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A Life History Approach to the Assessment and Management of Deepwater Fisheries in the Northeast Atlantic

by

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Abstract

It has been generally stated that fish exploited by deepwater fisheries cannot sustain high levels of fishing pressure because of their characteristic slow growth, longevity and low reproductive output. Irish surveys (1993-2000) allowed for studies of age, growth, fecundity and maturity of several deepwater teleosts and elasmobranchs. These data show that *Coryphaenoides rupestris* is slow growing and has low fecundity. Other teleosts displayed rather conservative life-history characteristics. The shark *Deania calceus* was slower growing than the teleosts and *Centrophorus squamosus* attained ages of up to 71 years. The implications of the life-history parameters for sustainable exploitation are discussed by way of comparison with continental shelf species from this region. These data allowed for the estimation of the rate of potential population increase that supports the view that deepwater species are more vulnerable to exploitation. Whilst there may be scope for compensatory changes in fecundity such scope is likely to be limited, especially for sharks. Fisheries management plans should consider these differing life-history traits. The very different life history strategies exhibited by shelf and deepwater species suggests that different management systems will be required for deepwater fisheries to those prosecuted on the shelf.

Introduction

The International Council for Exploration of the Sea defines deepwater fisheries as those in waters deeper than 400m-500m. Such fisheries have developed rapidly in recent years in ICES Sub-divisions VI and VII. This rapid expansion is due to the decline (or indeed collapse) of 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 *et al.*, 1999) whilst 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 well developed, such as the French mixed-species trawl fishery (Charuau *et al.*, 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 expansions 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.

ICES recognised the growing importance of these new fisheries and convened a Study Group (now a Working Group) in 1994. The advice from ICES based on the work of this group has consistently been to keep fishing effort at a low level until sufficient information is gathered to enable scientific-based management decisions (Gordon, 2001). The most recent ICES management advice (ICES, 2001) made reference to two categories of deepwater stocks:

Category 1, Developing new fisheries:

“Consistent with a precautionary approach, fishing should not be allowed to expand faster than acquisition of information necessary to provide a basis for sustainable exploitation.”

Category 2, Fully of overexploited fisheries:

“ICES recommends immediate reduction in these fisheries unless they can be shown to be sustainable.”

Stocks in Category 2 include most of stocks in ICES Sub-area VI and VII. Notable exceptions in this area were forkbeard and the squalid sharks that were assigned to Category 1. The latter advice was intended to apply to virgin stocks. However this term is not entirely appropriate for forkbeard or the sharks, for which fishing has taken place for most of the 1990's.

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 deep-water fishery might be expected to last (Haedrich *et al.*, 2001). Management should ideally be based on population dynamics, including fisheries-dependent and fisheries-independent data, for example abundance and biomass indices collected on an annual basis. Yet for deepwater species this sort of information is mostly lacking. Whilst 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 most of the data available relate to the life history of the target species. This paper presents the results of life history studies carried out at the Irish Marine Institute, over the last 10 years. Such information can in itself provide a framework for determining the sustainability of these species to exploitation. It is the purpose of this paper to use this information to inform the management of these deepwater fisheries.

Materials and Methods

A deepwater survey programme of the continental slopes of the Rockall Trough, Porcupine Bank and Porcupine Seabight was initiated in 1992. Together with data collected from commercial fishing vessels and port sampling, these surveys formed the basis of several primary biological studies of deepwater fish (Clarke, 2000; Kelly, 1997; Ronan *et al.*, 1993). The species for study were chosen on the basis of their importance to commercial fisheries and their abundance, species being chosen from the main taxa and distributional patterns in the region.

Studies of age, growth, maturity and fecundity of roundnose grenadier *Coryphaenoides rupestris* were carried out using specimens collected from trawl surveys (1993-1995) (Kelly *et al.*, 1998). Age estimation, using sectioned sagittal otoliths, was conducted and estimates of the parameters of the von Bertalanffy growth model were obtained with respect to pre-anus length and total weight. Size at maturity – from probit modelling – and age at maturity estimates were also obtained (Kelly *et al.*, 1997). Age estimation of juvenile *Coryphaenoides rupestris* was validated by analysis of the outer edge of the whole otoliths (Gordon *et al.*, 1995b). Fecundity analysis of this species was carried out for females in the range 63-95cm TL and in order to elucidate the reproductive cycle, an analysis of oocyte dynamics was also carried out (Kelly *et al.*, 1996)

Age estimates of bluemouth rockfish *Helicolenus dactylopterus* was carried out using sectioned sagittal otoliths and maturity at length and age were estimated from probit analysis (Kelly *et al.*, 1999). This study was carried out using samples from trawl surveys (1992-1993). Age estimation of greater forkbeard *Phycis blennoides* again using sectioned sagittal otoliths formed the basis of a growth study (Kelly, 1997). Age estimates of greater argentine *Argentina silus* were obtained from whole otoliths and estimates of the von Bertalanffy growth function were derived (Ronan *et al.*, 1993). In addition this study provided information on age at maturity and fecundity of females in the range 23-45 cm TL. Age estimation of the black scabbardfish *Aphanopus carbo* was conducted using sectioned otoliths (EC FAIR, 1999). Biological and life history data for the squaliform sharks; leafscale gulper shark *Centrophorus squamosus*, birdbeak dogfish *Deania calceus* and Portuguese dogfish *Centroscymnus coelolepis* are detailed in Clarke (2000) and Clarke *et al.* (in press). Age estimates for the first two sharks were obtained from sectioned dorsal fin spines. Fecundity and size at maturity data were obtained from trawl and longline caught specimens.

Life history data for shelf dwelling species were taken from several works and programmes currently underway. Information on size, age, growth, maturity and fecundity of the epibenthic species, grey gurnard *Eutrigla gurnardus* from the Irish Sea was presented by Connolly (1986). Size and age data for the two pelagic species; Celtic Sea stock of herring *Clupea harengus* and the western/southern combined stocks of Atlantic mackerel *Scomber scombrus* were

obtained from routine sampling programmes for these stocks. This information was used to derive the parameters of the von Bertalanffy growth function for both. Maturity at size and age data for both pelagic stocks were analysed by probit analysis to provide estimates of length and age at 50% maturity. It should be noted that the Celtic sea stock of *Clupea harengus* is primarily composed of autumn spawners. Therefore fish spawned in October, for example, are assigned to the age class of fish hypothetically spawned the following January. Data for *Gadus morhua* were obtained from information used in the ICES working group on the assessment of northern shelf demersal stocks (Officer, pers. comm.) whilst reproductive data were derived from a detailed study reported in Anon. (1995a).

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 were obtained from the method that assumes that this is the rate required to reduce a recruited population to 1% of its initial value (Hoenig, 1983). 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 r' - or surrogate r - (Jennings *et al.*, 1998) as follows;

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

Fecundity at size at maturity was used for *Argentina silus* and *Coryphaenoides rupestris*, 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 *Deania calceus* and from mean length at age in the case of *Centrophorus squamosus*.

A Beverton and Holt (1957) yield per recruit analysis was carried 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).

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 *Phycis blennoides* attaining ages of up to 9 years. The species that was estimated to reach the greatest age was *Centrophorus squamosus*, attaining an age of 70 years. *Coryphaenoides rupestris* was another long-lived species (60 years). Species with intermediate longevity were, in decreasing order, *Helicolenus dactylopterus* (43 years), *Argentina silus* (36 years), *Deania calceus* (35 years) and *Aphanopus carbo* (32 years).

Maturity was reached at largest proportion of maximum size in the case of *Centrophorus squamosus* (83 and 88 % for males and females respectively). The other sharks also mature at high proportions of maximum length. *Coryphaenoides rupestris* mature at about 50 % of maximum length but in terms of age at only about 18 % of maximum. *Helicolenus dactylopterus* also attained maturity at an advanced size, though at an earlier percentage of maximum age than *Coryphaenoides rupestris*. An interesting result was the differences in size and age at maturity between sexes for *Phycis blennoides*.

Greatest age at 50 % maturity was recorded for *Helicolenus dactylopterus* (15-16 years), though maturity was attained by this species at a smaller size than the other species except for *Phycis blennoides*, which reached maturity at smaller size and age than any of the other species. *Argentina silus* (4 years) also matures early, whilst *Coryphaenoides rupestris* matured later (10 years). Ages at maturity data were lacking for the sharks but these species all attain maturity at large size. 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 *P. blennoides*, followed by *Argentina silus*. Whilst *Coryphaenoides rupestris* displayed slow growth, the slowest growing of the teleosts examined was *H. dactylopterus*, which displayed slower growth than the shark *Deania calceus*.

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 point in the life history of that species reaches sexual maturity. Table 2 presents length and age at 50% maturity as ratios of maximum length and age in each case. The shelf dwelling species all reached sexual maturity at relatively small size and early age, in all cases first maturity being reached at less than 2 years. Except for *Scomber scombrus*, all the shelf species reached maturity before 50% of maximum size was attained. In contrast, of the deepwater species only *Coryphaenoides rupestris* 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 *Coryphaenoides rupestris* the deepwater species reached maturity between 20% and 70% of their life spans. Fecundity estimates were only available for two of the teleosts. *Argentina silus* females in the range 23-45 cm total length had fecundities in the approximate range 1,000 to 22,000. *Coryphaenoides rupestris* in the range 63-95 cm total length had fecundities in the approximate range 11,000 to 55,000.

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 slowest rates of all are those of the sharks.

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 1). 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.

Discussion

The percentage of maximum length at which maturity is reached was greatest in the case of the sharks (78-88%), agreeing with mean values calculated for elasmobranchs by Frisk *et al.* (2001). The deepwater teleosts matured at lower percentages of maximum length with the values for *Coryphaenoides rupestris* and *Phycis blennoides* less than 55% and in the range for the shelf-dwelling species. In contrast the shelf-dwelling species appear to reach sexual maturity whilst somatic growth proceeds. The ratio of age at maturity to maximum age represents the portion of time and growth that takes place before the investment adults make 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 agree well with published studies; Gordon *et al.* (1995a) 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 predicts moderate to low rates of growth towards large asymptotic size.

The ratios of age at maturity to maximum age for sharks are similar to those reported for shelf elasmobranchs by Frisk *et al.* (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 likelihood that these species have gestation periods of more than one and perhaps more than two years (Clarke 2000, Girard, 2000) coupled with the possibility that they have prolonged periods of rest between reproductive events (Clark and King, 1989; Clarke *et al.* in press) 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 *Squalus acanthias* (Gauld, 1979). However only *Centrophorus squamosus*, of the species in the present study shares with that species the tendency to develop batches of oocytes during pregnancy (Yano pers. comm.). 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 stock. In the absence of tagging data natural mortality is usually estimated using the technique of Rikhter and Efanov (1976) or of Hoenig (1983), the former method based on age at maturity, the latter on maximum age attained. The problems with using these approaches may be illustrated with reference to *Aphanopus carbo*. Morales Nin and Sena Carvalho (1996) using whole otoliths found ages of up to 8 years whilst the results reported in this study, from sectioned otoliths, were up to 32 years. The resultant differences in estimates of M from Hoenig's (1983) method; 0.57 and 0.14 respectively, give quite different ideas about productivity 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. *Coryphaenoides rupestris* and *Argentina silus* produce small numbers of large eggs (Kelly *et al.* 1996; Ronan *et al.*, 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 *Coryphaenoides rupestris*, but the results have been contradictory. The 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 that this species was a determinate spawner, though Allain (2001) considers fecundity to be indeterminate and that the number of batches produced each year is unknown. Spawning in *Argentina silus* 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 complicates comparisons between shelf and slope teleosts. *Eutrigla gurnardus* has an asynchronous strategy, spawning repeatedly throughout the breeding season (Connolly, 1986). *Scomber scombrus* also has a protracted spawning period (Anon., 1999). Thus, these species spread theory 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 *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 species than may be the case for teleosts.

These data illustrate the differences in growth and reproduction between shelf and slope. These differences can 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 *et al.*, 1996). 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 *et al.* (1998) a surrogate value – the potential rate of population increase (r') was derived from the available data for 4 deepwater species and 4 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 *et al.*, 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. Hoenig and Gruber (1990) suggested the possibility of ranking species according to their resilience to exploitation, based on life history characteristics. Smith *et al.* (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. Whilst this seems a very useful exercise for management purposes Smith *et al.* (1998) note the difficulties in obtaining all the parameters. In view of these difficulties, 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 very low rates of increase with shelf-dwelling sharks (Smith *et al.*, 1998; Walker and Hislop, 1998) but the possibility that the deepwater sharks have very long gestation periods of 2 or more years (Girard, 2000) and the likelihood that they have prolonged resting periods between reproductive events (Clark and King, 1989; Clarke *et al.*, in press) may indicate that these deepwater elasmobranchs are yet more vulnerable than their shelf-based relatives.

Most deepwater fisheries on the continental slopes west of Ireland and Britain are multi-species in character, with the possible exception of the pelagic trawl fishery for *Argentina silus* (though data on this fishery are lacking). Figure 2 illustrates the interactions between the main gear types in terms of the main species in the catch. *Coryphaenoides rupestris* is taken in the multi-species trawl fisheries with a range of species including *Argentina silus*, deepwater sharks, *Aphanopus carbo*, *Molva dypterygia* and others (Charuau *et al.*, 1995). Longline fisheries

on the upper slopes target *Molva molva* and *Brosme brosme* (Anon., 2000) whilst deeper down another longline fishery targets *Mora moro*, *Phycis blennoides* and the sharks (Pineiro *et al.*, 2001). The diversity of species in longline catches is less than from trawl, but sharks tend to dominate discards on longline (Connolly and Kelly, 1996).

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.

The simulations based on Beverton and Holt's (1957) yield per recruit model (Figure 1) 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 yield 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 preferable the intrinsic rate of population increase r . But depending on the rate of fishing mortality some species may decline, whilst others may sustain that level of exploitation. The lack of species-specific abundance indices may explain why, for example, well-known species such *Dipturus batis* almost disappeared from the Irish Sea (Dulvy *et al.*, 2000) whilst 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 most recent report of ICES WG Deep (Anon., 2001) most vulnerable species in the exploited deepwater assemblage in the waters west of Ireland and Scotland are the deepwater squalid sharks.

The results presented in this paper support the widely held view that deepwater species are more vulnerable to exploitation than shelf-dwelling species, and that their response rates to decreased fishing mortality will be lower. There is currently great debate both within ICES and European fisheries management agencies on appropriate management measures for deepwater species. The European Commission has proposed a series of TAC's to be introduced in 2002. However, it is still unclear whether a single management measure such as this will be successful and ICES has advised that a range of management measures may be required (Anon., 2000b).

The United Nations Food and Agriculture Organisation (FAO, 1995) presents guidelines for the adoption of the precautionary approach to fisheries management, research and technology. In terms of fisheries management, these FAO guidelines make reference to four "typical situations", but each is based on the level of exploitation of the fishery. With regard to deepwater fisheries perhaps it is now time to think more in terms of a "life history approach" where the biological traits of the species being caught are used in the formulation of management objectives. We echo the thoughts of Haedrich *et al.* (2001) that management plans for deepwater fisheries cannot follow those developed for traditional shelf stocks. Deepwater fisheries are based on species assemblages with completely different biological characteristics and this calls for a new approach, based on life history information.

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Table 1. Size and age at maturity (at 50% maturity in the population) and maximum size and age attained by some deepwater and continental shelf-dwelling species.

Species	Sex	L _{max}	Age _{max}	L ₅₀	Age ₅₀
<i>Argentina silus</i>	f	45	36	26	4
<i>Aphanopus carbo</i>		118	32		
<i>Coryphaenoides rupestris</i>	m	23*(106)	50	10*(48)	
<i>Coryphaenoides rupestris</i>	f	24*(111)	60	12*(57)	10
<i>Centrophorus squamosus</i>	f	145	70	128	44
<i>Centrophorus squamosus</i>	m	122	53	102	25
<i>Deania calceus</i>	f	119	35	105	27.5
<i>Deania calceus</i>	m	109	31	58	19
<i>Helicolenus dactylopterus</i>	m	38	43	26	15.5
<i>Helicolenus dactylopterus</i>	f	39	37	23	13
<i>Clupea harengus</i> Celtic Sea stock	f	33	11	20	1
<i>Scomber scombrus</i> Western/southern stock	f	46	21	29	1.5
<i>Gadus morhua</i> Irish Sea stock	f	100	10	50	2
<i>Eutrigla gurnardus</i>	f	39	21	18	1.5

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

Table 2. Life history parameters of some deepwater and continental shelf-dwelling species, derived from Irish Marine Institute studies.

Species	Sex	Longevity	Growth	L50/Lmax	Age50/Agemax	Fecundity	M
<i>Argentina silus</i>	f	36	0.14		0.11	4,478	0.13
<i>Aphanopus carbo</i>		32					0.14
<i>Coryphaenoides rupestris</i>	m	50	0.13	0.43			0.09
<i>Coryphaenoides rupestris</i>	f	60	0.1	0.5	0.16	13,083	0.08
<i>Centrophorus squamosus</i>	f	70		0.88	0.62	8	0.07
<i>Centrophorus squamosus</i>	m	53		0.83	0.47		0.09
<i>Deania calceus</i>	f	35	0.07	0.86	0.78	13	0.13
<i>Deania calceus</i>	m	31	0.13	0.78	0.61		0.16
<i>Helicolenus dactylopterus</i>	m	43	0.06	0.59	0.36		0.11
<i>Helicolenus dactylopterus</i>	f	37	0.09	0.58	0.35		0.12
<i>Clupea harengus</i> Celtic Sea stock	f	11	0.56	0.59	0.09	40,879	0.42
<i>Scomber scombrus</i> Western/southern stock	f	21	0.34	0.63	0.07	14,347	0.22
<i>Gadus morhua</i> Irish Sea stock	f	10	0.43	0.5	0.11	913,780	0.46
<i>Trigla gurnardus</i>	f	21	0.21	0.46	0.08	235,673	0.22

Table 3. Surrogate potential population replacement rate for four deepwater species compared with four continental shelf-dwelling species.

Species	Fecundity at L ₅₀	Age ₅₀	r'
<i>Centrophorus squamosus</i>	8	44	0.05
<i>Deania calceus</i>	13	26	0.10
<i>Coryphaenoides rupestris</i>	13,083	10	0.95
<i>Argentina silus</i>	4,478	4	2.10
<i>Eutrigla gurnardus</i>	14,347	1.5	6.38
<i>Gadus morhua</i>	913,780	2	6.86
<i>Clupea harengus</i>	40,879	1	10.62
<i>Scomber scombrus</i>	235,673	1.5	12.37

Table 4. Parameters used to fit Beverton and Holt (1957) yield per recruit model for hypothetical K and r strategist species.

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

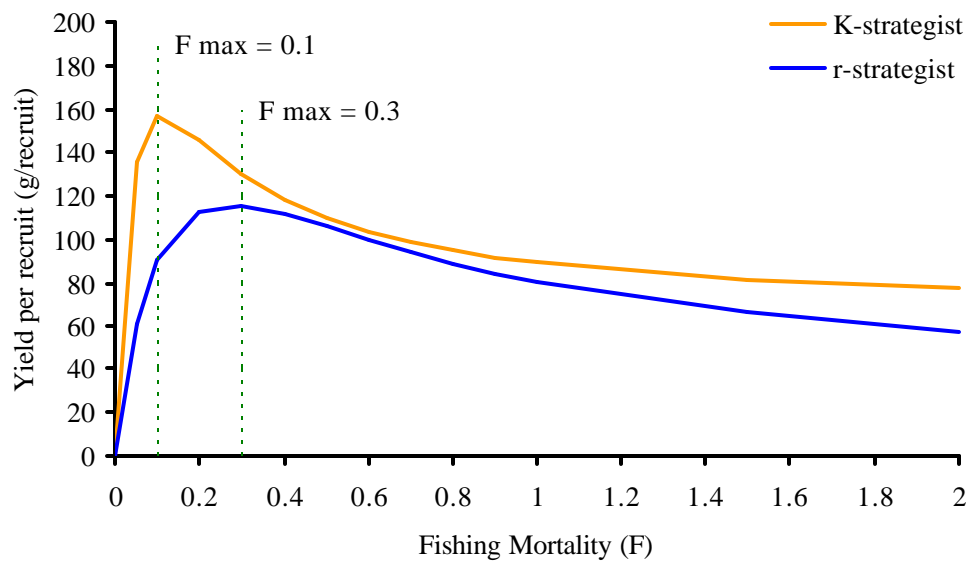


Figure 1. Simulations of the Beverton and Holt yield per recruit model for hypothetical K and r strategist fish populations.

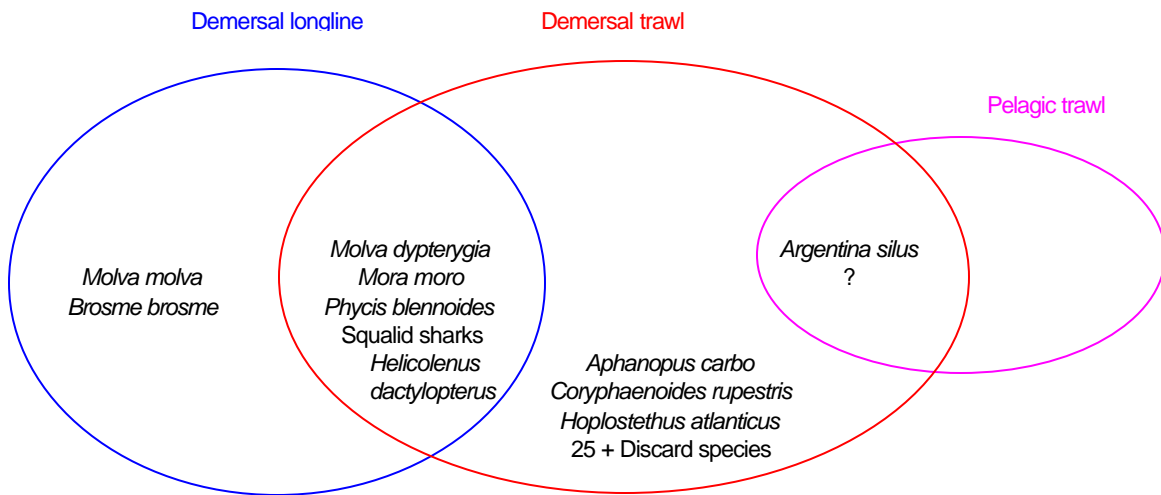


Figure 2. Schematic representation of the interactions between the main gear types in the area west of Ireland and Britain. Some species are caught by more than one gear. Data on by-catch in pelagic trawl fishery for *Argentina silus* are lacking. No data are available for gill net fisheries.