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Fecundity and maturity of orange roughy (*Hoplostethus atlanticus* Collett 1889) on the Porcupine Bank, Northeast Atlantic

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Synopsis The first, comprehensive analysis of the fecundity and reproductive maturity of orange roughy, *Hoplostethus atlanticus*, from a specific area in the Northeast Atlantic is reported. Specimens were collected from aboard vessels, targeting this species on the Porcupine Bank (ICES subarea VII), in waters of between 1400 m and 1,650 m depth. Between September and December 2002, a non-random, stratified, sampling protocol was implemented by on board fisheries biologists to collect mature female fish between 300 mm and 540 mm SL. Ovaries from 65 individuals, representing the majority of 10 mm SL size classes, formed the analytical sample. A novel, digital method of oocyte counting was developed, allowing digital images of oocytes to be annotated, counted and stored. Total fecundity ranged between 20,352 and 244,578 oocytes per female and mean total fecundity was estimated to be 97,368 oocytes per female (SD = 48,322). Relative fecundity was estimated to be 33,376 oocytes per kg (SD = 11,407). Fecundity was shown not to decrease with age. Macroscopic analyses showed that 50% of females were not mature until they reached 27.5 years and 37 cm SL. Comparison with stocks from the southern hemisphere indicate that orange roughy from the Northeast Atlantic mature at a larger size and generally have a higher mean fecundity than those found in the southern hemisphere. This may reflect differences in growth rates influenced by environmental variables and fishing pressure.

Keywords Trachichthyidae · Digital oocyte counting · Comparative deepwater productivity · Life history

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Introduction

Orange roughy, *Hoplostethus atlanticus*, is a benthopelagic species found at depths of between 450 m and 1,800 m in the Northeast Atlantic. The species is distributed between 35° and 65° N, summarised in Branch (2001), and has recently been subject to a sporadic, large-scale fishery, across its distribution. An Irish fishery for the species began off the west coast of Ireland in 2000, in an area that had previously

been exploited by the French fleet since 1992 (Gordon 2001). Fishing effort was initially concentrated to the Northwest of Ireland (ICES area VI), but populations of orange roughy in this region underwent severe depletion in subsequent years. Reported landings fell from 3,502 tonnes during 1991 to 138 tonnes during 2000, resulting in the translocation of fishing effort into the adjacent, ICES area VII.[1] The fishery for orange roughy is currently restricted by European legislation to a small number of topographic features on the continental slope along the Porcupine Bank (50°–54° N, 9° W) and in areas to the North bordering the Rockall trough.

Little is known of the basic biology of orange roughy in the Northeast Atlantic. Stock assessments are precautionary as a result and generally lack sufficient detail to allow the provision of confident stock management advice. Although it has been reported that spawning occurs during a brief period between the end of January and the middle of March,[2] (Du Buit 1995), the fecundity of the species within a discrete locality cannot be confirmed.

Based on the landings of orange roughy from commercial vessels fishing in an area, south of the sampling area of the current study, the total fecundity ranged between 70,000 and 385,000 oocytes (Du Buit 1995) and 50,000 and 380,000 oocytes.[2] Given that fecundity is known to vary between spatially distributed orange roughy populations, and that variation in the fecundity of such a long lived fish species may have a significant effect on stock dynamics and recovery, there is a general recognition of the need for area-specific data collection and fishery-wide data collation (Clark et al. 1994). In additon to the caveats, which must be placed on those data previously reported, no comprehensive analysis of fecundity and maturity relating length, weight and age, is available for this species, in the Northeast Atlantic.

[1] Anon 2002. Report of the working group on the biology and assessment of deep-sea fisheries resources. ICES document: CM 2002/ACFM:16.

[2] Berrehar C, Du Buit MH, Lorance P (1998). Orange roughy fishery in the Northeast Atlantic. ICES CM 1998/O:73 (poster).

Estimates of the fecundity of orange roughy are available from other areas, and in the Southwest Pacific are reported to be low in comparison to most commercial fish species taken on the continental shelf (Koslow et al. 1995). The mean fecundity of the species, from these areas, has been documented as ranging between 31,056 and 42,809 (Australia) and 36,000 101,440 oocytes (New Zealand) (Clark et al. 1994).

Given the rapid expansion of the fishery, knowledge of the basic biological parameters and how they differ between disparate regions is essential for contributing to stock assessment and stock stability analysis over time.

Materials and methods

Fecundity analysis

Ovary samples were obtained between August and December 2002, aboard commercial fishing boats targeting orange roughy from the continental slope of the Porcupine Bank (Fig. 1).

A non-random sampling protocol, designed to collect ovaries from five, mature females, in each 1 cm size class, over the standard length range of the population (approximately 30–55 cm SL), was implemented, at sea, by onboard fisheries biologists. All gonads sampled were in a maturing stage of development, and contained fully vitellogenic oocytes (Stage III of Pankhurst et al. 1987). Although the majority of predetermined size classes contained the target number of individuals, an under-representation of fish in the smaller and larger size classes was observed. Over the sampling period, a total of 68 pairs of ovaries were collected and stored on ice prior to processing ashore. Details of fish length (mm SL), weight (g), and catch position were recorded and otoliths removed for ageing.

Ovaries were removed and preserved in an aqueous solution of 5% formaldehyde (see Cailliet et al. 1986). Oocyte aggregation and clumping, commonly associated with this method in other species, were not observed.

The gravimetric method described by Bagenal and Braum (1978) was used to determine fecundity

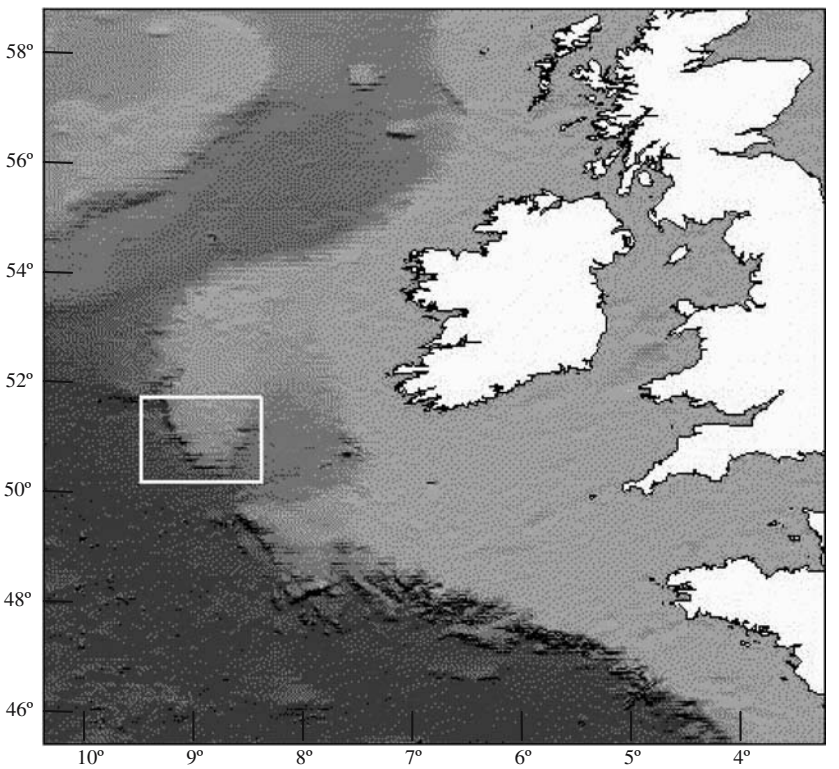

Fig. 1 Location of the Porcupine Bank sampling area (white box) for female orange roughy (*Hoplostethus atlanticus*), sampled during the fecundity analysis between August, and September 2002

(defined as the number of ripening oocytes in the female ovary prior to the next spawning event). All oocytes were scraped from both ovaries and washed and dried over a Buchner funnel using muslin cloth as a filter. The oocytes were then transferred into a 12 cm × 10 cm × 3 cm (length, weight and depth respectively) chamber of numbered gridsquares. The oocyte mass was then weighed, covered and refrigerated to prevent evaporation and weight change prior to further processing. Grid reference numbers were used to obtain random subsamples from the chamber. Subsamples were selected using a random numbers table to generate grid square locations and removed using a 1 cm × 1 cm glass cuvet pressed into the oocytes.

To determine the appropriate number of subsamples from each pair of ovaries to ensure a coefficient of variation of less than 5% (CV = SD/mean), a range of oocyte subsamples were removed and counted. Four subsamples of 1–2 g provided an approximate CV of 5%, similar to that reported (Koslow et al. 1995).

Oocyte sub-samples were placed into designed 25 mm × 25 mm × 2 mm counting chambers constructed of acryllic board of 2 mm thickness, glued onto glass microscope slides (8.5 cm × 2.5 cm). The volume of oocytes loaded into the chamber was carefully monitored to ensure that a single layer of oocytes was dispersed over the chamber bottom. The remaining volume of the chamber was filled with water to allow the oocytes to disperse and the chamber was then sealed with another microscope slide.

A digital image of the oocyte monolayer was captured for each of the 25 mm chambers. Maturing vitellogenic oocytes with a diameter of approximately 1.1 mm and above were recorded (Koslow et al. 1995). A novel, low-tech counting programme was developed to circumvent the tedium of microscope counting and the difficulties and expense associated with fully automated counting programmes (Murua et al. 2003). The programme, called ''Particle Counter'', was written in Visual Basic© (source code is available from the corresponding author). The counter decides

upon each oocyte being counted in the digital images of the counting chambers. Once the counter has clicked on each oocyte to be counted, the total count is then automatically exported to flat ASCII files for subsequent analyses.

The total fecundity of each female was estimated by

$$F_{xy} = \left(\frac{\mathrm{EW}_x}{\mathrm{SW}_{xy}}\right) * N_{xy} \quad (1)$$

where F_{xy} is the fecundity of oocyte mass x, subsample y; EW_x is the weight of the total oocyte mass x; SW_{xy} is the weight of oocyte mass x, subsample y, and N_{xy} the number of oocytes counted in oocyte mass x, subsample y (adapted from Gundersen et al. 1999). Relative fecundity was estimated by dividing the total fecundity of each fish by the weight of the fish in kilograms. As the ovaries were preserved in a 5% solution of formaldehyde for differing periods of time prior to sampling, exact oocyte diameters were not measured, as accurate and comparable measurements were not possible due to volume changes.

Of the 68 fish collected, 65 estimates of total fecundity were obtained. Three samples were rejected due to damage or other circumstances during preparation. Generalised linear models (GLM) were used to establish the relationships between fecundity and: length, weight, and age. The variance was non-constant so a ''gamma'' error distribution was used. A log link was used for the relationships between fecundity and length and weight. This is the equivalent of fitting a power curve aX^b (Bagenal and Braum 1978). For comparison with analyses from other populations, linear relationships were also established between the natural logarithm of fecundity and standard length (mm) and weight (g).

The relationship between fecundity and age has been hypothesised to decrease at older ages (Koslow et al. 1995). To test for senescence, two biologically reasonable models were fit to the data; one that does not allow and one that does allow for decreased fecundity with age. By comparing the goodness of fit using the Akaike Information Criteria (AIC) from both these models, it is possible to elucidate the presence and significance of reproductive senescence. The first is a classic asymptotic Michaelis–Mentin saturation curve (Beverton–Holt curve)

$$\mathrm{TF} = \frac{A}{\beta_1 + \beta_2 A} + \varepsilon \quad (2)$$

where TF is total fecundity, A is the age, β_1 and β_2 are the parameters to be estimated, and ε is a gamma-distributed error term. Given that fecundity does not begin until after maturity, we cannot assume a zero x-axis intercept. To accommodate this, Eq. (3) was re-formulated as

$$\mathrm{TF} = \frac{(A - \beta_0)}{\beta_1 + \beta_2 (A - \beta_0)} + \varepsilon \quad (3)$$

where β_0 is distance along the x-axis to where fecundity begins.

To allow for a decrease in fecundity at older ages, a more flexible form of the Michaelis–Mentin, an inverse quadratic (Nelder 1966) was used

$$\mathrm{TF} = \frac{(A - \beta_0)}{\beta_1 + \beta_2 (A - \beta_0) + \beta_3 (A - \beta_0)^2} + \varepsilon \quad (4)$$

where β_3 is a coefficient of decrease to be estimated. This approach does not have the symmetrical constraint of an ordinary quadratic (Nelder 1966) making it very useful for separating the two processes of increasing and decreasing fecundity with age. An ordinary quadratic regression was also fit for comparative purposes.

Ageing

A total of fifty otoliths from gravid females were aged by the Central Ageing Facility (CAF) at Queenscliff, Victoria, Australia. Otoliths were sectioned longitudinally and annuli counted from the primordium to the posterior edge. Eighteen otolith pairs broken during removal, transport or reading were rendered unsuitable for ageing and were removed from subsequent analysis.

Length and age at maturity

Two hundred and sixty two female fish were macroscopically staged at sea and considered to be mature if the gonads had reached maturity stage III or above (Pankhurst et al. 1987). Maturity ogives were constructed using logistic regression. All data analyses were performed using the R (2.0.1) open-source statistical software[3]

Results

The standard length and total weight of the 65 fish, sampled for fecundity, ranged between 362 and 544 mm and 1,387 and 5,206 g, respectively. Total fecundity ranged between 20,352 and 244,578 oocytes per female (mean 97,368, SD 48,322) and relative fecundity ranged between 9,701 and 64,493 oocytes per kg (mean 31,255, SD 11,407).

The results of the fecundity relationships are summarised in Table 1. Significant, yet highly variable, relationships exist between fecundity and length (Fig. 1) and weight (Fig. 2). Weight was the single best predictor of fecundity, explaining 40% of the variance. Significant linear relationships ($p \leq 0.001$) exist between log transformed fecundity (TF) and the variables standard length (mm) (SL) and total weight (g) (TW).

A significant saturation relationship was established between fecundity and age (Table 1). Using an inverse quadratic to allow for senescence (Eq. 3) proved non-significant, based on the goodness of fit AIC values.

Length and age at maturity

Length and age at maturity were determined as 378 mm SL (SE = 7.51 mm) and 27.54 years (SE = 1.46 years) (Figs. 3, 4), respectively.

Discussion

Orange roughy are known to be group synchronous spawners, spawning from January to February in the Northeast Atlantic (Du Buit 1995). Ovaries for the present study were obtained between August and October 2002 and were typical of early to mid-term gonadal development (Stage III of Pankhurst et al. 1987). All oocytes counted were fully vitellogenic. No hyaline oocytes, indicative of a recent spawning event, were present in the ovaries providing evidence that spawning had not yet occurred. As the fecundity of *H. atlanticus* is known to decline between two and four thousand oocytes per female, directly prior to spawning, it is generally recommended that ovaries are sampled prior to known or predicted periods of spawning[4] (Clark et al. 1994; Koslow et al. 1995). Sampling constrictions did not allow for sampling directly prior to spawning in the present study and no correction for atresia has been made.

Variability in fecundity

It is of note that none of the outlying points for the fecundity relationships could be attributed to processing error. The wide variability of fecundity with length and weight is consistent with some observations made on the species off New Zealand (Clark et al. 1994) although others reported less variability (Pankhurst and Conroy 1987). It has been proposed that the underlying age structure of the sampled fish could be the cause of the variability of fecundity with length (Clark et al. 1994). The hypothesis being that fish of the same length may differ widely in age. On the Porcupine Bank, fecundity was related to length, weight and age. The variability in these data is still prevalent when fecundity is related to age (Fig. 4) and was not of sufficient significance to explain the variability present when fecundity

[3] R Development Core Team (2004). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

[4] Bell JD (1989) Reproductive cycle and fecundity of orange roughy, *Hoplostethus atlanticus*, in south eastern Australia. Unpublished report of the fisheries institute, New South Wales Department of Agriculture.

Table 1 A summary of the relationships between total fecundity (TF) and maturity (fraction mature, *M*), and: length (SL in mm), total weight TW in (g) and age A_1 (for ages ≥ 18) and age A_2 (for ages ≥ 16) in years, for female orange roughy (*Hoplostethus atlanticus*), sampled on the Porcupine Bank between August and December 2002

Relationship	Predictor	*n*	Equation	AIC	PEV	*p*
Fecundity	Standard length	65	$TF = 9.83e{-}05\ SL^{3.375}$	1566.8	0.303	< 0.001
Fecundity	Standard length	65	$\ln(TF) = 3.52\ln(SL) - 10.229$	82.1	0.372	< 0.001
Fecundity	Weight	65	$TF = 8.220\ TW^{1.167}$	1559.3	0.372	< 0.001
Fecundity	Weight	65	$\ln(TF) = 1.38\ln(TW) + 0.38$	75.07	0.404	< 0.001
Fecundity	Age	50	$TF = (A_1{-}18)/(6.103e{-}06(A_1{-}18) + 5.913e{-}05)$	1143.4	0.399	< 0.001
Fecundity	Age	50	$TF = (A_2{-}16)/(2.85e{-}06(A_2{-}16) + 2.346e{-}08(A_2{-}16)^2 + 2.568e{-}04)$	1144.9	0.410	< 0.001
Fecundity	Age	50	$TF = 2464.196A - 10.235A - 14395$	1156.2	0.418	< 0.001
Maturity	Standard length	244	$M = 1/(1 + \exp(-(3.72e{-}02SL - 14.092)))$	90.7	0.720	< 0.001
Maturity	Age	244	$M = 1/(1 + \exp(-(2.18e{-}01A - 6.008)))$	78.8	0.759	< 0.001

Note: PEV is the proportion of explained variance and is equivalent to an r^2 value; AIC is the Akaike Information Criteria

was related to length. It is probable, therefore, that there are other causes for the variability of fecundity observed.

There are two possible explanations for the wide variability of fecundity in *H. atlanticus*; resource availability and individual reproductive success, both of which relate to the productivity of the deepwater habitat.

The continental slopes inhabited by *H. atlanticus* are dynamic regions with disparate production (Merret and Haedrich 1997). Homogenous production could be expected to produce species evolved with lower variability in fecundity, as observed in Greenland halibut (data from Gundersen et al. 1999). Equally, heterogeneous habitat productivity should produce species with high variability in fecundity.

Differences in food intake by individuals or contained populations resident over flat, undulating or seamount feeding areas, may affect oocyte numbers as a result of competition for resources and the frequency of food availability. Resources sufficient to exceed the metabolic threshold of daily energy requirements are necessary to deposit vitellogenic precursors within the liver and swim bladder, which directly influence the number of oocytes present within the ovary (Kjesbu et al. 1991). This exerts direct environmental control on the number of additional oocytes entering the layer of cells

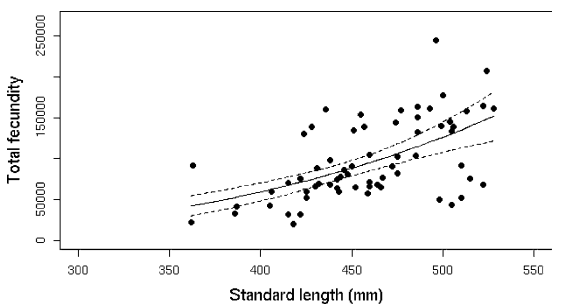

Fig. 2 The relationship between total fecundity and standard length (mm) in female orange roughy (*Hoplostethus atlanticus*), sampled on the Porcupine Bank between August and December 2002, $N = 65$. The dashed lines show the 95% confidence intervals around the mean response

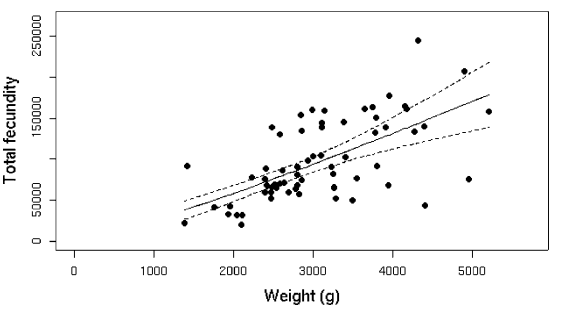

Fig. 3 The relationship between total fecundity and total weight (g) in female orange roughy (*Hoplostethus atlanticus*), sampled on the Porcupine Bank between August and December 2002, $N = 65$. The dashed lines show the 95% confidence intervals around the mean response

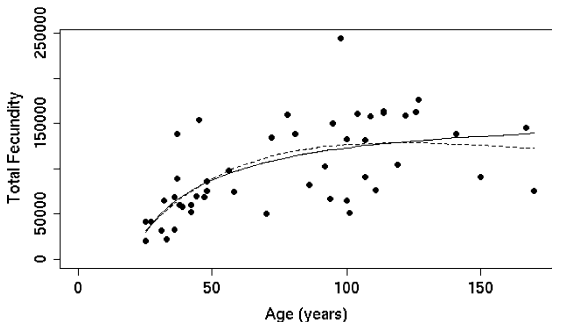

Fig. 4 The relationship between mean total fecundity and age (years) in female orange roughy (*Hoplostethus atlanticus*), sampled on the Porcupine Bank between August and September 2002, $N = 50$. The solid line is an asymptotic Michaelis–Mentin curve; the dashed line is a flexible inverse quadratic form of the Michaelis–Mentin

next to the epithelial lining of the ovary. Extra production and food availability could result in increased fecundity during this phase (Kjesbu et al. 1991). Fish from different production regimes would, therefore, be expected to have variable fecundity.

The fish sampled during the present study came from a number of different aggregations within a defined area off the Porcupine Bank. The variability in fecundity observed, suggests that fish may have travelled large distances to reach seamounts or sites of aggregation (Coburn and Doonan 1994; Francis and Clark 1998) and originated in areas characterised by widely disparate production regimes.

Interannual variability in production regimes may influence the spawning success of individuals by supporting a continuum of reproductive stragegies within the spawning population. The inherent investment of resources by individuals in their oocytes, dictates the size and number of oocytes produced, which thereafter affects the subsequent rate of juvenile survival. Individual fitness, when affected by environmental variability, has been shown to be of particular importance in determining fecundity in salmonids (Smoker et al. 2000).

Fecundity–age relationship

The relationship between fecundity and age has previously been modelled using a quadratic term in a linear regression (Koslow et al. 1995). This approach suffers from the confusion of the initial process of fecundity increase and the hypothesised decrease in older ages. There is no biological reason why the decrease should be the same as the increase. This is the only possibility when using an ordinary quadratic. A more natural approach would be to fit an inverse quadratic (Nelder 1966). An inverse quadratic is not symmetric and can capture the two separate processes of the initial fecundity increase with age and subsequent decrease at older ages. A one variable inverse polynomial (Eq. 2) is a Michaelis–Mentin saturation curve, which can be made to accommodate a possible decrease, by adding a quadratic term. The hypothesis of senescence is then readily testable using the AIC values.

Using this approach, a significant decrease in fecundity was not witnessed at older ages. Although it must be noted that the there are relatively few data points in this region and that the AIC values for both models are just marginally different. Further sampling of older fish might reveal a significant decrease of fecundity with age. Conversely to this analysis, fitting an ordinary quadratic in a multiple linear regression, established a significant quadratic relationship. The quadratic term showed fecundity declining with age ($t = -2.6$, 47 degrees of freedom, $p \leq 0.01$). The maximum fecundity, found by differentiating the relationship with respect to fecundity, was found to be at approximately 122 years.

Population comparisons

From a mixed, shore sample of the species, caught between 48° and 51° N, DuBuit (1995) estimated the total fecundity of orange roughy in the Northeast Atlantic to range between 70,000 and 380,000 oocytes per female. Although these fish showed a larger range of fecundity than fish from known locations on the Porcupine Bank (this study), direct comparison is impossible due to the lack of geographical information associated with these data. When considered with data from other fisheries, the evidence suggests that either; the fish sampled by DuBuit may have come from a distinct or relatively unexploited stock, or that the fecundity of orange roughy in the general

geographic area has declined over the period between the two studies (1995–2002). As the fecundity of orange roughy is known to vary between areas (Clark et al. 1994; Koslow et al. 1995) the lack of qualifying data, in this instance, emphasises the importance of spatially resolved data when interpreting life history traits of long lived organisms from dynamic and environmentally sensitive habitats.

Reproductive parameters of orange roughy from the Northeast Atlantic differ from those found elsewhere. The mean fecundity of *H. atlanticus* on the Porcupine seabight is generally higher than that reported from other fisheries for the species (Table 2). The exception to this generalisation, are fish from the Puysegur Bank, located to the southwest of the South Island of New Zealand, which have a mean fecundity of 101,440 oocytes per female (Clark et al. 1994). This population is in itself unusual, as its fecundity is over twice that of other orange roughy populations, which form New Zealand's commercial fishery for the species.

In the Northeast Atlantic (Porcupine Bank), the scaling exponent in the relationship between the length and fecundity of female orange roughy is estimated as 3.75. With the exception of the Puysegur population, where the scaling exponent has been calculated to be 5.01, this is generally greater than the exponent values of between 2.38 and 3.01 for the majority of the *H. Atlanticus* populations in New Zealand. The scale of the exponent for fish from the Porcupine Bank implies that there is a greater relative increase in the fecundity of large females from this area, than in females from typical New Zealand fisheries.

A plausible explanation for the relatively high fecundity of females from the Northeast Atlantic relates to body size. Similarly sized fish from the Porcupine Bank, Chatham Rise and East Tasman Rise have comparable fecundities. Estimates of the total fecundity of a mature female of 40 cm (SL) from these fisheries, of variable productivity, are 52,000, 65,000 and 42,000 oocytes, respectively. For these same size fish, fecundity estimates are comparable, although the overall population mean fecundity is higher on the Porcupine Bank (97,360) than on the Chatham Rise (53,660) and the East Tasman Rise (31,085) due to the presence of larger females (Table 2).

As fecundity, after the onset of maturity, is a function of size (Stearns 1992), it is therefore expected that mean population fecundity should be highest in populations where individuals are typically late maturing and of a large size at maturity. This represents a life history strategy balancing the costs and benefits of the age and size at maturation. For orange roughy in the Northeast Atlantic, the most successful and persistant strategy is to delay the onset of maturity and by so doing achieve a lifetime fecundity, which is maximised due to the large size and high reproductive output of individuals within the spawning population. This strategy assumes a relatively low natural mortality and, or, a low level of habitat productivity.

Table 2 A summary of the fecundity and length and age at maturity of *H. atlanticus* from three major fisheries, where data are available the fisheries are broken down into individual areas sampled

Area	Length range SL (cm)	Mean fecundity (female^{-1})	Mean relative fecundity (oocytes/kg)	Length at L_{50} maturity (cm)	Age at maturity (years)
NE Atlantic					
Porcupine Bank	36–51	97,368	33,376	38	27.5
Australia[a]					
Eastern Tasmania	32–45	31,085	31,085	32	25
New South Wales	27–42	42,787	42,787	28	
South Australia	32–45	35,339	35,339		
New Zealand[b]					
Challenger Plateau	25–40	36,790	27,270	26	
Cook Canyon	25–42	44,290	27,180	29	
Chatham Rise	30–42	53,660	31,480	32	29[c]
Puysegur Bank	30–45	101,440	49,530	30	
Ritchie Banks	30–40	44,010	28,550	32	

Sources:
[a]Koslow et al. (1995),
[b]Clark et al. (2000),
[c]Francis and Horn (1997).

Higher fecundity is suggested to be a secondary result of habitat productivity acting on growth rate. If the production regime is lower in the Northeast Atlantic than that of the Southwest Pacific and the age at maturity is inversely related to both growth rate and mortality (Roff 1984; Stearns and Crandall 1984; Stearns and Koella 1986, Stearns 1992), fish would be expected to have a slower growth rate (Minto and Nolan unpublished data) and would reach maturity at an older age and larger size (Stearns 1992; Smith and Skúlason 1996). Fish of similar size distribution to those in the Northeast Atlantic have also been reported from the Northwest Atlantic (Kulka et al. 2003) and in the recent fishery for the species in the Indian Ocean, where the age at maturity and growth rate also indicate low productivity[5]

Relative fecundity

The mean, relative fecundity for the orange roughy population on the Porcupine Bank ranged between 9,701 and 64,493 oocytes kg^{-1} (Mean 31,255; SD 11,407 oocytes kg^{-1}) and is similar to data reported from the orange roughy fisheries of New Zealand and Australia (Table 1). Berrehar et al.[2] estimated the mean relative fecundity for orange roughy sampled off the Hatton Bank, a discrete area north of the Porcupine Bank and separated from it by the Rockall trough and Rockall-Hatton Basin, to be 48 530 oocytes kg^{-1} (n = 45).[5] Although this figure is higher than the mean relative fecundity of fish from the Porcupine Bank, it is within the range of relative fecundities recorded. The higher mean relative fecundity may also be due to the exceptionally large size of fish present on the Hatton Bank (Horn et al. 1998) (Figs. 5 and 6).

Density dependence

Density dependence is widely regarded as the mechanism regulating population abundance in ''K-selected'' species (Fowler 1981). The form of K-selected density dependence, the relationship between population growth rate and population density, is predicted to be convex (Silby and Hone 2002). Any release from density dependent population regulation in orange roughy, such as a reduction in population density by commercial fishing, would be confounded by low fecundity and exaggerated response times (Koslow et al. 2000). As we do not have recruit to spawner data for the species, we are also unaware of at what stage density dependence occurs. This would require extensive sampling of the juvenile stages, of which there is very little known information.

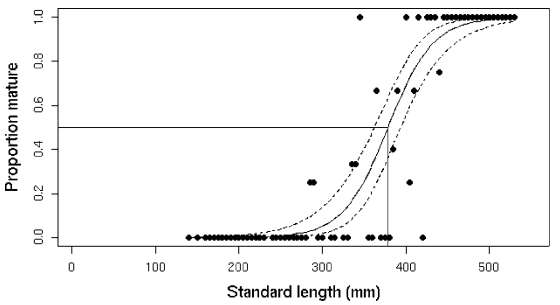

Fig. 5 Length based maturity ogive for female orange roughy (*Hoplostethus atlanticus*), sampled on the Porcupine Bank between August and December 2002, N = 244. L50 = 378 mm. Dashed lines represent the 95% confidence intervals

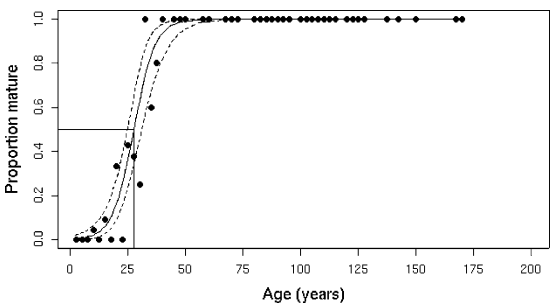

Fig. 6 Age based maturity ogive for female orange roughy (*Hoplostethus atlanticus*), sampled on the Porcupine Bank between August and December 2002, N = 244. A50 = 27.54 years. Dashed lines represent the 95% confidence intervals

[5] Anon 2001. FAO Report of the ad hoc meeting on management of deepwater fisheries resources of the southern Indian Ocean: Swakopmund, Namibia, 30 May–1 June 2001—ISSN 0429-9337.

Comparisons with co-habitants

The relatively low fecundity of orange roughy has been attributed to greater energetic input into individual oocytes, rather than the production of greater numbers of oocytes in a K selective manner (Koslow et al. 1995). In comparison to co-habitants of the Northeast Atlantic, *H. atlanticus* have a relatively low fecundity (Table 3) equivalent to that reported from other deep-water species with similar life histories, e.g. the deepwater oreos; smooth oreo, *Pseudocyttus maculates*, and black oreo, *Allocyttus niger* (Conroy and Pankhurst 1989).

Length and age at maturity

Differences in life-history chronology between populations of orange roughy are also evident when the relationship between length and age at maturity is examined. Given that Northeast Atlantic fish generally mature at a greater size and age than those from New Zealand and Australia, it is notable that the growth rate of New Zealand fish ($K = 0.06$) is greater than that of fish from the Northeast Atlantic (~0.05, Minto and Nolan unpublished data). Faster growth rates and larger standing biomass of the New Zealand populations, in particular, sustain the hypothesis that these waters have higher productivity than those of the Northeast Atlantic.

Table 3 A summary of fecundity ranges for deep-water orders in the Northeast Atlantic (Adapted from Merret and Haedrich 1997)

Order	Approximate maximum fecundity range (number of oocytes)
Gadiforms	1024–33,554,432
Anguilliformes & Notacanthiformes	256–1048,576
Aulopiformes	16–32,768
Ophidiiformes & perciformes	4–65,536
Miscellaneous	32–1048,576

Conclusion

Fecundity and maturity are essential life-history parameters to consider when assessing reproductive potential (Murua et al. 2003). Both are directly influenced by the environment, are reflected in subsequent recruitment, and can influence the ability of a stock to sustain commercial exploitation.

Given the accentuated life history patterns of orange roughy on the Porcupine Bank, it seems essential that all fishing be monitored and a precautionary approach adopted. Ongoing fisheries in the Southwest Pacific are sustained by a large biomass, lower age at maturity and greater environmental productivity. Although few life-history changes have occurred in the New Zealand populations of *H. atlanticus* (Clark et al. 2000), it is of particular note to emphasise that, to date, most recruits to this fishery are the product of spawning events which occurred prior to the exploitation of these stocks. Given that the time taken for fish to mature is greater than the current age of the fishery, the effects of the earliest exploitation should only begin to be seen over the next few years (The onset of maturity of female orange roughy occurs between 23.4 and 29.2 years in New Zealand, and the domestic fishery began in earnest in 1979 (Branch 2001)).

H. atlanticus exemplifies delayed life-history chronology in marine teleost fishes. Concern for the species and fishery in the northeast Atlantic is based on the low potential of the stock to recover from the removal of mature fish. Large size and late age at maturity contributes to the vulnerability of this population and makes the species particularly suceptable to increased mortality, such as that exerted by commercial exploitation. The lag phase between exploitation and the realisation of its effects is likely to exceed that of other commercial shelf fisheries for orange roughy and may be compounded by the disturbance of nursery areas and feeding grounds by a composite of environmental, ecological and commercial effects.

It is, therefore, essential that an appropriately weighted and conservative approach be adopted to the management of orange roughy on Porcupine Bank. It is also paramount and essential in

the long term that morphometric, meristic and genetic data be quickly gathered and disseminated on the specific populations, upon which assessments are made, in order to track changes, which will affect the stability of the population over time.

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