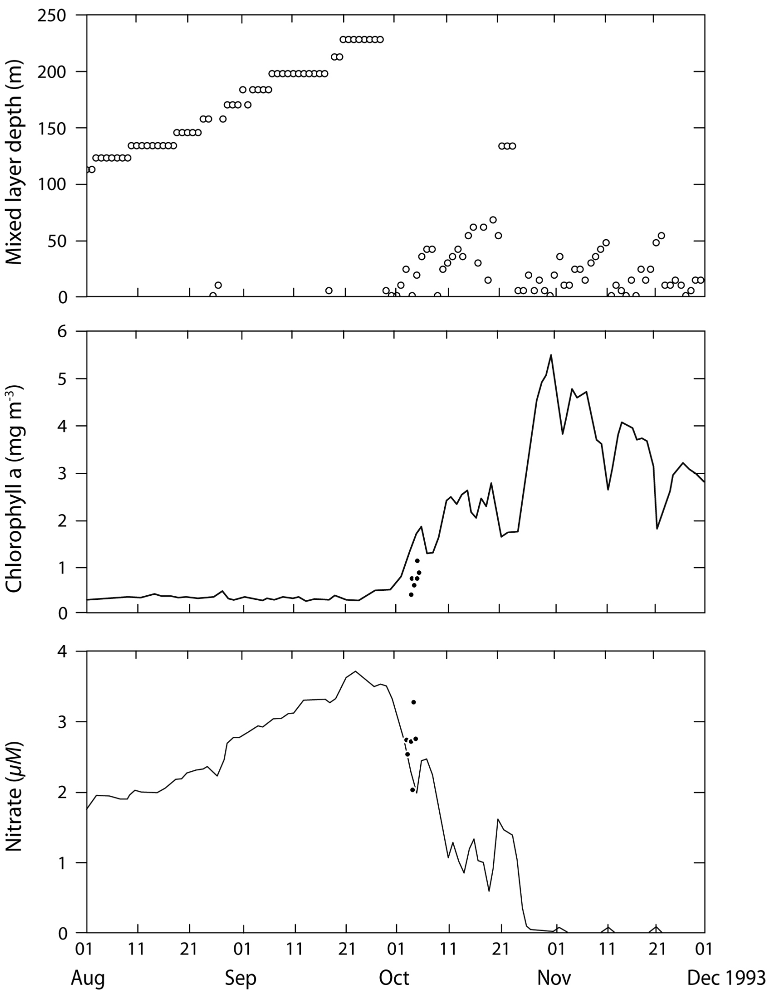

Figure 3.3.6: Modelled mixed layer depth, surface chlorophyll and nitrate concentrations August – November 1993. Filled dots on lower two panels are observations. Note that the grazing impact rate used in this model run gives unrealistically high chlorophyll concentrations. (after Hadfield & Sharples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

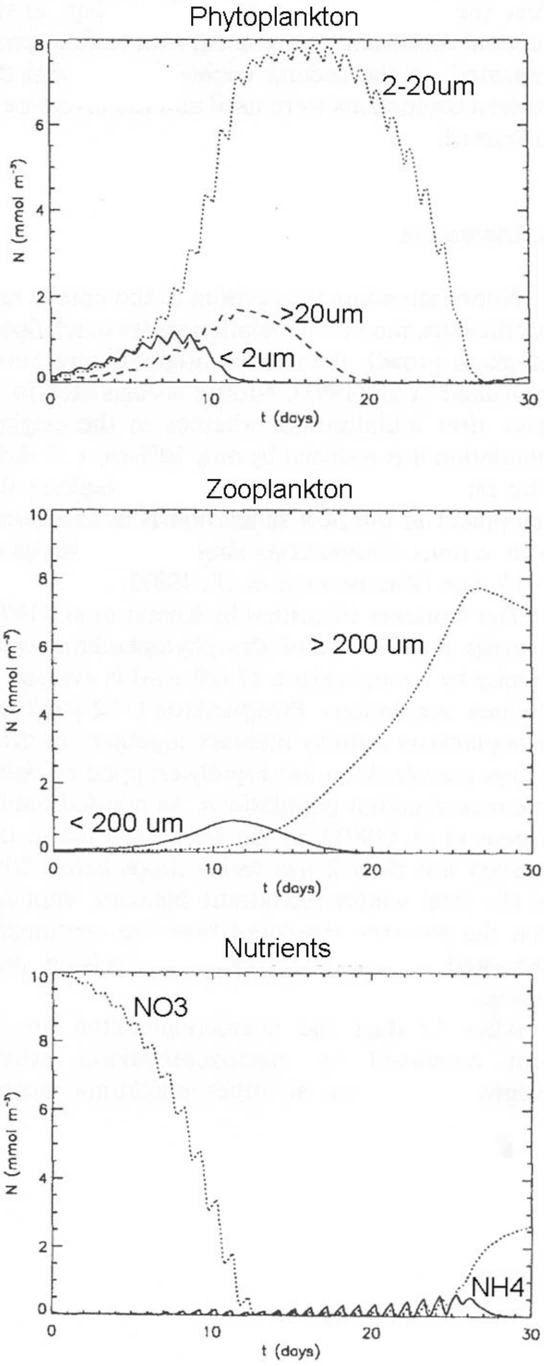

Figure 3.3.7: Model results in the mixed layer for three phytoplankton size fractions, two zooplankton size fractions and nitrate- and ammonia-nitrogen, for a 30 day period after a mixing event (after Hadfield et al. 1995). um = μm

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 NO_3-N was the most important source of N available when more than 55% of mean total N-uptake ($\Sigma\rho N$) 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 $\Sigma\rho N$ 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

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3.4 Microbial food web

Authors: Julie Hall, Mark James

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 phosphorcum* were also isolated.

Bacterial numbers in the WCSI region ranged from 1.1 to 27 x10^{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).

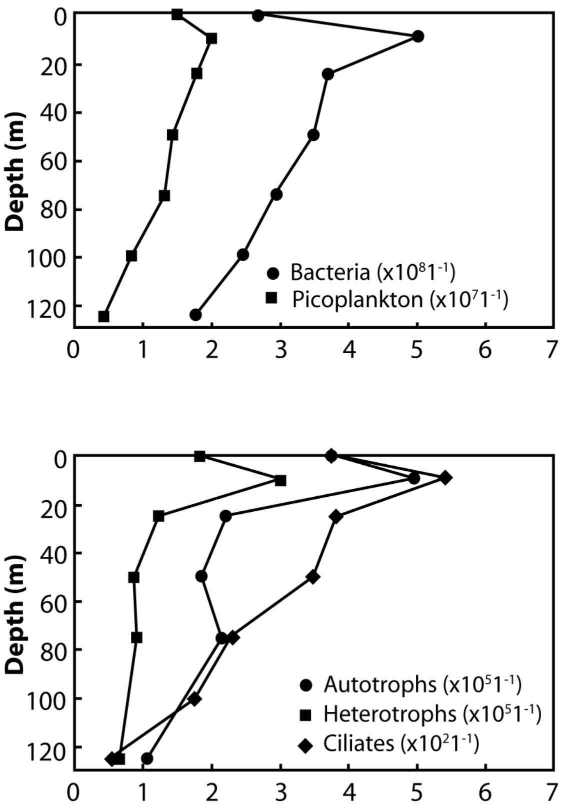

Figure 3.4.1: Profile of bacteria, picophytoplankton, flagellate and non-loricate ciliate numbers over the continental slope off Westland (from Hall et al. 1993). Note that greatest concentrations are found in the euphotic zone.

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 Chrysomonidida, Euglenida, Cryptomonadida and the Dinophycae 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 10^6 cells l^{-1} and in spring 2.2 and 0.69 x 10^6 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 μm^3 for ANF and 7.6 μm^3 for HNF and, in spring, of 47.5 and 76 μm^3 respectively.

The distribution of both HNF and ANF was closely related to the distribution of urea, NH_4, 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, bactivorous, 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 temperature 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 µg C l^{-1} in winter and 0.62 –15.37 µg 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

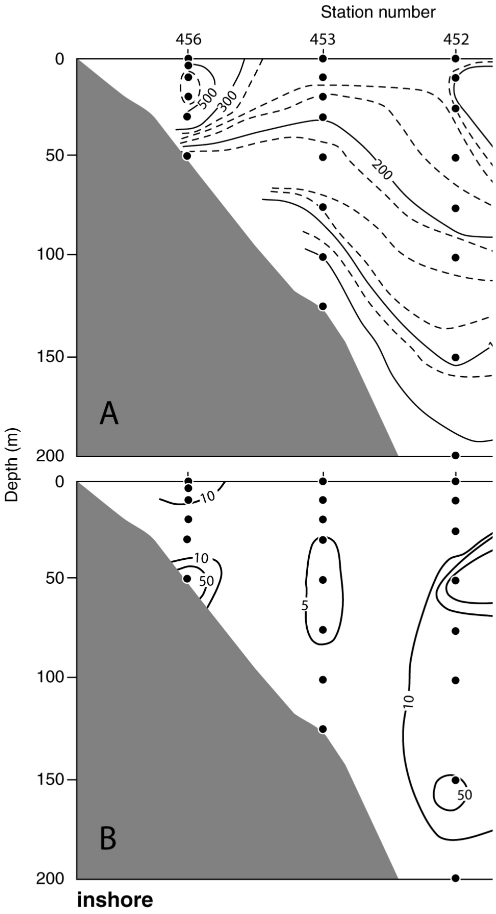

Figure 3.4.2: Vertical profiles of ciliate number off Westland, June/July 1990: (A) non-loricate ciliate abundance (no. l^{-1}) and (B) tintinnid abundance (no. l^{-1}) off Hokitika (from James & Hall 1995). Note that largest concentrations of ciliates occur inshore in water that has the greatest influence 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 $\mu g\ l^{-1}$. 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 µm 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 µm) and picophytoplankton (1.0 µm) 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 *a*) removed Percentage by microzooplankton grazing	% Production Percentage removed by Microzooplankton 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 µl $ind^{-1}h^{-1}$ (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 nl ind^{-1} h^{-1} for 0.5 µm and 1.0 µm beads respectively. These compare to clearance rates of 1.8 and 0.9 nl ind^{-1} 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 µl $ind^{-1}h^{-1}$ for bacteria sized fluorescent microspheres, 0.05–0.58 µl $ind^{-1}h^{-1}$ for labeled bacteria but 0.39–1.65 µl $ind^{-1}h^{-1}$ for picophytoplankton sized particles (James & Hall 1998). Larger taxa such as *Laboea* and tinnids had specific clearance rates up to 9.0 µl $ind^{-1}h^{-1}$. 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 $NH4^+$. 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.

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3.5 Zooplankton

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3.5.1 Introduction

Zooplankton animals are an essential link between the microscopic primary and secondary producers and the rest of the food web. They are a food source for fish larvae, adult fish, larger carnivorous zooplankton, and large filter-feeding marine animals. Not only are the large zooplankton important to the animals that feed on them but they potentially control the biomass of phytoplankton and microzoopankton through their feeding activities. Zooplankton also contribute to the recycling of organic and inorganic compounds through their metabolic activities, excretion and respiration and the transfer of particles to the sea floor by means of their faecal pellets and carcasses when they die.

This chapter reviews the characteristics of zooplankton communities in waters off West Coast, South Island (WCSI) emphasizing aspects relevant to early stage hoki larvae. Species composition, abundance, biomass and the trophic role of zooplankton are described. The vertical distribution of zooplankton communities and the physical processes that affect them are also discussed.

3.5.2 Species composition, distribution and biomass

Zooplankton species of continental shelf and slope waters off WCSI are typical of New Zealand near-surface coastal waters (Bradford 1985). Species whose densities are greatest nearest to shore are the copepods (*Acartia ensifer, Centropages aucklandicus, Paracalanus* c.f. *indicus, Euterpina acutifrons*) and the euphausiid *Nyctiphanes australis.* Other species have maximum concentrations over the outer shelf or over the continental slope: copepods (*Oithona similis, Clausocalanus ingens, C. pergens, Mesocalanus tenuicornis, Calocalanus sp., Mecynocera clausi*), appendicularia, amphipods and chaetognaths. Here we illustrate the different types of distribution with those groups that are important in the diet of early hoki larvae or are potential predators (Figure 3.5.1). Winter distributions are mostly similar to summer distributions except for some taxa (*Oithona* and Chaetognatha) whose main centre of distribution in summer is further inshore.

The herbivorous component of the zooplankton community is dominated by the copepods *Calocalanus minutus, Clausocalanus ingens, Clausocalanus jobei, Paracalanus indicus*; the larvacean *Oikopleura*, and the salps *Salpa fusiformis* and *Thalia democratica* (Bradford 1985). Common omnivorous species are the copepods *Acartia ensifera*, *Centropages aucklandicus* and *Oithona similis*, and the euphausiid *Nyctiphanes australis* (Bradford 1985). Common carnivores are the chaetognath *Serratosagitta tasmanica* and the amphipod *Themisto gaudichaudii*. The herbivores *Calocalanus, Paracalanus* and *Clausocalanus* are important items in the diet of early hoki larvae (Murdoch & Quigley 1994).

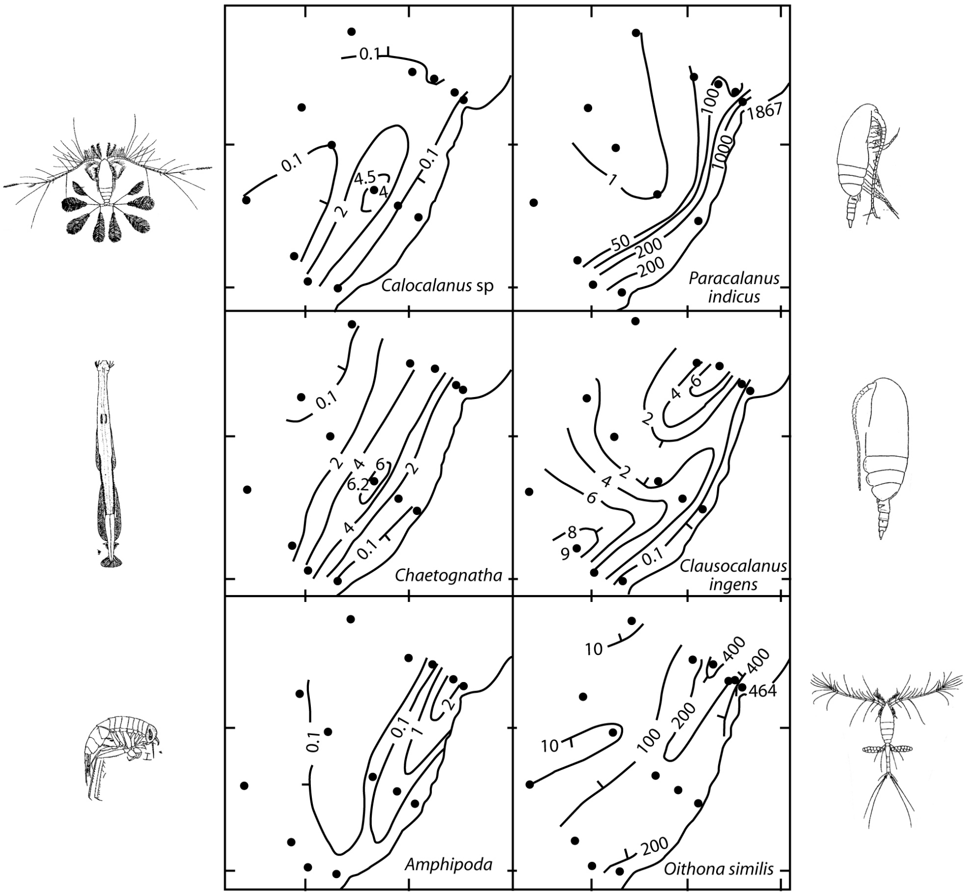

Figure 3.5.1: Winter distribution (numbers m^{-3}) off Westland of *Calocalanus* sp., *Paracalanus indicus*, Chaetognatha, *Clausocalanus ingens*, Amphipoda and *Oithona similis* (Bradford 1985).

The importance of small copepods such as *Calocalanus* (approximately 0.8 mm total length) is underestimated when sampled by a 200 µm mesh zooplankton net as maximum concentration of only 4 m^{-3} were found using such a net (Bradford 1985). When a 39 µm mesh net was used in conjunction with a plankton pump, very much higher densities of *Calocalanus* were revealed (100–600 m^{-3}) (Bradford-Grieve et al. 1996). It is clear that such small copepods more often than not pass through a 200 µm mesh net.

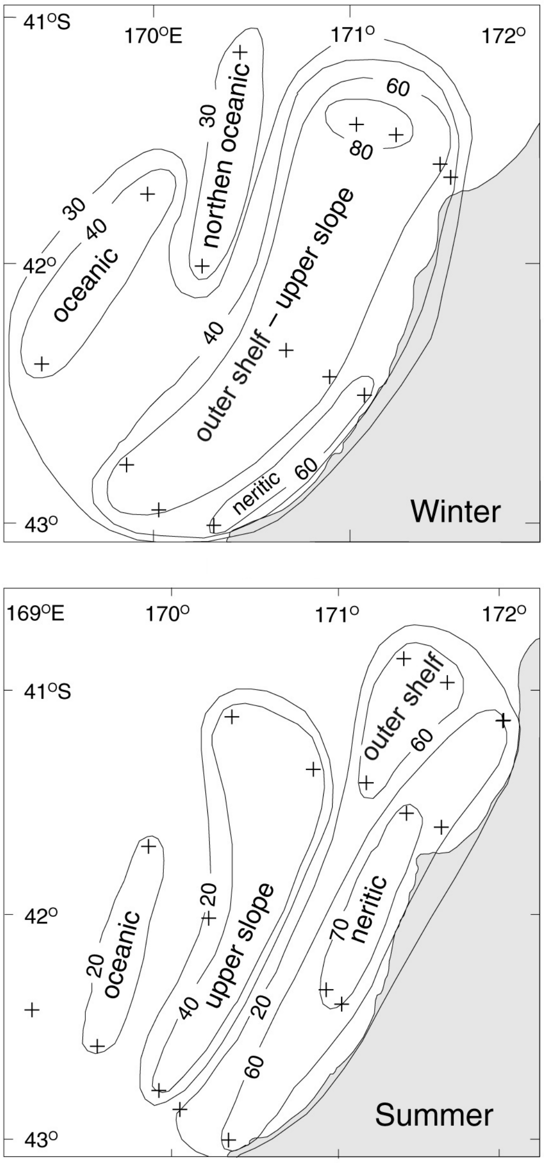

Figure 3.5.2: Geographic representation of the station similarities and their names in winter (June 1979) and summer (February 1982) (Bradford 1985).

Zooplankton populations off the WCSI can be sub-divided into nearshore (neritic), outer shelf / upper slope, and oceanic populations during both winter and summer (Bradford 1985; Bradford-Grieve et al. 1996) (Figure 3.5.2). Of particular interest is the outer shelf / upper slope population in winter as this is the environment in which hoki spawn their eggs. The inflow of oceanic subtropical water from the north along the upper continental slope in winter and *in situ* processes resulting from the deepening of the mixed layer (Bradford-Grieve et al. 1996) appear to result in an identifiable zooplankton population there in outer shelf / upper slope region. Copepod nauplii and copepodites, several genera of protozoa, and several copepod genera (*Oithona, Calocalanus, Microsetella, Clausocalanus, Mesocalanus* and *Paracalanus*) typify the outer shelf / upper slope community (Fig 3.5.2, top panel).

The zooplankton wet weight biomass in the surface 200 m in the oceanic Tasman Sea is less than 25 mg m^{-3} (Bradford 1980) and does not vary much seasonally (Figure 3.5.3). This relatively low background biomass lies within the range considered typical for subtropical waters (0–50 mg m^{-3}) (Heinrich 1962; Tranter 1962). The lack of a seasonal cycle and conspicuous offset in peak biomasses of oceanic zooplankton and phytoplankton suggests there is little decoupling of the phytoplankton and zooplankton cycles in WCSI offshore waters.

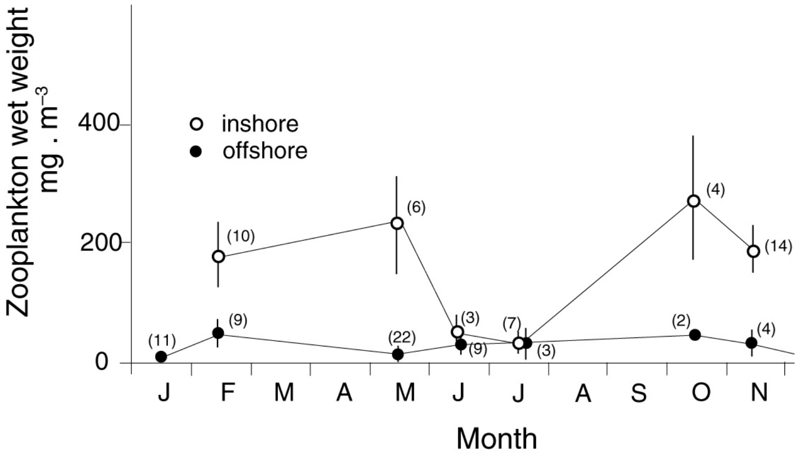

Figure 3.5.3: Collation of zooplankton wet weight biomass by month, inshore and offshore WCSI. Mean, ± one SE. Number of observations in brackets. Data from Bradford (1980, 1985), Bradford-Grieve et al. (1998), James (1989), and NIWA Marine database.

This picture of generally low biomass may be interrupted by isolated patches of greater zooplankton concentrations (Bradford 1980), which may be populated by gelatinous salps. The advection of offshore water towards the coast appears to introduce higher zooplankton populations into the region off WCSI than can be supported by the observed phytoplankton concentrations (Bradford 1985). Bradford deduced that the salp patches observed off the west coast of South Island had been transported from a localised region of greater primary productivity than the overall level found in the Tasman Sea. One such area may be located over the Challenger Plateau. This accumulation of salp biomass implies some kind of nutrient renewal and heightened primary production in surface waters although, as yet, we do not understand the physical processes that would cause such nutrient renewal (Figure 3.5.4).

Zooplankton biomass over the continental shelf is usually greater than offshore but varies considerably. The average upper limit of inshore WCSI zooplankton is about 200 $mg.m^{-3}$, although occasionally, biomasses greater than 1000 $mg.m^{-3}$ are encountered which are augmented by concentrations of krill (*Nyctiphanes australis*) or salps (Bradford 1985). Some of the variability over the shelf may be seasonal (Figure 3.5.3) with a definite winter minimum that is similar to the biomass found offshore. Spring, summer, and autumn biomasses may be several times larger than those found offshore.

Local concentrations of phytoplankton probably play an important role in determining the observed biomass of zooplankton (Bradford 1985). Greatest zooplankton biomass in the surface 50 m, both in winter and summer, occurred largely in nearshore waters where chlorophyll concentrations were greatest (Bradford-Grieve et al. 1998). In winter, over the WCSI continental slope, the minimum in zooplankton biomass coincided with minimum chlorophyll concentrations. But offshore beyond the slope, in winter and in summer, there was no relationship between zooplankton biomass and chlorophyll.

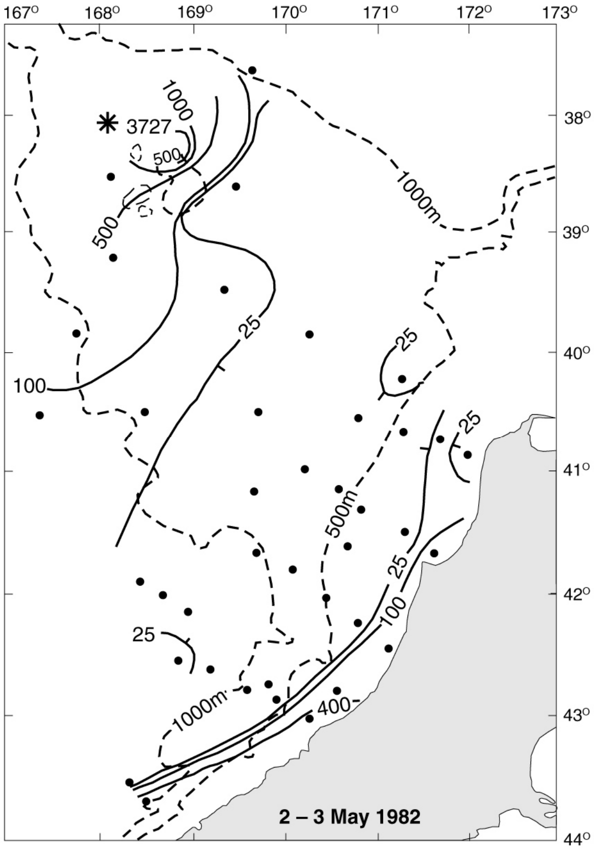

Figure 3.5.4: Distribution of zooplankton wet weight (mg m^{-3}) 0-200 m in May 1982 (original data from NIWA Voyage 1134) determined using the method described in Bradford (1972). Ticks directed towards regions of low concentration.

3.5.3 Feeding

Zooplankton feeding studies on this coast show that omnivory is a more dominant feeding mode than first thought (Bradford-Grieve et al. 1998). There was little evidence for day-night variation in grazing, except in offshore water in spring when grazing appeared to peak at night (Bradford-Grieve et al. 1998). The proportion of the basic metabolic requirements of zooplankton that was met by the consumption of phytoplankton was usually very small (1–4%). An exception occurred at one offshore location, sampled in winter, where 74% of basic metabolic requirements were met by grazing on phytoplankton. It is deduced that the bulk of the food required to support basic metabolic needs, growth and reproduction of zooplankton was being met from the consumption of microzooplankton and smaller zooplankton rather than phytoplankton.

Bradford-Grieve et al. (1998) linked the limited dependence of zooplankton on phytoplankton for food, the dominance of the microzooplankton as phytoplankton grazers (James and Hall 1998), with the relatively low biomass of phytoplankton and their relatively small cell size (less than 20 μm) (Bradford-Grieve et al. 1997). Off WCSI, phytoplankton less than 20 μm were 21–65% of integrated chlorophyll *a* but the absolute quantities of this size fraction were similar in winter and spring.

The impact of a food web dominated by microbial processes on larger zooplankton was illustrated using a one dimensional seven-component plankton-nutrient model immediately after an instantaneous increase in nutrients in the water column (Kumar et al. 1991; Hadfield et al. 1995). This model incorporated three size classes of phytoplankton (<2, 2-20, 20-200 μm) and two size classes of zooplankton: microzooplankton <200 μm which fed exclusively on picophytoplankton (<2 μm) and mesozooplankton (>200 μm) which fed on phytoplankton (2-20 and 20-200 μm) as well as microzooplankton. Initial conditions were taken from field data immediate after a hypothetical winter mixing event and the model was integrated for 30 days (Kumar et al. 1991). The theoretical sequence of events during the 30 days demonstrated large changes in population size and structure of the plankton over the weeks following a simulated mixing event accompanied by an injection of nutrients. Picophytoplankton achieved maximum concentrations within eight days of mixing (see Figure 3.3.7 in Section 3.3). They were rapidly cropped by the rising microzooplankton populations, the phytoplankton community shifted towards dominance by nanoplankton (2–20 μm) after about 10 days, and mesozooplankton populations greater than 200 μm rapidly grew at the expense of microzooplankton and phytoplankton after 20 days. Although these model results depend on a number of assumptions and simplifications, they suggest that increased primary production in this type of ecosystem would pass through to the larger zooplankton in less than one month. Field data that supports this analysis are presented next.

3.5.4 Vertical distribution and processes enhancing densities of larval hoki food

The vertical distribution of zooplankton greater than 39 μm is known in greatest detail from winter pump samples taken over the outer continental shelf and slope in June 1990, July 1988, August 1987 (Bradford-Grieve et al. 1996). These results showed that increased zooplankton biomass usually occurred near the shelf break when mixed-layers were deeper than 50 m. Different species had distinctive vertical distributions within and just below the mixed-layer.

To illustrate the important role of autumn / winter surface mixing in determining the concentrations and distribution of the food of hoki larvae, two continental slope locations with different mixed layer histories are compared (Figure 3.5.5). These two contrasting water columns had mixed layers at 75 m (T921) and 158 m (T944) (indicated by Dm in Figure 3.5.5). The latter water column was also capped, at the time of sampling, by less dense coastal water (Bradford-Grieve et al. 1996). In the upper 75 m at T921 chlorophyll concentrations greater than 0.1 mg.m^{-3} were found only in the mixed layer down to 50 m. In contrast, at T944, chlorophyll concentrations greater than 0.1 mg.m^{-3} were found throughout the deep mixed layer down to 150 m. *Calocalanus* spp., *Oithona similis* and *O. nana* were recorded in 2–3 times greater concentrations at T944 than at T921. *Oithona nana* was found in greatest concentrations at the bottom of the mixed layer, unlike *Calocalanus* spp. and *Oithona similis* that were concentrated in the mixed layer. *Paracalanus* c.f. *indicus* was confined to the surface, low-density water at T944.

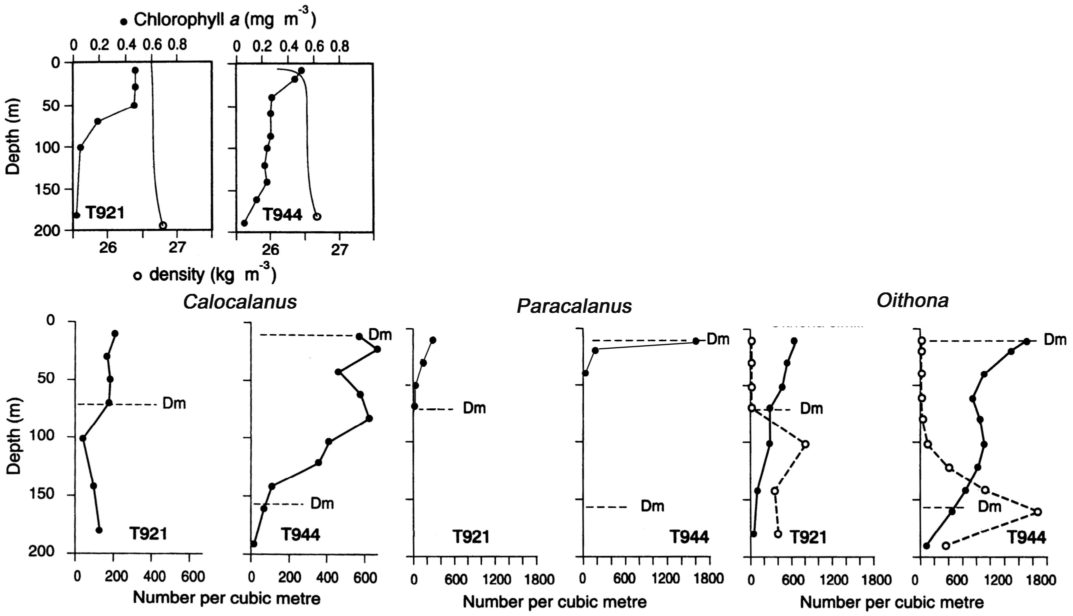

Figure 3.5.5: Vertical distribution of *Calocalanus* spp., *Paracalanus indicus, Oithona similis* (bullet), and *O. nana* (circle) (numbers m^{-3}) off WCSI in winter at stations T921 (oceanic) and T944 (capped oceanic) (Bradford-Grieve et al. 1996). D$_m$ = mixed layer depth

The occurrence of heightened larger zooplankton abundance in more deeply mixed water columns is consistent with the theoretical model of Kumar et al. (1991). That is, early winter surface mixing and deepening of the surface mixed layer enriches dissolved inorganic phytoplankton nutrients in the mixed layer, enhancing phytoplankton biomass accumulation and copepod nutrition leading to increased copepod reproduction (Bradford-Grieve et al. 1996). Thus, the concentrations and distribution of food prey items eaten by early stage hoki larvae can be directly linked to enrichment of nutrients in early winter.

3.5.5 Summary

The oceanic Tasman Sea supports a relatively low average biomass of zooplankton (25 mg m^{-3}) without a distinct seasonal cycle. The shelf off WCSI, supports higher biomasses of zooplankton (greater than 200 mg m^{-3}) with high variability. Some of this variability is seasonal, with a winter minimum.

Zooplankton species of continental shelf and slope waters off WCSI are typical of New Zealand near-surface coastal waters. Species whose densities are greatest nearest to shore are the copepods (*Acartia ensifera, Centropages aucklandicus, Paracalanus* c.f. *indicus, Euterpina acutifrons*) and the euphausiid *Nyctiphanes australis.* Other species have maximum concentrations over the outer shelf or over the continental slope: copepods (*Oithona similis, Clausocalanus ingens, C. pergens, Mesocalanus tenuicornis, Calocalanus sp. Mecynocera clausi*) and appendicularia, amphipods and chaetognaths. Distinct zooplankton communities off WCSI can be identified for neritic, outer shelf / upper slope, and oceanic environments. This association of characteristics may be due to advection of warmer water from the north and to *in situ* processes resulting from the deepening of the surface mixed-layer. It is the outer shelf / upper slope community into which hoki eggs are spawned. Therefore, as the mixed layer develops in autumn and early winter, species important in the diet of hoki larvae

(*Calocalanus* spp., *Paracalanus indicus, Oithona similis* and *O. nana*) achieve their greatest concentrations.

The proportion of basic metabolic requirements of zooplankton that were calculated to be met by the consumption of phytoplankton was usually very small (1–4%). It was deduced that the bulk of the food required to support basic metabolic needs, growth and reproduction of zooplankton were met from the consumption of microzooplankton and smaller zooplankton rather than phytoplankton. The limited dependence of larger zooplankton on phytoplankton for food is linked to the prevalence of microzooplankton over phytoplankton, and the small cell size of the phytoplankton (less than 20 μm). Simulations using a one dimensional, seven-component plankton-nutrient model immediately after an injection of nutrients into the water column suggest that material might flow through a system dominated by the microbial loop to the larger zooplankton in about 20 days. Field observations of the vertical distribution of small copepods in surface mixed layers of different depths are consistent with these interpretations. That is, *Calocalanus* spp., *Oithona similis* and *O. nana* were recorded concentrations in 2–3 times greater in the deep mixed layer compared with the shallower mixed layer. *Calocalanus*, in particular, is a favoured food of young hoki larvae (see section 2.2) leading to the conclusion that processes of nutrient renewal in deeply mixed water over the continental slope in June-August is apparently closely linked with the early survival of hoki larvae.

3.5.6 References

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3.6 Sediment and benthos

Authors: P. Keith Probert, Scott D. Nodder

3.6.1 Introduction

The benthos has a puzzling place in the West Coast, South Island (WCSI) shelf ecosystem. Benthic production seems to be low relative to planktonic energy input to the benthos (Probert 1986). Unfortunately, we know very little about the role of the benthos in the diets of all developmental stages of fish, especially commercially important species in the region. Here, knowledge of the sedimentary environment, benthic populations, biomass and productivity is summarized although we are unable to comment on the implications for fish. The possibilities that efficient bacterial remineralisation of phytodetritus, its export off the shelf and/or burial, invoke low benthic production are explored.

3.6.2 Sedimentary environment

The New Zealand continental shelf and slope is typified by marked variations in the sedimentary environment that reflect regional differences in tectonism, sediment supply and hydraulic regime (Carter 1975; Carter 1980). Shelves of northernmost and southernmost New Zealand are starved of modern terrigenous sediment due to their relative tectonic stability, absence of major rivers, and the trapping of river-borne sediments by coastal embayments, such as fiords and harbours (Carter 1975). Consequently, these shelf areas are mainly mantled by a combination of biogenic and/or relict sediments (Carter 1975; Nelson et al. 1988; Mitchell et al. 1989). In contrast, modern terrigenous sands and muds prevail off the west coast South Island (WCSI) and the east coast North Island. In these localities, rapid tectonic uplift of the New Zealand landmass provides a readily available source of land-derived sediment, which is delivered to the continental shelf by major river systems (Griffiths & Glasby 1985; Hicks & Shankar 2003).

Tectonics and bathymetry

The New Zealand landmass sits astride the tectonic boundary between the Pacific and Australian lithospheric plates. Along the eastern margin of North Island, the Pacific Plate is being consumed beneath the Australian Plate, while to the south of New Zealand, the opposite process is occurring. Since about 23 million years ago, in order to accommodate the tectonic stresses created by these two diametrically opposed subduction zones, the Alpine Fault has formed along the western and central parts of South Island (Wellman 1979; Walcott 1984). Increased rates of oblique convergence across the Pacific-Australian plate boundary since about 5–10 million years ago have resulted in the rapid uplift and subsequent erosion of the Southern Alps (Adams 1980; Walcott 1984; Kamp & Tippett 1993).

Tectonism has created a narrow continental shelf in a region characterised by Cenozoic compressional tectonics, regional uplift and fault reactivation, leading to the present-day basin-and-range topography off the WCSI (e.g., Nathan et al. 1986). The shelf reaches its narrowest extent of less than 5–10 km south of Jackson Head (Figure 3.6.1) where the Alpine Fault approaches the coastline. The shelf widens towards the north to 40–80 km north of Hokitika. Two prominent features, Hokitika Canyon and Cook Canyon, intersect the shelf margin opposite the mouths of their namesake rivers, resulting in steep local topography on an otherwise relatively flat, and featureless continental terrace (Norris 1978; Carter 1980). Exposure of consolidated rock and gravel, at Cape Foulwind and south of Cape Farewell at

Kahurangi Shoals, respectively, leads to localised bathymetric irregularities (e.g. van der Linden 1969; van der Linden & Norris 1974; Mitchell 1987).

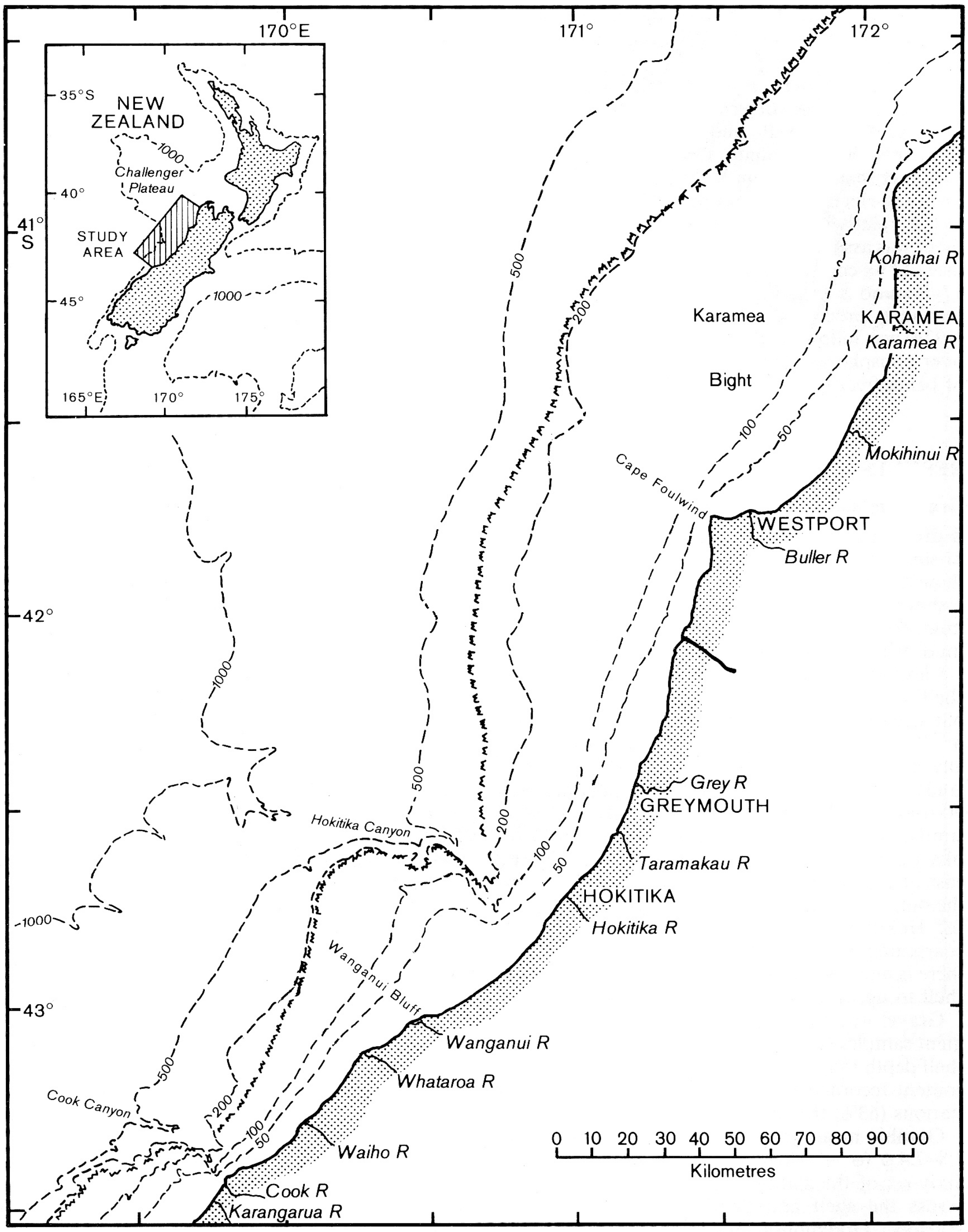

Figure 3.6.1: Bathymetry of the WCSI continental shelf and upper slope (after Eade 1972; Norris & van der Linden 1972; Norris 1979; Carter 1981), and inshore and offshore sediment trap positions. The shelf edge is marked by the darker broken line near the 200 m contour.

Sediment characteristics and composition

Sediment cover on the WCSI shelf comprises predominantly modern, terrigenous fine-grained sands and muds (Carter 1980; Stoffers et al. 1984; Probert & Swanson 1985) (Figure 3.6.2). In water depths of less than about 50 m, fine sands predominate, and grade seawards into muddy sands and sandy muds in mid-shelf areas (50–150 m). Carbonate-rich (greater than 50%) muds are present mainly at upper slope depths (greater than 500 m). On the outer shelf (150–220 m), relict and biogenic sands occur predominantly between Hokitika and Karamea (Stoffers et al. 1984). Well-sorted gravels and gravelly sands are a localised sedimentological feature of Kahurangi Shoals and Paturau Bank (van der Linden 1969; Chiswell & Bowman 1985). South of Hokitika, and in the vicinity of Hokitika Canyon, fine-grained muds and muddy sands are present in water depths as shallow as 50 m. The general fining of sediment grain size southwards along the WCSI shelf is accompanied by a prominent north-south reduction in sediment calcium carbonate content (i.e. greater than 20% at approximately 900 m depth in the south, compared with 200 m in the north) (Figure 3.6.3), and slight decreases in the ranges of sorting and skewness (i.e. better sorted and finer to the south: van der Linden 1969; Stoffers et al. 1984; Probert & Swanson 1985).

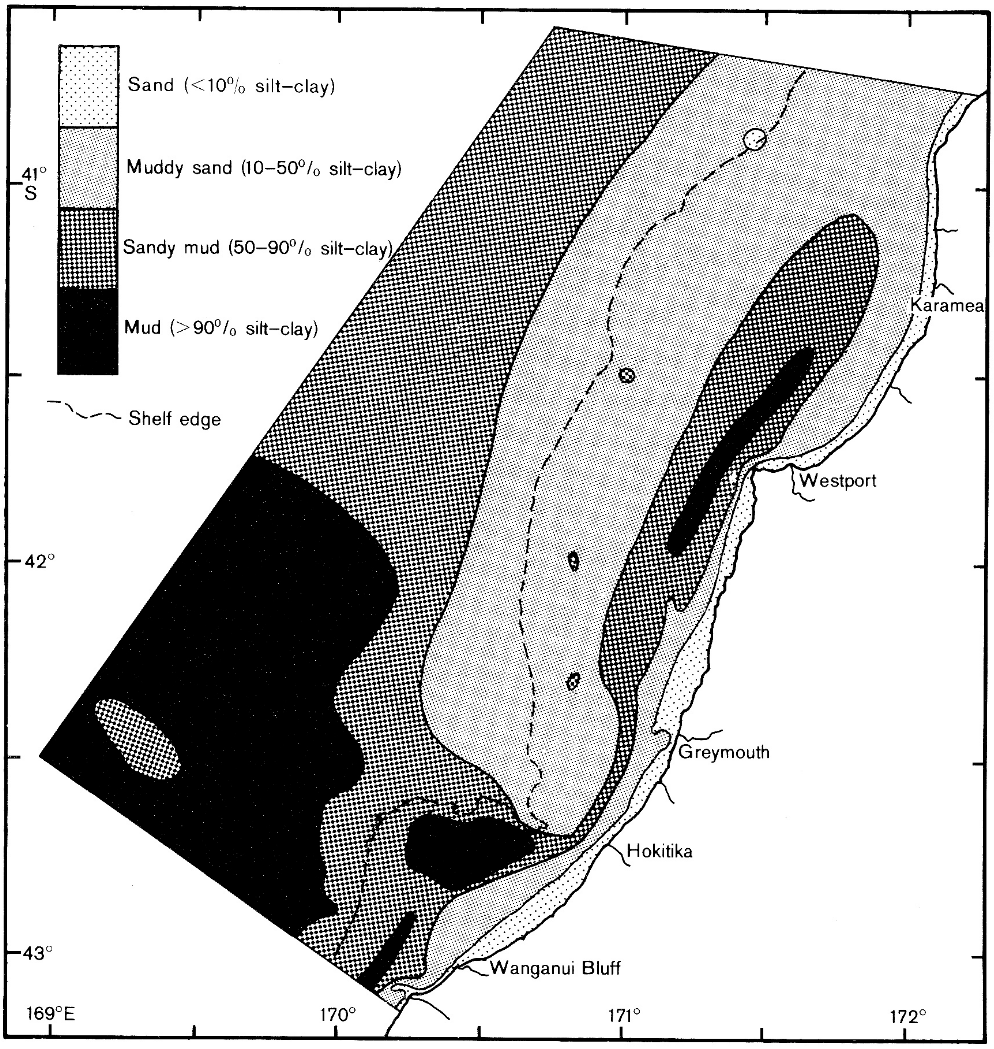

Figure 3.6.2: Distribution of major sediment types off WCSI (based on Carter 1980; Probert & Swanson 1985).

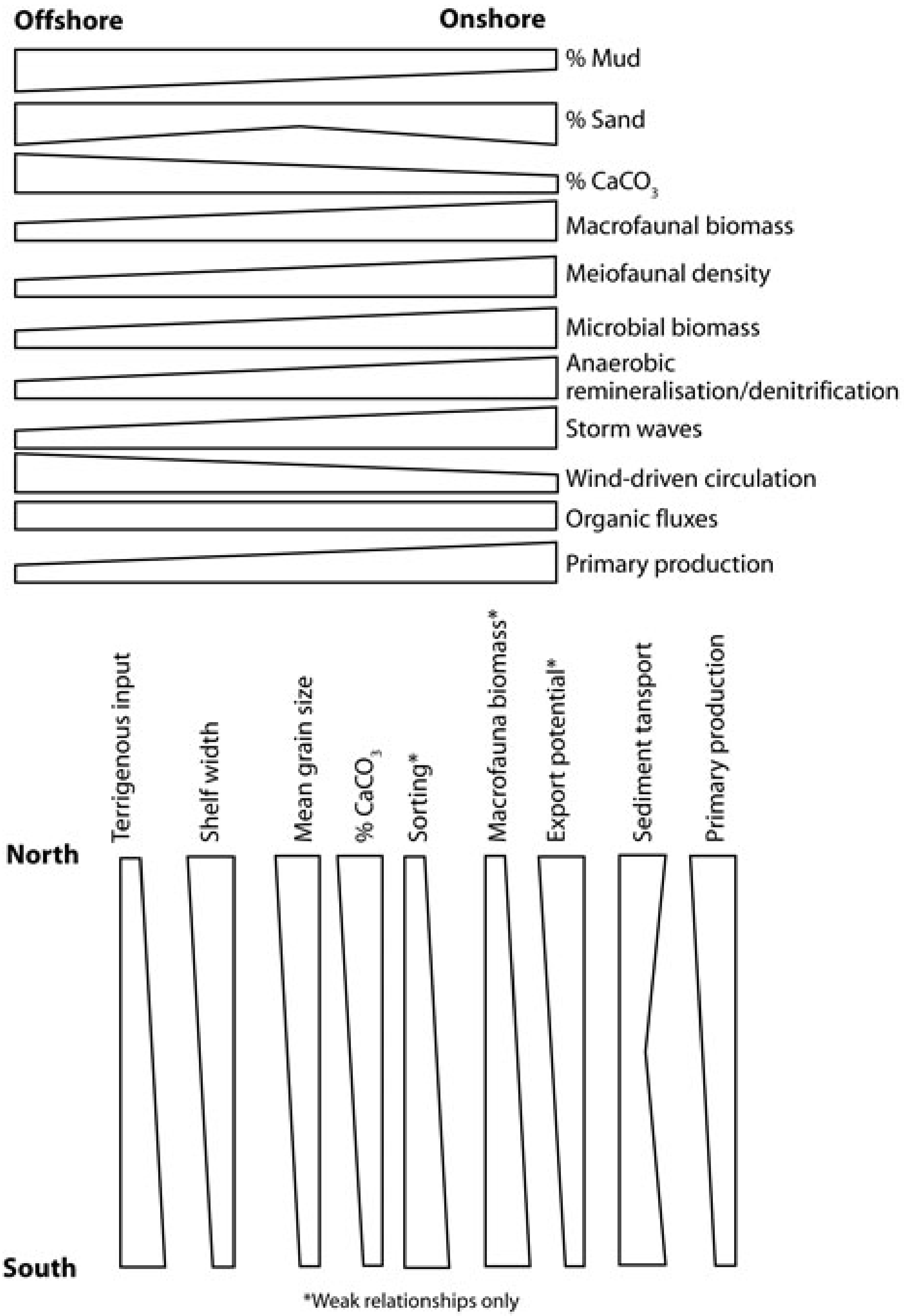

Figure 3.6.3: General trends in physical and biological factors, onshsore-offshore and north-south, over the west coast South Island shelf and upper slope.

Sedimentary processes

Rapid crustal uplift rates of 600±100 Mt yr^{-1} of rock have been estimated for the Southern Alps (Wellman 1979), but excessive erosion rates within steep river catchments (Adams 1980), aided by high average precipitation rates of 5–10 m y^{-1} (Griffiths 1979), result in little net mountain range uplift. Off the WCSI, therefore, specific annual suspended sediment yields of rivers draining the western Southern Alps may be less than 10 times higher than world average rates for mountainous areas (Adams 1980). Griffiths & Glasby (1985) estimated that 131 Mt y^{-1} of river-borne suspended sediment is delivered to the WCSI shelf north of Fiordland, though more recently Hicks & Shankar (2003) have estimated this input to be 69 Mt y^{-1}. Substantial amounts of sediment delivered to the WCSI shelf is likely to be funneled down the Hokitika and Cook canyons to the deep ocean (Adams 1980).

Sedimentation rates for the WCSI shelf are high and estimated to vary from 0.5–2.3 mm y^{-1} (van der Linden 1969; Norris 1978; Probert & Swanson 1985). Furthermore, north-south differences in sedimentation rates on the WCSI shelf are anticipated given present-day spatial variations in shelf width and sediment supply. In particular, reductions in shelf width, south of Hokitika, are concomitant with increases in suspended sediment discharge from local rivers (Carter 1980) and fine-grained, non-carbonate deposition (Probert & Swanson 1985). The combination of these factors might be expected to enhance modern sedimentation rates on the shelf in the southern part of the study area, although the narrow nature of the shelf here may also facilitate higher rates of off-shelf transport.

The predominant direction of sediment transport on the WCSI shelf is to the northeast due to the combined influence of hydraulic factors, such as storm-driven waves, longshore and oceanographic currents and tidal flows (Carter & Heath 1975). However, the dominant component of shelf circulation off the WCSI is southwards-propagating coastal-trapped waves that are generated by wind-forced flux through Cook Strait and have calculated velocities of up to 0.3 m s^{-1} (Cahill et al. 1991). Near-bottom alongshore current flows of 0.2–0.3 m s^{-1} have been recorded on the WCSI shelf (Stanton & Greig 1991; Stanton & Moore 1992), although mean flows of less than 0.04 m s^{-1} generally prevail (Heath 1982). For example, the Westland Current (Brodie 1960) has a mean northeastward flow, but attains low surface speeds of 0.01–0.1 m s^{-1} (Carter & Heath 1975), and exhibits considerable temporal variability as a function of the wind climate (Heath 1982; Chiswell & Bowman 1985; Stanton & Moore 1992).

Since the WCSI is a windward shore exposed to prevailing westerly winds, periodic coastal upwelling events (e.g. Bradford 1983; Heath & Gilmour 1987; Shirtcliffe et al. 1990) and northwards-directed currents, often with underlying south-going counter-currents (e.g. Stanton & Moore 1992), are prominent features of the region's physical oceanography. Similarly, the predominant wave approach direction is west-southwest with an average deep-water wave period and height of 8 s and 2.5 m (Pickrill & Mitchell 1979; Gorman et al. 2003a, b). Shoaling of waves in the nearshore environment leads to the generation of a northeast-directed longshore drift system (Furkert 1947; van der Linden 1969; Heath 1982). Storm-waves act as sediment suspension agents at inner to (possibly) mid-shelf depths and facilitate the movement of sediment by the otherwise weak mean west coast circulation, reinforced at times by the peak tidal flow, which is also to the northeast (Carter & Heath 1975; Heath 1984).

Whilst the Westland Current and wind-induced coastal upwelling are features of shelf circulation north of about Haast River, farther south the mean southward-flowing Southland Current predominates, with surface geostrophic flows in the coastal zone of up to 0.6 m s^{-1} towards the south (e.g. Stanton & Moore 1992). The Southland Current may, however, move off the shelf during times of strong northward wind stress, with a significant proportion of southwards transport in the current occurring below 500 m water depth (Heath 1982; Stanton & Moore 1992). The narrowness of the shelf and high sediment supply suggest that fine-grained sediments present beneath the Southland Current may be moved readily by flows within the current system.

Any effects of periodic upwelling along the WCSI are masked by the very high terrigenous input into the shelf environment (Stoffers et al. 1984). Thus, in contrast to sediments under typical upwelling regions (e.g. Diester-Haass 1978; Summerhayes et al. 1995), sediments on the WCSI shelf exhibit a near absence of siliceous organisms, sparse occurrence of benthic foraminifera, low organic contents (typically less than 0.5% above 500 m water depth) and high C:N ratios (9–15 over most of the outer to inner shelf environment and only more than 15 off the Grey River and south of Hokitika Canyon; Stoffers et al. 1984; Kaspar et al. 1985). These observations, in combination with reductions in calcium carbonate and increases in sediment supply towards the south (Probert & Swanson 1985), highlight the deposition of low quality, refractory terrestrial organic matter in the marine realm. Low C:N ratios (6–7) were recorded from the shelf-break/upper-slope off northern Karamea and on the upper slope north of Hokitika Canyon (Stoffers et al. 1984), but the low organic carbon content (approximately 0.5%) of these sediments possibly indicates that there is not a strong marine input of sedimentary carbon. Furthermore, the presence of authigenic glauconite pellets in relict outer shelf-upper slope sands northeast of Hokitika Canyon (Stoffers et al. 1984) suggests relatively slow deposition rates, perhaps facilitated by strong shelf-break currents (Carter 1980), and indicates that moderately reducing sediment conditions presently prevail. The influence of terrestrial material on deposition in the offshore WCSI environment is confirmed by the presence of lignin in levels ranging from 0.5 to 5 mg g dry sediment^{-1} (Probert & Swanson 1985). The assimilability of this terrestrial pool of carbon by shelf benthos has been questioned (Probert 1986), and its presence is perhaps corroborated by observations of high levels of relatively refractory aquatic humus (or "yellow substance") in offshore waters in autumn 1989 (e.g. g_{440} 0.04–0.11 m^{-1}, Davies-Colley 1992; Howard-Williams et al. 1995). Yellow substance may, however, be derived either from terrestrial sources or marine algal production processes (Davies-Colley 1992).

Sediment trap fluxes

Vertical fluxes of particulate material have been measured using free-floating, surface-tethered cylindrical sediment traps in WCSI shelf and slope environments over winter and spring 1993 (S. D. Nodder, unpubl. data; for methods refer to Nodder et al. 1994a; b; Nodder and Alexander, 1998; Nodder and Gall 1998). Information on total mass, particulate phosphorus (PP) and pigment fluxes have been collected; no data on fluxes of organic carbon or nitrogen are available.

In winter, WCSI inshore waters exhibited high average mass fluxes of 2000 and 3500 mg m^{-2} d^{-1} at 50 m and 80 m water depths, respectively, in a total depth of 100–150 m. Samples from the 80 m trap exhibited significant variability. Similar trends were observed for the PP flux, suggesting that increases in flux and variability with depth were probably related to localised resuspension of bottom sediments. Average PP fluxes were generally similar at offshore and inshore stations, except at the near-bottom sampling depths. Lower, though still moderately high, average mass fluxes of 300–1100 mg m^{-2} d^{-1} were observed in spring in upper slope waters (900–1100 m) over water depths ranging from 120 to 300 m. Both total mass and PP fluxes in these offshore waters in spring decreased markedly with water depth, with mass flux at 300 m almost 70% of the near-surface flux at 120 m. PP fluxes in spring were higher than in winter (by 1.5–4.0 x) in the offshore west coast region.

Pigment fluxes collected in winter from the west coast upper slope were dominated by chlorophyll *a*, the carotenoid fucoxanthin and phaeophorbide *a*2, a degradation product of chlorophyll *a*. Trace amounts of other pigments (less than 10 µg m^{-2} d^{-1}), such as 19'hexanoloxyfucoxanthin (19'HOF), peridinin and chlorophyll *b*, were also collected. A similar pigment assemblage was observed in spring, except at high flux rates (generally 2 x), with phaeophorbide *a1* and chlorophyll *c* pigments more conspicuous components. At one inshore station sampled in winter, phaeophorbides were prominent in the 80 m trap sample with chlorophyll *a* and fucoxanthin dominant at the shallow trap depth, suggesting a resuspension component in the deeper sample, as inferred from mass and PP fluxes.

Thus, from limited sediment trap data, it appears that localised resuspension is a prominent feature of the near-coastal WCSI environment and can cause increases in flux variability with increasing water depth from the sea surface. The observation that fluxes can exhibit considerable spatial and temporal variability is not unexpected given the highly changeable nature of the WCSI physical and biological environment (e.g. Bradford 1983; Stanton & Moore 1992). In addition, it seems that vertical particulate fluxes of phosphorus and photosynthetic pigments to the WCSI benthic environment are similar on the shelf as on the upper slope. There are likely, however, to be substantial differences in the magnitude of fluxes between seasons and in different years.

Mass flux values are comparable with fluxes measured in other shelf and slope environments (e.g. Monaco et al. 1990; Biscaye & Anderson 1994), reflecting similar rates of export production from surface waters. Substantial reductions in mass and PP fluxes with increasing depth, as observed at offshore WCSI stations in spring 1993, reflect particle degradation and decomposition processes as organic material sinks out of the upper water column. Similar observations have been made by other sediment trap studies in continental margin environments (e.g. VERTEX, Knauer et al. 1979; Martin et al. 1987). The magnitude of PP flux at WCSI shelf and upper slope sites in winter and spring is comparable to fluxes reported for the northeast Pacific, off the coast of Washington, USA, during coastal non-upwelling and open ocean conditions (Knauer et al. 1979). Pigment fluxes of chlorophyll *a* and, especially, fucoxanthin may reflect a diatom-dominated phytoplankton community that was found in WCSI offshore waters in winter and spring 1993 (Chang and Gall 1998), although increased importance of other pigments, such as 19'HOF, chlorophyll *c*'s, and peridinin, indicate other phytoplankton groups (i.e. prymnesiophytes, chromophytes and dinoflagellates, respectively) were important components of the sinking flux in spring. The prevalence of phaeophorbides in trap samples in spring perhaps reflects greater zooplankton grazing and/or increased phytoplankton senescence at the time of sampling (e.g. Welschmeyer & Lorenzen 1985).

The magnitude of WCSI pigment fluxes is, however, more similar to that of open ocean environments than of highly productive coastal environments elsewhere; e.g. Dabob Bay, Washington, where fluxes of chlorophyll *a* and total phaeopigments are 2–3 orders of magnitude higher than the west coast fluxes (e.g. Welschmeyer & Lorenzen 1985). The inference that fluxes of organic material in WCSI shelf and slope environments are more similar to those of open ocean environments has implications for benthic ecosystem functioning in terms of food quality and quantity. Since organic flux provides the primary energy source for the benthos, changes in the quality and quantity of this supply will influence the composition and trophic strategies of the benthos. The ephemeral nature of physical processes in the WCSI ecosystem, and seasonal fluctuations in sediment supply to the shelf via the west coast rivers, may tend to favour opportunistic benthic organisms.

Furthermore, burial and export of available organic material along the WCSI shelf-slope could be a significant, and as yet unquantified, "loss" term in any benthic ecosystem models (see Probert 1986). Burial and export results from high terrigenous supply and elevated sedimentation rates, the presence of natural "sinks", such as canyons, for shelf-derived sediments (known mechanisms for physical advection of material off the shelf, such as coastal squirts (Moore & Murdoch 1993)), and temporary changes in position of mean shelf circulation systems (e.g. Stanton & Moore 1992).

As indicated by Probert (1986), the importance of benthic microbial production on the WCSI shelf seems to be a function of several of these factors, but may have been overestimated. It was suggested that the immediate input of newly produced highly nutritious organic matter via sedimentation from phytoplankton blooms could be an important process by which material is provided directly to deposit feeders, thereby avoiding the microbial component of the food web. Although contradictory evidence from sediment traps is apparent (i.e. fluxes of rapidly degradable photosynthetic pigments were similar to open ocean fluxes, and not comparable to pigment fluxes measured in highly productive coastal environments), the traps were not deployed at the height of spring stratification and biomass accumulation, as predicted by existing one-dimensional mixed-layer models (Hadfield & Sharples 1996). Chlorophyll *a* biomass and nutrient levels, measured at the time of trap sampling, also suggest that the sampling programme was not conducted at the height of the phytoplankton accumulation (e.g. Bradford-Grieve et al. 1997). Thus, it is probable that the only sediment traps deployed in the WCSI environment to date did not sample the peak of any phytoplankton sedimentation event, even if it had occurred.

3.6.3 Benthos

Microbenthos

On the basis of ATP content, benthic bacterial biomass in surface (0–1 cm) sediment was measured during January – February 1983. Bacterial biomass at WCSI mid-shelf locations was found to decline significantly with water depth, from a mean of 560 mg C m^{-2} at inshore (22–32 m) stations, to 354 and 155 mg C m^{-2} at mid to outer shelf (112–199 m) and upper slope (484–935 m) stations respectively (Probert 1986; Probert unpubl.). These are comparable to values obtained for continental terrace sediments (Meyer-Reil 1987). Gillespie et al. (1982) examined the relative microbial activity of WCSI sediments. Both the rate of ^{14}C-glucose mineralisation (V_{max}) and ATP concentration declined by more than an order of magnitude from shelf to upper slope (shallower than 625 m) sites. Ratios of sulphate reduction to oxygen consumption indicated that the relative importance of anaerobic mineralisation of organic C decreased dramatically with increasing distance offshore. High ratios observed at nearshore stations suggested that a significant or even a major fraction of total C mineralisation within the sediments may occur through the anaerobic pathway. In this regard, lowered near-bottom oxygen concentrations (greater than 57% of saturation) have been recorded at mid-shelf depths (Bradford & Chang 1987). Kaspar et al. (1985) recorded higher denitrification capacity of sediments at shelf sites than on the upper slope. At an inner shelf (50 m) site 75% of net mineralised N was denitrified and thereby lost from the biologically available nitrogen pool, whereas at the deepest site (625 m) only 3% was denitrified. By markedly reducing the flux of $NH4^{+}$ and $NO3^{-}$ from some sediments, microbial denitrification may have an indirect regulating effect on primary production on the shelf.

Meiobenthos

Metazoan meiofauna was sampled during summer 1982 and summer 1983 from 22 box-core stations (less than 5 replicate subcores per sample) at water depths of 23–938 m off the WCSI. Stations were sited along four transects located approximately off Karamea, Westport, Greymouth, and Wanganui Bluff (Probert & Pilditch 1991). Total meiofaunal densities were generally highest at inshore stations and declined with water depth. Mean densities (0–5 cm) at inshore (23–32 m), mid to outer shelf (84–198 m) and upper slope (462–938 m) were 1132, 813, and 586 individuals per 10 cm^2 respectively. Nematodes comprised on average 80% of individuals, whilst the next most abundant group, harpacticoid copepods and nauplii, averaged 5%. In 5 cm cores, more than 75% of individuals occurred on average within the top 2 cm of sediment, and 90% in the top 3 cm. Sediment type, however, influenced the degree of vertical distribution. As the proportion of the silt-clay fraction increased from sands to muds, the meiofauna became increasingly confined to the uppermost layers. These results for meiofaunal density, composition, and vertical zonation are consistent with those from other studies of comparable shelf and upper slope environments (Higgins & Thiel 1988; Giere 1993).

Macrobenthic assemblages

Benthic macrofaunal samples were taken on the WCSI shelf and upper slope at 30 anchor-box dredge stations (32–1120 m) (Probert & Grove 1998), and at 18 (replicated) box-core stations (28–943 m) (Probert et al. 2001). Most samples were dominated by polychaetes (means of 36 and 54% of individuals), with bivalves and amphipods usually the next most abundant major taxa (means of approximately 9–13% of individuals). Major groupings identified by multivariate analysis from these two surveys were: (1) inner shelf stations at approximately 30–50 m on silty sand characterised by *Sthenelais* cf. *chathamensis*, *Nephtys* sp., *Aglaophamus macroura*, *Prionospio australiensis*, *Paraprionospio* aff. *pinnata*, *Magelona* cf. *dakini*, *Aricidea* sp., *Ampharete kerguelensis, Diplocirrus* sp. (Polychaeta), *Austrofusus glans* (Gastropoda) and *Maorimactra ordinaria* (Bivalvia); (2) mid-shelf to shelf-break stations at approximately 90–300 m on sandy mud characterised by *Aglaophamus verrilli*, *Lumbrineris ?brevicirra*, *Prionospio australiensis, Paraprionospio coora*, *Levinsenia* cf. *gracilis*, *Diplocirrus* sp. *Auchenoplax mesos* (Polychaeta), *Poroleda lanceolata* (Bivalvia) and *Ampelisca chiltoni* (Amphipoda); and (3) upper slope sandy mud or mud stations at approximately 440–1120 m where good discriminators were *Prionospio ehlersi* (Polychaeta), *Apseudes diversus* (Tanaidacea) and *Ophiozonella stellamaris* (Ophiuroidea).

In a survey of benthic infaunal communities of the New Zealand continental shelf and upper slope, McKnight (1969) included 37 stations off the WCSI between Cape Farewell (approximately 40° 30' S) and Jackson Head (approximately 44° 00' S) at water depths of 13–215 m. McKnight recognised communities mainly on the basis of their larger bivalves and echinoderms. Nevertheless, some correspondence with the groupings described above is evident. "*Venus* communities" were identified by McKnight from stations at water depths of 13–29 m on sand or muddy sand, and at 58–192 m on a variety of sediments from gravelly sand to mud. The predominant type of *Venus* community identified off the WCSI was a *Scalpomactra scalpellum* - *Maorimactra ordinaria* community, which McKnight described as a widespread open-shelf community occurring mainly on sandy substrata at depths of 20–60 m. This community is clearly identifiable with the inshore silty sand grouping for WCSI macrofauna described above. McKnight also identified "*Nemocardium* communities" off the west coast at 134–215 m, and these show similarities to the muddy, mid- to outer shelf macrobenthic community described above.

Macrobenthic community structure off the WCSI does not appear to be significantly influenced by upwelling. Instead, major influences are bathymetry and sediment type. Indeed, infaunal communities of the WCSI shelf are similar to those recorded from other (non-upwelling) New Zealand shelf regions characterised by modern terrigenous fine-grained sediments (McKnight 1969). WCSI macrobenthos appears largely to comprise deposit feeders, as would be expected for an area dominated by generally muddy sediments. Abundant deposit-feeding taxa include spionid, maldanid and ampharetid polychaetes, protobranch bivalves, apseudid tanaidaceans, urothoid and corophiid amphipods, amphiurid ophiuroids, and spatangoid echinoids.

The limited data available indicate that the study area supports a relatively sparse epifauna. Agassiz trawl samples were taken in January-February 1983 at 19 stations along four main transects at water depths of 28–955 m (NIWA benthic database). All the samples were small with, in most cases, less than 15 major groups represented per haul; these were mainly Polychaeta (primarily *Hyalinoecia tubicola, Chloeia inermis*, and *Aphrodita* sp.), Gastropoda, Paguridea, Brachyura, Asteroidea, Ophiuroidea, Echinoidea, Holothuroidea and Teleostei. By contrast, coarser sediments on the outer shelf farther north, off Cape Farewell, support a well developed invertebrate epifauna (McKnight 1968).

Benthic biomass and productivity

Estimates of macrofaunal density and wet weight biomass from box-core and anchor-box dredge surveys of the WCSI shelf and upper slope vary considerably, but nevertheless show significant inverse relationships with water depth (Probert 1984). Faunal density (1 mm sieve) was generally about 1000–3000 individuals m^{-2} at inshore (23–51 m) stations, 800–1000 individuals m^{-2} at mid-shelf to shelf-break (87–297 m) stations, and 350–550 individuals m^{-2} at upper slope (462–1120 m) stations, whilst macrofaunal biomass (1 mm sieve) for these zones was generally of the order of 50–150, 10–50, and 5–10 g wet wt m^{-2} respectively (Probert & Anderson 1986; Probert & Grove 1998). Only limited benthic biomass data are available for other sites on the New Zealand shelf, but these indicate that the west coast supports a lower biomass than the east coast (Neyman 1970; Probert & Anderson 1986), which may be attributable to contrasting patterns of surface primary productivity and seasonal variation in plankton biomass (Probert & Anderson 1986). Geographic distribution of benthic biomass on the New Zealand shelf appears to correspond broadly to the distribution of surface reactive phosphorous and surface primary productivity in the New Zealand region (Bradford & Roberts 1978). Off the WCSI, onshore-offshore and more tentatively north-south reductions in primary production may be apparent with "hot spots" of production in areas of upwelling, such as Cape Foulwind and Cape Farewell/Kahurangi Point (J. Grieve pers. comm., 2004; Chapter 3.3).

There is some evidence of a north to south increase in shelf macrobenthic biomass off WCSI (Probert & Anderson 1986) as mean grain-size decreases and sorting improves. There may be potential for a north-south decrease in export of shelf carbon since a simple analytical model indicates that there is a latitudinal change in the character of the near-bottom cross-shelf flow: north of about 42° 30' S there is zero cross-shelf flow at mid-shelf depths whereas south of 42° 30' S near-bottom flow has an onshore component (Heath 1982). On the other hand, the narrow shelf in this region might facilitate off-shelf export of carbon and sediment; large-scale sediment fans and remobilised deposits are evident in the deep ocean west of the shelf-break off Fiordland (P. Barnes, pers. comm., 2004).

Benthic biomass is typically high under upwelling regions unless surface productivity and organic flux is sufficient to lead to oxygen depletion of near-bottom water (Thiel 1978; Arntz et al. 1991). Pelagic primary production for the WCSI shelf is estimated, however, to average approximately 180 g C m^{-2} y^{-1}, a value more typical of temperate shelf seas (e.g. Platt & Subba Rao 1975; Cushing 1988). Macrobenthic biomass of the WCSI shelf averages approximately 2 g C m^{-2} (meio- and megabenthos are likely to make only minor contributions) (Probert 1986). This appears low relative to primary production if one takes, for instance, an average shelf benthic biomass for the world ocean of approximately 12 g C m^{-2} (Zenkevitch et al. 1960). Macrobenthic production of the WCSI shelf may, however, be comparable to other shelf systems if an average P:B ratio of approximately one is taken as a suitable literature value (e.g. Pace et al. 1984; Valiela 1995), but in the absence of measurements of benthic production for the WCSI shelf it remains unclear how tightly coupled are primary and benthic production. Probert (1986) has argued that benthic production on the WCSI shelf is relatively low.

Processes that may account for a disparity between primary production and benthic secondary production include efficient bacterial mineralisation of phytodetritus, its export and/or burial, and the relative importance of zooplankton production (Probert 1986). High wind stress may influence benthic secondary production off the west coast by decreasing the availability of primary production to the benthos and/or, at least to mid-shelf depths, through various costs to benthic energetics as a result of increased sediment transport (Emerson 1989). River-borne mud delivered to the WCSI shelf may accumulate nearshore as flocculated particles that would be vulnerable to resuspension. Resuspended sediment, as well as non-flocculated grains that have remained in suspension, would be readily transported by the mean circulation, tides and storm-driven components (Carter & Heath 1975). Rapid deposition of modern terrigenous sediment may favour the burial of metabolisable organic material. Low benthic biomass would be expected in sediments with high C:N ratios (e.g. Grebmeier et al. 1988), as observed on the WCSI shelf and slope.

Episodic upwelling may provide important, though irregular, pulses of organic flux to the benthos. The benthic environment of the WCSI shelf is one where there is also rapid deposition of fine-grained sediment, which itself is low in assimilable carbon. Such factors might be expected to favour production by meiofauna and small opportunistic macrofaunal species, particularly surface detritus-feeding polychaetes (see e.g. López-Jamar et al. 1992), able to respond to sedimentation events. Provisional estimates indicate that benthic metazoan production on the WCSI shelf and upper slope is predominantly meiofaunal (Probert 1986), and an abundance of spionid polychaetes may reflect the scope for opportunistic macrofauna (Probert et al. 2001). Nevertheless, in terms of gross composition of the larger infauna, the WCSI shelf benthos shows obvious similarities to muddy bottom assemblages that occur widely around New Zealand (McKnight 1969).

Energy flow models for different sedimentation regimes

Energy flow pathways of New Zealand shelf benthic systems are likely to differ substantially depending on the modern sedimentation regime. At one end of the spectrum are shelves with low modern sedimentation covered largely by coarser relict and biogenic sediments, such as occur off southern New Zealand, Otago-Canterbury and Northland (Carter 1975; Nelson et al. 1988). Under this regime, macrobenthic suspension feeders (*Venus*-type communities and associated sessile epifauna) are likely to be important in benthic energy flow. Also, mobile epifauna appear to be conspicuous in these systems. In contrast are those shelves with high modern sedimentation, covered largely by modern muddy sediments, and typified by the WCSI and Hawkes Bay-Wairarapa shelves (Carter 1975). Energy flow is here likely to be mainly via sediment micro- and meiobenthos and deposit-feeding macrobenthos (*Nemocardium*-type communities). Further research could profitably be undertaken to further elucidate the structure and function of these contrasting benthic systems.

3.6.4 Hoki offal dumping

In the mid 1980s, the discarding of processed offal at sea and the release of contents from burst fishing nets was thought to be an issue affecting water quality in the WCSI hoki spawning ground (Ministry of Fisheries 2011 and references therein). Photographs of the seabed showed an influx of scavenging fauna during the hoki spawning season, but there was little evidence of anoxic conditions above those already observed near the sea bed due to natural processes (Livingston & Rutherford 1988). This potential problem has largely been alleviated as most of the vessels now carry meal plants, most offal is processed on board and dumping offal at sea contravenes a code of practice.

3.6.5 Summary

The continental shelf and upper slope off the South Island west coast is characterised by modern terrigenous fine-grained sediments. Inshore (less than 50 m depth), sediment is predominantly fine sand to coarse silt. Silt-clay content increases towards mid-shelf depths, and areas of mud (less than 10% sand) occur at depths of approximately 90–140 m. Sediments tend to become coarser again on the outer shelf, and sandy mud (10–50% sand) or muddy sand (50–90% sand) covers the outer shelf and upper slope. Input of river-derived sediment is high and sedimentation rate for the shelf is estimated to average 1–2 mm y^{-1}. There are, however, a north-to-south increase in riverine input and a decrease in shelf width, corresponding with north-to-south decreases in mean grain size and the ranges of sorting and skewness. An increase in sediment carbonate content with water depth also indicates greater dilution of carbonate by detrital sediment to the south. Effects of periodic upwelling on sediment geochemistry appear to be masked by high terrigenous input: shelf sediments exhibit a near absence of siliceous organisms, sparse occurrence of benthic foraminifera, low organic contents and high C:N ratios. Anaerobic mineralisation of carbon and denitrification are likely to be important, at least on the inner shelf.

Mean meiofaunal density (approximately 80% nematodes) for the shelf and upper slope (less than 938 m) is 825 individuals 10 cm^{-2}. Benthic macrofauna of the shelf and upper slope largely comprises deposit feeders, and important taxa include spionid, maldanid and ampharetid polychaetes, protobranch bivalves, apseudid tanaidaceans, urothoid and corophiid amphipods, amphiurid ophiuroids, and spatangoid echinoids. Macrobenthic assemblages relate closely to bathymetry and sediment type, and include an inshore (less than 50 m) silty sand fauna, and mud bottom faunas at mid- to outer shelf (less than 300 m) and at upper slope (less than 1120 m) depths. Mean macrobenthic biomass for these zones is generally of the order of 50–150, 10–50, and 5–10 g wet wt m^{-2} respectively. Rapid sedimentation and episodic upwelling may promote an abundance of opportunistic taxa and high temporal variability of benthic populations. Benthic energy flow is likely to occur particularly via the sediment micro- and meiobenthos and deposit-feeding macrobenthos.

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4 LINKING ENVIRONMENTAL VARIABILITY AND HOKI LARVAL SURVIVAL

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4.1 Introduction

Fish with planktonic larvae usually produce a huge number of eggs when they spawn. A very small proportion of these eggs survive through early stages of development before metamorphosing into a juvenile fish, indicating that it is this period in their lives when they are at greatest risk (e.g. Buckley 1984 and references therein). To grow quickly and thus become less vulnerable to predation, first-feeding larvae need to have been spawned into an environment where their preferred food is in optimum concentrations at the stage when their yolk sac reserves are finished. Larvae must also be exposed to physical conditions that allow for their subsequent transport into suitable habitat. The frequency and duration of favourable conditions for larval feeding and transportation, and their timing relative to the spawning period and yolk sac absorption, are key factors in estimating the impact of ocean climate on the survival of fish larvae through to the juvenile stage.

There are numerous statistical studies that link larval survival and fish abundance to environmental indices or climate variables (e.g. Tyler 1992; Renwick et al. 1998; Bull & Livingston 2001; Beentjes & Renwick 2001; Tian et al. 2003; Maes et al. 2004; Waluda et al. 2004). These studies typically use variables such as sea surface temperatures, chlorophyll concentrations, wind statistics, or climate indices (e.g. ENSO) that measure various aspects of environmental variability. These variables have been correlated with fish abundance statistics that may be represented by relative year class strength indices or recruitment strength.

A number of recent studies and reviews have highlighted the importance of understanding the interaction between oceanographic conditions and fish recruitment (Beaugrand et al. 2003; Hinrichsen et al. 2003; Lynch et al. 2001; Platt et al. 2003; Lehodey et al. 2006; Castonguay et al. 2008). We have advanced our understanding of why hoki may spawn in deep water off West Coast, South Island (WCSI) in an environment that is potentially of rather low productivity and identified the mechanisms that may link climate variability to biological changes in ecosystems and fish populations. We may now be in a position to develop more specific hypotheses and devise a better method for predicting survival in hoki larvae.

In summer, away from the continental shelf and slope, there is a relatively stable food web consisting of pico- and nanophytoplankton, heterotrophic bacteria and flagellates, protozoan micrograzers and their predators. Dissolved inorganic nutrients are in very low concentrations and the whole system is oligotrophic, relying on recycled nutrients. This environment does not appear to favour the survival of larvae of hoki. The very low levels of nutrients found in the mixed layer (Section 3.2), the dominance of small sized cells in the phytoplankton and relatively low primary productivity and the dominance of urea and NH_4 in nitrogen uptake (Section 3.3), the relatively large biomass of bacteria (Section 3.4), and low zooplankton biomass (Section 3.5) do not appear to provide sufficient productivity of hoki larvae prey. The mixed layer depth increases in autumn and winter to greater than 100 m (Section 3.1) and the resulting entrainment of nutrients leads to a slight increase in chlorophyll concentrations autumn to spring (Murphy et al. 2001) but zooplankton biomass is relatively stable (see Figure 3.5.1).

Spawning hoki have evolved to take advantage of the enhanced but variable food availability over the WCSI continental slope in winter where the mixed layer may extend to depths greater than 100 m. Hoki also hedge their bets by spreading spawning over two months. In the more deeply mixed water over the continental slope, oceanic species of very small copepods (*Calocalanus* sp.), favoured by first feeding hoki larvae, attain much higher densities than they do offshore; *Calocalanus* spp. are absent further inshore.

Hoki larvae have been recorded off WCSI in concentrations ranging from less than 0.01 m^{-3} to more than 20 m^{-3} (Murdoch & Quigley 1994; Zeldis et al. 1998). The largest concentrations recorded were 27 m^{-3} in late July 1987, a year that resulted in a strong year class (e.g. Livingston 1990).

In this section we address questions associated with adequate food for the first feeding larvae of hoki and their transport inshore. We explore the mechanisms that might link environmental variability to these questions, and discuss why a recent study (Francis et al 2006) failed to find a link between this variability and hoki year class strengths. We acknowledge that other factors (e.g. availability of food for juveniles, predation on juveniles) may also influence the year class strength (YCS) of a cohort as it recruits to the fishery but there are no data to address these questions.

4.2 Factors affecting food availability for early hoki larvae

Winter surface mixing

There is circumstantial evidence that year-to-year variations in the year class strengths of hoki may be influenced by the timing of the onset of winter mixing and the pattern of its progression (Livingston 1990; Bradford-Grieve et al. 1996).

In winter, it has been noted that the mixed layer is typically at maximum depths along a region parallel to the coast over the continental slope, shoaling both inshore and offshore. The location of the maximum may be determined by the presence of a tongue of warm surface water extending from the north along the continental slope off WCSI. If we assume that, subsurface, this water is also warmer than the surrounding water, and that there is a tendency for surface waters to cool in winter to match the air temperature, then the warm tongue would have a tendency to mix more deeply than the water inshore and offshore to reach equilibrium with the atmosphere. It appears that hoki eggs are spawned into this region where mixed layers may be at a maximum. What, therefore, is the impact of the observed spatial and temporal variability in mixed layer depth on the feeding environment of hoki larvae?

Fieldwork carried out in water of different mixed layer depths showed that the depth of vertical mixing was related to concentrations of copepod nauplii and *Calocalanus* spp. that are dominant in the diet of first feeding hoki larvae (Murdoch & Quigley 1994). At locations over the continental slope where the mixed layers were more than 75 m deep and nitrate nitrogen concentrations were more than 3 µM, copepod nauplii, and *Calocalanus* spp. were in concentrations of 10,000–16,000 m^{-3} and 288–577 m^{-3} respectively (Bradford-Grieve et al. 1996). In contrast, at slope stations with mixed layers less than 85 m and nitrate nitrogen less than 2 µM, copepod nauplii, and *Calocalanus* spp. were in concentrations of 3,000–6,000 m^{-3} and 53–86 m^{-3} respectively. Therefore, depending on where and when hoki spawn, the first feeding larvae may find widely differing concentrations of their preferred food. In late July 1987, hoki were found in concentrations of 27 larvae m^{-3} (Murdoch 1992) at two locations where the water column conditions had high numbers of copepod nauplii and *Calocalanus*. These measured conditions were clearly suitable for the survival and growth of hoki larvae and may have been widespread in 1987 as this year produced a strong year class. This deduction is dependant on the acceptance of a hypothesis that in 1987 optimal feeding conditions were a dominant cause of high larval survival.

The link between mixing, nutrients and primary production was explored using a mixed layer model driven by the observed winds (Hadfield & Sharples 1996). Hindcasts of the depth of mixing were made for years with contrasting year class strengths in the adult population. In

1987 and 1988, years that contributed strong year classes to the adult hoki fishery (Sullivan et al. 1995), the early and gradual onset of winter mixing was associated with the replenishment of nitrate in surface waters to 1 µM by the end of June (Bradford-Grieve et al., 1996) (Figure 4.1). In 1990, when the hoki year class was weak, the hind cast winter mixing began later and nitrate replenishment reached 1 µM a month later, at the end of July. Mixing then progressed rapidly to depths greater than 200 m (Bradford-Grieve et al., 1996) and may have curtailed net primary production through light-limitation of photosynthesis. The early, extra, primary production, mediated by increased nitrate, which occurred in 1987 and 1988 would then have flowed into the rest of the planktonic food web in time for the peak of egg laying in late July early August (see Figure 2.2.1).

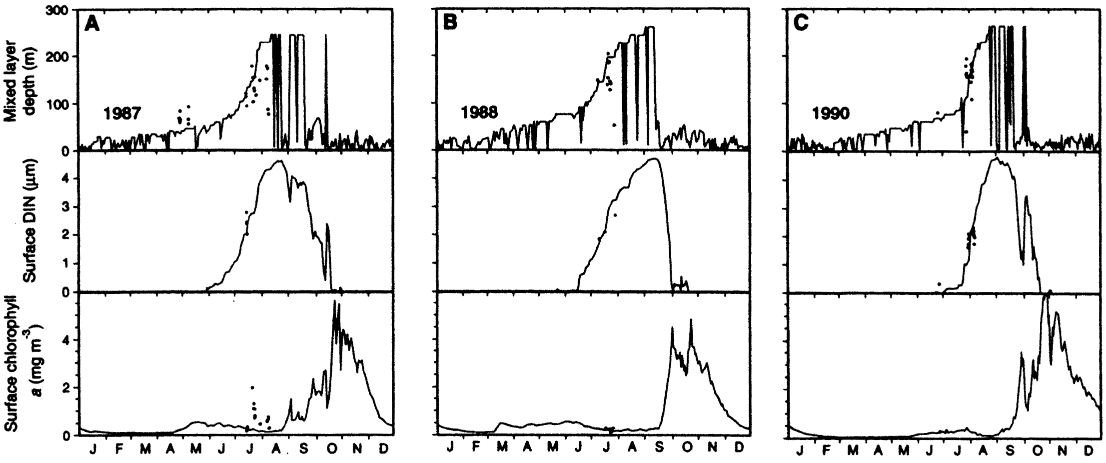

Figure 4.1: Depth of the mixed layer (Y axis), surface dissolved inorganic nitrogen and surface chlorophyll *a* over the continental slope off WCSI in A, 1987; B, 1988; C, 1990 from the model of Hadfield & Sharples 1996 (from Bradford-Grieve et al. 1996). The dots represent actual observations.

Based on an analysis undertaken with a 7-compartment nutrient-plankton model (Kumar et al. 1991; Hadfield et al. 1995) we postulated that it takes more than 20 days from an injection of extra phytoplankton nutrients into a deep mixed layer to pass through the food web to the larger zooplankton (such as *Calocalanus*). Therefore, deepening of the mixed layer would have to have occurred about one month before hoki eggs hatched for first feeding and growth to occur.

Spawning occurs over a period stretching from mid July to the end of August peaking in late July to early August (e.g. Zeldis et al. 1998). Weather-driven models of the development of the mixed layer over the continental slope 1980–1994 (Hadfield & Sharples 1996) show year to year variation in the maximum depth and the timing and progression of mixing. For example, in 1984, winter surface mixing was 100 m by mid July and reached a maximum of 120 m (see Figure 3.1.4). In 1992, not only was the modelled maximum surface mixing to greater than 300 m but it reached 150 m in mid July.

The deeper that surface water mix, the lower the average availability of light to growing phytoplankton. On the other hand, the more deeply a water column mixes, the greater the quantities of nutrients that are brought into the surface waters. Therefore, there has to be the right balance between nutrients and light to generate phytoplankton growth in winter.

The photic zone is about 75 m deep in oceanic water beyond the slope off WCSI in winter (Chang & Bradford 1985). When the mixed layer is greater than the depth of the photic zone, Sverdup's concept of "critical depth" is relevant: for net phytoplankton growth to occur the mixed layer depth has to be less than the critical depth where total vertically integrated phytoplankton production equals total respiration. At 42°S the critical depth may vary from 70 – 260 m in June a range which depends on incident radiation, (calculated using the critical depth formulation $1/K\ Z_{CR}(1-e^{-kz}{}_{CR}) = I_c/I_o$, where the compensation depth $I_c = 0.6$ mol photons $m^{-2}\ d^{-1}$ (*see* Siegel et al. 2002 for Sverdrup's value), $K = 0.07\ m^{-1}$ (see Chang & Bradford 1985 for June), and I_o is the flux of incident radiation. The trajectories of critical depth and mixed layer depth show that the minimum in the critical depth in June (the month when the sun is lowest in the sky) and the maximum in the mixed layer depth (August-September) do not coincide, often leaving a window in July when the mixed layer is much shallower than the critical depth so that net phytoplankton growth may occur if sufficient nutrients are available (see Figure 4.4). This window may be necessary for adequate concentrations of small copepods to develop.

The corollary of this is that if surface mixing starts late so that the injection of nutrients is late relative to hoki spawning or if it starts early but proceeds rapidly to near or beyond the critical depth, then any extra production linked to deepening of the mixed layer will be too late or not extensive enough to support adequate growth and accumulation of small copepods.

The pattern of winter mixed layer development is not the only process that potentially creates variability in nitrate concentrations in the mixed layer. From 1996–2002 the Tasman Sea was much warmer than usual (Sutton et al. 2005). Measurements showed that warming occurred down to at least 800 m and was accompanied by sea surface elevation. The elevation of sea surface heights during 1998 appear to have been the result of anomalously strong downward Ekman pumping during 1998 when the seasonal reversal in wind stress curl (a measure of the sense and strength of rotation in the wind) was disrupted (Bowen et al. 2006). They also note that this downwelling is highly correlated with the Southern Oscillation Index (correlation coefficient 0.8) and that other similar downwelling events have probably occurred during the last 50 years.

It is highly likely that this warming event altered the distribution of nutrients (nitrate) with depth. If we examine data from between 250–800 m (Figure 3.2.4), we see that temperature and nitrate concentrations are negatively correlated. If we assume that there is a relationship between temperature and nitrate at depth, then in the recent warm years the reservoir of nitrate that lies beneath the summer thermocline may have decreased. Therefore, the nitrate that is needed to drive an optimum autumn / winter increase in primary productivity and flow of organic matter into the preferred food of hoki larvae, may have been absent.

Therefore, the hypothesis that the survival of hoki larvae over the continental slope off WCSI depends on the timing and pattern of autumn / winter surface mixing coupled with the underlying oceanographic structure was formulated. Sufficient nitrate and other phytoplankton nutrients must be mixed into the upper water layers to allow the rate of primary production to increase and leave enough time before the hoki eggs are spawned for this additional primary productivity to flow through into food available for hoki at the point of yolk sac absorption.

Capping of slope water by coastal water

Another hydrographic event of potential significance to zooplankton productivity is the capping of continental slope water at the surface by low salinity, low density shelf water that has been displaced off shore and which then prevents deep mixing.

There are two situations when capping of the water column has been observed. The first was during offshore transport of surface coastal water during wind-driven upwelling (Bradford 1983). On this occasion low salinity, more highly stratified water was displaced offshore over the outer shelf and upper slope by inshore upwelled colder and more saline water. The impact of this was to double the rate of phytoplankton production per day which was at a minimum

(0.11–0.18 d^{-1}) offshore and at a maximum (0.57 d^{-1}) in the coastal water immediately adjacent to the upwelled water (Chang & Bradford 1985). In the upwelled water closest to the coast, phytoplankton doublings per day were intermediate (0.33 d^{-1}), apparently lowered by the attenuation of light by re-suspended sediment from the seafloor and by low light-saturated photosynthetic capacity (evidenced by low C:Chl ratios) in the photic zone (Chang & Bradford 1985).

The second situation leading to capping of the water column above the continental occurred when offshore-directed plumes (50 km long) of inshore water south of the Hokitika Canyon occurred under non-upwelling conditions (Moore & Murdoch 1993). These plumes are linked to coastally trapped wave activity propagating from Cook Strait and are transient phenomena recurring south of the Hokitika Canyon. Once offshore, the plumes resulted in stratification of previously deeply mixed offshore waters thus preventing downward mixing of phytoplankton from the photic zone. In time, chlorophyll in the relic mixed layer was reduced presumably by the grazing of zooplankton (Figure 4.2). The appearance and complete disappearance of a plume in the surface temperature signal may take 3 days although satellite-observed chlorophyll suggests the biological impact lasts several weeks.

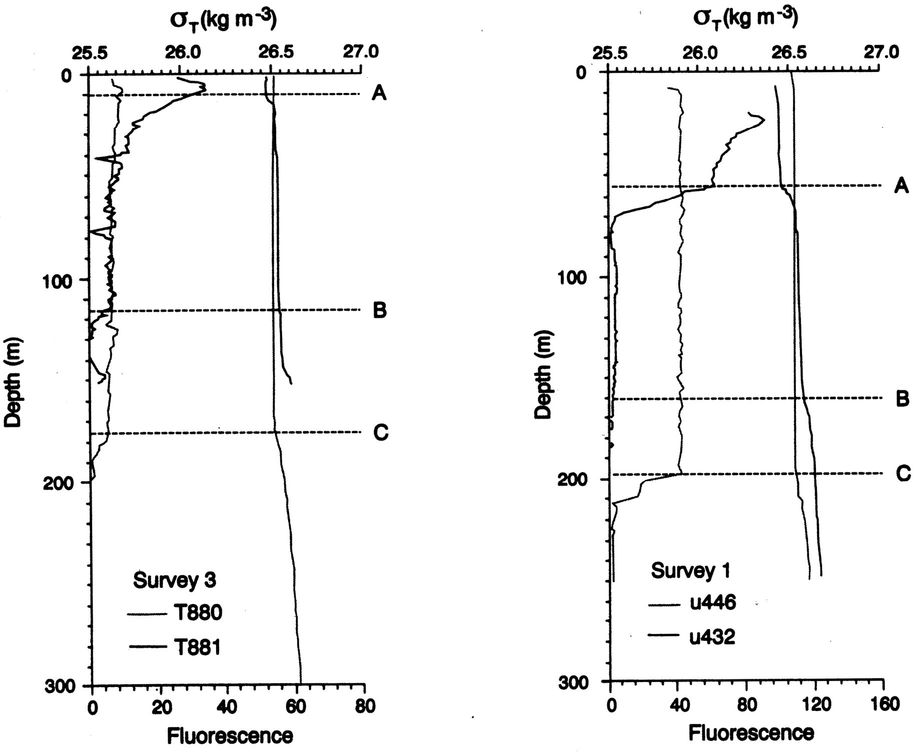

Figure 4.2: Profiles of phytoplankton fluorescence (left) and density (right) within (T881, U432) and outside (T880, U446) plume-affected waters WCSI . Horizontal lines indicate the pycnocline at the base of the plume (A), bottom of the relic mixed layer (B), and bottom of the mixed layer in plume-affected waters (C) (from Moore & Murdoch 1993). Note the decline in phytoplankton between 55 and 200 m in water affected by the plume (fine line) compared with water unaffected by the plume (thick line).

The capping of deeply mixed water theoretically results in two effects depending on the time that has elapsed since capping. The first effect is an increase in average light available to phytoplankton through stabilisation of the water column. This increases primary production until nutrients are exhausted. In the water column beneath the cap the replenishment of the relic mixed layer with phytoplankton ceases when mixing ceases and grazing rapidly exhausts the supply of food to planktonic animals. The impact of the offshore transport of coastal water and capping of the deeply mixed layer on the food of hoki larvae is difficult to judge. Locally, such events could cause a reduction in the quality of the food environment below the capping water but the water of the plume at the sea surface becomes more productive. Although these events seem to be relatively short-lived, their frequency of occurrence is not known and there is insufficient data on the vertical distribution of larvae in relation to the plume or on the threshold planktonic densities that impact hoki larval survival.

4.3 Factors affecting inshore transport

There is strong evidence that the shelf is the preferred habitat of juvenile fish (James & Unwin 1996; Zeldis et al. 1998). Regardless of how well-fed they are, early stage hoki larvae survival rates may ultimately depend on whether or not they are carried inshore onto the continental shelf.

Off WCSI, there are several physical processes that are capable of carrying larval fish onshore or offshore. The interaction of these processes with fish distribution strongly depends on the vertical distribution of hoki larvae. The small amount of evidence on vertical distribution showed that off WCSI hoki larvae were found in greatest concentrations below about 75 m down to 190 m in late July 1987 (Murdoch & Quigley 1994) and off Tasmania at depths of 20 m to 90–120 m (Thresher et al. 1989). Thresher et al. also showed that the depth of maximum abundance was 60 m and below during the night and 40 m and below during the day. The vertical distribution of hoki larvae is potentially a result of where they are spawned in the water column (300 m: Langley 1993), vertical mixing processes and larval behaviour. Until we have more detail about their usual vertical distribution we cannot be sure exactly how onshore / offshore flows will affect horizontal larval distribution.

Coastal upwelling under the influence of southerly winds is known to occur in sporadic events of several days along the WCSI coast and rarely reaches a discernable steady state (Stanton & Moore 1992). There are upwelling favourable winds more than 50% of the time. During wind driven upwelling there is a subsurface drift towards the shore and a counter drift offshore at the surface. Analysis of alongshore winds and temperature records on moored current meters showed that low temperatures at 50 m were associated with upwelling-favourable wind (Stanton & Moore 1992). Cross sectional observations through an upwelling event (Bradford 1983) indicated that water with a temperature, salinity and dissolved inorganic nutrient content representative of water found at slightly less that 100 m depth offshore was located near the sea surface close inshore. This, as well as the observations of Zeldis et al. (1998), strongly suggests that hoki larvae found deeper than 100 m would drift inshore. Similar results were demonstrated in the Cook Strait Canyon where hoki eggs spawned at depths of 200m within the Canyon were advected by upwelling into the shallow coastal region off Cape Campbell where they subsequently hatched (Murdoch et al. 1990).

Conversely, if any larvae were in the surface layer impacted by the wind (the Ekman layer), estimated to be about 30 m thick (Stanton and Moore 1992), they would drift offshore with the low density, near-surface coastal water. In theory, north easterly wind conditions would reverse the process with near-surface larvae drifting towards the shore and those in the deeper water column being carried offshore.

Transient seaward-directed plumes of inshore water associated with the Hokitika Canyon are another possible transport mechanism (Moore & Murdoch 1993). These plumes extend well beyond the shelf and are associated with both strong offshore and onshore flows near the surface (Murdoch 1992). Contemporaneous maps of less than 5mm and greater than 5 mm hoki larvae showed that older larvae were found nearer to shore than younger larvae suggesting a net benefit accrued from the presence of a plume (Murdoch 1992).

Other poorly known phenomena could impact the continental shelf region off WCSI from time to time. The presence of eddies was evident in current meter records (Cahill et al. 1991; Stanton & Moore 1992) but little is known about their impact on the biological system on WCSI. There is also evidence of wholesale exchange of coastal water during a period when a large amount of freshwater impacted shelf water but was later exchanged over a very short period (Heath & Ridgeway 1985); no mechanism was suggested and the vertical extent of the transport is unclear.

4.4 Environmental variation and hoki YCS

In this section we discuss a study (Francis et al. 2006), and some subsequent analyses, that unsuccessfully attempted to find environmental predictors of hoki YCS, even though environmental variables were considered, which, according to arguments advanced in the preceding sections, should be closely linked with larval survival.

A first point to note is that the problem of predicting YCS for fish stocks is inherently difficult. Myers (1998) pointed out that although apparent environment–YCS relationships have been found and published for many fish stocks, a high proportion of these have not been verified by subsequent testing. In the case of hoki, some subsequent testing occurred. Bull & Livingston (2001) found that strong hoki YCSs were associated with cooler sea surface temperatures and a negative Southern Oscillation Index. Subsequently, Francis et al. (2006), took a more rigorous approach and used revised model estimates of YCS, an additional six year's data, and included surface nitrate concentrations that were considered to be a possible test of the nutrient / larval survival hypothesis, previously mentioned, to investigate predictors of YCS. Francis et al. (2006) were unable to find any predictive power of practical significance despite the theoretical support for them. Nevertheless, it is notable that the relationship between YCS and nitrate changed with time from being negative in the period 1980–1989 to positive in the period 1989–2000 (Figure 4.3). It is interesting to note that the period from 1990–1996 represented one of the more extensive periods of positive departures of the Multivariate ENSO index (Wolter & Timlin 2011) since 1950. The significance of an extended El Niño event to the behaviour of the ocean is not yet understood.

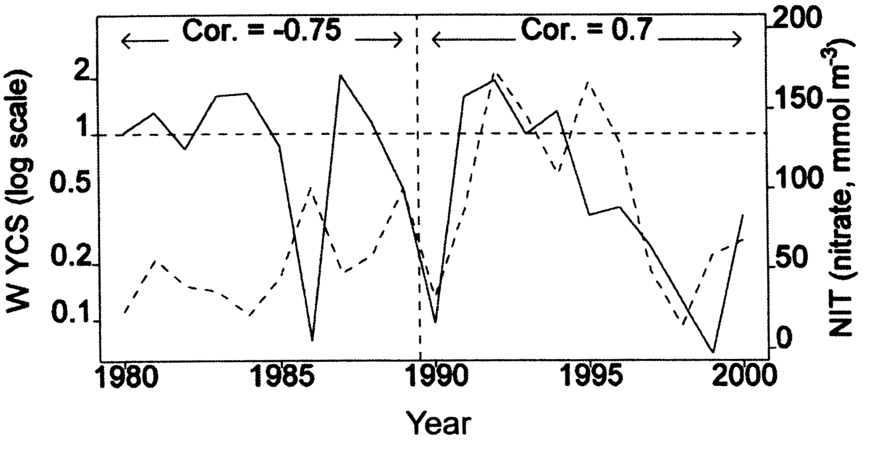

Figure 4.3: Comparison between WCSI YCS (solid line, left axis) and nitrate (dashed line, right axis: 5-month time integral of nitrate concentration, mmol m^{-3}).

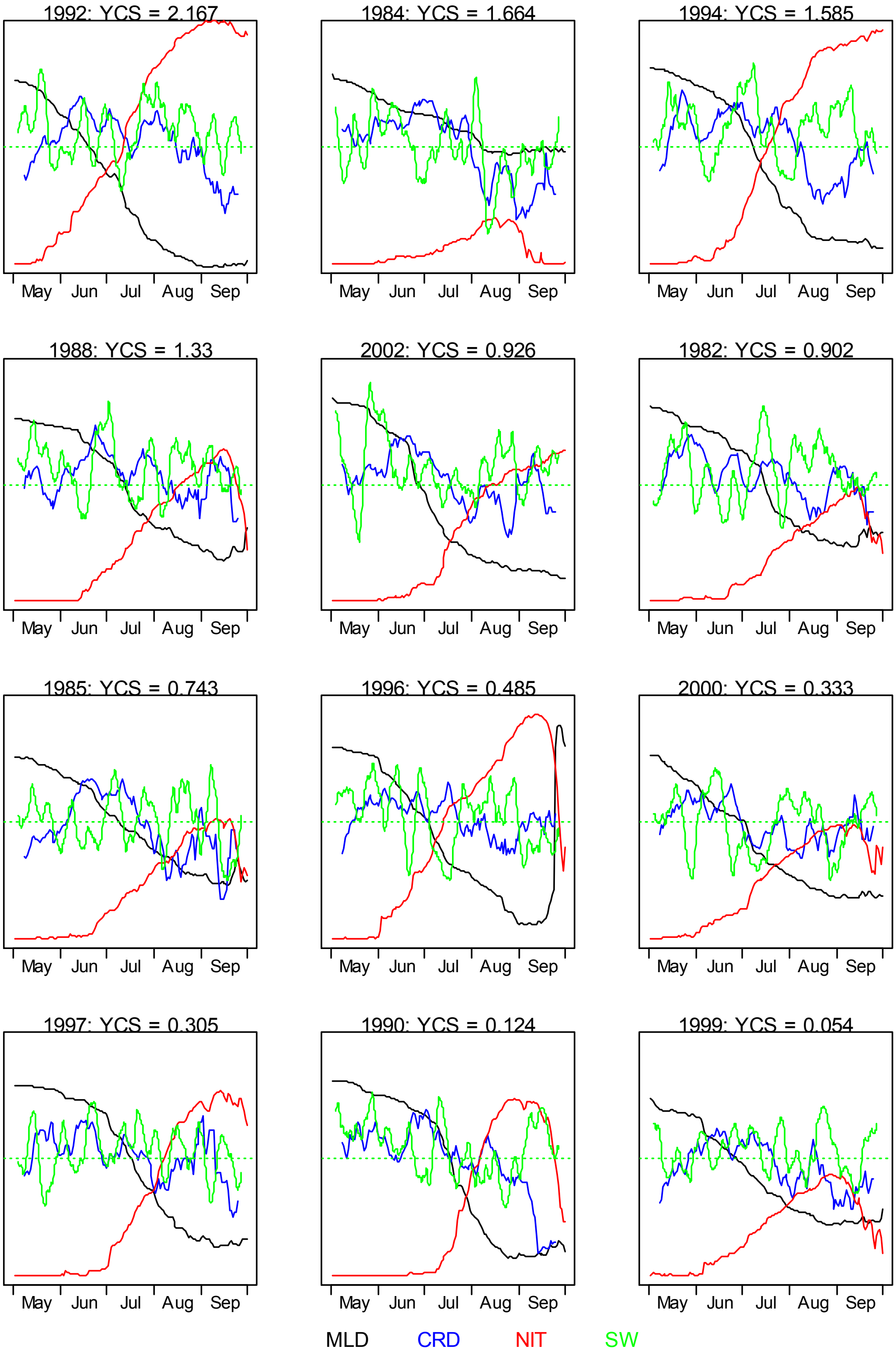

Figure 4.4A: Training set of data used to formulate hypotheses about environmental predictors of year-class strength (YCS). Each panel corresponds to one year and shows plots of four environmental variables against time: modelled mixed layer depth (MLD) (0-300 m), surface nitrate NIT (0–6 μM), strength of the SW wind (SW) (-15 − +15 ms^{-1}), and calculated critical depth (CRD) (0–300 m). The panels are ordered by decreasing model estimates of YCS and the person formulating the hypotheses knew the YCS, but not the year, for each panel.

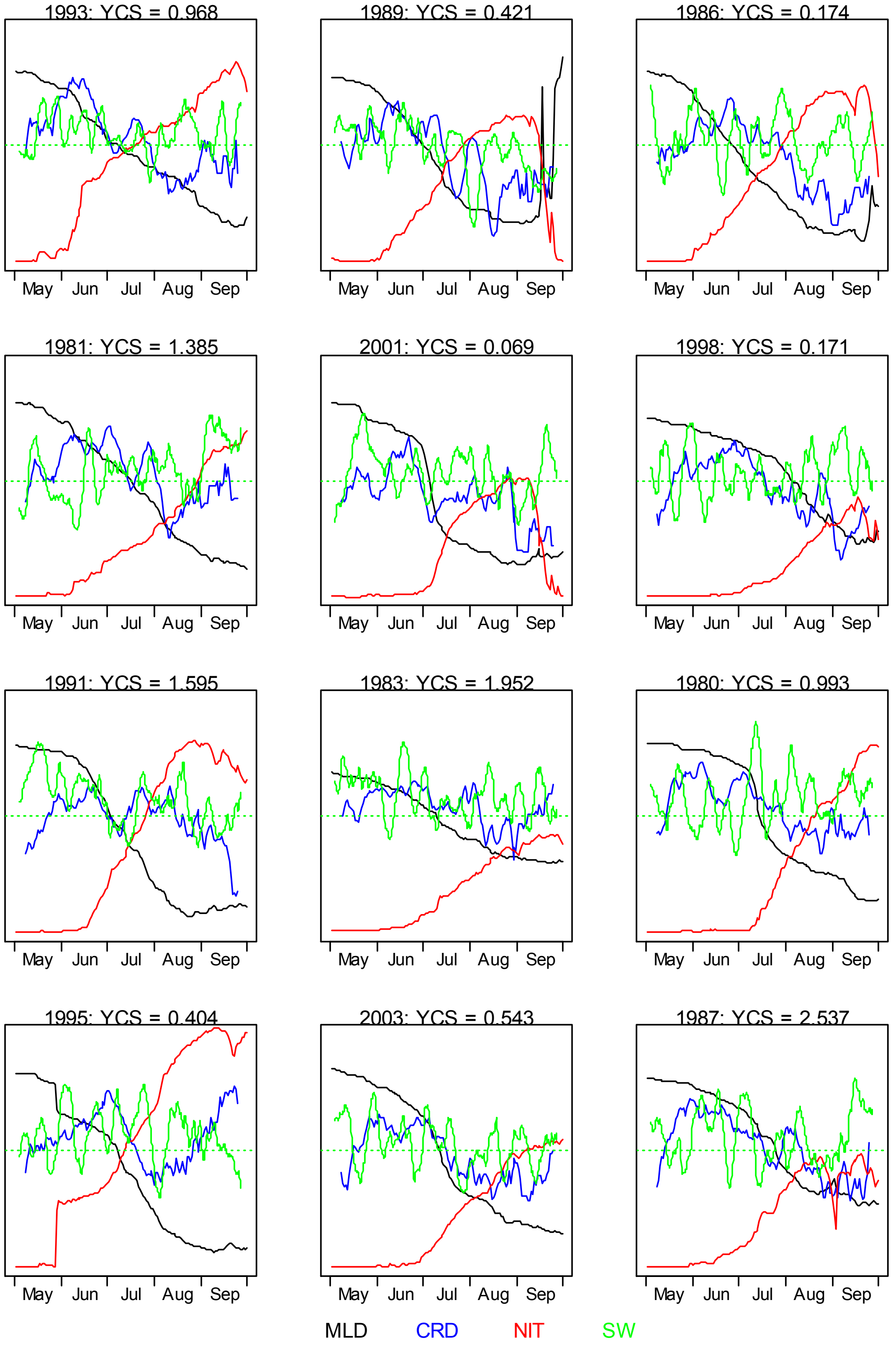

Figure 4.4B: Test set of data used to test hypotheses about environmental predictors of year-class strength (YCS). Each panel corresponds to one year and shows plots of four environmental variables against time: modelled mixed layer depth (MLD) (0–300 m), surface nitrate NIT (0–6 μM), strength of the SW wind (SW) (-15 – +15 ms^{-1}), and calculated critical depth (CRD) (0–300 m). The panels are randomly ordered, and the person formulating the hypotheses knew neither the YCS nor the year, for each panel.

A weakness in the approach of Francis et al. (2006) is that all environmental variables were averaged over time within each year. In this report we describe some subsequent analyses that considered how each environmental variable varied with time between 1 May and 30 September. Four variables were considered: mixed layer depth, the critical depth, surface nitrate, and the strength of the SW winds. The data for the 24 years 1980–2003 were divided into two parts, each containing 12 years – a training set (Figure 4.4A), and a test set (Figure 4.4B) – in such a way that the YCSs associated with each part covered a similar range. The training set was used to formulate hypotheses about the relationship between the environmental variables and YCSs, and the test set was used to test these hypotheses. The person formulating the hypotheses saw plots of both the training and the test environmental data sets. In the case of the training set, the person formulating the hypotheses knew the YCS but not the year for each panel and for the test data set, the person formulating the hypothesis knew neither the YCS nor the year.

After an examination of the training set, three potential predictors of YCS were selected: the day number (counting from 1 May) on which surface nitrate first exceeded 0.5 μM; the day number on which the mixed layer depth first equalled the critical depth; and the depth at which the critical depth first equalled the mixed layer depth. Only the third of these actually showed much correlation with YCS in the training set (Figure 4.5C). However, the hypothesis that mixed layer depth is correlated with YCS was not supported by the test set (Figure 4.5F).

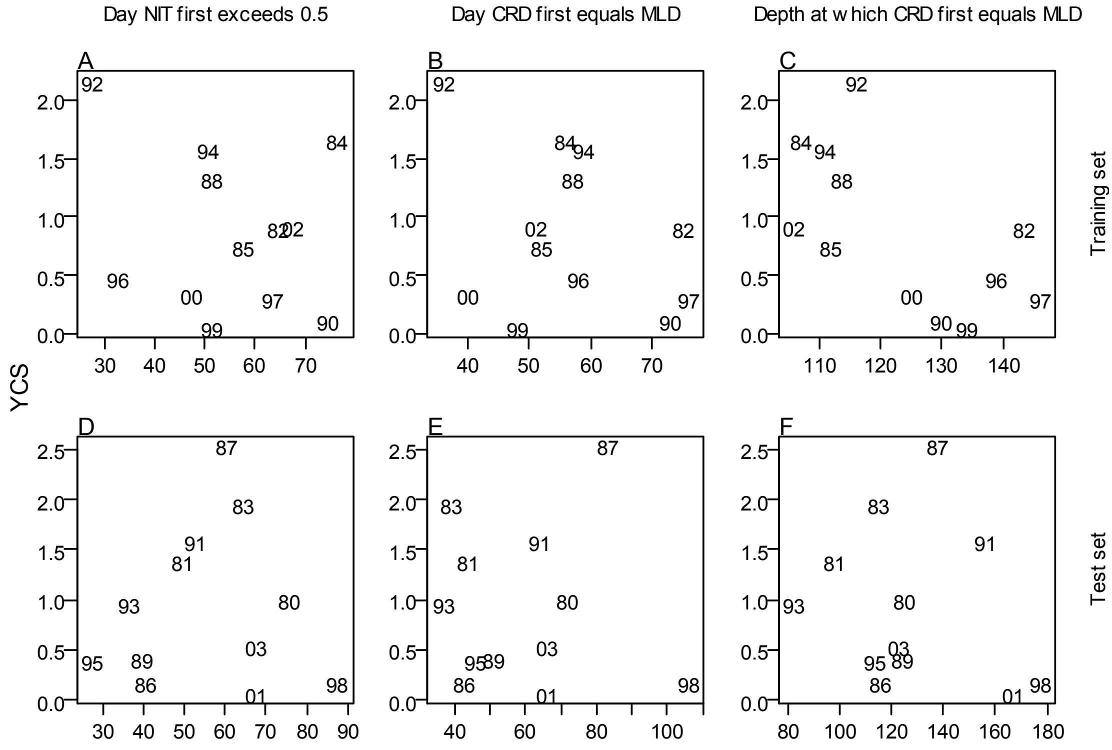

Figure 4.5: Plots of model estimates of YCS (y-axis) vs three potential predictors of YCS (x-axis) for the years in the training set (upper panels), and those in the test set (lower panels). The predictors are: the day number (counting from 1 May) on which surface nitrate first exceeded 0.5 μM (left panels); the day number on which the mixed layer depth first equalled the critical depth (middle panels); and the depth at which the critical depth first equalled the mixed layer depth (right panels). Each plotted point represents a year (e.g. 1992 is plotted as '92').

Several problems may be contributing to our failure to predict YCS. The first may be our lack of data on the detailed impact of environmental variability over the whole spawning season. From about mid June to mid August there appear to be daily pulses (Murdoch & Quigley 1994) of billions of spawned eggs which lead to hundreds of millions of larvae per day. These larvae are scattered across the changing seasonal progression of mixed layer depth, critical depth, nitrate concentrations and south-westerly winds. Therefore, unless there is some highly negative long term event over a large fraction of the spawning season, then there may not be a resulting YCS signal big enough to detect, integrated over the spawning season.

Second, our time series are quite short (only 24 y), and the number of potential environmental predictors is large. This means that there is a high probability of finding a false correlation and it is not possible to be confident about the strength of an environment–YCS relationship (Francis 2006).

Third, a possible reason for the failure to predict YCS is that some phenomena that may be important to the survival of hoki larvae, at least in some years, are not captured in the environmental variables used by Francis et al. (2006) or in the current report. This is true of eddies, transient offshore-directed plumes, and capping of slope water that are discussed above. Also, nothing is known about year-to-year variation in the vertical distribution of hoki larvae. If variation in vertical distribution of larvae is substantial, then along-shore winds that are usually favourable for the inshore transport of larvae would be much less so, in years when the larvae were much shallower, or deeper, than normal.

A fourth reason may be the quality of the environmental and YCS data. Most of the environmental data in Figure 4.4 are derived from a model or from empirical equations rather than actual measurements. Although there were some data to validate the modelled mixed layer depth and surface nitrate concentrations (Hadfield & Sharples 1996), these data were not extensive and may not have been sufficient to give real confidence that year to year variability was being accurately portrayed.

Finally the YCS data are derived from a stock assessment model which combines data from what are assumed to be two distinct spawning stocks of hoki. The stock hypothesis used by this model (see Section 2.1) may be wrong, and so the YCS used by Francis et al. (2006) may not be representative of the fish that spawn in WCSI (the western stock). Even if the stock hypothesis is correct and these YCS are truly representative of the western stock, there is room for error. Francis et al. (2006) assumed that YCS was determined primarily by the extent of larval survival, and thus chose environmental variables that might predict this survival. It could be that juvenile survival is variable enough to substantially affect YCS. In this case, variables that were useful predictors of larval survival would not necessarily be good for predicting YCS. Francis et al. (2006) also changed the model so that model estimates of YCS changed substantially from those used in earlier studies.

4.5 Advancing our ability to predict YCS of hoki from environmental variables

In the preceding discussion of the physical oceanographic processes that may be linked to the survival and inshore transport of young larvae, what stands out is:

1. our lack of basic data on the proportion of juvenile hoki on Chatham Rise that were spawned on WCSI;
2. a lack of verification that model-estimated year class strength indices are indicative of the annual survival rates of larvae and juveniles;
3. our lack of basic data on the vertical distribution of young hoki larvae in relation to their physical environment;

4. our lack of basic data on the minimum level of food that a first feeding larva needs in order to survive;
5. our lack of measured nitrate concentration profiles that are linked to an understanding of the oceanographic processes occurring in the Tasman Sea and further afield including ENSO events;
6. our lack of basic data and understanding of the links between mixed layer depth, phytoplankton growth, nutrients, light and small copepod growth with time;
7. our lack of basic data on the spatial and temporal variability in inshore / offshore transport in relation to the vertical and horizontal distribution of young fish;
8. a need for novel approaches to modelling YCS and larval survival that are capable of incorporating non-linear effects.

Any future examination of the predictive power of environmental data (e.g. temperature) should ideally include postulated mechanisms by which the identified environmental variable acts on year class strength. Schematic concepts need to be developed offering relatively well-understood, fairly well-defined frameworks for the identification and elaboration of important mechanistic linkages between climate variability and fishstock dynamics.

4.6 Summary

Preliminary results suggested that year-to-year variations in the year class strengths of hoki may be influenced by the timing of winter mixing and the pattern of its progression. It is reasonable to hypothesise that sufficient nitrate and other phytoplankton nutrients must be mixed into the upper water layers to allow the rate of primary production to increase and leave enough time before the hoki eggs are spawned for this additional primary productivity to flow through into the food of hoki.

Further analysis, using revised estimates of YCS, an additional six years data, and including surface nitrate concentrations as a test of the nitrate / larval survival hypothesis, was used to investigate predictors of YCS in more detail, but failed to replicate the earlier results. No predictive power of practical significance was found in this analysis.

However, it is interesting to note that the relationship between YCS and nitrate changed with time from being significantly negative in the period 1980–1989 to significantly positive in the period 1989–2000. The period from 1990–1996 represented one of the more extensive periods of positive departures of the multivariate ENSO index since 1950 and the significance of such an extended El Niño event on the behaviour of the ocean is not yet understood.

There are other reasons why the relationship between oceanographic processes and year class strength may be more complex than at first suspected.

To evaluate these hypotheses, we need a greater understanding of the impact of ENSO events on the ocean and time series of data are required to verify model outputs.

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