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A synopsis of the biology of ling (*Genypterus blacodes*) and a history of its fishery and assessment in New Zealand

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EXECUTIVE SUMMARY

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The ling, *Genypterus blacodes*, is an important and abundant commercial species on the New Zealand continental shelf and also supports fisheries off Chile, Argentina, Falkland Islands, and Australia. Scientific research on this species accelerated since the early 1980s, resulting in the production of numerous papers and reports. Some of the reports are unpublished or occur in 'grey' literature and are not readily accessible. This report aims to review the available literature and data on ling, primarily to provide synopses on the biology and life history of the species from worldwide sources, but also to provide references should the reader wish to investigate particular aspects in more detail. In addition, the report describes the history and development of the New Zealand fisheries for ling and summarises the assessment and management of ling in New Zealand waters.

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[1] Pachyornis Science, New Zealand.

1. INTRODUCTION

The ling, *Genypterus blacodes* (Foster, 1801), is an important and abundant commercial species on the New Zealand continental shelf. Published scientific research on this species commenced in New Zealand in 1938 (Graham 1938, Shorland 1938). Limited information available on the species was available before the early 1980s, but since then large quantities of data have been collected resulting in the production of numerous papers and reports. However, some of the data and reports are unpublished or occur in 'grey' literature not readily accessible to the wider community. Because ling occurs, and there is a commercial fishery, in all of the Southern Hemisphere's oceans, reports on aspects of its biology and fisheries have also been produced in other countries, particularly Chile, Argentina, and Australia.

1.1 Overview of text

This report aims to review the available literature and data to provide synopses on:

- the biology and life history of ling from worldwide sources,
- the history and development of the New Zealand fisheries for ling, and
- the assessment and management of ling in New Zealand waters.

The synopsis of the biology and life history draws on studies of ling from New Zealand and elsewhere, and in all cases the location of data collection is noted. It is likely that the biology of a single species occurring in several widespread locations will be relatively consistent between areas. This review, therefore, provides the most comprehensive summary of ling biology to date, but also highlights any between-area differences. Unless otherwise stated, all references to ling length are total length.

The text relating to ling fisheries and their assessment and management deals almost exclusively with the New Zealand experience. However, some reference is made to studies from other areas where these provide interesting contrasts or present methods that could be applicable to the New Zealand situation.

1.2 Species of ling

Ling (*Genypterus blacodes*) belong to the cusk eel family (Order Ophidiiformes, Family Ophidiidae). The order Ophidiiformes was identified by Cohen & Nielsen (1978) using a combination of characters. One or more specialised characters shared by all presumed ophidiiforms have yet to be discovered. Cusk eels are a group of benthic fishes occurring in all oceans from the shallows to depths of at least 4000 m. The taxonomic classification of Genus *Genypterus* (and the Family Ophidiidae in general) is open to some conjecture. Nielsen et al. (1999) reviewed the status of names given to *Genypterus* species, but gave no references to any work that had rigorously studied the problem. They retained the following four valid species: *G. blacodes, G. capensis, G. chilensis,* and *G. tigerinus*. The name *G. maculatus* was recorded as a junior homonym and was retained pending a decision from the International Commission. *Genypterus brasiliensis* was recorded as a junior synonym of *G. blacodes*. As at 2022 on FishBase, six *Genypterus* species were recognised: *G. blacodes*, *G. brasiliensis*, *G. capensis*, *G. chilensis*, *G. maculatus*, and *G. tigerinus* (Froese & Pauly 2000).

Paulin et al. (1989) listed six species of cusk eel (Family Ophidiidae) from New Zealand waters but noted that all, except *G. blacodes*, were rare. Only two were in the genus *Genypterus*, i.e., *G. blacodes*, and the northern ling, *G. microstomus*. However, in the most recent revision of taxonomic name status, Nielsen et al. (1999) synonymised *G. microstomus* with *G. blacodes*.

Comparisons of partial sequences of mitochondria1 DNA (mtDNA) between *Genypterus* species from New Zealand, Australia, and South Africa showed *G. blacodes* from New Zealand and Australia to be a separate species from both the rock ling, *G. tigerinus*, from Australia, and the kingclip, *G. capensis*, from South Africa (Smith & Paulin 2003). Genetic differences between *G. blacodes* from New Zealand and Tasmania were small with only 5 out of 575 mtDNA nucleotides differing. A fourth postulated species, the banded ling, *G. microstomus*, based on a few small specimens from New Zealand and Australia, could not be distinguished from *G. blacodes*, leading to the conclusion that *G. microstomus* was a junior synonym of *G. blacodes* (Smith & Paulin 2003). Using five microsatellite pairs, Canales-Aguirre et al. (2010a) found significant genetic differences between *G. blacodes, G. chilensis*, and *G. maculatus* in Chilean waters, indicating that *G. maculatus* was a valid species.

The conclusions of Smith & Paulin (2003) were very similar to those of Daley et al. (2000) and Ward et al. (2001) who analysed microsatellite DNA and mtDNA to determine whether the orange and pink morphs of *G. blacodes* were genetically distinct, and to examine the genetic difference between *G. blacodes*, *G. tigerinus*, and *G. capensis*. They concluded that the orange and pink morphs were probably juvenile and adult forms, respectively, of a single species. However, in contrast to Smith & Paulin (2003), Daley et al. (2000) concluded that *G. blacodes* from Australia and *G. capensis* from South Africa are more closely related to each other than either is to *G. tigerinus* from Australia.

Specimens of the six species of *Genypterus* were compared using a Polymerase Chain Reaction (PCR) technique followed by phylogenetic analysis (Forensically Informative Nucleotide Sequencing) (Santaclara et al. 2014). The developed methodology used the mitochondrial cytochrome oxidase subunit I gene (COXI) as molecular marker. The work was completed to enable the identification of the species in any kind of commercial product, from fresh or frozen fish, to a cooked meal. All six species (*G. blacodes*, *G. brasiliensis*, *G. capensis*, *G. chilensis*, *G. maculatus*, *G. tigerinus*) were differentiable. Relatively close relationships were apparent between *G. chilensis* and *G. maculatus*, as well as between *G. blacodes* and *G. tigerinus.*

Ayling & Cox (1982) described *G. blacodes* (Figure 1) as a robust eel-like fish with a bluntly pointed snout and an undershot jaw. Its dorsal and anal fins are continuous with its caudal fin. It has slender, two-rayed pelvic fins set well forward beneath the lower jaw, where they may be mistaken for chin barbels. The fish is orange-pink dorsally, with occasional splotches of brown, but is paler ventrally. The skin is covered with very fine scales and a thick coating of mucus. Ayling & Cox (1982) wrote (rather unfairly, in the opinion of the current author) that “the ling must surely be one of the most repulsive of the fishes found in New Zealand waters”.

As is with many species, *G. blacodes* has several common names. The FAO standard English name is the pink cusk-eel. Names commonly used in countries landing significant quantities of this fish are as follows:

New Zealand	ling, and its Māori names hoka and hokarāri
Australia	ling, rock ling, pink ling
Chile	congrio dorado
Argentina	abadejo

The species is also sometimes referred to as kingclip, the common name for *G. capensis* off southern Africa. In Australia, ‘rock ling’ is more generally used to describe *G. tigerinus*.

Figure 1: Ling (*Genypterus blacodes*). (Photo by Peter Marriott, NIWA.)

Studies of *G. blacodes* aimed primarily at stock differentiation have produced ranges and mean values for a variety of morphometric and meristic parameters. Chong Lay-Son (1984) analysed 10 meristic and 20 morphometric characteristics for ling off the coast of central Chile and compared some of these parameters with similar ones derived from off the coast of Argentina (from Chocair et al. 1969, cited by Chong Lay-Son 1984). Colman (1995) analysed five morphometric characteristics for ling from various parts of the New Zealand continental shelf. Ling have no dorsal or anal spines but do have 141–164 dorsal soft rays, 101–126 anal soft rays, and 68–70 vertebrae (Nakamura et al. 1986, Nielsen et al. 1999).

Meristics and morphometrics were also used as part of a study to test whether more than one species of *Genypterus* occurred in New Zealand and Australian waters (Smith & Paulin 2003). Several of the meristic characters overlapped published ranges for other *Genypterus* species, leading to the conclusion that meristics and morphometrics are of limited use for the identification of *Genypterus* species in general.

2. BIOLOGY and LIFE HISTORY

2.1 Geographical distribution

Genypterus blacodes has been recorded from the continental shelves around New Zealand, southern Australia including Tasmania, and South America from northern Chile south to Patagonia and north to Uruguay, including the Falkland Islands (Froese & Pauly 2020).

In New Zealand waters they occur around the entire continental shelf in depths from about 10 to 1200 m, although they are most abundant in depths of 50–800 m south of 39° S (Anderson et al. 1998). Ling were recorded in over 80% of New Zealand research bottom trawl tows in depths from 350 to 750 m (Anderson et al. 1998). They are a predominantly demersal species, caught regularly over both smooth trawlable and rocky untrawlable substrates, but have been captured in midwater, both feeding and spawning (Livingston 1990) predominantly in depths from 350 to 750 m (Bagley et al. 2000). Little is known about the distribution of juvenile ling, although they have been recorded from shallow depths out to about 500 m (O’Driscoll et al. 2003). When they are about 40 cm total length they begin to appear in trawl samples over most of the adult range (O’Driscoll et al. 2003).

In Australian waters they occur from Western Australia as far north as 33° S, across the Great Australian Bight and around Tasmania to New South Wales, with their northern limit off the east coast being about 32° S (Tilzey 1994). They are found between depths of 20 to 1000 m, although appear most abundant in the 300–550 m depth range (Tilzey 1994).

Off South America, ling occur in the Pacific Ocean off Chile from Coquimbo (29° S) to the southern border with Argentina (Paredes & Bravo 2005) and in the Atlantic off Argentina and around the Falkland Islands northwards to at least Uruguay (34° S). They occur on the shelf and continental slope in depths from 45 to 700 m, although appear most abundant off Chile between 200 and 400 m (Tascheri et al. 2003) and off Argentina between about 60 and 200 m (Renzi 1986, Villarino 1998, Cordo 2004). The preferred depth range of ling off South America appeared to be shallower than the preferred depth range off New Zealand and Australia. In Falkland waters, however, ling occur mostly over rocky substrata off the continental slope, between 100 and 1000 m (Brickle et al. 2003), but is perhaps most abundant in depths of 150–300 m (Nyegaard et al. 2004). Records of *G. blacodes* off Brazil and Peru may be extreme outliers or misidentified specimens of *G. brasiliensis* or *G. chilensis*, respectively (Froese & Pauly 2020).

2.2 Stock structure

Investigations of ling stock structure have searched for differences in morphometrics and meristics, genetics, life-history parameters, and population size and age structures. A summary below of studies by country indicates that multiple stocks are likely present around New Zealand and off South America but perhaps not Australia. There is probably substantial within-country gene flow between adjacent populations—a situation similar to that for *G. capensis* off South Africa (Henriques et al. 2017). Extensive genetic sampling of high-resolution genetic markers may resolve within-country uncertainty (Papa et al. 2021).

New Zealand

Colman (1995) analysed the morphometrics of heads and otoliths of ling from south of about 41° S using fish with total lengths of 70–100 cm. Otolith morphometrics indicated two distinct groups: northern (comprising Chatham Rise, Canterbury, and west coast South Island) and southern (comprising all the Campbell Plateau, Puysegur Bank, and the Stewart-Snares shelf). Male fish from off Otago fitted best in the southern group, but females were more aligned with the northern group. Head measurements also indicated a clear north-south split, with Otago fish being more clearly aligned with the southern group. Generally, fish from the northern areas had longer heads, narrower interorbital widths, and thinner otoliths than southern fish. A sample of seven males from the Bounty Plateau were distinct from both the northern and southern groups.

Meristics and morphometrics were also used as part of an investigation of the species and stock structure of *Genypterus* species in New Zealand and Australian waters (Smith & Paulin 2003). The counts and measurements had similar ranges to those produced by Daley et al. (2000) for Australian fish. There were no significant differences between northern and southern New Zealand ling in any of the characteristics, leading to the conclusion that meristics and morphometrics were of limited use in the distinction of *Genypterus* populations.

The distribution of alleles in two polymorphic enzymes from 395 ling samples from five areas (north-east North Island, Cook Strait, west coast South Island, Canterbury Bight, Pukaki Rise) were analysed (Smith 1979). One (phosphoglucomutase) exhibited no areal differences in allele frequency. The other (glucosephosphate isomerase) exhibited no statistical differences in all the between-location pairwise comparisons, but differences were indicated when the Pukaki Rise sample was compared with the grouped data from the four northern locations. The probability of a difference increased when the Canterbury Bight data were removed from the combined group. Hence, Smith (1979) concluded that the Pukaki Rise ling were from a stock separate to that providing all the other samples, and that the two stocks were separated by the Subtropical Convergence. In an expansion of the 1979 study, Smith & Francis (1982) analysed the glucosephosphate isomerase allele frequency from a greater spatial and temporal range of samples. Despite the large sample size (n = 1743), there was no overall allelic heterogeneity. However, after pooling regional samples and considering hydrological conditions, Smith & Francis (1982) suggested that there were two or three ling stocks: one incorporating ling around North Island and the coastal areas around South Island as far south as the Snares Islands; a southern stock on the northern section of the Campbell Plateau (i.e., Pukaki Rise and Auckland Islands); and a possible third stock around Campbell Island. The Chatham Rise was proposed as an area of mixing between the mainland and southern stocks.

New Zealand *G. blacodes* specimens from three locations (Bay of Plenty, Chatham Rise, and the Campbell Plateau) were tested at two regions of the mtDNA: the cytochrome *b* and control region (Roberts et al. 2002, Smith & Paulin 2003). There was no evidence for any geographical structure from cytochrome *b* sequence variation, but molecular variation among the control region haplotypes indicated significant variation between the Campbell Plateau and both the Bay of Plenty and Chatham Rise, indicating 'northern' and 'southern' stocks. There was a greater significant difference in control region haplotype frequencies between the New Zealand and Tasmanian populations, indicating that the New Zealand populations were more closely related to each other than to *G. blacodes* from Tasmania. Papa et al. (2021) reviewed all genetic studies of ling in New Zealand waters and concluded that there was limited gene flow between stocks from the mainland (including Chatham Rise) and the Campbell Plateau, most likely due to the subtropical front acting as a barrier to migration.

Age-length data for ling from around the South Island were grouped by sex and five areas (i.e., Chatham Rise, Bounty Plateau, Sub-Antarctic including Puysegur Bank, west coast South Island, and Cook Strait) and the resulting von Bertalanffy curves were compared using a maximum likelihood method (Horn 2005). Pairwise comparisons indicated highly significant differences in growth across all five areas. Other comparisons of growth parameters have produced the same differentiation between areas (Horn 1993b, 2021).

Using information from published studies of genetics and morphology, from trends in catches, and from life history characteristics, Horn (2005) concluded that there were at least five distinct ling stocks in New Zealand waters: Chatham Rise, Sub-Antarctic (comprising Campbell Plateau, Pukaki Rise, Stewart-Snares shelf, and Puysegur Bank), Bounty Plateau, Cook Strait, and west coast South Island. Life history data (i.e., growth parameters, size and age at maturity, location and timing of spawning, estimates of recruitment strength) were found to be the most useful, but fishery-dependent data (i.e., fishery age-frequency distributions, trends in catch per unit of effort) also supported stock differentiation. Horn (2005) considered it unlikely, however, that any of the defined stocks were genetically distinct; mixing between them at the egg, larval, and adult stages appeared inevitable. But because most fish in each stock were believed to spend a large proportion of their lives geographically separated from those in other areas, management assuming five major stocks was recommended.

The viability of using otolith contour shape analyses to inform the stock structure of ling was examined by comparing otoliths from the northern (Fishery Management Area LIN 5) and southern (LIN 6) regions of the postulated Sub-Antarctic biological stock, with another comparison between the Sub-Antarctic and Chatham Rise areas (Ladroit et al. 2017). Otolith images were analysed to produce sets of 17 physical characteristic descriptors along with 50 elliptical Fourier descriptors, and these were applied in a Linear Descriptive Analysis. For the Chatham Rise versus Sub-Antarctic comparison, the percentage of successful classifications was 77.4%, a level indicative of a differentiation between ling from these two areas. For the north-south Sub-Antarctic comparison, the success rate was 50–55%, strongly indicative of no differentiation. The stock structure indicated by these two results was the same as that derived from other sets of biological characteristics, indicating, therefore, that otolith shape analysis could usefully inform the stock structure of ling.

There have been suggestions that the postulated Sub-Antarctic stock actually comprises two distinct biological stocks, based on the presence of at least two spawning areas (Horn 2005) and on reported differences in trace element concentrations in ling from Puysegur Bank, Auckland Islands, and

Campbell Island (Ashoka 2009). Using a discriminant analysis of profiles of trace metal concentrations in ling flesh, Ashoka (2009) produced an overall cross validation classification success rate of 90% between fish from three areas of the postulated Sub-Antarctic stock. Subsequent analyses of estimated research survey biomass distribution, by season (Appendix C of Horn et al. 2013b) and across years (Appendix B of Roberts 2016), have supported the hypothesis that the Sub-Antarctic area holds a single stock, but that there is some seasonal movement of adult fish, probably related to spawning. Otolith morphology also supported a single Sub-Antarctic stock (Ladroit et al. 2017).

Chile

Canales-Aguirre et al. (2010a) used five pairs of microsatellite primers previously isolated from *G. blacodes* in Australia by Ward & Reilly (2001) to demonstrate significant genetic differences between *G. blacodes*, *G. chilensis*, and *G. maculatus* in Chilean waters. Valenzuela et al. (1999) had previously distinguished the same three species using three different electrophoretic techniques: gel isoelectrofocusing, two-dimensional polyacrylamide gel electrophoresis, and capillary zone electrophoresis. Each technique was successful, but capillary zone electrophoresis was the preferred technique owing to its use of small amounts of reagents, short separation times permitting fast comparative analysis, data reproducibility, and ease of use.

Ling off the coast of Chile are believed to comprise northern and southern stocks, separated at about 47° S, based on differences in biological parameters (Baker et al. 2014). Individuals from the southern area had slower growth rates and reached larger asymptotic sizes (Wiff et al. 2007), possessed higher survival rates (Wiff et al. 2011), had higher lengths at 50% maturity, and females had lower mean monthly gonadosomatic indices (Baker et al. 2014) and matured later (Wiff et al. 2019), compared with the northern area fish. Baker et al. (2014) concluded that the significant between-area differences in life-history traits agreed with the trade-offs predicted by the life history theory of Charnov & Berrigan (1991), where females from the northern area have developed a life-history strategy which favours earlier maturation and a proportionally greater investment in reproduction than females from the southern area.

Previous studies, however, were not able to identify any stock differentiation along the Chilean coast. Based on otolith morphometry, Chong (1993) and Brito et al. (2008) showed that overlaps in the physical characteristics of otoliths existed between age groups of fish from different zones, despite some morphometric differences between zones. Both authors concluded, however, that the studies were not sufficient to rule out the presence of multiple stocks. Canales-Aguirre et al. (2010b) used three microsatellites to study the genetic variability of *G. blacodes* primarily south of 50° S and reported no differentiation in the genetic structure between northern and southern zones. However, Baker et al. (2014) challenged those results based on the close proximity of sampling locations in the northern and southern zones together with the low power of the statistical results. Since 2005, Chilean stock assessments have been conducted assuming two independent stocks; one in the northern area (41° 28.6'–47° S) and other in the southern area (47°–57° S), with separate recruitment for each and no migration between them (Wiff et al. 2020).

Wiff et al. (2019, 2020) evaluated differences in the shape of 253 sagittal otoliths of ling in the fjords and inner channels of three administrative regions in Chilean Patagonia (two in the northern area and one in the southern area, as defined in the previous paragraph). Images of otolith contour were modelled using wavelet transformation, and discriminant analysis was used to classify the resulting contour descriptors. Results indicated that this method was useful in modelling ling otolith contours, and discriminant analyses showed differences between fishing grounds across the latitudinal gradient, thus strengthening the hypothesis that ling comprise at least two separated stock units in Chile. The two northern fishing grounds that were geographically close showed higher levels of misclassification.

Australia

Daley et al. (2000) examined meristic and morphometric characters (most being the same as those examined by Colman 1995) of *G. blacodes* from Australian waters (eastern Tasmania, western

Tasmania, eastern Victoria, western Victoria, and New South Wales). They found that some meristic characteristics (e.g., counts of vertebrae, gill rakers, and pyloric caecae) exhibited little variation between areas, and others (e.g., fin ray counts) showed broad ranges with no clear modes. Morphometric characteristics also exhibited no regional differences, although the analysis was confounded by limited success in compensating for regional differences in mean fish size. Genetic analyses (allozyme electrophoresis, DNA microsatellites, and mitochondrial DNA sequencing) also produced no significant geographical differences (Daley et al. 2000). Hence, the authors could not refute the hypothesis of a single ling stock in Australian waters.

An analysis of allozyme variation and microsatellite DNA in *G. blacodes* off south-eastern Australia found no significant differences between ling from five sample locations (Ward & Reilly 2001, Ward et al. 2001), so the null hypothesis of a single ling stock off Australia could not be rejected.

2.3 Length and weight relationships

Length-weight relationships have been produced for several postulated ling stocks in all areas where they occur, often with separate equations by sex (Table 1).

A relationship between head length (HL, cm) and total length (TL, cm) was developed for ling off Argentina to enable length-frequency distributions to be estimated for commercial catches where the fish had been processed but the heads retained (Villarino & Aubone 2000). The linear relationship was: TL = 0.737638 + HL * 4.632991. Head length was defined as the distance between snout tip and the most posterior point of the gill operculum. No significant differences were found between sexes or between size groups over the length range 53–80 cm TL.

Morison et al. (1999) used a sample of 230 fish to produce a relationship between total and standard fish length (both in cm), i.e.:

$$TL = 1.0301 * SL + 0.3844$$

Table 1: Estimated length-weight parameters: weight = *a*(length)^b (weight in g, length in cm total length). All parameter sets are for total (not gutted) weight. WCSI, west coast South Island. NZ is New Zealand.

Location	Female		Male		Combined		Reference
	a	*b*	*a*	*b*	*a*	*b*	
NZ, Chatham Rise	0.00128	3.29	0.00122	3.30	0.00127	3.29	Edwards 2017
NZ, Sub-Antarctic	0.00128	3.30	0.00206	3.19	0.00146	3.27	Edwards 2017
NZ, WCSI	0.00101	3.34	0.00135	3.28	0.00110	3.33	Edwards 2017
NZ, Bounty Plateau	0.00136	3.30	0.00220	3.19	0.00146	3.28	Edwards 2017
NZ, Cook Strait	0.000536	3.51	0.00187	3.23	0.00102	3.37	Edwards 2017
Australia, south-east	–	–	–	–	0.00293	3.139	Bruce et al. 2002
Chile, north of 41.5° S	–	–	–	–	0.001950	3.198	Arancibia et al. 2015
Chile, central-south	0.0018	3.188	0.0019	3.176	–	–	Tascheri et al. 2003
Chile, c. 42.5° S	0.001625	3.242	0.003475	3.044	–	–	Wiff et al. 2019
Chile, c. 44.3° S	0.001054	3.339	0.001204	3.304	–	–	Wiff et al. 2019
Argentina	0.002945	3.107	0.005865	2.948	0.003650	3.057	Renzi 1986
Argentina	–	–	–	–	0.001068	3.348	Cordo 2004

2.4 Otolith structure

The microstructure of otoliths (sagitta and lapillus) of ling larvae and juveniles from off Argentina has been described. The sagittae and lapilli of early larvae (length < 10 mm) were round and disc-shaped

(Morioka et al. 2001). With further growth, two different structural areas were observed in the sagittae only, causing them to become elongated. The structures were defined by Morioka et al. (2001) as the compressed increments fusion (CIF, a dark band of compressed increments in fish larger than 8 mm, generally formed at about increments 24–29) and the accessory growth centre (AGC, a fan-shaped structure in sagittae of fish larger than 15 mm, generally formed from increments 37–43). The formation of the CIF appeared to be associated with the appearance of caudal fin structure, and the AGC formed about the time of appearance of all other fin ray structures. Morioka & Machinandiarena (2001) found that increments were generally formed at a rate of 1 per day in both structures. However, in fish that were not feeding, less than one increment per day was visible (using a light microscope at a maximum magnification of ×1000). Sub-daily increments were observed frequently in sagittae (particularly those from fish longer than 20 mm and older than about 50 days), whereas there was a good correlation between lapillus increment counts and known age in days. Morioka & Machinandiarena (2001) concluded that the lapilli provided the clearest and most accurate source of data for daily increment analysis in juvenile ling. Increment width in both structures reached a maximum around increments 30–40 and became narrower thereafter. Morioka & Machinandiarena (2001) and Morioka et al. (2001) produced images of micro-increments in the otoliths of juvenile ling.

Brito et al. (2008) measured otolith length, width, thickness, and dry weight, as well as fish length and weight, for about 5000 ling off Chile sampled in various years between 1982 and 2004. The samples were from two areas; one each in the northern and southern Chilean fisheries zones (i.e., north or south of 47° S). Linear relationships calculated for each pair of metrics by area and year were tabulated by the authors. Two additional Chilean studies calculated relationships between fish TL (cm) and otolith radius (R, mm, along the nucleus-rostrum axis), by sex, as follows:

	Male	Female	Reference
North of 47° S	$TL = 12.5 * R - 9.1$	$TL = 14.5 * R - 22.3$	Wiff et al. (2007)
South of 47° S	$TL = 10.3 * R + 7.8$	$TL = 13.0 * R - 8.9$	Wiff et al. (2007)
South of 47° S	$TL = 5.4468 * R^{1.3837}$	$TL = 5.3316 * R^{1.3913}$	Chong & Aguayo (1990)

Viera (2011) compared some otoliths morphometrics of *G. blacodes* and *G. brasiliensis* captured in waters off northern Argentina and Uruguay. The following relationships between fish TL (mm) and otolith length (O_L, mm), width (O_W, mm), and weight (O_G, g) were calculated from 364 *G. blacodes* (length range 28–93 cm):

$O_L = 0.0166 * TL + 2.0372$ ($r^2 = 0.86$)
$O_W = 0.0073 * TL + 0.7946$ ($r^2 = 0.84$)
$O_G = 0.0155 * e^{0.0036 * TL}$ ($r^2 = 0.88$)

Linear relationships between fish TL (cm) and otolith radius (V, mm, along a transverse section between the nucleus and ventral edge) for New Zealand ling from the Chatham Rise and Sub-Antarctic, by sex, were calculated using data analysed by Morrongiello et al. (2021) with sample sizes of approximately 250 per area-sex combination.

	Male	Female
Chatham Rise	$TL = 16.0 * V + 13.0$ ($r^2 = 0.88$)	$TL = 20.1 * V + 1.1$ ($r^2 = 0.91$)
Sub-Antarctic	$TL = 12.7 * V + 24.4$ ($r^2 = 0.82$)	$TL = 16.6 * V + 13.9$ ($r^2 = 0.84$)

The shape of adult ling otoliths was found to vary between putative stocks off New Zealand (Ladroit et al. 2017) and Chile (Wiff et al. 2020), indicating that analyses of otolith contours may be a useful technique in stock separation studies.

Otoliths of *G. blacodes* were occasionally found to be completely or partially transparent and ‘crystalline’ in appearance (Villarino 1997, D’Atri 2006, author’s unpublished information). This characteristic is believed to be a consequence of the otolith being composed primarily of vaterite (a polymorph of calcium carbonate that is glassy in appearance) rather than the normal aragonite form of calcium carbonate (but see Pracheil et al. (2019) for a discussion of the prevalence of species that routinely have otoliths with a non-aragonite composition). D’Atri (2006) found that it was most common for only one of an otolith pair to be crystalline (3% of fish from a sample of about 9700), but that both otoliths were sometimes affected (an additional 1.5% of fish), and even less commonly only the otolith border was transparent (0.1%). Morales-Nin (1985) estimated that about 3% of *G. capensis* were similarly affected, although her observations found that partial decalcification was the most common condition. The cause of the anomaly in otoliths of *G. capensis* was likely owing to a fault in the carbonate-protein binding mechanism. Note also that Morales-Nin (1985) determined that the crystalline otoliths of *G. capensis* were composed primarily of calcite (another polymorph of calcium carbonate), rather than vaterite, and were found to contain significantly more protein than ‘normal’ otoliths (0.55% relative to 0.40%). No analyses of the calcium carbonate polymorph composition of *G. blacodes* otoliths were found.

2.5 Age determination and growth

Juvenile

Ling larvae were assumed to be 2 mm at one day after hatching, based on a yolk-sac absorbed larva of 2.2 mm found off Argentina (Morioka et al. 2001). Based on assumed daily growth increments in lapilli, the instantaneous growth rate was found to be quite rapid initially (greater than 5% of body length per day until about day 30), but then declined rapidly (to less than 1% of body length per day by day 100). The caudal fin structure appeared between about days 24 to 29 (8–11 mm), and the remaining fin ray structure formed generally between days 37 to 43 (15–19 mm). Morioka et al. (2001) concluded that ling grew to about 17 cm one year after hatching.

Adult

Studies of ling growth have been reported from the four general areas where ling make up a significant fishery, i.e., Argentina (Wrzesiński 1984, Villarino 1997, 2004, D’Atri 2006), Australia (Withell & Wankowski 1989, Smith et al. 1996, Morison et al. 1999, Kalish et al. 2002), Chile (Chong & Aguayo 1990, Ojeda et al. 2001, Tascheri et al. 2003, Wiff et al. 2007, Brito et al. 2008), and New Zealand (Horn 1993b, 2021, Edwards 2017). All have used sagittal otoliths, although preparation methods have varied (e.g., whole untreated otoliths, whole ground otoliths, untreated or baked transverse cross-sections, and untreated or baked thin transverse sections). Fitted von Bertalanffy parameters were an output from most of the studies (Table 2). At all locations, female ling grew faster and reached a larger asymptotic size than males. It was clear that the use of sectioned otoliths was necessary to produce accurate ages for large/old ling, but smaller/younger specimens (i.e., perhaps up to an age of about 10 years) could probably be successfully aged using whole otoliths. The remainder of this section examines the available studies essentially in chronological order.

Wrzesiński (1984) used otoliths from research trawl surveys between 40–50° S off Argentina. They were prepared by breaking transversely and burning the broken edge, then reading the edge immersed in glycerine and illuminated by incident light. White opaque zones were counted and about 4% of otoliths were unreadable. Interpretation of otolith zones was difficult, particularly for old fish. Fish were aged from 3 to 31 years. Von Bertalanffy curves were fitted to data from northern and southern areas separately (Table 2), but the curves fitted the older age data poorly. No between-sex comparisons of growth were reported, nor was any validation study attempted.

Withell & Wankowski (1989) collected otoliths from research trawl surveys in eastern Bass Strait, Australia. They were examined whole and in section (a slice 0.5–0.6 mm thick through the dorso-ventral axis, mounted on a slide in clear mountant under a coverslip). The authors stated that all annuli were visible on both sectioned and whole otoliths, but sections were considered preferable because the annuli were more distinct. Individual annuli often comprised many fine aggregated translucent bands rather than a single broad translucent band. In general, the inner annuli were more irregular and difficult to interpret than the outer ones. Fish were aged from 2 to 21 years. A single von Bertalanffy curve fitted all the data well; data from both sexes were combined (Table 2). Withell & Wankowski

(1989) attempted to validate their study by looking for modal progression between years in length-frequency distributions, and examining the marginal increment of otoliths over a season, but neither of these techniques was successful.

Chong & Aguayo (1990) obtained otolith samples monthly over a 10-month period from commercial trawl operations off the Chilean coast. The lateral surfaces of whole untreated otoliths were ground down on carborundum paper. The preparations were soaked in water for 24 hours, then viewed through a stereomicroscope with illumination by reflected light. Fish were aged only up to 16 years even though some were longer that 140 cm. Von Bertalanffy curves were fitted to the data separately by sex, and sexual differentiation in growth was reported (Table 2). Mean lengths at younger ages were back-calculated from a relationship between otolith radial measurements (nucleus to rostral tip) and fish length. Chong & Aguayo (1990) attempted a partial validation of their technique by classifying otolith margins as either translucent or opaque. They reported that about 60–70% of otoliths had a translucent margin in winter (April to September), and 80–90% had an opaque margin in summer to early autumn, thus indicating a probable annual formation of the zones.

Horn (1993b) obtained samples of otoliths from research and commercial trawl operations from four areas of the New Zealand continental shelf (i.e., Chatham Rise, west coast South Island (WCSI), Sub-Antarctic, Bounty Plateau). Otoliths were broken transversely through the nucleus, the broken surface polished with fine sandpaper, and then heated in an oven (275 °C for 10–30 minutes dependent on otolith size) until amber coloured. The sections were coated with clear oil and examined under a stereomicroscope (×30) with illumination by reflected light. Translucent zones were counted. Horn (1993b) noted that the clearest banding generally occurred beside the sulcus or along either of the long axes of the prepared otolith surface. Banding was indistinct laterally. In general, zonation was clearer on otoliths from males than females. Fish were aged from 2 to 35 years. Von Bertalanffy parameters were calculated for each sampled area, separately by sex (Table 2). Significant between-sex differences in growth were noted, with females growing larger than males. It was also apparent that growth rates varied between areas. Growth of Sub-Antarctic ling was significantly slower than for fish from the three other sampled areas.

Horn (1993b) attempted a partial validation of his technique by examining modes in length-frequency distributions taken 6 months apart (and counting zones in otoliths of fish from these modes), and by an examination of otolith marginal increment and marginal state. It was noted that it was difficult to precisely define opaque-translucent boundaries (because of the frequent diffuse nature of the zones), which led to a relatively high level of within-sample variability. However, the available data implied that translucent material became visible at the margin in late winter, and that most fish were laying down opaque material during summer. Four relatively indistinct juvenile modes were apparent in the length-frequency distributions, and the number of zones visible in otoliths from each mode generally increased by one for each consecutive mode. Consequently, it appeared likely that juvenile and adult ling lay down one opaque and one translucent otolith band annually. Horn (1993b) recommended that ling be aged using cross-sectioned rather than whole otoliths, because in whole otoliths the identification of zones at the margins of large specimens becomes difficult owing to the otolith thickening rather than increasing in width (Figure 2), a conclusion similar to that drawn for *G. capensis* by Japp (1990).

Table 2: Von Bertalanffy parameters estimated for ling (by sex, and sexes combined), showing location, sampling period, the number of aged fish (N), and age range for each parameter set, as well as details of the age determination method. NZ is New Zealand; NI is North Island.

Location	Data years	N	Male			Female			Sexes combined			Range (years)	Otolith preparation method	Reference
			L_∞	K	t_0	L_∞	K	t_0	L_∞	K	t_0			
NZ, Chatham Rise	1989–92	1 601	119.0	0.108	-1.24	160.1	0.076	-1.05				2–35	Baked cross-section	Horn 1993b
NZ, Sub-Antarctic	1989–91	940	95.1	0.194	0.16	125.7	0.113	-0.67				2–30	Baked cross-section	Horn 1993b
NZ, Bounty Plateau	1992	121	123.2	0.128	0.28	158.4	0.079	-0.7				3–27	Baked cross-section	Horn 1993b
NZ, WCSI	1991	371	146.1	0.087	-0.13	165.9	0.09	0.22				3–35	Baked cross-section	Horn 1993b
NZ, Chatham Rise			115.2	0.12	-0.86	158.7	0.08	-0.89	132.8	0.10	-0.83	2–33	Baked cross-section	Edwards 2017
NZ, Sub-Antarctic			97.3	0.16	-1.16	116.6	0.12	-1.30	107.7	0.14	-1.10	3–30	Baked cross-section	Edwards 2017
NZ, Bounty Plateau			126.3	0.11	-1.71	145.1	0.09	-1.43	134.0	0.10	-1.36	8–21	Baked cross-section	Edwards 2017
NZ, WCSI			141.0	0.09	-1.18	164.2	0.08	-0.75	160.2	0.08	-1.16	2–28	Baked cross-section	Edwards 2017
NZ, Cook Strait			148.2	0.10	-0.93	162.1	0.11	-0.08	151.6	0.11	-0.38	4–24	Baked cross-section	Edwards 2017
NZ, east coast NI			147.9	0.10	-1.01	151.2	0.14	0.70	144.5	0.13	0.29	7–15	Baked cross-section	Edwards 2017
NZ, Chatham Rise	1989–2020	24 207	111.0	0.15	-0.1	148.7	0.101	-0.1				1–46	Baked cross-section, t_0 set to -0.1	Horn 2021
NZ, Sub-Antarctic	1989–2020	23 217	92.6	0.215	-0.1	109.9	0.163	-0.1				1–37	Baked cross-section, t_0 set to -0.1	Horn 2021
NZ, Bounty Plateau	1989–2020	1 170	121.9	0.133	-0.1	143.1	0.107	-0.1				5–41	Baked cross-section, t_0 set to -0.1	Horn 2021
NZ, WCSI	1989–2020	12 861	134.4	0.116	-0.1	157.7	0.0978	-0.1				2–38	Baked cross-section, t_0 set to -0.1	Horn 2021
NZ, Cook Strait	1999–2020	6 021	142.6	0.122	-0.1	159.6	0.112	-0.1				2–32	Baked cross-section, t_0 set to -0.1	Horn 2021
NZ, Sub-Antarctic	1989–2020	23 000	92.0	0.20	-0.42	111.8	0.14	-0.83				2–34	Baked cross-section	Mormede et al. 2021a
Chile, c. 37° S	1984	3 720	117.5	0.18	-0.54	134.8	0.14	-0.67				1–14	Ground-down whole otoliths	Chong & Aguayo 1990
Chile	1982–96		105.4	0.20	-0.92	126.2	0.152	-1.18					Some back-calculation	Ojeda et al. 2001
Chile, central-south	2002–03	833	81.5	0.292	-1.5	96.3	0.207	-1.3				1–12	Whole & section, with some back-calculation	Tascheri et al. 2003
Chile, 41–47° S	1982–2004	19 581	97.2	0.241	-0.844	117.4	0.184	-0.591	111.5	0.186	-0.912	1–16	Ground-down whole otoliths	Wiff et al. 2007
Chile, 47–57° S	1982–2004	27 445	101.0	0.209	-1.756	123.2	0.165	-1.248	123.4	0.147	-1.779	1–16	Ground-down whole otoliths	Wiff et al. 2007
Argentina, <45° S	1973	530							126.5	0.1	0.844	3–30	Break & burn cross-sections	Wrzesinski 1984
Argentina, >45° S	1973	329							121.6	0.1	0.733	3–31	Break & burn cross-sections	Wrzesinski 1984
Argentina	1996–2001	5 906	110.7	0.17	-0.61	130.5	0.14	-0.66	119.9	0.15	-0.63	1–37	Whole otoliths and cross-sections	D'Atri 2006, 2009
Bass Strait, Australia	1984–85	377							135.5	0.095	-1.4	2–21	Transverse thin sections	Withell & Wankowski 1989
SE Australia	1979	400	112.5	0.167	-0.769	126	0.151	-0.791				2–21	Transverse thin sections	Morison et al. 1999
SE Australia	1994–95		96.2	0.198	-1.83	117.8	0.14	-2.19				1–28	Transverse thin sections	Morison et al. 1999
SE Australia									101.3	0.179	-2.045		Transverse thin sections	Thompson & He 2001

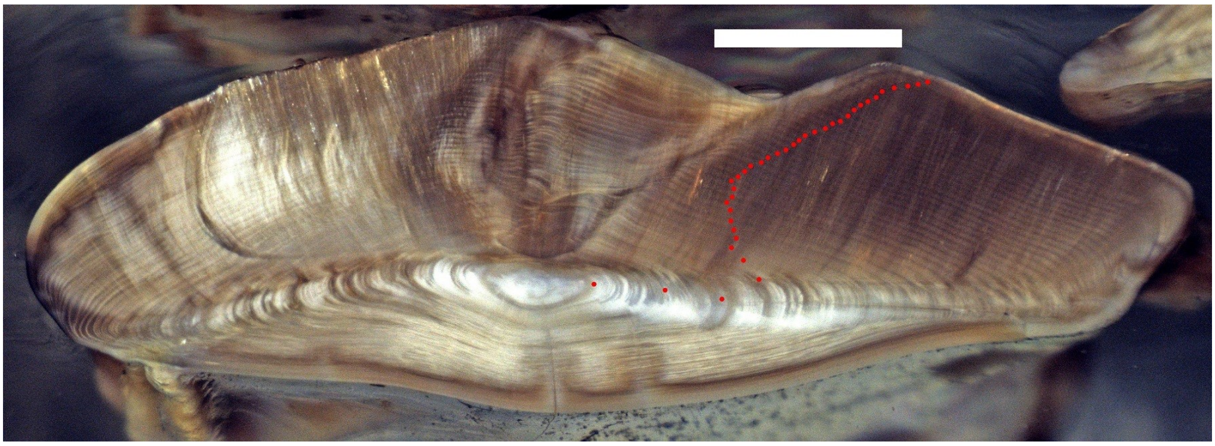

Figure 2: Otolith cross-section from a 130 cm male ling (from Chatham Rise, New Zealand) that can be relatively clearly aged as 38 years. The counted dark zones are indicated by red dots. Sub-annual zones are apparent in the first four years of growth and the second zone is relatively diffuse and indistinct. This section provides a clear example of how, for old fish, otoliths continue to increase steadily in thickness but little in width. White bar = 2 mm. (From Horn 2021.)

Ling have been reported spawning in New Zealand waters from late winter to summer (Horn 2005). This potential for protracted spawning has implications for the interpretation of early otolith growth. Horn (1993b) noted that the nuclei of ling otoliths could be either translucent or opaque with a translucent ring surrounding it. He suggested that otoliths with opaque nuclei were probably from fish spawned early in the season, and later spawned fish had translucent nuclei. A 'birthday' of 1 October (approximating mid spawning season) was set for ling; translucent material is being laid down in the otolith at this time. Hence, Horn (1993b) concluded that ling are, on average, about 0.3 years old at the completion of the translucent part of the nucleus and about 1.3 years old at completion of the first 'true' annual zone. However, this characteristic clearly has the potential to introduce some ageing error; i.e., is an otolith with an opaque nucleus surrounded by a small, but clearly defined translucent zone from a late spawned fish from year class *X* or and early spawned fish from year class *X*+1?

Villarino (1997) examined whole otoliths from juvenile ling off Argentina and showed that the annual translucent growth ring was formed between the months of February to November. Villarino (1997, 2004) counted approximately 340 assumed daily growth zones from the first readable daily ring out to the completion point of the first translucent annual zone. The measured distance from the primordium to the completion of the first translucent annual zone (along the longitudinal axis to the rostrum) was generally around 3100–3300 µm. According to Villarino (2004) there could be up to four translucent bands inside the first true annual zone. It was also common for the first three annual translucent zones to be split and to find multiple discontinuous or faint false zones in the juvenile part of the otolith.

Smith et al. (1996) and Morison et al. (1999) obtained otoliths from several years and sites off southern Australia. They examined 0.25 mm transverse sections from untreated otoliths, set in clear mountant on glass slides, and viewed with transmitted light under a stereomicroscope (×6 or ×10). Fish were aged from 2 to 28 years, and von Bertalanffy curves were presented, by sex, for the various samples (Table 2). Thompson & He (2001) reported a von Bertalanffy equation for both sexes combined (Table 2), using all the available data from south-east Australia, which included those from the two Australian studies cited above.

Kalish et al. (2002) analysed levels of ^{14}C in the otolith cores of eleven ling from Bass Strait, Tasmania, that had been aged previously using counts of zones in transverse otolith sections. Birth dates assigned to individual fish on the basis of zone counts agreed well with birth dates predicted from the ^{14}C calibration curve of Kalish (1993), indicating that otolith-based estimates were likely to be accurate. There was also good agreement in zone counts within and between laboratories, leading

Kalish et al. (2002) to conclude that otolith cross-section zone count ages for ling were likely to be relatively precise, i.e., ± 2 years.

Tascheri et al. (2003) examined otoliths collected from off central-south Chile in 2002–03. Most commonly, the proximal surface of the otolith was ground, then examined after soaking in water to clarify the growth zones. However, where otoliths were difficult to analyse whole due to their opacity, they were baked and sectioned transversely. A comparison of the two methods found no significant differences in age estimation between whole ground or baked sectioned otoliths, although all examples in this comparison were estimated to be less than 10 years old (Table 2). The study found fish aged to 13 years, and there were few fish longer than 110 cm in the sample. An examination of otolith marginal state over 12 months indicated that a translucent slow growth zone and an opaque fast growth zone formed annually, with the translucent margin predominating from May to July.

D'Atri (2006, 2009) prepared pairs of sagitta from Argentinian ling using up to three preparation techniques per pair; i.e., whole otoliths polished on the proximal surface until the first annual zone was visible, transverse cross-sections of untreated otoliths, and transverse cross-sections where the reading surface was burned to produce a greater contrast between translucent and opaque zones. Whole otoliths and untreated sections were hydrated for at least 24 hours before examination. Burning of the cross-sections was found to be particularly useful to enable satisfactory readings from otoliths of ling larger than about 100 cm; it was effective in allowing readings from 90% of untreated cross-sections previously classified as unreadable. Overall, about 3% of otoliths were unreadable. Ling were aged from 1 year (17 cm) to 36 years (127 cm female), and female size-at-age was found to be significantly greater than that for males from about age 5 years (Table 2).

Wiff et al. (2007) determined the ages of large samples of ling from the northern and southern zones off Chile. Before examination, otoliths were polished on their proximal surfaces until the first annual zone was visible and were rehydrated for at least 24 hours. They were then examined in water or oil on a black background, illuminated with reflected light, under a stereomicroscope at ×10 magnification, and translucent zones were counted to produce growth parameters by sex (Table 2).

Brito et al. (2008) tested an artificial neural network model as a means to determine the age of ling using metrics from otoliths and whole fish. Otolith length, width, thickness, and weight, and fish length, weight, and sex were related to previously determined ages from otoliths using a training set of data, and the resulting model was subsequently applied to another set of metrics to see how well the predicted and 'actual' (i.e., previously determined) ages matched. The relationship between predicted and actual age had an R^2 value of 0.75. Brito et al. (2008) concluded that, when there was lower data availability, some of the seven input variables could be removed without affecting the prediction power. Further work was recommended, however, to improve the age-estimation model.

Von Bertalanffy parameters (with 95% confidence intervals) were produced as part of a study to provide updated informative priors (used in stock assessment modelling) for the natural mortality rate for each of the recognised New Zealand ling stocks (Edwards 2017). The recommendations on priors were based on life-history theory, and, to provide the necessary growth and maturity parameter estimates, all available life-history data were re-analysed (Table 2). Data were used only where there were a minimum of nine points for each sex-age bin. Mormede et al. (2021a) updated the von Bertalanffy parameters (and also presented Schnute growth parameters) as part of an assessment of the Sub-Antarctic stock.

Contreras et al. (2018) applied non-Gaussian distributions and a Bayesian approach to model growth variability of Chilean ling, using back-calculated length-at-age data derived from otolith radii measurements in aged fish. The authors assumed that errors in the von Bertalanffy growth function followed a Students-*t* distribution, based on the presence of some individuals with high length-at-age values. Only fish with estimated ages between 1 and 13 years (with a length range of 41–127 cm) were included in the analysis; fish older than 13 years were available but lacked ring radius information. It was concluded that a Students-*t* model with mixed effects best described the back-calculated data.

The effects of climate and fish stock size on the growth of ling from Chatham Rise and the Sub-Antarctic, New Zealand, were investigated by Morrongiello et al. (2021) using measurements of annual otolith growth increments, after first showing that otolith growth was linearly related to fish length. Chatham Rise ling growth was lower in years following large ling spawning stock biomass (*SSB*), but *SSB* had a negligible impact on Sub-Antarctic ling growth. A synergistic impact of fishing pressure and the Interdecadal Pacific Oscillation (IPO) on ling growth was detected: growth was positively related to IPO at low biomass, but negatively related to IPO at high biomass suggesting a release from density-dependent growth control. Mean otolith growth increments (along the nucleus-ventral margin axis) are listed, by area and sex, in Table 3.

Table 3: Mean otolith growth increment widths (µm, with standard deviations (S.D.)), by growth year, along a transverse section between the nucleus and ventral edge. Data are presented by area (Chatham Rise, Sub-Antarctic) and sex. Data for growth year 2 relates to the otolith increment that formed between the first and second 'birthdays', etc. There are no data from the first year of life.

	Chatham male		Chatham female		Sub-Antarctic male		Sub-Antarctic female	
Growth year	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
2	574	139	608	162	616	149	631	172
3	599	138	602	137	700	180	675	173
4	502	115	513	113	551	140	553	146
5	431	106	429	103	416	112	419	118
6	360	87	382	95	328	82	336	84
7	305	73	329	83	273	70	275	72
8	276	75	297	75	233	68	238	63
9	249	61	264	62	192	54	205	53
10	220	52	243	57	167	46	193	53
11	196	49	224	56	145	39	168	46
12	179	47	209	58	130	37	156	40
13	157	43	192	48	121	34	139	39
14	144	51	180	51	107	33	128	35
15	135	47	168	48	101	30	117	30
16	124	45	159	48	93	28	112	32
17	116	45	142	49	91	27	107	33
18	106	45	130	37	86	26	101	30
19	96	36	120	33	76	24	90	33
20	97	47	103	22	78	20	91	31

An age determination protocol document for ling described the methodologies used for otolith preparation and interpretation, ageing procedures, and the estimation of ageing precision (Horn 2021). The method of baking and subsequent cross-sectioning of otoliths that is used to age ling from New Zealand was described, with digital image examples to illustrate the zone interpretation used in determining fish age. Difficulties and idiosyncrasies related to ageing prepared otoliths were also documented. The wide variation in length-at-age for ling in New Zealand waters related to sex and location was reported (Table 2).

Ling was one of a set of species examined in an Australian study to quantify age-reading error (Punt et al. 2008). The work aimed to determine a method to construct age-reading error matrices that accounted for both ageing bias and ageing imprecision, for use in stock assessment modelling. The method had some shortcomings, however, when sample sizes were small, when age-reading error was correlated among readers, when both readers' results were biased, and for ages that were poorly represented in the sample. Coefficients of variation of age-reading error versus true ling age (assuming the primary reader produced true age) were 0.2 at age 2, 0.1 at age 6, and 0.06 at age 15 years. Of all the species examined in the study, ling was found to be one of the least precise.

Ling from New Zealand (Chatham Rise and Sub-Antarctic) was one of 53 species whose growth parameters were used to evaluate the influence of ecological and environmental drivers of growth of deep-sea teleosts, with the aim being to understand the evolution of life history parameters across the depth continuum (Black et al. 2021). No conclusions specific to ling were drawn.

2.6 Natural mortality

The natural mortality parameter (*M*) is an important determinant of productivity within age- and length-structured stock assessment models, but it is difficult to estimate. For New Zealand's ling stocks, *M* was first estimated by Horn (1993a) to be 0.18 yr^{-1} based primarily on the equation $M = \log_e 100$ / maximum age. That estimate was reviewed by Horn (2000), who concluded that the best estimates of *M* were 0.18 for males and 0.16 for females. The data indicative of a sexually differentiated *M* were not convincing, however, so the 0.18 value was retained for stock assessment purposes. Subsequently, Horn (2008) used a variety of age-based methods to predict *M* for New Zealand's primary ling stocks, and, while there was considerable variation within stocks across estimation methods and sexes, it appeared that *M* was probably less than 0.18 for Chatham Rise ling and greater than 0.18 for west coast South Island (WCSI) and Cook Strait fish. The recommended *M* values by stock were: Chatham Rise, 0.13; Sub-Antarctic, 0.19; WCSI, 0.23; Cook Strait, 0.25. The higher values for the latter two stocks were based primarily on the absence of older age classes in the catch from these areas (Horn 2008). In general, subsequent assessments of New Zealand ling stocks retained $M = 0.18$ for most 'base case' model runs, but alternative runs using different fixed *M* values, or runs estimating *M* as either a fixed value or as an age-dependent ogive, were regularly evaluated (see Horn (2008) and subsequent ling assessment reports, e.g., McGregor (2015), Roberts (2016), and Dunn & Ballara (2019)). The estimation of age-dependent ogives for *M* generally produced 'logical' results with *M* being greatest for very young and very old fish (e.g., often around 0.3–0.4 yr^{-1}) and least in the years following first maturity (e.g., around 0.1 yr^{-1}).

It became apparent in subsequent assessments, however, that the model outcomes could be very sensitive to the chosen value of *M*, and any *M* values estimated during modelling often depended on the data-weighting assumptions within the model (e.g., Dunn et al. 2013). Following a Sub-Antarctic ling stock assessment, Roberts (2016) recommended an investigation of sex-specific *M*. Subsequently, a study by Edwards (2017) aimed to provide updated informative prior values for *M* for each ling stock, based on both theoretical (i.e., known correlations between *M* and other life-history characteristics, specifically age, growth, and maturity) and empirical (i.e., data based) models. Estimates of *M* for females (but not males) from the theoretical and empirical models were consistent, and while the length-based models produced male *M* values that were higher than those for females, the age-based models predicted that they were similar between sexes. Some of the estimated male *M* values were simply too high, leading Edwards (2017) to reject all the male values. The theoretical derivation of female *M* appeared sound, however, and produced values of: Chatham Rise, 0.13; Sub-Antarctic, 0.16; WCSI, 0.15; Cook Strait, 0.12 (although the overlapping credibility intervals for all these estimates indicated a value of about 0.14 yr^{-1} for all stocks). Hence, only the Chatham Rise and Sub-Antarctic values were similar to the age-based estimates of Horn (2008), leading Edwards (2017) to suggest that older females were not being observed in the WCSI and Cook Strait catches, possibly because of the migration of larger females to other areas.

Estimates of *M* for Chilean ling have been made using two types of models; i.e., those based on the theoretical maximum longevity ($T_{\max}$) and those where *M* was associated with the instantaneous rate of individual growth (*K*). Using the first model type, Ojeda et al. (1986, cited by Arancibia et al. 2015) estimated male *M* to be in the range 0.22–0.30 yr^{-1} and *M* for females to be 0.18–0.26 yr^{-1}. Wiff et al. (2011) used the second type of model to estimate *M* (with confidence bounds) for sexes combined and reported that Pauly's (1980) method was the most suitable, producing values of 0.27 (CI: 0.13–0.47) for the northern zone (north of 47° S) and 0.23 (CI: 0.11–0.40) for the southern zone. Arancibia et al. (2015) trialled five models but rejected two based on $T_{\max}$ because the estimates were too high to agree with known characteristics of the ling life history. The other models (based on *K*) gave mean estimates of 0.35 for males and 0.27 for females from northern Chile, with comparable values of 0.32 and 0.25

for southern fish. As in the New Zealand studies, male M values were higher than those for females, although overall the Chilean estimates are higher than those from New Zealand. Arancibia et al. (2015) did note, however, that because their estimates were strongly K-dependent there was considerable potential for variation in M estimates.

For ling off Argentina, Cordo (1999) used a variety of models that relate M to longevity or to growth parameters (as described above for Chilean ling) to produce estimates that varied between 0.15 and 0.24 yr^{-1}. Cordo suggested that a mean M of 0.2 with bounds of 0.15 and 0.25 could be used in ling stock assessment models.

Morison et al. (1999) completed a catch curve analysis of a 1979 research sample from off south-eastern Australia (assumed to be from a near-virgin stock) to produce a range of M values from 0.12–0.42 yr^{-1} depending on the data set and the range of ages included in the estimate. They concluded that the best estimate of M was 0.34 for both sexes combined but noted that assumptions of constant mortality and recruitment may invalidate this method. Methods based on $T_{\max}$ generally gave lower estimates in the range 0.16–0.22. When Morison et al. (2012) estimated combined-sex M in assessments modelling separate sexes, the estimated value was 0.23 or 0.25 yr^{-1}, and the models showed sex-specific differences in selectivities (domed in males, logistic in females). Selectivities and M can be confounded, but different behaviour and availability of ling sexes is also plausible, and research into the role of ling refuges was recommended by Morison et al. (2012). Whitten et al. (2013) stated that there was some evidence from Australian catch curves developed by Smith et al. (1996) and Morison et al. (1999) that M for older ling may be lower than for younger ling. However, M was treated as an estimable combined-sex constant in their stock assessment models, with estimates in the range 0.20 to 0.24 (Whitten et al. 2013).

2.7 Gonad development

The macroscopic and microscopic structure of ling ovaries were described from samples collected off Argentina (Louge et al. 1992, Machinandiarena et al. 1998, 2003). Descriptions of the microscopic and macroscopic structure of ovaries and testes from Chilean ling samples were provided by Aguayo et al. (2001) and Wiff et al. (2019), and for ovaries only by Paredes & Bravo (2005).

Machinandiarena et al. (2003) produced a five-stage macroscopic classification of ovarian development based on changes in the appearance and size of the ovary (Table 4), illustrated with colour images. They concluded that the main difficulty in ovary stage identification was the differentiation of advanced maturation (late stage 2) versus spawning (stage 3), due to the large ovary volume attained prior to spawning. Consequently, the decrease in the thickness of the ovary wall membrane and whether oocytes can be observed through it were considered to be the characteristics fundamental for the identification of the spawning stage.

The microscopic and macroscopic descriptions by Aguayo et al. (2001) and Wiff et al. (2019) from Chilean samples (Table 5) were also illustrated with images. Note that there are some differences between Aguayo et al. (2001) and Machinandiarena et al. (2003) in ovarian classifications, e.g., spawning females are classified as stage 4 or 3, respectively.

A sample of 128 spawning female ling collected off Argentina during January produced ovaries containing groups of growing oocytes joined by post-ovulatory follicles, with eggs ranging in diameter from 30 to 1400 μm (Machinandiarena et al. 1998). The frequency distribution of egg sizes was continuous, but with modes of oocytes in maturation (200–900 μm) and hydrated (1000–1400 μm), indicating that ling are partial spawners with an unstructured pattern of oocyte development. The presence of post-ovulatory follicles in distinctly different phases of resorption, but still joined to hydrated eggs, indicated that spawning occurred frequently. However, the scarcity of hydrated oocytes observed in the ovaries suggested that the number off eggs released at each spawning episode was low. After releasing the hydrated components, a new batch of oocytes completes maturation and is rapidly released in a new spawning episode. Machinandiarena et al. (1998) believed that the characteristics of a continuous egg size distribution and continuous phases of resorption would make it difficult to estimate reproductive frequency or calculate partial fecundity. However, Wiff et al. (2019) presented multi-modal oocyte size-frequency distributions, with modes comprising vitellogenic (600 µm), mature (700 µm), and hydrated (900 µm) oocytes, respectively, and these authors produced estimates of batch fecundity (see Section 2.9).

Machinandiarena et al. (1998) described a five-stage sequence of oocyte maturation (and presented micrographs to illustrate the stages). Note that these microscopic stages are not intended to match with the macroscopic stages 1–5 in Table 4. The categories are as follows:

- Previtellogenic oocytes (egg diameter 30–150 µm). Oocytes have a spherical nucleus with peripheral nucleoli.
- Oocytes with cortical alveoli (160–320 µm). Oocytes have colourless cortical alveoli in the cytoplasm, principally around the nucleus.
- Oocytes in primary vitellogenesis (350–480 µm). Oocytes have small yolk globules between the cytoplasmic alveoli.
- Oocytes in secondary vitellogenesis (~650 µm). Oocytes have cytoplasm loaded with large yolk globules and a nucleus with an irregular outline. In the final phase of this stage the nucleus migrates towards the edge of the oocyte.
- Oocytes in final maturation or hydration. Oocytes can, in the histological section, reach a diameter of 900 µm but have an irregular shape due to shrinkage caused by dehydration during the histological processing. The nucleus is not visible because of the disintegration of the nuclear membrane.

Macroscopic descriptions of whole ovaries, and microscopic descriptions of whole oocytes and histological sections (with micrographs), were presented by Paredes & Bravo (2005) for four developmental stages: unyolked perinucleus stage, unyolked yoke-vesicle stage, yolked stage, and ripe stage. The whole oocyte descriptions are as follows:

- Unyolked perinucleus stage (diameter < 250 µm). Transparent but becoming granular and translucent with increasing size. Visible nucleus. Homogenous cytoplasm.
- Unyolked yoke-vesicle stage (> 250 µm). Granular and translucent, but becoming darker with increasing size.
- Yolked stage (< 900 µm). The prehydration phase, with oocytes completely opaque except for previteline border. [Average diameter 731 µm; Wiff et al. 2019.]
- Ripe stage (> 900 µm). Oocytes translucent except for the oil droplet. [Average diameter 944 µm; Wiff et al. 2019.]

Samples collected off Argentina during March produced ovaries in stages of reversion, whereas those from September were in a developing phase (Louge et al. 1992). Three stages of reversion were described. In the stages of early and intermediate reversion, the ovary is flaccid and bloody. Its membrane wall is whitish and translucent, which allows the inner contents to be seen, and there is marked vascularisation. At early reversion, the ovary contains late ripening eggs and post-ovulatory follicles, with large inter-oocyte spaces. At intermediate reversion, the eggs turn atresic. However, together with atresic oocytes, there are also immature and, to a lesser extent, retracted oocytes with signs of yolk. In the resting or final reversion phase (Stage V of Machinandiarena et al. 2003), the gonad is smooth and pink, the wall is thick, and it is not possible to see the eggs inside. In this final reversal state, the resting ovary is made up of only immature oocytes—unlike the previous reversal stages—and the developing eggs are light yellow, with the extent of vascularisation being much less relative to the previous stages. When female ling are in reproductive condition, the lamellae contain oocytes at different developmental stages: previtellogenic, primary growth, and vitellogenic oocytes (Cohen et al. 2016). Based on the mixture of stages of oocytes occurring in spawning and recently spawned gonads, it is probable that ling are partial spawners (Louge et al. 1992, Paredes & Bravo 2005, Wiff et al. 2019). *Genypterus chilensis* exhibited similar characteristics and were also believed to be partial spawners (Chong & Gonzales 2009).

The ovary is elongated and bi-lobed ventrally, with a fibromuscular membrane wall that changes in thickness depending on the stage of gonadal maturation. In cross section, it has a tree-like structure. The ovarian fluid of *G. blacodes* is viscous, and during the spawning season it shows large amounts of mucus that fills the ovarian lumen, a characteristic that distinguishes this species from many other teleosts. Freijo et al. (2009) and Cohen et al. (2016) investigated the physiological significance of the glycoproteins secreted by the luminal epithelium of the ovarian lamellae of *G. blacodes*. At the beginning of the cycle, during the resting season, the epithelium is squamous in appearance, while during the spawning season it is columnar. Morphological changes during the spawning season were associated with a secretory activity of mucus, which was intensified during ovarian maturity, suggesting that ling release masses of eggs enveloped in mucus, and not individual eggs as in most other externally fertilising species. In addition, the oocytes of *G. blacodes* had only small oil droplets, suggesting that this species could spawn demersal gelatinous masses of eggs that attach to the substrate. Analyses of the carbohydrate composition of ling oocytes showed that the oil droplets and zona radiata or outer egg membrane contained glycoconjugates (Díaz et al. 2012, Cohen et al. 2015, 2016). The zona radiata controls the interaction of eggs with water and protects the embryo from microorganisms, and it is known that sometimes the surface glycoconjugates become sticky in contact with water, thus permitting eggs to be fixed to the substrate and also binding sperm to the egg surface. Cohen et al. (2016) concluded that the secretory role of the epithelium, and the glycoconjugates produced, are strongly linked to the reproductive strategy of *G. blacodes*, whereby the release of oocytes wrapped in mucous masses enhances the fertilisation mechanism of the eggs in a highly dispersive environment and also ensures greater egg survival. The works by Freijo et al. (2009), Díaz et al. (2012), and Cohen et al. (2015, 2016) were all illustrated with histological sections of ovaries. Wiff et al. (2019) presented histological sections of testes.

Table 4: Macroscopic classification of ling ovarian development (from Machinandiarena et al. 2003).

Stage	Stage name	Description
1	Juvenile	Small, pink, slightly swollen ovaries, with a thin and translucent ovary wall membrane. Oocytes are not visible through the membrane.
2	Maturing	Pinkish, compact ovaries, larger than in Stage 1, with little vascularisation in the membrane. Oocytes are not visible through the off-white membrane, but are visible when the membrane is cut.
3	Spawning	Large orange or pink ovaries. The membrane is translucent and vascularised, and oocytes are visible through it. The interior of the gonad can be compact or have a tree-like structure, with opaque and hydrated oocytes. Parenchymal attachments (indicating the locations of previously spawned oocytes) are also apparent.
4	Post-spawning	Flaccid ovaries, smaller than in Stage 3, with increased vascularisation in the tunic. The membrane is whitish and thickened, and no oocytes are differentiable through it (although Louge et al. (1992) noted that at the early stages of post-spawning the membrane was still translucent). Residual opaque oocytes can be detected in rare cases. The colour of the interior of the gonads varies from orange to dark pink.
5	Resting	Ovaries further reduced in size. The membrane is flaccid and whitish, generally with no vascularisation, and differentiable oocytes are visible through it. The interior of the gonad is compact and dark pink.

Table 5: Macroscopic and microscopic classification of ling ovaries and testes (from Aguayo et al. 2001 and Wiff et al. 2019).

Sex & stage	Stage name	Macroscopic description	Histomorphological description
Female 1	Immature	Small ovary. Initially the ovaries are threadlike, but at a more advanced stage they have a flattened, tubular section narrower at the ends. Ivory white colour.	Ovigerous lamellae in parallel arrangement, with abundant previtellogenic reserve oocytes, all with multinucleolar central germinative vesicles. Basophilic homogeneous cytoplasm.
Female 2	Maturing	Medium-sized pink ovary, narrower at the posterior end, and covered by a tough, smooth membrane. Ovigerous lamellae (clusters with oocytes) are visible with the naked eye.	Simultaneous presence of reserve and vesicular oocytes, with a clear predominance of oocytes at the beginning of exogenous vitellogenesis, most of which have fine eosinophilic granules in the cytoplasm. At the end of the stage, oocytes loaded with large yolk granules appear.
Female 3	Mature	Ovary swollen, and coloured pink or pale yellow. It is covered by a resistant, smooth membrane; there is little or no mucous discharge. Oocytes with a diameter less than 0.9 mm. This is the phase prior to oocyte hydration. This stage includes ovaries that have recently undergone partial spawning.	Yolked ovary. The predominant oocytes, loaded with large yolk granules, are accompanied by immature reserve and vesicular oocytes.
Female 4	Spawning	Large swollen, light yellow ovary with hydrated oocytes. It is covered by a resistant, smooth membrane and contains a large amount of transparent mucus. The oocytes flow freely when the abdomen is pressed. Oocyte diameter greater than 0.9 mm.	Terminal maturation, with the presence of oocytes with migrating and hydrated germinative vesicles, accompanied by post-ovulatory follicles. This stage exhibits the maximum development of the zona radiata and follicular-thecal layer.
Female 5	Spent and regressing	Ovary appears less swollen and is light brown to pinkish in colour. Visible ovigerous lamellae, flaccid in appearance. Small number of oocytes in the process of reabsorption. At the end of this stage, the ovary becomes pink, with greater turgidity.	Distended ovigerous lamellae with large spaces occupied by connective tissue. Immature reserve and vesicular oocytes predominate. Presence of residual or atresic follicles and oocytes. Macrophages and lymphocytes are scattered in the parenchyma. Dilated blood vessels. The histological organisation is similar to stage 1, but differs in that stage 5 exhibits flaccid lamellae, of greater length and diameter.
Male 1	Immature	Testes small and flat with smooth edges; pale yellow.	Initiation of spermatogenesis. Predominance of spermatogonia and primary spermatocytes.
Male 2	Maturing	Small testes, thicker than in the previous phase. Pale yellow. When pressed, no opaque white liquid flows.	Spermatocytogenesis reflected in the marked proliferation of secondary spermatocytes and round spermatids. Few cysts or tubules with sperm.
Male 3	Mature	Medium sized testes, with thickened lobes and a slight increase in length. Colour opaque white. When pressed, opaque white viscous liquid flows.	Initiation of spermiohistogenesis, characterised by the predominance of sperm over other germ cells, both in cysts and in tubules.
Male 4	Spawning	Testes have increased in length and thickness; ivory white. When pressed, white milky semen flows.	Active spermiohistogenesis where spermatozoa predominate, and are abundant in the testis ducts.
Male 5	Spent and regressing	Yellowish-white testes. When pressed, little or no semen flows. As the regression progresses, the thickness of the lobes decreases.	Abundance of spermatogonia on the few small cysts with spermatocytes and spermatids, both in the thick septa and in the region of the testis cortex. Residual sperm in the lumen of the evacuation ducts.

2.8 Sexual maturity

New Zealand

Maturity ogives and lengths where 50% of fish were mature (L_{50}) were estimated for putative ling stocks in New Zealand waters using macroscopically determined gonad stages and gonadosomatic indices (GSI) (Horn 2005). Many of the data (particularly from Chatham Rise and Sub-Antarctic trawl surveys) were collected before or after the recognised peak spawning times. Also, many of these research fish were classified as stage 2 (‘resting’), which included large individuals resting following spawning, and small fish that had yet to spawn for the first time. Stage 2 fish constituted a high proportion of the sample, and classifying all of them as mature or all as immature markedly altered the ogives. Frequency plots of binned GSIs by maturity stage were used to determine likely GSI ‘cut-offs’ between immature (stage 1) and mature (stages 3–5). These cut-off values (GSI of 0.25% for males, 0.75% for females) were used to allocate stage 2 fish with GSI values to either the immature or mature groups. Horn (2005) examined ogives excluding stage 2 fish, and including stage 2 fish if a GSI was available to allocate them to a maturity group. However, he rejected the ‘include stage 2’ ogives because the difference in GSIs between pre- and post-mature fish varied between seasons and areas, whereas the likely maturity status of non-stage 2 fish was believed to be well known. There were apparent differences in L_{50} between areas for both sexes (Table 6), although Horn (2005) noted that some of the ogives were likely biased owing to the relatively large numbers of large fish that were classified as being stage 1 and the general lack of data from the peak spawning times. The WCSI ogives were believed to be the most reliable for New Zealand ling because they were based on data from the winter spawning season.

Maturity ogives by age, from converted length-based ogives, were also estimated from the Chatham Rise and Sub-Antarctic trawl surveys series by Horn (2005) because large numbers of aged and maturity staged fish were available from these (Table 6). These ogives were used in subsequent assessments of New Zealand ling stocks (Fisheries New Zealand 2022), but note the previous caveats about the potentially biased nature of these data. The estimated A_{50} values are for the WCSI stock and are likely more reliable than those for other New Zealand stocks.

As part of a re-evaluation of ling biological parameters in a study to produce priors for M, Edwards (2017) estimated L_{50} values under the assumption that the age-at-maturity is equal to the age at which growth starts to slow (i.e., the point of maximum inflexion of the growth curve describing weight-at-age), because resources will be diverted towards gamete production at that point in the life cycle (Jensen 1996). Ogive parameters for the maturity-at-length and -at-age were produced separately by sex for each ling stock (Table 6). For all stocks the length- and age-at-maturity was noticeably larger for females. The estimates of A_{50} by Horn (2005) and Edwards (2017) were similar for males, but Edwards’ estimates for females were 1.6 to 3.7 years higher.

Table 6: Estimates of L_{50} (cm, with 95% CIs in parentheses) and A_{50} (years) for New Zealand ling, by area. –, no data.

Parameter	Chatham Rise	Sub-Antarctic	WCSI	Cook Strait	Reference
L_{50} female	96.6 (94.9–98.5)	86.2 (85.5–86.9)	87.4 (84.5–90.0)	–	Horn 2005
L_{50} female	106.4 (101.2–112.7)	84.4 (83.0–85.8)	106.2 (104.0–108.3)	123.6 (117.6–131.8)	Edwards 2017
L_{50} male	72.0 (71.6–72.6)	67.9 (67.5–68.3)	70.4 (68.5–71.9)	–	Horn 2005
L_{50} male	73.4 (72.4–74.3)	67.9 (66.5–68.8)	71.4 (65.8–75.9)	–	Edwards 2017
A_{50} female	11.9	8.9	8.4	–	Horn 2005
A_{50} female	14.5	10.5	12.1	12.5	Edwards 2017
A_{50} male	8.1	6.7	6.3	–	Horn 2005
A_{50} male	7.8	6.5	5.8	–	Edwards 2017

Chile

The mean size at which 50% of female ling attain sexual maturity (L_{50}) off southern Chile was estimated using both measurements of GSI and fits of logistic functions to percentage mature by size to be 90–91 cm (Chong 1993) and 84–86 cm (Paredes & Bravo 2005). Aguayo et al. (2001) analysed extensive data from 1985 to 2000 and presented annual logistic fits (with associated ogive parameters) to proportion mature data derived macroscopically. Estimated L_{50} values ranged from 85 to 100 cm, but a 'best estimate' L_{50} of 82.2 cm (and an age of 6 years) was chosen based on histological examinations of ovaries from 1999. However, the L_{50} estimated by Aguayo et al. (2001) using histological data was significantly different between samples collected in 1999 (L_{50} = 82.2 cm) and 2000 (93.5 cm). Baker et al. (2014) found that the L_{50} (based on macroscopic observations) for females differed between the northern and southern Chilean zones, being 88.0 cm (CI: 87.2–88.5) for the north and 91.0 cm (CI: 90.3–91.9) for the south. Arancibia et al. (2015) reported an L_{50} of 114 cm for the northern area.

Aguayo et al. (2001) suggested that the marked variation in Chilean estimates may be caused by the frequent difficulty in macroscopically determining the state of sexual maturity (hence their preference for a microscopically based estimate), and that there are inter-annual variations in the spawning season that can affect the proportions-at-length between mature and immature females. In addition, Baker at al. (2014) suggested that difficulties in obtaining a random on-board sample, differing experience levels of on-board observers, differences between landings in the relative availability of large females (potentially attributable to different fishing practices), and whether the sampled fishing covered the peak reproductive period, could all add to variation in L_{50} between years or samples.

In contrast to the findings of Aguayo et al. (2001), Wiff et al. (2019) found that macroscopic maturity staging of female ling agreed 78% of the time with histological designations. Using data collected during 2018 only, the L_{50} estimated using histology was 84.8 cm (95% CI: 81.8–87.5), with macroscopy it was 86.3 cm (95% CI: 83.7–88.5), and from GSIs it was 87.8 cm (95% CI: 85.6–89.4). The estimated maturity ogive and the L_{50} values did not vary significantly between the three methods. Significant differences in maturity ogives across regions were found, however, supporting the previous findings of Baker et al. (2014) that northern females matured at a smaller size compared with those from the southern region. Using data collected from 2005 to 2017, Wiff et al. (2019) estimated northern L_{50} values to be 96.9 cm (95% CI: 95.4–98.8) from macroscopic examinations and 88.4 cm (95% CI: 87.1–89.7) from GSI analyses. In the southern region, comparable values were 106.8 cm (95% CI: 102.9–111.0) and 96.1 cm (95% CI: 92.2–100.0), respectively. Flores et al. (2020) re-analysed the GSI data from 2005 to 2017 and estimated L_{50} values of 87.2 cm (86.0–88.4) and 93.6 cm (90.2–96.0) for the northern and southern regions, respectively. Parameters for logistic fits to the sets of maturity data were provided (Wiff et al. 2019, Flores et al. 2020).

The log-log relationship between gutted weight and gonad weight of females was linear with a slope of one across all active maturity stages (i.e., stages 2–4) (Wiff et al. 2019, Flores et al. 2020). Also, a General Linear Model examining the influence on GSI of three predictors (sexual maturity stage, liver weight index, and a condition index) found that maturity stage explained 87% of the deviance, while the remaining predictors explained less than 1.5% (Wiff et al. 2019). Hence, GSI is a good indicator of the reproductive condition of ling and is not significantly influenced by fish size. Reported peak GSI values for mature females were reported in the range of 4–7% (Aguayo et al. 2001, Paredes & Bravo 2005, Wiff et al. 2019). Flores et al. (2020) suggested that females change from immature to mature at a GSI of 1.39%.

As expected, female GSI changed in line with gonad development. Fish with immature ovaries (stages 1 and 2) had GSI values less than 1%, but GSI increased markedly with stages 3 and 4 until reaching around 6.5% (Wiff et al. 2019). The variation in the liver weight index was similar to the GSI variation; it increased between stages 1 and 2 until attaining a relatively constant level of about 6% when in advanced stages of maturity (stages 3–4), then decreased markedly at the conclusion of spawning. Changes in the condition index exhibited a different pattern, i.e., a slight increase between stages 1 and 2, then a decrease in stages 3 to 5. These findings may indicate how energy is sourced for oocyte production, with energy obtained mainly from feeding during reproduction, but immediately post-spawning they recover energy from body reserves, mainly from the liver (Wiff et al. 2019).

In males, Wiff et al. (2019) found that correspondence between macroscopic and histological maturity staging was poor (i.e., correct only 11% of the time), indicating that the use of macroscopy in this sex was not reliable, because changes in gamete development were not clearly expressed in size, shape, and gonad colour. These authors did, however, estimate an L_{50} for the southern region in 2018 from macroscopic data to be 77.9 cm (95% CI: 75.6–79.7). Also, a maturity ogive fitted to macroscopic data from the northern region in 2005–2017 indicated an L_{50} of 78.9 cm (95% CI: 78.1–79.5). The L_{50} values were significantly different between sexes; males first mature at a smaller size than females (Wiff et al. 2019). Aguayo et al. (2001) used a histological analysis of a sample of males from 1999 to produce an L_{50} of 70 ± 4 cm, equating to an age of 5 years.

Argentina

Cordo et al. (2002) estimated a maturity ogive and L_{50} value for female ling off Argentina using histological analyses of gonads collected during research surveys in late summer of 1997 and 1998 to determine whether specimens were immature or mature. Their estimate of L_{50} was 70.5 cm. Cordo (2004) reported an L_{50} value of 70.8 cm seemingly using the same data from 1997–98. Previous estimates made using macroscopic examinations of gonads of both sexes collected during January to March of 1996 and 1997 produced L_{50} values of 72 cm and 75.8 cm by year (Wöhler et al. 1999). Cordo et al. (2002) and Cordo (2004) suggested that the differences observed between their estimates and those of Wöhler et al. (1999) were due to the difficulty of macroscopically determining the stage of maturation in specimens close to the size of first maturation.

D'Atri (2006) analysed data from a series of research surveys from 1996 to 2001 (including the data described in the previous paragraph) in an area of known ling spawning that occurs during summer in waters shallower than 200 m between 44° and 48° S. Gonads of males and females were classified macroscopically as either juvenile or mature adult using the maturation scale of Machinandiarena et al. (1998), and L_{50} values 71.0 cm for females and 69.4 cm for males were estimated from fitted logistic maturity ogives. Using age data developed in the same study, D'Atri (2006) estimated mean age-at-first-maturity to be 5.2 years for females and either 4.8 years (based on estimated ages of staged fish) or 5.3 years (based on lengths converted to ages) for males.

Australia

Smith et al. (1995) plotted GSI against length for female ling, by month, for samples from the western Bass Strait and concluded that they matured at about 60 cm, based on the length where relatively high GSIs started to occur. For males, maturity length was not clear because there was little variation in GSI across all size classes. For females, GSIs were highest in winter, particularly in August, with individual GSIs up to 5%. The highest individual male GSI was 0.74%, but monthly means for males longer than 60 cm were never above 0.2%. Lyle & Ford (1993) reported an L_{50} of 72 cm for female ling off Tasmania.

2.9 Spawning biology and early life history

The eggs of *G. blacodes* are undescribed, but those of the closely related *G. capensis* are pelagic and spherical, 1.18–1.30 mm in diameter, and have a single oil globule 0.09–0.11 mm (Brownell 1979). Freijo et al. (2009) found that the epithelium of the *G. blacodes* ovarian lamellae performed a secretory role, which was intensified during ovarian maturity, suggesting the release of masses of eggs enveloped in mucus. Similarly, Breder & Rosen (1966) stated that members of the Family Ophidiidae produced oval, pelagic eggs in a gelatinous mass. Based on the relatively low fecundity of ling, the small oil droplets in eggs, and the likelihood that spawned egg masses in mucus attach to the substrate, Freijo et al. (2009) postulated that some kind of parental care of eggs could exist, and the eggs could be deposited in nests. Similarly, Cordo (2004) noted that the very low or null frequency of cannibalism, as well as the frequent capture of isolated large females accompanied by one or more juveniles, could indicate a commitment to parental care.

In aquaculture conditions, however, the related *G. chilensis* spawned gelatinous masses of floating eggs overnight, with an average of 82 000 eggs, and a maximum of 285 000 eggs, per mass (Vega et al. 2018). After 4 to 5 days of incubation, pelagic larvae about 5 mm long hatched. The gelatinous mass dissolved during incubation, with live eggs continuing to float and dead ones sinking. It was not clear in this instance, however, whether there was suitable substrate to attach eggs to (if substrate attachment is the normal reproductive behaviour).

Dumorné (2018) assessed the spermatic functions (motility, mitochondrial membrane potential, cytoplasm membrane integrity and viability, DNA integrity and fertility) and the effects of pH, salinity, and temperature on sperm motility of *G. blacodes*. The structure of the spermatozoa, studied using electron microscopy, was found to be a primitive uniflagellated type, differentiated into a head, midpiece, and flagellum (Dumorné et al. 2018b). The short mid-piece contained 4 or 5 mitochondria. Sperm motility was initiated on contact with a hyperosmotic swimming medium. The longest motility duration was recorded at 4 °C, and the maximum percentage of motile cells was recorded at 8 °C in 100% seawater (Dumorné et al. 2018a). Spermatozoa density was 5.35×10^9 mL^{-1}, and 73.9 ± 17% were fertile. This work aimed to establish a baseline of research to develop and optimise protocols for artificial reproduction of the species.

Some Ophidiiform species (e.g., *Ophidion marginatum*) are known to use sound during courtship behaviour (Rountree & Bowers-Altman 2002). Based on observations of *Ophidium* spp., Breder & Rosen (1966) postulated that the gas bladders attached to the ribs and vertebral column of ling were “used by the male to produce sounds of significance in courtship and mating activities”, but this has yet to be confirmed for this species. However, males and females of *Genypterus maculatus* and *G. chilensis* maintained in aquaria produced two sound types, mainly between 7 and 10 pm (Parmentier et al. 2018). These sounds were probably related to courtship behaviour because floating eggs were found after night calls. The anatomy of the sonic structures were similar in both sexes of both species (i.e., three pairs of sonic muscles, a neural arch that pivots on the first vertebral body, and a thick swim-bladder with unusual features). Parmentier et al. (2018) concluded that both sexes were capable of sound production, although precedence from shallow ophidiids and sonic fishes in general suggests that males are more likely to produce courtship calls.

Several studies have indicated that *G. blacodes* are partial or batch spawners (e.g., Machinandiarena et al. 1998, Arancibia et al. 2015, Wiff et al. 2019). Machinandiarena et al. (1998) found post-ovulatory follicles joined to hydrated eggs, indicating that spawning occurred frequently, and that the scarcity of hydrated oocytes at any time in an ovary indicated that the number off eggs released at each spawning episode was low. Aguayo et al. (2001) examined the daily frequency of females with hydrated gonads, and (based on sparse data) postulated that the average time between spawned batches was 22 days and that four batches of eggs could be produced each season. The likelihood of skipped spawning (where some females do not mature during a reproductive cycle) and its potential causes in ling was discussed by Flores et al. (2020).

There have been several investigations of the fecundity of *G. blacodes* off Chile (Table 7). While some of the studies described their results as being ‘total’ fecundity (and Chong (1993) stated that his estimates were of the total number of eggs that could be spawned in a season), the current author believes that all estimates were of ‘partial’ fecundity (i.e., the number of eggs that would be spawned in one of several batches produced in a single season). Chong (1993) estimated fecundity for 51 ling off southern Chile in 1992, assuming that the oocytes with diameters greater than 0.333 mm (i.e., oocyte size at the beginning of the vitellogenesis process, determined by histological analysis) represented the total number that could be released in a spawning episode. Linear regressions relating total fecundity to body weight and length were calculated. Aguayo et al. (2001) estimated fecundity for 28 females (lengths 85–120 cm) from southern Chilean waters in 1999; they had ovaries in an advanced stage of development and contained some oocytes with diameters greater than 0.65 mm. One ovary contained 1 225 000 oocytes, a value much higher than the rest (c. 60 000–700 000), and was removed from the analysis primarily because Chong (1993) found no observations greater than 450 000 oocytes. Aguayo et al. (2001) concluded that an exponential curve best fitted the remaining data and, consequently, that the contribution by younger fish (3–6-year-olds) amounted to only 1.4% of the total egg production. Parades & Bravo (2005) revisited the data analysed by Aguayo et al. (2001). They also noted the one high value "which fell above the general tendency observed", but still used that point to produce a mean batch fecundity of 333 330 oocytes per fish in the sample. Best fits to the relationships between batch fecundity and total fish weight or length were found to be linear.

Table 7: Regression equations relating batch fecundity (*F*) to total length (TL, cm) and weight (W, g), for ling off Chile. Where available, r^2 values are presented in parentheses. W_G, gutted weight.

Fecundity by length	Fecundity by weight	Reference
$F = 21952 * \mathrm{TL} - 1600514$ (0.62)	$F = 160.99 * W - 21311$ (0.74)	Chong 1993
$F = 0.0054 * \mathrm{TL}^{3.8165}$ (0.23)	–	Aguayo et al. 2001
$F = 16003 * \mathrm{TL} - 1321311$ (0.33)	$F = 73.94 * W - 139356$ (0.45)	Parades & Bravo 2005
$F = 1507.5 * \mathrm{TL} - 101040$ (0.25)	$F = 9.2 * W - 3883.9$ (0.32)	Arancibia et al. 2015
$F = 1386 * \exp(\mathrm{TL} * 0.0393)$	$F = 15.5 * W - 2686.5$	Wiff et al. 2019
–	$F = 18.5 * W_G - 4490.1$	Wiff et al. 2019

Arancibia et al. (2015) analysed data from 20 Chilean ling of lengths 100–135 cm caught north of 41.5° S in 2014. Individual batch fecundity ranged from 30 000 to 130 000 oocytes (mean of 65 000). The estimated linear relationships between batch fecundity and both length and weight were poorly correlated. Wiff et al. (2019) and Flores et al. (2020) analysed the ovaries of 36 fish (11 mature and 25 with hydrated oocytes) collected in October–November 2018. The estimated fecundity relationships were exponential for length and linear for weight (Table 7). Relative fecundity was estimated to be 15 (range 6–26) oocytes per gram of body weight, and the size of the oocytes was independent of the size of the female. Individual batch fecundity ranged from 31 107 to 144 267 (mean of 74 238) spawned oocytes per female (Flores et al. 2020). Wiff et al. (2019) and Flores et al. (2020) showed that fecundity at a specific size was not significantly different between fish from inshore (fjord) waters compared with offshore waters (from Chong 1993). The reproductive potential of *G. blacodes* (as measured by fecundity) was lower than four other major (gadoid) commercial species off southern Chile, suggesting that it is a species with low resilience to exploitation (Flores et al. 2020).

The larval development and early life history of *G. blacodes* from coastal waters off south-eastern Australia was described by Furlani (1998). Larvae are shorter than 2.5 mm at time of hatching, develop notochord flexion at about 8–12 mm, and adopt a benthic habit when longer than about 25 mm. Formation of fins occur at the following sizes: caudal 7.8–9.4 mm; anal 7.8–9.9 mm; dorsal 7.8–13.4 mm; pelvic 8.1–11.8 mm; pectoral 10.3–13.4 mm. Small teeth along both jaws occur in preflexion larvae larger than 4.5 mm. The larvae are lightly pigmented with colour along the lateral midline of the tail anteriorly and posteriorly from about 8 mm. Furlani (1998) illustrated larvae of lengths 4.1, 9.4, and 15.6 mm. The larval development of the closely related *G. capensis* has also been described and illustrated (Olivar & Sabatés 1989) and exhibits some similarities to that for *G. blacodes*.

In an investigation of the seasonal distribution of ling across the area containing New Zealand's Sub-Antarctic ling stock, Horn et al. (2013b) found that substantial biomass of adult fish occurred on the Campbell Plateau throughout the year. The authors postulated that this could be a consequence of one or more scenarios relating to spawning behaviour, i.e.:

- A sizeable proportion of adult ling may not spawn annually, and so do not travel to the spawning grounds in spring-summer.
- Residence time on the spawning grounds may be short relative to the length of the spawning season, resulting in abundant pre- or post-spawn fish in the non-spawning areas.
- Spawning may occur widely throughout Fisheries Management Areas (FMAs) 5 and 6, although it is known to be concentrated in two areas.

No New Zealand evidence to support or reject the first two points was available, although Flores et al. (2020) suggested that 10% of females skipped spawning in the fjords of southern Chile. It was apparent, however, that running ripe female ling occurred sporadically across the Campbell Plateau, mainly from October to December (Horn 2005), so spawning probably did occur outside main spawning grounds.

2.10 Spawning locations and times

New Zealand

Horn (2005) examined all available fish sample databases for records of ‘running ripe’ ling. Spawning females were recorded off northern WCSI from July to September. Spawning males were also common in August. In Cook Strait, spawning males and females are relatively abundant from June to September, but few data were available from this area in other months. On the Chatham Rise, spawning females were abundant from July to October, mainly just west of the Chatham Islands, and to a lesser extent at a separate location on the western Chatham Rise from September to November. For the Sub-Antarctic ling stock, spawning fish were abundant at Puysegur Bank and the Solander Corridor from October to December, and spawning females were also present at those locations in August and September. There was also an indication that spawning can occur over much of the Campbell Plateau from October to December, but with the activity clearly more concentrated near the margins of the Stewart-Snares shelf. On the Bounty Plateau, spawning males and females were abundant from October to February, with spawning females also relatively abundant in September. There were anecdotal reports of spawning females occurring in the Bay of Plenty and off Cape Kidnappers (Horn 2005). Roberts (1987) recorded a ‘pre-spawning’ aggregation of ling in October, just north of North Cape, where many ovaries were either maturing or ripe and some contained 50% hyaline eggs.

Fishing for ling on the main New Zealand grounds (Chatham Rise, Sub-Antarctic, WCSI) generally occurs in depths of 400–600 m (Horn 2004b) and most spawning fish are caught in this depth range. On the Bounty Plateau, however, spawning (and fishing) tends to be concentrated between 150 and 300 m (Horn 2004b).

Argentina

Hatching dates, estimated by back-calculations of assumed daily growth increments in lapilli otoliths of 25 larval and juvenile ling from off Argentina, ranged from December to June (Morioka et al. 2001). This conclusion was supported by observations of staged ling gonads (microscopic, macroscopic, and GSI-based staging) where spawning fish were most abundant between December and May (Machinadiarena et al. 1998, 2003, Louge et al. 1992). In particular, on the Argentinian Patagonian Platform, ling spawning occurred between 45° and 47° S in the San Jorge Gulf area, in summer, in areas about 100 m deep; the greatest summer concentrations of ling were observed at this depth and area (Machinadiarena et al. 1998). These aggregations resulted from the movement of ling towards the coast (Renzi 1986, Villarino 1998), apparently intent on reproduction. The presence in San Jorge Gulf of larvae particularly in March (Machinadiarena 1996) and juveniles smaller than about 55 cm throughout the year (Villarino 1998) reinforced the conclusion that this was the major spawning area for ling off Argentina (Cordo 2004). Machinandiarena (1996) detected additional larvae and juveniles, however, in autumn on the platform between 37° and 41° S, suggesting the existence of another spawning area to the north of San Jorge Gulf.

Chile

Aguayo et al. (2001) reported that the main reproductive period for ling in southern Chile (south of 47° S) ran from September to November. Arancibia et al. (2015) examined various technical reports and concluded that the main spawning areas for ling in Chile occur between 41.5° S and 47° S, and, in that area, GSI values increased from May–June, to reach maximums in August–September. In the far north of Chile (north of 41.5° S), female GSI values were highest from August to October (Arancibia et al. 2015). Similarly, at a latitude of about 40° S, Sandoval-Ramírez (2015) found high proportions of mature individuals present from August to November, but no spawning fish. Based on the analyses of GSI values and sexual maturity states, it appeared likely that ling spawning occurred most intensely in the northern area of the fishery (41.5–47° S), and secondarily in the southern area (47–57° S).

In the main region (41.5–47° S), Aguayo et al. (2001) reported intensive spawning between November and December. Ichthyoplanktonic studies carried out in inland waters of this area during November reported the highest occurrences of eggs and larvae of the *Genypterus* genus north of 47° S (Bustos et al. 2008, 2011), which coincided with the higher incidence of mature female ling observed by Wiff et al. (2019). In the southern region (47–57° S), mature individuals were present from August to April, with spawning occurring from August to November, based on GSI, mean oocyte diameter, and macroscopic examination of ovaries (Paredes & Bravo 2005).

Wiff et al. (2019) examined spawning activity in more detail in some areas of the northern region during 2018. They found that reproductive activity started in June for all fish sizes, but that smaller females (c. 84 cm) had less intense participation (maximum GSI 2.3%, with a peak recorded between August and September), whereas the reproductive participation of larger females was of greater intensity (maximum GSI 3%) and duration, with a peak between September and October, a lag of one month compared with smaller fish. In inner-fjord fishing grounds, abundant mature individuals were observed in the Gulf of Ancud (c. 42° S) during spring and from the Gala region (c. 45° S) during winter (Rubilar et al. 2000). In outer waters, based on the GSI, a main spawning area was identified between 41.5° S and 47° S mainly in late spring to early summer (Aguayo et al. 2001). It was apparent, therefore, that there were important and separate areas of ling spawning in both offshore and inshore (i.e., fjord) waters of Chile.

Australia

Smith et al. (1995) concluded that in western Bass Strait the main spawning period for ling occurred in winter–spring at depths of 450–550 m based on peaks in female GSI, which was similar to the May to October spawning period based on the presence of mature females proposed by Kailola et al. (1993). Spawning aggregations were also reported off Strahan (Tasmania), Lakes Entrance (Victoria), and Gabo Island (New South Wales) in spring (Bruce et al. 2002).

Genypterus species larvae were caught in shelf and slope waters off New South Wales from April to September, and in coastal waters off Sydney from April to August, but these may have included *G. tigerinus* as well as *G. blacodes* (Bruce et al. 2002). These larval records are indicative of spawning from late autumn to early spring.

2.11 Recruitment

Castillo-Jordán et al. (2015) investigated recruitment patterns across 30 Southern Hemisphere fish stocks, including ling stocks from Australia, New Zealand, and Chile, using data from 1980 to 2010. Three dominant recruitment pattern trends were identified, suggesting that there are both regional and global influences on recruitment patterns across multiples species. Ling from eastern Australia, eastern and southern New Zealand, and southern Chile exhibited similar recruitment trends with a pattern (i.e., Trend 3 of Castillo-Jordán et al. 2015) that had low stable values from 1980 to 1990, a rapid increase from 1991 to 1996, a decrease until 2000 followed by a short recovery, followed by a rapid decline towards 2010. Trend 3 was negatively correlated with the Southern Oscillation Index.

Patterns of recruitment strength were estimated in stock assessment analyses of New Zealand ling stocks using available series of catch-at-age data from commercial fisheries and research surveys, and these patterns were found to vary markedly between stocks (Horn 2005). This was one of the characteristics used by Horn (2005) to postulate the existence of at least five separate ling stocks in New Zealand waters. Updated estimated recruitment series for the putative New Zealand stocks are presented annually (e.g., Fisheries New Zealand 2022). Estimated patterns of recruitment strength were regular outputs from ling assessments in areas outside New Zealand (e.g., Arancibia et al. 2010, Whitten & Punt 2014, Cordue 2018).

Wiff et al. (2018) used a meta-analysis to estimate the stock-recruitment relationships (called ‘steepness’ and denoted as *h*) for Chilean fish stocks. This parameter is related to the slope of the stock-recruitment relationship and is defined as the proportion of unexploited recruitment produced when spawning biomass has been reduced to 20% of its unexploited size. Their estimate of *h* for ling was 0.59, with the 95% confidence interval for the mean being 0.51–0.66 and the 95% prediction interval being 0.28–0.91.

2.12 Migration

Areal differences in size frequencies indicative of changing depth preferences with changes in fish size, and seasonal movements probably associated with spawning, have been noted for ling in various locations.

In waters off Tasmania, Australia, ling occurred between 20 and 800 m, but with juveniles less than 40 cm being most common on the shelf and larger adults being prevalent at about 600 m (Tilzey 1994). Similarly off New Zealand, although the distribution of ling less than 40 cm was poorly described, there were records of juvenile fish up to 2 years old from shallow inshore areas, particularly in the Bay of Plenty and off the central east coasts of North Island and South Island, although most occurred in depths from 200 to 500 m (O’Driscoll et al. 2003). Mormede et al. (2021b) showed that in the Sub-Antarctic region, ling less than 40 cm occurred almost exclusively in two areas: the southern Stewart-Snares shelf, and the Auckland Islands Shelf. Immature fish (c. 40–67 cm) had a distribution similar to adults (O’Driscoll et al. 2003). Although the distributions of fish of all sizes exhibited considerable overlap, the data provided by O’Driscoll et al. (2003) showed a clear trend of increasing depth with increasing fish size. Concentrations of juvenile fish (less than 60 cm) were recorded in inshore waters (i.e., depths of 50–100 m) of Argentina (Cordo 2004), particularly in the San Jorge Gulf (Villarino 1998), and although larger fish also occurred in these shallower areas they tended to predominate in deeper waters.

Seasonal trends in the distribution of biomass within New Zealand’s Sub-Antarctic ling stock were investigated by Horn et al. (2013b). The areal trends were indicative of ling moving towards, and concentrating in, the north-western spawning grounds during spring and summer, then migrating back east (particularly from Puysegur Bank and onto the eastern Campbell Plateau) during autumn and winter. There are insufficient data to evaluate any spawning migration trends for other New Zealand ling stocks. Instances of Australian ling moving from deeper to inshore waters at sites off western Tasmania, eastern Bass Strait, and southern New South Wales were believed to be a consequence of adult migration to spawning locations (Bruce et al. 2002).

Off Argentina, ling are distributed between 34° and 54° S but mainly are concentrated between 44° and 48° S, with low densities year-round in other parts of the range (Villarino 1998). In winter and spring the highest concentrations were located between 41° and 48° S, mainly on the continental slope, and in summer they were between 43.5° and 48.5° S, generally closer to the coast on the continental shelf relative to winter-spring (Renzi 1986). These aggregations, particularly in the San Jorge Gulf region, resulted from the movement of ling towards their summer spawning areas near the coast (Renzi 1986, Villarino 1998). During autumn, the mean length of adults was found to increase with increasing latitude and depth. Sex ratios also varied across time and region, indicative of some between-sex differences in migration (Renzi 1986). On the continental shelf during winter there were twice as many females as males, whereas in samples from the San Matias and San Jorge Gulfs, and in the spring and summer seasons, a ratio of two males to one female was observed.

2.13 Feeding

The diet of ling has been studied extensively in all areas where it occurs. The largest study examined 1540 stomachs containing prey from New Zealand’s Chatham Rise, with samples collected over three years, mainly from late December to late January, and concluded that ling is a benthic generalist (Dunn et al. 2010). Diet was characterised by benthic crustaceans (mainly *Munida gracilis* and

Metanephrops challengeri), demersal fishes (mainly Macrourids), and scavenged offal from fishing vessels. The most important predictors of diet variability were depth, fish length, and vessel type (i.e., whether the sample was collected from a commercial or research vessel; this predictor is probably aliasing for a spatial effect), but the model explained only 12% of the deviance, indicating most of the variability in diet could not be explained by the available predictors. Galatheids (mainly *M. gracilis*) occurred in 50% of stomachs but contributed only 7% of prey weight. Scampi (*M. challengeri*) were a relatively large crustacean prey and contributed a similar weight to galatheids despite occurring in only 9% of stomachs. The fish prey included benthic species, such as Anguilliformes and flatfish, demersal species such as hoki (*Macruronus novaezelandiae*), mesopelagic species such as myctophids, and three instances of cannibalism, but the most important fish prey were demersal macrourids, which were found in 17% of stomachs, contributed 16% of prey weight, and consisted of at least seven species. The greatest percentage weight was from discarded fish remains (30%), which were predominantly severed heads and/or tails of the pelagic jack mackerel *Trachurus* species, or heads of other fishes with no other accompanying remains, e.g., one stomach contained only four hoki heads. The presence of a lamb chop bone reaffirmed the opportunistic scavenging behaviour of ling.

Dunn et al. (2010) found that, by prey weight, Galatheidae and Pandalidae were most important in the diet of smaller ling of 32.7–58.8 cm; Galatheidae, Pandalidae, Goneplacidae, and Macrouridae were most important in intermediate sized ling of 58.9–82.9 cm; Galatheidae, Nephropidae, Macrouridae, and discarded fish were most important in larger ling of 83.0–149.7 cm, with Anguilliformes also important for the largest fish (103.8–149.7 cm). The ontogenetic diet shifts in ling were consistent with gape-size limited predation. The overall diet and ontogenetic shift in diet was similar to that reported in previous studies around New Zealand (Mitchell 1984, Clark 1985a), Tasmania (Blaber & Bulman 1987), and the Falkland Islands (Nyegaard et al. 2004). Dietary differences by depth showed that Galatheidae, Pandalidae, and Goneplacidae were most important in waters 255–381 m deep; Galatheidae and Nephropidae were most important at 382–428 m; Galatheidae, Nephropidae, Mysidae, Macrouridae, and discarded fishes were most important at 429–791 m, with fish prey dominant at 562–791 m (Dunn et al. 2010). The changes in diet with depth are likely to be a direct response to changes in prey availability.

In other studies of ling around New Zealand, Graham (1938, 1956) noted that, in general, prey of ling comprised fishes, cephalopods, and crustaceans. On the Campbell Plateau, ling fed predominantly on fishes, including the Macrourids hoki and javelinfish (*Lepidorhynchus denticulatus*) (Kerstan & Sahrhage 1980). Mitchell (1984) examined 358 stomachs with prey from multiple areas and identified 42 prey species, mainly Pisces and Crustacea (with *Macruronus novaezelandiae* and *Munida gregaria* being the main prey species), but also Mollusca, Annelida, and Bryozoa. Small ling (30–80 cm) preyed largely on crustaceans, whereas large ling (80–160 cm) preyed on fish. Diet also varied by location and season (e.g., hoki off WCSI and southern blue whiting on Campbell Plateau were taken predominantly when those species were spawning (Mitchell 1984)). During the hoki spawning season in Cook Strait, Livingston (1990) examined 19 non-empty ling stomachs and found that all were feeding in midwater on hoki.

Clark (1985a) found that ling (50 non-empty stomachs) on Campbell Plateau were predominantly benthic feeders preying on natant decapods (principally *Campylonotus rathbunae*), rattails (mainly *Coelorinchus fasciatus*), small hoki, and morid fishes (*Austrophycis marginata*). The principal prey of smaller ling (70–100 cm) were natant decapods and rattails (with an estimated average weight of 16 g per prey item), whereas hoki were the predominant prey of larger ling (101–130 cm) (average 68 g per prey). Average prey weight was estimated to be 0.26% of average predator weight. Based on his Campbell Plateau sample, Clark (1985b) concluded that ling were neither specialists nor generalists, and that small ling and large hoki had relatively similar diets.

A sample of 242 non-empty stomachs off eastern Tasmania indicated that ling were epibenthic piscivores consuming mainly javelinfish, hoki, and *Helicolenus* sp. (accounting for 79% of energy intake), but also took larger crustaceans (10% of energy, predominantly *Munida*) and squid (10%) (Blaber & Bulman 1987). Temporal changes in diet were observed: hoki predominated in autumn, *Munida* in winter, and Macrourids (*Coelorinchus* sp. and javelinfish) in summer. From 93 non-empty stomachs off south-eastern Australia, Bulman et al. (2001) found that the diet was primarily benthic fish (81% by weight), with the remainder a mix of benthic and pelagic invertebrates. Ling were assigned to the benthic piscivore guild (Blaber & Bulman 1987, Bulman et al. 2001).

Ling around Falkland Islands (496 non-empty stomachs sampled during August 2001–September 2002) had key prey species of rockcod (*Patagonotothen* sp.), benthic isopods, and Patagonian grenadier (*Macruronus magellanicus*) (Nyegaard et al. 2004). Ling smaller than 50 cm fed mainly on crustaceans (benthic isopods) and small fishes (rockcod). For ling of lengths 50–100 cm, the diet shifted away from crustaceans towards *Patagonotothen* sp. and finally towards larger fishes such as *M. magellanicus* and *Micromesistius australis* for even larger fish. Niche breadth increased with increasing predator size. Larger ling generally selected larger individuals of the same prey species, with the exception of the Patagonian squid *Loligo gahi*, where all ingested squid were of similar size, regardless of the predator length. The main prey species varied substantially between the five consecutive seasons studied and appeared to follow the seasonal abundance and availability of prey. Some spatial variability in the diet was likely driven by water mass differences (i.e., temperate and sub-Antarctic waters occurring north-west and south-east, respectively, of the Falklands). The rockcod, which is available throughout the year around the Falkland Islands, was the basis of the ling diet. However, ling took advantage of other seasonally abundant prey species during their seasonal migrations (e.g., *L. gahi*). Nyegaard et al. (2004) concluded that ling scavenged on discards from fishing vessels, with this source providing more than half of prey weight in four of five seasonal samples (under the assumption that all *M. magellanicus* and *M. australis* were discards).

Off Argentina, the diet of ling (351 non-empty stomachs) comprised primarily demersal and benthic fish (70%, mainly notothenids and hake), crustaceans (18%, mainly stomatapods and isopods), and cephalopods (9%) (Renzi 1986). Fish prey dominated across all three depth zones (< 100, 100–150, > 150 m, with the total depth range from 45 to 350 m), but cephalopods increased with increasing depth and crustaceans decreased. The diet of fish less than 72 cm was dominated by crustaceans but with almost equal amounts of fish; the diets of larger fish were dominated by fish with some crustaceans and cephalopods. Areal differences in diet appeared to be aliasing for fish size, and there was no apparent seasonal variation. Renzi (1986) recorded instances of cannibalism on small ling. In Argentina's San Jorge Gulf, Sánchez & Prenski (1996) found stomatopods to be the main dietary component of ling shorter than 90 cm, with *Munida* being moderately important across all predator sizes, and fish (primarily *Merluccius hubbsi*) dominating the diet of larger ling. Seasonal variations in diet were detected, primarily relating to stomatopods, *M. hubbsi*, and euphausiids.

A small sample (47 non-empty stomachs) from the central Chilean coast in depths of 290–380 m showed ling to be primarily ichthyophagus (*Coelorinchus fasciatus* was the most abundant fish), but with significant components of a benthic Pandalid shrimp (*Heterocarpus reedi*) and mantis shrimp (*Pterygosquilla armata*) (Bahamonde & Zavala 1981). Pool et al. (1997) analysed 458 non-empty stomachs sampled from inshore and offshore waters of the northern and southern Chilean regions in 1995–96. Grenadier (*Macruronus magellanicus*) was the most important prey species across areas and seasons, with other fish species (particularly *Coelorinchus fasciatus*, *Salilota australis*, Myctophidae, *Micromesistius australis*) accounting for almost all the remaining diet, and only a small component of crustacea and cephalopods. Seasonal differences in consumption rates were apparent for some prey species, particularly *Macruronus magellanicus* and *Micromesistius australis*. There was no apparent trend in the selectivity of prey by size. Estimates (by prey type) of instantaneous gastric evacuation rate (0.05–0.06), digestion time (2.3–3.3 days), average prey weight, and daily ration as a percentage of the predator's biomass were also produced (Pool et al. 1997). A sample of 71 non-empty stomachs from off southern Chile in November 2008 showed the main component by weight to be alfonsino (*Beryx splendens*) (51% by weight), followed by cannibalised ling (11%) (Arancibia et al. 2010). The indices of relative importance (IRI), however, indicated that the main dietary component was copepods (IRI 25%, found in half of the stomachs), followed by 'fish remains' (19%), and alfonsino (17%).

All the studies summarised above showed that the diet of ling can vary markedly between areas, seasons, predator sizes, and depths, although most prey items were obtained by benthic foraging. Dietary variation can be demonstrated by examining the component of small macrourids. In New Zealand (Mitchell 1984, Clark 1985a, Dunn et al. 2010), Australia (Blaber & Bulman 1987), and Chile (Bahamonde & Zavala 1981) they comprised a large component of the diets (e.g., *Coelorinchus*, *Lepidorhynchus*). However, macrourids were found only sporadically in Falkland Islands ling (Nyegaard et al. 2004) and not at all on the Argentinean shelf (Renzi 1986). Although *Coelorinchus fasciatus* is a common macrourid in the south-west Atlantic, it occurs usually deeper (> 300 m) than the common feeding grounds of ling in the south-west Atlantic (100–250 m; Renzi 1986, Nyegaard et al. 2004), thus being unavailable as ling prey. In contrast, ling off Chile, Australia, and New Zealand are abundant deeper than 300 m and *Coelorinchus fasciatus* is commonly consumed in those three areas (Bahamonde & Zavala 1981, Clark 1985a, Blaber & Bulman 1987, Dunn et al. 2010). Small macrourids were uncommon in the diet of small ling from New Zealand but very important for medium and large fish (Dunn et al. 2010), and in Australia they were consumed more often in summer than autumn or winter (Blaber & Bulman 1987). It is clear that ling are benthic generalists and are able to feed predominantly on whichever benthic fish and crustaceans are present in their habitat, as well as on other taxa and scavenged material, with the only limitation seemingly being gape size.

Because ling is predominantly a benthic forager it is potentially vulnerable to any negative impacts of bottom trawling on benthic fauna (Dunn et al. 2010). By being benthic generalists, however, ling have an ability to switch prey (including to scavenged material rejected from trawlers), which may help to mitigate this negative effect. Scavenging of discarded offal and wounded crustacean and fish escapees from trawl nets could provide a substantial positive feedback from the commercial fishery to the ling population. Scavenging was most pronounced in intermediate sized ling and may be less frequent in smaller individuals because they are less able to forage widely and cannot as easily ingest animal remains such as discarded offal (Dunn et al. 2010). Scavenging by ling has been reported only around the Falkland Islands (Nyegaard et al. 2004) and on New Zealand's Chatham Rise (Dunn et al. 2010), which suggests ling are facultative scavengers.

The trophic level of ling off central Chile was estimated to be between 4.18 and 4.48 based on $\delta^{15}N$ values and reported stomach content data (Hückstädt et al. 2007) and 4.67 ± 0.47 based on predator and baseline $\delta^{15}N$ values (Espejo et al. 2018). Knight & Jiang (2009) estimated a trophic level of 4.34 ± 0.77 using dietary data from FishBase (Froese & Pauly 2000). Davenport & Bax (2003) used hierarchical clustering of stable nitrogen and carbon values of fish and invertebrates off south-eastern Australia to produce five trophic groups. Ling were in a group that was highly piscivorous with enriched $\delta^{15}N$ and $\delta^{13}C$ values, indicating a diet of prey with a relatively high trophic position. Two estimates of trophic level for New Zealand ling were calculated by Durante et al. (2022); bulk $\delta^{15}N$ values from fish muscle tissue indicated a trophic level of 4.03 ± 0.18, and a compound-specific stable isotope analysis of amino acids indicated a level of 4.61 ± 0.22. The trophic level from pre-1996 samples was estimated to be about 0.2 lower than samples from the post-2000 period, with the shift postulated to be a result of a greater reliance on phytoplankton-based production (relative to macroalgae-based) in the later period (Durante et al. 2022).

The digestive canal of ling was described in detail by Salinas et al. (2020), based on 12 individuals collected off southern Chile. It consisted of a short tubular oesophagus with thick walls that transitioned to a J-shaped stomach also with thick walls. This combined section comprised approximately 40% of the total length of the digestive canal. The J-shaped stomach allowed a better distension capacity and, therefore, the intake and storage of large amounts of food. A thick muscular stomach wall suggested a strong crushing mechanism acting on food prior to its passage to the intestine. The stomach ended in a pyloric sphincter (which regulated the flow of partially digested food from the stomach) connecting to a thin-walled intestine. The anterior region of the intestine had 4–5 pairs of pyloric caeca and comprised about 30% of the canal length. The posterior intestine (without pyloric caeca) had a smaller diameter compared with the anterior region. Salinas et al. (2020) concluded that the digestive system was typical of a carnivorous benthic fish adapted to feed on fish and crustaceans.

2.14 Predators

The South American sea lion (*Otaria flavescens*) was reported to prey on *G. blacodes* off the coast of Argentina (Koen-Alonso et al. 2000), with ling contributing estimated wet weights of 0.7% and 3.4% to the diets of females and males, respectively. Off Chile, George-Nascimento et al. (1985) found *Genypterus* species to contribute an estimated one-third of the sea lion diet; they used otoliths to identify partially digested fish, so could not separate the three *Genypterus* prey species. Based on analyses of stable isotopes of carbon and nitrogen, *G. blacodes* was determined to be a prey species of the South American sea lion off the southern Patagonian coast of Argentina (Zenteno et al. 2015) and a minor contributor (less than 2.8%) to the sea lion diet off central Chile (Hückstädt et al. 2007).

For New Zealand sea lion (*Phocarctos hookeri*) at Campbell Islands, ling was a relatively minor dietary component by occurrence and prey number (c. 1%) but was estimated to comprise about 9% of prey mass, with average ling prey length and weight being 70 cm and 3.7 kg, respectively (Roberts & Lalas 2015). Those authors concluded that ling were taken more often by male sea lions able to forage further offshore in deeper waters. Koen-Alonso et al. (2000) similarly reported a greater consumption of ling by male, relative to female, South American sea lions.

Ling was reported as a minor dietary component of Peale's dolphin (*Lagenorhynchus australis*) off southern Argentinian Patagonia (Schiavini et al. 1997). In a sample of 118 non-empty sperm whale (*Physeter catodon*) stomachs from Cook Strait, New Zealand, examined in 1963–64, 12 contained ling (Gaskin & Cawthorn 1967). Ling was one of the most abundant teleost species recorded, with up to six per stomach, and records occurred year-round. Some ling, however, had likely been stripped from longlines because two had hooks in their mouths.

Reports of ling being the prey of other teleosts are rare. They were classified as a minor component of the diet of the Argentine hake (*Merluccius hubbsi*) on the Patagonian shelf off Argentina (Belleggia et al. 2014) but were not identified in the diet of southern hake (677 stomachs with prey) in New Zealand waters (Dunn et al. 2010). Sánchez & Prenski (1996) recorded juvenile ling in 15% of the stomachs of *Genypterus brasiliensis* during spring only in the San Jorge Gulf off Argentina. Juvenile ling comprised 2% by weight of the diet of tiger flathead (*Neoplatycephalus richardsoni*) off south-eastern Australia (Bulman et al. 2001), and a small component of the diet of red cod (*Pseudophycis bacchus*) at various New Zealand locations (Habib 1975). One report of ling in the diets of elasmobranchs was found: in 8584 non-empty stomachs of the blue shark (*Prionace glauca*) sampled around New Zealand, one contained a ling (Horn et al. 2013a). Ling have been reported in the stomachs of jumbo squid (*Dosidicus gigas*) off the central Chilean coast (Ibáñez et al. 2015).

DNA from faecal samples used to characterise the diet of the Westland petrel (*Procellaria westlandica*) included genetic material from several relatively large teleosts, including ling (Querejeta et al. 2022). The presence of such material in the diet of this relatively shallow diving bird was concluded to be a consequence of feeding on offal and other remains scavenged from commercial fishing vessels.

An ecosystem model of the south-east Australian marine ecosystem (where ling is an important trawl fishery catch) had tiger flathead (*N. richardsoni*) as the most influential predator on ling (particularly on ling up to age 5 years, but even including those as old as 11 years), taking more than an order of magnitude more than the next most important predator (Audzijonyte et al. 2015). In that model, other predators on juvenile ling were listed (in order of importance) as gelatinous zooplankton, deepwater demersal finfish, cephalopods, orange roughy, sharks, and pinnipeds. Predators of large ling were listed as tiger flathead, pinnipeds, and gulper sharks. The information source of the predation by tiger flathead was not given by Audzijonyte et al. (2015). Bulman et al. (2001) reported that ling comprised 2% of the tiger flathead diet but noted that these prey were probably ‘the young of the year’ (i.e., ling up to 1 year old), which is at odds with the parametrisation of the ecosystem model, but more in line with the usual size of tiger flathead (i.e., commonly 35–55 cm long, but up to 65 cm (Froese & Pauly (2000)).

Cannibalism occurs rarely in New Zealand waters; it was recorded in 3 out of 1540 ling stomachs with prey (Dunn et al. 2010). Some small ling were cannibalised off Argentina (Renzi 1986) and southern Chile (Pool et al. 1997). Arancibia et al. (2010) reported that cannibalised ling made up 11% by weight of ling diet off Chile in November 2008, but it comprised only one preyed ling in 71 stomachs containing food items.

2.15 Parasitology

Lists of parasites recorded from *G. blacodes* were derived primarily from Hewitt & Hine (1972), Grabda & Ślósarczyk (1981), and Hine et al. (2000) for New Zealand; Riffo (1994) and Muñoz & Olmos (2008) for the south-eastern Pacific Ocean; and Sardella et al. (1998) for the south-western Atlantic Ocean. Subsequently there were additional records reported from the latter two areas, but none found for New Zealand since Hine et al. (2000). No records of parasites reported from *G. blacodes* in Australian waters were located. Table 8 lists records of identified parasites by geographical area.

The nematode *Pseudoterranova decipiens* (a member of a genus that, along with *Anisarkis*, is responsible for many cases of anisakiasis in humans) was found to have both the highest prevalence and abundance of any parasites in flesh samples of ling from Valdivia, Chile (Torres et al. 2014). Ling was one of a suite of species noted in a review of the potential risk of fish-borne nematode infections in humans (Eiras et al. 2016). Ling is an intermediate host for several parasites (i.e., *Corynosoma semerme*, *Pseudoterranova decipiens*, *Anisarkis simplex*, *Contracaecum* sp.) that are known to be primarily hosted by marine mammals, particularly pinnipeds (Lehnert et al. 2019).

One of the most commonly observed parasites of ling is the copepod *Sphyrion laevigatum*, conspicuous because of its size (up to about 7 cm in length) with a modified cephalothorax that embeds deeply in the flesh of the host. The parasite creates scars deep in the flesh of the fish, causing an aesthetic problem that can reduce its market value (Brickle et al. 2003). Gayevskaya & Kovaleva (1984) reported that up to 56% of *G. blacodes* examined in the 1970s from samples in the Falklands-Patagonian region were infected with between 1 and 14 *S. laevigatum*. Subsequently around 1990, in a sample of 719 ling ranging in size from 35 to 145 cm, there was a prevalence of infection of 49% (Brickle et al. (2003). The number of parasites per fish ranged from 0 to 24, but with only 2% of the sample having more than five parasites. Fish as small as 35 cm were infected. There was a significant increase in mean abundance of parasites with increasing fish age and length (Brickle et al. 2003). Similarly, Sardella et al. (1998) found a significant correlation between host length and both prevalence and mean intensity of *S. laevigatum* in ling off the Argentinian coast. Brickle et al. (2003) compared the prevalence of infection by *S. laevigatum* across three fishing grounds around the Falkland Islands and found that for the largest host size class (110–149 cm) there were significant differences between the southern grounds, relative to the northern and western grounds. Peña-Rehbein et al. (2013) concluded that *S. laevigatum* tended to cluster, and that variations in the number of parasites per host could be described by a negative binomial distribution (although the maximum number of parasites observed per host in their data was only two). However, the data provided by Brickle et al. (2003) are indicative of a negative exponential relationship in the number of parasites per host. The nematode *Cucullanus genypteri* in ling off the Argentinian coast also exhibited a significant correlation between host length and both prevalence and mean intensity, as well as a latitudinal trend in mean intensity (Sardella et al. 1997).

Other microbiological infections reported for ling comprise mycobacteria and birnaviruses. Mycobacteria, which can survive under environmental conditions that are intolerable for most other bacteria, were isolated from 9 of 20 samples of Argentinian ling that had been held at temperatures below -18 °C (Mediel et al. 2000). An infectious pancreatic necrosis virus (a birnavirus) that is a serious disease particularly of farmed salmonids was identified in ling from Macquarie Harbour, western Tasmania (Crane et al. 2000). The identification followed the discovery of the virus in farmed Atlantic salmon in the harbour, and subsequent testing of wild fishes adjacent to the marine farms.

Table 8: Parasites recorded in specimens of *G. blacodes* from New Zealand, the south-eastern Pacific, and the south-western Atlantic Oceans. (Continued on next page)

Parasite	Location	New Zealand	SE Pacific	SW Atlantic
Microsporidia				
Species unidentified	muscle		Torres at al. 2014	
Protozoa: Sporozoa				
Auerbachia anomala	gall bladder	Meglitsch 1968		
Ceratomyxa recta	urinary bladder	Meglitsch 1960		
Cerotomyxa inversa	gall bladder	Meglitsch 1960	George-Nascimento et al. 2004	
Cerotomyxa hokarari	gall bladder		George-Nascimento et al. 2004	
Sphaerospora sp.	gall bladder	Meglitsch 1970		
Myxozoa				
Kudoa sp.	muscle		Torres at al. 2014	
Digenea				
Derogenes varicus	stomach	Manter 1954		
Lecithochirium genypteri	stomach	Manter 1954	Riffo 1994	Sardella et al. 1998
Pseudopecoelus sewelli	intestines	Hine et al. 2000		
Tricotyledonia genypteri	stomach	Manter 1954, Fyfe 1954		
Aporocotyle ymakara	heart & blood vessels		Villalba & Fernández 1986, Riffo 1994	Hernández-Orts et al. 2012
Aporocotyle mariachristinae	heart & blood vessels			Hernández-Orts et al. 2012
Cestoda				
Anoncocephalus chilensis	intestine	Grabda & Slósarczyk 1981	Riffo 1994, Suriano & Labriola 1998	Sardella et al. 1998
Grillotia sp.	muscle, body cavity	Grabda & Slósarczyk 1981		
Gymnorhynchus sp.	muscle	Hine et al. 2000		
Hepatoxylon trichiuri	body cavity	Grabda & Slósarczyk 1981, Sin et al. 1992	Cattan 1977, Riffo 1994	
Scolex polymorphus	intestine			Sardella et al. 1998

Parasite	Location	New Zealand	SE Pacific	SW Atlantic
Nematoda				
Anisakis simplex	muscle, body cavity	Grabda & Slósarczyk 1981	Torres et al. 1983, 2014, Fernández & Villalba 1985, Riffo 1994	Sardella et al. 1998
Anisakis physeteris	not recorded			Eiras et al. 2016
Capillaria sp.	muscle	Grabda & Slósarczyk 1981		
Cucullanus genypteri	intestine	Hine et al. 2000	George-Nascimento & Muñoz 1997, Riffo 1994	Sardella et al. 1997, 1998
Pseudoterranova decipiens	muscle, body cavity	Grabda & Slósarczyk 1981	Torres et al. 1983, 2014, Fernández & Villalba 1985, Riffo 1994	Sardella et al. 1998
Hysterothylacium aduncum	body cavity, digestive tract	Grabda & Slósarczyk 1981	Riffo 1994	Sardella et al. 1998, Navone et al. 1998
Contracaecum sp.	body cavity, digestive tract		Riffo 1994	Sardella et al. 1998
Acanthocephala				
Corynosoma semerme	muscle, body cavity	Grabda & Slósarczyk 1981	Riffo 1994, Torres et al. 2014	
Corynosoma sp.	mesentery			Sardella et al. 1998
Echinorhynchus sp.	intestine			Sardella et al. 1998
Copepoda				
Chondracanthus genypteri	oral cavity	Grabda & Slósarczyk 1981		Sardella et al. 1998
Lepeophtheirus distinctus	not recorded	Hewitt 1963		
Sphyrion laevigatum	body surface	Grabda & Slósarczyk 1981	Peña-Rehbein et al. 2013, Donoso 2017	Sardella et al. 1998, Brickle et al. 2003
Isopoda				
Livoneca raynaudii	not recorded	Hurley 1961		

2.16 Ecosystem studies

Ling were included in a study to determine the trophic guilds of fishes on the Chatham Rise, New Zealand (Dunn et al. 2009). A 'guild' is a group of functionally similar animals in a community that exploit the same type of environmental resources in a similar way, with an emphasis on similarity in prey and in predators. The analysis used square root transformed prey weight data. Ling were included in the analysis as four separate groups based on fish size (less than or greater than 2510 g) and depth of capture (shallower or deeper than 500 m), and were found to be components of three of the ten identified trophic guilds. Small ling from both shallow and deep waters were in a group with red cod (*Pseudophycis bachus*), sea perch (*Helicolenus* spp.), and oblique banded rattail (*Caelorinchus aspercephalus*), with the main prey categories contributing to the similarity in diet for this group being benthic crustaceans, particularly galatheids. Large ling shallower than 500 m were in a group with smooth skate (*Dipturus innominatus*), with the main prey categories being discarded fish from commercial fishing, benthic crustaceans (particularly *Metanephrops* spp.), and other fish. Large deeper ling were grouped with giant stargazer (*Kathetostoma giganteum*), barracouta (*Thyrsites atun*), shovelnose dogfish (*Deania calcea*), spiny dogfish (*Squalus acanthias*), hake (*Merluccius australis*), large hoki (*Macruronus novaezelandiae*), and large arrow squid (*Nototodarus sloanii*). The main prey contributing to the similarity in this group were fishes (particularly Macrouridae and Merlucciidae), with a substantial contribution from cephalopods. Diet breadth (an indication of prey diversity) was also estimated for each predator category, and the four ling groups had Shannon-Wiener indices ranging from 1.93 to 2.13, indicative of relatively broad diets.

Several investigations of demersal fish assemblages in New Zealand waters using data from research trawl surveys have been reported. Beentjes et al. (2002) examined data from off the east coast South Island (Pegasus Bay, and North and South Canterbury bights, in 10–400 m depths). Ling were classified in the outer shelf assemblage (200–400 m), and, although their full depth range was not represented, they were the sixth most abundant species in that depth range. Seasonal comparisons showed that ling were more abundant in the south of the study area during summer. A later analysis of the same east coast South Island survey series (from 1991 to 2018) found that ling was one of a set of high-value species exhibiting a strong positive relationship between catches from fisheries-dependent and fisheries-independent data (Durante et al. 2020). Jacob et al. (1998) analysed data from 1983 to 1986 off south-eastern New Zealand (Sub-Antarctic), spanning 80–787 m depths, and placed ling in the deepwater assemblage (300–800 m), with the main associated families being Merlucciidae, Macrouridae, Argentinidae, and Chimaeridae. Bull et al. (2001) investigated Chatham Rise fish communities in 200–800 m depths. Ling had a preferred depth range of 305–710 m (with a point estimate of 490 m) and were slightly more abundant on the south relative to the north Chatham Rise. They were overall the fourth most abundant species and were a dominant species in both the 350–550 m (occurred in 99% of tows) and 550–800 m (94% of tows) zones. All three studies found that depth was the primary variable influencing assemblages, with secondary effects generally being latitude and bottom temperature.

Assemblage studies from the extent of the New Zealand Exclusive Economic Zone (EEZ) have used New Zealand research trawl data from depths of ~4 to 1500 m. Francis et al. (2002) identified four primary assemblages, with ling being a dominant species in the upper continental slope group (occurring in 43% of tows and being the third most caught species in that assemblage). Point estimate preferences for ling were a depth of 480 m and latitude of 48° S. Most of the explainable variation in species composition was associated with depth and latitude. Leathwick et al. (2006) incorporated a wider range of environmental variables and found that the most influential predictors were depth, temperature, salinity, and chlorophyll-*a*. They identified 16 fish assemblages, with ling being recorded in all of them. Ling were particularly important, however, in five assemblages: Challenger Plateau shallow upper slope (~400 m); Chatham Rise shallow upper slope (~370 m); Campbell Plateau shallow upper slope (~515 m); Chatham Rise mid upper slope (~550 m); and Campbell Plateau mid upper slope (~720 m). These areas tended to be characterised by moderately cold temperatures and low salinity. Stephenson et al. (2020) used high resolution environmental data and presence/absence data of demersal fish species in research trawls to define 30 distinct fish assemblages. Ling was one of a small number of widespread species that occurred in most of the 30 groups but was particularly dominant in a set of intermediate depth groups (340–600 m mean depths) characterised primarily by cool temperatures, high oxygen, and low salinity levels, south of the Subtropical Front. Ling were often associated with javelinfish and hoki.

Two end-to-end ecosystem models incorporating ling as major components have been reported, one for the Chatham Rise, New Zealand (McGregor et al. 2019), and the other off south-eastern Australia (Audzijonyte et al. 2013, 2015). The Australian model explored how reductions in size-at-age of fished species (up to 6% in 50 years) would affect stock recovery after the implementation of a fishing moratorium. Reduced size-at-age for ling resulted in reduced relative biomass, reduced fisheries catches, and increased predation mortality, with larger effects during scenarios of higher mortality rates due to fisheries. Very strong trophic interactions were observed between tiger flathead (*Neoplatycephalus richardsoni*) and ling, owing to flathead being parametrised as the major predator on ling (but see Section 2.14). Small reductions in the body size of flathead had positive effects on ling, involving both predation of flathead on ling and competition between the two species. Following the cessation of fishing there was a boom followed by a decrease in ling biomass, with the increase caused by the fast response of ling to the cessation of fishing, followed by increased abundance of large flathead producing greater predation mortality on ling. The New Zealand model (McGregor et al. 2019) was set up to investigate the potential for understanding system-wide responses to fisheries management strategies in one of New Zealand's largest fishing grounds. Ling were incorporated in the model as a single species age-structured group. It was a moderately important component of the model, with a 'keystoneness' (a measure of the effect that the ling group has on the rest of the ecosystem) ranking of 11 out of 37 vertebrate and macro-invertebrate groups. Ling was well defined in terms of abundance estimates, biological parameters, and diet. The model estimate of its biomass trend was found to be very similar to stock assessment model results. There was slight poor performance relating to estimates of its size-at-age, with the estimated lengths of younger aged fish being larger than actual biological parameters indicated.

The consumption to biomass ratio (C_y) at the population level is the number of times a population eats its own weight during a certain period of time (usually a year, y) and is a metric often required in multispecies models in aquatic ecosystems. The estimation of this measure of interaction between predator and prey usually relies on numerous assumptions. Wiff et al. (2015), using a general modelling framework, estimated the mean C_y for separate non-stationary northern and southern populations of ling off Chile over years 1978 to 2004 to be 1.72 and 1.21 yr^{-1}, respectively. The model used known growth parameters, length-frequency data, and a dietary assimilation rate (0.769) based on a reanalysis of daily ration data (mean ration 7.12 g day^{-1}) from Pool et al. (1997).

The stable isotopes of carbon and nitrogen were used to investigate trophic relationships of fish and invertebrates on the continental shelf of south-eastern Australia (Davenport & Bax 20103. Hierarchical clustering separated the 87 fish species into five groups. The group including ling comprised highly piscivorous species with enriched δ^{15}N and δ^{13}C values, indicating a diet of prey with a high trophic position that have high δ^{15}N values (i.e., fish, cephalopods, polychaetes). This hypothesis was supported by data from stomach content analyses of the predators in the group.

The diet of the Argentine hake, *Merluccius hubbsi*, an opportunistic predator in the San Jorge Gulf (Argentina) ecosystem, changed markedly from 2011 to 2014, with much greater consumption of *Munida gregaria* compared with the years from 2005 to 2011 (Belleggia et al. 2017). The main predators of *M. gregaria*, which included *G. blacodes*, exhibited decreased abundance and catches in the years analysed, leading to the conclusion that top-down trophic dynamic control occurred in the studied ecosystem.

The effects of a large-scale offshore Marine Protected Area (MPA) on the Southwest Atlantic Patagonian Shelf (43° S, 63° W) on demersal fish abundance was assessed by analysing the fishing effort and catch at 152 stations concentrated near the protection boundaries before and after the MPA establishment (Alemany et al. 2013). The Argentine hake was the prime species being investigated, and it, along with with *Genypterus blacodes*, *Macruronus magellanicus*, and *Patagonotothen ramsayi*, showed marked increases in abundance, supporting the case for offshore, large-scale MPAs. Punt et al. (2016b) used simulation to explore the effect of spatial closures to achieve goals relating to conservation and utilisation of fishery resources, with an operating model based on *G. blacodes* off southern Australia. They concluded that when a large fraction of the total area is closed, stock size is substantially larger than the target at the end of the projection period.

The responses of key New Zealand fisheries species (including ling) to climate-associated change over the remainder of the 21st century, based on reviews of their biological and ecological characteristics, were investigated by Cummings et al. (2021). While it was concluded that climate change posed no known challenges to future ling production, this finding arose primarily because there was little available information to postulate a definite impact. Based on expert opinion, however, it was concluded that most biological characteristics of ling (e.g., stock size and distribution, growth, mortality, reproduction, and migrations) were likely to undergo climate-related changes (both positive and negative) in the following decades. Likely effects on ling growth rates of changing sea temperatures were investigated by Morrongiello et al. (2021) (see Section 2.5).

2.17 Habitat and behaviour

Based on underwater video recordings and distributions of commercial fishing, ling are known to occur over a wide variety of substrate types, including soft muddy and sandy flats, stony bottoms, and rocky reefs (Bruce et al. 2002, Horn 2004b, Piasente et al. 2004, Leathwick et al. 2006).

Characteristics of ling habitat and behaviour were derived from images and video footage obtained using NIWA’s Deep Towed Imaging System (DTIS) during several research surveys, primarily on the Chatham Rise, but also at other locations around New Zealand. Conclusions relating to ling, made by NIWA staff who viewed the videos to record the observed fauna (NIWA, unpublished data), were:

- Ling occurred on a wide range of substrate types, i.e., relatively flat muddy and sandy sediments, substrates predominantly covered by shells or cobbles, and reef areas often with abundant epibenthos.
- When encountered by the camera they rarely exhibited an escape response (in contrast to other ‘eel-like’ fishes), and generally just remained in the flood-lit area with their tails rhythmically moving, holding station in the current. One fish followed the camera.
- They appeared to use their slender pelvic fins on their chin to ‘feel’ the surface of fine substrates, presumably searching for prey (Figure 3).
- They were observed stationary on relatively open substrates, appearing to hide or shelter behind isolated objects, i.e., rocks and sponges (Figure 3).
- They were observed sheltering in holes and crevices in reefs (Figure 4). It was not clear whether this behaviour provided protection against predators, provided a location where ling could remain ‘on station’ with very little energy expenditure in areas with relatively strong currents, or provided a hiding place from where prey ambushes could be launched.

Towed underwater video recordings made as part of marine biological and resource surveys off south-eastern Australia (National Oceans Office, Project OP2000-SE02) recorded 85 adult ling from an area comprising a canyon and terraced slope between 300 and 700 m. Ling were found to be very abundant on the canyon rim, an area with abundant outcrops and subcrops (i.e., outcrops largely buried with alluvial sediments), relative to areas of cobbles, pebbles, and fine sediments. In the outcrop-subcrop areas, ling were most strongly associated with cracks and crevices and structural epibenthos (predominantly sponges). Other ling (16% of observations) were associated with mud-pebble debris fields, depression features in sediment bottoms, and on unstructured sediments. There were no observations of ling in burrows or on areas of sediment characterised by sand ripples. Little flight response upon encountering the video lights was recorded for ling in all habitat types. The observations were interpreted as ling making use of structured habitat as refuges when they were not actively foraging (Alan Williams, CSIRO, pers. comm.).

Species of *Genypterus* and other Ophidiiformes have been regularly described as fish that created burrows in soft substrates. Some of these reports were clearly based on actual observations of the behaviour (e.g., Rountree & Bowers-Altman 2002), and videos of cusk eels burrowing are available (e.g., Rountree 2003). Evidence-based studies of this behaviour appeared to be most abundant for cusk eels of the genera *Ophidion* and *Chilaria*, and it was probably a means of predator avoidance or hiding to ambush prey. There were some references to *Genypterus* species in burrows. Macpherson (1983) stated that *Genypterus capensis* "are nocturnal feeders and probably live in burrows at the bottom, in small holes in the mud, or in caves during daytime. This behaviour has also been observed in some species of *Genypterus* off the coast of Chile." However, no reference to any Chilean study was provided. In a checklist of fishes off Tasmania, *G. blacodes* was reported by Last et al. (1983) to occur "in depths of 20–800 m, where it burrows in soft sand or mud"; no source for this statement was given. *Genypterus blacodes* were reported as being observed occupying burrows in mud substrate at Patterson Inlet, Stewart Island, New Zealand, during scuba-diving (Mitchell 1984). Recent discussions with fisheries biologists have suggested that given the location and depth, the observed fish could easily have been *Conger* species. Although neither of New Zealand's conger species have been reported as burrowers, the biological knowledge of both congers is sparse, and several Congridae in other parts of the world do exhibit burrowing behaviour (e.g., Levy et al. 1988). Given that there were no recorded examples of ling looking out of burrows in soft sediments in the many hours of video footage examined from ling depths around New Zealand (NIWA, unpublished data) and south-eastern Australia (CSIRO, unpublished data), it is considered most likely that *G. blacodes* rarely, if ever, constructed, or dwelt in, burrows. It is clear, however, that ling frequently sheltered in natural holes and crevices in or under rocky features (see Figure 4).

The behaviour of ling when encountering a trawl net was investigated using cameras mounted on the trawl. Ling were motionless or randomly swimming when first encountered by the trawl, whereupon they responded with a startled burst of high-speed swimming away from the trawl (Piasente et al. 2004). Ling entered the trawl close to the bottom and remained on or close to the bottom panel. They swam in an anguilliform mode, where the posterior half of the body is flexed laterally. When in the net ahead of the codend, ling (lengths 50–80 cm) were observed swimming both forward and aft in a relaxed manner, with occasional burst-swimming forward, but were sometimes motionless and quickly overrun by the trawl. Contact with other fish or the trawl evoked haphazard burst-swimming manoeuvres. Smaller ling were able to escape by burst-swimming through meshes in the anterior part of the trawl. After reaching the codend, most ling accumulated ahead of the other mass of fish and swam forward at the same speed as the trawl, with some large individuals observed swimming up and down the length of the codend (Piasente & Eayrs 2000, Piasente et al. 2004).

The proportion of red muscle to white muscle in fish appears to be dependent on the activity of the species: greater red muscle is associated with a greater activity level. Ling have only a very small amount of red muscle, present as a thin strip just below the skin along the caudal section of the lateral line, a characteristic consistent with it being a sedentary species (Ashoka et al. 2011).

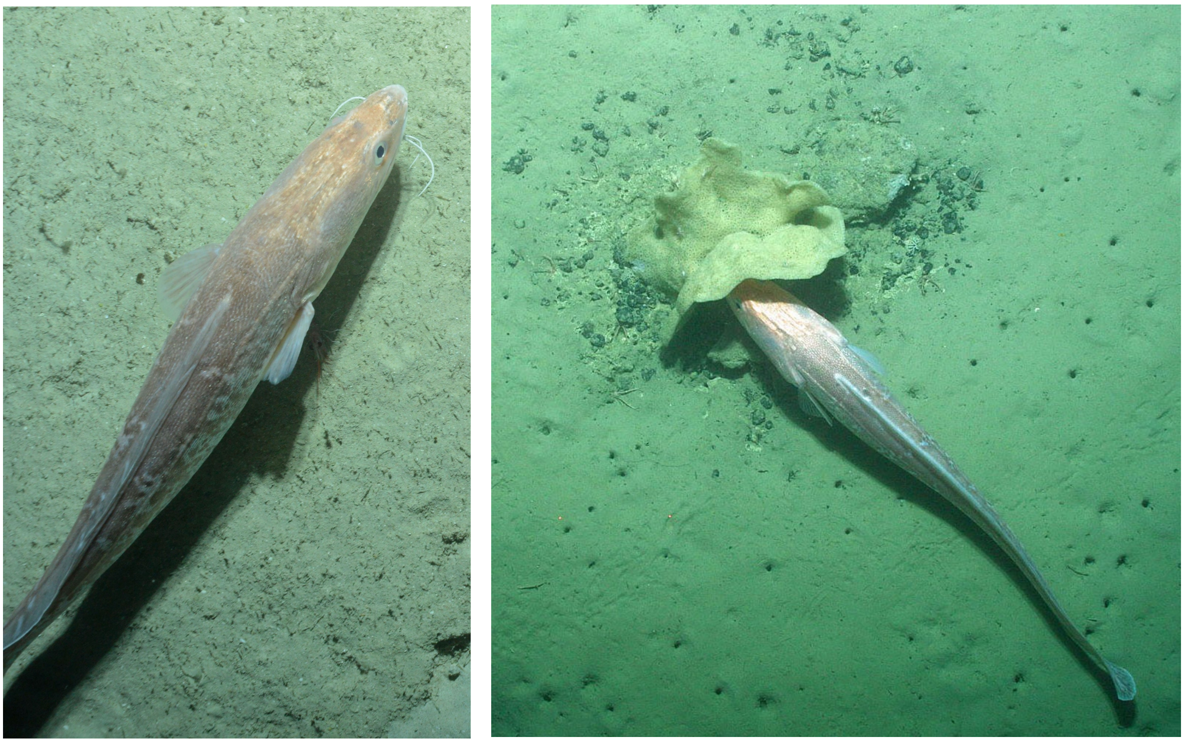

Figure 3: NIWA's Deep Towed Imaging System images of ling; (left panel) using its pelvic fin 'barbels' to 'feel' the substrate, (right panel) stationary ling sheltering behind a sponge. (Photos by NIWA.)

Figure 4: NIWA's Deep Towed Imaging System image of a ling (see head at top left of image) sheltering in a crevice under a rock outcrop with associated epibenthos, and a small fish (possibly a dwarf cod, *Notophycis marginata*, a common ling prey species) at centre of frame. (Photo by NIWA.)

2.18 Fishery selectivity

Only one instance of experimental determination of trawl mesh selectivity of ling was found. Bruce et al. (2002) reported logistic trawl gear selectivity curves for a range of trawl mesh sizes based on field trials and for a sample from a commercial fish market (Table 9). As would be expected for a fish with a cylindrical body shape, a codend mesh hung on the square allows more escapement of larger fish than the same sized mesh hung on the diamond.

Table 9: Logistic gear selectivity parameters for three codend mesh configurations and from a market sample. L_{50}, length at 50% selectivity (cm); *k*, the logistic growth rate or steepness of the curve.

Codend mesh	90 mm diamond	90 mm square	102 mm square	Market
L_{50}	42.93	52.4	57.07	35.18
k	0.3197	0.2000	0.3485	0.3533

In an investigation of gill net selectivity, Hickford et al. (1997) found that a small sample (n = 8) of ling caught in 3.5 inch (~90 mm) mesh had a mean length of 65 cm.

Selectivity ogives for specific fisheries or research surveys were regular outputs of stock assessment models for New Zealand ling (e.g., McGregor 2015, Dunn & Ballara 2019, Mormede et al. 2021b), and for assessments elsewhere (e.g., Contreras et al. 2013, Whitten & Punt 2014, Cordue 2018). These outputs were generally of selectivity by age class rather than by fish size but could easily be converted to size selectivity by using appropriate age-at-length information. It was apparent, however, that fishery selectivity ogives derived in models could be influenced by the relative weightings given to the input series of proportions-at-age data, as well as by the model parametrisation of both the natural mortality rate and the ogives themselves (e.g., Dunn & Ballara 2019).

2.19 Biochemistry

A proximate analysis of muscle from New Zealand ling found it comprised water (88.1%), protein (17.2%), fat (0.2%), and ash (1.0%) (Konosu et al. 1978). Those authors also provided a detailed analysis of the nitrogenous constituents of the flesh and the amino acid composition of the muscle proteins. Two proximate analyses of ling muscle from off the southern Argentinian coast reported: 77.7% water, 15.3% protein, 5.0% lipids, and 2.6% ash, and an energetic value of 5.6 kJ G^{-1} wet mass (Eder & Lewis 2005); and 81.25–82.8% water, 15.2–16.25% protein, 0.55–1.1% fat, and 1.1–1.3% ash (Chiodi 1971). Both studies indicated that there was seasonal variation in the proximate composition, particularly in lipid values, with Chiodi (1971) showing that fats were at their minimum in June (i.e., at spawning time, when the gonads had their peak lipid concentrations) and maximum in December–February. Ling muscle off south-eastern Australia comprised 0.35% lipids (Armstrong et al. 1991). The composition of the lipids was also evaluated from the Australian sample (means calculated from the data for 10 individual fish): saturated fatty acids, 31.9%; polyunsaturated fatty acids, 39.2%; docosahexaenoic acid, 22.2%; eicosapentaenoic acid, 4.6%; arachidonic acid, 3.7% (Armstrong et al. 1991). Marques et al. (2019) tested ling fillets from an unspecified location and found that all the lipids comprised polyunsaturated fatty acids; there were 0.28 mg g^{-1} of cholesterol, and no carbohydrates. The energetic value of ling flesh was reported to be 5.60 kJ g^{-1} (Eder & Lewis 2005) and 2.93 kJ g^{-1} (Marques et al. 2019).

As part of an investigation of the changing diet of the South American sea lion off Argentina, Zenteno et al. (2015) determined the ratios of stable isotopes of carbon and nitrogen in the muscle of ling, one of the sea lion's potential prey. Values of $\delta^{13}C$ and $\delta^{15}N$ (‰, mean ± SD) were, respectively, -14.7 ± 0.4 and 18.0 ± 0.3 off northern-central Patagonia and -17.2 ± 0.8 and 18.3 ± 0.5 off southern Patagonia. A comparable study off central Chile produced values of -13.68 and 20.71, respectively (Hückstädt et al. 2007). A sample of three ling from the southern Chilean fjords produced a $\delta^{15}N$ value of 16.29 ± 0.25 (Espejo et a. 2018). Values of $\delta^{13}C$ and $\delta^{15}N$ (‰, mean ± SD) from a sample of 18 ling off south-eastern Australia (using white muscle from the caudal region) were reported to be -17.2± 0.6

and 13.1 ± 0.7, respectively (Davenport & Bax 2003). Durante et al. (2022) determined $\delta^{13}C$ and $\delta^{15}N$ values (‰, mean ± SE) for ling off north-eastern South Island, New Zealand, from fish harvested before 1996 and after 2000, and concluded that the changes in values over time ($\delta^{13}C$ and $\delta^{15}N$, pre-1996, -17.6 ± 0.2 and 14.1 ± 0.2; post-2000, -16.6 ± 0.2 and 14.6 ± 0.3) were a consequence of a shift by ling to be more reliant on phytoplankton-based production (relative to macroalgae-based) in the later period.

A comprehensive analysis of trace element concentrations examined ling fillets collected off southern New Zealand (Ashoka 2009, Ashoka et al. 2011). Mean concentrations (mg kg^{-1} dry weight) are listed in Table 10. The distributions of trace elements were found to be generally not homogeneous along the fillet. In white muscle, increases in concentration towards the tail end of the fish were observed for 11 metals (Li, Na, Ca, V, Fe, Cu, Zn, Sr, Ag, Cd, U), whereas the reverse trend was observed for Mn, As, and Se, and no trends were observed for Mg, K, Rb, and Cs. Concentrations of 10 metals (Li, Na, Ca, V, Mn, Cu, Se, Ag, Cd, U) were significantly higher in the belly flap, and concentrations of four metals (K, Rb, Sr, Cs) were significantly lower in the belly flap. In addition, the concentrations of several metals (Fe, Cu, Zn, Ag, Cd) were found to be 3–4 times greater in red than in white muscle.

There were other reported trace element analyses of ling muscle. Those results were reported as mg kg^{-1} wet weight but were converted to mg kg^{-1} dry weight by Ashoka (2009), assuming the average water content of muscle was 80%, to enable comparisons with her results. The mg kg^{-1} dry weight values follow. Kobayashi et al. (1979) analysed ling caught off New Zealand and Patagonia and reported values for Se (0.08), Zn (9.3), Pb (0.07), and As (1.17). These values, with the exception of Pb, were very much lower than those of Ashoka (2009). Vlieg et al. (1991) reported values for Na (5100), Mg (1650), K (19 900), Ca (750), Zn (32), and As (14), which all compared well to those of Ashoka (2009). However, their values for Mn (1.2), Cu (3) and Fe (38) were considerably higher than Ashoka's, while a value of 1.8 for Se (Vlieg 1990) was half of the value obtained by Ashoka (2009).

Ashoka (2009) also compared trace element levels in three tissue types: muscle, liver, and bone (Table 10). The accumulation of trace metals in fish tissues depends on the physiological role of the organ, and, for most detectable elements, the concentrations were significantly different in all three tissues. The liver, for example, is actively involved in the uptake and storage of heavy metals, and levels of both Ag and Cd were found to be significantly higher in the liver than in the other tissue types. Analyses of trends between element concentrations and ling size indicated that trace metal levels in both muscle and bone did not generally show any significant trends with size, but, in the liver, the element concentrations generally decreased with increasing size. Ashoka (2009) suggested that trace metal concentrations in either muscle or bone (but not liver) could therefore be acceptable for stock discrimination purposes.

Concentrations of mercury were measured in ling collected around New Zealand between 1976 and the early 1980s, with most samples being of dorsal muscle directly posterior to the left operculum (van den Broek et al. 1981, Fenaughty et al. 1988). Mean values (mg kg^{-1} wet weight, with sample size and standard error in parentheses) were 0.94 (31, 0.10) from Auckland Islands, 0.73 (34, 0.07) from WCSI, 0.64 (29, 0.09) off Southland, 0.52 (178, 0.03) on Campbell Plateau, 0.39 (73, 0.04) on Pukaki Rise, and 0.31 (222, 0.02) off east coast South Island (ECSI). In all areas, mercury content of the flesh increased (a non-linear increasing function) with length and presumably also with age. Comparison of mercury levels in standardised samples comprising New Zealand ling of lengths likely to be aged about 14 years showed no significant differences between sexes but did indicate geographical differences in concentrations (Timperly & Tracey 1997). Fish from the Chatham Rise had, on average, lower levels (c. 0.36 mg kg^{-1}) than those from the Campbell Plateau and WCSI (c. 0.65 mg kg^{-1}). Within the Campbell Plateau, ling from the Auckland Islands shelf had the highest mercury levels of the study (c. 1.01 mg kg^{-1}), but the sample size was relatively small. Muscle tissue from five ling sampled off south-eastern Australia had a mean mercury concentration of 0.73 mg kg^{-1} wet weight (Walker 1988).

Results of a programme to investigate levels of heavy metals in marine organisms were also reported by Fenaughty et al. (1988). Samples of ling muscle tissue from ECSI ($n = 6$) and Campbell Plateau ($n = 30$) collected around 1979 were analysed. Mean values (mg kg^{-1} wet weight) for ECSI and Campbell Plateau, respectively, were: Cd, 0.02 and 0.02; Cu, 0.44 and 0.96; Zn, 3.85 and 7.66; Pb, 0.15 and 0.18. With the exception of Zn, these values are all higher than those of Ashoka (2009) after conversion to mg kg^{-1} dry weight. No detectable levels of organochloride pesticides were found in 11 ling from Campbell Plateau (Fenaughty et al. 1988). The cadmium level in muscle from three ling from the southern Chilean fjords was 0.38 ± 0.47 µg g^{-1} dry weight (Espejo et al. 2018).

Levels of radioactive polonium per wet weight of fillets in six ling sampled off Argentina were found to be 31.3 ± 9.1 mBq kg^{-1} (Colangelo et al. 1994). The polonium activity levels in ling were the lowest of the seven marine species tested.

Table 10: Concentrations (mean ± standard deviation) of elements in ling, in muscle, liver, and bone (from Ashoka 2009). –, measurements were not within quality control specifications. Values in brackets denote method detection limits. Superscripts of the same letter indicate that mean values for that element are not significantly different between the tissues.

Element	Concentrations (mg kg^{-1} dry weight)		
	Muscle	Liver	Bone
Li	0.14 ± 0.04	0.05 ± 0.03	1.3 ± 0.1
B	2.2 ± 0.8	(<0.039)	1.8 ± 0.3
Na	8000 ± 1000	–	–
Mg	1400 ± 200	400 ± 300	–
K	15000 ± 1000	4000 ± 2000	400 ± 100
Ca	700 ± 200	300 ± 300	–
V	0.013 ± 0.004	0.04 ± 0.003	0.19 ± 0.09
Cr	0.04 ± 0.04 ^{a}	(<0.127) ^{ab}	(<0.0681) ^{b}
Mn	0.43 ± 0.07	1 ± 1	20 ± 7
Fe	6 ± 3	90 ± 70	–
Co	0.010 ± 0.004	0.15 ± 0.09	0.027 ± 0.003
Ni	0.1 ± 0.2 ^{a}	0.2 ± 0.2 ^{a}	0.27 ± 0.01
Cu	1.0 ± 0.3	15 ± 9	0.20 ± 0.6
Zn	24 ± 3	40 ± 20	73 ± 5
As	18 ± 9	4 ± 3	0.11 ± 0.05
Se	3.5 ± 0.7 ^{a}	3 ± 2 ^{a}	(<0.479)
Rb	3.4 ± 0.5	1.0 ± 0.5	0.07 ± 0.03
Sr	–	2 ± 1	–
Y	(<0.000903) ^{a}	0.0004 ± 0.0003 ^{a}	(<0.00905)
Ag	(<0.00168) ^{a}	0.5 ± 0.4	(<0.0121) ^{a}
Cd	0.02 ± 0.02 ^{a}	1 ± 1	0.014 ± 0.008 ^{a}
Cs	0.19 ± 0.05	0.04 ± 0.02	0.005 ± 0.002
Ba	(<0.030) ^{a}	(<0.0125) ^{a}	2.3 ± 0.6
La	0.001 ± 0.001 ^{a}	(<0.00131) ^{a}	(<0.00677) ^{a}
Ce	0.001 ± 0.001 ^{a}	(<0.00192) ^{a}	(<0.0168)
Pb	0.03 ± 0.03 ^{ab}	(<0.0174) ^{a}	0.05 ± 0.03 ^{b}
U	(<0.00176)	0.0012 ± 0.0009	0.06 ± 0.02

A lectin (a protein found mainly in legumes and grains that binds to carbohydrates) was isolated from the external mucus of ling by Oda et al. (1984a) and was found to contain large amounts of the amino acid lysine. A mitogenic lectin in the skin mucus of the ling (referred to as *G. capensis*, but caught off New Zealand so almost certainly *G. blacodes*) was purified by Toda et al. (1996). These lectins can stimulate the transformation of cells from the resting phase to blast-like cells that experience growth and development, and they may also function as inhibitors against colonisation or invasion of potential pathogenic micro-organisms. The authors did not investigate whether the mitogenic lectins stimulated cell growth, but Oda et al (1984b) did find that they prevented fertilisation in mice by both agglutinating sperm and attaching to the zona pellucida of the ova.

Capillary zone electrophoresis (CZE) was used to study the effect of frozen storage on the electrophoretic patterns of sarcoplasmic proteins extracted from ling fillets (Larraín et al. 2002). Profiles were found to be independent of fish freshness: frozen fish showed the same protein profile as their fresh counterpart. CZE, a rapid, simple, and reproducible technique, enabled correct identification of frozen ling stored at -18 or -30 °C from 0 to 180 days.

Ling was one of five fish species from different suborders used to examine phylogenetic relationships by comparing the electrophoretic properties and tissue distributions of the lactate dehydrogenase isoenzyme LDH M_4 (Thompson & Baldwin 1983). Eye, heart, liver, and muscle tissues were analysed. Unlike the other species examined, ling muscle LDH M_4 exhibited three electrophoretic bands when stained for protein, which the authors found difficult to explain.

The vitamin A content of liver oil sampled from ling in Cook Strait slowly decreased from a maximum value of 0.7% during January–February to a minimum value of 0.5% during July–August (Shorland 1938). Changes in the vitamin content of the oil were suggested to be related to spawning, when the vitamin reserves would be used up to a much greater extent than the oil itself. Shorland (1939) found no significant seasonal variation in fatty acid composition of the liver. The liver vitamin A content in eight ling samples off Argentina ranged from 1800 to 840 IU g^{-1}, and the liver comprised up to 50% fat at times outside the spawning season (Chiodi 1971). Marques et al. (2019) reported the vitamin A, D, B_6, and B_{12} contents of ling fillets but did not state the origin of the fish.

The skin of ling is primarily composed of collagen, which has many commercial applications. Hofman & Newberry (2011) investigated the effects of temperature and solvents on the denaturation of the collagen molecule in ling skin, findings which had implications for processing, storage, and later use of ling collagen as an ingredient in other products.

Levels of trimethylamine oxide (TMAO) in the white muscle of ling were 184–291 mg/100 g wet weight (Summers et al. 2017). TMAO contributes significantly to loss of seafood quality during post-harvest storage. The ling values were in the middle of the range for all tested New Zealand species and were below levels considered to be indicative of poor quality. A higher TMAO mean value of 389 mg had been reported previously (Konosu et al. 1978), the difference likely owing to variations across seasons and habitats (Summers et al. 2017).

The changes in freshness of ling over a 6-month period, when stored at -18 °C or -30 °C, and when canned in brine or distilled water, were evaluated by examining changes in pH, total volatile basic nitrogen, and nucleotide levels (Abugoch et al. 2005). Little change was observed in both pH and nitrogen, whereas the nucleotide levels indicated slightly reduced levels of freshness, particularly in the canning process, but not to levels that compromised the freshness of the product. Trials with salting ling fillets found that the species provided an excellent alternative to salted cod (Avdalov & Lasa 1995). The drying process took two weeks and produced a product which, when cooked after successive washes to remove the salt, had an excellent taste and texture.

2.20 Aquaculture

Aquaculture of *G. blacodes* has been trialled in Chile (Dumorné 2018), although it appeared that this has primarily involved keeping wild captured fish alive in tanks near processing facilities to enable the industry to control the time of processing. Salinas et al. (2020) researched the morpho-histology of the digestive canal of *G. blacodes* to provide information to support their nutritional management in captive conditions. The authors reported that ling had a digestive system typical of a carnivorous benthic fish adapted to feed on fish and crustaceans and showed potential as a species for Chilean aquaculture diversification. Spermatic functions and the effects of pH, salinity, and temperature on sperm motility of *G. blacodes* were assessed by Dumorné (2018) with an aim to develop and optimise protocols for artificial reproduction of the species.

Genypterus blacodes juveniles (*n* = 60, mean weight 20 g) were obtained from captive brood-stock and acclimated for seven weeks in raceway tanks (temperature 15.2 ± 1.9 °C) at Puerto Montt, Chile (Serrano et al. 2021). Three diets were trialled over 12 weeks: a control diet, and two diets containing 5% or 10% of *Schizochytrium limacinum* (a microalga) meal, respectively, formulated to replace 0, 28, and 56% of total dietary fish oil with microalgae. All the experimental diets were accepted by the fish and the survival rate was 97%. The average live weight gain (c. 25 g) did not differ between treatments, indicating that *S. limacinum* meal was a sustainable alternative ingredient for the dietary substitution of fish oil in commercial feed for *G. blacodes*.

Juveniles of the closely related *G. chilensis* produced by wild parents in culture conditions and fed on a diet of commercial marine fish pellets reached a harvest weight of 2 kg after between 18 and 26 months (Vega et al. 2015). The mortality rate of eggs during cultured incubation was found to be high, however (Vega et al. 2018). Vega et al. (2012) tested the efficiency of two incubation systems for *G. chilensis* egg masses, one with a closed water circuit and the other with an open water circuit; the former system produced greater egg survival.

3. THE NEW ZEALAND LING FISHERY

3.1 Māori fisheries (pre-European)

Analyses by Leach & Boocock (1993) of Māori midden contents from 84 sites showed ling to be the sixth most abundant teleost species, accounting for a minimum of 430 individual fish, or 3.5% of the total minimum number of all individual teleosts identified. The data indicated that the relative abundance of ling in middens over time declined, being 3.9% in the archaic period (i.e., before c. AD 1500), 3.4% in the classic period (i.e., c. AD 1500–1769), and 2.0% in the post-European period (i.e., c. AD 1769–1840). Minimum numbers of individuals from each of the three periods were 265, 130, and 35, respectively. Leach & Boocock (1993) noted that the midden data were heavily weighted overall towards South Island archaeological sites, but that there were more classic assemblages from the North Island relative to the South Island; both these factors could bias comparisons across species and over time (discussed further by Leach (2006)). For ling, 391 of the minimum 430 individuals were from southern South Island sites, with all but three of the remaining fish being from either northern South Island or the Chatham Islands.

In a subsequent review, Leach (2006) compiled data from 126 sites, recording a minimum number of 713 ling which comprised a weighted mean value of 1.8% of the total minimum number of all individual fish identified (i.e., weighted in proportion to the size of each assemblage to prevent very small assemblages from unduly influencing the averages). Ling occurred in small numbers at sites around the South Island, and, to a lesser extent, in Cook Strait and at the Chatham Islands. A site at Tiwai Point, at the mouth of Bluff Harbour, was unusual in that 30% of the individual fish (31 out of the 103 total) were ling, along with 41 red cod. Leach (2006) suggested that ling (and red cod) at Tiwai Point were caught in Bluff Harbour, as Graham (1956) recorded ling venturing into Otago Harbour at times. Using data from five sites occupied over a sustained period of time, Leach (2006) found that only one had a significant change in ling abundance over time (the Black Rocks site at Cape Palliser, southern North Island, showed a reduction). It was stressed, however, that temporal changes in the catch rates of any species could be influenced by seasonality of site occupation, as well as temporal changes in weather patterns, fishing technology and methods, and species abundance.

In an evaluation of midden remains from the Otago-Catlins region, ling were present in 22 of the 30 sites, and it was one of the more abundant species (Smith 2013). Ling remains were less abundant in the archaic period (relative to the classic period), but the limited number and size of classic period assemblages meant that the observed variation in ling abundance could easily be a sampling effect.

In conclusion, ling appear to have been taken occasionally by Māori throughout their occupation of New Zealand, with most catches being from around South Island. Ling were probably not targeted but were likely a bycatch of hook and line fisheries for other species in coastal waters 30–70 m deep (Graham 1956, Paulin 2007). The amount of catch was unlikely to have impacted the ling stock size.

3.2 History and development of the commercial fishery

Historically there have been two main fishing methods for ling: line and trawl (Dunn & Ballara 2019). The development of ling fisheries, by area and time period, is described below. The New Zealand Exclusive Economic Zone (EEZ) as established on 1 April 1978 (Figure 5). Quota Management Areas (QMAs) for ling fishstocks were used for reporting ling catches from the start of the 1986–87 fishing year (1 October 1986) when the Individual Transferable Quota (ITQ) system was introduced (Figure 5). Before this time, foreign fishing vessels received catch allocations, and reported catches, using the statistical areas denoted A–H in Figure 6.

The commercial catch history for the ling fishery in New Zealand waters has been derived from a variety of sources. Data on landings before 1983 are from Paul & Robertson (1979), King (1985), Patchell & McKoy (1985), and Francis & Paul (2013). Data from 1983 to 1986 are from the Fisheries Statistics Unit (FSU) database and data from 1987 to the present are from the Quota Monitoring System (QMS) database, both administered by Fisheries New Zealand (Ministry for Primary Industries) (and formerly by the Ministry of Agriculture and Fisheries (MAF) and the Ministry of Fisheries).

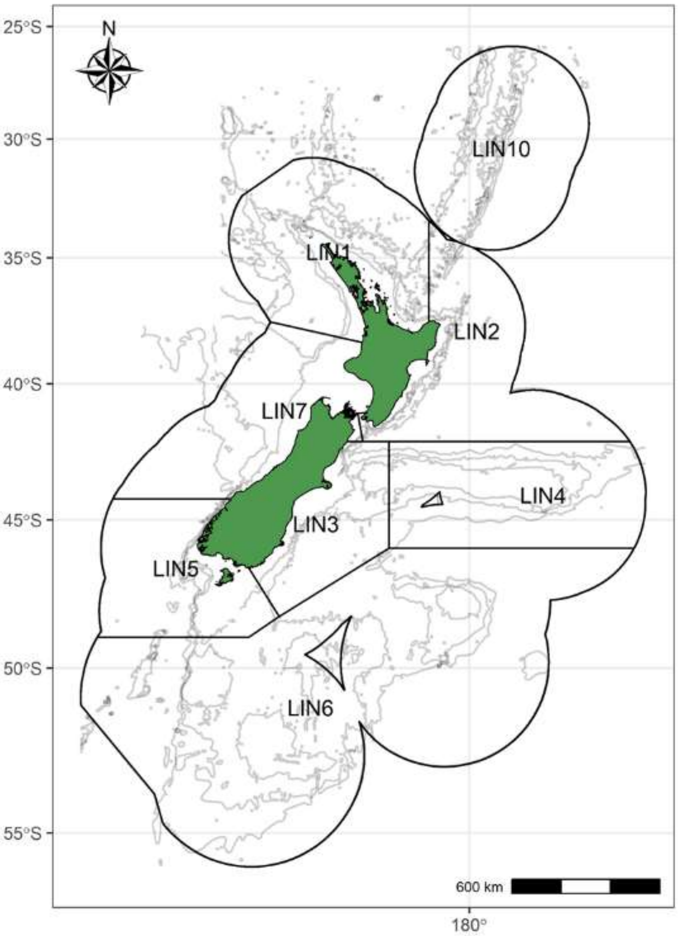

Figure 5: The New Zealand EEZ, and Quota Management Areas for ling (from Mormede et al. 2021a).

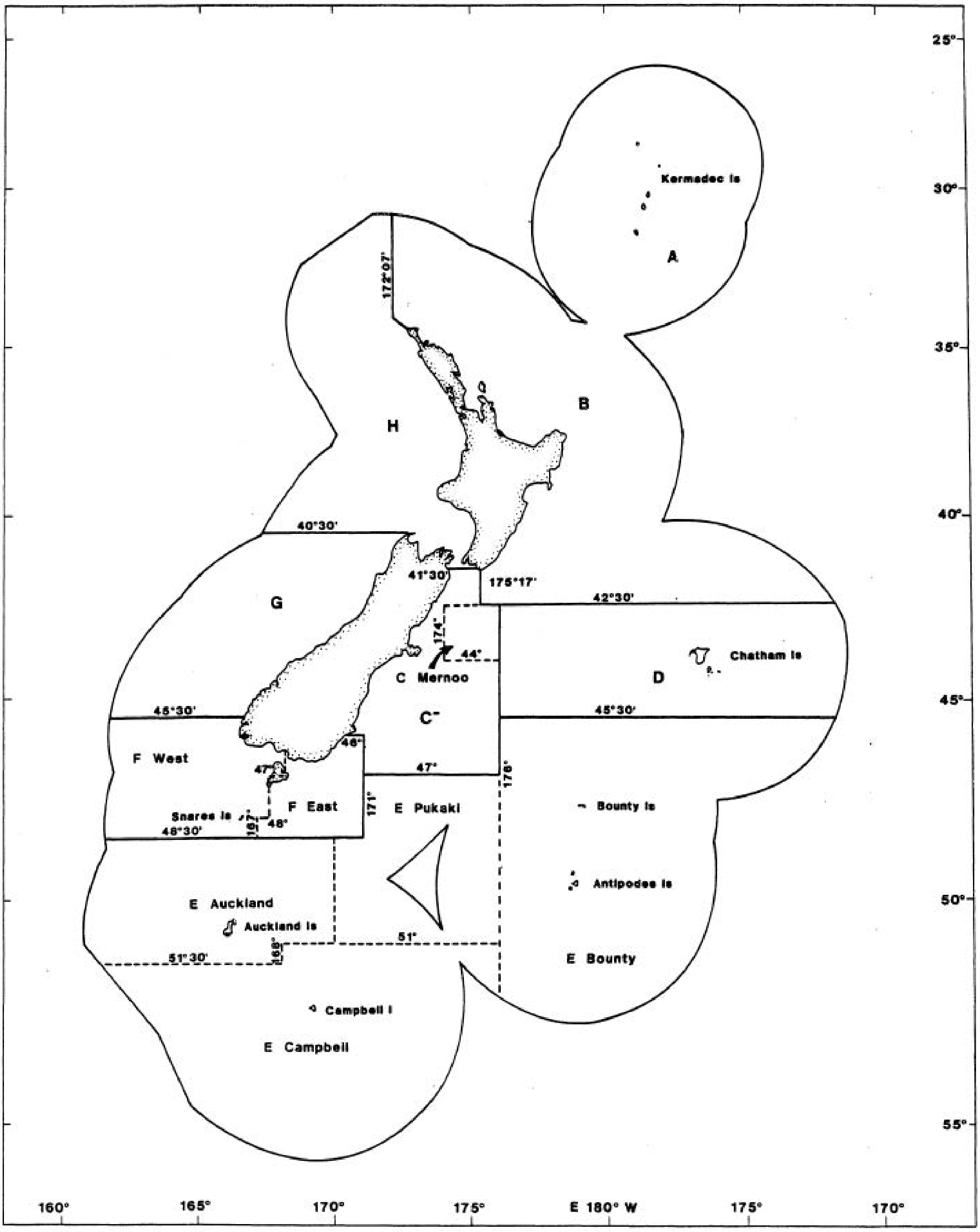

Figure 6: New Zealand fisheries statistical areas used by foreign deepwater fishing vessels before 1978 (from King et al. 1985).

3.2.1 Initial development of commercial fisheries

Francis & Paul (2013) tabulated reported domestic and foreign landings from 1931 to 1982 (Table 11) and described in detail their sources and methods of compilation. Landings from 1931–73 were from Annual Reports on Fisheries, compiled by the Marine Department until 1971 and the Ministry of Agriculture and Fisheries until 1973 as a component of their Annual Reports to Parliament. Domestic landings from 1974–82 were from FSU records published by King (1985). Foreign landings from 1979−82 were obtained from deepwater trawl logbook data obtained from the FSU database. There was no comprehensive source of foreign fishing landings before 1979, but some published and unpublished sources enabled a partial record. Francis & Paul (2013) noted that their landings data were not precise or accurate and were probably underestimated, possibly by a large degree. Their results comprised only reported landings; they did not include unreported landings, customary or recreational landings, or catch that was discarded.

The New Zealand domestic fishery had probably been catching ling since the early 20th century, but in relatively small quantities only (Graham 1956). Total domestic fish landings were first reported in the Annual Reports on Fisheries in 1915, but there was no breakdown by species until 1931. However, extrapolating from the data on fleet size and composition presented by Francis & Paul (2013), landings from 1915 to 1930 were likely to have been less than 200 t annually. The landings compilation by Francis & Paul (2013) showed that, from the 1930s to the mid-1950s, domestic catches were predominantly from off the eastern coast of South Island and, to a lesser extent, the lower eastern coast of North Island (Table 11). The eastern South Island area maintained its dominance as a fishery until the mid-1970s but was eventually superseded by the lower eastern North Island and west coast South Island, which exhibited rapidly increasing catches from the late 1970s until 1982. The majority of ling landings from these areas were likely to have been from line fisheries, followed by setnet fisheries, both as a target species and a bycatch of more ‘traditional’ species like hāpuku, *Polyprion oxygeneios* (see appendix 1 of Francis & Paul 2013).

Catches by foreign vessels, likely starting from about 1968 (Francis & Paul 2013) were poorly known before 1979, although some information from 1972 to 1977 was provided by Paul & Robertson (1979). From 1975 until 1978, most ling landings were taken by Japanese longliners on the Chatham Rise (Table 12) with a smaller proportion taken using the same method off the west coast of South Island. In 1977, Japanese and Korean longliners reported a combined catch of 22 692 t of ling from foreign deepwater reporting areas C and D (i.e., Chatham Rise, see Figure 6) (Patchell & McKoy 1985). Most of the trawl landings of ling by foreign vessels before 1978 were believed to have been taken from the Puysegur Bank region.

Table 11: Reported domestic and foreign landings of ling, in tonnes, from 1931 to 1982, by Fishery Management Areas (FMA) (from Francis & Paul 2013).

	Domestic								Foreign									Domestic and Foreign									Total
Year	FMA 1	FMA 2	FMA 3	FMA 4	FMA 5	FMA 7	FMA 8	FMA 9	FMA 1	FMA 2	FMA 3	FMA 4	FMA 5	FMA 6	FMA 7	FMA 8	FMA 9	FMA 1	FMA 2	FMA 3	FMA 4	FMA 5	FMA 6	FMA 7	FMA 8	FMA 9	
1931	0	0	11	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	1	0	0	0	0	12
1932	0	63	14	0	2	26	9	0	0	0	0	0	0	0	0	0	0	0	63	14	0	2	0	26	9	0	114
1933	0	146	59	0	1	46	21	0	0	0	0	0	0	0	0	0	0	0	146	59	0	1	0	46	21	0	273
1934	0	217	70	0	1	63	31	0	0	0	0	0	0	0	0	0	0	0	217	70	0	1	0	63	31	0	382
1935	0	146	124	0	1	45	21	0	0	0	0	0	0	0	0	0	0	0	146	124	0	1	0	45	21	0	337
1936	0	133	103	0	1	42	19	0	0	0	0	0	0	0	0	0	0	0	133	103	0	1	0	42	19	0	298
1937	0	91	320	0	1	44	13	0	0	0	0	0	0	0	0	0	0	0	91	320	0	1	0	44	13	0	469
1938	0	66	280	0	24	28	9	0	0	0	0	0	0	0	0	0	0	0	66	280	0	24	0	28	9	0	407
1939	0	40	320	0	16	21	5	0	0	0	0	0	0	0	0	0	0	0	40	320	0	16	0	21	5	0	402
1940	1	85	286	0	21	35	11	0	0	0	0	0	0	0	0	0	0	1	85	286	0	21	0	35	11	0	439
1941	0	64	308	0	22	32	8	0	0	0	0	0	0	0	0	0	0	0	64	308	0	22	0	32	8	0	434
1942	0	54	254	0	24	22	7	0	0	0	0	0	0	0	0	0	0	0	54	254	0	24	0	22	7	0	361
1943	0	83	264	0	19	29	11	0	0	0	0	0	0	0	0	0	0	0	83	264	0	19	0	29	11	0	406
1944	0	103	224	0	13	32	14	0	0	0	0	0	0	0	0	0	0	0	103	224	0	13	0	32	14	0	386
1945	1	122	199	0	13	39	41	0	0	0	0	0	0	0	0	0	0	1	122	199	0	13	0	39	41	0	415
1946	0	153	348	0	9	50	28	0	0	0	0	0	0	0	0	0	0	0	153	348	0	9	0	50	28	0	588
1947	0	203	474	0	24	68	28	0	0	0	0	0	0	0	0	0	0	0	203	474	0	24	0	68	28	0	797
1948	0	120	403	0	24	49	17	0	0	0	0	0	0	0	0	0	0	0	120	403	0	24	0	49	17	0	613
1949	0	108	402	0	20	50	17	0	0	0	0	0	0	0	0	0	0	0	108	402	0	20	0	50	17	0	597
1950	0	84	352	0	29	49	12	0	0	0	0	0	0	0	0	0	0	0	84	352	0	29	0	49	12	0	526
1951	0	60	230	0	16	25	9	0	0	0	0	0	0	0	0	0	0	0	60	230	0	16	0	25	9	0	340
1952	0	69	235	0	16	26	10	0	0	0	0	0	0	0	0	0	0	0	69	235	0	16	0	26	10	0	356
1953	0	62	212	0	19	24	10	0	0	0	0	0	0	0	0	0	0	0	62	212	0	19	0	24	10	0	327
1954	0	75	208	0	7	31	13	0	0	0	0	0	0	0	0	0	0	0	75	208	0	7	0	31	13	0	334
1955	0	48	160	0	6	20	7	0	0	0	0	0	0	0	0	0	0	0	48	160	0	6	0	20	7	0	241
1956	0	27	155	0	4	12	3	0	0	0	0	0	0	0	0	0	0	0	27	155	0	4	0	12	3	0	201
1957	0	34	175	0	8	15	4	0	0	0	0	0	0	0	0	0	0	0	34	175	0	8	0	15	4	0	236
1958	0	43	178	0	15	23	5	0	0	0	0	0	0	0	0	0	0	0	43	178	0	15	0	23	5	0	264
1959	0	39	157	0	13	22	5	0	0	0	0	0	0	0	0	0	0	0	39	157	0	13	0	22	5	0	236
1960	0	26	196	0	21	16	3	0	0	0	0	0	0	0	0	0	0	0	26	196	0	21	0	16	3	0	262
1961	0	25	230	0	20	16	3	0	0	0	0	0	0	0	0	0	0	0	25	230	0	20	0	16	3	0	294
1962	1	27	211	0	13	13	3	0	0	0	0	0	0	0	0	0	0	1	27	211	0	13	0	13	3	0	268
1963	1	17	213	0	14	10	1	0	0	0	0	0	0	0	0	0	0	1	17	213	0	14	0	10	1	0	256
1964	1	20	223	0	16	12	1	0	0	0	0	0	0	0	0	0	0	1	20	223	0	16	0	12	1	0	273
1965	1	21	195	0	24	11	2	0	0	0	0	0	0	0	0	0	0	1	21	195	0	24	0	11	2	0	254
1966	5	52	141	0	16	15	2	0	0	0	0	0	0	0	0	0	0	5	52	141	0	16	0	15	2	0	231

	Domestic								Foreign									Domestic and Foreign									Total
Year	FMA 1	FMA 2	FMA 3	FMA 4	FMA 5	FMA 7	FMA 8	FMA 9	FMA 1	FMA 2	FMA 3	FMA 4	FMA 5	FMA 6	FMA 7	FMA 8	FMA 9	FMA 1	FMA 2	FMA 3	FMA 4	FMA 5	FMA 6	FMA 7	FMA 8	FMA 9	
1967	7	40	106	0	14	34	2	0	0	0	0	0	0	0	0	0	0	7	40	106	0	14	0	34	2	0	203
1968	7	55	88	0	11	39	3	0	0	0	0	0	0	0	0	0	0	7	55	88	0	11	0	39	3	0	203
1969	5	52	154	0	10	19	4	0	0	0	0	0	0	0	0	0	0	5	52	154	0	10	0	19	4	0	244
1970	6	67	167	0	14	46	5	0	0	0	0	0	0	0	0	0	0	6	67	167	0	14	0	46	5	0	305
1971	4	49	186	0	19	34	3	0	0	0	17	0	1	1	0	0	0	4	49	203	0	20	1	34	3	0	314
1972	6	37	196	0	20	31	2	0	0	0	326	6	2	0	0	0	0	6	37	522	6	22	0	31	2	0	626
1973	18	73	263	0	23	37	4	0	0	0	1 162	0	0	0	0	0	0	18	73	1 425	0	23	0	37	4	0	1 580
1974	9	102	203	3	44	65	9	0	0	0	372	39	291	44	8	0	0	9	102	575	42	334	44	73	9	0	1 188
1975	2	70	218	0	32	155	6	0	0	0	1 552	15	1 481	344	59	4	1	2	70	1 770	15	1 513	344	214	10	1	3 939
1976	1	60	195	0	30	152	5	0	0	0	1 372	14	2 600	0	1 578	4	1	1	60	1 567	14	2 630	0	1 730	9	1	6 012
1977	4	100	237	0	22	172	9	0	0	0	912	466	1 661	0	2 614	15	5	4	100	1 149	466	1 683	0	2 786	24	5	6 217
1978	23	143	249	0	18	207	9	0	0	1	238	0	2 497	391	22	2	1	23	144	487	0	2 515	391	229	12	1	3 802
1979	79	207	243	0	32	338	15	0	0	21	556	246	4 368	1 431	100	1	3	79	228	799	246	4 400	1 431	438	16	3	7 640
1980	112	205	150	0	45	505	12	2	0	0	115	182	4 019	933	411	0	0	112	205	265	182	4 064	933	916	12	2	6 691
1981	192	429	215	0	38	634	32	16	0	0	212	444	3 538	636	354	0	0	192	429	427	444	3 576	636	988	32	16	6 740
1982	271	625	250	0	13	842	23	36	0	0	674	435	2 096	317	343	0	13	271	625	924	435	2 110	317	1 185	23	49	5 939

Table 12: Reported landings (t) from 1972 to 1987–88 by New Zealand domestic and foreign chartered vessels, and foreign licensed vessels. Foreign licensed data from 1972 to 1977 from Paul & Robertson (1979); other data from 1972 to 1983 from MAF; data from 1983–84 to 1985–86 from FSU; data from 1986–87 to 1987–88 from QMS. –, no data available.

				Foreign licensed					
	New Zealand			Longline	Trawl				Grand
Fishing year	Domestic	Chartered	Total	(Japan + Korea)	Japan	Korea	USSR	Total	total
1972*	292	0	292	0	–	0	400	400	692
1973*	418	0	418	0	–	0	500	500	918
1974*	435	0	435	0	568	0	800	1 368	1 803
1975*	483	0	483	9 269	2 180	0	0	11 499	11 932
1976*	443	0	443	19 381	5 108	0	1 300	25 789	26 232
1977*	544	0	544	28 633	5 014	200	700	34 547	35 091
1978–79†	649	24	673	8 904	3 151	133	452	12 640	13 313
1979–80†	914	2 598	3 512	3 501	3 856	226	245	7 828	11 340
1980–81†	1 031	–	–	–	–	–	–	–	–
1981–82†	1 556	2 423	3 979	0	2 087	56	247	2 391	6 370
1982–83†	2 060	2 501	4 561	0	1 256	27	40	1 322	5 883
1983‡	2 695	1 523	4 218	0	982	33	48	1 063	5 281
1983–84§	2 705	2 500	5 205	0	2 145	173	174	2 491	7 696
1984–85§	2 646	2 166	4 812	0	1 934	77	130	2 141	6 953
1985–86§	2 126	2 948	5 074	0	2 050	48	33	2 131	7 205
1986–87§	2 469	3 177	5 646	0	1 261	13	21	1 294	6 940
1987–88§	2 212	5 030	7 242	0	624	27	8	659	7 901

* Reported by calendar years. Domestic data from Francis & Paul (2013).
† Reported April 1 to March 31 (except domestic vessels, which reported by calendar year). Domestic data from Francis & Paul (2013).
‡ Reported April 1 to Sept 30 (except domestic vessels, which reported by calendar year).
§ Reported Oct 1 to Sept 30.

3.2.2 Foreign licensed fisheries, 1978–79 to 1982–83

With the declaration of the EEZ in 1978, landings by foreign licensed and foreign chartered vessels were reported by deepwater area (Figure 6), for fishing years beginning 1 April. Foreign longline landings still dominated the ling catch in 1978–79, but declined markedly in 1979–80, and were negligible in subsequent years (Table 12).

The Fisheries Research Division (FRD) of MAF was concerned at the high level of effort directed into the longline fishery in 1977, so recommended that only 24 000 t of all species be allocated for foreign longlining in 1978–79. Japan took only 31% of their 9000 t allocation (fees had to be paid for all fish quota accepted) and missed the first nine months of the fishing year. Korea was allocated 15 000 t. Longline vessels from both countries took 8904 t of ling that year, almost exclusively from the Chatham Rise in deepwater areas C and D (Table 12).

In 1979–80, a Total Allowable Catch (TAC) of 25 500 t for all fish species caught by longline was allocated for the EEZ (13 000 t to Japan, 12 500 t to Korea). FRD had recommended a TAC of 25 000 t for ling only, to apply to all fishing methods, and with specific limits in some areas (i.e., deepwater area C, 3000 t; area D, 15 000 t; area G, 2000 t). Japan accepted 3500 t of their allocation but sent no longliners to the EEZ. Korea caught about 3500 t of ling by longline.

For 1980–81, the EEZ longline TAC for all species was set at 28 000 t, with 25 500 t of that allocated to foreign licensed and foreign chartered vessels (Patchell & McKoy 1985). Korea took only 1190 t of its allocation; Japan took none. No catch data from the foreign licensed and foreign chartered fleets were available for that year. The total ling quota for the EEZ was reduced to 20 000 t, but the TAC for deepwater area G was increased to 4000 t. Late in 1980, it was recommended that controls be placed on the catch of fish by joint-venture companies and that 8000 t of the longline allocation be transferred to foreign licensed trawlers for the rest of the 1980–81 fishing year (Patchell & McKoy 1985).

In 1981–82, a bottom longline TAC of 23 000 t for all species was set, with 2000 t of this reserved for the domestic fleet. Korea made no requests for an allocation, and Japan subsequently declined the allocation of 7000 t it initially requested. This essentially ended the participation of foreign longline vessels in the New Zealand ling fishery.

In 1982–83 the longline TAC for all species was again set at 23 000 t, but with 3000 t reserved for the domestic fleet. As in the previous year, Japan declined the allocation it initially requested, and Korea made no request. FRD recommended a ling TAC, for all methods, of 20 000 t with specific deepwater area limits (i.e., C, 3000 t; D, 10 000 t; E, 3000 t; F, 2000 t; G, 2000 t). The limits finally set (for all methods) for ling were 20 000 t for the EEZ, with 2000 t limits in each of areas F and area E north of 49° S and west of 169° E.

Catches of ling by trawl from 1978–79 to 1982–83 were taken primarily by Japanese vessels and foreign vessels chartered by New Zealand companies (Table 12). Relatively small components of the trawl catch were also taken by Korean, Russian, and New Zealand domestic vessels. The main target trawl fishery for ling was in deepwater area F at Puysegur Bank and the Solander Corridor where ling congregate to spawn from September to December. Heavy fishing pressure in this area before the declaration of the EEZ led to the closure of the Puysegur Bank area from October 1977 to January 1978 (Patchell & McKoy 1985). No quota controls on trawling were introduced until the 1982–83 fishing year, when a catch-per-unit-effort (CPUE) analysis indicated an apparent decline in the ling stock size (Patchell 1980, 1983). Consequently, as noted above, 2000 t quotas for all methods were set in each of deepwater areas F and part of E.

3.2.3 All fisheries, 1983–84 to 1985–86

Changes in management occurred in 1983 with the introduction of the deepwater policy. The timing of the fishing year was changed to begin on 1 October. For the 1983–84 fishing year, the ling TACs of 2000 t in each of deepwater areas E and F were allocated to individual quota holders and foreign licensed vessels, and 6000 t of ling outside these areas was also allocated to quota holders. This left 10 000 t of ling available for all other sectors. The longline TAC for all species of 23 000 t was maintained, and ling allocations by area remained at the 1982–83 levels.

In 1984–85, FRD recommended that trawl and longline quotas be combined, but this did not eventuate. The longline TAC for all species was reduced markedly to 10 000 t and this could be caught only in deepwater area D. Quotas were introduced for trawl-caught ling in areas B, C, D, F, G, and H and for line-caught ling in area D (Table 13). The fisheries in area F and part of E were brought under a single TAC of 3000 t in 1984 (when the southern boundary of area F was extended to 49° S), and industry was warned of likely future reductions. There were no limits placed on ling catches from area A and modified area E (Patchell & McKoy 1985). These TACs totalling 17 500 t were based on trawl survey results and catch histories (Patchell & McKoy 1985).

The 1985–86 fishing year saw the allocation of recommended catch limits to the new set of Fishery Management Areas (FMAs). The recommendations were for all ling fisheries combined, with a total TAC for the EEZ of 18 000 t (Table 14) (McGregor & McKoy 1986). The allocations to FMA were based largely on the previous allocations to deepwater areas, except that the previous allocation of 6000 t to line vessels on the eastern Chatham Rise was shifted to make up most of the 7000 t quota for the Sub-Antarctic FMA (equivalent to LIN 6 shown on Figure 5).

Table 13: 1984–85 ling quotas (t) by deepwater areas (see Figure 6).

	Quota	
Area	Trawl	Line
B	1 000	–
C	1 200	–
D	4 300	6 000
F	3 000	–
G & H	2 000	–

Table 14: 1985–86 recommended ling TACs (t) by Fishery Management Area (FMA). See Section 3.2.4 and Table 15 for information on the relationships between FMAs and the subsequent ling QMAs.

FMA	TAC
1 & 2	1 000
3	1 200
4	4 300
5	2 500
6	7 000
7, 8 & 9	2 000

Reported catches from 1983–84 to 1985–86 were split relatively equally between New Zealand domestic vessels, New Zealand chartered trawlers, and foreign licensed trawlers, to produce annual landings of about 7000 t. There was no foreign longline fishing, but small domestic line vessels did take catches of ling.

3.2.4 All fisheries, from 1986–87

At the introduction of the ITQ system from the 1986–87 fishing year, quota owners were able to catch their quota by whatever method they wished. Recommended TACs for ling for the 1986–87 fishing year totalled 18 100 t. Relative to 1985–86, however, some adjustments were made to the area groupings to which the quotas applied, to allow more convenient administration within the ITQ system, i.e., areas east and west of Northland (FMAs 1 and 9) were combined, and the lower east coast of North Island (FMA 2) became a separate reporting area (McGregor & McKoy 1986). Thus, the Quota Management Areas for ling were defined (see Figure 5). The actual TACs gazetted for 1986–87 were generally similar to the TAC recommendations (Table 15) (Hurst 1988). There have been no subsequent changes to the boundaries of these administrative QMAs (Fisheries New Zealand 2021). The QMA boundaries for ling largely mirror the FMA boundaries, except that FMAs 1 and 9 are combined, as are FMAs 7 and 8 (Table 15).

Although ling in New Zealand were managed as eight administrative QMAs from the 1986–87 fishing year, five of these (LIN 3, 4, 5, 6, and 7) have produced about 95% of the ling landings (Dunn & Ballara 2019). Reported landings by administrative fishstock (i.e., ling QMA) since 1983–84 (Table 16) are updated and presented annually in the Fisheries New Zealand Plenary Reports (e.g., Fisheries New Zealand 2022). The Plenary documents also provide updated annual estimates of catches by fishing method (trawl and line) for each of the postulated biological ling stocks, as well as references to the most recent assessments of each of these stocks.

Table 15: 1986–87 recommended and gazetted ling TACs (t) by ling Quota Management Areas (QMA, see Figure 5), and the equivalent Fishery Management Areas (FMA).

		TAC	
Ling QMA	FMA	Recommended	Gazetted
LIN 1	1 & 9	200	200
LIN 2	2	900	910
LIN 3	3	1 200	1 850
LIN 4	4	4 300	4 300
LIN 5	5	2 500	2 500
LIN 6	6	7 000	7 000
LIN 7	7 & 8	2 000	1 960
LIN 10	10	–	10

Table 16: Reported landings (t) of ling by Fishstock from 1983–84 to 2020–21 and actual Total Allowable Commercial Catches (TACCs, t) from 1986–87 to 2020–21. Estimated landings for LIN 7 from 1987–88 to 1992–93 include an adjustment for ling bycatch of hoki trawlers, based on records from vessels carrying observers. QMS data from 1986–87 to 2020–21. (Table from Fisheries New Zealand 2022 and continued on next page.)

Fishstock		LIN 1		LIN 2		LIN 3		LIN 4		LIN 5
FMA (s)		1 & 9		2		3		4		5
	Landings	TACC	Landings	TACC	Landings	TACC	Landings	TACC	Landings	TACC
1983–84*	141	–	594	–	1 306	–	352	–	2 605	–
1984–85*	94	–	391	–	1 067	–	356	–	1 824	–
1985–86*	88	–	316	–	1 243	–	280	–	2 089	–
1986–87	77	200	254	910	1 311	1 850	465	4 300	1 859	2 500
1987–88	68	237	124	918	1 562	1 909	280	4 400	2 213	2 506
1988–89	216	237	570	955	1 665	1 917	232	4 400	2 375	2 506
1989–90	121	265	736	977	1 876	2 137	587	4 401	2 277	2 706
1990–91	210	265	951	977	2 419	2 160	2 372	4 401	2 285	2 706
1991–92	241	265	818	977	2 430	2 160	4 716	4 401	3 863	2 706
1992–93	253	265	944	980	2 246	2 162	4 100	4 401	2 546	2 706
1993–94	241	265	779	980	2 171	2 167	3 920	4 401	2 460	2 706
1994–95	261	265	848	980	2 679	2 810	5 072	5 720	2 557	3 001
1995–96	245	265	1 042	980	2 956	2 810	4 632	5 720	3 137	3 001
1996–97	313	265	1 187	982	2 963	2 810	4 087	5 720	3 438	3 001
1997–98	303	265	1 032	982	2 916	2 810	5 215	5 720	3 321	3 001
1998–99	208	265	1 070	982	2 706	2 810	4 642	5 720	2 937	3 001
1999–00	313	265	983	982	2 799	2 810	4 402	5 720	3 136	3 001
2000–01	296	265	1 105	982	2 330	2 060	3 861	4 200	3 430	3 001
2001–02	303	265	1 034	982	2 164	2 060	3 602	4 200	3 295	3 001
2002–03	246	400	996	982	2 529	2 060	2 997	4 200	2 939	3 001
2003–04	249	400	1 044	982	1 990	2 060	2 618	4 200	2 899	3 001
2004–05	283	400	936	982	1 597	2 060	2 758	4 200	3 584	3 595
2005–06	364	400	780	982	1 711	2 060	1 769	4 200	3 522	3 595
2006–07	301	400	874	982	2 089	2 060	2 113	4 200	3 731	3 595
2007–08	381	400	792	982	1 778	2 060	2 383	4 200	4 145	3 595
2008–09	320	400	634	982	1 751	2 060	2 000	4 200	3 232	3 595
2009–10	386	400	584	982	1 718	2 060	2 026	4 200	3 034	3 595
2010–11	438	400	670	982	1 665	2 060	1 572	4 200	3 856	3 595
2011–12	384	400	504	982	1 292	2 060	2 305	4 200	3 649	3 595
2012–13	383	400	579	982	1 475	2 060	2 181	4 200	3 610	3 595
2013–14	380	400	673	982	1 442	2 060	2 373	4 200	3 935	3 595
2014–15	374	400	673	982	1 325	2 060	2 246	4 200	3 924	3 595
2015–16	422	400	702	982	1 440	2 060	2 659	4 200	3 868	3 595
2016–17	404	400	1 022	982	1 808	2 060	2 565	4 200	3 356	3 595
2017–18	415	400	1 106	982	2 171	2 060	2 636	4 200	4 034	3 595
2018–19	383	400	939	982	2 016	2 060	2 044	4 200	4 596	4 735
2019–20	371	400	756	982	1 685	2 060	1 778	4 200	4 678	4 735
2020–21	319	400	645	982	1 489	2 060	2 103	4 200	4 950	4 735

Table 16: — *continued.*

Fishstock		LIN 6			LIN 7		LIN 10		
FMA (s)		6			7 & 8		10		Total
	Landings	TACC	Reported Landings	Estimated Landings	TACC	Landings	TACC	Landings§	TACC
1983–84*	869	–	1 552	–	–	0	–	7 696	–
1984–85*	1 283	–	1 705	–	–	0	–	6 953	–
1985–86*	1 489	–	1 458	–	–	0	–	7 205	–
1986–87	956	7 000	1 851	–	1 960	0	10	6 940	18 730
1987–88	1 710	7 000	1 853	1 777	2 008	0	10	7 901	18 988
1988–89	340	7 000	2 956	2 844	2 150	0	10	8 404	19 175
1989–90	935	7 000	2 452	3 171	2 176	0	10	9 028	19 672
1990–91	2 738	7 000	2 531	3 149	2 192	< 1	10	13 506	19 711
1991–92	3 459	7 000	2 251	2 728	2 192	0	10	17 778	19 711
1992–93	6 501	7 000	2 475	2 817	2 212	< 1	10	19 065	19 737
1993–94	4 249	7 000	2 142	–	2 213	0	10	15 961	19 741
1994–95	5 477	7 100	2 946	–	2 225	0	10	19 841	22 111
1995–96	6 314	7 100	3 102	–	2 225	0	10	21 428	22 111
1996–97	7 510	7 100	3 024	–	2 225	0	10	22 522	22 113
1997–98	7 331	7 100	3 027	–	2 225	0	10	23 145	22 113
1998–99	6 112	7 100	3 345	–	2 225	0	10	21 034	22 113
1999–00	6 707	7 100	3 274	–	2 225	0	10	21 615	22 113
2000–01	6 177	7 100	3 352	–	2 225	0	10	20 552	19 843
2001–02	5 945	7 100	3 219	–	2 225	0	10	19 561	19 843
2002–03	6 283	7 100	2 918	–	2 225	0	10	18 903	19 978
2003–04	7 032	7 100	2 926	–	2 225	0	10	18 760	19 978
2004–05	5 506	8 505	2 522	–	2 225	0	10	17 189	21 977
2005–06	3 553	8 505	2 479	–	2 225	0	10	14 184	21 977
2006–07	4 696	8 505	2 295	–	2 225	0	10	16 102	21 977
2007–08	4 502	8 505	2 282	–	2 225	0	10	16 264	21 977
2008–09	2 977	8 505	2 223	–	2 225	0	10	13 137	21 977
2009–10	2 414	8 505	2 446	–	2 474	0	10	12 609	22 226
2010–11	1 335	8 505	2 800	–	2 474	0	10	12 337	22 226
2011–12	2 047	8 505	2 771	–	2 474	0	10	12 953	22 226
2012–13	3 102	8 505	3 010	–	2 474	0	10	14 339	22 226
2013–14	3 221	8 505	3 200	–	3 080	0	10	15 224	23 192
2014–15	3 115	8 505	3 343	–	3 080	0	10	15 002	23 192
2015–16	2 222	8 505	3 340	–	3 080	0	10	14 654	23 192
2016–17	2 473	8 505	3 428	–	3 080	0	10	15 056	23 192
2017–18	4 846	8 505	3 487	–	3 080	0	10	18 694	23 192
2018–19	3 706	8 505	3 059	–	3 080	0	10	16 743	23 972
2019–20	3 972	8 505	3 216	–	3 387	0	10	16 456	24 279
2020–21	3 916	8 505	3 308		3 387	< 1	10	16 730	24 279

* FSU data.

§ Includes landings from unknown areas before 1986–87, and areas outside the EEZ since 1995–96.

The reported catch (Table 16) will not be an accurate record of actual catch. Reported totals will generally (but not always) be an underestimate of total mortality due to fishing, owing to ling being dumped or sent to meal and being killed by fishing gear but not landed on the vessel (e.g., mortality associated with trawl mesh escapement). Such outcomes for ling are believed to be negligible. It is likely, however, that up to the mid-1990s some ling bycatch from the west coast hoki fishery was not reported (see Table 16, reported and estimated landings in LIN 7). Also, some catch from LIN 7 was probably reported against other ling stocks (probably LIN 3, 5, and 6). The likely levels of misreporting were moderate, being about 250–400 t in each year from 1989–90 to 1991–92 (Dunn 2003).

A detailed descriptive analysis of the ling fisheries showing the distribution of catches by area and method since 1989–90 was presented by Dunn & Ballara (2019). There were two main fishing methods for ling: line (primarily bottom longline, but with minor catches taken by trot line and dahn line) and trawl (primarily bottom trawl, but with a small midwater trawl component). The principal grounds for smaller domestic vessels (both trawl and line vessels) were off the west coast of South Island and the east coast of both main islands south of East Cape. For large trawlers, the main sources of ling were Puysegur Bank and the slope of the Stewart-Snares shelf and waters in the Auckland Islands area, and the Chatham Rise, primarily as bycatch of target fisheries for hoki, but with some target fishing particularly in the Puysegur region.

Before 1989, the New Zealand domestic line fishery was conducted by relatively small vessels that completed short trips. In 1989, several larger longliners with autoline equipment joined the domestic fleet, resulting in a large increase in the catches of ling off the east and south of South Island (i.e., LIN 3, 4, 5, and 6). Horn (2004b) reviewed the auto-longline fishery using data collected by observers from 1993 to 2003, examining changes over time in the location and depth of sets, the topography types fished, the efficiency of the automatic baiters, and rates of hook loss and hook saturation. Data from between 1994–95 and 1999–2000 collected during an industry-run logbook programme were also available (Langley 2001). Following the 2000–01 fishing year, there was a declining trend in catches taken by longline vessels in most areas, offset, to some extent, by increased trawl landings (Dunn & Ballara 2019). Most catches by line fishing, by both the smaller 'inshore' vessels and the large autoliners, were from target fishing. Finucci et al. (2020) provided pictorial distributions of all reported longline sets targeting ling in New Zealand waters from 2002 to 2018. The descriptive analysis also showed small catches of ling by setnet and fish pots, primarily off the eastern South Island coast (Dunn & Ballara 2019).

3.2.5 Changes in quota allocations

The TACs for each of the ling QMAs gazetted for the start of the 1986–87 fishing year were based on recommendations from FRD. Subsequently, allocations of recreational and customary catches were added to most of the administrative fishstocks in the New Zealand Quota Management System. Consequently, quota allocations to commercial fishers became known as Total Allowable Commercial Catches (TACCs) (see Table 16).

It is apparent, from Table 16, that TACCs for all ling QMA stocks have changed over time. Most changes between years were relatively small (i.e., generally less than 100 t between adjacent years). These increases were a consequence of quota appeals where fishers who received no quota, or less quota than they believed they were entitled to, were able to demonstrate a pre-quota catch history, thus entitling them to a subsequent allocation.

Some adjacent year increases and decreases were substantial, however, and were a consequence of fishery management decisions. These are described below:

- Under the Adaptive Management Programme (AMP), the TACC for LIN 1 was increased to 400 t from 1 October 2002, and it remained at this level when LIN 1 was removed from the AMP on 30 September 2009. (The AMP was a mechanism for increasing the TACC where the Ministry has limited information on stock size. It aimed to provide information concerning the effects of fishing on uncertain stocks. To mitigate risk, the AMP included monitoring and review programmes, and an onus on the industry to fulfil their defined commitments.)
- In an AMP proposal for the 1994–95 fishing year, TACCs for LIN 3 and LIN 4 were increased by about 30% to 2810 t and 5720 t, respectively; these levels were expected to allow any decline in biomass to be detected by trawl surveys of the Chatham Rise (with CV of 10% or less) over the 5 years following the increase. These stocks were removed from the AMP from 1 October 1998, with TACCs maintained at the increased level. However, from 1 October 2000, the TACCs for LIN 3 and LIN 4 were reduced by about 27% to 2060 t and 4200 t, respectively, as a consequence of a stock assessment that indicated a current biomass level close to B_{MAY} and a likelihood that recent levels of catch were not sustainable (Horn et al. 2000).
- From 1 October 2004, the TACCs for LIN 5 and LIN 6 were increased by about 20% to 3595 t and 8505 t, respectively, following an assessment that estimated current biomass to be about 85% of B_0, implying that the stock could sustain catch levels higher than the TACC (Horn 2004a). The LIN 5 TACC was increased by a further 10% (to 3955 t) from 1 October 2013 following an assessment indicating a current stock size of 89% B_0 for the LIN 5&6 stock, a level well above the management target of 40% B_0 (Horn et al. 2013b). From 1 October 2018, a TACC of 4735 t was applied for LIN 5, following an assessment indicating that the current stock size of LIN 5&6 was well above the management target of 40% B_0 at around 90% B_0 (Masi 2019).

- From 1 October 2009, the TACC for LIN 7 was increased from 2225 t to 2474 t, and further increased to 3080 t from 1 October 2013. These two changes followed stock assessments which, although indicating that the current status of the WCSI LIN 7 stock was highly uncertain, concluded that current stock size was likely to be well above the management target of 40% B_0 (Horn 2009, Dunn et al. 2013). From 1 October 2019, the LIN 7 TACC was increased by another 10% to 3387 t when an assessment indicated that the stock was very likely to be above the biomass target (40% B_0), and that biomass was likely to remain about the same even if future catches increased by around 10% (Dunn & Ballara 2019).

3.3 Fishery interactions

Target fisheries for ling in New Zealand waters interacted with other species, both fish and non-fish. Data collected at sea by Fisheries New Zealand observers on trawl and line vessels were analysed to provide lists of bycatch species as well as estimates of the bycatch of fish (quota and non-quota species), marine invertebrates, marine mammals, and seabirds.

Observers have made detailed set-by-set records of retained catch by species or species group for a portion of the ling longline fleet (primarily the large autoline vessels) in each year since 1992–93 (Anderson 2014, Finucci et al. 2020). Records of discarded catch, however, were not recorded before 1999–2000 and were poorly covered in some years since then (particularly between 2008–09 and 2011–12). In the target ling line fishery from 2002–03 to 2017–18, when observers were present, ling accounted for about 65% of the total estimated catch (Finucci et al. 2020). Over 250 non-target species or species groups were identified, most being non-commercial species, including invertebrates, caught in low numbers. The main non-target species were spiny dogfish *Squalus acanthias* (17% of the catch), ribaldo *Mora moro* (3.3%), rough skate *Zearaja nasuta* (2.7%), black cod *Paranotothenia magellanica* (1.7%), smooth skate *Dipturus innominatus* (1.5%), sea perch *Helicolenus* spp. (1.4%), pale ghost shark *Hydrolagus bemisi* (1.2%), red cod *Pseudophycis bachus* (1.2%), and shovelnose dogfish *Deania calcea* (1.1%). Species relatively frequently caught and almost always discarded were congers (*Bassanago* spp.), unspecified deepwater dogfish, and carpet shark (*Cephaloscyllium isabellum*). About 68% of spiny dogfish were also discarded. Invertebrates collectively accounted for under 0.5% of the catch and most were discarded; starfish alone accounted for about 0.2% of the catch (Finucci et al. 2020).

The economic impact of spiny dogfish in a New Zealand ling longline fishery was assessed for the purpose of guiding early-stage bycatch reduction device (BRD) development (Howard et al. 2019). Based on fishing lines in the upper quartile for spiny dogfish CPUE (193 dogfish per thousand hooks), 0.4 ling were lost for every dogfish caught, and the opportunity cost of dogfish bycatch in lost ling was estimated to be 0.23 NZD per hook. Thus, a cost-neutral BRD would need to eliminate lines with large dogfish catches and cost less than 23 cents per unit per use.

It was apparent that the presence of an observer on ling longline vessels clearly influenced the reporting of bycatch (Burns & Kerr 2008). With observer presence, every day ling were taken by bottom longline, both quota and non-quota bycatch were reported. Without observers, however, commercial fishers reported quota species bycatch on 82% of days fished, and non-quota bycatch on only 50% of days fished.

While there is some target trawling for ling, most ling trawl catches are taken by a fishery targeting a mix of species: hoki (*Macruronus novaezelandiae*), hake (*Merluccius australis*), ling, silver warehou (*Seriolella punctata*), and white warehou (*S. caerulea*). In an analysis of observer data from 2002–03 to 2016–17, over 800 bycatch species or species groups were identified in that fishery, most being non-commercial species, including invertebrate species, caught in low numbers (Anderson et al. 2019). Hoki accounted for about 73% of the total estimated catch, with the other main catch species being hake (6.7% of the catch), ling (5.2%), silver warehou (3.9%), javelinfish *Lepidorhynchus denticulatus* (1.9%), unspecified Macrouridae rattails (1.6%), spiny dogfish (1.4%), and white warehou (1.3%). Of these, javelinfish (37% discarded), unspecified rattails (43%), and spiny dogfish

(69%) were the fish species with the largest rate of observed discarding in this fishery. Other species frequently caught and generally discarded included shovelnose dogfish, Baxter's dogfish *Etmopterus granulosus*, redbait *Emmelichthys nitidus*, silverside *Argentina elongata*, leafscale gulper shark *Centrophorus squamosus*, and silver dory *Cyttus novaezealandiae*.

Captures of New Zealand fur seals (*Arctocephalus forsteri*) in trawls targeting ling were estimated to occur at a rate of between 1 and 2 per 100 tows, during 2002–03 to 2014–15 (Abraham & Berkenbusch 2017). The tows occurred mainly at Puysegur Bank, near Snares Island, and off west coast South Island. Trawl tows targeting middle depth species (which included the hoki, hake, ling, and warehou target fishery) had a capture rate of fur seals similar to that of ling target tows.

Estimates of incidental captures of seabirds were available for trawl fisheries from 2002–03 to 2016–17 and for longline fisheries from 1998–99 to 2016–17 (Abraham & Richard 2019). In the ling longline fishery, capture rates were highest in the early 2000s at around 40–60 individual birds per 100 sets. Since the mid-2000s, rates have been generally lower at around 10 birds per 100 sets. White-chinned petrel (*Procellaria aequinoctialis*) was the most commonly reported species, being roughly an order of magnitude more abundant than the following species of Salvin's albatross (*Thalassarche salvini*), grey petrel (*Procellaria cinerea*), and New Zealand white-capped albatross (*Thalassarche cauta steadi*). Captures by the target ling trawl fishery were generally lower than 6 birds per 100 trawls, with white-chinned petrels and sooty shearwaters (*Puffinus griseus*) being the species most often caught (Abraham & Richard 2019). The middle depths trawl fishery had a similar capture rate of about 5 birds per 100 trawls.

Seabird captures reported by observers on New Zealand longline fishing vessels from 1998 to 2004 were examined by FMA (Waugh et al. 2008). Although the data were not split up by fishery, they were split by fishing method. Consequently, virtually all the FMA 1 captures by bottom longline would have been by the snapper target fishery, while those from FMAs 3–7 were probably when targeting ling. Grey petrel, the most numerous species (372 individuals), was taken predominantly (86% of records) in the Sub-Antarctic (FMA 6), and secondarily (9%) on the Chatham Rise (FMA 4). Captures of Salvin's albatross (130 birds) were similarly distributed: 85% from FMA 6 and 13% from FMA 4. The next most abundant species, sooty shearwater (94 birds), was taken almost exclusively (94%) from off Southland (FMA 5).

An analysis of annual potential fatalities (APF) by fishery using data from 2006–07 to 2012–13 (Richard & Abraham 2015) depended on assumptions that were made about the extent of cryptic mortalities (birds that are killed by the fishing activity but not brought on-board the fishing vessel or included in captures reported by fisheries observers). Captures by the target ling trawl fishery were estimated to be 163 birds annually, made up primarily of New Zealand white-capped albatross, Salvin's albatross, sooty shearwater, white-chinned petrel, and southern Buller's albatross (*Thalassarche bulleri bulleri*). Bottom longline fisheries targeting ling were analysed as two fleets based on vessel size, i.e., less than, or greater than 34 m. The large vessel fleet had an APF of 122 birds, with white-chinned petrel, New Zealand white-capped albatross, Salvin's albatross, and southern Buller's albatross accounting for 98 of them. The small vessel fleet had a larger APF of 692 birds, over half being Salvin's albatross (375), with Chatham Island albatross (*Thalassarche eremita*), white-chinned petrel, southern Buller's albatross, grey petrel, and New Zealand white-capped albatross accounting for a further 236 birds. In an analysis of risk by species, three species regularly taken by ling fisheries were in the 'Very high risk' category (i.e., Salvin's albatross, southern Buller's albatross, New Zealand white-capped albatross), and Chatham Island albatross was in the 'High risk' category (Richard & Abraham 2015). A subsequent analysis of data from 2014–15 to 2016–17 (Richard et al. 2020) estimated total fishery-related deaths for the three years combined to be 428 for the large vessel ling longline fleet and 1150 for the small vessel ling fleet, numbers smaller than those estimated for the previous seven years, particularly for the small vessel fleet.

The point estimates of APF for inshore and small-vessel fisheries (including the small-vessel ling bottom longline fishery) had wide bounds as a consequence of low levels of observer coverage

(Richard & Abraham 2015). Also, many New Zealand seabirds migrate outside the EEZ and may interact with other Southern Hemisphere fisheries, including those targeting ling (e.g., Favero et al. 2013, Techow et al. 2016).

Considerable effort has gone into mitigating the catches of seabirds by longline fisheries for ling and other species (e.g., Baird 2001, Smith 2001). For ling bottom longline fisheries, effective mitigation methods included the removal of hooks for 30 m on both sides of floats, the use long snoods to allow the baited hooks to quickly sink beyond the reach of birds, and the effective use of a tori line (Smith 2001, Seco Pon 2007).

3.4 Recreational fisheries

The extent of recreational catches of ling is poorly known but is likely to be small. Some data were available from surveys of recreational fishers. A survey of the North region in 1993–94 estimated the annual recreational catch from LIN 1 (see Figure 5) as 10 000 fish, with a CV of 0.23 (Bradford 1997). Assuming a mean fish weight in the range of 1.5 to 4 kg, this equated to a harvest of 15–40 t. A national diary survey in 1996 recorded recreational catch from LIN 1, 5, and 7, but the estimated harvests (LIN 1, 3000 fish; LIN 5, less than 500; LIN 7, less than 500) were too low to provide reliable estimates of catch tonnage (Bradford 1998).

National Panel Surveys were conducted throughout the 2011–12 and 2017–18 fishing years using face-to-face interviews of a random sample of about 30 000 New Zealand households to recruit a panel of fishers and non-fishers for a full year (Wynne-Jones et al. 2014, 2019). The panel members were contacted regularly about their fishing activities and harvest information in standardised phone interviews. In 2011–12, three fishers reported catching ling in LIN 1 (4 trips) and four fishers reported catches in LIN 2 (5 trips). In 2017–18, two fishers reported catching ling in LIN 2 (2 trips), one fisher reported a catch in LIN 3 (1 trip), and three fishers reported catches in LIN 7 (3 trips). Estimates of total nationwide ling catch were 1334 and 320 fish in 2011–12 and 2017–18, respectively, both with wide CVs. These estimates were markedly different to those from the 1990's surveys (Bradford 1997, 1998).

3.5 Stock assessment history

3.5.1 New Zealand stock assessments

The initial TACCs of ling allocated to the FMAs established from the 1985–86 fishing year were based on 'expert evaluation' of trawl survey results and previous catch levels (Patchell & McKoy 1985). First attempts at stock assessments occurred in the early 1990s, after standardised trawl survey series using the research vessel *Tangaroa* commenced on the Chatham Rise and Sub-Antarctic and produced estimates of current biomass based on using area swept between the trawl doors (Horn 1993a). Estimates of virgin biomass (B_0) were derived by examining trial values of B_0 in stock reduction analyses that were constrained to give particular levels of mean instantaneous fishing mortality (F) over the known period of exploitation. It was stressed that the biomass estimates were very preliminary, however, being based on uncertain estimates of mortality rates (M and F) and on few relative biomass indices from trawl surveys (Horn 1993a). Yield per recruit analyses were completed for administrative ling stocks LIN 3–7 to produce estimates of $F_{0.1}$, thus enabling estimates of Maximum Constant Yield (MCY) based on the formula MCY = 0.25 $F_{0.1}$ B_0 (Horn 1993a). The MCY estimates for LIN 3–7 were comparable with the TACCs current at that time (they ranged from 11% lower to 46% higher than the TACCs).

Stock assessments using the MIAEL (Minimum Integrated Average Expected Loss) estimation technique of Cordue (1998) to produce bounded estimates of B_0 and MCY were first completed for stocks LIN 3–7 (using the groupings LIN 3&4, LIN 5&6 excluding the Bounty Platform, and LIN 7) by Horn & Cordue (1996). This method produced a 'performance index' which was a percentage measure of how well the unknown quantity was pinpointed within its given bounds; an index of 100% implied perfect information. The model inputs comprised biological data, catch histories, and relative abundance indices from trawl surveys. That assessment, and a subsequent update (Horn 1997), suggested recent catch levels and current TACCs for LIN 3&4, LIN 5&6 were probably sustainable in the short term at least, but that the status of LIN 7 was poorly known. Subsequent assessments using the MIAEL method analysed four biological stocks: Chatham Rise (LIN 3 and LIN 4), Campbell Plateau and Stewart-Snares shelf (LIN 5, and LIN 6 west of 176° E), Bounty Plateau (LIN 6 east of 176° E), and west coast South Island (LIN 7 west of Cape Farewell). These biological stocks were referred to as LIN 3&4, LIN 5&6, LIN 6B, and LIN 7WC, respectively. The last MIAEL analyses of ling (Horn 2002) concluded that the assessments of LIN 3&4, LIN 5&6, and LIN 6B appeared to be reasonably reliable, based on their performance indices (i.e., about 50–70% for estimates of B_0, and 70–95% for estimates of current biomass). The LIN 7WC assessment was the least reliable of the four presented, with a performance index of about 35% for estimates of B_0.

Stock assessments of ling from the 2002–03 fishing year onwards were completed using CASAL (C++ algorithmic stock assessment laboratory), a generalised age- or length-structured population model (Bull et al. 2012), where parameters were estimated using Bayesian estimation. Generally, only the mode of the joint posterior (MPD) distribution was estimated in preliminary runs, but for final runs the full posterior distribution was sampled using Markov chain Monte Carlo (MCMC) methods. Horn & Dunn (2003) used CASAL to assess ling in QMAs 3–6 and parts of QMAs 2 and 7 as five biological stocks: the four noted previously (LIN 3&4, LIN 5&6, LIN 6B, and LIN 7WC), plus a fifth stock in the Cook Strait region denoted as LIN 7CK (Figure 7). Note that QMA 3 (east coast South Island) was divided at about 46° S near the Otago Peninsula, with northern catches and biological data being attributed to the Chatham Rise stock, and southern catches and biological data attributed to the Sub-Antarctic stock. The assessments incorporated all relevant biological parameters, the commercial catch histories, relative abundance indices, and series of catch-at-age and catch-at-length data. MPD assessments were presented for all stocks, and MCMC assessments were presented for LIN 3&4, LIN 5&6, and LIN 7WC (Horn & Dunn 2003).

Assessments of stocks LIN 3&4, LIN 5&6, and LIN 7WC have been conducted regularly since 2003 (e.g., McGregor 2015, Dunn & Ballara 2019, Mormede et al. 2021b) (see Fisheries New Zealand (2022) and subsequent iterations of that plenary document for the latest assessments). The Bounty Plateau stock (LIN 6B) was assessed again only once (Horn 2007). There is no TACC exclusive to that stock; it forms part of administrative stock LIN 6. The LIN 6B fishery has been almost exclusively target longline, so economic considerations will likely regulate catches from this area (i.e., effort will reduce as catch rates become economically marginal). The Cook Strait stock (LIN 7CK) was assessed sporadically, with the last accepted assessment being that produced by Horn & Francis (2013) for the 2010–11 fishing year. A subsequent LIN 7CK assessment (Dunn et al. 2013) was considered unsuitable for the provision of management advice because the model failed to accurately represent declines in resource abundance evident from CPUE values, which had been declining since 2001.

Assessments of ling around most of North Island (i.e., administrative fishstocks LIN 1 and LIN 2) were attempted using CPUE analyses, but only the assessment for the LIN 2 fishery (Roux 2015) was accepted for management advice (Fisheries New Zealand 2022).

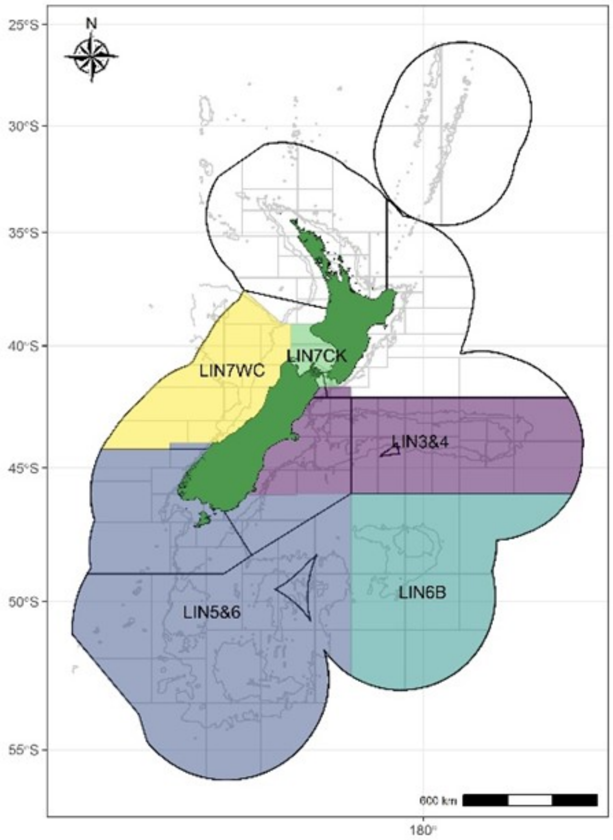

Figure 7: Biological stock boundaries used for the assessment of ling in New Zealand (from Mormede et al. 2021a).

3.5.2 International stock assessments

Ling stocks off Argentina were assessed using dynamic production models: a biomass dynamic model (Cordo 2001b) and a more complex age-structured production model (Cordo 2001b, 2007). Both model types were fitted to CPUE data obtained from the commercial fishing fleet (e.g., Cordo 2001a). A comparison of the 2001 and 2007 assessments indicated a declining stock size, which led to recommendations to reduce fishing effort for part of the year at the spawning grounds (Cordo 2007).

The population dynamics of Chilean *G. blacodes* was investigated using a discrete time stage-structured matrix model (González-Olivares et al. 2009). The work aimed to describe the population growth rates for ling, carry out a perturbation analysis of the survival and fecundity rates, and compare population dynamics with and without fishing. The fished population had a negative growth rate, while there was a positive and significantly different (but relatively low, i.e., 1.08) growth rate for the harvested population. The population growth rate was most sensitive to variations in adult survival in the age class 7–10 years. The authors recommended developing management strategies to preserve these fish that were just above the age at first maturity, because small variations in their survival markedly altered the dynamics of the whole population, threatening the sustainability of the ling fishery. Flores et al. (2020) suggested that the relatively sedentary behaviour, mating strategy, occurrence of skipped spawning, and low fecundity of ling were driving the low rate of population renewal and low resilience to fishery exploitation apparent for Chilean ling populations.

Arancibia et al. (2010) compared the implementation of two multi-species stock assessment approaches applied to the Chilean southern demersal fishery, i.e., an ecosystem-based approach to fisheries management based on ecosystem indicators (Ecopath software with Ecosim, EwE), and a structural cohort analysis type model formulated as a multispecies virtual population analysis (MSVPA). The fishery resources incorporated in both models were southern hake (*Merluccius* *australis*), grenadier (*Macruronus magellanicus*), southern blue whiting (*Micromesistius australis*) and ling (*Genypterus blacodes*), with the ray (*Dipturus flavirostris*) and Patagonian toothfish (*Dissostichus eleginoides*) also included in EwE. Predation by adults of the main species (including cannibalism) was found to be the main component of natural mortality. The EwE model was found to be strongly influenced by both the top-down effect of fishing and predators, and by bottom-up changes related to groups at low levels in the food web, including primary production. Arancibia et al. (2010) noted that because the two model types required different data inputs, it was possible to evaluate different, but complementary, questions in the dual modelling process. It was suggested that single species management based on Maximum Sustainable Yield (MSY) may not be an optimal for the Chilean southern demersal fishery because it was not possible to reach and maintain MSY simultaneously in all target species. The MSVPA model was further developed by Jurado-Molina et al. (2016), who found that estimates of ling abundance from that model were similar to those from a single-species model.

Single-species assessments of Chilean ling were carried out using Automatic Differentiation Model Builder (ADMB) software (Contreras et al. 2013). The age-structured model had sexes combined and assessed two stock units (northern and southern zones). The evaluation incorporated relevant biological parameters, updated maturity ogives, catch histories, CPUE series, and catch-at-age series for different fleets of the resource by zone. Stocks in both areas were assessed to be over-exploited, each with spawning stock biomasses of about 16% B_0.

Assessments of Australian ling stocks have been completed using the software packages Stock Synthesis (e.g., Whitten & Punt 2014) and CASAL (e.g., Cordue 2018). A case study using the Australian ling assessment was conducted to evaluate the effects of closed areas and spatial variation in growth and exploitation rate when estimating spawning biomass (Punt et al. 2015, 2016a). The performance of spatially-aggregated assessments when estimating spawning stock biomass was found to depend on the interactions among spatial variation in growth, in exploitation rate, and in knowledge of the spatial areas over which growth and exploitation rate are homogeneous. Biomass estimates could vary markedly when spatial variability in somatic growth was ignored. Ling was also one of a suite of assessed Australian species incorporated in a retrospective analysis conducted to quantify the extent of uncertainty associated with estimates of spawning stock biomass in relative and absolute terms (Punt et al. 2018).

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