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

Editors

J.M. Bradford-Grieve¹ M.E. Livingston²

> ¹NIWA Private Bag 14901 Wellington 6241

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CONTRIBUTORS

J.M. Bradford-Grieve¹

F.H. Chang¹

R. J. Davies-Colley²

R.I.C.C. Francis¹

M.G. Hadfield¹

J.A. Hall²

 $R.J.\ Hurst^l$

M.R. James²

¹NIWA

Private Bag 14901

Wellington 6241

²NIWA

P.O. Box 11-115

Hamilton 3251

³Ministry of Fisheries

P.O. Box 1020

Wellington 6140

⁴Department of Marine Science

University of Otago

P.O. Box 56

Dunedin 9054

⁵NIWA

P.O. Box 8602

Riccarton 8440

Now c/o World Fisheries Project, Gizo, Solomon Islands.

M.E. Livingston³

M.I. Moore

R.C. Murdoch¹

S.D. Nodder¹

R. O'Driscoll¹

P.K. Probert⁴

A.-M. Schwarz⁵

P.J.H. Sutton¹

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EXECUTIVE SUMMARY

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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 As well as recent work, the report includes previously unpublished work from research initiated during the West Coast Marine Ecosystem programme, 1979–1989.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 coastaltrapped 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 (NO₃-N) peaks. Nitrogen is available in three forms. "New" nitrogen is in the form of NO₃ and regenerated nitrogen is in the form of ammonia (NH₄) and urea. Nutrient limitation in summer results in small cells dominating phytoplankton populations, decreased production rate based on regenerated (recycled) NH₄ 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 NO₃ uptake and ambient NO₃-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, NO₃-N is the most important source of nitrogen available, although the less than 2 µm size fraction of phytoplankton is a major user of NH₄ 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 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, 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.

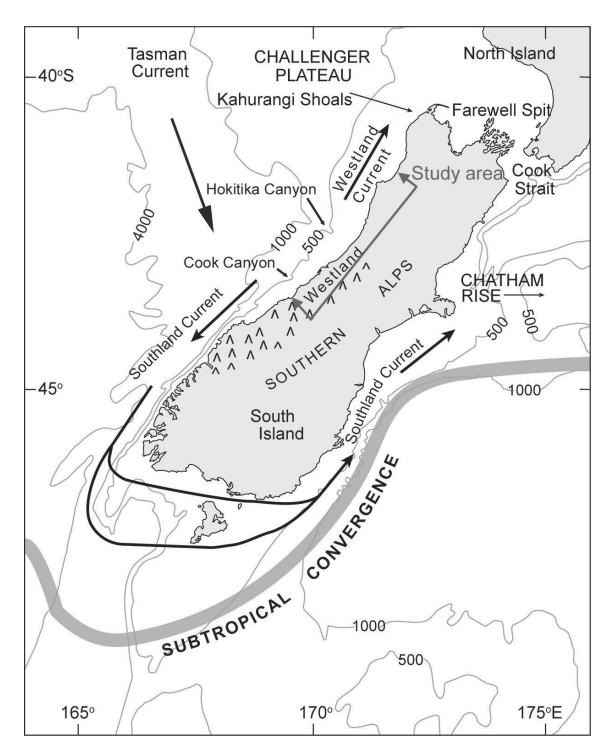


Figure 1.1: Bathymetric chart of South Island, New Zealand indicating the region of the West Coast South Island (WCSI) studied during the West Coast Ecosystem Programme and geographic names mentioned in the text. See also Figure 3.6.1 for a more detailed bathymetry.

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.

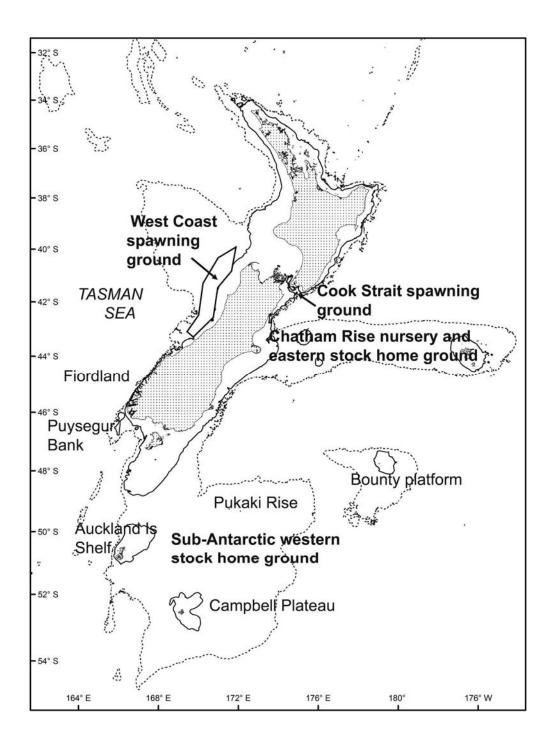


Figure 2.1.1: Spawning grounds and home grounds of western and eastern stocks of hoki.

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)).

			9	Spawning			No	n-spawnin	g fisheries	TACC
Fishing			Cook	_	Sub-	Chatham		-	Total	
Year	WCSI	Puysegur	Strait	ECSI	Antarctic	and ECSI	ECNI	Unrep.	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 prespawning 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 twintrawl 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.

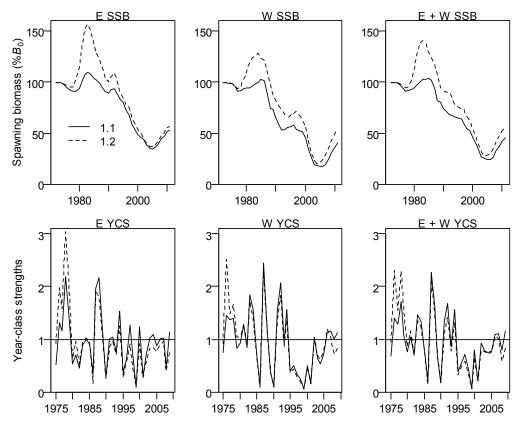


Figure 2.1.2: Estimated spawning biomass trajectories (SSB, upper panels) and year-class strengths (YCS, lower panels) for the E (left panels), W (middle panels) and E + W stocks (right panels) from the base case model (Run 1.1) and one of the sensitivities (Run 1.2). Plotted values are medians of marginal 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

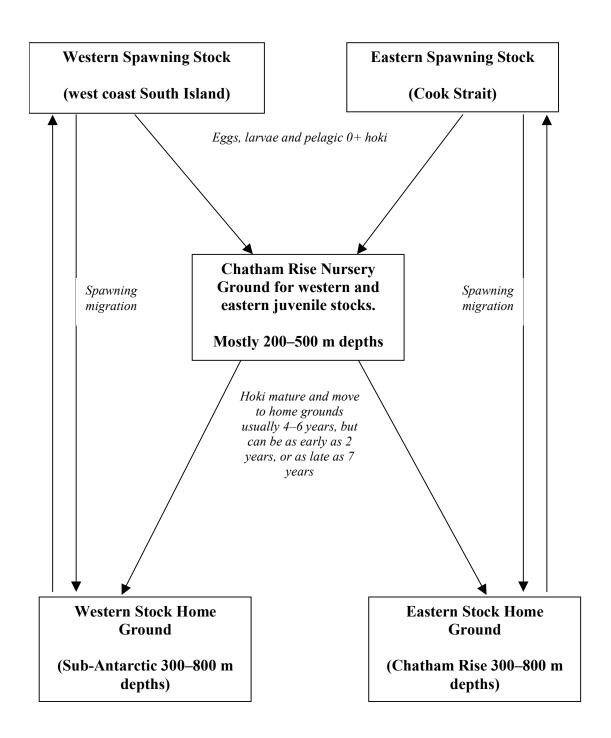


Figure 2.1.3: Current view of the life-cycle of hoki from Livingston (1990).

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.

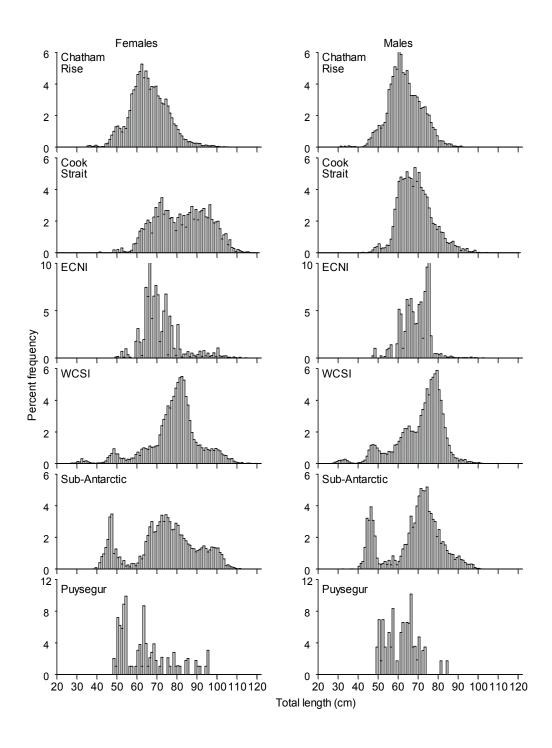


Figure 2.1.4: Comparison of length frequencies of hoki taken in commercial catches from different areas. Example is from the 2006–07 fishing year (Ballara et al. 2008).

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

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).

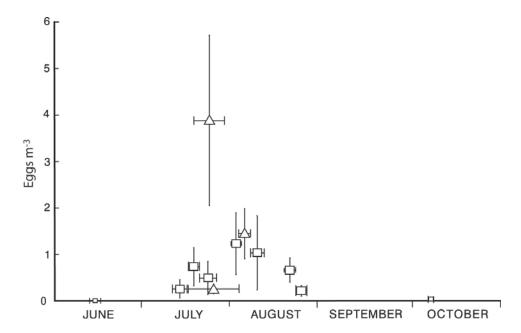


Figure 2.2.1: Mean \pm 1 S.D. of density of hoki eggs in the upper 0-200 m for each survey by date as sampled by bongo net. Horizontal bars represent start and finish dates. Squares and triangles represent Ministry of Fisheries and NIWA surveys, respectively (Zeldis et al. 1998).

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).

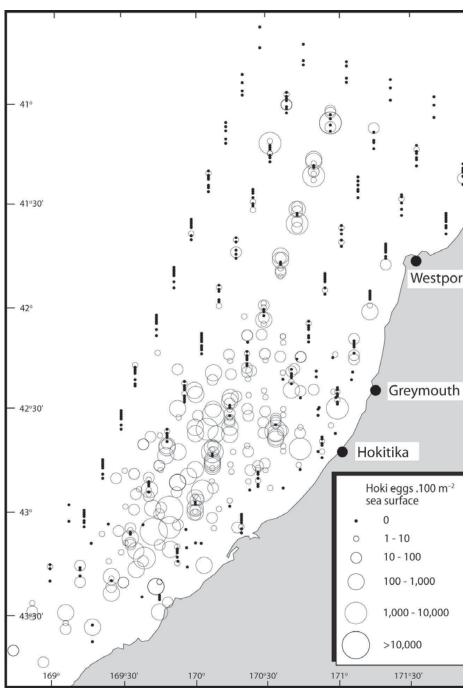


Figure 2.2.2: Distribution and abundance of hoki eggs from all surveys (Zeldis et al. 1998).

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).

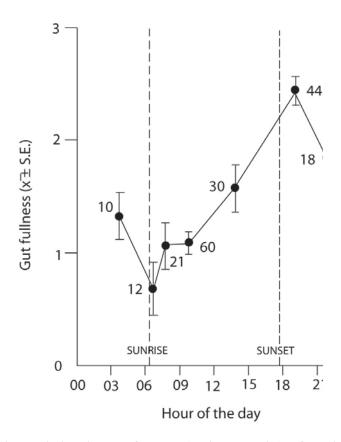


Figure 2.2.3: Diel variation in gut fullness (arbitrary units) of hoki larvae (number of observations listed besides each data point) collected from Cook Strait, September 1987 (Murdoch 1992).

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.

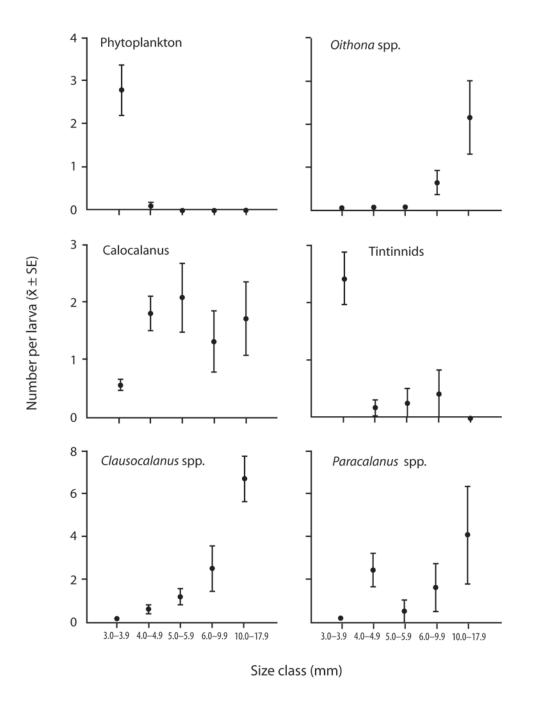


Figure 2.2.4: Mean number of selected prey types, approximately in order of increasing size, per hoki larva for the different size classes examined. The numbers of larvae for each size class were 130, 52, 19, 12, and 12 mm, respectively (Murdoch 1990).

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).

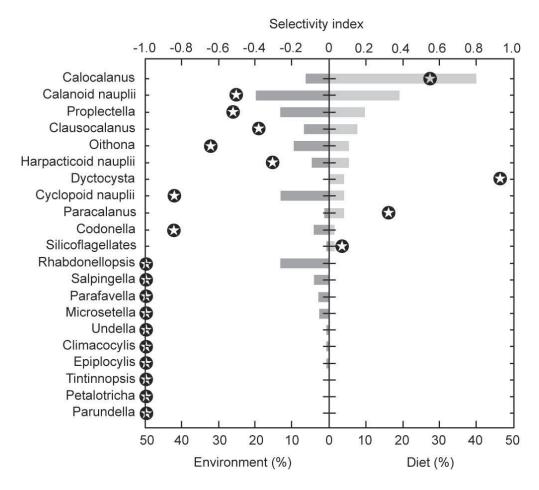


Figure 2.2.5: Percentages of different planktonic species in the environment (left) and diet (right) of hoki larvae. The value of the alpha Selectivity Index for each species is denoted by a star. Values greater than 0 represent positive selection, and values less than 0 represent negative selection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

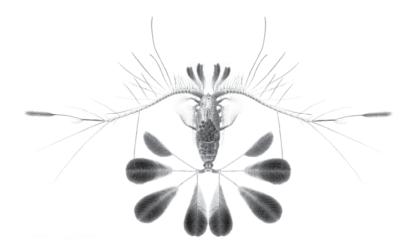


Figure 2.2.6: Morphology of the calanoid copepod genus *Calocalanus pavo* to show the features that apparently aid flotation when at rest (Giesbrecht 1892).

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).

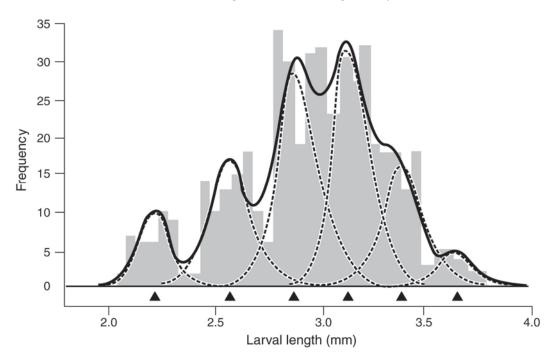


Figure 2.2.7: Histogram of size frequency distribution of hoki larvae from one sample collected within a patch. Results of a modal analysis are also shown, indicating the position of the normal distributions associated with each cohort (dotted lines), the estimated mean length of each cohort (triangles),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

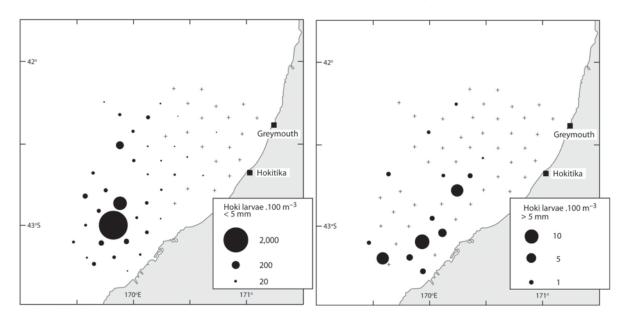


Figure 2.2.8: Abundance of hoki larvae less than 5 mm standard length (left panel) and greater than 5 mm standard length (right panel) off Westland, July 1987 (from Murdoch 1992).

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.

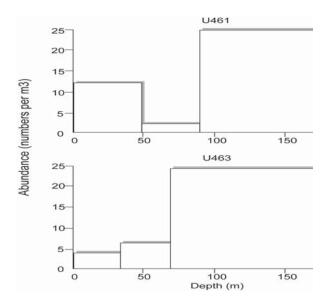


Figure 2.2.9: Vertical distribution of hoki larvae in the upper 200 m of the water column from two plankton net tow series off Westland (Murdoch & Quigley 1994).

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%).

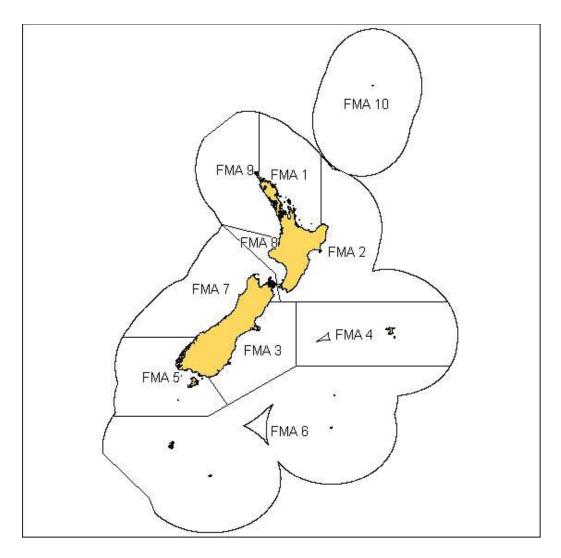


Figure 2.3.1: New Zealand Fishery Management Areas

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) Hoki	QMA Part	Area WCSI ¹	Average catch 1986-87 to 1995-96 (t) 131 800	Average catch 1996-97 to 2005-06 (t) 81	QMA7/ WCSI catch as a % of total EEZ catch (t) 1986-87 to 1995-96 63	QMA7/ WCSI catch as a % of total EEZ catch (t) 1996-97 to 2005-06 40
	HOK1			050		
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 2 1 7	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	
Inshore	Blue mackerel Elephant fish Red gurnard	Location W, TB TB WC, TB	Period R & spent Jan-Feb RR Mar-Apr, Oct	WC: low WC, TB: mod	
	Rig Rough skate School shark Tarakihi	WC, TB	Mature eggs Mar-Apr RR Mar-Apr	WC, TB: low WC, TB: low WC: mod-high, TB: low-mod WC, TB: low	
Inshore & mid depths	Barracouta	WC, N, TB	RR Jul-Oct, Feb	WC: low; TB: mod	
•	Jack mackerel (<i>T. declivis</i>) Jack mackerel (<i>T. murphyi</i>) Northern spiny	WC, TB WC, TB	Peak RR Nov, extends Jan-Mar RR Jan-Feb, R & spent Jul-Aug	WC: low	
Mid depths	dogfish Sea perch Smooth skate Spiny dogfish Alfonsino	WC, TB	Mature eggs Mar-Apr	WC: low WC: low WC, TB: low WC: low-mod	
deptilis	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 Hake Ling Lookdown dory Pale ghost shark Ray's bream	WC, WC, WC, WC	R Jun-Sep R Jun-Oct RR Aug-Sep Spent Jun-Aug	WC: low-high; TB: low WC: low-high; TB: low WC: mod, TB: low WC: low WC: low WC: low	
	Red cod Ribaldo Silver warehou Silverside	WC, WC WC,	RR Jul-Sep R Jul-Aug R Jul-Oct	WC: TB: low-mod WC: low WC: low; TB: mod WC: low	
Deep	White warehou Moonfish Orange roughy	WC, Challenger Plateau	R Jul-Sep RR Jun-Aug	WC: low WC 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).

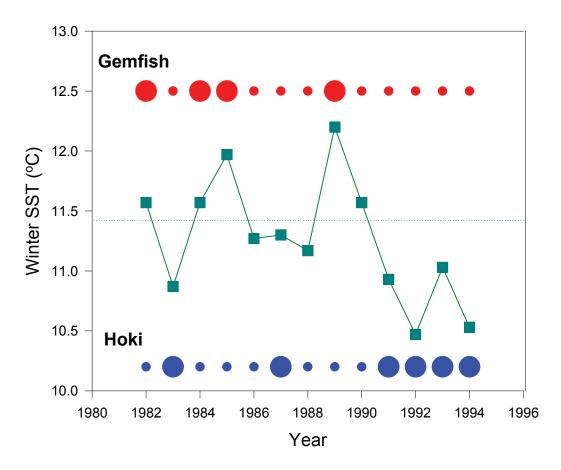


Figure 2.3.2: Patterns of gemfish (red circles) and hoki (blue circles) recruitment (circle size denotes strong or weak year class strength) and winter sea surface temperature (green).

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).

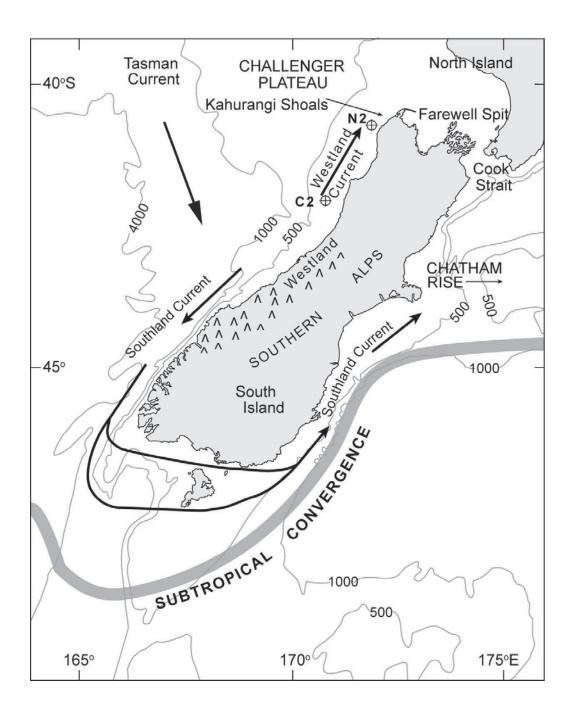


Figure 3.1.1: General Circulation features off Westland, bathymetry and location of current meter moorings (adapted from Moore & Murdoch 1993).

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.