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A REVIEW OF ORANGE ROUGHY *HOPLOSTETHUS ATLANTICUS* FISHERIES, ESTIMATION METHODS, BIOLOGY AND STOCK STRUCTURE

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Orange roughy *Hoplostethus atlanticus* are unusual fish. They form dense aggregations that have fuelled lucrative fisheries at great depths (600–1 400 m), especially off Namibia, New Zealand and Australia. They are thought to be very long-lived (>100 years, maturity at 22–40 years), and to have exceptionally low natural mortality ($M = 0.045 - 0.064$ year^{-1}) and slow growth rates ($K = 0.055 - 0.070$ year^{-1}). In addition, they spawn large eggs and have low fecundity. These factors combine to make orange roughy highly susceptible to overfishing; most stocks are below 30% of pristine levels. Assessments are obtained from indices of catch rate and trawl, acoustic and egg surveys. Acoustic estimates are the most direct, but are confounded by the species' low target strength (-50 to -53 dB) – attributable to the wax-filled swim bladder. Extracellular wax esters are stored in abundance and comprise mostly mono-unsaturated fatty acids, with low concentrations of the ω-3 fatty acid family. This unusual composition (resultant from the species' diet) ensures neutral buoyancy. Stock separation has been inferred mainly from biological studies, but genetic studies have also found differences among stocks within New Zealand and Australia. Deep-water habitat may be damaged by trawling operations and may take many years to recover, so in some quarters there is a call for a portion of suitable habitat to be set aside for preservation. Although Namibian orange roughy are shallower, smaller and younger than those in other stocks, the Namibian fishery sustained high catches for only a few years before quotas were reduced, from 12 000 to 1 875 tons. Three management lessons are suggested for developing orange roughy fisheries based on the Namibian experience: (1) imposition of catch limits during exploratory fishing; (2) starting the acoustic surveys earlier in the fishery, if possible; (3) greater reliance on trends in catch rate until a survey series has been established.

Key words: age determination, aggregations, assessment, biology, diet, distribution, fisheries, genetics, habitat, *Hoplostethus atlanticus*, lipids, Namibia, orange roughy, reproduction, review, stock structure, surveys

The orange roughy *Hoplostethus atlanticus* is an unusual fish species. It is thought to be extremely long-lived (>100 years), only reaching maturity after 20–30 years. In addition, it aggregates densely, permitting catches of 50 tons per minute (Ross and Smith 1997). Orange roughy are highly sought after, one of the attractions being that the fillets can withstand several cycles of freezing and thawing (Merrett and Haedrich 1997); their market price in early 2001 was US$10–13 per kg for fillets. The combination of these factors makes the species highly susceptible to overfishing. Commercial fishing for orange roughy only started in 1979. The relatively late start can be explained by the great depths (>500 m) and difficult terrain on which they are found. The trawl fisheries use advanced technology to locate and exploit the aggregations, and exploratory fishing (which is expensive) can still be unrewarding (Strutt 2001). Their longevity, high density and great depths are not the only remarkable features of orange roughy; relative to many other fish species, they have large eggs, low fecundity, a high lipid content (with an atypical composition) and marked avoidance behaviour.

The Namibian fishery is a case study on how the unusual features of orange roughy can lead to difficulties in management, exacerbated by the sparse data available at the start of a developing fishery (Boyer *et al*. 2001). Scientists and managers were required to provide information and advice about a fishery operating in conditions very different from the existing local fisheries. Such information is available in numerous papers that have been written on the species, but many of these papers are unpublished assessment documents or internal reports and so are difficult to obtain. Furthermore, no overall synthesis of this literature exists, although Clark (1996) summarizes the methods used for biomass estimation, and Tracey and Horn (1999) review age determination studies. Research results from Namibia are now part of this extensive literature, and an overall summary

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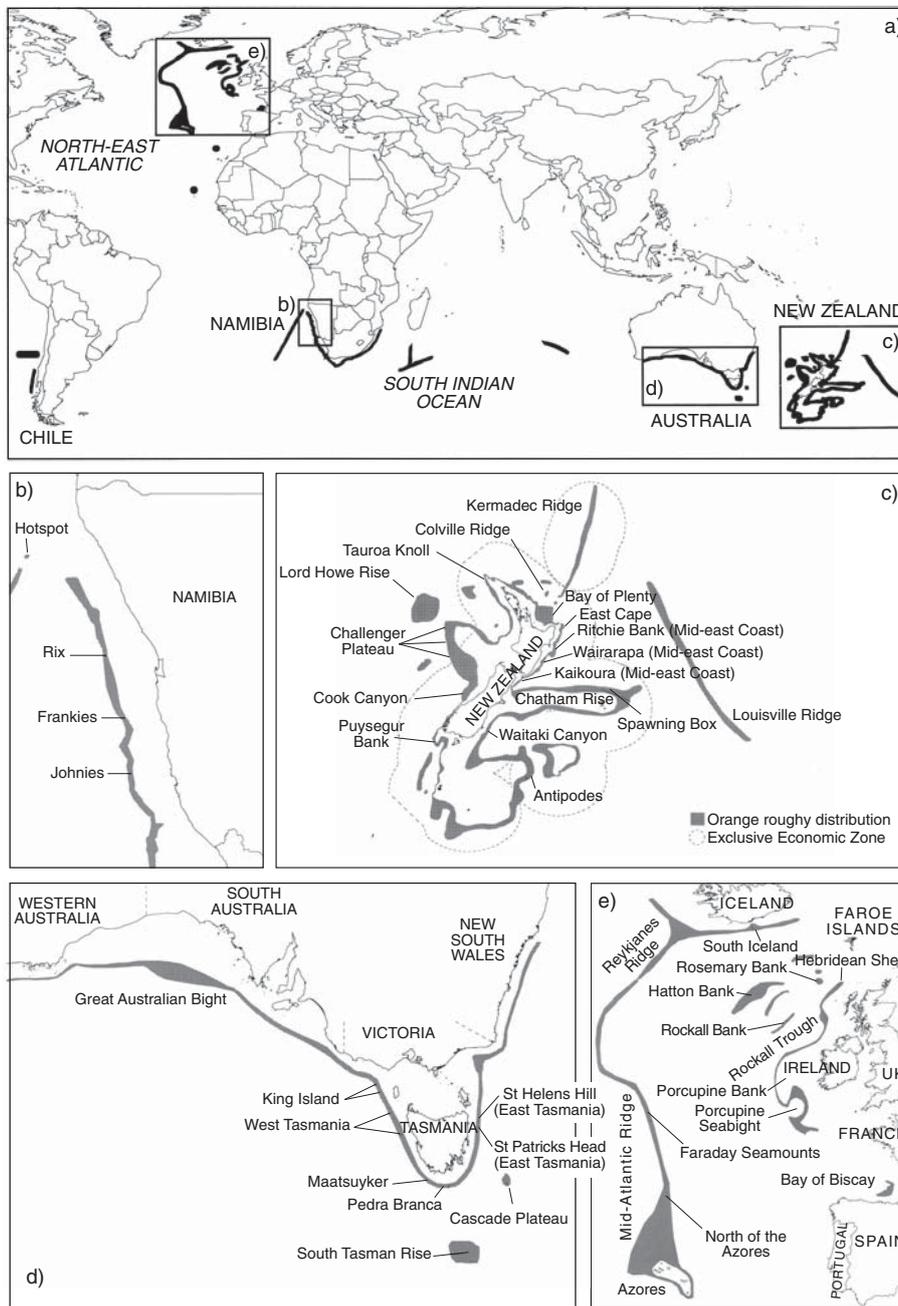Fig. 1: Distribution of orange roughy (a) worldwide, with insets of the distribution (b) off Namibia, (c) around new Zealand, (d) around Australia, and (e) in the North-East Atlantic. Primary sources – Kotlyar (1996), Branch (1998), Magnússon and Magnússon (1998), Clark (1999, 2001), Gordon (1999), Tracey and Horn (1999), Bax (2000), Strutt (2000), Anderson (2001), Hareide and Garnes (2001), Hope (2001)

of Namibian and other fisheries would be an invaluable tool for managing orange roughy fisheries, both old and new.

The purpose of this paper is to review orange roughy research, in Namibia and worldwide, and to give information on the species' habitat and identification, as well as a history of fisheries and methods of abundance estimation around the world. A description is given of orange roughy life history, the controversy around age determination is outlined, and information presented on diet, aggregating behaviour and anomalous lipid composition. Further, the usefulness of different methods for determining orange roughy stock structure is examined before an assessment of the potential impacts on the environment of deep-water orange roughy trawling is presented.

Orange roughy have a worldwide distribution (Fig. 1a) in temperate regions at depths ranging from 450 to 1 800 m (Paulin 1979, Merrett and Wheeler 1983, Bell *et al.* 1992, Dr J. D. M. Gordon, Scottish Association for Marine Science, Oban, pers. comm.[1]). Exploratory fishing (and expensive side-scan sonar surveys) for orange roughy off Namibia focused on depths of 800–1 200 m, which are typical of the established fisheries for the species off Australia and New Zealand and in the North-East Atlantic (Merrett and Wheeler 1983, Coburn and Doonan 1994, Magnússon and Magnússon 1995, Ross and Smith 1997). However, Namibian orange roughy occur shallower (600–800 m) than in other locations (Boyer and Hampton 2001). Off Namibia, suitable temperatures (3–9°C) are shallower than in other fisheries; worldwide, most large catches are recorded at 4.5–6.5°C (Clark 1997, Strutt 2001). This tight range of water temperature is considered more important than depth in determining orange roughy occurrence. One exception to this rule is north of the Azores, where orange roughy are most prevalent at temperatures of 8.2–8.9°C, and are even caught at 10.2–11.2°C in depths of 500–600 m (Hareide and Garnes 2001). Fishable aggregations are usually found on hard ground on topographical features such as seamounts, drop-off features or canyons (Clark 1999, Boyer and Hampton 2001), but orange roughy are also caught on areas of soft substratum, where they are more dispersed.

The fish is bright orange. There is a great variety in fish size from region to region, but length frequency distributions in a particular region are normally strongly unimodal (juveniles are rarely caught) and do not change over time (e.g. Horn *et al.* 1998, Anderson 2001, Clark 2001). Off Namibia, orange roughy are generally smaller than in other orange roughy fisheries, with a standard length[2] (*SL*) of 20–32 cm, except on the Hotspot ground, where the range is 24–52 cm (A. Rees, Gendor Fishing, Swakopmund, Namibia, pers. comm.). Around Australia and New Zealand adults are typically 20–50 cm long (Anderson 2001), with extremes at Cook Canyon (14–40 cm) and Colville Ridge (38–57 cm; Anderson 2001). Off Chile, nearly all fish are 29–49 cm long. Throughout the North-East Atlantic, orange roughy are considerably larger than in the southern hemisphere, with most fish 40–58 cm (Charuau *et al.* 1995, Du Buit 1995, Thomsen 1998, Gordon 1999). The largest recorded specimens are those from the Faroese catches, which can reach 62 cm and a body mass of 7 kg (Thomsen 1998).

Despite the differences in length, orange roughy stocks worldwide constitute a single species (*Hoplostethus atlanticus* Collett 1896) in the family Trachichthyidae within the order Beryciformes. *H. atlanticus* is the only species in the family with any commercial value. A formal description and identification key for some trachichthyids off New Zealand is included in Paulin (1979), but 19 of the 43 trachichthyid species have been described since 1979 (Froese and Pauly 2000). The beryciforms are reviewed by Kotlyar (1996). The common name for the Trachichthyidae is "slimeheads", perhaps a reason why New Zealand marketing firms coined the less repulsive name "orange roughy" to sell exports from New Zealand (Merrett and Haedrich 1997).

HISTORY OF ORANGE ROUGHY FISHERIES

Orange roughy trawl fisheries have developed off Namibia, New Zealand and Australia, in the North-East Atlantic and the southern Indian Ocean, and off Chile (Fig. 1). In most cases, the stock has been rapidly fished down to (and often below) the long-term sustainable yield. Fisheries managers in Namibia used these experiences as a basis for setting precautionary target biomass levels and restricting effort at the start of the fishery.

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[1] A maximum depth of 1 809 m in the North-East Atlantic is erroneously reported as 1 908 m in several unpublished documents (J. D. M. Gordon, pers. comm.)

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[2] Where measurements were reported as total length (*TL*), they have been converted to standard length (*SL*) throughout the paper using the relationship in Horn *et al.* (1998): $SL = 0.839\,TL - 1.53$. Alternative formulations are given by Magnússon and Magnússon (1995) for Icelandic fish ($SL = 0.8118\,TL$) and by Tracey and Horn (1999) for orange roughy from the Challenger Plateau ($SL = 0.828\,TL - 1.35$)
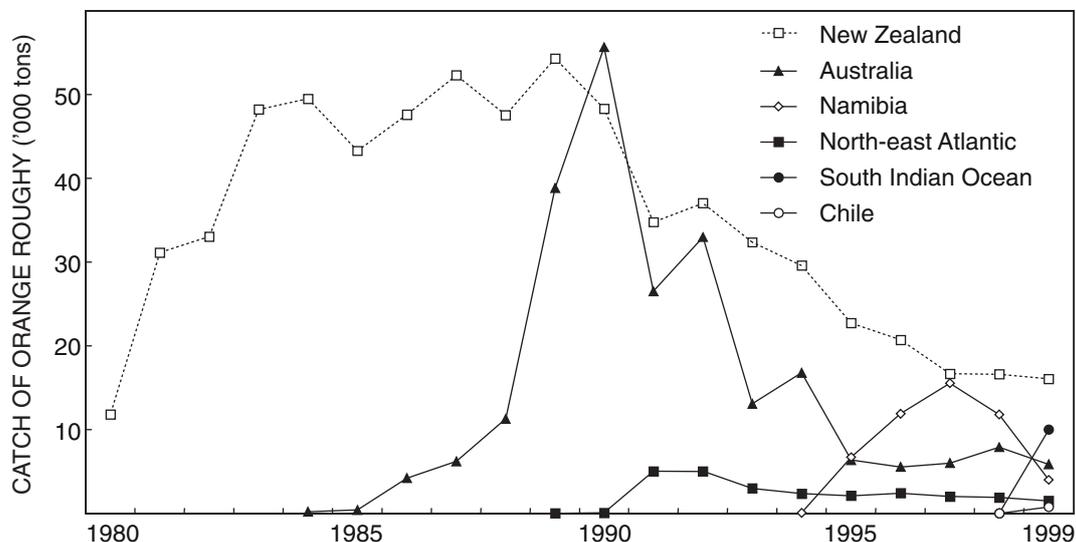
Fig. 2: Catch history of orange roughy around the world. The catches shown represent the year in which the fishing season ended. Most of the North-East Atlantic catches were made by France, the Faroe Islands and Iceland, and the remainder (<100 tons per year) by Ireland, the United Kingdom, Spain and Norway (catch data for 1999 incomplete). The 1983 and 1984 catches for New Zealand correspond to 15-month periods owing to a change in the timing of the season. Overruns are included only for Australia. For New Zealand assessment purposes, overruns are assumed to be 30% until 1984, gradually reduced to 10% in 1992 and reduced further to 5% after 1994–95 (Annala *et al.* 2000). Sources – New Zealand, Annala *et al.* (2000); Australia, Bax (2000); Namibia, McAllister and Kirchner (in press); North-East Atlantic, ICES (2000); South Indian Ocean fishery, Strutt (2001); Chile, government statistics (www.sernapesca.cl)

Namibia

After much initial exploration by a single company in 1994, four distinct spawning areas were located; they still form the basis of the fishery (Fig. 1). Hotspot and Johnies were discovered in 1995 and Rix and Frankies in 1996. Total catches reached 15 500 tons in 1997 (Fig. 2). Catch limits were imposed in 1997, and the fishery was opened to three companies, with at most five vessels in the fishery. The management goal in Namibia was to fish the spawning biomass down to 50% of its pristine level. However, initial assessments (Branch 1998) were overly optimistic and, despite the limited number of vessels as well as the application of a number of aspects of precautionary management, the aggregating biomass dropped to 10–50% of pristine levels in just six years (Boyer *et al*. 2001). Biomasses on Hotspot, Johnies and Frankies are now considered likely to be well below 30% of virgin biomass (Brandão 1999, Kirchner and McAllister 2000). The *TAC* (Total Allowable Catch) was accordingly reduced from 12 000 tons in 1998 to 1 875 tons in 2000.

New Zealand

The New Zealand fishery remains the largest in the world, with a far greater variety and number of fishing grounds than in any other region. Initial catches were by foreign trawlers in the late 1970s, but the domestic fishery developed rapidly from 1979. Exploitation focused on the Spawning Box on the Chatham Rise for the first few years of the fishery, but spread to a number of other areas around New Zealand (Fig. 1) as new grounds were found at regular intervals (Clark 1995). Annual reported catches from 1982/83 to 1989/90 were 40 000–55 000 tons, but had decreased with reductions in quotas to the present level of 16 000 tons by 1996/97 (Fig. 2). The target biomass level (to maximize the average yield of a fluctuating population) is 30% of pristine biomass (Annala *et al.* 2000). However, many New Zealand stocks are already thought to have fallen below this level, including the East Cape, Mid-east Coast, north-east Chatham Rise, Puysegur Bank, Challenger Plateau and Cook Canyon stocks (Annala *et al.* 2000).

Australia

After limited success from 1985 to 1988, a major spawning aggregation (St Helens) was discovered off eastern Tasmania in 1989 (Fig. 1). In the same year, smaller non-spawning aggregations were located south of Tasmania on Maatsuyker and Pedra Branca. Together with the Cascade Plateau, these areas form the South-East fishery. Annual catches ranged from 26 000 to 54 000 tons per year between 1989 and 1992 (Fig. 2) before the imposition of *TAC*s halted the "orange roughy rush". By 1996, annual catches had been reduced to their current level of around 4 000 tons plus an additional 1 700–3 700 tons outside the South-East fishery (Smith and Wayte in press). The additional Australian catches are mostly from a spawning aggregation on the South Tasman Rise, but also from the Great Australian Bight (Smith and Wayte in press). In 1999, 34 vessels reported orange roughy catches, down from a high of 67 in 1990 (Bax 2000). The management aim for the fishery is to maintain the spawning biomass of orange roughy above 30% of that in 1988, but the Southern, Eastern and Western Zone stocks are all below this target (Bax 2000).

North-East Atlantic

Early Russian exploration for deep-water species in the North-East Atlantic resulted in some catches of orange roughy (Troyanovsky and Lisovsky 1995), but French vessels fishing on the Hatton Bank landed most of the catch in the 1990s (Thomsen 1998). French vessels landed 5 000 tons of orange roughy in 1991, but this declined to 1 000–1 300 tons per year from 1995 to 1999 (ICES 2000). A recent assessment of area VI indicated that the biomass had declined to 27–29% of unexploited biomass (ICES 2000), and there are indications from catch rates that the biomass in some areas has been fished down rapidly (Lorance and Dupouy 2001).

The Faroese Fishing Laboratory (Faroe Islands) conducted 28 exploratory cruises for orange roughy between 1992 and 1998, starting south and west of the Faroe Islands, in the Hatton Bank area, south of Iceland on the Reykjanes Ridge, and later on the Mid-Atlantic Ridge north of the Azores (Thomsen 1998). Most commercial catches (nearly all by a single vessel) have been taken north of the Azores, peaking at 1 300 tons in 1996.

Icelandic trawlers started fishing orange roughy south of Iceland in 1991, with catches peaking at 700 tons in 1993 after an exploratory survey (Magnússon and Magnússon 1995). Annual catches have been <100 tons since 1995 (ICES 2000). Sporadic, scattered catches (<70 tons per year) have also been recorded by Spain, Ireland, the United Kingdom and Norway, and an exploratory permit has been granted in Azorean waters.

South Indian Ocean fishery

Fishing began in 1999 on seamounts south of Madagascar on the South-West Indian Ridge (Strutt 2000, 2001). In total, 10 000 tons of orange roughy (and other deep-water species) were landed in both 1999 and 2000, but the "fleet" increased from 6 to 35 vessels between the two seasons, and many vessels lost money in 2000 (Strutt 2001).

Fisheries elsewhere

Catches ranging between 400 and 5 535 tons have been taken since 1988 on the Lord Howe Rise and Challenger Plateau, in international waters between Australia and New Zealand (Bax 2000). Seamounts on the Louisville Ridge, east of New Zealand, have also been fished since the mid-1990s (Clark 1999). The Chilean fishery for orange roughy has concentrated around the Juan Fernandez archipelago, and off southern Chile. In 1999, 779 tons of orange roughy were caught, and in 2000 the *TAC* of 1 580 tons was taken in less than eight weeks (Hope 2001).

SURVEYS AND OTHER ASSESSMENT TOOLS

Surveys are one of the most important management tools for orange roughy because they provide estimates of trends in biomass. Collecting basic biological information (although essential for stock assessment) does not help in estimating trends because age and length frequencies change little from year to year. In a developing fishery, an early start to a survey series is essential because trends will only become apparent after 2–3 surveys. In Namibia, the first surveys were conducted in the third year of the fishery, which in hindsight may have been one year too late.

Surveys can be used in one of two ways: as an estimate of absolute biomass, or as a relative index of abundance. Egg surveys and acoustic surveys may provide useful absolute estimates of biomass, whereas

trawl surveys, acoustic surveys and analysis of catch per unit effort (*cpue*) have provided relative indices. Bias-corrected swept-area estimates of abundance from commercial trawl data have not provided good absolute estimates for orange roughy. Clark (1996) reviews survey techniques in New Zealand.

Trawl surveys

Trawl surveys have been used for orange roughy mainly in New Zealand, but also in Australia and Namibia. They are used only as relative estimates of abundance, primarily because the interaction between orange roughy and trawling gear is poorly understood. Limited trawl surveys in Namibia (performed together with acoustic surveys) verified the acoustic trend (Boyer and Hampton 2001), but did not approach the scale of the New Zealand trawl surveys.

Clark (1996) reports the results of 24 trawl surveys off New Zealand. There, a two-phase stratified random survey was used on flatter areas in an attempt to provide estimates with lower *CV*s (Francis 1984); on seamounts, the methodology initially involved tows in random directions starting on the apices of the rises (Clark 1994), and later evolved into a more systematic "star" design (Bull *et al.* 2000). Trawl surveys showed strong trends in biomass on the Chatham Rise and Challenger Plateau, with *CV*s generally from 11 to 27% (Clark 1996). However, two recent trawl surveys on the Chatham Rise had *CV*s of 34% (1992) and 67% (1994), perhaps because of very low levels of biomass (Clark 1995, Francis *et al.* 1995) or because reduced fishing (and hence less disruption) in those years had allowed much denser aggregations to form. An additional problem on the Chatham Rise was that the trawl surveys in a small area (the Spawning Box) were thought to index the entire Chatham Rise, but are now used only as an index for the north-east Chatham Rise (Annala *et al.* 2000). Trawl surveys on the Chatham Rise have therefore been discontinued. Trawl-survey series elsewhere in New Zealand have been difficult to interpret, because different vessels were used in different years. For example, the East Coast surveys from 1986 to 1991 were not used in stock assessments because they were not regarded as comparable (Field *et al.* 1994).

Two trawl surveys off Australia (Evans and Pullen 1986, Bulman *et al.* 1994), produced unreliable results, primarily because little trawling was done on rough ground. For example, Bulman *et al.* (1994) estimated orange roughy biomass at 5 044 tons in a region that included the St Helens aggregation, which had an estimated pristine biomass of about 100 000 tons (Kloser

et al. 1996). Trawl surveys have therefore been viewed with disfavour by both industry and scientists in Australia (Ross and Smith 1997). Part of the problem is the range of bottom types: orange roughy may be present on flat grounds, on the tops and sides of seamounts, and near deep canyons. Gear performance and catchability can vary on these different features. The very high densities of orange roughy can also cause gear saturation, and provide problems with processing time in the short time available for the surveys.

Trawl surveys do, however, have a number of advantages: the methodology is well-established, results are quickly calculated, and specialized equipment and vessels are not required. They also provide a method for assessing biomass outside the dense aggregations, which egg and acoustic surveys are unable to do. In addition, a variety of randomly sampled biological information can be obtained, which can be used to determine trends in biological parameters, and to estimate growth and natural mortality.

Analysis of catch per unit effort

In most fisheries, a vast amount of commercial data is available for analysis. Usually, some form of *cpue* analysis provides an index that is presumed to track changes in abundance. In the Namibian fishery, unstandardized *cpue* declined to 16–62% of initial values within 1–2 years (Branch and Roberts 1998a). A method of standardizing *cpue* indices for vessel type, power and nationality was developed by Doonan (1991), but the pattern of change is generally similar for standardized and unstandardized (e.g. tons per tow) measures of *cpue* (Clark 1996). *Cpue* indices for New Zealand have declined dramatically to just 1–8% of the initial values for the Chatham Rise, Challenger Plateau, Ritchie Bank and Cook Canyon (Clark 1992, Clark and Tracey 1994, Field *et al.* 1994, Clark and Field 1995, Annala *et al.* 2000). Although such declines were initially thought to be more precipitous than reality (Clark 1996, Koslow *et al.* 1997, Branch and Roberts 1998a), they are now thought to provide a good indication of general trends in orange roughy fisheries (Bax 2000, Clark *et al.* 2000). Accordingly, standardized and unstandardized *cpue* indices are used to provide assessment advice for New Zealand stocks on the Mid-east Coast, Chatham Rise hill complexes and Challenger Plateau fisheries (Annala *et al.* 2000), for the French fishery in the North-East Atlantic (ICES 2000), and as part of Namibian and Australian assessments (Bax 2000, Kirchner and McAllister 2000).

Commercial swept-area estimates

A method was developed by Branch (1998) to estimate the absolute abundance of orange roughy off Namibia, when surveys had not yet been conducted. Commercial catch data were converted to swept-area estimates (using the wingspread of the nets, the bottom distance of the tows, and post-stratified estimates of the area of the aggregations based on catch locations). Major biases include uncertain catchability, the directed (non-random) nature of tows, and uncertainty in how to define the area occupied by the aggregations. Extensive working group discussions were used to obtain consensus probability distributions for these biases, which were in turn used to convert the swept-area estimates into absolute abundance estimates. This method was used by Branch (1998), Branch and Roberts (1998b) and Brandão (2000) to provide a series of abundance estimates for the Namibian fishery.

The unexploited median biomass inside the aggregations was estimated to be 117 000–135 000 tons using this method, comparing favourably with the 1997 acoustic estimate of 121 000 tons (Boyer and Hampton 2001). However, the Branch (1998) method gave median estimates of 175 000–179 000 tons outside the aggregations, whereas the acoustic surveys assumed that biomass outside the aggregations was zero. Later acoustic surveys provided dramatically reduced estimates of abundance: 26 000 tons in 1998, and 2 900 tons for Frankies only in 1999 (Boyer and Hampton 2001). When combined with the subsequent catch history, it is clear that the biomass estimates using this swept-area method were many times too high, resulting in excess optimism about the future of the fishery. Kirchner and McAllister (in press) address one problem with this method by improving the procedure for estimating the area of aggregation, but the consensus method of obtaining realistic distributions for the biases is still problematic.

Egg surveys

Egg surveys have been used off New Zealand and Australia to estimate spawning stocks of orange roughy. Two methods are in use: the daily fecundity reduction method (DFRM) developed by Lo *et al.* (1992) and the annual egg production method (AEPM; Saville 1964). The DFRM has been used to assess the New Zealand Ritchie Bank, East Cape, Mid-east Coast and Northwest Chatham Rise spawning grounds, with estimated *CV*s between 46 and 80% (Field *et al.* 1994, Francis *et al.* 1997, Zeldis *et al.* 1997a, 1997b). The AEPM method was applied to the Australian St

Helens aggregation, obtaining an estimate congruent with acoustic and stock reduction analyses, with a *CV* of 41–47% (Koslow *et al.* 1995a). It is likely that the AEPM method is more robust because it does not require assumptions about fish turnover in the aggregations, but it requires the whole spawning period to be covered, needing up to six weeks of vessel time (Clark 1996).

Egg surveys have the potential to provide estimates of absolute biomass, but high associated variances render them unsuitable as a basis for relative indices. Survey design and data analysis can also be complicated. Specialized equipment and experienced staff are required, and sampling must be intensive in and around the core area (Clark 1996). Egg surveys are only possible when orange roughy aggregate in a single high-density locality. Egg surveys are not currently conducted on any orange roughy stocks, mainly because of the many assumptions that must be made to obtain biomass estimates.

Acoustic surveys

As orange roughy form dense aggregations, they appear to be ideal candidates for acoustic surveys. Acoustic survey equipment is described in Coombs (1994, 2000), Kloser *et al.* (1996, 2000) and Boyer and Hampton (2001). Such surveys provide good relative indices, but there are a number of factors that complicate their conversion to absolute abundance.

Annual acoustic surveys (Huse *et al.* 1997, Dalen *et al.* 1998, Staalesen *et al.* 1999) are the main basis for biomass estimates of Namibian orange roughy and are performed on the Rix, Frankies and Johnies grounds. Boyer and Hampton (2001) summarize and discuss these surveys. Acoustic estimates of orange roughy biomass off Namibia declined rapidly from 1997 to 1999 (by more than an order of magnitude), and the aggregations became more difficult to locate during the surveys (Boyer and Hampton 2001). These findings were instrumental in causing the Namibian *TAC* to be reduced from 12 000 tons in 1997–98 to 1 875 tons in 2000–01. The Chatham Rise in New Zealand was acoustically assessed in 1986, 1995, 1998 (twice) and 1999 (respectively Do and Coombs 1989, Clark 1996, Doonan *et al.* 1999, Bull *et al.* 2000, Kloser *et al.* 2000), although the 1986 survey was intended as a test project only. The St Helens aggregation off Australia was assessed from 1990 to 1993, with very low sampling *CV*s (7–15%), ideal for relative indices of abundance. However, because there were many potential sources of bias, *CV*s of around 40% were assigned for stock

assessment purposes (Bax 2000).

Problems with target strength[3] measurement are notorious. Orange roughy have low target strength because their swimbladders are filled with lipids instead of gas (Do and Coombs 1989, McClatchie and Ye 2000). No estimates of target strength are available for Namibian orange roughy, so the target strength estimates obtained for the New Zealand and Australian stocks were used for the Namibian survey analysis, after adjustment for the smaller average size of Namibian orange roughy. A 27 cm Namibian fish will have a target strength 1.8 or 2.3 dB lower than a "typical" 35 cm Australasian fish[4] (using the equations in McClatchie *et al.* 1999 and Kloser *et al.* 2000 respectively).

Estimates of target strength (for a fish 35 cm long) have ranged from -36.0 dB, based on dead orange roughy in a tank (Do and Coombs 1989), to -41 dB using the reduction in mean backscatter during commercial fishing (Elliott and Kloser 1993), to values of -47.2 dB (using modelling) or -53 dB (tethered at depth, Kloser *et al.* 1997). Attempts to obtain target strengths of individuals *in situ* were initially unsuccessful because orange roughy display marked avoidance behaviour (Koslow *et al.* 1995b), although dominant modes *in situ* at -50 dB have been attributed to orange roughy (Kloser *et al.* 1997). McClatchie *et al.* (1999) measured target strength of live orange roughy in an aquarium, obtaining a value of -46.3 dB. McClatchie and Ye (2000) modelled the lipid composition of orange roughy, adjusting it for changes in backscatter at the temperatures and pressures where the species is found, and obtained a predicted target strength of -48.3 dB. They demonstrated that *in situ* measurements of -50 dB should be increased by 2.5 dB to -47.5 dB to account for avoidance behaviour. McClatchie and his co-workers conclude that their experimental and *in situ* measurements converge at about -48 dB, but other recent measurements of individual *in situ* orange roughy have produced lower target strengths of -50 to -51 dB (McClatchie and Coombs 2000), -51.5 dB (Kloser *et al.* 2000) and -51 to -53 dB (M. A. Soule, Marine & Coastal Management, Cape Town, pers. comm.). Barr *et al.* (2000) discuss the problem of destructive interference when obtaining individual estimates of target strength; this arises because orange roughy swimbladders are not gas-filled.

A major problem with acoustic methods is estimating the biomass of orange roughy within the acoustic "dead zone". The dead zone is that zone just above

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[3] Target strength is the ratio of the reflected (echo) intensity at 1 m from the organism to the intensity that strikes it

[4] Throughout, target strengths have been converted to the equivalent for a fish of 35 cm *SL*

the seabed where fish cannot be detected because of interference by the leading edge of the echo from the bottom. This region may be 7–24 m at the centre of the beam on hills with slopes of 10–20° (Cordue 1996). On flat grounds, the dead zone is 6–11 m (Boyer and Hampton 2001), but just 2–6 m when deep-towed transducers are used (Kloser 1996). On St Helens, the mean dead zone was as much as 24–32 m on the steepest slopes, but a deep-towed transducer reduced this zone to a maximum of 14–16 m (Kloser 1996, Kloser *et al.* 1996). A vessel-mounted transducer could therefore underestimate biomass by a factor of 1.4–2.0 on steep ground (Kloser *et al.* 1996) and by a factor of 1.3–1.7 on flat ground (Boyer and Hampton 2001).

Acoustic backscatter cannot always be attributed to orange roughy, because of possible intermingling with other species; fortunately, surveyed plumes often comprise >99% orange roughy (e.g. Kloser *et al.* 2000, McClatchie *et al.* 2000, Boyer and Hampton 2001). Even with such monospecific aggregations, species identification is a problem because of the low target strength of orange roughy. Kloser *et al.* (1997) estimate that a single 50 cm morid cod may be equivalent (acoustically) to 79 orange roughy. Off Namibia, 5–15% of the backscatter in aggregations is estimated to come from other species (Boyer and Hampton 2001). Trawling is normally used to determine the composition of aggregations of fish, although this is not an ideal solution because avoidance (Koslow *et al.* 1995b) and herding effects (Kloser *et al.* 1997) may bias trawl compositions. The vertical range covered by trawls may also fall entirely within the acoustic dead zone. Aggregations known to be multispecific may also occur on untrawlable ground, thwarting this method of determining species composition. This problem prevents acoustic surveys being used on feeding aggregations south of Tasmania (Koslow *et al.* 1997). On St Helens, the species identification problem has been addressed by using acoustic signals at three different wavelengths (12, 38 and 120 kHz), so providing better discrimination than a single-wavelength system (Koslow and Kloser 1999). Such a system can distinguish between orange roughy and schools of macrourids and deep-water cods.

A further problem with acoustic estimates is that they have to be conducted on areas of aggregation with sufficient densities of orange roughy (generally spawning aggregations). In the Namibian survey in 1999, densities were not high enough to provide estimates on Johnies or Rix, where most of the fishing was being conducted (Boyer and Hampton 2001). Acoustic estimates are typically extrapolated to account for dispersed orange roughy and for fish outside the survey

area. Point estimates on the Northwest Chatham Rise ranged from 10 000 to 31 000 tons, depending on the assumptions used for the extrapolation (Bull *et al.* 2000, Francis and Bull 2000).

Despite all these problems, the acoustic surveys off Namibia provided a good basis for subsequent management decisions, and tallied with *cpue* and simultaneous swept-area survey estimates. The St Helens series also provided absolute estimates of biomass that concurred with estimates obtained from an egg survey, and with stock reduction analyses. Acoustic surveys on the Chatham Rise in New Zealand also play an influential role in stock assessment results. On balance, therefore, acoustic estimates appear to be the best method of monitoring dense concentrations of orange roughy, if the required equipment and technical expertise are available.

BIOLOGY AND BEHAVIOUR OF ORANGE ROUGHY

Salient features of orange roughy biology include their very low fecundity, slow growth and great longevity (although the last two are currently controversial). Possible reasons for the formation of dense spawning and feeding aggregations have been discussed in the literature. The feeding patterns of orange roughy may explain their anomalous lipid content.

Reproduction and egg development

Orange roughy are synchronous spawners that form dense aggregations within which spawning takes place over a period of 2–3 weeks. In the southern hemisphere, spawning usually starts in mid July (Pankhurst and Conroy 1987, Pankhurst *et al.* 1987, Pankhurst 1988, Bell *et al.* 1992, Zeldis 1993), but occasionally it begins in June (Bell *et al.* 1992). Off the Faroe Islands, the main spawning season is between late January and early March (Thomsen 1998); off Iceland, spawners first appear in November and spawning continues until March (Magnússon and Magnússon 1995). There is separation of the sexes in these spawning aggregations, with some indications that females remain in deeper water than males (Pankhurst 1988, Francis 1996). Off New Zealand, not all mature females spawn: up to half the adult population remains outside the spawning aggregations (Bell *et al.* 1992, Zeldis *et al.* 1997a). Such non-reproductive females only constitute 1–2% of French-caught orange roughy (Gordon 1999). Mean length

at maturity is 24 cm off Namibia, 29–32 cm off New Zealand, 34 cm off Tasmania and 39–42 cm in the North-East Atlantic (Horn *et al.* 1998, Thomsen 1998, Gordon 1999).

Absolute fecundity is low around Australia and New Zealand, with reported means ranging between 28 180 and 49 530 eggs female^{-1}, and relative fecundity is also low: 22 000–49 000 eggs kg body mass^{-1} (Pankhurst and Conroy 1987, Clark *et al.* 1994, 2000, Koslow *et al.* 1995a). Higher absolute fecundities of 70 000 –380 000 eggs female^{-1} have been reported for larger individuals (*SL* 43–53 cm) in the North-East Atlantic (Du Buit 1995), but relative fecundity is similar: 48 530 eggs kg body mass^{-1} (Gordon 1999). Fecundity increased significantly off eastern Tasmania after a decline in stock size (Koslow *et al.* 1995a), but there was no evidence of such an increase on the Challenger Plateau (Clark *et al.* 1994). On the Chatham Rise, fecundity actually decreased (Clark *et al.* 2000) under exploitation. There appears to be a slight decline in fecundity after the age of 60 (Koslow *et al.* 1995a), but this relationship is weak. The gonadosomatic index (*GSI*, ratio of gonad to body weight) ranged from 9.3 to 11.1% over a period of 11 years for ripe females on the Chatham Rise, New Zealand (Clark *et al.* 2000), and was 6% in the French fishery (Gordon 1999).

Unfertilized and newly fertilized eggs have about 200 small, bright orange oil globules that coalesce to a single globule (0.47–0.67 mm diameter) in fertilized eggs by the 4-cell stage (Zeldis *et al.* 1998). The egg itself has a diameter of 2.0–2.5 mm (Pankhurst and Conroy 1987, Bulman and Koslow 1995, Du Buit 1995, Zeldis *et al.* 1998, Gordon 1999), larger than that of 82 of the 84 fish species listed by Pauly and Pullin (1988). The eggs are buoyant and rise to a depth of about 200 m at estimated rates of 12.5–23.8 m h^{-1} (Bulman and Koslow 1995, Zeldis *et al.* 1995). Most egg development is at this depth before the eggs lose their buoyancy and sink, probably hatching near the seabed (Bulman and Koslow 1995, Zeldis *et al.* 1995). Egg distribution is extremely patchy, decreasing over 10–15 km to just 0.1% of the density in spawning centres (Zeldis 1993). Time to hatching has been estimated at 175 h under natural conditions (Bulman and Koslow 1995), but at constant temperatures it is 312 h at 7°C (Bulman and Koslow 1995), 278 h at 8°C, 235 h at 10°C and 146 h at 12°C (Zeldis *et al.* 1995, 1998). Eggs cultured at 6°C (typical bottom temperatures) did not hatch (Zeldis *et al.* 1998). The development of the eggs from fertilization to hatching (in 29 stages) is described by Zeldis *et al.* (1998), who also staged and described the damaged eggs. These descriptions are a crucial step in obtaining

abundance estimates from egg surveys, because many eggs are damaged during survey tows (Zeldis *et al.* 1998).

Hatched orange roughy do not start feeding for about a month (Grimes and Zeldis 1993). Young fish (0+ and 1+ cohorts) are rarely encountered during trawling operations and have only been reported at three locations: off the west coast of North Island, New Zealand, at 250 m (Gauldie 1998), on the North Chatham Rise, 50–175 km from the main spawning aggregation (Zeldis *et al.* 1995), and at Frankies, Namibia (B. I. Staalesen, National Marine Information and Research Centre, Swakopmund, pers. comm.). Young orange roughy grow very slowly, with validated standard lengths of 3.1, 5.5 and 7.6 cm for ages 1, 2 and 3 (Mace *et al.* 1990). Validation for New Zealand orange roughy was recently extended to age 4, giving a 5-year-old fish a length of c. 12.4 cm (Tracey and Horn 1999). That study also noted that growth rates were about three times greater in summer (January and February) than in winter (late May to early September).

Growth, age and mortality

A wide range of ages has been ascribed to orange roughy, and there is continued controversy in this area of research. In part, this debate has stemmed from incredulity that a relatively small fish could be so long-lived (e.g. Gauldie and Cremer 1998). However, published estimates of ages greater than 80 years for rockfish (*Sebastes* spp., Bennett *et al.* 1982), and ≥100 years for oreo dories (Oreosomatidae, Stewart *et al.* 1995), have led to wider acceptance of the 100+ years reported for orange roughy. Indeed, a recent paper lists six *Sebastes* species with maximum ages ≥100 years (Cailliet *et al.* 2001). The above groups live at similar depths and in similar conditions to orange roughy. Cailliet *et al.* (2001) hypothesize that great longevity may result from altered physiological processes in conditions of low temperature, high pressure, low oxygen concentration and little food. For Namibian stock assessments (following those in Australia and New Zealand), orange roughy are presumed to be extremely long-lived (Branch 1998). To some extent, this presumption is based on the precautionary principle (F.A.O. 1997), because an extremely long-lived species would be much more susceptible to overfishing than one with a shorter life expectancy.

Several methods of age determination have been applied to orange roughy: circuli in scales, micro-increments in otoliths, annuli in whole otoliths and sectioned otoliths, and radiometric dating. Ages obtained from scales (7–8 years) and otolith micro-

increments (<18 years) are the lowest, whereas sectioned otoliths and radiometric dating give greatest maximum ages (≥100 years). A major problem with the age determination methods applied to orange roughy is the lack of validation past the first four years, a problem in common with many other fish age and growth studies worldwide (Beamish and McFarlane 1983). An exhaustive review of published and unpublished studies on age and growth of orange roughy, and a description of the methods of otolith preparation and reading, is given by Tracey and Horn (1999).

Kotlyar (1981) concluded that scales did not contain any useful zonation pattern. Nevertheless, Gauldie *et al.* (1991) examined the chemistry of orange roughy scales and discovered matching peaks and troughs in calcium and fluorine, from the spiny external to the smooth internal part of each scale. If the peaks and troughs in fluorine were annual, then the fish examined had a maximum age of 7–8 years. The number of visible rings on one of the scales was 76, but Gauldie and his co-workers presumed that these did not represent annual rings.

A technique of age determination based on micro-increments in orange roughy otoliths was developed and extended in a series of papers by Gauldie and associates (Gauldie and Nelson 1988, Gauldie *et al.* 1989, 1995, Gauldie 1990a, b,). Micro-increments are rings 1–5 μm wide that are assumed to be laid down daily in orange roughy; counting these rings yields maximum ages of 15–18 years. A plausible mechanism for daily growth rings is developed by Gauldie and Nelson (1988), and micro-increments in the trevally *Caranx georgianus* are shown to be obligatory and laid down daily (Gauldie and Radtke 1990). Gauldie *et al.* (1995) indicated that strontium variation in orange roughy otoliths had a similar periodicity to micro-increments, but that there were on average 253 micro-increments between peaks in micro-increment width. Fusion of micro-increments into checks could account for some of the difference between 253 and 365 (if the peaks were annual), but this mechanism alone is not sufficient to explain the discrepancy. Romanek and Gauldie (1996) describe a model that attempts to predict the width of micro-increments using endolymph chemistry and temperature. An experimental test of the method showed that the width of the micro-increments at the posterior edge of the otolith was correlated ($r = 0.59$) with the theoretical measurements (Gauldie and Romanek 1998). However, Tracey and Horn (1999) point out that the estimates in the Romanek and Gauldie (1996) model have bounds of two orders of magnitude, and also that no validation of daily growth rings has yet been published. Gauldie (1998) studied whole otoliths from a catch of 67 juve-

nile orange roughy, and concluded that there was no relationship between micro-increment counts (extrapolated to the whole sample from four otoliths) and hyaline zones. His micro-increment analysis assigned ages of 16 months (7 cm) and 32 months (15 cm) to the two modes in the length-frequency distribution, which would seem to argue against the validity of this method, given the 12-month periods between spawning in orange roughy.

Various check rings and marks are visible on orange roughy otoliths, and this mechanism has been used to assign ages to orange roughy under the assumption that these rings are annual. Early attempts either ended in failure to determine an acceptable age from otoliths (Linkowski and Liwoch 1986), or concluded that age estimates resulting from whole otoliths were not reliable (Gauldie 1987, 1988). Ring counts from thin sections of otoliths did not correspond to ring counts from whole otoliths (Gauldie 1987, 1988). However, validation of the hyaline (translucent) zones in whole otoliths has been successful up to an age of four years, using modal analysis of length-frequency distributions of small juveniles (Mace *et al.* 1990, Tracey and Horn 1999), and extrapolated to maximum ages in excess of 50 years (Mace *et al.* 1990). The relationship between counts made on whole and sectioned otoliths was examined by Smith *et al.* (1995). Counts were similar until about 20 annuli, but thereafter counts on sectioned otoliths were much higher. Whole otoliths gave maximum age as 38 years, whereas sectioned otoliths put maximum age at 125 years (Smith *et al.* 1995). Similar ages for sectioned otoliths (21–156 years) were obtained by CSIRO (1995). Attempts at reading otoliths from the French catch were abandoned for fish >30 cm (Charuau *et al.* 1995). Estimates of age of orange roughy from the Faroe Islands were also only attempted for smaller fish, with ages of >30 years assigned to fish 45 cm long (Thomsen 1998). In rockfish *Sebastes alutus* and *S. diploproa*, maximum ages of 50–80 years have been obtained from sectioned otoliths and only 25 years from whole otoliths (Bennett *et al.* 1982, Stanley 1986), a result akin to that for orange roughy.

Radiometric age determination is the latest method to be used for orange roughy. This method had been developed for *S. diploproa* and *S. mentella*. For those species, sectioned otoliths gave more accurate estimates of age than whole otoliths (Bennett *et al.* 1982, Campana *et al.* 1990), confirming longevities of 75–80 years for those species. However, radiometric age determination does not always support ages from sectioned otoliths: in three species of tropical snapper (Lutjanidae), the whole otolith ring count agreed better with the radiometrically determined age (Milton *et al.* 1995). The radiometric method relies on the in-

corporation of ^{226}Ra in the otolith, where it decays to ^{210}Pb. The radium isotope has a much longer half-life (1 600 years) than the lead isotope (22.3 years), so the ratio of ^{210}Pb : ^{226}Ra can provide a measure of the time elapsed since the ^{226}Ra was incorporated into the otolith. A maximum age of 149 ± 12 years for orange roughy was obtained using this method (Fenton *et al.* 1991). Naturally, this extreme longevity proved controversial, and West and Gauldie (1994) attacked a number of assumptions made in that analysis, concluding that uncontrolled errors might invalidate the approach. West and Gauldie (1994) had three principal concerns:

- it is probable that one of the intermediate products (^{222}Rn) diffuses out of the otolith;
- the sources and sinks of ^{210}Pb, ^{226}Ra and other intermediates have not been quantified;
- an assumed otolith-mass growth model uses "ages" produced by other methods of age determination, and is potentially tautological.

Smith *et al.* (1995) address the problem of the mass-growth model, incorporating estimates of growth rate from sectioned otoliths. They conclude that maximum age is either 101 or 125 years, depending on the assumptions made. Francis (1995) provides two approaches to avoid the problem of tautology, and re-estimates maximum age as having a lower bound of 84 years, with a "most likely" value of 194 years for one of the samples.

The controversy over the assumptions behind radiometric age determination has continued. Whitehead and Ditchburn (1996) demonstrated that excess ^{210}Pb is incorporated into the outer layers of otoliths from old fish – artificially inflating age estimates. Gauldie and Cremer (1998) used measurements of ^{214}Bi as a proxy for ^{222}Rn to show that ^{222}Rn diffuses out of the otoliths, and they also report that there is variable uptake of ^{226}Ra into the otoliths. A general note of caution was injected into the debate by Proctor and Thresher (1998). They stress that the handling of otoliths after collection may influence trace element composition. Changes are marked for sodium, potassium, sulphur and chlorine, but calcium and strontium are relatively unaffected. These findings cast some doubt on the trace element analyses on scales carried out by Gauldie *et al.* (1991), and the studies on strontium variation in otoliths that Gauldie *et al.* (1995) used as evidence for micro-increment analysis. However, they also raise questions about whether radiometric age determination could be affected in a similar manner.

Despite the overall concerns about the assumptions underlying the radiometric method of age determination, there is still stronger evidence for extreme longevity
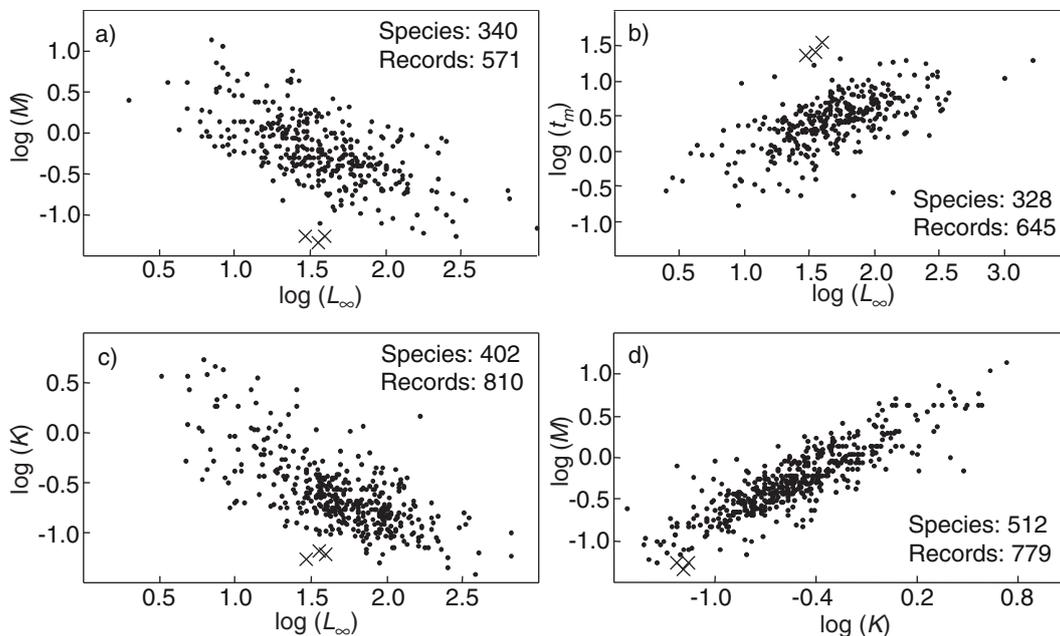
Fig. 3: Population parameters for orange roughy (crosses) compared to those for other fish species (dots). L_∞ and K are the asymptotic length (cm) and growth rate (year^{-1}) parameters in the Von Bertalanffy growth equation, t_m is the age at maturity (years), and M is natural mortality (year^{-1}). Where there are several records for a species, the mean of the logged values for that species is plotted. The total number (excluding orange roughy) of records and species is shown on the graphs

than for the younger ages proposed by Gauldie and his associates (Tracey and Horn 1999). The overall conclusion from the radiometric and sectioning data is that the maximum age of orange roughy is at least 84 years, and probably well over 100 years. In addition, the decline of orange roughy stocks in many areas under very conservative levels of harvest adds further weight to the argument for great longevity.

The methods described in FishBase (1999) and Froese and Pauly (2000) were used to obtain the estimated parameters of the Von Bertalanffy growth equation, L_∞ ("maximum" length) and K (instantaneous growth rate), and the instantaneous rate of natural mortality (M), for all possible fish species. The age at maturity (t_m) for these species was calculated from the length at maturity and the Von Bertalanffy parameters in FishBase (1999). Lengths were converted to total length where possible. In order to avoid bias towards well-studied species, one data point was plotted per species, by taking the mean of the logged values for L_∞, K, etc. For orange roughy, these parameters were obtained from the most recent Namibian, Australian and New Zealand stock assessments (Annala *et al.* 2000, Bax 2000, Kirchner and McAllister 2000).

When L_∞ is plotted against M (0.045–0.064 year^{-1}), K (0.055–0.07 year^{-1}) and t_m (23–40 years) it is clear that orange roughy grow much slower and have a much lower natural mortality, and an older age at maturity, than any of the other species for which data are available (Fig. 3). These findings further reinforce the status of orange roughy as an unusual fish species.

Values of t_m plotted in Figure 3 are those used in stock assessment reports for Namibia, New Zealand and Australia, and are obtained by converting length at maturity to age using a Von Bertalanffy growth curve. Francis and Horn (1997) propose an alternative method of estimating t_m by looking at the "transition zone" in sectioned otoliths. Using this method, Namibian orange roughy (from Rix and Johnies) have the youngest t_m values of any orange roughy examined: 21.8 years, compared to 23.4–29.2 years for New Zealand stocks and 35.4 years for Hatton Bank (Horn *et al.* 1998). The implications of this research are twofold: first, it provides evidence that delaying the age at maturity results in larger adult fish, explaining the difference in adult sizes in different areas around the world; second, it provides the first data on age of Namibian orange roughy.

Aggregating behaviour

Orange roughy form dense single-species aggregations on hard ground, often on such features as seamounts and canyons. Catch rates on these aggregations can be astonishingly high: reported rates off Namibia, New Zealand and Australia have exceeded 10 tons for each minute that the trawl gear is in contact with the bottom (Pankhurst 1988, Clark 1995, Koslow 1997, Koslow *et al.* 1997, Branch 1998), and may reach 50 tons per minute of bottom time (Ross and Smith 1997). These catch rates are obtained with trawl nets that have a wingspread of just 15–20 m and headline heights of around 5 m. Off Namibia, individual aggregations are normally 0.1–1.0 miles long along the acoustic trackline, and are typically located at the top of a gully or drop-off feature (Boyer and Hampton 2001). Acoustic data show that aggregations may be concentrated on the bottom, or may form into dynamic plumes reaching 200 m off the bottom (Kloser *et al.* 1996, McClatchie *et al.* 2000, Boyer and Hampton 2001).

Aggregations form primarily for spawning but also develop outside the spawning season. Non-spawning aggregations off New Zealand are most dense in spring and summer (Clark 1995). Spawning aggregations appear to be made up of fish that migrate into an area to spawn during winter, and then return to their normal locality (Bell *et al.* 1992, Coburn and Doonan 1994). Francis and Clark (1998) used L_{50} (the length at which 50% of mature females are spawners) to infer spawning migrations over hundreds of kilometres on the Chatham Rise. Aggregation densities are highest during the spawning season, but a resident population remains throughout the year (Bell *et al.* 1992), presumably to feed. The density inside aggregations can be so great that it cannot apparently be maintained just by the productivity of the occupied water column (Koslow 1997, Williams and Koslow 1997). However, the currents around the topographic features are strong (0.1–0.4 m s^{-1}) and may import organisms through advection (Koslow 1997, Williams and Koslow 1997).

The aggregations may serve a subsidiary purpose as a mechanism of predator avoidance. Orange roughy aggregations display marked avoidance behaviour, reacting to acoustic cameras as much as 130 m away and even to an iron bar (30×8×1 cm) at a distance of 60 m (Koslow *et al.* 1995b). In one instance, a 200 m high plume compacted to a 25 m pyramid of fish in reaction to a towed acoustic body (McClatchie *et al.* 2000). Orange roughy have a pronounced lateral line (Paulin 1979) and a high degree of visual specialization (Pankhurst 1987); these adaptations may allow them to detect movements of adjacent fish and to respond quickly (Koslow 1996). There is some evidence that fishing pressure disrupts schooling behaviour of orange roughy (Clark and Tracey 1991): the closure to fishing of the Spawning Box on the Chatham Rise resulted in the formation of smaller and denser aggregations there (Clark *et al.* 2000).

Although avoidance of acoustic gear is well documented, individuals can be approached closely with submersibles. Lindsay *et al.* (2000) observed orange roughy in the South Indian Ocean gathering in twos and threes outside the spawning season, and de Pontual and Troadec (1998) reported that orange roughy in the North-East Atlantic were very passive and could even be touched with a submersible arm.

In spawning aggregations, there is marked sexual segregation: individual tows rarely catch equal proportions of males and females (Pankhurst 1988, Lyle *et al.* 1990, Bulman *et al.* 1994, Francis 1996). In the early days of the Namibian fishery, sex ratios were strongly skewed, with 66–71% males on four voyages in 1995 and 1996 (A. Rees, unpublished data, cited by Branch 1998). Sex ratios depend strongly on when and where catches are made (Francis 1996). In some areas (e.g. South Chatham Rise), females dominate throughout the fishery (Francis 1996), whereas on other grounds, especially over seamounts, catches are initially male-dominated and later female-dominated (Francis 1996). In the Spawning Box on the Chatham Rise, the sex ratio was close to 50% for the years 1984–1990, but in 1992 only 28% of the survey catch was male, and in 1994 this dropped further to 14% male (Clark *et al.* 2000).

Diet and feeding

Orange roughy are opportunistic predators that consume a wide variety of invertebrate and fish species. Their prey includes fish, squid, amphipods, mysids and decapod crustaceans, depending on the local abundance of these prey items (Liwoch and Linkowski 1986, Gordon and Duncan 1987, Rosecchi *et al.* 1988, Bulman and Koslow 1992, Thomsen 1998). Rates of food consumption have been estimated at 0.91% (juveniles) and 1.15% (adults) of body mass per day (Bulman and Koslow 1992).

It is likely that orange roughy starve during the spawning season (the proportion of empty stomachs increases then) and that feeding only recommences at the end of the spawning season (Liwoch and Linkowski 1986, Bulman and Koslow 1992, Lesch 1995). Clark *et al.* (2000) found that 85% of all fish caught in the Spawning Box had empty or almost empty stomachs. Feeding is most intense during March and early April, when the gonads are developing (Liwoch and Linkowski 1986). Outside the spawning season, there is some indication that the incidence of

feeding is greater in the aggregations (Bulman and Koslow 1992), perhaps serving to explain the existence of a resident population of orange roughy on those grounds.

Orange roughy metabolism is high: 0.11ℓ O_2 kg wet weight^{-1} h^{-1} for juveniles and 0.14 for adults. These values are similar to those of active mesopelagic fish and lead to exceptionally poor growth efficiencies of about 5% (Bulman and Koslow 1992, Koslow 1997). The high metabolic rates in adults may be related to their strong locomotory ability and avoidance response to perceived threats (Koslow *et al.* 1995b; Koslow 1996).

Flesh composition

Orange roughy command high prices on the US market, primarily because of their firm white flesh, amenability to different sauces and the wide variety of ways in which they can be cooked. There is a layer of lipids (oils) beneath the skin, which are almost entirely (98–100%) wax esters (Bakes *et al.* 1995). Most fish, including the closely related *Hoplostethus mediterraneus*, have a large proportion of triacylglycerols (and not wax esters) in their flesh (Sargent *et al.* 1983), so orange roughy are unusual in this respect. The oils are removed during preparation, partly because of their laxative quality (Judd and Westerkov 1989, cited in Merrett and Haedrich 1997). However, the esters are not harmful to pigs and are therefore presumed to be perfectly safe for human consumption (James *et al.* 1986). A number of studies have focused on the properties and composition of wax esters in orange roughy.

Wax esters are contained primarily in the muscles, belly flap, liver, pyloric caeca, cranial cavity and swimbladder of orange roughy (Sargent *et al.* 1983). The swimbladder, instead of containing gas, contains 82–90% wax esters (Bakes *et al.* 1995), perhaps playing a role in maintaining neutral buoyancy in the cold water they inhabit (Phleger and Grigor 1990). Lipid concentration in orange roughy muscle is high: 3.9–10.4% (Hayashi and Takagi 1980, Grigor *et al.* 1983, Sargent *et al.* 1983, Vlieg and Body 1988, Phleger and Grigor 1990, Sigurgisladóttir and Pálmadóttir 1993, Bakes *et al.* 1995). The wax esters in muscles may be used as metabolic reserves, or aid in insulation (Bakes *et al.* 1995). A strong argument is made by Phleger (1998) that wax esters are primarily used by orange roughy in maintaining buoyancy: first, they are stored extracellularly where lipase activity is absent, and hence are unlikely to contribute as metabolic reserves; second, they have much greater positive buoyancy (0.165 g mℓ^{-1}) than triacylglycerols

(0.095 g mℓ^{-1}, Phleger 1998).

Many species of fish have large quantities of polyunsaturated fatty acids in the ω-3 fatty acid family, especially eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), which are thought to prevent coronary heart disease and other related diseases (Iacono and Dougherty 1993). However, orange roughy have the lowest recorded concentrations of EPA and DHA of any marine fish, just 2.3–3.3% (Sigurgisladóttir and Pálmadóttir 1993, Bakes *et al.* 1995), lower than any of the other 39 species in the two studies listed. Not only are EPA and DHA concentrations low in orange roughy, so are other polyunsaturated fatty acids: monounsaturated fatty acids constitute 82–94% of the fatty acids in orange roughy (Hayashi and Takagi 1980, Grigor *et al.* 1983, Sargent *et al.* 1983, Vlieg and Body 1988, Sigurgisladóttir and Pálmadóttir 1993, Bakes *et al.* 1995), compared to a mean of 31% (*SD* 11.8%) for 34 other species listed by Sigurgisladóttir and Pálmadóttir (1993).

The fatty acid and wax ester composition in orange roughy is thought to originate in their diet, which is varied but does include myctophids that are rich in wax esters (Grigor *et al.* 1990, Phleger 1998). Species like oreo dories, which are conspecific with orange roughy, feed on salps and have low levels of wax esters in their flesh (Clark *et al.* 1989). It is intriguing that the fish species with the most similar lipid composition to the orange roughy is the coelacanth *Latimeria chalumnae*, an unusual species in its own right. Not only does the coelacanth have a swimbladder invested with wax esters, but lipids constitute 30–71% (dry weight) of the muscles, and are deposited extracellularly (Nevenzel *et al.* 1966). In addition, coelacanths have an extremely low percentage of polyunsaturated fatty acids in the organ lipids (Nevenzel *et al.* 1966). Coelacanths live at depths of 100–300 m, and feed mainly on myctophids and squid (Thomson 1991), a diet similar to that of orange roughy.

Mercury concentration in orange roughy flesh is high, averaging 0.5 mg kg^{-1} on the Chatham Rise (Van den Broek and Tracey 1981) and 0.42 mg kg^{-1} in the North-East Atlantic (Cronin *et al.* 1996). In the latter study orange roughy had the highest mercury concentration of the six deep-sea fish species examined. Cronin *et al.* (1996) found that mercury concentration increased with age, an indication that orange roughy may be long-lived.

GENETICS AND STOCK STRUCTURE

Research on orange roughy stock structure has produced equivocal results. On the one hand, studies

Table I: Summary of stock structure results from different studies on orange roughy. Different stocks are represented by the same letter if that study found no difference between the stocks. Study types are loosely arranged from those that easily discriminate between stocks, to those that do not. Abbreviations for different areas are *New Zealand* — East Cape (EC), Bay of Plenty (BP), Ritchie Bank (RB), Wairarapa (Wa), Cook Canyon (CC), Kaikoura (Ka), Chatham Rise (CR), Waitaki (Wi), Puysegur Bank (Pu), West Coast (WC), Challenger Plateau (Ch), Lord Howe Rise (LH); *Australia* — Western Australia (We), Great Australian Bight (GA), South Australia (So), Western Tasmania (WT), Maatsuyker (Ma), Cascade Plateau (Ca), Eastern Tasmania (ET), St Helens (SH), New South Wales (NS); *Other* — South Africa (SA), Namibia (Na), west of the British Isles (BI).

Study	Method	New Zealand												Australia									Other		
		EC	BP	RB	Wa	CC	Ka	CR	Wi	Pu	WC	Ch	LH	We	GA	So	WT	Ma	Ca	ET	SH	NS	SA	Na	BI
Elliott *et al.* (1995)	Morphometrics													a	b	c	c	d	e	f	g	h			
Haddon and Willis (1995)	Morphometrics									a			b												e
CSIRO (1995)	Otolith chemistry													b	c	a	c			a		d			
Edmonds *et al.* (1991)	Otolith chemistry													a		b				b					
CSIRO (1995)	Otolith shape					b										a									
Lester *et al.* (1988)	Parasite analysis							a				c													
Ward and Elliott (1993)	Standard length													a	d	a	e	b	a	f	c	g			
Bell *et al.* (1992)	Fecundity, spawning time, length at maturity														bc				a			d			
Horn *et al.* (1998)	Length at maturity		a	a				a		a		c					a			a		b		b	d
Horn *et al.* (1998)	Age at maturity		a	a				c		a		b												b	d
Horn *et al.* (1998)	Mean radius to transition zone		a	a				c		a		c												b	d
Smith *et al.* (1997)	Random amplified polymorphic DNA			a				a	b	c															
Smith *et al.* (1996)	Mitochondrial DNA restrictions			a				a	b	b															
Elliott *et al.* (1994)	Mitochondrial DNA restrictions										a	a													b
Smolenski *et al.* (1993)	Mitochondrial DNA restrictions							a						a	a	a	a			a		a			b
Ovenden *et al.* (1989)	Mitochondrial DNA restrictions													a	a	a	a			b		b	a		
Baker *et al.* (1995)	Mitochondrial DNA cytochrome *b* sequencing							a		a		a	a	a	a	a	a						a		
Smith *et al.* (1997)	Mitochondrial DNA haplotypes		a	a			a	ab	b	a															
Smith *et al.* (1997)	Allozymes (11 loci)		a	a				a	b	c															
Smith and Benson (1997)	Allozymes (11 loci)	a	a	a	a		a	b																	
Elliott *et al.* (1994)	Allozymes (11 loci)											a		a	a	a		a	a	a	a	a			b
Ward and Elliott (1993)	Allozymes (11 loci)				a									a	a			a	a	a	a	a			
Elliott and Ward (1992)	Allozymes (11 loci)											a		a	a			a	a	a	a	a			b
Smith (1986)	Allozymes (12 loci)		a	a	a		a	a				a	a												
Baker *et al.* (1992)	DNA fingerprints							a																	a

that focused on environmental characteristics of the fish have generally found differences between stocks; on the other hand, some genetic studies have not found differences between even very widely separated regions (Table I). Based on these findings, the four Namibian aggregations are assumed to be separate stocks.

Environmental characteristics depend on the surroundings of the fish during its life. Studies on trace elements in otoliths (Edmonds *et al.* 1991, CSIRO 1995), otolith structure (CSIRO 1995), morphometric differences (Elliott *et al.* 1995, Haddon and Willis 1995) and parasite analysis (Lester *et al.* 1988) have found significant differences among virtually every stock examined (Table I). The length of adult orange roughy may also be significantly different from one aggregation to the other (Ward and Elliott 1993, Elliott *et al.* 1995, Huse *et al.* 1997, A. Rees, unpublished data cited by Branch 1998). The transition zone in orange roughy otoliths is thought to mark the onset of maturity (Francis and Horn 1997). The mean radius to the transition zone, as well as the lengths and ages at maturity obtained using this method, differ among New Zealand populations and they also differ from Namibian and Hatton Bank populations (Horn *et al.* 1998). Orange roughy off New South Wales have a different time of spawning, greater fecundity and a smaller length at maturity than other populations off Australia (Bell *et al.* 1992). All of these studies suggest that adult orange roughy are relatively sedentary, and that stocks are fairly discrete.

Genetic studies, which reveal inheritance patterns, have generally failed to discriminate between stocks (Table I). Restriction site analysis of mitochondrial DNA (mtDNA) has been used with the most success. For example, the technique has shown that the Waitaki and Puysegur Bank stocks are different from other New Zealand stocks (Smith *et al.* 1996), that New South Wales orange roughy form a different stock from other Australian orange roughy (Smolenski *et al.* 1993), and that orange roughy off the British Isles are distinct from those off Australia (Elliott *et al.* 1994). The technique has also been used to show that eastern Tasmania and western Tasmania orange roughy are different stocks (Ovenden *et al.* 1989). Other genetic methods have generally proved less successful: including direct sequencing of the mitochondrial cytochrome *b* gene (Baker *et al.* 1995), analysis of polymorphic allozymes (Smith 1986, Elliott and Ward 1992, Ward and Elliot 1993, Elliott *et al.* 1994) and examination of DNA fingerprints (Baker *et al.* 1992). One allozyme study could not even distinguish New Zealand orange roughy from those off South Africa (Smith 1986). However, later allozyme studies did find genetic differences. For in-

stance, Smith and Benson (1997) did distinguish between adjacent East Coast and Chatham Rise stocks and also revealed genetic heterogeneity within the Chatham Rise stock itself. A later genetic study (Smith *et al.* 1997) overturns the earlier patterns in the discriminatory power of different techniques, finding differences between most locations in New Zealand using allozymes and random amplified polymorphic DNA (RAPD) fragments, but fewer differences using mtDNA haplotypes.

A thought-provoking study on New Zealand orange roughy by Smith *et al.* (1991) reported a reduction in genetic diversity on the Chatham Rise, the Challenger Plateau and the East Coast between 1982 and 1988. The authors postulated that this may have been caused by greater mortality of larger fish, which might be more heterozygous. However, Ward and Elliott (1993) found no evidence for a link between mean length and levels of heterozygosity in Australian populations of orange roughy, and a later study (Smith and Benson 1997) found no significant decline in heterozygosity between 1982 and 1994 on the sites studied by Smith *et al.* (1991).

Of the genetic techniques used, mtDNA restriction-site analysis provides the best discriminatory power, and the results appear to echo the finding from environmental characteristics that stock differences may be present over distances of <500 km (Edmonds *et al.* 1991, Elliott *et al.* 1995). Genetic data may have poor discriminatory power because of the extreme longevity of orange roughy, which has two important consequences. First, genetic changes accumulate very slowly in long-lived species; second, the number of migrants per year need to be extremely small to allow genetic divergence. For example, Smith *et al.* (1996) estimated that the effective number of migrants could be less than two per generation between the northern and southern sites off New Zealand to allow the observed genetic separation between these regions.

TAGGING STUDIES?

Tagging is an obvious way of resolving the debates over both age and growth and stock structure in orange roughy. Unfortunately, no successful tagging has been reported to date, primarily because of the great depths at which orange roughy live. Orange roughy are not always killed by the ascent and have been kept alive for up to five days after capture (Gordon 1999, McClatchie *et al.* 1999), but it is difficult to return them alive to their preferred depths. Tagging has been attempted using break-away hooks on other deep-water species, including alfonsino *Beryx splendens*

(Grimes *et al.* 1983, Horn 1989), but this approach was deemed inappropriate for orange roughy because the species is not caught by longlining (CSIRO 1995, Hareide and Garnes 2001). IFREMER and Collège de France have pursued a variety of methods of marking (by tetracycline injection) and recapturing orange roughy (Gordon 1999), but only one method was successful: they used a submersible to net, inject and cage orange roughy, retrieving two live fish after one month. Results from electron microscope examination of those otoliths have not yet been published.

POTENTIAL TRAWL DAMAGE TO BENTHIC COMMUNITIES

The deep ocean contains the last untapped sources of fish in the oceans. Probert *et al.* (1997) examined the contents of trawls hauled over pristine orange roughy habitat, and inferred possible impacts on the benthic community. The largest benthic bycatch was of corals, and they suggested that such coral patches may take more than 100 years to recover from the effects of trawling. Clark (1999) examined the serial depletion of orange roughy on successive seamounts and questioned the sustainability of the species, especially given that the trawl gear may have long-lasting impacts on the habitat. McAllister and Kirchner (in press) use a Bayesian decision analysis to conclude that sharp declines off Namibia, on Rix and possibly also on Frankies, can be explained best by disturbance attributable to fishing pressure. Brandão and Butterworth (2000) also show that catch removals alone cannot explain the decrease in abundance off Namibia. There is additional evidence from orange roughy surveys on the Chatham Rise that trawling damages the habitat (Clark *et al.* 2000). There, fishing resulted in declines in the abundance of 10 out of 18 bycatch species, and an increase in only one species. These studies suggest that some portion of the suitable deep-water habitat in each fishing area needs to be set aside as a no-fishing zone because conservative catch rates may not be enough to prevent the overfishing of orange roughy stocks. New Zealand has already set aside a number of "no-fishing" seamounts.

CONCLUSIONS

Namibian orange roughy live shallower (600–800 m), are smaller and have a younger age at maturity (22 years) than other orange roughy stocks around the world. They might therefore be slightly more productive than other stocks. Management of Namibian orange roughy has benefited from worldwide research and lessons from other orange roughy fisheries. For instance, precautionary management included limiting the number of vessels to no more than five, assuming that productivity was low owing to the great longevity of the species, setting a target of 50% of pristine spawning biomass instead of the 30% used elsewhere, applying separate *TAC*s to each aggregation based on stock structure studies, and the early introduction of stock assessments and acoustic surveys. Despite these actions, biomass declined by 50–90% in six years, and *TAC*s were reduced from 12 000 to 1 875 tons in two years. In hindsight, the following improvements could have been made:

- The imposition of *TAC*s during the exploratory phase; despite limited effort, exploratory catches were higher than survey results would have allowed.
- Starting the acoustic series earlier than in the third year. However, availability of equipment and expertise and knowledge of the area of the aggregations precluded this from happening.
- Attaching greater importance to declines in commercial *cpue* in the early years of the fishery. Declining *cpue* (Branch and Roberts 1998a) was at odds with the high estimated biomass obtained from commercial swept-area data (Branch 1998), but *cpue* was not then believed to track changes in abundance reliably.

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