Differences in habitat selection of male and female megrim (*Lepidorhombus whiffiagonis*, Walbaum) to the west of Ireland. A result of differences in life-history strategies between the sexes?

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Abstract

The sex ratio in the catches of megrim (*Lepidorhombus whiffiagonis*, Walbaum) varied systematically with depth on three independent trawl survey series off the west coast of Ireland. Female megrim dominated the shallow catches, while males were more common in catches from deeper waters. The size difference between the sexes alone cannot explain this pattern because it remained evident when fish length was taken into account. Therefore size-specific habitat preferences or size-selective fishing mortality cannot fully explain the observed trend in the sex ratio of megrim. Female megrim grow to a larger size, at a faster rate than males and it is likely that their differences in habitat preferences are related to this. Shallower waters are warmer during the growing season and are likely to provide better conditions for fast growth. An understanding of the mechanisms behind these patterns is an important consideration in the management and conservation of this fish stock, which might be particularly vulnerable because the commercial landings are to a large extent dominated by female megrim.

Key words: flatfish; megrim; sex ratio; life-history; habitat selection

1. Introduction

The sex ratio of fish can be difficult to estimate, as differences in morphology and behaviour between the sexes can influence their catchability (Trippel, 2003). These differences in catchability between males and females are particularly common in flatfish (Beverton, 1964; Rijnsdorp and Witthames, 2005), although they have also been noted for other species (e.g. cod: Armstrong et al., 2004). It is important to understand these differences between the sexes if one aims to obtain unbiased samples from a population, for example for the purpose of stock assessment.

Skewed sex ratios can occur if the sexes suffer different mortality after parental care has ceased. Differences in mortality between the sexes could arise from differences in size, spawning or feeding behaviour or energy requirements (Rijnsdorp and Ibelings, 1989; Sterns, 2000). Because many flatfish species display sexual dimorphism in growth and behaviour, they are often subject to different mortality rates between the sexes (Beverton, 1964; Fahy and Fannon, 1991; Landa et al., 1996; Sánchez et al., 1998; Bromley, 2000; Landa and Pineiro, 2000), but due to lack of sexually disaggregated data, most flatfish stocks are assessed without separating the sexes (e.g. ICES, 2008b).

Skewed sex ratios are not uncommon in survey or commercial catches (e.g. Hannan, 2002; Robson, 2004; King et al., 2006). However it is difficult to determine whether this reflects the sex ratio in the population or results from differences in catchability and associated fishing mortality between the sexes (e.g. Armstrong et al., 2004; Rijnsdorp and Witthames, 2005). In addition to this, differences in distribution of the sexes have been noted for many species, resulting in spatial trends in their sex ratio (Trippel, 2003). Some of these trends might be the result of differences in migration behaviour during the spawning season (e.g. Warnes and Jones, 1995; Morgan and Trippel, 1996; Stoner et al., 1999). However, trends in sex ratio have also been observed outside the spawning season for a number of flatfish species (Swain and Morin, 1996; Swain, 1997; Poulard et al., 1999; González and Paz, 2005). In many of these cases, the proportion of males increased with increasing bottom depth. Bottom depth, in turn, is often related to temperature, prey distribution, productivity, dissolved oxygen levels and salinity (Swain and Morin, 1997) and is therefore a useful indicator of habitat for groundfish.

Swain (1997) suggested that differences in temperature preferences between male and female American plaice (*Hippoglossoides platessoides*) determined the differences in their distribution in the southern Gulf of St.Lawrence. He proposed that females might prefer warmer waters, as it allows them to have a higher growth rate. Swain and Morin (1996; 1997) also found that females of the same species had a larger stock range than males, possibly reflecting more intensive foraging activity amongst females. The sex ratio of megrim (*Lepidorhombus whiffiagonis*) in the Celtic sea and the Bay of Biscay has also been observed to vary with depth; females were relatively more abundant in shallow water, while males were more common in deep water (Boon, 1984; Poulard et al., 1999), but no explanation has been proposed as yet.

Megrim are a valuable by-catch of the Irish mixed fisheries. The highest densities of megrim are usually found close to the continental break (100-300m; Sánchez et al. 1998; Poulard et al. 1999). Spawning of megrim in this area takes place between February and April (Anon., 2001). Du Buit (1984) found that megrim to the west of Scotland mainly prey on fish (mostly sprat and small gadoids) and small crustaceans. Similar results were obtained for megrim in the Celtic Sea (Pinnegar *et al.*, 2003; Du Buit, 1992). Significant differences in growth between sexes appear after the age of two, around the time of first maturation: females grow faster and reach older ages and larger sizes than males (Landa et al., 1996; Landa and Pineiro, 2000; Robson, 2004).

Megrim are caught in large numbers on the groundfish surveys that are undertaken by the Marine Institute in waters around Ireland in the 1st and 4th quarter of each year. In recent years, the Marine Institute has also undertaken surveys that target monkfish but which also commonly catch megrim. The present paper is aimed at investigating the structure of spatial patterns in the sex ratio of megrim in Irish waters and exploring the mechanisms that might underlie these patterns.

2. Methods

Data were collected on three survey series consisting of:

- Six Quarter-4 IBTS Irish Groundfish Surveys, carried out on RV "Celtic Explorer" in October and November of 2003-8

- Five Quarter-1 Biological Sampling Groundfish Surveys, carried out on RV "Celtic Voyager" in February and March of 2004-5, and 2007-9
- Two monkfish surveys, carried out on chartered commercial vessels in January and December of 2006-7 and 2007-8

On both groundfish survey series, trawling took place during daylight hours only using a GOV trawl (ICES, 1999). The gear was towed over the bottom at 3 knots for 30 minutes per tow. The mesh size of the groundfish gear was graded from 80mm in the wings to 30mm at the cod-end. The cod-end was fitted with a 12mm liner. The average door spread was 60m for the Q1 groundfish surveys and 110m for the Q4 groundfish surveys which use a larger trawl (door spread was measured by acoustic door mounted distance sensors). On the monkfish surveys, trawling took place around the clock using a standard commercial monkfish otter trawl and a tow duration of one hour. The mesh size of the monkfish gear was 120mm in the wings and 100mm at the cod-end which was fitted with a 20mm liner. The average door spread was 85m. On the monkfish surveys megrim were retained from a length of around 18cm. The groundfish survey gear retained megrim from around 12cm due to the smaller mesh size. The gears used on the surveys are not optimal for catching flatfish, however, catch numbers of megrim were high enough to obtain reasonable sample numbers (in excess of 1000 fish for most surveys). Table 1 provides details on the spatial and depth coverage and sample numbers of the surveys.

Sampling stations between 6°W and 12°30'W were selected for analysis, this excludes stations on the Porcupine Bank, which were only sampled on the monkfish surveys and stations in the Irish Sea, which were only sampled on some of the groundfish surveys. It needs to be noted that the spatial coverage of the Q1 groundfish surveys was considerably smaller and more variable than that of the other surveys. Table 1 provides some summary statistics for the surveys and Figure 1 shows the station positions.

The entire catch was generally sorted by sex and measured (total length). Occasionally, if the megrim catch was very large, sub-samples of the catch were sexed and measured. The numbers-at-length were subsequently raised to the total catch by the ratio of the catch weight to the sample weight. Megrim were sexed by holding the fish up to the light and checking for the presence of ovaries. Small fish were dissected if their sex was not obvious. The sagittal otoliths were removed from a length-stratified sub-sample of the catch and read whole under reflected light. Length-at-age was estimated by applying an Age-Length Key (ALK; Fridriksson, 1934) to the raised length frequency of the total catch, separately for each sex and depth class.

Additional information on length-at-age was obtained from routine sampling of landings from commercial trawlers to assess the growth pattern throughout the year. Data from 2001 to 2008 were combined and the mean length-at-age was estimated by applying an ALK to the total length frequency distribution of the samples for each quarter. The standardised mean length was then estimated for each age class in each quarter by subtracting the annual mean length-at-age from the quarterly mean length-at-age to investigate growth throughout the year.

Data on the temperature near the bottom were obtained from a CTD dataset from the International Council for the Exploration of the Sea (ICES) oceanographic database (ICES, 2008a) as well as CTD data held at the Marine Institute (Ireland). The dataset was limited to a similar geographic range covered by the survey data (6-12°30'W; 50-57°N). The average of measurements taken within 10m off the bottom was taken as the near-bottom temperature. If the deepest measurement was more than 10m from the bottom it was omitted. Data from 1957-2008 were combined in order to give a general impression of the patterns in bottom temperature at different times of the year.

3. Results

Due to the difference in growth between males and females, large megrim tend to be females, while small megrim are more likely to be males. This pattern is observed on both the groundfish surveys and the monkfish surveys (Figure 2). The monkfish surveys use larger mesh size than the groundfish surveys, allowing more small fish to escape, therefore the number of males in the monkfish survey catches is quite low. Figure 2 also shows that in the Q4 groundfish survey catches, the highest abundance of females was found around 200m depth, while males were most abundant around 275m. The catches of monkfish survey series are dominated by females due to the size selectivity of the gear. Nevertheless, the proportion of males in the catches does increase with depth. The Q1 groundfish did not extend beyond 200m depth.

When the length class of the fish is taken into account, trends remain in the proportion of females-at-depth and these trends are nearly identical for all three survey series (Figure 3). Megrim under 20cm consist mostly of males except at shallow depths. For size classes 20-25cm and 25-30cm the proportion females decreases with depth and most megrim over 35cm are females as males rarely grow to that size.

The Q4 groundfish survey was the only survey for which enough data were available to investigate the mean length-at-age by depth. Figure 4 shows that the females showed a strong trend with depth: their length-at-age decreased with depth for all ages. Two-year-old fish in shallow water were larger than three-year-old fish in deep water, this pattern can also be seen for other age classes. The mean length-at-age of males appeared to be lowest around 200-250m and slightly higher towards the edges of their distribution.

Figure 5 shows the standardised mean length-at-age of megrim throughout the year (standardised length is the quarterly mean length-at-age minus the average mean length-at-age for the whole year; data from commercial samples). For most age classes the mean length-at-age did not change much between the first and second quarter of the year, most of the growth appears to take place between the second and the last quarter of the year. The sex of these fish was not routinely recorded but because these data are obtained from commercial catches, it can be assumed that most of the sampled fish were female (Laurenson and Macdonald (2008) estimate that up to 91% of the commercial landings of megrim are females.)

Figure 5 also shows the seasonal changes in bottom temperature; at bottom depths of around 100m the temperature increases throughout the year and is highest in the last quarter. In deeper water the temperature remains more stable throughout the year.

4. Discussion

The results show that, once size selectivity has been taken into account, the three survey series showed very similar patterns in the sex ratio of megrim. This indicates that the observed difference in depth distribution of males and females is not likely to be an artefact, but a consistent observation over a number of years, seasons and gear types. Other studies have also identified trends in the sex ratio of megrim using a number of different vessels and gear configurations (Boon, 1984; Warnes and Jones 1995; Poulard et al. 1999). However, none of them proposed an explanation for the patterns found. The present study also covers a larger geographical area and time span within and between years than previous work and it is the first to disentangle the effect of length and depth on the sex ratio in the catches (Figure 3). The present work shows that the difference in distribution between males and females cannot be explained by their size difference alone.

The difference in depth distribution suggests that male and female megrim have different habitat preferences (independent of their size difference). Perhaps this is not surprising as the two sexes have quite different life-histories. In many flatfish species (including megrim), females grow not only larger, but also faster than males, while producing a larger amount of gonadal material and suffering lower mortality (Beverton, 1964; Fahy and Fannon, 1991; Landa et al., 1996; Pauly, 1994; Rijnsdorp and Witthames, 2005; Sánchez et al., 1998; Landa and Pineiro, 2000). Many of these characteristics are consistent with the findings that fecundity is directly related to size, while the reproductive output of male flatfish does not seem to increase once a critical size has been reached (Rijnsdorp, 1994; Rijnsdorp and Witthames, 2005). So there is a strong incentive for females to quickly attain a large size while for males a large size appears to be less important.

A full megrim ovary can comprise of more than 10% of the total body weight (even before the oocytes hydrate; Q1 survey data) so the reproductive output of females is likely to be considerable. The reproductive output of males is unknown but the condition of both male and female megrim appears to decrease between Q4 and Q1. On average, mature females lost around 6% of their body weight in areas where the Q4 and subsequent Q1 survey overlapped. Males lost around 7% of their body weight. At the time of the Q4 survey, the gonads of many adult fish were starting to develop, while most adult fish were spent at the time of the Q1 survey. It is not surprising that females lose body weight during the spawning season because of the large volume of oocytes they produce. However, it is somewhat surprising that males lose at least as much body weight as the females as the relative size of the testes is small. However, the male reproductive output is unknown, and the loss of condition suggests that the energy demands for milt production and/or behavioural aspects might be considerable. Males of other flatfish species are known to stay in spawning condition longer whilst females spawn for a shorter time (Bromley, 2000). It is also possible that megrim feed less or not at all during the spawning season.

The spawning season of megrim in the Celtic Sea takes place in early spring (Aubin-Ottenheimer, 1987). Megrim in spawning condition were found on the Q1 surveys at depths ranging from 90m to 170m but it is possible that spawning occurs in deeper waters because sampling in Q1 did not extend beyond 185m. An ichthyoplankton survey carried out in April 2000 around Ireland (Dransfeld *et al.* 2004) showed high concentrations of megrim larvae to the south-west of Ireland between the 100m and 500m depth contours. Commercial catch logbook data combined with positional data from Vessel Monitoring Systems (VMS) shows that the catches of megrim per unit effort are high in this area throughout the year (Marine Institute, unpublished data) so there is no evidence of a major spawning migration from the commercial catches. The different surveys also observed an unchanging pattern in the sex ratio in autumn (Q4 groundfish), winter (monkfish) and spring (Q1 groundfish). If the differences in depth distributions between the sexes were related to spawning migrations, one would expect to see differences between the surveys taking place before, during and after the spawning season. However this is not the case so it is unlikely that the differences in depth distributions between males and females are related to sex-specific spawning migrations.

Du Buit (1992) and Pinnegar *et al.* (2003) found that megrim in the Celtic Sea mainly prey on fish and that the prey species composition changes with size. Unfortunately neither study distinguished between the sexes. Vassilopoulou (2006) studied the diet of the four-spot megrim (*L. boscii*) and she found that female *L. boscii* stomachs contained relatively larger prey species than those of males although she found no differences in stomach fullness. Studies on other flatfish species have shown that females require a higher food intake than males (Lozán, 1992; Stoner et al., 1999; Villarroel et al., 2001). So it is possible that differences in habitat preferences between males and females result also from a higher food intake requirement for females. A detailed study of food intake of *L. whiffiagonis* would be required to confirm this hypothesis.

Landa *et al.* (1996) found that growth rates of megrim from the Bay of Biscay varied with depth. In accordance with the present study, they found that females in shallow water were larger at age than those at deeper depths and proposed that variable growth at different depths might be related to density dependence. Another possibility is that higher summer temperatures in shallow waters might allow for faster growth. The finding that growth mainly takes place in the second half of the year (Figure 5) lends some weight to the argument that megrim in shallow water grow faster than those in deeper water because of higher temperatures in those waters during the growing season. Apart from faster somatic growth, higher temperatures in the last quarter of the year might also allow the production of a larger amount gondal growth in the period leading up to the spawning season.

The findings outlined here do not provide conclusive evidence for the reasons behind the difference in depth distribution, but it is clear that females grow faster and to a larger size than males and therefore they might have different requirements from their habitats. Because depth is likely to be related to temperature, prey distribution, productivity, oxygen levels and salinity (Swain and Morin, 1997) it will be difficult to establish which of these factors drives the difference in depth preference between males and females. The bottom temperature data seem to provide a plausible explanation for the female preference for relatively shallow water as temperatures are highest there during the season when most of the growth takes place. This is in accordance with the findings of Swain (1997) for American plaice.

The trend in the sex ratio of megrim off Ireland was very pronounced, however it is likely that other species also display differences in distribution of the sexes, particularly for species with strong sexual dimorphism. Sexual dimorphism is common in flatfish, particularly species attaining a large size (Rijnsdorp and

Witthames, 2005). As differences in growth rate are likely to impact on the habitat requirements of the sexes, one might expect to find spatial trends in the sex ratio of many flatfish populations.

An understanding of the differences in habitat selection and life-history strategies of males and females can improve sampling design and inform fisheries management advice. Many flatfish stocks are assessed without distinguishing between the sexes, despite well-known differences in weight-at-age (e.g. ICES, 2008b). Any bias in sampling due to differences in distribution between the sexes can therefore have important consequences on the stock assessment. Additionally, applying age-length keys without distinguishing between the sexes will result in increased uncertainty in the assessment as sex-related differences in length proliferate into the age structure of the assessment model. An understanding of the differences between males and females is also required for the use of female-only spawning stock biomass estimates (Marshall et al., 2003), which might provide an improved index of reproductive potential, particularly in a fishery where the catches are dominated by females.

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References

Anon., 2001. Distribution and biology of anglerfish and megrim in waters to the west of Scotland. European Commission - DG XIV Study Contract 98/096. 88pp.

Armstrong, M.J., Gerritsen, H.D., Allen, M., McCurdy, W.J., Peel, J.A.D., 2004. Variability in maturity and growth in a heavily exploited stock: cod (*Gadus morhua* L.) in the Irish Sea. ICES J. Mar. Sci., 61(1), 98-112.

Aubin-Ottenheimer, G., 1987. Bilan des connaissances sur la cardine (*Lepidorhombus whiffiagonis*). Etude du stock sur de Mer Celtique (In French). Rev. Trav. Inst. Pêches Marit., 49(3-4): 205-214.

Beverton, R.J.H., 1964. Differential catchability of male and female plaice in the North sea and its effect on estimates of stock abundance. Rapp. P.-v. Réun. Cons. int. Explor. Mer., 155, 103-122.

Boon, M.J., 1984. The UK megrim fishery in ICES sub-area VII: A preliminary analysis. ICES CM 1984/G:17. 14pp.

Bromley, P.J., 2000. Growth, sexual maturation and spawning in Central North Sea plaice (*Pleuronectes platessa* L.), and the generation of maturity ogives from commercial catch data. J. Sea Res., 44: 27-43.

Dransfeld, L., Dwane, O., McCarney, C., Kelly, C.J., Danilowicz, B.S. and Fives, J.M., 2004. Larval distribution of commercial fish species in waters around Ireland. Irish Fish. Invest., 13: 39pp.

Du Buit, M.H., 1984. Prédation de la cardine (*Lepidorhombus whiffiagonis* W.) au nord et à la ouest de l'Ecosse (In French). J. Cons. int. Explor. Mer., 41, 194-198.

Du Buit, M.H., 1992. Alimentation de la Cardine, *Lepidorhombus whiffiagonis* en Mer Celtique (In French). Cah. Biol. Mar., 33: 501-514.

Fahy, E., Fannon, E., 1991. The exploitation of megrim *Lepidorhombus whiffiagonis* by the demersal fleet. Irish Fish. Invest. Ser. B No. 38, Department of the Marine, Dublin. 20pp.

Fridriksson, A., 1934. On the calculation of age-distribution within a stock of cod by means of relatively few age-determinations as a key to measurements on a large scale. Rapp. P.-v. Réun. Cons. int. Explor. Mer., 86(6): 1-5.

González, C., Paz, X., 2005. Distribution of American plaice (*Hippoglossoides platessoides*) on the Grand Bank (NAFO Divisions 3NO), 1995-2004. NAFO SCR, 05/30. Ser No. N5118, 16pp.

Hannan, J.F., 2002. Age, growth and population dynamics of lemon sole *Microstomus kitt* (Walbaum 1792) sampled off the west coast of Ireland, Thesis. Galway-Mayo Institute of Technology, Galway, Ireland.

ICES, 1999. Manual for the International Bottom Trawl Surveys. Revision VI. ICES CM 1999/D:2, ICES, Lisbon, Portugal. 49pp.

ICES, 2008a. ICES Oceanographic Database. http://www.ices.dk/Ocean/

ICES, 2008b. Report of the Working Group on the Assessment of Southern Shelf Stocks of Hake, Monk and Megrim (WGHMM), ICES, Copenhagen.

King, P.A., Hannan, J.F., McGrath, D., Veldon, M., 2006. Population dynamics, age, growth and maturity of lemon sole *Microstomus Kitt* (Walbaum 1792) sampled between 2000-2002 off the west coast of Ireland. Irish Fish Invest, 16, 1-28.

Landa, J., Piñeiro, C., 2000. Megrim (*Lepidorhombus whiffiagonis*) growth in the North-eastern Atlantic based on back-calculation of otolith rings. ICES Journal of Marine Science, 57(4), 1077-1090.

Landa, J., Piñeiro, C., Perez, N., 1996. Megrim (*Lepidorhombus whiffiagonis*) growth patterns in the northeast Atlantic. Fisheries Research, 26(3-4), 279-294.

Laurenson, C. and Macdonald, P., 2008. Collection of fisheries and biological data on megrim in sub-area IVa. Scottish industry/science partnership (SISP). Report No 05/08.

Lozán, J.L., 1992. Sexual differences in food intake, digestive tract size, and growth performance of the dab, *Limanda limanda* L. Neth. J. Sea Res., 29, 223-227.

Marshall, C.T., O'Brien, L., Tomkiewicz, J., Köster, F.W., Kraus, G., Morgan, M.J., Saborido-Rey, F., Blanchard, J.L., Secor, D.H., Wright, P.J., Mukhina, N.V., Björnsson, H., 2003. Developing alternative indices of reproductive potential for use in fisheries management: Cases studies for stocks spanning an information gradient. J. Northw. Atl. Fish. Sci., 33, 161-190.

Morgan, M.J., Trippel, E.A., 1996. Skewed sex ratios in spawning shoals of Atlantic cod (*Gadus morhua*). ICES J. Mar. Sci., 53, 820-826.

Pauly, D., 1994. On the sex of fish and the gender of scientists - collected essays in fisheries science. Fish and fisheries series. Chapman and Hall, London, 272pp.

Pinnegar, J.K., Trenkel, V.M., Tidd, A.N., Dawson, W.A., Du Buit, M.H., 2003. Does diet in Celtic Sea fishes reflect prey availability? Journal of Fish Biology, 63 (Supplement A), 197-212.

Poulard, J.C., Peronnet, I., Rivoalen, J.J., 1999. Depth and spatial distributions of *Lepidorhombus whiffiagonis* (Walbaum, 1792) by age group in Celtic Sea and Bay of Biscay. ICES CM, G:43, 11pp.

Rijnsdorp, A.D., 1994. Population-regulating processing during the adult phase in flatfish. Neth. J. Sea Res., 32(2): 207-223.

Rijnsdorp, A.D., Ibelings, B., 1989. Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice *Pleuronectes platessa* L. J. Fish. Biol., 35: 401-415.

Rijnsdorp, A.D., Witthames, P., 2005. Ecology of reproduction. In, R. Gibson (Editor), Flatfishes. Biology and exploitation. Fish and aquatic resources. Blackwell publishing, Oxford, pp. 68-93.

Robson, S.M., 2004. Age, growth reproductive biology and population dynamics of the common megrim (Lepidorhombus Whiffiagonus, Waldbaum, 1792) from off the west coast of Ireland. PhD Thesis, Galway-Mayo Institute of Technology, Galway, 231pp.

Sánchez, F., Pérez, N., Landa, J., 1998. Distribution and abundance of megrim (*Lepidorhombus boscii* and *Lepidorhombus whiffiagonis*) on the northern Spanish shelf. ICES Journal of Marine Science, 55(3): 494-514.

Sterns, S.C., 2000. Life history evolution: successes, limitations, and prospects. Naturwissenschaften, 87: 476-486.

Stoner, W.A., Beja, A.J., Manderson, J.P., Phelan, B.A., Stehlik, L.L., Pessutti, J.P., 1999. Behaviour of winter flounder, Pseudopleuronectes americanus, during the reproductive season, laboratory and field observations on spawning, feeding, and locomotion. Fish Bull, 97(4): 999-1016.

Swain, D.P., 1997. Sex-specific temperature distribution of American plaice (*Hippoglossoides platessoides*) and its relation to age and abundance. Can. J. Fish. Aquat. Sci., 54, 1077-1087.

Swain, D.P., Morin, R., 1996. Relationships between geographic distribution and abundance of American plaice (*Hippoglossoides platessoides*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci., 53, 106-119.

Swain, D.P., Morin, R., 1997. Effects of age, sex and abundance on the bathymetric pattern of American plaice in the southern Gulf of St Lawrence. Journal of Fish Biology, 50(1), 181-200.

Trippel, E.A., 2003. Estimation of Male Reproductive Success of Marine Fishes. J. Northw. Atl. Fish. Sci., 33, 81-113.

Vassilopoulou, V., 2006. Dietary habits of the deep-sea flatfish *Lepidorhombus boscii* in north-eastern Mediterranean waters. J. Fish. Biol., 69, 1202-1220.

Villarroel, J.C., Acuña, E.H., Andrade, M.J., 2001. Feeding and distribution of the bigeye flounder *Hippoglossina macrops* off Northern Chile. Mar. Freshw. Res., 52(6), 833-841.

Warnes, S., Jones, B.W., 1995. Species distribution from English Celtic Sea groundfish surveys, 1984 to 1991. Fisheries research technical report number 98, MAFF, Lowestoft.

Figures

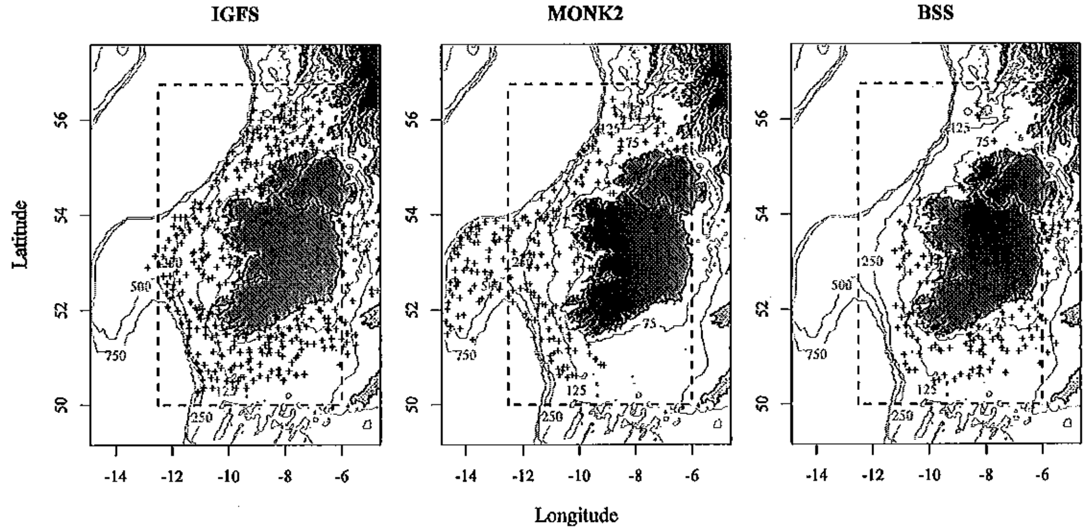

Figure 1. The station positions of the Q4 groundfish surveys (2003-8), monkfish surveys (2006-7) and the Q1 groundfish surveys (2004-9). The dataset was limited to the area indicated by the dashed rectangle so the spatial coverage of the surveys would be similar. Depth contours are shown in grey (depth in m).

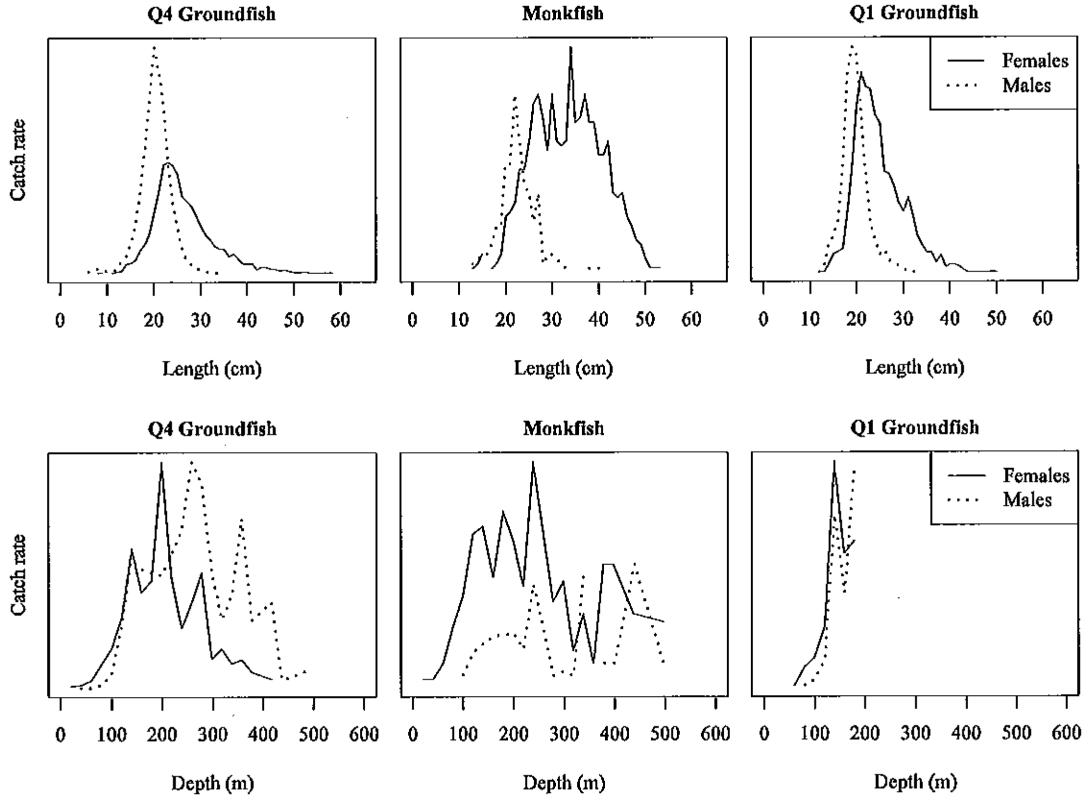

Figure 2. Top row: The length distribution of males and females for the three survey series. Females dominate the catches from 20-25cm upwards for all survey series. The monkfish survey catches contain very few fish under 20cm. Bottom row: the depth distribution of males and females for the three survey series. Females catch rates are highest between 100-300m while males are most abundant between 250-350m. Catch rates were estimated by standardising the catch numbers per minute towed and are shown on a relative scale.

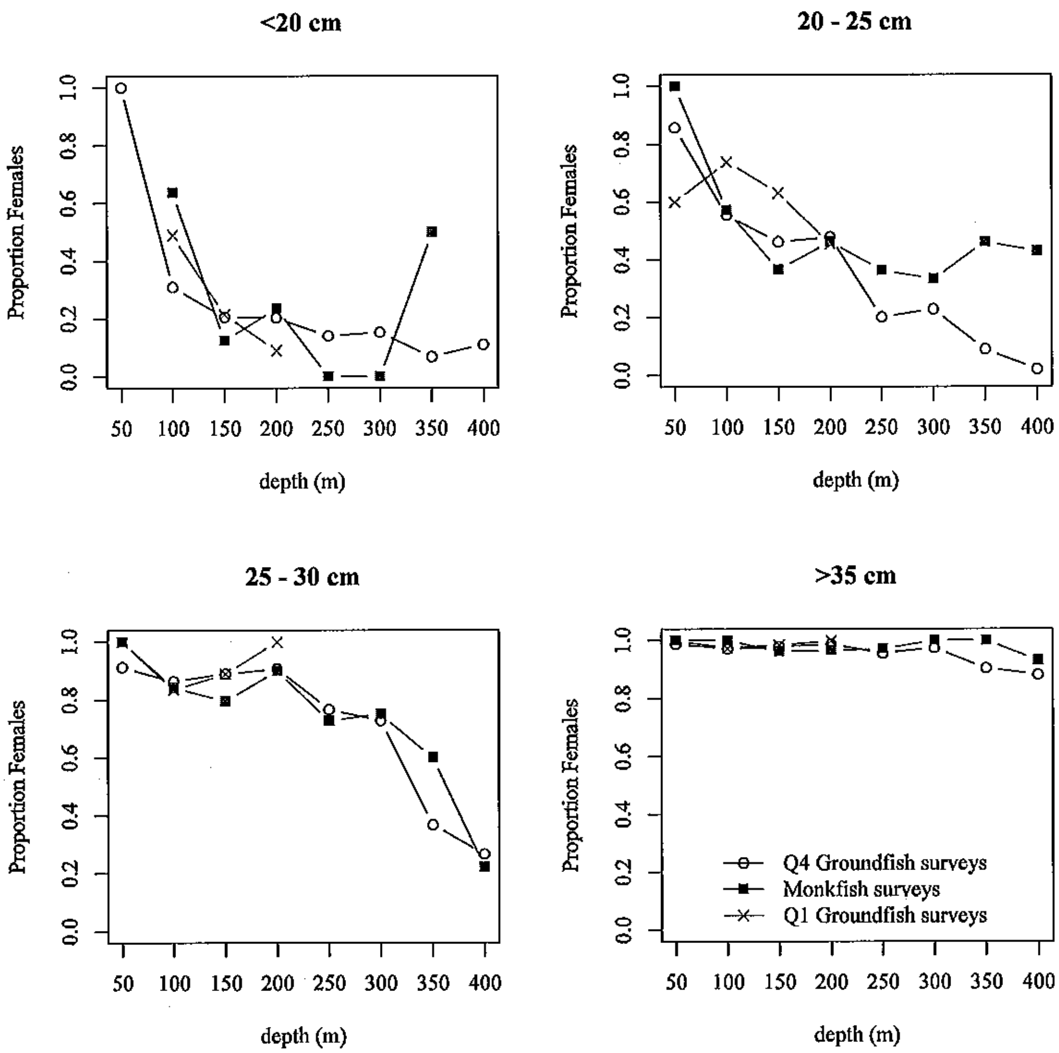

Figure 3. The sex ratio at depth for four size classes of megrim. The three survey series show very similar patterns: for all size classes under 35cm the sex ratio decreases with depth and nearly all fish over 35cm are 100% female.

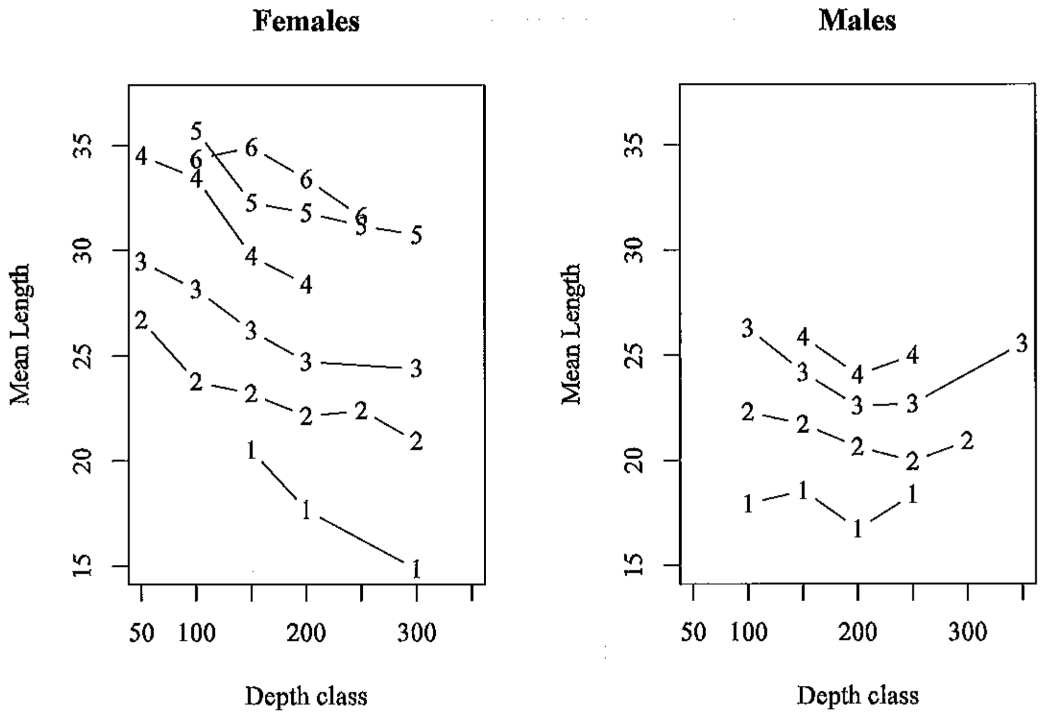

Figure 4. The mean length-at-age of megrim from the Q4 groundfish survey. Ages for which fewer than 5 fish were aged per depth class were omitted. The length-at-age of females shows a strong decreasing trend with depth for all ages while males show a U-shaped trend.

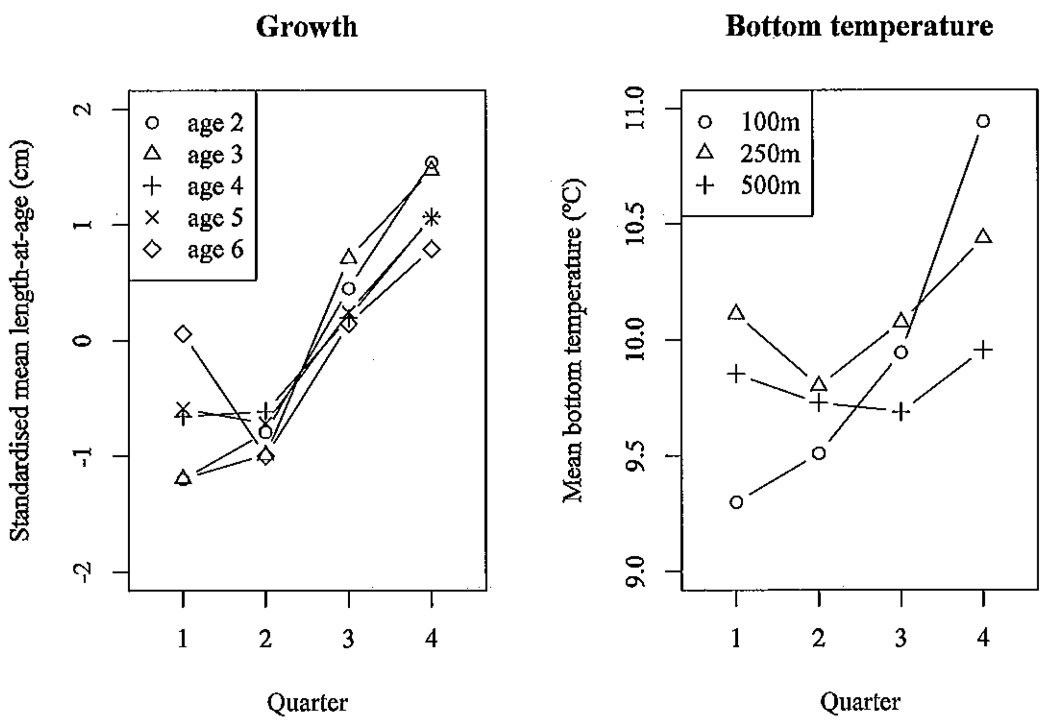

Figure 5. The left panel shows the standardised mean length-at-age by quarter from commercial landings in 2001-2009. Most of the growth appears to take place between the second and fourth quarter of the year. The right panel shows the bottom

temperature profile at different bottom depths. At 100m bottom depths the temperature shows a strong seasonal pattern while it is more stable in deeper waters.