A LIFE HISTORY APPROACH TO THE ASSESSMENT OF DEEPWATER FISHERIES IN THE NORTHEAST ATLANTIC
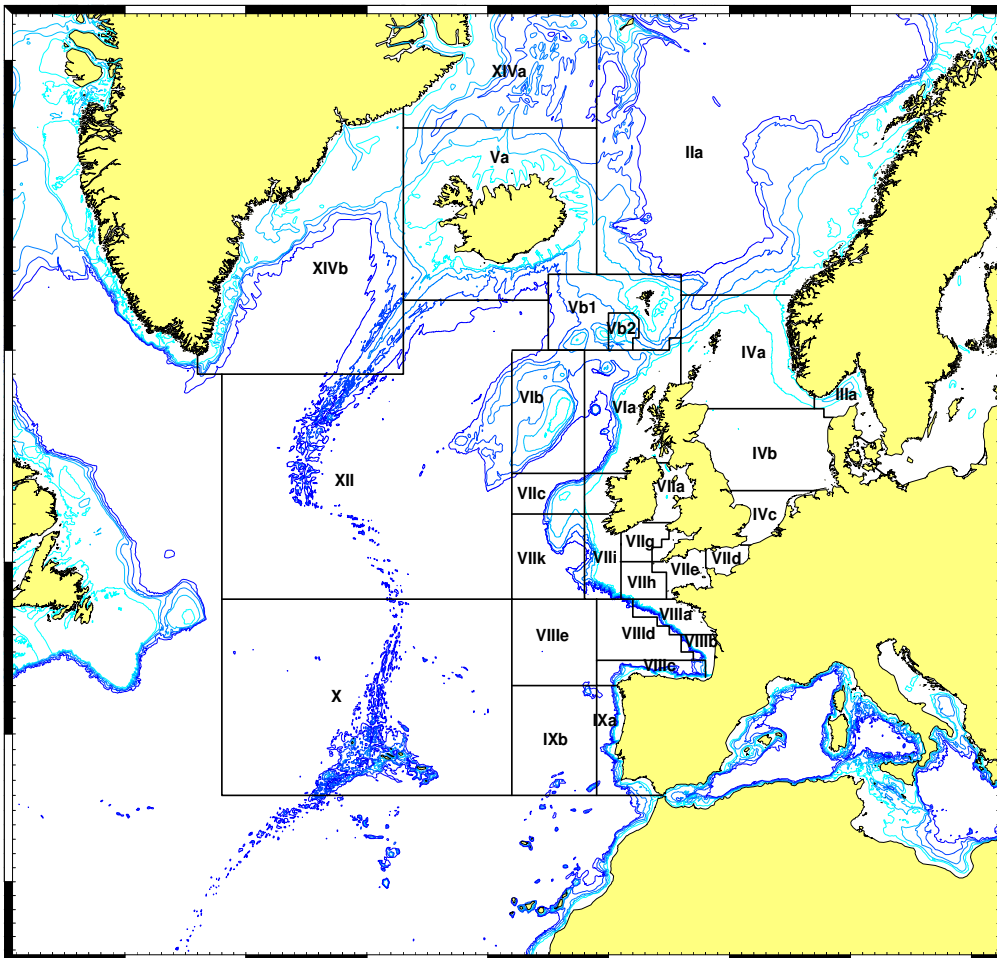
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1. INTRODUCTION

It has been generally stated that deepwater fishes cannot sustain high levels of exploitation because of their characteristic slow growth, longevity and low reproductive output. However deepwater fish species display a wide variety of life-history strategies, occupying diverse positions along the *K-r* continuum. Many teleosts display intermediate or conservative life-history characteristics, but the squalid sharks are more stringent *K*-strategists. Data were used in life-history analyses to assess the sustainability of these mixed-species deepwater fisheries. While there may be scope for compensatory changes in fecundity such scope is likely to be limited, especially for sharks.

The International Council for Exploration of the Sea (ICES) defines deepwater fisheries as those in waters deeper than 400–500 m. Such fisheries have developed rapidly in recent years in ICES Sub-divisions VI and VII (Figure 1).   This rapid expansion is due to the decline (or indeed collapse) of

Figure 1
Map of ICES Sub-areas and divisions, NE Atlantic

many traditional stocks. Some of these deepwater fisheries are long established, for example the Norwegian longline fishery for ling (*Molva molva*) and tusk (*Brosme brosme*) (Connolly, Kelly and Clarke 1999) while others are by now well established, for example the pelagic trawl fisheries for blue whiting (*Micromesistius poutassou*) and greater argentine (*Argentina silus*) (Gordon 2001). Others have developed in the last 10 years but are now quite advanced, such as the French mixed-species trawl fishery (Charuau, Du Pouy and Lorance 1995) and the Spanish deepwater longline fisheries for sharks, forkbeard (*Phycis blennoides*) and mora (*Mora moro*) (Pineiro *et al*. 2001). In most recent years further expansion of fishing to grounds such as Hatton Bank for Greenland halibut (*Reinhardtius hippoglossoides*), blue ling (*Molva dypterygia*) and sharks (Langedal and Hareide 2000, Pineiro *et al*. 2001) have taken place, and a new fishery for orange roughy west of Ireland has developed in most recent years.

Despite the established nature of many Northeast Atlantic deepwater fisheries, data for routine stock assessments are sparse and the lack of adequate, up-to-date information has prevented stock assessments being carried out in ICES since 2000 (Anon. 2002). Most deepwater fisheries in this area are mixed-species fisheries and this leads to problems in assessment and management. Though most deepwater species conform to the general K-selected life history mode, there is considerable variation within these mixed species assemblages in terms of vulnerability to overexploitation (Clarke *et al*. 2003). Dulvy *et al*. (2000) highlighted the dangers of exploiting a mixed-species assemblage; the local extirpation of the most vulnerable species may proceed unnoticed as happened in the case of common skate (*Dipturus batis*) in the Irish Sea. Various authors have used basic life history information as a tool in assessing the resilience of species to exploitation (Brander 1981, Jennings, Reynolds and Mills 1998). The ICES Advisory Committee on Fisheries Management took a simple approach and ranked deepwater species in the NE Atlantic according to a range of life history variables and used this to illustrate the differing risks associated with stock depletion in these species. A more complicated approach was taken by Smith, Au and Show (1998) who calculated "intrinsic rebound potentials" for 26 shark species, incorporating density dependence terms in their analyses. These authors point out that even simple life history data are difficult to collect, so the maximum benefit should be obtained from them.

Most deepwater fisheries developed recently. But already there is strong evidence from around the world that such fisheries may not be sustainable. It is unclear whether roundnose grenadier (*Coryphaenoides rupestris*) in the Northwest Atlantic will ever recover (Atkinson 1995) and there is evidence that many stocks of orange roughy (*Hoplostethus atlanticus*) in New Zealand have followed a similar fate (Clark 2001). It is clear that assembling data needed for conventional management will take a long time, in fact often longer than a deepwater fishery might be expected to last (Haedrich, Merrett and O'Dea. 2001). Management should ideally be based on population dynamics, including fisheries-dependent and fisheries-independent data, for example catch numbers at age and abundance and biomass indices collected on an annual basis. Yet for deepwater species this sort of information is mostly lacking. While great efforts have been taken to collect and refine time-series of catch and effort data, this process is only slowly allowing for assessments to be carried out. For deepwater stocks much of the data available relate to life history of target species. This paper aims to demonstrate that even basic life history information can, in itself, provide a framework for the advisory process for deepwater fisheries.

2. MATERIALS AND METHODS

Life history parameters and derived variables for the main deepwater species presented by Clarke *et al*. (2003) were augmented with data from the literature (Table 1). The basic parameters were maximum size (cm), maximum age, Brody growth coefficient (K), natural mortality (M), length at maturity (L_{50}) and age at maturity (Age_{50}). The ratios of size and age at maturity to maximum size and age were derived. These ratios provide a more meaningful indication of when in the fish's growth, or life span, maturity actually is attained.

Table 1

Life history parameters of the deepwater and continental shelf dwelling species derived
from Irish Marine Institute studies

The parameters are: maximum size and size at 50% maturity (cm), maximum age and age at 50% maturity (yrs),
Brody growth coefficient (K) in yrs^{-1}, ratio of size and age at 50% maturity to maximum observed values and
the instantaneous rate of natural mortality (M). Maximum size and age are as observed in these studies.

Species	Sex	L_{max}	Age_{max}	L_{50}	Age_{50}	K	L_{50}/L_{max}	Age_{50}/Age_{max}	M
Argentina silus	F	45	36	26	4	0.14		0.11	0.13
Aphanopus carbo		118	32						0.14
Coryphaenoides rupestris	M	23*(106)	50	10*(48)		0.13	0.43		0.09
Coryphaenoides rupestris	F	24*(111)	60	12*(57)	10	0.1	0.5	0.16	0.08
Centrophorus squamosus	F	145	70	128	44		0.88	0.62	0.07
Centrophorus squamosus	M	122	53	102	25		0.83	0.47	0.09
Deania calceus	F	119	35	105	27.5	0.07	0.86	0.78	0.13
Deania calceus	M	109	31	58	19	0.13	0.78	0.61	0.16
Helicolenus dactylopterus	M	38	43	26	15.5	0.06	0.59	0.36	0.11
Helicolenus dactylopterus	F	39	37	23	13	0.09	0.58	0.35	0.12
Clupea harengus Celtic Sea stock	F	33	11	20	1	0.56	0.59	0.09	0.42
Scomber scombrus Western/southern stock	F	46	21	29	1.5	0.34	0.63	0.07	0.22
Gadus morhua Irish Sea stock	F	100	10	50	2	0.43	0.5	0.11	0.46
Eutrigla gurnardus	F	39	21	18	1.5	0.21	0.46	0.08	0.22

* Length measurements for *Coryphaenoides rupestris* are pre-anus length, with total length in parenthesis. All
  other measurements are total length apart from *Eutrigla gurnardus* which are fork length.

Longevity and length data for ling and blue ling were obtained from Bergstad and Hareide
(1996). Size and age at maturity data for ling, blue ling and tusk were obtained from Magnusson *et al.*
(1997), using median of male and female values. Longevity and length data for tusk were obtained
from Magnusson *et al.* (1997) and an estimate of M from Anon. (1996). Maximum age of orange
roughy and cardinalfish (*Epigonus telescopus*) were taken from Talman *et al.* (2002). For orange
roughy, an estimate of M, L_{50} and maximum size were taken from Branch (2001), and references
therein. For greater forkbeard, longevity and growth data were obtained from Casas and Pineiro (2001)
and an estimate of M derived from data therein using the technique of Rikhter and Efanov (1976).
Maturity data for this species were obtained from Kelly (1997). Life history data on blue whiting were

obtained from routine sampling programmes underway in the Irish Marine Institute, while an estimate of M was obtained from Anon. (2003). The life history data above, were used to rank the main deepwater species in order of increasing conservatism in life history mode. The most conservative species was assigned the lowest rank for each life history trait.

The economic value of each species was calculated from records of average Irish prices in Ireland (Marine Institute 2003) and used to rank the species in order of price a tonne. Species that form aggregations that are targeted by the commercial fisheries were assigned ranks of 1, and those that are, in general, dispersed were assigned a rank of 2. Along with the economic value of the species this information can be used to highlight which species are more vulnerable in terms of attractiveness to fishing.

These data were used to derive further biological variables for these species. The ratios of size and age at maturity to maximum size and age were derived. These provide a more meaningful indication of when in the fishes' growth, or life span, maturity actually is attained. Estimates of natural mortality in this study (Table 1) were obtained using a method that assumes that this is the rate required to reduce a recruited population to 1 percent of its initial value (Annala and Sullivan 1996). In the present case, maximum age was taken to be the greatest observed age in samples. Estimates of fecundity and age at maturity were used to derive the potential rate of population increase the surrogate r' – (Jennings, Reynolds and Mills 1998) as follows

$$r' = \ln \text{(fecundity at length at 50\% maturity)/age at 50\% maturity}$$

Fecundity at size at maturity was used for greater argentine and roundnose grenadier, but for the sharks, mean observed ovarian fecundity was used because there was no evidence of increased fecundity with size (Clarke 2000, Girard and Du Buit 1999). Age at maturity was not estimated directly for the sharks but predicted from the von Bertalanffy growth function for birdbeak dogfish (*Deania calceus*) and from mean length at age in the case of leafscale gulper shark (*Centrophorus squamosus*).

A Beverton and Holt (1957) yield per recruit analysis was done for two hypothetical species, one with a *K*-strategist life history, and the other with a more *r*-selected mode. This model assumes that fish growth is expressed by the von Bertalanffy growth function and that mortality is exponential (Ricker 1975).

3.   RESULTS

Length and age data of the deepwater species are presented in Table 1 along with those of the shelf species. Maximum age attained (longevity) by these deepwater species varies. The shortest-lived species was forkbeard attaining ages of 9 years. The species that was estimated to reach the greatest age was leafscale gulper shark, attaining an age of 70 years. Roundnose grenadier was another long-lived species (60 years). Species with intermediate longevity were, in decreasing order, blue-mouth redfish (*Helicolenus dactylopterus*) (43 years), greater argentine (36 years), birdbeak dogfish (35 years) and black scabbardfish (*Aphanopus carbo*) (32 years). The maximum ages reported were as determined from the studies outlined above. Apart from the work carried out for roundnose grenadier (Gordon, Merrett and Haedrich *et al*. 1995) and grey gurnard (*Eutrigla gurnardus*) (Connolly 1986) where marginal increment analysis was employed, these studies did not include any validation of the age estimates that were obtained.

Greatest age at 50 percent maturity was recorded for blue-mouth redfish (15.5 years) though maturity was attained by this species at a smaller size than the other species except for forkbeard. Forkbeard reached maturity at smaller size and age than any of the other species. Greater argentine (4 years) also matures early, while roundnose grenadier matured later (10 years). The deepwater species were longer lived than the shelf species and thus the estimates of natural mortality for the

deepwater species were lower. The Brody growth coefficients (K) of the deepwater species indicate that they grow more slowly, reaching asymptotic size at a lower rate than the shelf species. Species displaying fastest growth, in terms of the Brody growth coefficient (K) from the von Bertalanffy growth model was forkbeard, followed by greater argentine. While roundnose grenadier displayed slow growth, the slowest growing of all species examined was blue-mouth redfish, displaying slower growth than the shark birdbeak dogfish. Though blue whiting reaches over 50 percent of maximum length before maturity, it matures at a relatively young age and is fast growing compared to the others ($K = 0.19$) (Table 2).

Table 2

Life history and economic parameters for deepwater species taken in fisheries
west of Ireland and Britain

The parameters are: maximum size and size at 50% maturity (cm), maximum age and age at 50% maturity (yrs), Brody growth coefficient (K) in yrs^{-1}, ratio of size and age at 50% maturity to maximum observed values, the instantaneous rate of natural mortality (M) and market price (€/tonne). The behavioural rank is (B) = 1 for dispersed species and 2 for those forming aggregations that are fished upon.

Species	Sex	L_{max}	Age_{max}	L_{50}	Age_{50}	K	L_{50}/L_{max}	Age_{50}/Age_{max}	M	€/t	B
Centrophorus squamosus	F	145	70	128	44		0.88	0.62	0.07	1 389	1
Hoplostethus atlanticus	F	69	180	52	35	0.06	0.75	0.19	0.05	2 603	2
Epigonus telescopus	u	60	38							1 270	2
Helicolenus dactylopterus	F	39	37	23	13	0.09	0.58	0.35	0.12		1
Deania calceus	F	119	35	105	27.5	0.07	0.86	0.78	0.13	0	1
Coryphaenoides rupestris	F	24	60	12	10	0.1	0.5	0.16	0.08	1 206	1
Aphanopus carbo		118	32						0.14	1 533	1
Brosme brosme	u	90	20	42.5	9		0.47	0.45	0.11	1 138	1
Molva molva	u	169	20	67.5	6		0.40	0.30		1 247	1
Molva dypterygia	u	120	30	50	7		0.42	0.23	0.15	1 273	2
Phycis blennoides	F	75	14	32	3.2	0.08	0.43	0.23	0.12	1 122	1
Argentina silus	F	45	36	26	4	0.14		0.11	0.13	118	2
Micromisteus poutassou	u	42	13	22.5	1.5	0.19	0.54	0.12	0.2	99	2

A more useful biological parameter than length or age at which 50% of the population reaches maturity is one that provides an indication of the age for the species when it reaches sexual maturity. Table 1 presents length and age at 50% maturity as ratios of maximum length and age in each case. Maturity was reached at largest proportion of maximum size in the case of the leafscale gulper shark (83 and 88% for males and females respectively). The other sharks also mature at high proportions of their maximum length. Roundnose grenadier mature at around 50% of maximum length but in terms of age at only about 18% of maximum. Blue-mouth redfish also attained maturity at an advanced size, though at an earlier percentage of maximum age than roundnose grenadier. The shelf dwelling species all reached sexual maturity at relatively small size and early age; in all cases first maturity was reached at less than 2 years. In contrast, of the deepwater species only roundnose grenadier matured at less than 50% of maximum size. Contrasting patterns of maturity with respect to age are also apparent. The shelf dwellers all matured in the first 12% of their life spans. Apart from roundnose grenadier the deepwater species reached maturity between 20 and 70% of their life spans. Fecundity estimates were only available for two of the teleosts. Greater Argentine females in the range 26.5–45 cm total length

had fecundities in the approximate range 4 478 to 16 284 ova. Roundnose grenadier in the range 63–95 cm TL had fecundities in the approximate range 11 000 to 55 000 ova.

Table 2 presents the above data, combined with additional data from various literature sources, to present an overall picture of the varying life histories in the deepwater fisheries. Orange roughy was the most valuable species (2 603 €/t). Most of the remaining true deepwater species commanded lower market prices, between about €1 100 and 1 500 €/t. The pelagic deepwater species had much lower market prices. Combined with the behavioural ranking, the economic data give some indication of vulnerability. For example, a high-value aggregating species such as orange roughy offers considerable incentive to fisheries. Combined with its conservative life history mode, these characteristics render it particularly vulnerable to exploitation.

The potential rate of population increase for four deepwater species and four shelf dwelling species is presented in Table 3, in order of increasing rate. These values show that the deepwater species all have slower rates of population increase than the shelf-dwelling species. The lowest rates of all are those of the sharks.

Table 3

Surrogate potential population replacement rate for four deepwater species compared with 4 continental shelf-dwelling species, calculated as fecundity at L_{50}/Age_{50}

Species	Fecundity at L_{50}	Age_{50}	r' ln (fecundity at L_{50}/Age_{50})
Centrophorus squamosus	8	44	0.05
Deania calceus	13	26	0.10
Coryphaenoides rupestris	13 083	10	0.95
Argentina silus	4 478	4	2.10
Eutrigla gurnardus	14 347	1.5	6.38
Gadus morhua	913 780	2	6.86
Clupea harengus	40 879	1	10.62
Scomber scombrus	235,673	1.5	12.37

The Beverton and Holt yield per recruit simulations show some important differences between fisheries based on *K*- and *r*-strategists. *K*-strategist-based fisheries produce maximum yield at lower rates of fishing mortality than those based on *r*-strategists (Figure 2). Thus, *r*-strategists may be harvested at higher rates of fishing mortality than those based on *K*-strategists. The parameters used as inputs to this analysis are given in Table 4.

Table 4

Parameters used to fit Beverton and Holt (1957) yield per recruit model for hypothetical *K* and *r*-strategist species.

Instantaneous rate of natural mortality M, the Brody growth coefficient K in yrs[-1] and the asymptotic weight in grams W_∞ from the von Bertalanffy growth function.

	K-strategist	r-strategist
M (natural mortality)	0.09	0.2
K (Brody growth coefficient)	0.08	0.37
W_∞ (g)	2000	700

4. DISCUSSION

The percentage of maximum length at which maturity is reached was greatest in the case of the sharks (78–88%), which agrees with mean values calculated for elasmobranchs by Frisk, Miller and Fogarty (2001). The deepwater teleosts matured at lower percentages of maximum length with the values for roundnose grenadier and forkbeard less than 55% and in the range for the shelf-dwelling species. The shelf-dwelling species appear to reach sexual maturity while somatic growth proceeds. The ratio of age-at-maturity to maximum age represents the portion of time and growth that takes place before the adults invest in reproduction. Again, the sharks had the highest values, indicating that they live most of their lives before they mature. These contrasts between shelf and slope species agree well with published studies; Gordon *et al*. (1995) notes that slope dwelling fish only mature when somatic growth has slowed or ceased, indicating that on the deepwater slopes, energy is available for growth or reproduction, but not both (Merrett and Haedrich 1997). Estimates of the Brody growth coefficient (K) for the deepwater species predict moderate to low rates of growth to asymptotic size.

Figure 2
Simulations of the Beverton and Holt yield per recruit model
for hypothetical *K* and *r*-strategist fish populations
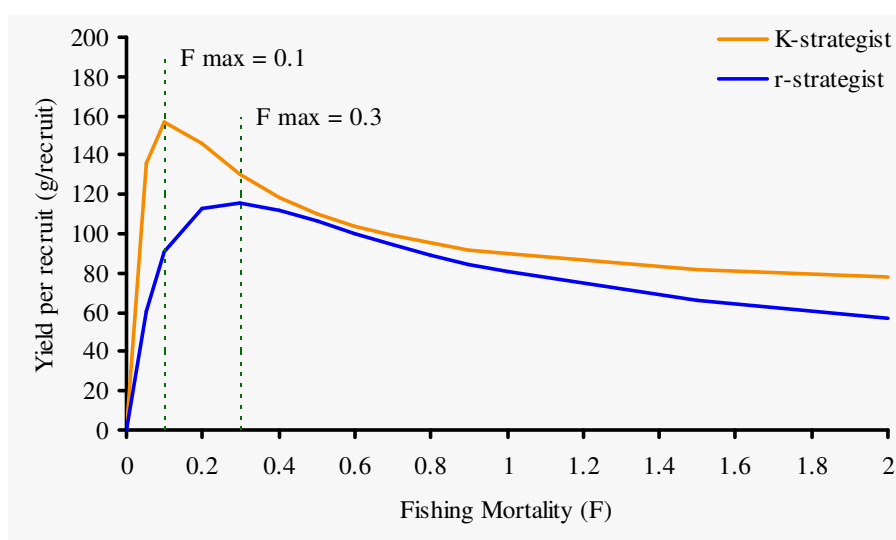
The ratios of age at maturity to maximum age for sharks are similar to those reported for shelf elasmobranchs by Frisk, Miller and Fogarty (2001). These authors tentatively suggest that compensatory responses to exploitation may explain earlier maturation in the sharks relative to other – unexploited – vertebrate classes. However, the high likelihood that these species have gestation periods of more than one, and perhaps more than two, years (Girard 2000) coupled with the possibility that they have prolonged periods of rest between reproductive events (Clark and King 1989, Clarke, Connolly and Bracken 2001) might indicate that the scope for compensatory change is limited. There have been reports of density dependent changes in fecundity in the shelf-dwelling squalid shark spiny dogfish (*Squalus acanthias*) (Gauld 1979). However Portuguese dogfish (*Centroscymnus coelolepis*) and birdbeak dogfish do not develop subsequent batches of oocytes during gestation. This seems to support the view that the scope for compensatory changes in deepwater sharks is more limited than might be the case for their shelf-dwelling relatives.

The dangers of not validating age have been illustrated by Beamish and McFarlane (1983). The errors in ageing the Pacific ocean perch (*Sebastes alutus*) led to a management strategy that was less conservative than was prudent, given the great longevity and low natural mortality of that species. In the absence of tagging data, natural mortality is often estimated using the techniques of Rikhter and Efanov (1976), orHoenig (1983) or is based on maximum age attained by a stock or species (Annala and Sullivan 1996). The problems with using these approaches may be illustrated with reference to

black scabbardfish (*Aphanopus carbo*). Morales and Carvalho (1996), using whole otoliths, found ages of up to eight years while the results reported in this study from sectioned otoliths were up to 32 years. The resultant differences in estimates of M from the method used in this study, 0.57 and 0.14 respectively, give quite different results about the maximum yield of this species. Again, the need for validation of age is underlined.

Available data on reproduction in teleosts further strengthens the contrasts between shelf and slope. Roundnose grenadier and greater argentine produce small numbers of large eggs (Kelly, Connolly and Bracken 1996, Ronan, Bracken and Malloy 1993) that are characteristic of species inhabiting low-energy environments (Ekau 1991). There are difficulties in translating these fecundity data into annual egg production estimates. There have been several studies of reproduction in roundnose grenadier, but the results have been contradictory. Their spawning is prolonged throughout the year (Allain 2001, Bergstad 1990, Gordon and Hunter 1994, Kelly *et al*. 1996, Magnusson and Magnusson 1995), however Kelly *et al*. (1996) found this species to be a determinate spawner, though Allain (2001) considers fecundity to be indeterminate and that the number of egg batches produced each year is unknown. Spawning in greater argentine proceeds throughout the year (Magnusson 1988, Ronan *et al*. 1993) though there may be seasonal peaks in spawning intensity (Anon. 1995b). There is no published information on the nature of spawning in this species. Differing spawning strategies complicate comparisons between shelf and slope teleosts. The grey gurnard has an asynchronous strategy, spawning repeatedly throughout the breeding season (Connolly 1986). The Atlantic mackerel (*Scomber scombrus*) also has a protracted spawning period (Anon. 1999). Thus, these species spread their reproductive effort over time to counteract environmental variability by adopting a "bet hedging" strategy (Lambert and Ware 1984). This approach accommodates environmentally induced poor recruitment by increasing the temporal scale of reproductive output relative to that of the environmental fluctuation (Merrett and Haedrich 1997).

The deepwater sharks have much lower fecundities than the slope-dwelling teleosts, but share similar values with shelf-based relatives such as spiny dogfish (*Squalus acanthias*) (Holden and Meadows 1964). These species produce a small number of well-developed young, with a better chance of survival. This tends to support the idea that stock-recruitment relationships are more defined in these viviparous elasmobranchs than may be the case for many teleosts.

This study illustrates the differences in growth and reproduction between shelf and slope species. These differences might be illustrated using the concept of the *K–r* continuum. *K*-strategists tend to inhabit environments where there is little fluctuation, they achieve success by attaining large size, deferred reproduction and producing smaller numbers of more developed offspring (Begon, Harper and Townsend 1996). However there has been much criticism of the *K–r* concept. Stearns (1992) examines the evolution of life history traits and suggests that earlier authors had tended to consider that so-called *K*-strategists evolved under density-dependent conditions, while *r*-strategists evolved in density-independent conditions, a theory that he considers incorrect. Boyce (1984) states that this theory should only be applied to density-dependent models, a point which Stearns (1992) also makes. The deficiencies in this concept should be noted. The use of the model in the current study is by way of an simple generalization of the dichotomy in life-history strategies in these species, and does not consider the selection pressures on individual organisms that produced these traits.

The intrinsic rate of natural increase (*r*) is the rate at which a population increases in size per individual in unit time. It is calculated as the mean number of offspring produced by an individual in its lifetime divided by the average time between the birth of an individual and the birth of the first offspring of that individual – cohort generation time (Begon *et al*. 1996). Given the uncertainties in reproductive biology of deepwater teleosts and elasmobranchs, it was not possible to calculate *r*. However, following the method of Jennings, Reynolds and Mills (1998), a surrogate value – the potential rate of population increase (*r'*) – was derived from the available data for four deepwater species and four shelf species. In this approach, fecundity at age at maturity provides an index of reproductive output and age at maturity an index of cohort generation time (Jennings, Greenstreet and Reynolds 1999). Ranking the species according to *r'* suggests that the sharks are least resilient to

fishing, followed by the slope teleosts. The shelf dwellers display markedly higher rates of potential population increase. There are no published estimates of the intrinsic rate of population increase (*r*) for the shelf species in this study. Jennings, Reynolds and Mills (1998) state that *r* could not be calculated for such species because available data were from stocks that had already been exploited, and reduced life-spans would bias the estimates. These authors suggest that *r'* is a useful surrogate, and produced estimates of this parameter for a range of shelf species. The parameter *r'* incorporates the fecundity at L_{50}, a surrogate for the mean annual egg production and Age_{50}, a substitute value for cohort generation time. Due to uncertainties in the estimates of annual egg-production (see above), *r* was not calculated for the deepwater species, and the surrogate estimate (*r'*) was used instead.

Hoenig and Gruber (1990) suggested the possibility of ranking species according to their resilience to exploitation, based on life history characteristics. Smith, Au and Show (1998) calculated "intrinsic rebound potentials" for 26 shark species, incorporating density dependence terms in their analyses. Brander (1981) ranked skate species according to the total mortality the populations could withstand without collapsing. This approach was also taken by Walker and Hislop (1998) for North Sea skates. Smith *et al.* (1998) note the difficulties in obtaining all the necessary data, therefore it seems prudent to maximise the usefulness of such information for assessment purposes.

These estimates of potential population increase suggest that these deepwater species are less resilient to fishing pressure and that they will respond more slowly to decreased exploitation than those on the continental shelf. The deepwater sharks share their low rates of increase with shelf-dwelling sharks (Smith, Au and Show 1998, Walker and Hislop 1998) but the possibility that the deepwater sharks have long gestation periods of two or more years (Girard 2000) and the likelihood that they have prolonged resting periods between reproductive events (Clark and King 1989, Clarke, Connolly and Bracken 2001) may indicate that these deepwater elasmobranchs are more vulnerable than their shelf-based relatives.

However, life history models are limited in their application for stock assessment purposes., provide only a static view of the population that does not consider possible density-dependent factors. More importantly, this method does not allow any direct measure of how to set management targets. But, these methods can be a useful aid in situations of poor fisheries data. Combined with data on trends in abundance, they can highlight the potential of particular species to recover, if fishing effort is reduced. They can be used to classify species in a fishery along a continuum of relative resilience to exploitation. Another application is to provide informed decisions about prior distributions of the rate of increase for surplus production models.

Most deepwater fisheries on the continental slopes of the ICES area are multi-species in character, with the possible exception of the pelagic trawl fishery for greater argentine (though data from this fishery are lacking). Figure 3 illustrates the interactions between the main gear types in terms of the main species in the catch. Roundnose grenadier is taken in the multi-species trawl fisheries with a range of species including greater argentine, deepwater sharks, black scabbardfish, blue ling and other species (Charuau, Du Pouy and Lorance 1995). Longline fisheries on the upper slopes target ling and tusk (Anon. 2000) while in deep waters another longline fishery targets mora, forkbeard and the sharks (Pineiro, Casas and Banon 2001). The diversity of species in longline catches is less than from trawl, but sharks tend to dominate the discards from longline harvests (Connolly and Kelly 1996). Orange roughy is taken in the mixed trawl fishery along with roundnose grenadier, and also in a directed fishery using specialised trawl gear, along with the cardinal fish.

Management of these fisheries should consider the vulnerability of each of the species. The ICES Working Group on the Biology and Assessment of Deep-sea Fisheries Resources has ranked the main deepwater species in order of their vulnerability, based on various life history parameters. In relation to these multi-species deepwater fisheries the question arises, how can a range of species be managed when they have a range of differing life history traits, though generally conforming to the *K*-strategist mode?

Figure 3

Schematic representation of the interactions between the main deepwater fishing gear types
in the area west of Ireland and Britain

Some species are caught by more than one gear. Data on bycatch in the pelagic trawl fishery for
Argentina silus are lacking. No data are available for gillnet fisheries.
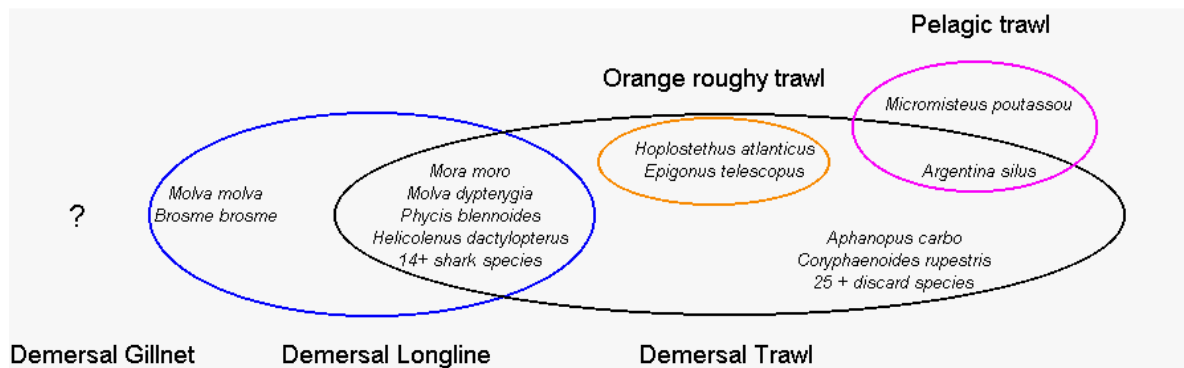
The simulations based on Beverton and Holt's (1957) yield per recruit model (Figure 2) show some important differences between species with what might be termed *K*-strategist life histories and those with *r* strategies. Fisheries based on *K*-strategists (such as the deepwater species in this study) achieve maximum yields at lower rates of fishing mortality (F) than those based on *r*-strategists. Thus *r*-strategists (analogous to the shelf-dwelling species) can sustain higher fishing mortalities. The resilience of these species can be gauged by *r'* or preferably the intrinsic rate of population increase *r*. But depending on the rate of fishing mortality some species may decline, while others may sustain that level of exploitation. The lack of species-specific abundance indices may explain why, for example, well-known species such as the common skate almost disappeared from the Irish Sea (Dulvy *et al*. 2000) while other skates were more resilient to fishing. This highlights the dangers of exploiting multi-species assemblages without taking into account the differing life-histories of the species involved. Framing management objectives may involve choosing the most vulnerable species and setting reference points for fishing mortality based on guidelines based on the precautionary approach. According to the results of this study and the ICES report on deepwater fisheries (Anon. 2001) the most vulnerable species in the exploited deepwater assemblage in the waters west of Ireland and Scotland are the deepwater squalid sharks.

Haedrich, Merrett and O'Dea. (2001) stated that management plans for deepwater fisheries cannot follow those developed for traditional shelf stocks. Indeed this statement could apply to traditional stocks also. The usual approach of providing single species advice for each species has been seen to be flawed and is now being changed. ICES is now aiming at providing advice on fisheries, rather than single stocks. The current advice for Irish Sea demersal fisheries, for example, is that fisheries should only proceed when there are no catches of cod or whiting (ICES 2003). This advice is based on analytical catch-at-age assessments that are not possible with deepwater species. However, basic life-history data can be used to produce fleet-based assessments of risk and support fisheries-based advice.

To frame fisheries-based advice for deepwater species, the first step should be to determine the species relationships in each fishery and for each depth range. This analysis can be used to evaluate the current and advised TACs, or effort levels. In other words, a TAC of 1 000 t for roundnose grenadier would entail certain amount of sharks, blue ling, black scabbard and orange roughy, for example. The life history analyses provide guidance on which species are most at risk, and can be used by managers to decide on which species are priorities for management decisions. Then a series of scenarios can be run, based on catch or effort levels for the species that have been deemed as priorities. Such an approach along with incorporation of technical interactions, could underpin fishery-based management advice for mixed-species deepwater fisheries.

5.   LITERATURE CITED

Allain, V. 2001. Reproductive strategies of three deepwater benthopelagic fishes from the northeast Atlantic Ocean. *Fis. Res.*, 51: 165–176.

Annala, J.H. & K.J. Sullivan 1996. Report from the fishery assessment plenary, April–May 1996: stock assessments and yield estimates. NIWA: Wellington. *Unpublished Report*.

Anon. 1995a. Estimation of fish biomass in the Irish Sea by means of the annual egg production method. Belfast: Queen's University of Belfast. Unpublished Report to European Commission.

Anon. 1995b. Report on the Study Group on the Biology and Assessment of Deep-sea Fisheries Resources. *ICES CM* 1995/Assessment: 4.

Anon. 1996. Report on the Study Group on the Biology and Assessment of Deep-sea fisheries resources. *ICES CM 2000* Assess:8.

Anon. 1999. Report of the Working Group on Mackerel and Horse Mackerel Egg Surveys. *ICES CM* 1999/G:5

Anon. 2000. Report on the Study Group on the Biology and Assessment of Deep-sea fisheries resources. *ICES CM 2000* ACFM:8.

Anon. 2001. Report of the Working Group on Biology and Assessment of deep-sea Fisheries Resources. *ICES CM* 2001/ACFM:23.

Anon. 2002.   Report of the Working Group on Biology and Assessment of deep-sea Fisheries Resources. *ICES CM* 2002/ACFM: 16

Atkinson, D.B. 1995. The biology and fishery of roundnose grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the north west Atlantic. In *Proceedings of NATO Advanced Workshop on deepwater fisheries of the north Atlantic Slope.* (Ed. A.L. Hopper). Amsterdam: Kluwer. pp. 51–111.

Beamish, R.J. & G.A. Mc Farlane 1983. The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fis. Soc.*, 112 (6): 735–743.

Begon, M., J.L. Harper, & C.R. Townsend 1996. Ecology. London: Blackwell Scientific, 1068 pp.

Bergstad, O.A. 1990. Distribution, population structure, growth and reproduction of the roundnose grenadier in the deep waters of the Skagerrak. *Mar. Biol.*, 107: 25–39.

Bergstad, O.A. and N.-R. Hareide 1996. Ling, blue ling and tusk of the north-east Atlantic. Bergen: Report to Institute of Marine Research.

Beverton, R.J.H. & S.J. Holt 1957. On the dynamics of exploited fish populations. *Ministry of Agriculture, Fisheries and Food Fisheries Investigations*, Series II, no. 19. 533 pp.

Boyce, M.S. 1984. Restitution of *r*- and *K*- selection as a model of density-dependent natural selection. *Ann. Rev. Ecol. Syst.* 15: 427–448.

Branch, T. 2001. A review of orange roughy *Hoplostethus atlanticus* fisheries, estimation methods, biology and stock structure. *South African Journal of Marine Science*., 23: 181-203.

Brander, K. 1981. Disappearance of Common skate *Raja batis* from the Irish Sea. *Nature*, 290: 48–49.

Casas, J. M. and C. Piñeiro, 2000. Growth and age estimation of greater forkbeard (Phycis blennoides Brünnich, 1768) in the north and westh of the Iberian Peninsula (ICES Division VIIIc and IXa). *Fisheries Research* 47 (19-25). 7 p.

Charuau, A., H. Du Pouy, & P. Lorance 1995. French exploitation of the deepwater fisheries of the north Atlantic. In *Proceedings of NATO Advanced Workshop on deepwater fisheries of the north Atlantic Slope.* (Ed. A.L. Hopper). Amsterdam: Kluwer. pp. 337–356.

Clark, M. 2001. Are deepwater fisheries sustainable? – the example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fis. Res.*, 51: 123–135.

Clark, M. R. & K.J. King 1989. Deepwater fish resources off North Island New Zealand: results of a trawl survey, May 1985–June 1986. Wellington: Ministry of Agriculture and Fisheries. New Zealand Fisheries Technical Report, No. 11.

Clarke, M. 2000. Aspects of the biology of three exploited deepwater sharks *Centrophorus squamosus, Centroscymnus coelolepis* and *Deania calceus* (Elasmobranchii, Squalidae) from the continental slopes of the Rockall Trough and Porcupine Bank. Dublin: National University of Ireland. *Unpublished Ph.D. Thesis*, 310 pp.

Clarke, M.W., P.L. Connolly, & J.J. Bracken 2001. Aspects of reproduction of the deepwater sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* from west of Ireland and Scotland. *J. Mar. Biol. Ass. U.K.*. 81: 1019–1029.

Clarke, M.W., P.L. Connolly & J.J. Bracken 2002. Age estimation of the exploited deepwater shark *Centrophorus squamosus* from the continental slopes of the Rockall Trough and Porcupine Bank. *J. Fish Biol.*, 60: 501–514.

Clarke, M.W., P.L. Connolly & J.J. Bracken 2002. Catch, discarding, age estimation, growth and maturity of the squalid shark *Deania calceus* west and north of Ireland. *Fis. Res.* 56: 139–153.

Clarke, M.W., C.J. Kelly, P.L. Connolly and J.J. Bracken. 2003. A life history approach to the assessment and management of deepwater fisheries in the northeast Atlantic. Journal of Northwest Atlantic Fisheries Science. 31: 401-411.

Connolly, P.L. 1986. Aspects of the biology of the gurnard (Pisces; Triglidae) from the Irish Sea. Dublin: National University of Ireland. *Unpublished Ph.D. Thesis*, 394 pp.

Connolly, P.L. & C.J. Kelly 1996. Catch and discards from experimental trawl and longline fishing in the Rockall Trough. *J. Fish Biol.*, 49 (Supplement A): 132–144.

Connolly, P.L., C.K. Kelly & M.W. Clarke 1999. Longline survey of the eastern slopes of the Rockall Trough. Dublin: Marine Institute Fisheries Leaflet, No. 180.

Dulvy, N.K., J.D. Metcalfe, J. Glanville, M.G. Pawson & J.D. Reynolds 2000. Fishery stability, local extinctions and shifts in community structure in skates. *Cons. Biol.*, 14: 283–293.

EC Fair 1999. Developing deepwater fisheries. Oban: Scottish Association for Marine Sciences. Report to European Commission.

Ekau, W. 1991. Reproduction in high Antarctic fishes (Notothenioidei). *Meerforschung*, 33: 159–167.

FAO. 1995. Precautionary approach to fisheries. Rome: FAO. Fisheries Technical Paper, 350/1.52 pp.

Frisk, M.G., T.J. Miller & M.J. Fogarty 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Can. J.Fis. Aq. Sci.*, 58: 969–981.

Gauld, J. 1979. Reproduction and fecundity of the Scottish–Norwegian stock of spurdog, *Squalus acanthias* (L.). *ICES CM* 1979/H:54.

Girard, M. 2000. Distribution et reproduction de deux especes de requins de grands fonds, les <<sikis>>, *Centrophorus squamosus* et *Centroscymnus coelolepis* exploites ddans l'Atlantique Nord-est. Rennes: ENSAR. Unpublished Ph.D. Thesis.

Girard, M., & M. H. Dubuit 1999. Reproductive biology of two deepwater sharks from the British Isles, *Centroscymnus coelolepis* and *Centrophorus squamosus* (Chondrichthyes: Squalidae). *J. Mar. Biol. Ass. U.K.* 79: 923−931.

Gordon, J.D.M. 1999. Management considerations of deepwater shark fisheries. In Shotton, R. (Ed) Case studies of the management of elasmobranch fisheries. FAO Fish. Tech. Paper No. 378/2: 774–819. FAO, Rome.

Gordon, J.D.M. 2001. Deepwater fish and fisheries: introduction. *Fis. Res.*, 51: 105–111.

Gordon, J.D.M. & J.E. Hunter 1994. Study of deep water fish stocks to the west of Scotland. Scottish Association for Marine Science, Oban, Unpublished Report.

Gordon, J.D.M., N.R. Merrett & R.L. Haedrich 1995. Environmental and biological aspects of slope dwelling fishes of the North Atlantic slope. . In *Proceedings of NATO Advanced Workshop on deepwater fisheries of the north Atlantic Slope.* (Ed. A.L. Hopper). Amsterdam: Kluwer. pp 1-27.

Gordon, J.D.M., S.C. Swan, C.J. Kelly & N.-R. Hareide 1995b. Age determination of juvenile roundnose grenadier *Coryphaenoides rupestris*, a deep water macrourid fish: a preliminary report. *ICES CM* 1995/G:6, 6pp.

Haedrich, R.L., N.R. Merrett & N.R. O'Dea 2001. Can ecological knowledge catch up with deepwater fishing? A North Atlantic perspective. *Fis. Res.*, 51: 113–122.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. *Fis. Bull.* (US), 82: 898–903.

Hoenig, J.M. & S.H. Gruber 1990. Life–history patterns in the elasmobranchs: implications for fisheries management. *NOAA Technical Report NMFS*, no. 90, 1–16.

Holden, M.J. & P.S. Meadows 1964. The fecundity of spurdog (*Squalus acanthias* L.) and its use for age determination. *J.Mar. Biol. Ass. U.K.* 42: 179–197.

ICES 2003. Report of the Advisory Committee for Fisheries Management 2003. Copenhagen: International Council for the Exploration of the Sea.

Jennings, S., J.D. Reynolds & S.C. Mills 1998. Life history correlates of responses to fisheries exploitation. *Proc. R. Soc.Lon., Series B, Biological Series*. 265: 333–339.

Jennings, S., S.R.P. Greenstreet & J.D. Reynolds 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. An. Ecol.*, 68: 617–627.

Kelly, C.J. 1997. Aspects of the biology of three deep water fish species from the continental slope of the Rockall Trough. Dublin: National University of Ireland. Unpublished Ph.D. Thesis.

Kelly, C.J., P.L. Connolly & J.J. Bracken 1996. Maturity, oocyte dynamics and fecundity of the roundnose grenadier from the Rockall Trough. *J. Fish Biol.*, 49 (Supplement A): 5–17.

Kelly, C.J., P.L. Connolly & J.J. Bracken 1997. Age estimation, growth, maturity and distribution of the roundnose grenadier from the Rockall Trough. *J. Fish Biol.*, 50: 1–17.

Kelly, C.J., P.L. Connolly & J.J. Bracken 1999. Age estimation, growth, maturity and distribution of the bluemouth rockfish *Helicolenus d. dactylopterus* (Delaroche 1809) from the Rockall Trough. *ICES J. Mar. Sci.*, 56: 61–74.

Kelly, C.J., P.L. Connolly & M.W. Clarke 1998. The deepwater fisheries of the Rockall Trough: some insights gleaned from Irish survey data. *ICES CM* 1998/O:40. 22pp.

Lambert, T.C. & D.M. Ware 1984 Reproductive strategies of demersal and pelagic spawning fish. *Can. J. Fish.Aq. Sci.*, 41: 1565–1569.

Langedal, G. & N.-R. Hareide 2000 Rapport fra Forsoksfiske med line pa Hatton Bank. Bergen: Directorate of Fisheries. Unpublished Report.

Magnusson, J.V. 1988. On silver smelt (*Argentina silus* Asc.) in Icelandic waters. *ICES C.M.1998* G:39

Magnusson, J.V., O.A. Bergstad, N.-R. Hareide, J.Magnusson and J. Reinert 1997. Ling, blue ling and tusk of the northeast Atlantic. Copenhagen: Nordic Council of Ministers.

Magnusson, J.V. & J. Magnusson 1995. The distribution, relative abundance and biology of the deep-sea fishes of the Icelandic slope and Reykjanes Ridge. In: Hopper, A.G. (Ed.) Deepwater Fisheries of the North Atlantic Oceanic Slope. Kluwer, Amsterdam, pp. 161–199.

Marine Institute 2003. The Stockbook, Galway: Marine Institute, 389 pp.

Merrett, N.R. & R.L. Haedrich 1997. Deep-sea Demersal Fish and Fisheries. London: Chapman Hall. 283 pp.

Morales Nin, B. & D. Sena–Carvalho 1996. Age and growth of the black scabbardfish (*Aphanopus carbo*) off Madeira. *Fis. Res.*, 25: 239–251.

Pineiro, C.G., M. Casas & R. Banon 2001. The deepwater fisheries exploited by Spanish fleets in the Northeast Atlantic: a review of the current status. *Fis. Res.*, 51: 311–320.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Ottawa: Department of Fisheries and Oceans, Bulletin of the Fisheries Research Board of Canada. No. 191, 382 pp.

Rikhter, V.A. & V.N. Efanov 1976. On one of the approaches to estimation of natural mortality of fish populations. *ICNAF Research Document*, 76/VI/8, 12 pp.

Ronan, M.P., J.J. Bracken & J.P. Molloy 1993. Determination of biological characteristics of the greater argentine (*Argentina silus*) west of Ireland and Scotland. Dublin: University College Dublin. Report to the Commission of the European Communities, no. MA 2.605.

Smith, A.E., D.W. Au & C. Show 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Mar. Freshw. Res.*, 49: 663–678.

Stearns, S.C. 1992. *The evolution of life histories*. Oxford: Oxford University Press. 243 pp.

Talman, S., Krusic-Golub, K., Robertson, S. and Green, C. 2002. Age Estimation of deepwater fish species from the eastern north Atlantic. Queenscliff: Draft Report to An Bord Iascaigh Mhara (The Irish Sea Fisheries Board). 77 pp

Walker, P.A. & J.R.G. Hislop 1998. Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. *ICES J. Mar. Sci.*, 55: 392–402.