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Fisheries ecology of common wolffish, *Anarhichas lupus*, in the North Sea

by

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Declaration

The material contained within this thesis has not previously been submitted for a degree at the University of Durham or any other university.

Abstract

The common wolffish (*Anarhichas lupus*), a benthivorous species, is widely dispersed, although not abundant in the North Sea north of 54°N latitude. Despite being widely distributed in sub Arctic and cold North Atlantic waters, little is known of the ecology of this species in the North Sea. This thesis aimed to provide ecological information for this species at the southern limit of its range in the Northeast Atlantic. North Sea common wolffish are regarded as sedentary in habit and mainly inhabited depths ranging from 60 m to 150 m. The bottom temperatures where this species were found in the North Sea ranged between 3°C and 12°C. The common wolffish is a by-catch species for the North Sea bottom trawl fishery. The long-term catch data and CPUE (catch per unit effort) indicated that the stock abundance of North Sea common wolffish has been decreasing over the last decades. However, it is suggested from VPA (virtual population analysis) and Yield-per-recruit analysis, that the North Sea common wolffish stock is still in a safe condition but has been overexploited. The means of total mortality (Z), natural mortality (M) and fishing mortality (F) of this species for 1996-1998 were 0.47, 0.17 and 0.30, respectively.

Both resting metabolic rate (RMR) and maximum metabolic rate (MMR) were low for this species. RMR and MMR were measured for six adult common wolffish (mean weight, 1.39kg) at 5° C and 10° C. At 5° C the mean RMR± SE was 12.18 ± 1.6 mgO$_2$ kg^{-1}h^{-1}, and mean MMR ± SE was 70.65 ± 7.63 mgO$_2$ kg^{-1}h^{-1}. At 10° C the mean RMR± SE was 25.43 ± 1.31 mgO$_2$ kg^{-1}h^{-1}, and mean MMR ± SE was 113.84 ± 16.26 mgO$_2$ kg^{-1}h^{-1}. Absolute metabolic scope was 53% greater at 10°C than at 5°C.

The main food for common wolffish in the North Sea were Decapoda comprising 39 % of the overall diet by occurrence, with hermit crabs (Paguridae) being the dominant species. Other important dietary components were Bivalvia (20 %) and Gastropoda (12 %). Sea urchins (Echinidae), which are important prey of common wolffish in eastern Newfoundland, Gulf of Maine and Iceland, but typically of low energy value, occupied only 7 % of the diet. During the autumn/winter season, wolffish consumed less food compared with the remainder of the year.

From this study, von Bertalanffy growth parameters for common wolffish in the North Sea were calculated to be: for male, $L_\infty = 111.2$ cm, $t_0 = -0.43$ and $K = 0.12$; and for female, $L_\infty = 115.1$ cm, $t_0 = -0.39$ and $K = 0.11$, making North Sea common wolffish the fastest growing stock of this species reported. The fast growth of North Sea common wolffish may be a result of the higher energy content of the diet or greater metabolic scope available for food processing. This increased metabolic scope being associated with life in the warmer North Sea, in comparison to those stocks found elsewhere in the range of this typically sub-Arctic species. The maximum age found for this species in the North Sea was 18 years old. Median length at sexual maturity of male and female common wolffish is at 51.9 cm and 50.4 cm respectively, with the age of sexual maturity being achieved at 4-5 years in the North Sea. The spawning season of North Sea common wolffish is from October through to February. The fecundity varied with the body weight of females, from several thousand to 12,000 eggs. Ripe egg sizes ranged from 5 mm to 6.5 mm. Spermatozoa were found in mature male individuals throughout the whole year with the highest peak in October.

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Chapter 1 Introduction

1.1 World fisheries

The marine environment covers 70% of the surface of our planet, and contains a massive variety of organisms. The marine life represents an invaluable resource for humans, of which fish are among the most important. Fish are a highly nutritious food source and serve as a valuable supplement in diets lacking essential components such as the vitamins and minerals necessary for humans to maintain their body tissues. They also provide medicine and raw materials for humans all over the world. So far, more than 32,000 species of fish have been recorded worldwide (Castro and Huber, 1996). Fisheries have a long history. It has been shown that humans used tools to catch marine life during the Stone Age (Castro and Huber, 1996).

At the end of this century, worldwide, men and women will consume more fish than any other type of animal protein. It is estimated that 15-20% of all animal protein comes from fish (FAO, 1999). The consumption of the produce of fisheries increased to 15.7 kg per caput (live weight equivalent) in 1996 according to FAO reports. Over 30 countries, mainly located in Africa, Latin America, Asia and islands in the oceans, depend on fish as the principle source of protein. Fish are not only a food resource for humans, but also provide a source of work and income for people. In 1996, it was estimated that over 30 million people derived an income from fisheries and aquaculture. The majority of these were from developing countries.

In the 1996 total world fish production (including aquaculture) reached 121 million tonnes while the total catch of marine animals was 75 million tonnes and was 91% of total world catch (Fig. 1.1). The total catch of marine fish has increased rapidly with an annual growth of 6% since the beginning half of this century. The quantity of total catch in 1996 had increased by 147% compared with that of 1961. The value of global trade in fishery products reached £34.5 billion in 1996, with developing countries attaining a net commercial surplus of £9.9 billion. Improvements in aquaculture and expansion of inland fisheries have increased fisheries output in developing countries. Increasing fishing power and new fishing grounds were also responsible for increasing total catches. Moreover, there were significant increases in the yield of mesopelagic fish such as tuna and marlin in tropical areas (e.g. Western Indian Ocean) (FAO,

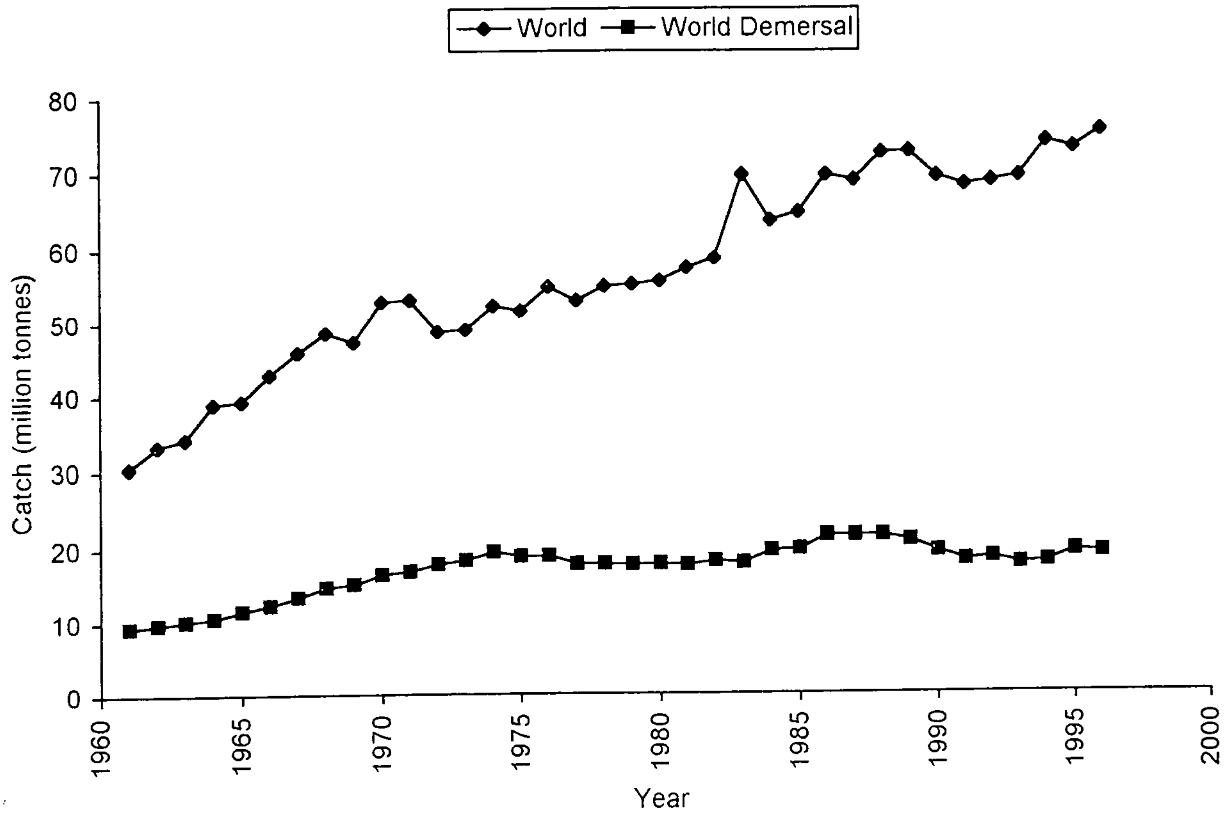


Fig. 1.1 Total world catch of marine fish and demersal fish from 1961 to 1998 (data from FAO, 1999).

1999). However, the total catch of demersal fish has not increased since 1975. The yield of demersal fishes varied between 1.7 million and 2.1 million tones between 1975 and 1996. The biomass of the main target species has been reducing since the last century (Smith, 1994). The total catch of demersal fish has been maintained at its current level due to increases in catches of less important fish and by catch species.

Most fishing activities are operated within the 200 m depth contour of continental shelves. Because of good mixing of nutrients within shallow waters, these areas have high primary and secondary production, providing essential food for fish larvae and invertebrates. The nutrient supply seems to play a particularly important role with respect to pelagic fishes (Cushing, 1982; Gerking, 1994). The abundance of pelagic species is enhanced by upwelling systems in tropical zones and is associated with tidal mixing of nutrient-poor surface water and nutrient-rich bottom waters in the temperate zone (Laevastu, 1993). Environment changes lead to substantial fluctuations in the population of pelagic species. Demersal fish species are unlike pelagic fish in that their population sizes are relatively steady, and in most species the factors influencing population dynamics are often the fish density and food competition (Cushing, 1982).

Human activities have strongly influenced fish populations both directly and indirectly. The direct effects are through catching them. The indirect effects are the changes in their living environment (e.g. pollution). These influences may cause their populations to decline or become unbalanced. From the fisheries viewpoint, continuous intense fishing pressure may reduce the reproductive capacity of a fish population and then cause a collapse in their numbers. Overfishing is becoming the major problem of the fisheries industry worldwide. This is not a new phenomenon, but one which has failed to be solved. The process of effective fisheries management, to ensure the exploitation of renewable resources, has become a necessary and urgent task for fisheries scientists to address.

1.2 Fisheries resources and fisheries management

From the last century to the beginning of this one, it was widely believed that humans were able to exploit marine resources endlessly due to the magnitude of the ocean (Smith, 1994). Advanced technology (e.g. sonar, diesel engine, fishing gear) enabled humans to exploit the marine resources efficiently and also brought wealth for fishermen. However, over exploitation has caused a collapse of some fish populations, and in some cases endangered fish species. In modern times, the Peruvian anchovy (*Engraulis mordax*) fishery and the North Sea herring (*Clupea harengus*) fishery have shown that, like other organisms on earth, humans have to live within the constraints of finite natural resources (Hilborn and Walters, 1992). This global limit for all natural fish stocks seems not far off and the marine fishes have been utilised to maximum capacity during the final years of this century (FAO, 1997). The reasonable exploitation of renewable resources like fish have become a key area of applied ecology.

Fisheries activities are not in a static system, and cannot be operated and rebuilt at will by management (Hilborn and Walters, 1992). When a virgin fishing ground is found and fishing fleets enter this area to begin catching, the commercial fisheries have always developed initially through a dynamic progress of several stages (Fig. 1.2). Initially, the new fishing ground is discovered and fishing industries propagate information about the place with a potentially abundant stock. At this phase, both yield and fishing effort are still low. Secondly, there follows a period of rapid growth of catch and effort resulting from initial success. After the growth phase, the fishery achieves full development. At this stage, the yield is close to the long-term sustainable level. However, the rapid development typically results in an overshoot of the sustainable level, and causes declining rates of fishing catch and reduced abundance of fish stock. Most fisheries often continue in the overexploitation stage so that both the yield and fishing effort reach the highest level, while the resource is declining to the lowest level. After the overexploitation stage some fisheries may enter the collapse stage where the yield is decreasing with increasing fishing effort. If the collapse is not too severe, the declining catch rates often reduce the fishing pressure because the fishermen find that it is not worthwhile to continue fishing. This stock may recover on its own but this may be a gradual process, and is usually incomplete.

The basic concept of fisheries management is used to assess the status and potential yield of a specific stock, and to provide information about catch quantity, fishing season, gears and fishing effort and the best way to maintain a sustainable fishery. However, fisheries management involves not only biological factors but also economic and social issues. If fisheries management were considered in terms of

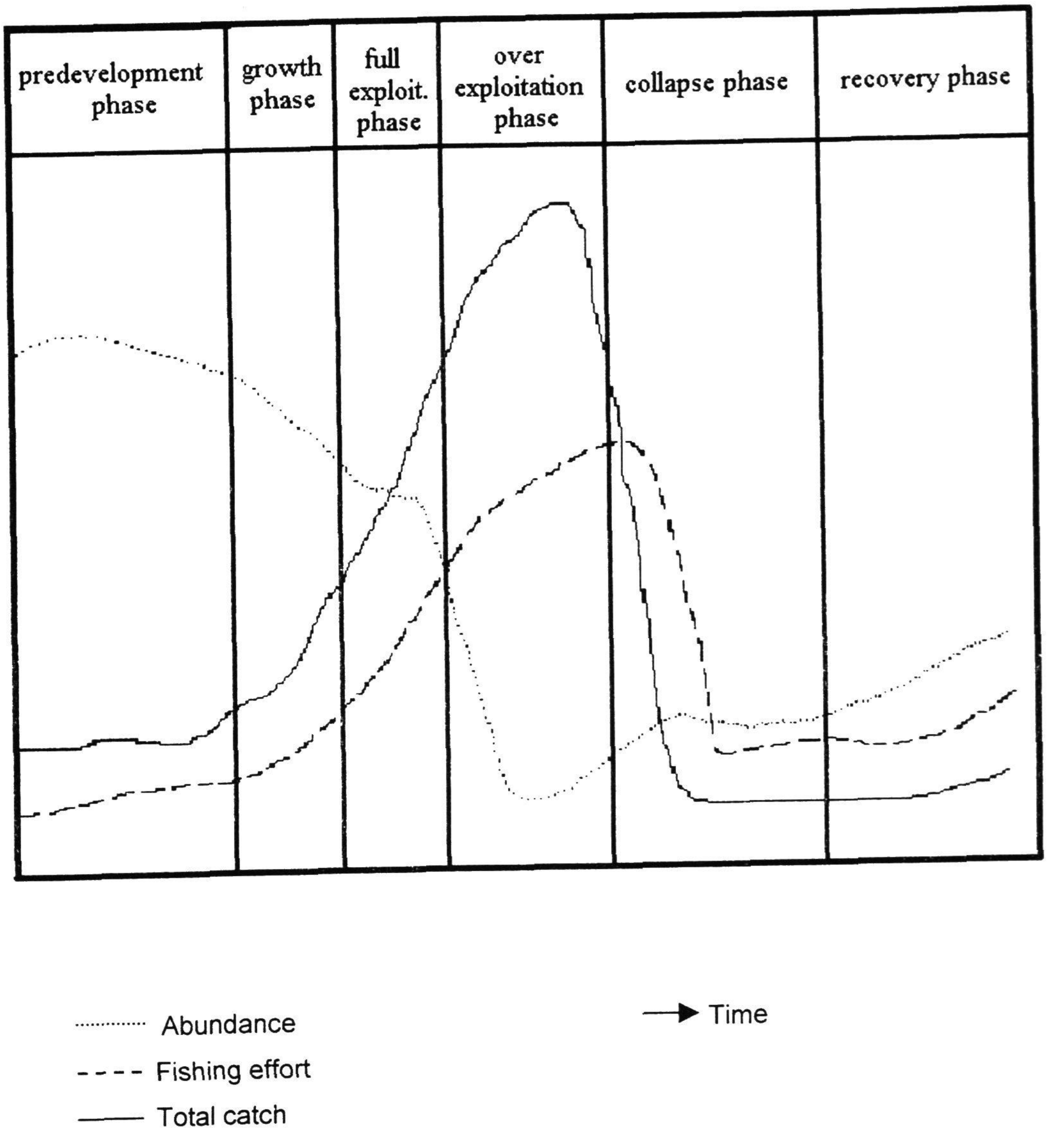


Fig. 1.2. Different phases of development of uncontrolled fisheries. Redrawn from Hilborn and Walters (1992).

biological factors only, the simplest way to a fishery would be to determine the size of the stock and then choose the appropriate fishing effort to catch the largest yield continuously. Such management is for the benefit of the target species while optimising catches. The maximum sustainable yield (MSY) is a traditional model of this concept (Hilborn and Walters, 1992). From the economic view, the purpose of a fishery is to create income rather than produce fish, therefore costs in catching have to be considered. A simple economic demand for management is to maximise the gross profit from the fishery by using moderate costs. The maximum economic yield (MEY) is the typical theory of this concept (Hilborn and Walters, 1992). Nevertheless, fishermen are an essential component in fishery industries, since they represent the fishing effort, which is influenced by human behaviour. Thus, all fisheries management have to find which of several alternatives will bring the most desirable outcome. Fisheries management can therefore involve a complex mix of biological, political and economic decisions, where several countries may exploit the same fish stocks. This may need international cooperation to be accomplished (e.g. Food and Agriculture Organization, Northwest Atlantic Fisheries Organization, International Council for the Exploration of the Sea).

Whatever the requirements of fisheries management, assessment of stock abundance is the foundation for successful management. Stock assessment plays different roles in the stages of fishery development and should play an important role in modifying the fisheries system for pursuing optimum yields following unpredictable changes of fisheries in response to changes in the environment. To carry out stock assessment, two biological characteristics of the target species provide essential information. First, information about the growth and longevity of the target species enable us to find the potential for the size of allowable catches (Royce, 1996). Secondly, knowledge of the behaviour patterns of target fish in terms of migration and distribution may help to avoid the collapse of the stock. Therefore, it is necessary to study the ecology of target species before trying to proceed with fisheries management for that species.

1.3 The role of fisheries ecology

In order to achieve a sustainable yield of marine fish, it is necessary to determine and understand the distribution, abundance and movement of the target and by catch fish species and to understand the significance of these behaviours. In fisheries science, most studies are concerned with groups of interbreeding individuals of the same species, called populations; with other groups of different species, in fixed areas, called communities; and with the mechanisms of all communities and their living environment in a given area, called an ecosystem. The ecosystem could be regarded as the true resource unit for the fishery industries to deal with, because fishing activities on the stock of target species will influence the structure of a given ecosystem through feeding competition and food availability. Therefore, it is necessary to realise the role of any species of target fish in an ecosystem. Fisheries ecology is applied to the study of interrelationships among organisms and the interrelationships with their environments. The main aspects of fisheries ecology studies are as follows:

1. Each population of a species has its own limited distribution and abundance in a given area. A key aspect of understanding the ecology of exploited fish species is the characterisation of behavioural and physiological responses to the physical and biotic environment. An understanding of life history traits and response to change in the environment is also important.
2. To determine variations in abundance of fish stocks. The survival, growth, and reproduction of individuals within a population, and community structure will influence the variation in stock abundance.
3. To quantify and understand the temporal and spatial dynamics of fish populations. The movement and migration of any species are determined by its life history, pattern of distribution, rhythms of diel and seasonal activities, and properties of feeding, spawning and overwintering. These studies can improve catches by exploiting periodic fish aggregations efficiently, but are more important for defining stock separation characteristics and enabling the protection of vulnerable stages of the life cycle.
4. The main disturbances on the marine environment and fish resources by humans include overfishing and water pollution. Fisheries ecology has a key role for helping to maintain the ecosystem balance and the renewal of fish stocks. Knowledge of fisheries ecology may enable us to estimate the optimum catch of marine organisms without severely damaging the environment and overexploiting stocks, although it is recognised that in several cases this objective has not been achieved (Royce, 1996)

It is clear that the concepts of fisheries ecology are wide-ranging and complex. However, in order to attempt appropriate fisheries management, a knowledge of several aspects of fisheries ecology is a prerequisite.

1.4 Why study common wolffish?

The United Kingdom is an island country, which is composed of several isles in the Northeast Atlantic area of continental shelf, and as such, has abundant marine resources. The total fish production of the UK was about 1 million tonnes with a total value of £1.9 billion in 1996 (FAO statistical 1996 records). This value accounted for 4.4% of total expenditure in food according to statistical reports (MAFF, 1999). Fish therefore provide a significant proportion of animal protein in the UK. The total catch of marine fish and shellfish of the UK occupied 88% of total fish production, most of which was caught at sea.

The North Sea is a traditional and important fishing ground in the Northeast Atlantic (Cushing, 1968). The North Sea has become an important economic area in Europe. After the Common Fisheries Policy (CFP) of the EC was adopted in 1983, the North Sea became the UK's most important fishing ground. In 1997, total UK catches in the North Sea occupied 40% of the total UK catch (MAFF, 1999). The fishing fleets of other EU or non-EU countries also operate in this region. Thus, any stock collapse in the North Sea would strongly influence the fishery industries of UK.

Historical fish landing data for the North Sea since 1973 is shown in Fig. 1.3. The highest catch occurred in 1974 at 3,671,619 tonnes, and then the amount caught declined gradually. In the 1980s, fish landings were stable at an average level of 2.65 million tones, but during the 1990s, catches fluctuated widely and the lowest catch of 2,255,739 tonnes occurred in 1996. Generally, the total catch of demersal fishes displayed the same trend as for all fishes landed in the North Sea (Fig. 1.3), the yield was more stable and ranged between 1.0 and 1.4 million tonnes except in 1973.

The main demersal species in the North Sea for fishery industries are cod (*Gadus morhua*), dab (*Limanda limanda*), haddock (*Melanogrammus aeglefinus)*, lemon sole (*Microstomus kitt*), megrim (*Lepidorhombus whiffiagonis*), monkfish (*Lophius piscatorius*), plaice (*Pleuronectes platessa*), saithe (*Pollachius virens*), sand eel

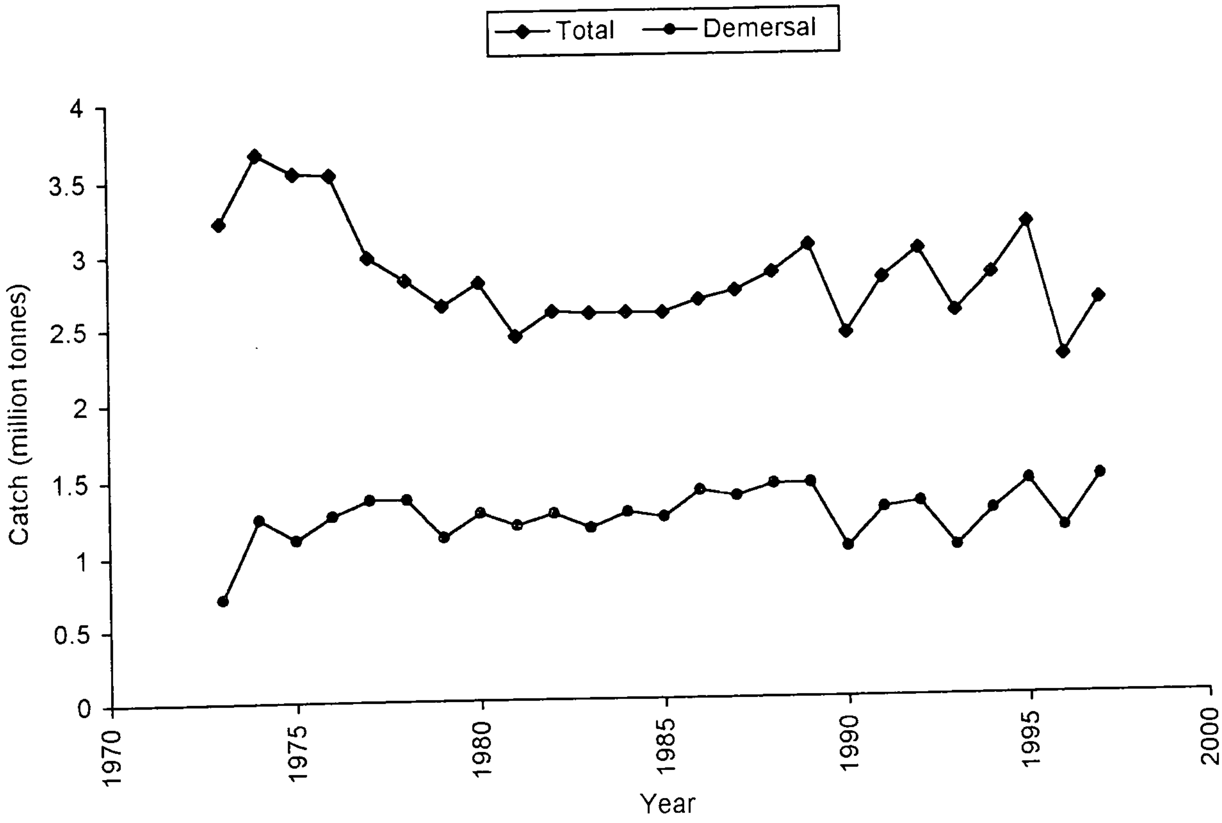


Fig 1.3. Total catch and demersal fish catch from the North Sea between 1973 and 1997 (data from FAO, 1999).

(*Ammodytes tobianus*) and whiting (*Merlangius merlangus*). The dominant species of pelagic catches are herring, horse mackerel (*Trachurus trachurus*) and mackerel (*Scomber scombrus*). These species and some shellfish such as crabs, prawns, scallops and whelks have represented more than 90% of the total catch from the North Sea for the last decade.

Since the International Council for the Exploration of the Sea (ICES) was established in 1902, there have been many fisheries biology studies of exploited fish in the North Sea, carried out with the cooperation of scientists from member countries. There were a number of pioneering fisheries studies in the North Sea in the late 19th century (Smith, 1994) but studies on the whole of the North Sea principally began with the ICES cooperation. Moreover, after the stocks of main target species such as herring, cod, and haddock collapsed or became severely depleted in the North Sea, fishery scientists gave more attention to the study of these species (e.g. Graham, 1935; Beverton and Holt, 1957; Gulland, 1956; Cushing, 1967, 1980; Daan, 1987; Smith, 1994). Most of the studies have been carried out on the dominant groups such as gadoids, pleuronectiforms, clupeids and scombrids. This has resulted in the creation of detailed databases of information concerning these species by ICES since the beginning of the 1970s (ICES, 1999). However, there is still little information on a number of less important species such as dogfish (Scyliorhinidae, Squalidae), skate and rays (Rajidae) and common wolffish (*Anarhichas lupus*) although research work on skate has recently increased (Walker and Hislop, 1998). Such species play significant ecological roles in the North Sea demersal community. Alteration in the species composition will tend to influence the population growth and trophic interactions of other species (Nikolsky, 1963). There is some evidence that the ray/skate communities of the North Sea have become dominated by small fast-growing, early maturing species such as starry ray (*Raja radiata*) as a result of intensive fishing of the larger, more desirable species such as thornback ray (*Raja clavata*) (Walker and Hislop, 1998) Therefore, to pursue both single-species and multi-species fisheries management, it is necessary to consider the interactions and relationships between species. Moreover, different species behave in different ways when encountering different types of fishing gear and a lack of understanding of the broad range of responses by species has resulted in mismanagement (Hilborn and Walters, 1992).

The common wolffish is also known as the Atlantic wolffish or striped wolffish, and often known commercially as catfish. They are often caught by commercial fisheries by trawling and longline fishing. The catch records of this species can be found dating back to the beginning of this century for some regions such as the Barents Sea and North Sea. Common wolffish are widely distributed over a broad range of depths and are not found in dense concentrations. Therefore the common wolffish is not subject to a specialised fishery but rather occurs as by catch in trawling for other species. Nevertheless, there has been recently increased interest in the species. The increasing interest in the common wolffish as a food resource is expected to cause increased pressure on the species, although it is not caught in sufficient quantities to be of economic importance by comparison to the main target species such as gadoids and flatfish (Falk-Petersen *et al.*, 1990). Its flesh is of excellent quality according to fishermen. The meat is highly prized and commands a high price in the fish market. In the UK, the value of common wolffish landings reached £1.6 million in 1997. This value occupied 0.3 % of the whole value of marine fish landed in UK. Furthermore, in recent years the European aquaculture industries, particularly in Norway, have shown a major interest in culturing wolffishes (Moksness, 1994). This is because their large larvae are easy to rear on artificial feed and relatively high survival rates have been achieved with a combination of both natural and artificial foods (Moksness *et al.* 1989; Moksness, 1990; Johannessen *et al.*, 1993; Stefanussen *et al.*, 1993; Pavlov and Moksness, 1994; Moksness, 1994). However, little is still known of the life history of the common wolffish, and this also applies to the abundance, feeding, growth and reproductive strategy of natural populations.

Over the last decade the UK has become the main country that captures the common wolffish in the North Sea (the UK takes ~80% of all North Sea common wolfish, ICES Statistics Database, 1998), but little is still known of the fisheries ecology of the North Sea wolffish. Moreover, the North Sea has become the most important fishing ground for some EU countries and has quite a complex ecosystem. Therefore, it is appropriate to carry out research on common wolfish.

1.5 Wolffish biology

1.5.1 The family of wolffishes

The wolffishes, also known by commercial fishermen as catfishes, belong to the suborder Blenniodei and family Anarhichadidae. There are three species in the same genus: common wolffish (*Anarhichas lupus* L.), spotted wolffish (*Anarhichas minor* Olafs.) and northern wolffish (*Anarhichas denticulatus* Kr.). Wolffish are large, blenny-like, benthic species that have robust heads and tapering bodies. They are widely distributed on both sides of the North Atlantic at depths of 5 m to 800 m. However, the common wolffish is the most abundant and widespread of the three species. It is usually found at depths between 15 m to 350 m, while the northern wolffish inhabits much deeper, cooler water. Studies have shown that common wolffish are found in the Barents Sea, the White Sea, along the Norwegian coasts, the North Sea, Skagerrak, Icelandic waters, off the coast of Greenland, off eastern Canada (especially Newfoundland) and the northeast coast of the United States, covering areas from the north temperate zone (e.g. North Sea) to the Arctic zone (e.g. Barents Sea). However, spotted wolffish and northern wolffish are not found in the North Sea, Skagerrak or off the northeast coast of the United States (Barsukov, 1959; Jónsson, 1982). All three wolffish species may move short distances but longer movements of 200-500 nautical miles have been shown from mark-recapture work in Icelandic waters (Jónsson, 1982), the Newfoundland area (Templeman, 1984), Barents Sea (Albikovskaya, 1982) and off Greenland (Hansen, 1958). Movements of common wolffish off Iceland appear to represent an inshore-offshore migration associated with the spawning-feeding cycle (Jónsson, 1982). All three wolffish species are mostly found at temperatures between 0°C to 5°C (Albikovskaya, 1982). The common wolffish and spotted wolffish are of commercial importance. The northern wolffish is not utilised because its flesh is too soft and watery (Smidt, 1981). The growth rate is slowest for the common wolffish, higher for spotted wolffish, and fastest for northern wolffish and varies in different regions (Beese and Kändler, 1969). The growth rate in weight for spotted wolffish is 2-4 times higher than for common wolffish from growth of captive juvenile wolffish of wild origin (Moksness, 1994). The maximum total length (TL) for the northern wolffish is about 200 cm and for the common wolffish and spotted wolffish it is about 125 cm. Commercial catch data of common wolffish shows that the TL of captured wolffish was usually less than 110 cm (Jónsson, 1982; Smidt, 1981). All wolffish species may live for between 20 and 25 years (Beese and

Kändler, 1969), but this depends on the area and temperature in which the wolffish live (Jónsson, 1982).

The biology of the three species is still little known, especially for the spotted wolffish and the northern wolffish. More studies have concentrated on the common wolffish because of its higher potential value and more widespread distribution.

1.5.2 Distribution and habitat temperature

The common wolffish is a non-shoaling benthic fish with a relatively sedentary nature. They inhabit mainly stony areas, but are also found on sandy or muddy substrates. They are widely distributed in the northern part of the Atlantic and adjacent northern seas, ranging from the Barents Sea to the Bay of Biscay in the east and from Greenland waters to Cape Cod in the west (Albikovskya, 1982; Jónsson, 1982). However, these are absolute limits and very few common wolffish are captured as far south as the Bay of Biscay.

The common wolffish can be found over a relatively wide range of depths and temperatures. In the Barents Sea common wolffish were caught from 18 m to 380 m in depth and in the Gulf of Maine at 2 m to 435 m (Barsukov, 1959). In Icelandic waters they occupied a depth zone extending from 8 m to 450 m (Jónsson, 1982). In Greenland waters they have been recorded from 14 m to 550 m in depth (Jónsson, 1982) and off Newfoundland from 1 m to 500 m depth (Albikovskya 1982). They tend to show a seasonal inshore-offshore migration pattern (Keats *et al.*, 1985). This species appears to migrate from shallow waters in spring and summer (feeding season) to deeper waters during autumn and winter to spawn (Barsukov, 1959; Jónsson, 1982; Templeman, 1984). However, Keats *et al.* (1985) found egg guarding by male common wolfish in < 10 m water in off Newfoundland, so this is not always true.

Jónsson (1982) states of the common wolffish: "The catfish, with its body tapering back to a slender caudal peduncle and a small weak tail fin has not the appearance of a good swimmer." Although swimming performance trials have not been carried out on this species, the body form is typical of poor swimmers, which tend not to move long distances (Webb, 1979; Pauly, 1994). Jónsson (1982) carried out tagging experiments in Iceland which showed that common wolffish did not tend to range more than 150 km from the tagging area in search of food and spawning grounds within 3 months of release. Templeman (1984) also supported this result from his tagging experiment of all three species of wolffish in Newfoundland. Thus, the common wolffish does not appear to undertake large-scale migrations. Nevertheless, even small-scale movements between habitats for different purpose such as feeding and spawning may greatly enhance the survival of fishes (Northcote, 1998).

The common wolffish is a cold-water species. Beese and Kändler (1969) suggested that wolffish have a wide range of temperature tolerance from -1°C to 10°C with 1°C to 4°C the favoured range, based on their research off Norway, Iceland and in the North Sea. Kotthaus and Krefft (1957) found common wolffish inhabited the waters off Iceland at 1.8°C to 7.1°C and in Greenland waters at 1.3°C to 5.5°C. In the Barents Sea common wolffish have been found at temperatures ranging from 1°C to 7.4°C (Barsukov, 1959) and off North America at 1° C to 11° C (Bigelow and Schroeder, 1953). Off Newfoundland common wolffish were found over the range -1.4°C to 11°C with the apparent optimum -0.4°C to 4.0°C. The species has also been recorded at temperatures ranging between 0°C and 14°C in the White Sea (Pavlov and Novikov, 1993). In general, the optimal temperature ranges for common wolffish might be considered to be 4°C to 11°C in nature. But this viewpoint has to be considered with respect to their life strategy and their migratory behaviour, because the common wolffish display quite complex strategies of feeding, growth and reproduction.

1.5.3 Food, tooth change and behaviour

Albikovskaya (1983) has provided a general description of the dental system of common wolffish. The common wolffish has well-developed teeth on the intermaxillae, mandibles, palate bones and vomer. Canine-shaped teeth on the frontal parts of the maxillae and mandibles are used to tear food organisms that live on or in the seabed. Conical and round teeth on the vomer and palate bones are used to crush the hard skeletons of bottom living organisms. These wear down quickly and are replaced by new ones annually. Jónsson (1982) provided the first detailed report on the tooth replacement of common wolffish. He mentioned that common wolffish were unlike most fish which renew their teeth gradually as they are worn down by use but instead wolffish replace their teeth once a year. Jónsson (1982) divided the conditions of teeth into 5 stages as (i) old firm teeth (ii) old loose teeth (iii) toothless (iv) new loose teeth (v) new firm teeth. He suggested that tooth replacement occurs from September until December or even early January. Firstly, the teeth are worn by the hard-shelled diet, which has loosened the old teeth by September. The fish then pass through an intermediate toothless period during which they appear to feed little or not at all, until a new set of teeth grows. However, the proportion of these stages of tooth replacement differed by sex and by month in his study. Thus, at any time in autumn and winter there may be some feeding wolfish with an operative dentition.

Analysis of stomach contents of the common wolffish indicate the great variety of organisms, including hydroids, crustaceans, molluscs, echinoderms and fish, that are eaten (Jónsson, 1982; Albikovskaya, 1983; Keats *et al.*, 1986). The common wolffish forages on a variety of prey according to the benthic communities which exist in the locality. Sameoto *et al.* (1994) researching zooplankton prey selection by larval common wolffish (< 30 mm TL) in the Nova Scotia shelf basin showed that they preyed primarily on the high concentrations of *Calanus finmarchicus* stage V and hyperiid amphipods but did not feed on euphausiids. Pavlov and Novikov (1993) analysed the gut contents of juveniles of the common wolffish (< 28 cm), and found that most contained crabs, cod eggs and large quantities of fish larvae. Falk-Petersen *et al.* (1990) found that the stomach contents of larval wolffish from northern Norwegian waters consisted of various crustaceans and fish larvae. The diet of adult common wolffish in eastern Newfoundland was predominantly green sea urchin (*Strongylocentrotus droebachiensis*) (Keats *et al.*, 1986), while echinoderms and decapods were important in deep water off Newfoundland. Molluscs such as whelks (Buccinidae) and scallops (Pectinidae) were the most important prey in the Northwest Atlantic (Templeman, 1985). Jónsson (1982) reported that in Icelandic waters, sea urchins (Echinidae), horse mussel (*Modiolus modiolus*), brittlestars (Ophiuroidea) and fish were the main prey. He also noted that the stomachs of common wolffish were usually filled with food from July to mid-September but were mostly empty from late September to early January. He suggested that this is correlated to the spawning season and tooth replacement. Other studies have also showed reduced feeding during the breeding season, particularly in females just prior to egg laying and for males guarding egg mass (Keats *et al.*, 1986). It is thought females resume feeding shortly following spawning, and males resume feeding shortly after the eggs hatch (Pavlov and Novikov, 1993). Keats *et al.* (1985) suggested that behaviour differences in sex could be used to determine the sex-specific costs of reproduction.

It is very difficult to observe the feeding behaviour of wolffish in relation to life history events in their true natural state. However, Moksness *et al.* (1989) reported observations made in the laboratory. They identified four main stages (i) larval stage - larvae are mostly pelagic, but they also can be seen lying on the bottom; (ii) pelagic stage - fish take food pelagically at this stage and show little interest in food at bottom; (iii) first bottom stage - when feeding, they come up to take food falling into the water, but as food starts accumulating at the bottom, they prefer to take food there; (iv) second bottom stage - almost total bottom feeding. They also suggested that the larvae and juveniles of common wolffish are more active than older fish but less active compared with larvae of other fish species.

1.5.4 Growth

For the common wolffish the specific growth rate, SGR, has been commonly used to describe the growth rate, particularly in aquaculture studies (Moksness *et al.*, 1989, 1990, 1994; Stefanussen *et al.*, 1993; Falk-Petersen *et al.*, 1990; Palov and Novikov, 1993).

The growth rate of wolffish larvae are somewhat variable in different areas. In the White Sea the growth rate was about 2.1 % day^{-1} (Palov and Novikov, 1993), and in northern Norway was near 3.6% day^{-1} (Falk-Petersen *et al.*, 1990). Moksness *et al.* (1990, 1994) also observed the SGR of larvae reared under laboratory conditions varied between 2.9% and 3.6 % day^{-1}. Growth rate in length is lowest for common wolffish compared with spotted wolffish and northern wolffish, and males grow faster than females (Beese and Kändler, 1969; Jónsson, 1982). Jónsson (1982) reported that in Icelandic waters the first year's growth is about 10-11 cm in length after which the growth rate slows down and the average annual growth up to the age of 18 years is 4.4 cm. Moksness (1994) observed the growth rate of this species in captivity beginning from egg hatching. These experiments showed that common wolffish reached a mean weight of 0.37 kg and a maximum of 1.25 kg after 2 years and an average weight of 0.84 kg and a maximum of 2.28 kg after 3 years.

For wolffish, only the otoliths are used for ageing, and other methods have not been favoured (Jónsson, 1982). The scales are too small and length-frequency methods are inappropriate due to the wide variety in monthly catch numbers. However, the innermost rings of otoliths are often difficult to read because the thickness increases each year. Wolffish otoliths are very small in relation to body size and can therefore be difficult to extract, particularly, since the skull is extremely tough.

Pavlov and Novikov (1993) found that the size was lower in the White Sea than in the North Sea and Skagerrak in the older age groups. Jónsson (1982) compared the relationship between age and length of common wolffish with data by other authors for Iceland, the Barents Sea, the North Sea, and Norwegian coast. Growth appeared to be most rapid in the Barents Sea and slowest in combined samples from the North Sea and Norweigan coast.

1.5.5 Reproduction

(1) Males

The testes belong to the percoid type (Keats *et al.*, 1985). Seminiferous tubules are radially distributed from the periphery of the gonad to the duct deferens situated on the dorsal surface of the testes (Johannessen *et al.* 1990). The sizes of the testes do not vary much over the whole year, and is only 0.15 % of total body weight. Normally running males produce less than 2-3 ml of milt when stripped (Johannessen *et al.*, 1990; Pavlov and Moksness, 1994). Usually most males are ripe over almost the whole year and the GSI of mature male fish fluctuated from 0.1 % to 0.3% (Pavlov and Novikov, 1993). Running-ripe males have a papilla on the urogenital pore which easily distinguishes them from the non-ripe males (Johannessen *et al.*, 1990).

(2) Females

The ovaries of the common wolffish are of the paired and close type. Ripening females display a gradual increase in abdominal girth. In addition, all ova are a uniform round shape. Hence there seems to be no marked, rapid swelling of the eggs and multiple spawning seems to be impossible (Keats *et al* 1985; Johannessen *et al.* 1990). The ripe eggs are relatively large and can be between 5.0 mm - 6.9 mm in diameter, but are usually 5.5 mm - 6.0 mm.

According to Barsukov (1959), Jónsson (1982), and Pavlov and Moksness (1996), the fecundity of common wolffish ranges from 7,000 - 40,000 eggs. Templeman (1986) showed that there is a strong correlation between fecundity and body size. Beese and Kändler (1969) also described the relationship of fecundity with body length and body weight.

(3) Maturity

Moksness (1994) mentioned that sexual maturity of common wolffish may occur at a relatively small size. Females were mature at > 0.5 kg, males at > 1kg. Beese and Kändler (1969) suggested that female common wolffish become mature one year earlier and at a smaller size than the males. The smallest mature female caught was recorded at Iceland and was 25 cm (age 7 years). Another one was 26 cm aged 6 years.

(4) Reproductive Behaviour

Johannessen *et al.* (1993) carried out studies of reproductive behaviour of common wolffish in the laboratory and made the following observations.

(i) Males seemed to be quite passive during courtship. The males rolled over on to their side and bent their bodies up from the bottom to form a U shape, followed by stretching, and bending repeatedly. They called this " side - bending" which is a general reproductive behaviour pattern.

(ii) Females have several behaviour patterns during spawning. Courtship may start 4-5 months prior to spawning. About 30-50 hours before spawning, the females turn over on their sides. This behaviour has been termed "side-resting" and included three stages: side-lying phase (12 - 24 h), labour phase (3 - 6 h) and resting phase. After the resting phase, the females start to spawn. The duration of egg depositing varied between 3 and 7 hours. Finally, in a period of 6 - 10 hours the mucus gradually dissolves causing the aggregation of eggs to become a firm round mass.

Based on their observations of spawning behaviour and morphological characteristics:

(i) Males develop a papilla on the urogenital opening which may serve as a copulatory organ.

(ii) The sperm is active in undiluted seminal fluid.

(iii) The common wolffish has relatively small testes since fertilisation is external.

(iv) Males and females were observed to lie close together with physical contact between their sexual openings.

Johannessen *et al.* (1990) strongly suggest that in the common wolffish, fertilisation of the eggs is internal.

(5) Spawning Season

Barsukov (1959) presented data to show that common wolffish spawned in shallow water in the White Sea during July and August. Pavlov and Novikov (1993) reported that common wolffish reproduced at 15 m to 40 m depth during the spawning period in August and September in the White Sea. Beese and Kändler (1969) found the females almost ready to spawn off Greenland during July with a peak in September to October. Jónsson (1982) mentioned that in Iceland, common wolffish migrated from the shallow waters to deeper water in the autumn to spawn. They stayed in the spawning area from September to January with a peak in fish numbers in October. Off Newfoundland the period of reproduction occurred from mid-August to October and was in shallow water < 14m deep (Keats *et al.*, 1985). Pavlov and Novikov (1993) suggest this species breed mainly at depths of 70 m -300 m in the North Atlantic. In the White Sea the larvae hatch from early April to the middle of May (Pavlov and Novikov 1993). Off the north Norwegian coast the larvae begin to hatch during the first half of April (Falk-Petersen *et al.* 1990), while off the Newfoundland coast the larvae appear to hatch earlier by the middle of December (Keats *et al.*, 1985).

(6) Parental care

Each female produces only one egg mass during the spawning season (Powles, 1967). The common wolffish displays parental care behaviour and only males protect the egg masses which are deposited in holes (Keats *et al.*, 1985; Pavlov and Novikov, 1993; Johanssenn *et al.*, 1990). However, Jónsson (1982) reported a contradictory observation of a female wolffish, which spawned in an Iceland aquarium, protecting her egg mass against attacking fish.

1.6 Development of aims

There is still relatively little known about the biology or fishery characteristics of the common wolfish in the North Sea. The common wolffish is not currently one of the most important species in the demersal fishery caught targets. Hence, it is not subject to a specific fishery and occurs as by catch from trawling or other fishing methods. The fishing gears mainly catch older fish. The yield of the common wolffish shows significantly seasonal variation (Pavlov and Novikov, 1993). They suggested that this probably reflects feeding activity, mobility of fish and their migration for breeding.

Among the three species of wolffish, the growth rate of common wolffish is lowest. Although there are some reports which discuss the quality and quantity of food consumed by wolffish, the metabolism and energy transfer during growth are not fully known. There are only some studies on the protein metabolism of captive juvenile common wolffish related to the effects of temperature (McCarthy *et al.*, 1998, 1999). However, the factors that influence growth rates in different areas are unclear. The growth rate of wild common wolffish is likely to reflect the ecosystem that they inhabit, and might be limited by temperature, food availability or digestion and assimilation.

Beese and Kändler (1969) described the relationship between age and length for common wolffish by the von Bertalanffy equation. However, considering the age-length data and largest recorded fish from other reports (Jónsson, 1982; Albikovskaya 1982), this equation overestimates the length of common wolffish in comparison to real data. Therefore, more data is needed to improve and recalculate the parameters.

Wolffish display most of the characteristics of a *k-selection* strategy such as low growth rate, low fecundity, and large body size. The minimum mature size of the common wolffish (female > 0.5 kg, male > 1 kg) is lower than that of the spotted wolffish (female > 4 kg, male >8 kg) (Moksness, 1994). Common wolffish display geographical and depth-related variations in their reproductive season. Their spawning time is different in different areas. Pavlov and Moksness (1994) suggest the main environmental factor, which apparently determines time of maturation, is the photoperiod. For marine fishes, the egg sizes of different species increase with increasing depths due to lower food availability in deeper water. Wolffish have quite large egg sizes, but they deposit their eggs both in shallow and deeper water (Keats *et al.*, 1985). Thus, it seems that wolffish have a complex reproductive strategy. How this behaviour relates to the North Sea population is unclear.

There has been increased work on growth rate, reproduction, and feeding of wolffish in captivity recently (e.g. Moksness *et al.*, 1989; Moksness, 1990; Stefanussen *et al.*, 1993; Moksness, 1994; Pavlov and Moksness, 1994). They show that the artificial fertilisation of eggs is still unsuccessful. There remains a high mortality rate of cultured wolffish larvae and juveniles because of cannibalism, starvation and infection. But higher growth can be achieved in wolffish using artificial pellets rather than natural diets. More and more evidence shows that wolffish could be cultured successfully in the future. However, there is currently limited information concerning the costs of maintenance of body tissues over a range of temperatures. Also, how large is their metabolic scope to cope with feeding and somatic growth? This information is essential for developing the aquaculture of this species, as well as for providing data on the energetics of wild fish production.

The common wolffish seem to represent one of the top benthos consumers in the North Sea ecosystem and in some geographical areas such as the Gulf of Maine it is a keystone benthic predator, influencing the structure of benthic communities (Keats *et al.*, 1986; Hagen and Mann, 1992). Therefore an understanding of its diet and interactions with other fauna in the North Sea is desirable.

Since the common wolffish has been of increasing interest to European countries for several decades, the catch has noticeably increased over the last 20 years in the North Atlantic. However, in some areas such as Greenland, catches and abundance have declined dramatically (Smidt, 1981). Therefore, the stock assessment for this species should be approached now because the yield began to decrease from the beginning of this decade.

1.7 Research concept and format

The biological study of any fishery must examine the dynamics of fish population. This analysis of population dynamics involves measurement of birth, death, growth, reproduction and movement of the fish. But more specifically two questions were asked:

(1) What are the biological features of common wolffish in the North Sea?
(2) What is the status of the exploited North Sea wolffish stock and are current fishing pressures appropriate?

There is still little information on the population dynamics of wolffish anywhere in the North Atlantic at present. Recent literature on the common wolffish has focussed on either diet in the wild or growth rate and survival in captivity. The latter information is mainly concerned with the development of wolfish aquaculture. Increasingly, fishery managers are seeking to manage multi-species fisheries so as to optimise catches without detriment to the target species. These concepts are increasingly being applied in order to try and minimise excessive impact on by catch species, which may be important to the ecosystem function. As benthic top predators, common wolffish may play such a role, and excessive depletion of stock may influence ecosystem function.

To answer the above two questions, this study aims to carry out relevant laboratory and field studies on common wolffish to provide an insight into the fisheries ecology of this species in the North Sea, and focuses on temporal and spatial distribution, respiratory energy budget, feeding, age and growth, reproduction and stock assessment. These data are the key to describing the population structure and trophic function of common wolffish in the North Sea for the purpose of fisheries management and ecosystem study. Furthermore, some aspects (e.g. respiratory energy budget) could offer useful information for the aquaculture industry.

The subject matter of the remaining chapters is outlined below.

Chapter 2 comprises the collection and analysis of fishing data for common wolffish, and provides the basic and essential information for North Sea wolffish stock analysis in relation to other fish landings. Such fishing data includes not only the location of fishing effort, length distribution and weight of fish landings, but also the temperature and depth of fishing ground, fishing powers and fishing gear. These studies can provide a preliminary analysis of the spatial and temporal distribution patterns of the common wolffish in the North Sea.

Chapter 3 undertakes to examine several components of the energy budget. A fish consumes food not only to maintain the body tissues for survival but also for locomotion, growth and reproduction. From an energetic viewpoint, the energy that the fish absorbs must be equal to the sum of the energy output in activities and heat loss. Energy budget characteristics differ between fish species, presumably in response to natural selection for appropriate metabolic strategies. Thus, the energy budget can provide a framework for seeking to understand the survival strategies used by different fish species. In this chapter, respirometry was used to determine the respiratory energy budget of common wolffish.

Chapter 4 is concerned with the age and growth, reproduction, and diet of common wolffish. To do any work on population dynamics, the age-length key is basic information that must be established. The pattern and timing of growth also needs to be measured. Measurement of the spawning season, fecundity, and reproductive behaviour, should enable an understanding of the reproductive strategies of North Sea wolffish. From the diet analysis, the feeding behaviour of common wolffish in relation to their habitat may be understood.

Chapter 5 seeks to estimate the population dynamics of the common wolffish in the North Sea. In order to estimate growth, total mortality rate and to incorporate these in a model that provides an estimate of the abundance and yield to be expected from various amounts of fishing effort, requires data on the age and size composition of captured fish, growth rate of fish, and the CPUE by age. Given these data over a period, one can estimate the variation in year class strength and relate this to changes in of fishing effort. Today the most common method currently used in temperate fisheries stock assessment is called virtual population analysis (VPA) or cohort analysis. It is one of the most powerful techniques for the analysis fish stock where the catch-at-age data are available. Once stock size was determined, fishing size-selectivity as well as changes in vulnerability over time could be predicted. However, VPA needs some parameters such as the growth coefficient K, maximum TL, temperature, and the fishing effort. The result of Chapters 2 and 4 are used to provide the necessary parameters. Examination of the trade-off between catching a large number of fish early in their life span and catching smaller numbers of older fish is very important for sustainable fishing. The yield per recruit model which considered the dependence of yield upon growth, age at first recruitment and fishing mortality can provide an answer for the optimum regime of catching wolffish. Even without fishing, mortality from natural causes still occurs. The stock will expand to the maximum abundance the environment capacity allows. Hence the numbers of offspring a female could produce is influenced by the environment in which it lives. The population can decline if fishing mortality is higher than the net rate of reproduction. Here demographic analysis under several fishing scenarios is used to assess fishing effects.

Chapter 6 provides a broad discussion of the results obtained from the laboratory and field studies and their relation to other work. It integrates the information from previous chapters, and from an ecological viewpoint, considers the role of common wolffish in the North Sea environment, and of likely factors, which may shift (or have shifted) the role played by wolffish. The chapter also summarises the situation for the fishery of North Sea wolfish and its likely future.

Chapter 2 Temporal and spatial variations in abundance of common wolffish in the North Sea

2.1 Introduction

2.1.1 Basic statistical fishing data

In open sea environments such as the North Sea, stocks of fishes are the communal property of all relevant nations. However, many fishermen and fisheries scientists have found that the more heavily such stocks are exploited, the more the catches have declined. It is generally recognised that many stocks of fishes have been overfished and decreased in abundance all over the world (Mangel *et al.*, 1996). As a consequence, most countries have begun to study the biology of relevant stocks and their population dynamics and increasingly cooperate internationally (Lim *et al.*, 1995). Fisheries studies often need the collection of long-term information including biotic and abiotic data. However, some fundamental fishing data are easy to obtain, and provide useful information for fisheries management.

In considering the population dynamics of an exploited stock, the fisheries scientist has to estimate the effects of fishing on this stock. However, this can be done only by linking the variations in growth, distribution, reproduction, age composition and total mortality rate with the changes in abundance of fish (Royce, 1996). The essentials for such correlations are correct and consistent data, obtained from the appropriate, scientific statistical system. These data usually include the amount of fishing related to the time and unit area, and catch in weight or number of target species by time and area. The divisions of area must be chosen to agree with the wellknown or probable stock's location (e.g. ICES divisions, NAFO divisions) and also have to be combined with depth information. The time divisions should include the fishing periods or season, and reference to fish habits and temperature by month, quarter or year.

Such biological data are also useful to the fisheries industries, especially when commercial data such as trends in value of fish, amount of fishing boats, employment, kinds of fishing equipment used and time spent in fishing are available. When these data are combined together, this information assists government or fisheries organisations to decide their fisheries management policy.

To study the relationship of commercial fish with their environment, basic fishing data also plays an important role. The complete data on catch according to species, time, exact location, weight, depth of fishing and fishing effort provides useful information in fisheries ecology studies. Moreover, additional data and material such as the size, sex, otoliths, gonads, and stomach of landed fish that are measured or obtained from the fishing market, enable assessment of living habits of commercial species in terms of age composition, somatic growth, feeding pattern, migration, reproduction, distribution and mortality. This can provide a framework for establishing the life history and biology of commercial fish species.

2.1.2 The North Sea

The North Sea covers an area of 575,300 km^2 in northwest Europe. It extends through 11° of latitude from the English Channel (51° N to 62° N) off Norwegian waters, and covers the longitude range 4° W to 8° E adjacent to the Skagerrak. Its northern and southern boundaries open into the Atlantic and this invokes oceanic influences. Moreover, there are geographical and topographical factors, which modulate the environmental characteristics of the North Sea greatly.

The North Sea is situated adjacent to the western edge of the European continental shelf (Fig. 2.1). The south part of the North Sea (< 54° N) is usually shallower than 50 m while the central region lies between 50 m and 100 m in depth. The north part of the North Sea (between 58° N and 62° N) from Scotland to Norwegian waters is situated in the range of the 100m – 200m isobath. The Rinne area (near the Norwegian coast) is deeper than 200 m. The bottom of the North Sea is covered mostly with sand but some of the deeper areas have a mud surface. Typically, coastal areas have some scattered stony patches mixed with gravel and sand. The North Sea receives Atlantic water by a strong current from the north around the Shetland Islands. Several currents bring Atlantic water into the north part of North Sea with one deep cold-water current entering the Rinne from Arctic. Currents form the north flow down the east coast of

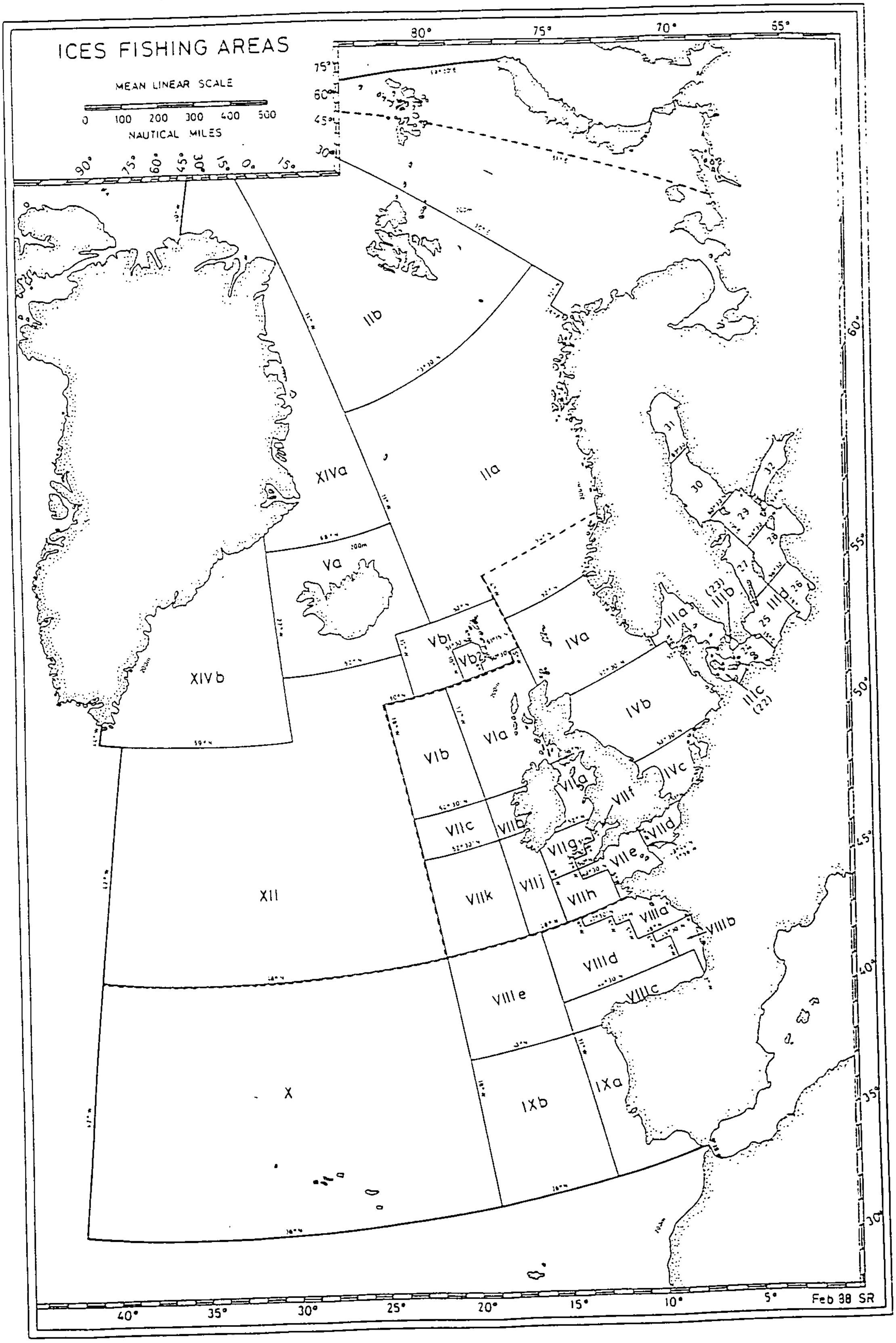


Fig. 2.1. The ICES fishing area divisions for the northeast Atlantic. The divisions IVa, IVb and IVc represent the North Sea. (Reproduced with permission of ICES).

Scotland and England and then turn east in the Dogger Banks. The drift comes through the English Channel and joins the eastern-flowing current in the central part of the North Sea and continuously flows along the Norwegian coast (MAFF, 1981). The cold water and warmer water mixed here result in a marine fauna which is rich in variety, containing elements of cold and temperate water faunas. Moreover, the continental shelf edge is a significant barrier to population expansion for many benthic species, especially benthic fishes (Hayward and Ryland, 1995). However, the North Sea is an open system, which should not be considered in isolation from the west of Scotland shelf, the Skagerrak and the English Channel (ICES, 1993).

Temperature is accepted to be one of the most important of the physical environmental factors that influence the life histories of marine organisms (Jobling, 1994). The shallow south part of the North Sea is much warmer than the water in the north area during the summer. In contrast, this area cools rapidly and is then cooler than the water in the north during the winter. In the north the water is deeper, and the temperature does not fluctuate so intensely. However, a thermocline is formed in this region.

The relatively large area of the North Sea comprises a complex and characteristic ecosystem. The primary producers are almost completely planktonic organisms. Steele (1974) has established the ratio of energy conversion between primary producers and consumers in the North Sea to be 1:0.1-0.3. The marine fauna including the dominant groups of invertebrate (e.g. crustaceans, molluscs, Annelida) and vertebrate groups (e.g. Pisces) have been described by Hayward and Ryland (1995). These organisms form complex food webs in the North Sea. The primary producers are consumed by herbivore planktons. The herbivores are then taken by invertebrate carnivores, pelagic fish and benthos. The invertebrate organisms are consumed by pelagic fish and demersal fish. Finally, the demersal fishes also take pelagic fish and benthos as food. Many species have been shown to exhibit complicated relationships with other organisms in the North Sea (e.g. herring (Hardy, 1924)).

There are about 224 species of fish existing in the North Sea (ICES, 1993). This geographical area has been economically important for fisheries industries throughout the histories of the nations around it. Twelve fish species provide over 95 percent of the total catch in the North Sea, and are principally gadoids, clupeids and flatfish (Pitcher and Hart, 1982). Many fisheries scientists have studied these fish species of the North Sea since the end of the 19th century (Smith, 1994). The divisions of the whole Northeast Atlantic area divided by ICES are shown in Fig. 2.1. The North Sea area comprises the divisions of IVa, IVb and IVc.

2.1.3 Fishing gear

Many gears have been designed to catch a wide variety of fish species since the prehistoric age. These fishing gears have evolved to their present forms through many modifications that were made to catch specific kinds of fish with greater efficiency (Pitcher and Hart, 1982). The greatest changes of fishing gears have occurred since the end of the last century because high mechanical power has become available for vessels. A number of materials have also been innovated and improved to make more efficient fishing gears. Now, most commercial fishing catches are caught by trawls, purse seine, line fishing, and gill net (Royce, 1996). However, most demersal fishes are captured by trawls and large amounts of pelagic fishes are caught by purse seine. This is because these two types of gear have greater efficiency and better selectivity compared with other gears (Engås, 1994).

There are many fishing gears used in the North Sea. These include the beam trawl, otter trawl, pair trawl, midwater trawl, Danish anchor seine, Scottish fly-seine, pair fly-seine, purse seine, drift net, long line, shank nets and others (Greenstreet *et al.*, 1999a). However, the most important fishing gears used in the North Sea are trawls (Greenstreet *et al.*, 1999a). The second most important fishing gears are seine types. These gears are effective for the principal demersal and benthic target fish species, which are predominant in the North Sea. Only a small quantity of the total catch is caught by other fishing gears.

2.1.4 Aim of this chapter

The aim of the work presented in this chapter was to determine temporal and spatial variations in abundance of common wolffish in the North Sea through analysis of statistical fishing data. Such information is important for use in considering other aspects of the fisheries biology of this species later in this study (chapters 3,4,5).

2.2 Materials and Methods

2.2.1 Historical fishing data

Historical fishing data for common wolffish in the UK were calculated from the statistical fisheries year books which were published by MAFF and SOAEFD (and its predecessors) from 1905 to 1997. The statistical catch data of common wolffish of the whole Northeast Atlantic and the North Sea were obtained from the fisheries databases of FAO and ICES from 1971 to 1997. Wolffish catch data for the Northwest Atlantic was not analysed because the catch data from NAFO reports were combined for two species of the wolffish family (*A. lupus* and *A. minor*). Also NAFO reports available contained only five years data (1991-1995).

2.2.2 Hydrological and topographical data of the North Sea

The bottom temperatures of the North Sea for 1996-1998 were obtained from ship surveys, which were carried out by ICES and CEFAS. The data used were only for the bottom temperature in summer (June-August) and winter (December-February). Data for spring and autumn seasons were unavailable. The Surfer package software (Golden Software Ltd.) was used to present these data.

The depths of the North Sea fishing ground from where the common wolffish were captured were obtained from CEFAS ground surveys and the admiralty sea charts published by the Hydrographic Office of the navy. The bottom substrate composition of the North Sea was obtained from the 'Atlas of the Seas around the British Isles', which was published by MAFF, (1981) and from evidence gathered in a CEFAS ground survey in which I participated (August 1998).

2.2.3 Fish samples from commercial landings at North Shields and from ground fish surveys by FRS (SOAEFD) and CEFAS

Total length of common wolffish were measured to the nearest centimetre and recorded monthly from commercial landings for January 1996 - November 1998 at North Shields, northeast England. The months of each season in this study were defined as spring (March – May), summer (June – August), autumn (September – November) and winter (December – February). The fishing areas and boats' names were also recorded. The division of fishing areas followed the system of alphanumeric coding that is used in the UK. Each division of fishing area was half a degree of Latitude in length and a degree of longitude in width. The alphanumeric codes for divisions of the North Sea were 30 to 52 from south to north and E6 to F7 from west to east. Most of the common wolffish had been gutted in the boats soon after they were captured. Therefore, the ungutted weight data of common wolffish was unavailable from most commercial landings. Total weight of common wolffish landings by month was obtained from MAFF records in North Shields. In this study about one third of the total catch of common wolffish landed at North Shields were measured (3,121 kg in 1996, 3,019 kg in 1997 and 575 kg in 1998). However, these measured individuals were randomised during collection. Moreover, the fishing areas of these samples also covered the whole fishing regions of boats that landed common wolffish at North Shields. Therefore, the samples are believed to be adequate and unbiased. Moreover, since they covered much of the fishing area for common wolffish in the North Sea (> 80% of area), they are probably representative for other ports.

Some samples of common wolffish were collected from the boat 'Scotia' (FRS) in August 1996 and the boat 'Cirolana' (CEFAS) in August 1998 during ground fish surveys in the North Sea. Both boats used bottom trawls as the fishing gear (also see section 2.2.5). The sample areas of the two boats for common wolffish were from 54° N to 62° N and 2° W to 7° E.

2.2.4 Fishing effort and catch per unit effort (CPUE)

The fishing effort (e.g. working hours, days, and fishing gear) of the boats that caught common wolffish and landed them in North Shields were obtained from MAFF records during 1996-1998. In addition, the horsepower (kW) of each boat was also determined (MAFF, North Shields).

To minimise the effect of varying of fishing power between boats, which influences the catchability of fish by boats. The horsepower was standardised to 200 kW for calculating the CPUE. This value was determined by averaging the horsepower of boats that captured common wolffish in the North Sea. In this study "kg per 200kW×hr" was used to represent a unit for CPUE analysis. In > 99 % of catches of common wolffish

North Shields boats used bottom trawls. Therefore capture method was similar in most cases.

2.2.5 CEFAS historical catch data

For comparison of CPUE calculated from commercial landings, CPUE from ground fish surveys by CEFAS for 1977-1998 was also calculated. These surveys were carried out by 'RV Cirolana', which was built in 1970 and is 72 m in length, 1,594 tons gross and 2,200 hp. Each cruise was conducted every year between July and September. There were 74 GOV fishing stations in the whole North Sea (62 stations above 54° N). The sampling areas were at the same fishing stations over this period. The bottom trawl was used as the fishing gear during these surveys. Standard fishing speed was 4 knots measured as trawl speed over the ground. Each haul lasted 1 hour until 1992. The net opening width and height, and trawling depth were also recorded during sampling. However, ICES have standardised the fishing gear and methods for the international bottom trawl surveys in the North Sea since 1992 (ICES, 1992). The lining of the cod-end consists of 400 stretched meshes of 20 mm each, with a total length of 8 m. The total circumference of the lining is 600 meshes and total buoyancy of the floats on the net is 172 kg. Each hauls last 30 minutes. The unit for this CPUE was "number of fish per hour". Therefore, the catch number in calculating CPUE has been doubled since 1992 because the hauls last half an hour.

2.3 Results

2.3.1 The fishing area for common wolffish in the North Sea

The fishing areas in this study for common wolffish covered most of ICES areas IVa and IVb (54 °N to 60° N) (Fig. 2.2). There were no records of common wolffish caught south of 54° N latitude (area IVc) in this study. Therefore, the latitude 54° N reasonably represents the southern limit of distribution for common wolffish in the North Sea. North Shields was quite an important fishing port for landing common wolffish caught in the North Sea and especially those captured near the southern limit of their range.

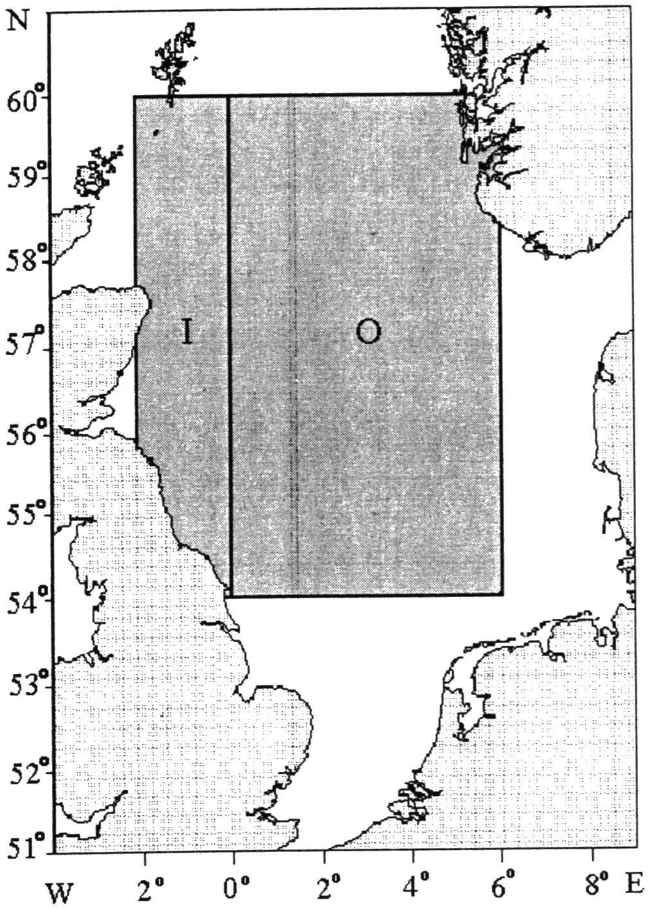


Fig. 2.2. Sampling area of common wolffish in this study (shaded area). The area between 2° W to 0° (I) is defined as inshore for UK fishing boats in this study. The area ranging from 0° to 6 °E (O) is defined as offshore. Samples were obtained from commercial landings at North Shields and ground fish surveys carried out by FRS (Aberdeen) and CEFAS (Lowestoft).

2.3.2 The topography of the North Sea

An isobath diagram of the North Sea is displayed in Fig. 2.3. Depths increase with increasing latitude, with a maximum depth of up to 200 m. Most of the southern half of the North Sea is shallow, and the 50 m contour runs approximately north-eastwards from the English coast at ~54° N. The depth at which common wolffish were caught were between 30 m and 200 m and mostly in 60 m-150 m. The bottom deposits of the North Sea were classified broadly into mud, sand, gravel or mixtures of these components. The substrates of bottom that the common wolffish inhabited were mostly in mixtures of sand and gravel. But the bottom off northeast England (54° N-56° N) where common wolffish were caught is a rocky area. This area was an important fishing ground for common wolffish by fishing boats from North Shields.

2.3.3 The bottom temperature of the North Sea

The bottom temperature of the North Sea for 1996-1998 is shown in Fig. 2.4. In the summer, the temperature was warmer in the southern area and in coastal waters. The temperature distribution was strongly influenced by the 50 m depth contour. Additionally, the topography also affected the temperature. The central and northern part of the North Sea is deep and did not show intense seasonal changes in temperature. In contrast, winter temperatures were colder in shallow and coastal waters, especially in the southern part of the North Sea. The North Sea bottom temperature varied from 5°C to 18°C in summer and from 0°C to 9°C in winter. Summer temperatures in1998 were warmer compared with those of 1996 and 1997 (Fig. 2.4.a, Fig.2.4.c, Fig. 2.4.e). The winter temperature in 1996 was cooler than that in 1997. From these temperature distribution maps, the temperatures common wolffish inhabited were between 5°C to 12°C (Fig 2.4.b, Fig. 2.4.d) and had a mean value of 8.3°C for 1996-1998 in the North Sea.

2.3.4 The general historical fishing data of the UK in the North Sea

The fish landings data for the North Sea by the UK is shown in Fig. 2.5. Both the total catch and demersal catch showed similar trends for the last thirty years. The yields of all fishes and demersal fishes caught by UK boats were highest at near 1,000 tonnes and about 800 tonnes in the 1960s but have since declined. The yield from the pelagic

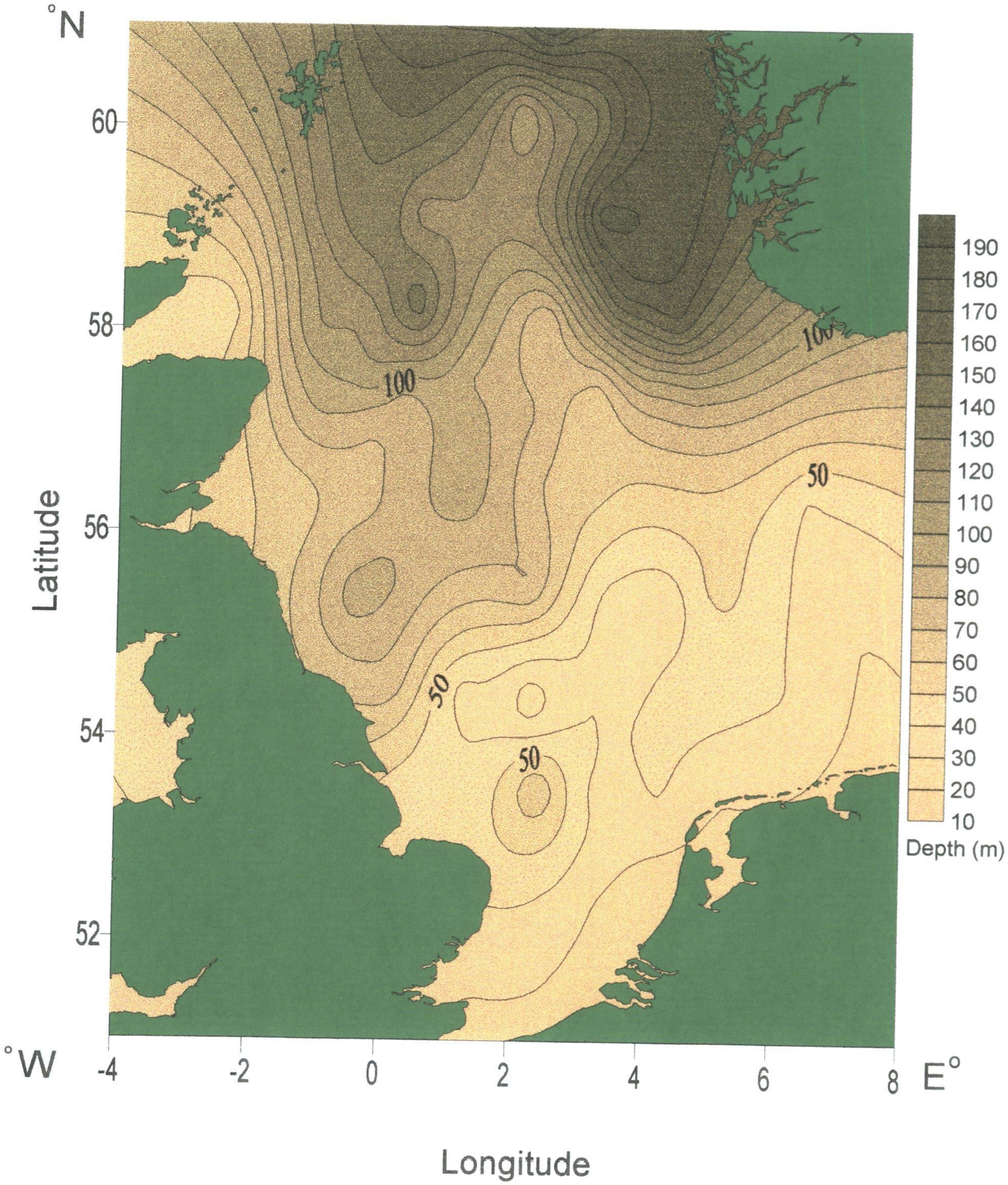


Fig. 2.3. The isobaths of the seabed of the North Sea. Depth increases with increasing latitude. The first contour begins at 10 m.

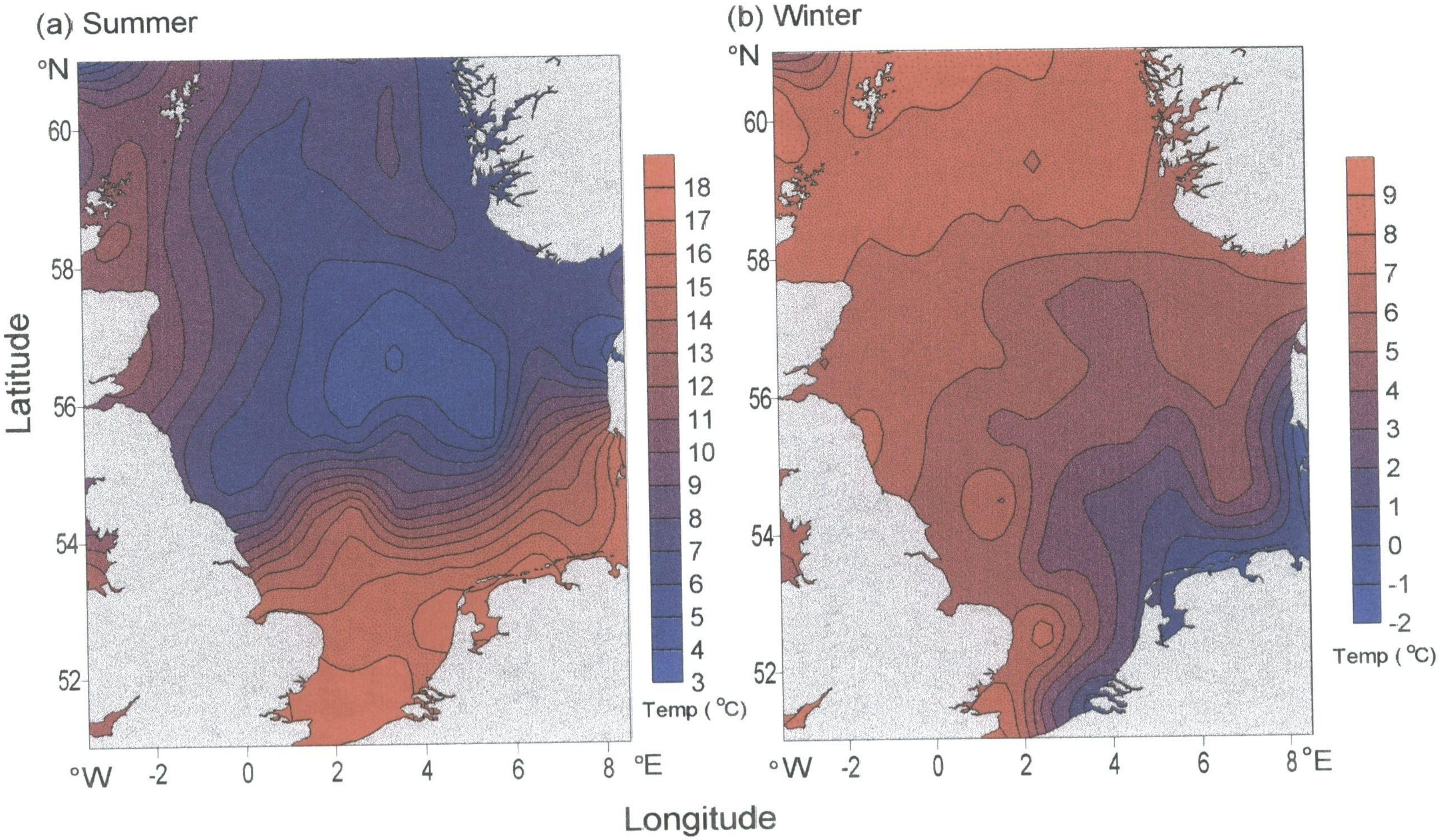


Fig. 2.4a & b. The seasonal variation in bottom temperature of the North Sea for 1996. (a) summer season, (b) winter season.

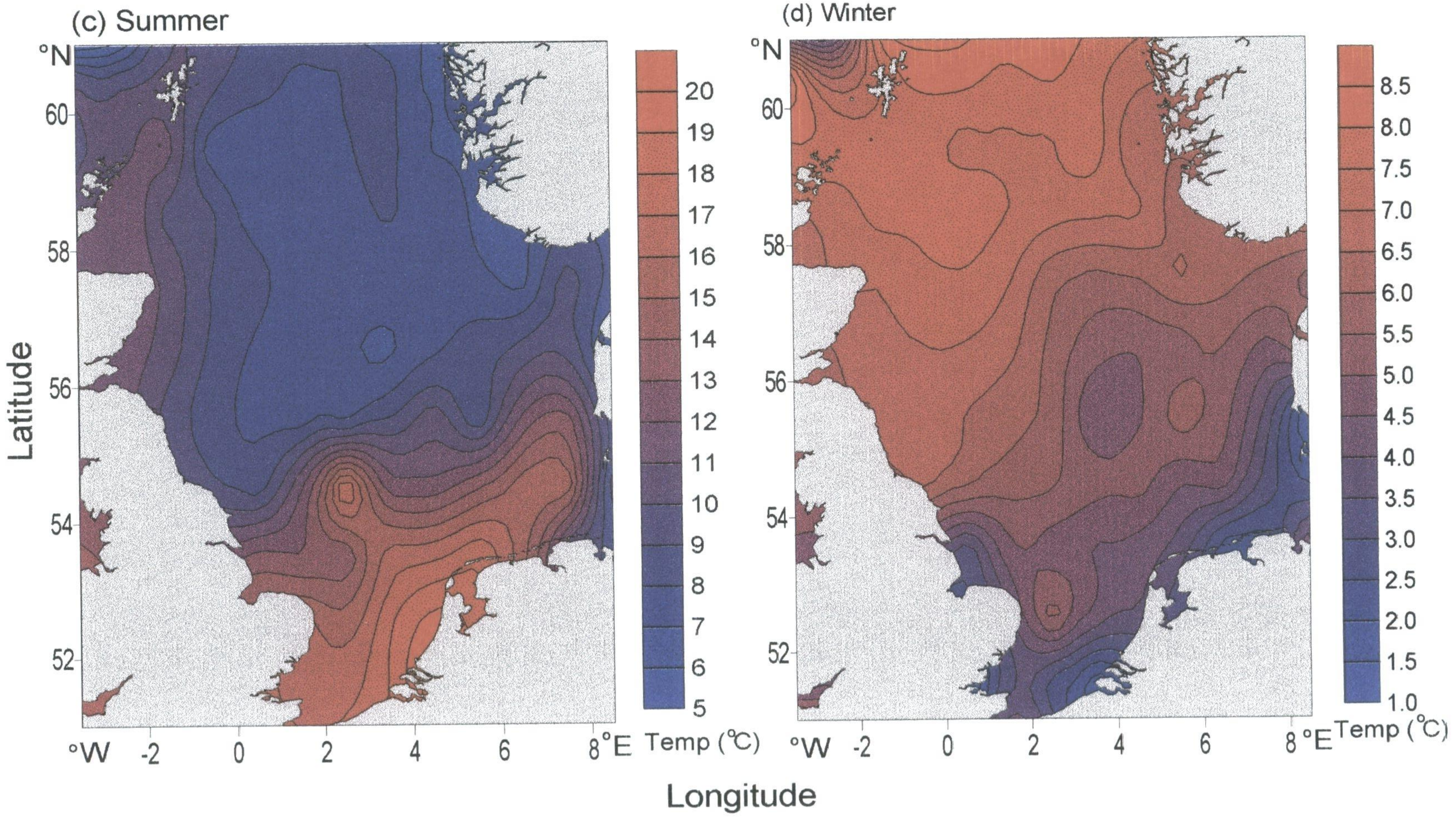


Fig. 2.4c & d. The seasonal variation in bottom temperature of the North Sea for 1997. (c) summer season, (d) winter season.

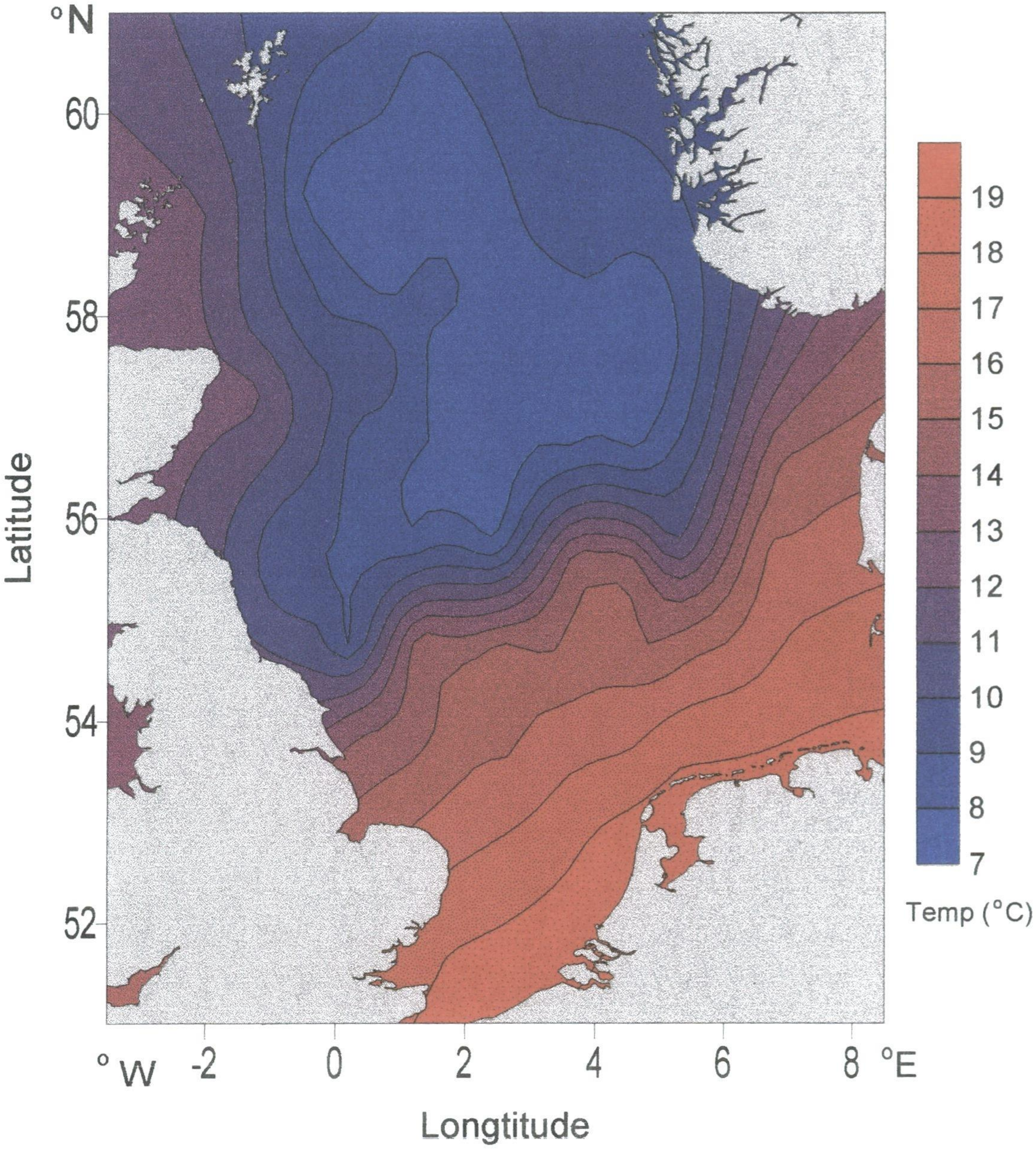


Fig 2.4e. The bottom temperature of the North Sea for summer 1998.

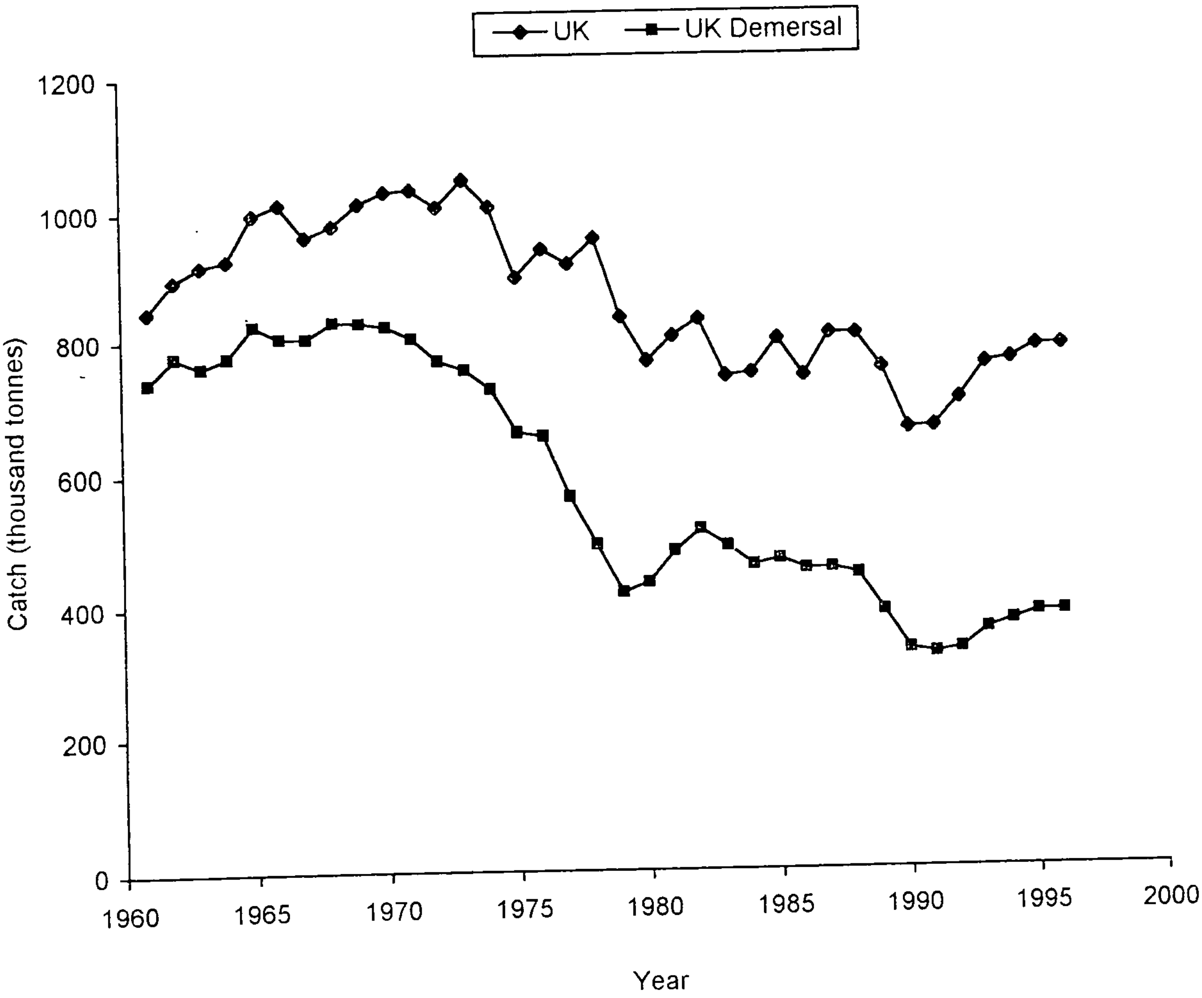


Fig. 2.5. Total catch of all fishes and demersal fish species by UK fishing boats for 1961-1996.

fishery occupied less than 20 % of total catch in the 1960s but has increased gradually to 50% of the total catch during the last ten years. The catches of demersal species have declined by 50 % over the last 30 years.

2.3.5 The catch data of common wolffish in the Northeast Atlantic

The amount of common wolffish landed in the Northeast Atlantic (42° W-30° E and 48° N-90° N) is shown in Fig. 2.6. The yield of common wolffish was highest in 1975 (50,000 tonnes) then declined rapidly to 20,000 tonnes in 1981. After 1981, catches were very stable at about 22,000 tonnes until 1995 when they increased to 31,000 tonnes by 1997. However, the average landings of common wolffish have declined by 40 % over the last 30 years. There were more than ten countries' fishing boats in this immense area. The principal areas for catching common wolffish are in Icelandic waters (Va), and the Barents Sea (I), in Norwegian waters (IIa, IIb), and in the North Sea (IVa, IVb). The Icelandic waters are the most important area for catching common wolffish in the Northeast Atlantic. After 1980, the yield for this area accounted for an average of 45 % of the total catch and has been an average of 12,450 tonnes over the last 27 years. The catch in this area has been more stable compared with other areas. The yields of common wolffish in the Barents Sea and in Norwegian waters declined to their lowest levels at the beginning of 1990s, but have increased again from 1996.

The yield of the common wolffish in the North Sea is displayed in Fig 2.7. The highest catch of 2,561 tonnes occurred in 1983 after which yield declined stepwise to the lowest catch in 1996 of 1,144 tonnes. The catches of common wolffish by UK fishing boats followed the same pattern as overall catches in the North Sea. However, after 1989, the catch of common wolffish by UK fishing vessels occupied more than 80% of total catch by all countries because some countries such as Belgium and Denmark reduced catches of the common wolffish (ICES, 1999). Therefore, the UK became and remains the most important country for landing wolffish caught in the North Sea.

The total catch of the wolffish by the UK since 1910 is shown in Fig 2.8. There were no landings data during World War I and there were low catches during the period of World War II. In this century, the highest catch occurred in 1928 (12,768 tonnes) after

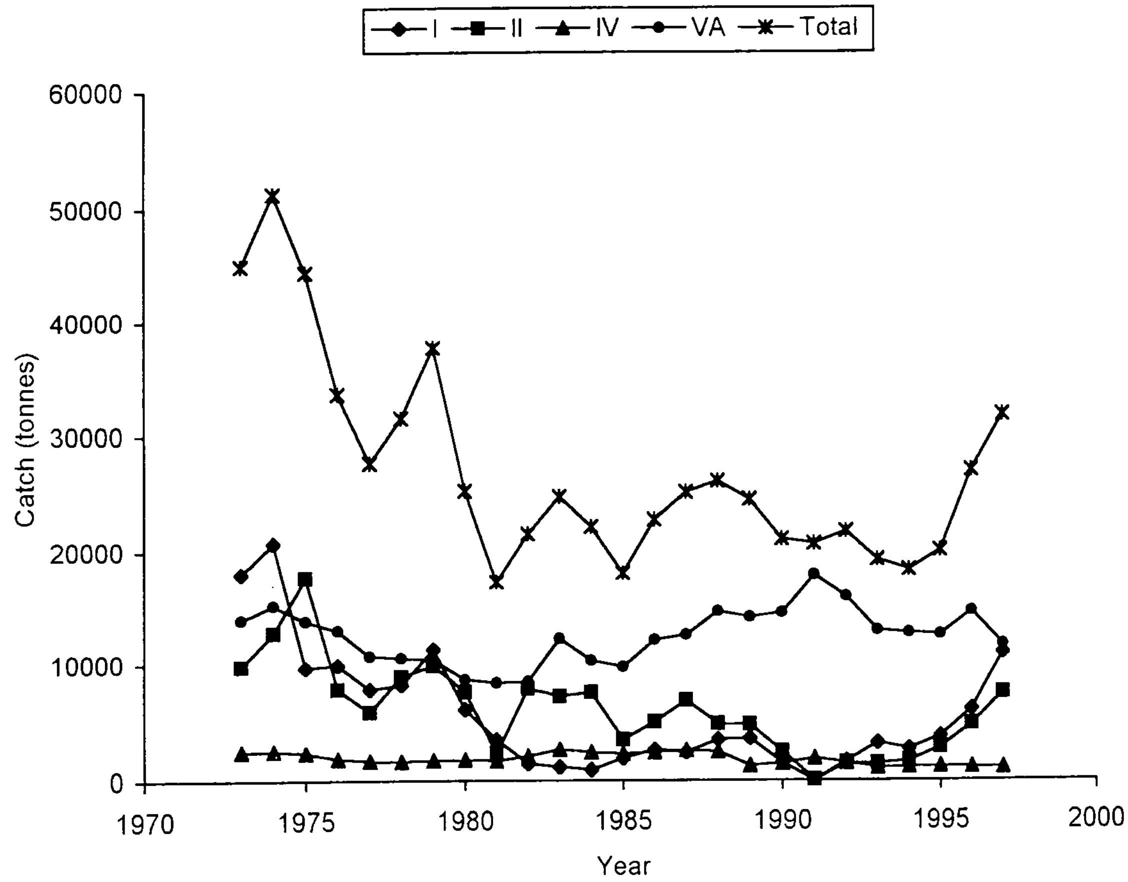


Fig. 2.6. Total catch of common wolffish of different areas in the northeast Atlantic for 1973-1997. (I: Barents Sea, II: Norwegian waters, IV: North Sea, and VA: Icelandic waters).

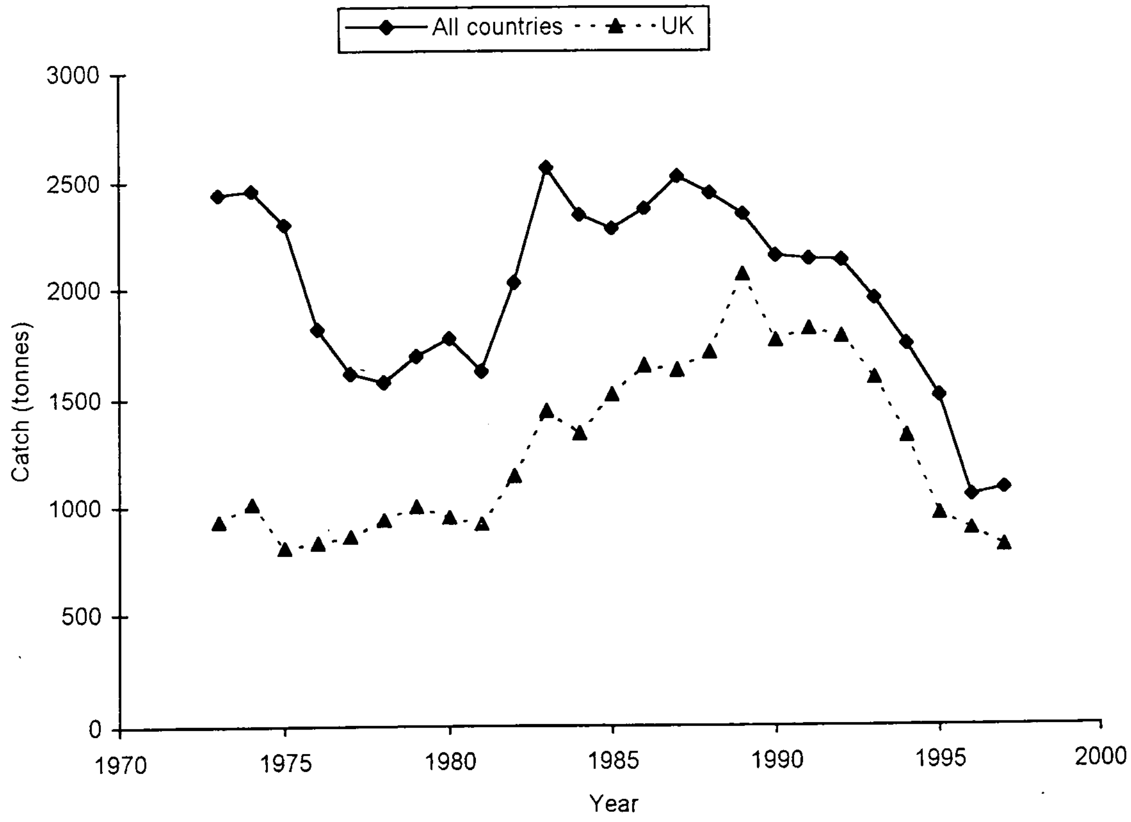


Fig 2.7. Total catch of common wolffish in the North Sea by all countries and by the UK for 1973-1997.

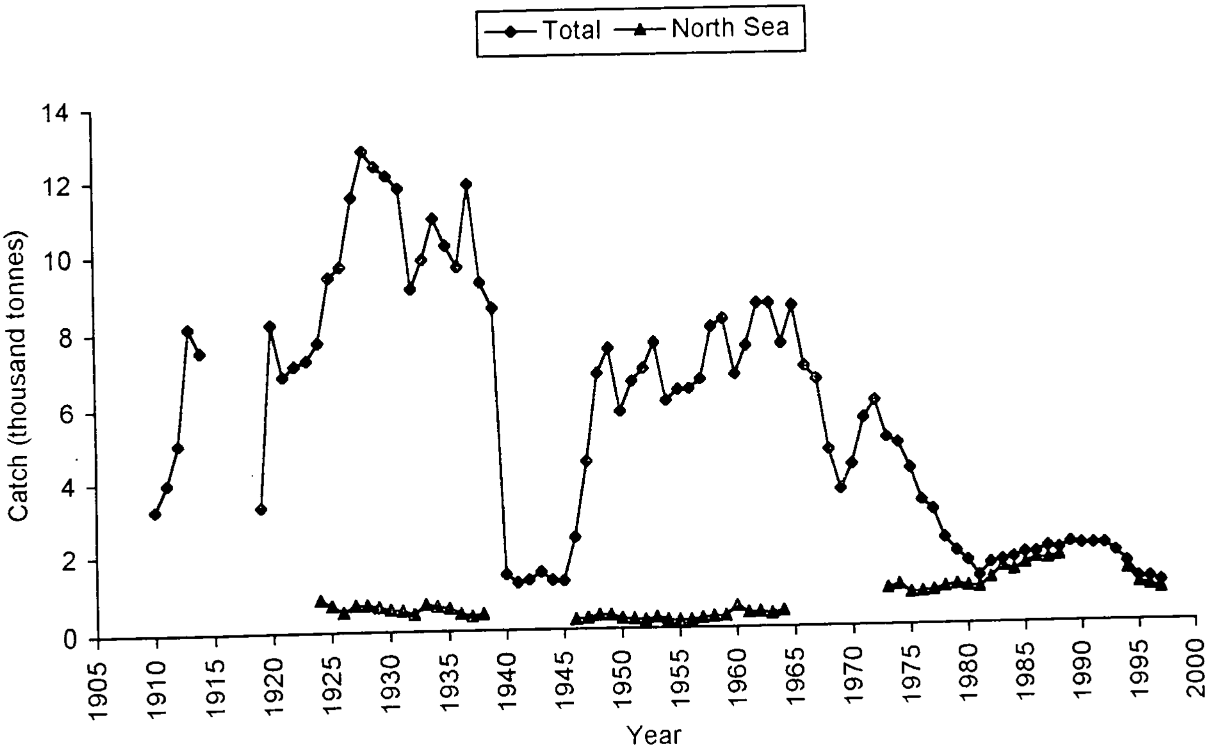


Fig 2.8. Total catch of wolffish in the North Atlantic and the North Sea by UK boats for 1910-1997. (Total catch of wolffish in the North Atlantic by UK boats included common wolffish and spotted wolffish since the UK fisheries statistical year books mixed them as 'catfish' in category. Total catch of wolffish in the North Sea only included common wolffish.)

which yield declined gradually but was still over 6,000 tonnes until 1972. However, after 1972, the yield of wolffish declined sharply to 1,206 tonnes in 1981, rose slowly between 1982 and 1994 with a mean catch of 1,600 tonnes until 1994 and has reduced again to about 1,100 tonnes.

The yield of common wolffish was low in the North Sea from 1924 to 1964, and for those years where data was available was less than 1,000 tonnes. However, the yield of common wolffish in the North Sea increased from 1974 with annual landings of more than 1,000 tonnes. From 1981, the catches from the North Sea occupied about 90% of total catch by the UK. The North Sea has been the main fishing ground for common woffish by UK fishing boats since 1981. The yield of common wolffish caught in area IVb is about two times that from IVa. In the North Sea, most of common wolffish were captured in bottom trawls. Other fishing gears such as purse seine only captured small amounts of common wolffish.

The relationship between total demersal catch in the North Sea by UK fishing boats and catch of common wolffish in the North Sea landed in the UK is shown in the Fig. 2.9. When the amount of North Sea demersal fishes landed tended to decrease, the quantity of wolffish caught in the North Sea increased. However, the catch rate of wolffish increased with increasing fishing effort in the North Sea (Fig. 2.10). Although, there is no report of fishing effort for UK boats by MAFF after 1990, the statistics yearbook mentioned that fishing effort was highest at the beginning of the 1990s, and gradually declined after 1992 through management measures. Therefore, the catch rate of common wolffish in the North Sea by UK boats appears to have been strongly influenced by variations in total fishing effort. The variation in value of common wolffish per tonne by year is shown in Fig 2.11. The price of common wolffish was relatively low, at under £350 per tonne before 1983, after which it increased sharply to the highest level of £1,500 per tonne in 1995.

The fish market of Peterhead lands the highest amount of common wolffish in the UK (Fig. 2.12). More than 30 % of total UK common wolffish catch has been landed there for several decades and the proportion of catch landed here has increased further in the last 5 years even though total landings have declined.

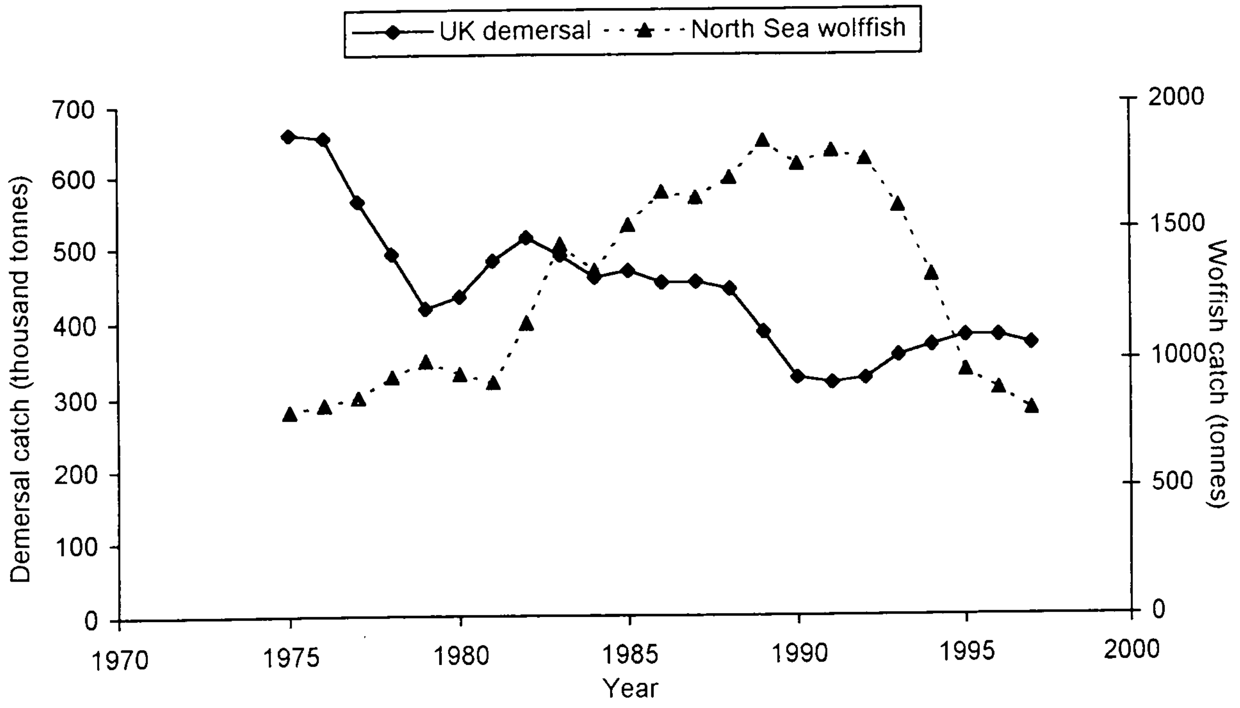


Fig. 2.9. Total catch of demersal fishes and wolffish in the North Sea by UK fishing boats for 1975 -1997

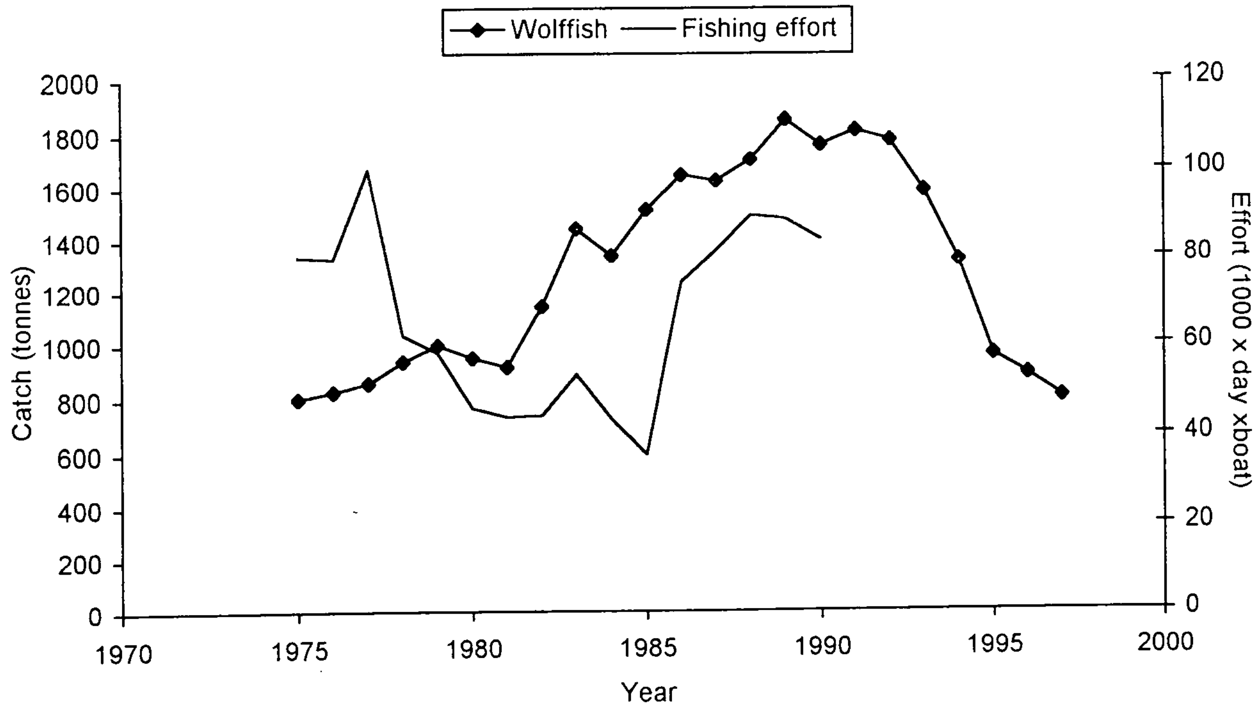


Fig. 2.10. Total catch of North Sea wolffish by UK fishing boats for 1975-1997 and fishing effort of UK boats operating in the North Sea for 1975-1990.

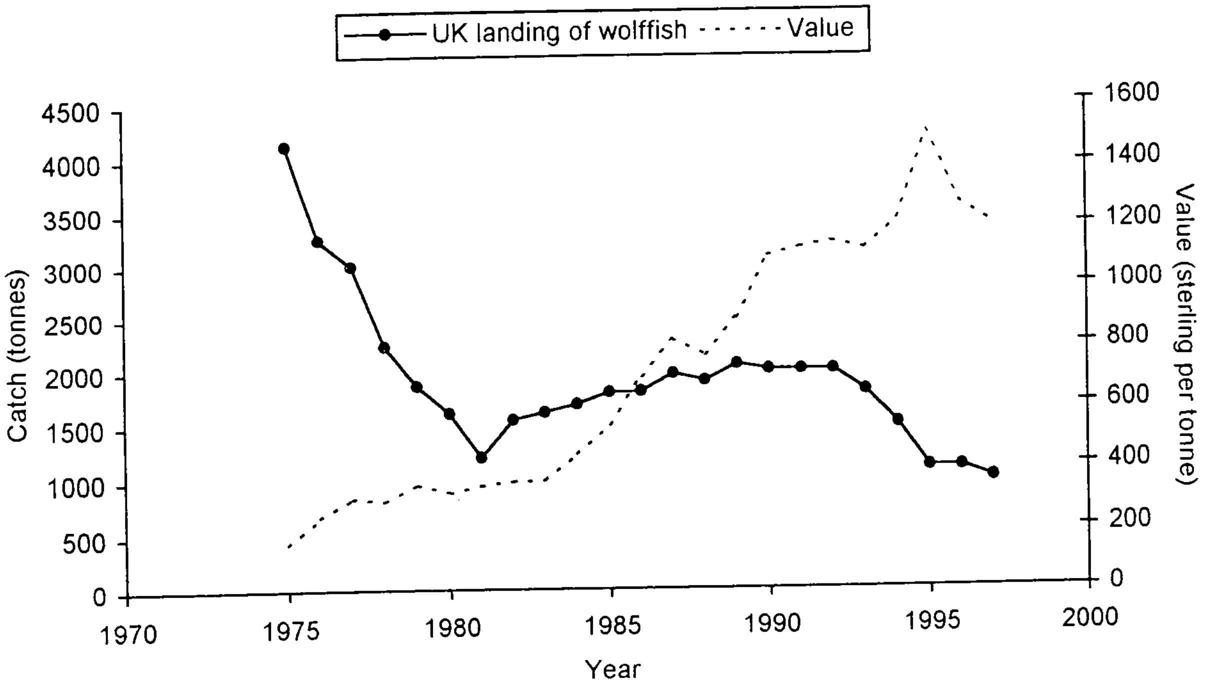


Fig. 2.11. Total catch of North Sea wolffish landed in the UK and the value of wolffish per tonne in the UK for 1975-1997.

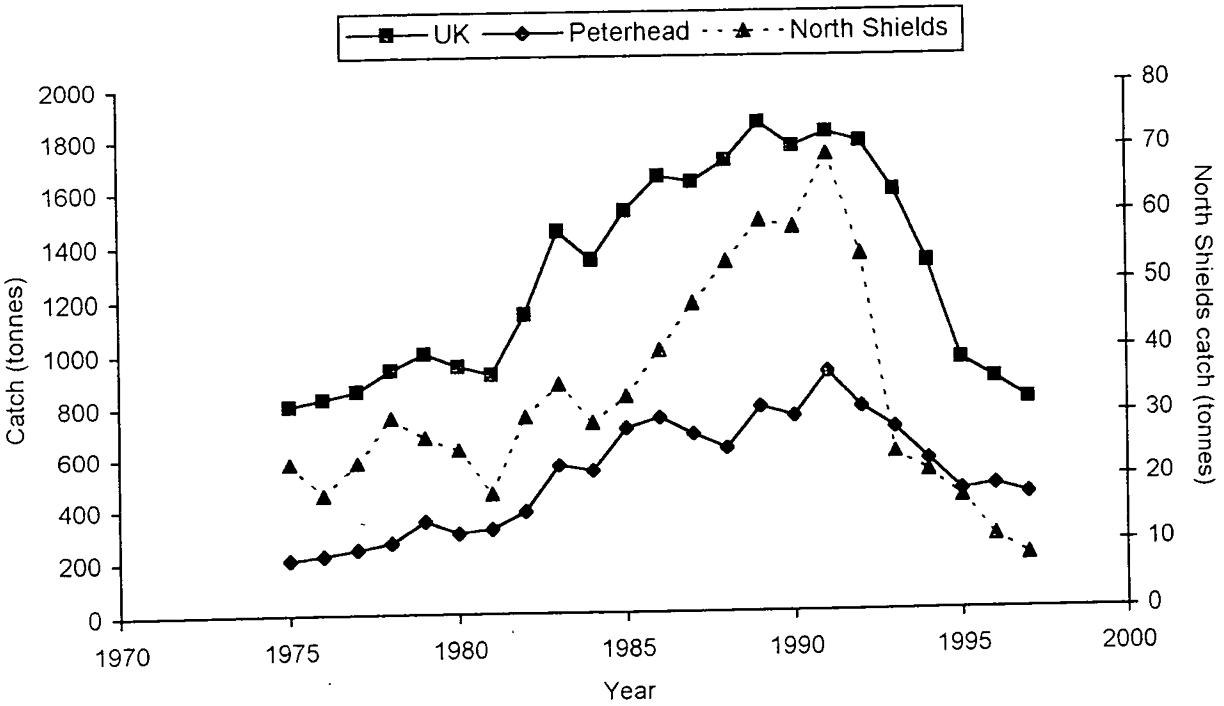


Fig 2.12. Total catch of North Sea wolffish landed in the UK, at Peterhead (Scotland) and at North Shields (England) for 1975-1997.

2.3.6 The catch data of common wolffish at North Shields

A total of 148 fishing vessels were registered in North Shields in 1995 but this had decreased to 111 in 1997. The total tonnage was reduced from 2,981 to 2,147 for 1995-1997. The total engine power also declined from 18,660 kW to 14,684 kW over this period. There were 53 vessels recorded that caught common wolffish in the North Sea and landed them at North Shields during 1996-1998. The engine powers for these boats, which captured common wolffish ranged from 82 kW to 447 kW with a mean value of 199.2 kW. The working days for these vessels varied between 1 day and 5 days for each cruise depending on the distance travelled from port and the boat size. More than 99% of wolffish were caught using the following gears: trawls including heavy trawl, light trawl, beam trawl and paired trawl. The mesh size of these boats was between 7 cm and 10 cm although there is no size limit for common wolffish. Occasionally, common wolffish were caught by purse seine during summer but less than 1% of total catch of common wolffish landed at North Shields were caught using purse seine. There were no records by of capture long-line for the common wolffish at North Shields. The fishing area of boats that landed common wolffish at North Shields was in a rectangle from 54° N to 59° N and 2° W to 6° E. This range covered the majority of the area that common wolffish inhabited in the North Sea.

The historical catch data of common wolffish landed at North Shields is shown in Fig. 2.12. The quantity of common wolffish landed in North Shields was over 100 tonnes before 1953. During the period for 1955-1975, the amount of catch declined gradually from 60 tonnes to 20 tonnes except for four years when it increased again up to 65 tonnes in 1990. However, the quantity of wolfish landed decreased to the lowest historical value of 8 tonnes in 1997, the same as the level during World War II.

Although, the amount of common wolffish landed in North Shields was small compared with that in Peterhead and other ports such as Whitby, Aberdeen and Grimsby, the trends in catch variation for North Shields were similar to that of Peterhead and that of the whole UK (Fig. 2.12).

2.3.7 Length distribution of common wolffish in the North Sea for 1996-1998

A total of 2676 common wolffish captured by commercial fisheries and ground fish surveys (20 individuals) were measured during 1996-1998, of which 920 common wolffish were examined in 1996, 1,492 were examined in 1997 and 264 were examined in 1998. The total length distribution of common wolffish combined for the 3 years is shown in Fig 2.13. There were no common wolffish landed by commercial fisheries with a body length under 32 cm despite requests to a number of boats to retain any very small common wolffish encountered, and despite there being no size limit for wolffish. The TL frequency distribution of common wolffish ranged from 32 to 108 cm for males and 36 to 102 cm for females. The length distribution for common wolffish displayed a trend of near normal distribution. Most of the common wolffish, which were caught in the North Sea, ranged between 41 cm and 70 cm in total length with a peak at the 61-65 cm size group. Female common wolffish were twice as common in landings as male common wolffish in the size groups of 51-55 cm and 56-60 cm. By contrast the size groups of 66-70 cm, 71-75 cm and larger than 81 cm contained twice as many males as females. However, the sex ratio (male:female) for all common wolffish landed in North Shields was 1.13:1. There was no significant difference in numbers of male and female common wolffish landed (Chi-square, $\chi^2 = 0.06$, $P > 0.05$).

The total length distribution of the common wolffish displayed each year for 1996-1998 is shown in Fig. 2.14. Initially, the body length distribution followed the same trend as described above. However, common wolffish with body lengths smaller than 50 cm were captured proportionately much more in 1997 (30.4%) and 1998 (31.4%) compared with those in 1996 (24.8%). The proportion of captured common wolffish larger than 75 cm in 1997 (6.9%) and in 1998 (5%) decreased gradually compared with that of in 1996 (10.7%). The sex ratio (male:female) of caught common wolffish for each year was 1:1.1, 1.1:1 and 1.5:1 for 1996-1998, respectively. The mean total length ± SE for male common wolffish, female common wolffish and all common wolffish from 1996 to 1998 were as follows: for 1996, male were 62.16 ± 0.99 cm (n = 218), females were 58.95 ± 0.74 cm (n = 237) and all fish were 58.97 ± 0.41 cm (n = 920); for 1997, males were 58.09 ± 0.38 cm (n = 634), females were 57.79 ± 0.42 cm

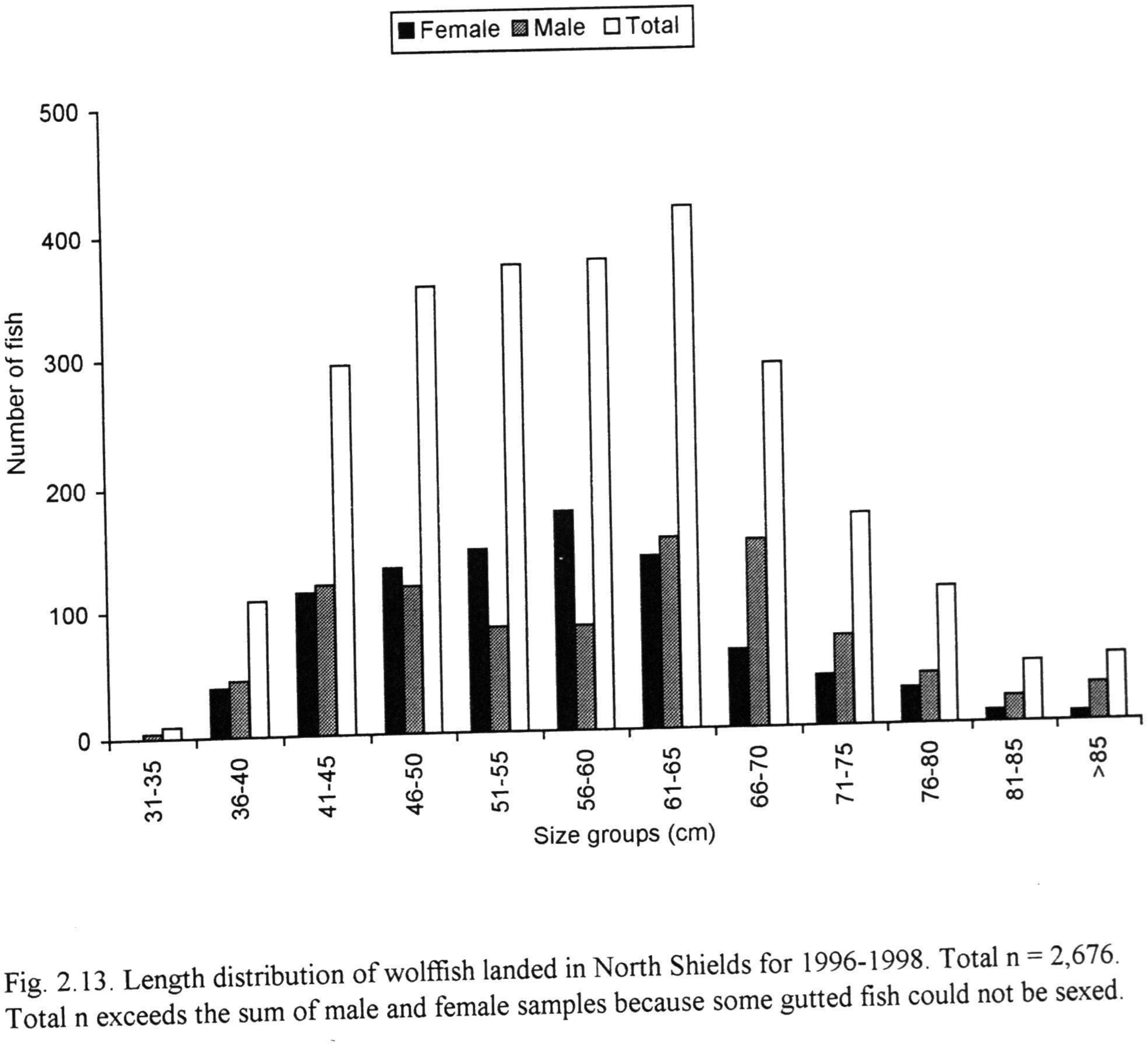


Fig. 2.13. Length distribution of wolffish landed in North Shields for 1996-1998. Total n = 2,676. Total n exceeds the sum of male and female samples because some gutted fish could not be sexed.

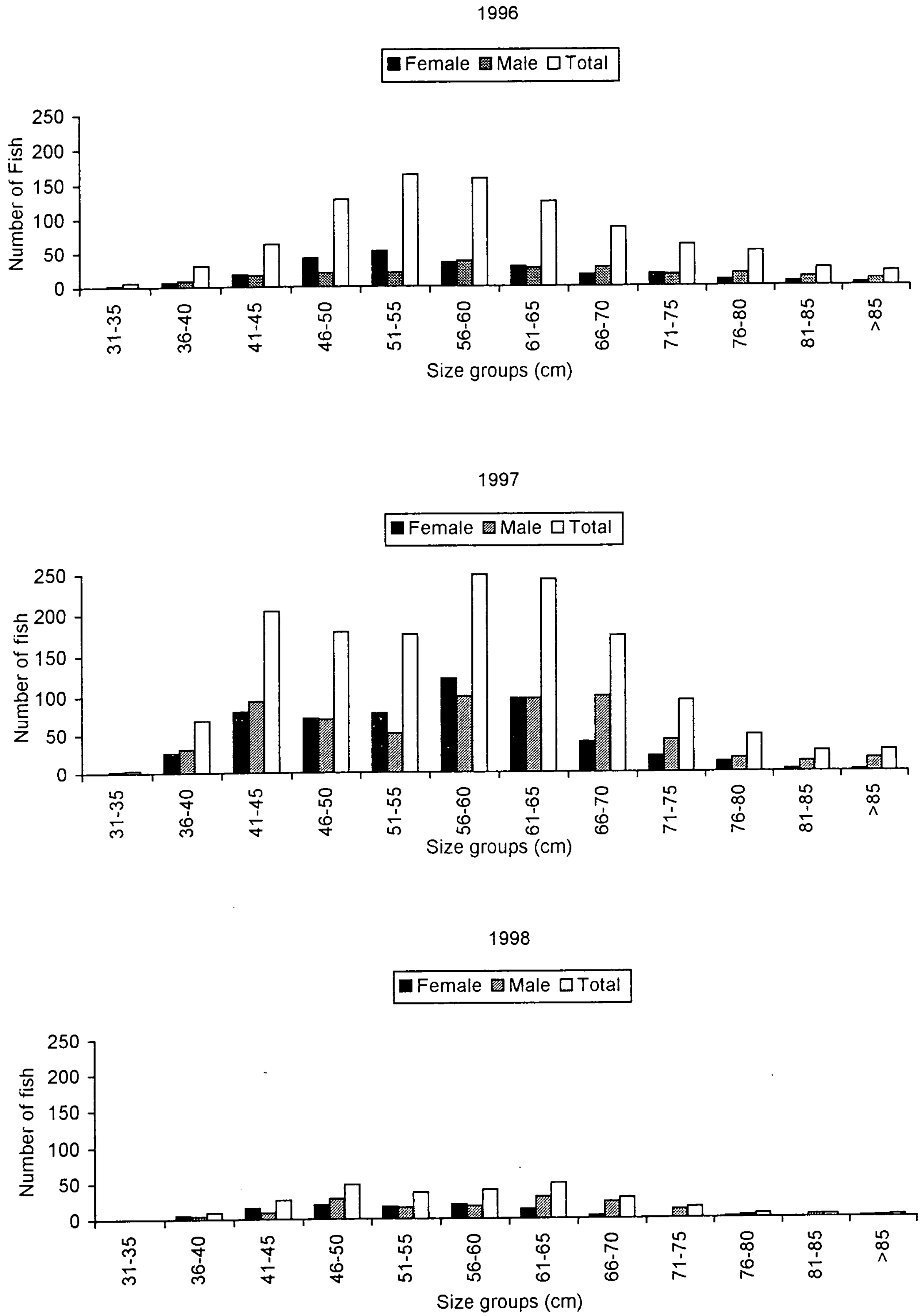


Fig. 2.14. Length distribution of common wolffish landed in North Shields for each year during 1996 to 1998.

(n = 552) and all fish were 57.65 ± 0.32 cm (n = 1492); for 1998, males were 58.09 ± 0.82 cm (n = 149), females were 53.38 ± 0.92 cm (n = 97) and all fish were 57.37 ± 0.65 cm (n = 264).The mean length of male common wolffish was larger than of females in each year. The mean length of both sexes combined were similar between 1996 and 1998.

The catch of common wolffish in relation to the distance from coastline and season is shown in Fig. 2.15. The inshore areas in this study were defined as distance less than 60 nautical miles (E8-E9 in alphanumeric codes) from the coastline (Fig. 2.2). The areas over this distance (F0-F7) were termed offshore in this study. Spring and summer were the seasons in which the larger catches of common wolffish landed at North Shields were taken. During spring , most common wolffish were captured in the offshore area and were of a wide size range. In contrast, during the other seasons, most common wolffish were caught in inshore areas off Northumbria (38E8-38E9 in alphanumeric codes). The body sizes of common wolffish caught inshore during the autumn and winter seasons were mostly less than 55 cm in length. The length division of 55 cm approximates to the size at which most (~70%) North Sea common wolffish are mature (Chapter 4). The sex ratio (male:female) of common wolffish was 1.1:1 for both inshore and offshore combined all seasons.

The length distribution of common wolffish in relation to the depth of fishing ground (<70 m or ≥ 70m) is shown in the Fig 2.16. The pattern was similar to that occurring between inshore and offshore categories. This is because the depth of the North Sea increases from the west to east and from south to north. However, there was a wider size range of common wolffish captured in shallow waters during the spring and autumn season compared with that in the inshore area. More precise assessments in relation to distance from shore or depth were not felt to be appropriate because of the long duration of tows and that landed common wolffish often came form several adjacent squares.

The length distribution of common wolffish, which were caught by CEFAS groundfish surveys for 1977-1998 is shown in relation to depth in Fig. 2.17. The body length

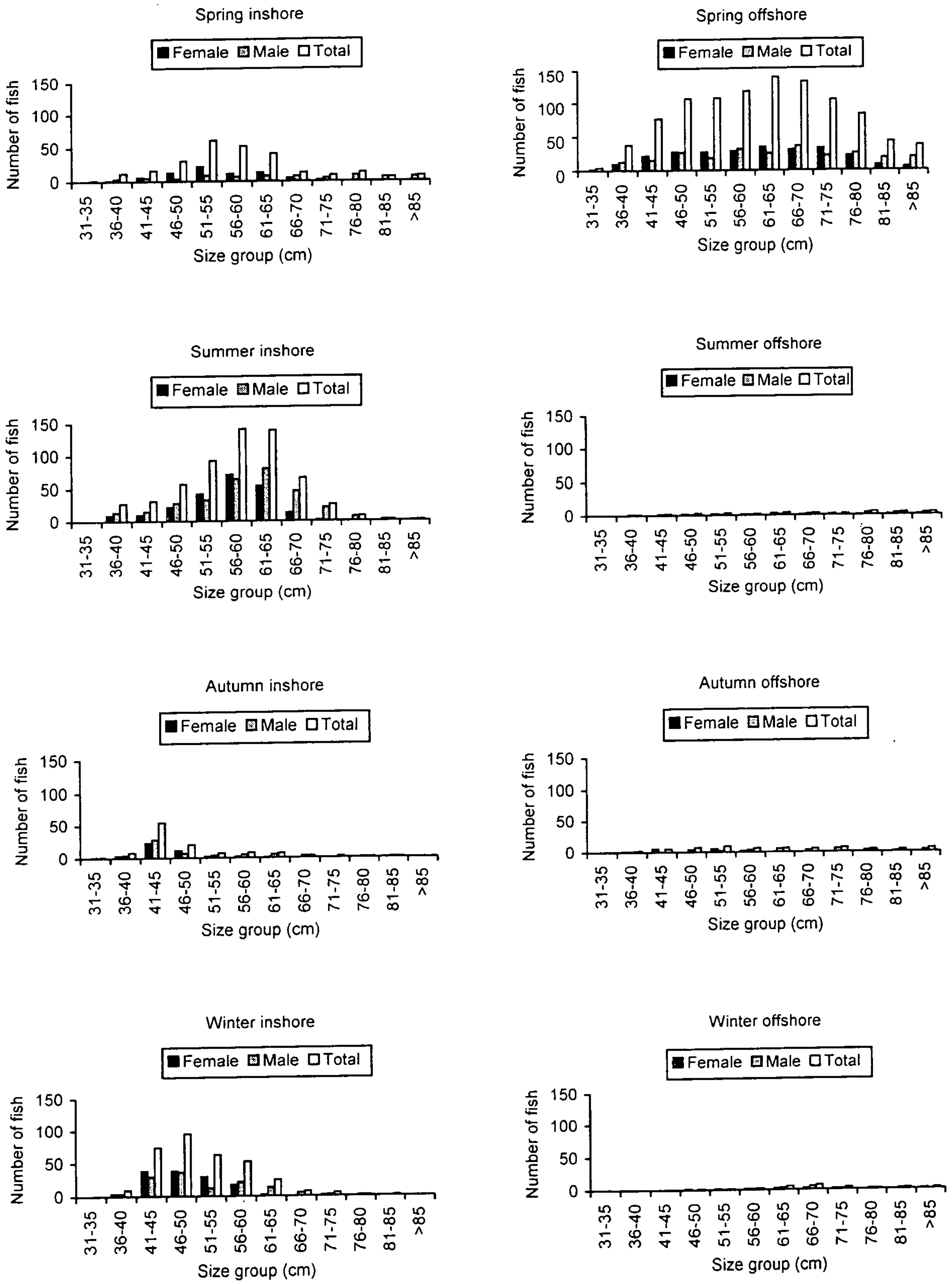


Fig 2.15. Length distribution of wolffish captured from inshore and offshore areas of the North Sea.

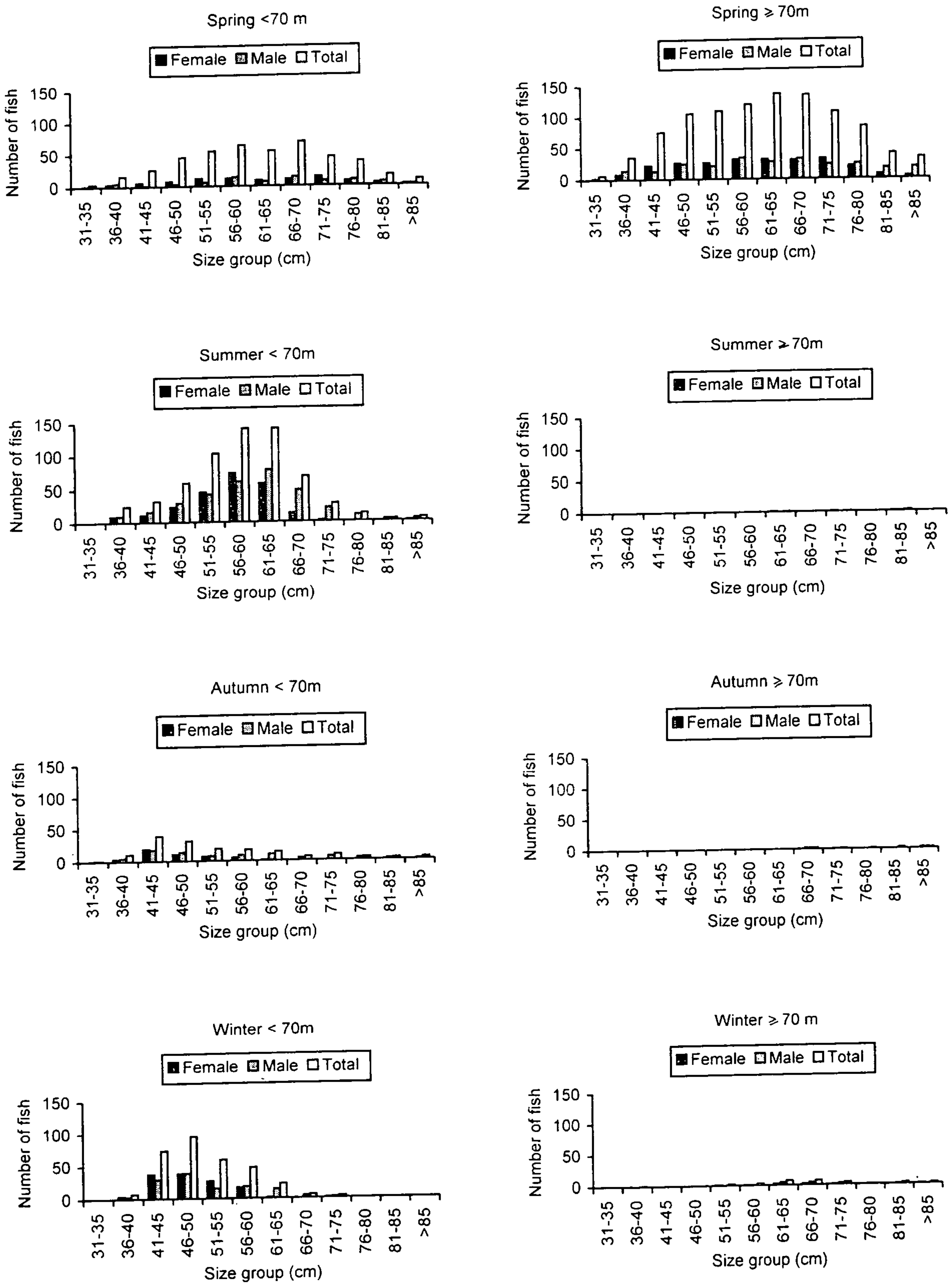


Fig. 2.16. Length distribution of wolffish captured in <70m areas and > 70m areas of the North Sea.

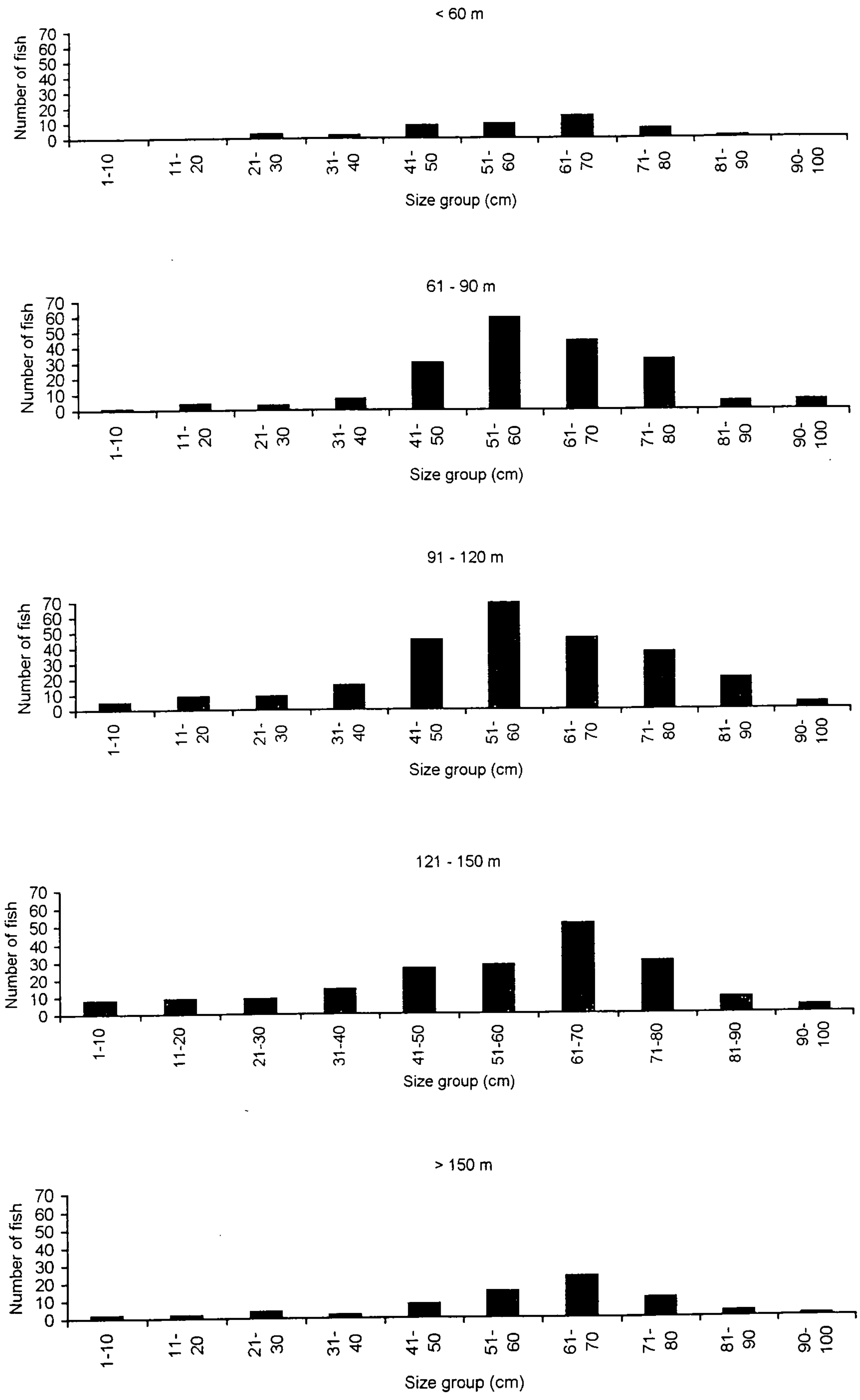


Fig 2.17. Length distribution of wolffish captured in different depths in North Sea by CEFAS ground fish surveys for 1977-1998. Total n = 753.

distribution was similar to that from commercial landings with the majority in the range of 41-80 cm at each depth. The depths inhabited by common wolffish in the North Sea were mostly between 61 m and 150 m (Fig. 2.17). Few common wolffish were captured in water shallower than 60 m, but only 9% of CEFAS trawls were at depths < 60 m. The smallest common wolffish (< 10 cm) were found only in water deeper than 60 m, but were distributed through other depth categories in proportion to the total catch of common wolffish occurring there. In CEFAS surveys, larger common wolffish (> 55 cm, mature) tended to be caught in deeper waters than small (chi-square, df = 1, $\chi^2 = 367.13$, $P < 0.001$). There was a significant but weak linear relationship between common wolffish body length and capture depth (Fig. 2. 18) with larger wolffish tending to be captured in deeper water (n = 57, $r^2 = 0.12$, $P < 0.05$).

2.3.8 Catch per unit effort for common wolffish in the North Sea

The monthly variation of CPUE and quantity of common wolffish landed at North Shields for 1996-1998 is shown in Fig. 2.19. The catch rate for common wolffish in the North Sea increased gradually from December and was highest in May and June before decreasing sharply in August and September. Monthly fluctuations of CPUE were intense. However, the CPUE was relative higher in the period of March-August for each year. The highest CPUE occurred in the summer season for each year while catches were moderately high but not at their peak. Both CPUE and yield of common wolffish were lowest in the autumn season for 1996-1998. Monthly landings of common wolffish were highest in May for 1996 and 1997. However, the CPUE was not as high as expected, 0.9 (kg/(200kW·h)) and 0.8 (kg/(200kW·h)) respectively. The highest CPUE, 2.2 (kg/(200kW·h)) occurred in the August 1998, but the CPUE for other months in 1998 were lower than in the previous two years.

The average CPUE of each year for 1996-1998 is shown in Fig. 2.20. The CPUE of common wolffish in 1997 was highest (kg/(200kW·h)) among the three years and that of 1998 was about half the value (kg/(200kW·h)) of 1997. Both catch and CPUE were lowest in 1998.

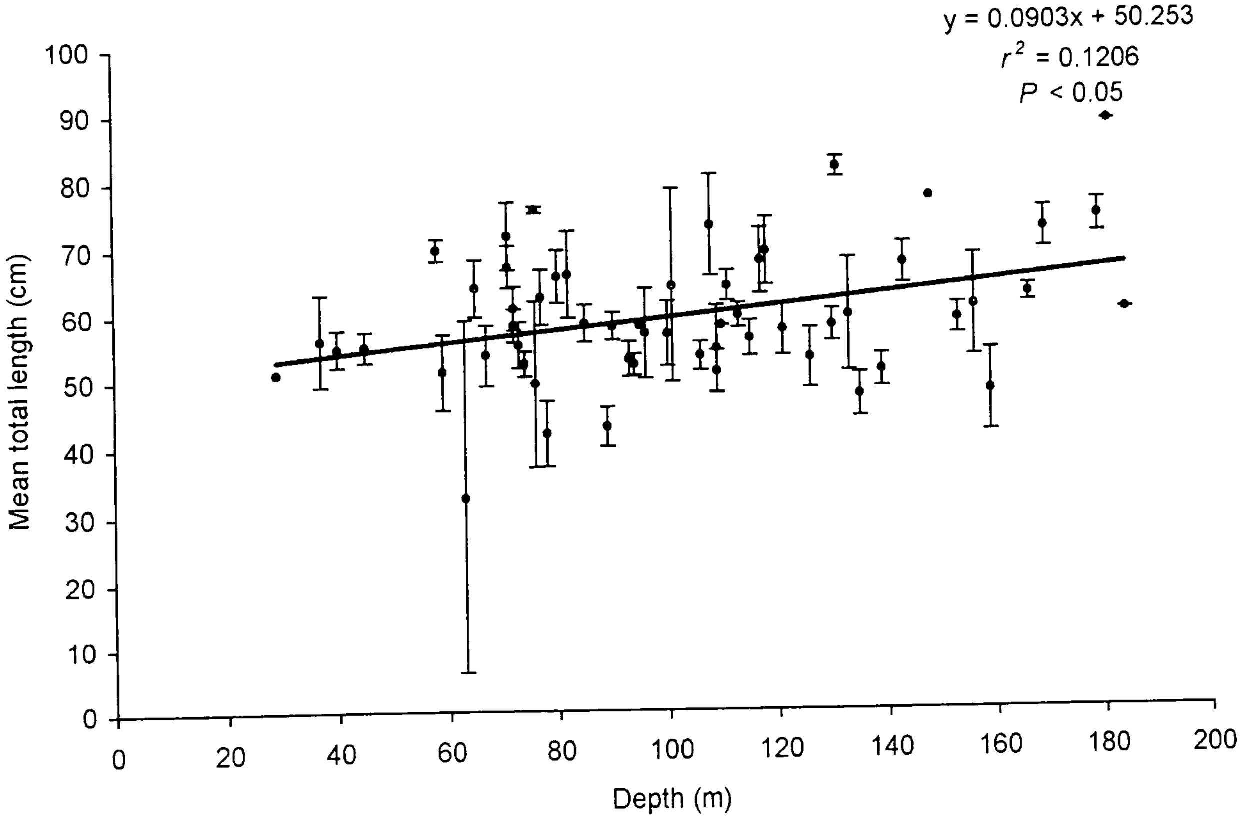


Fig. 2.18. The relationship between the lengths of captured wolffish and water depth at capture site in the North Sea. Bars represent standard errors. (Data obtained from CEFAS ground fish surveys).

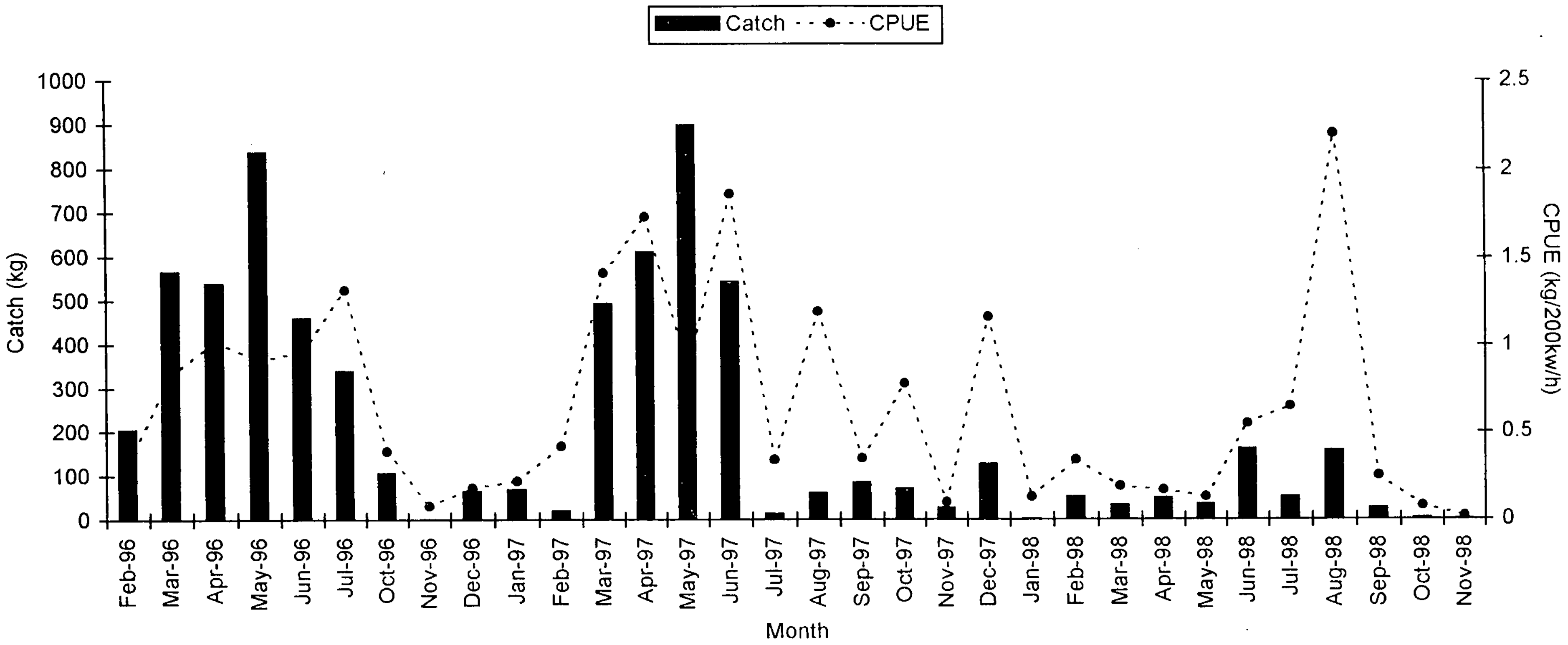


Fig. 2.19. Monthly variations of catch and CPUE of common wolffish landed at North Shields from February 1996 to November 1998.

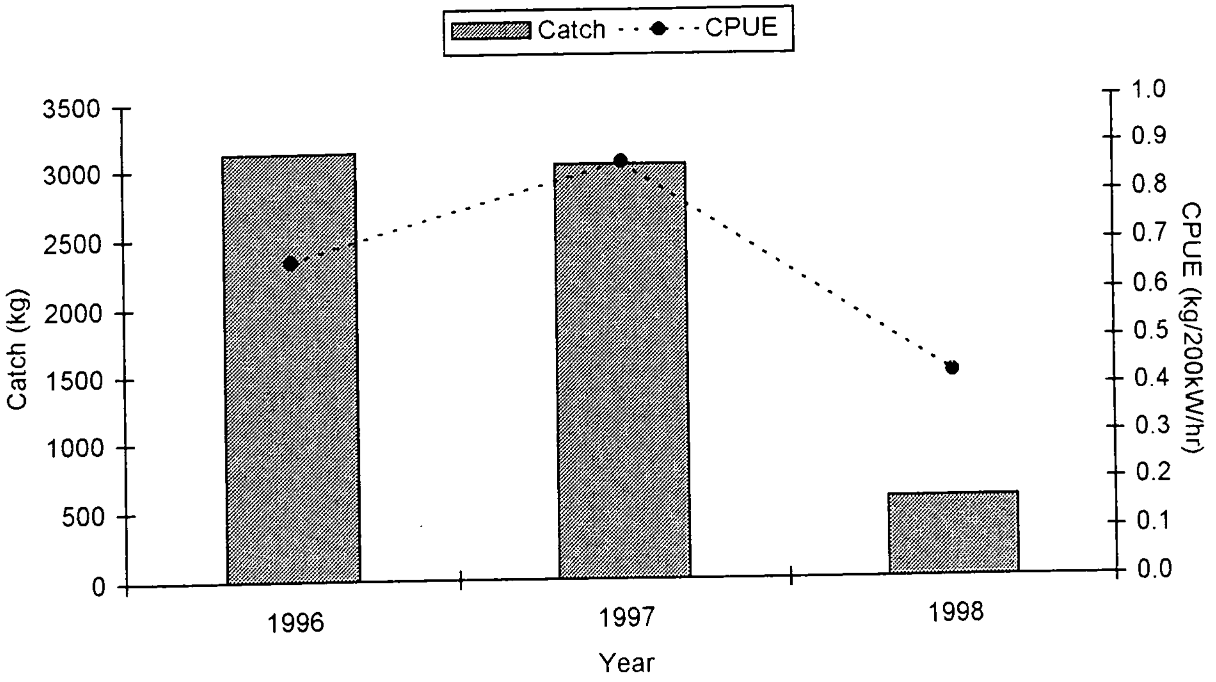


Fig. 2.20. Yearly variations of catch and CPUE of sampled wolffish landed at North Shields for 1996-1998.

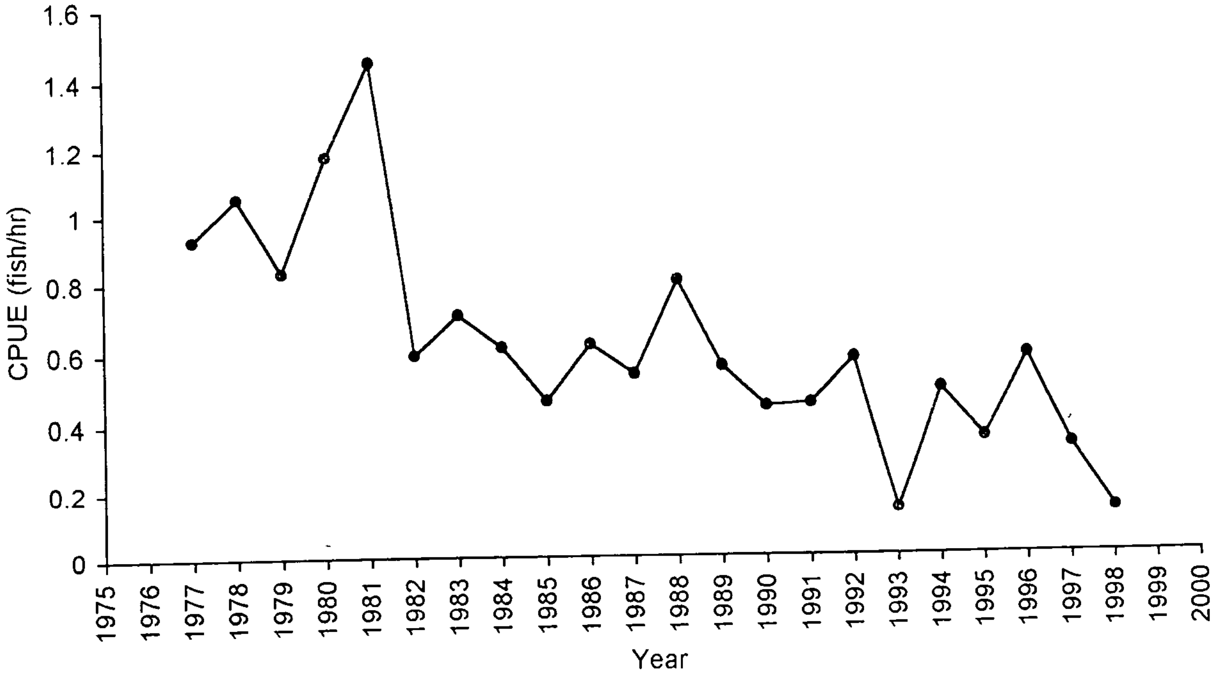


Fig. 2.21. Yearly variations of mean CPUE of wolffish for 1977-1998 from CEFAS summer ground fish surveys.

The relationship between environmental factors and CPUE is shown in Table 2.1.The value of CPUE was significantly influenced by both season and distance from shore (inshore, offshore), but season and distance had no significant interaction. The result of ANOVA and Tukey-tests are shown in Table 2.1. The CPUE of common wolffish in spring was significantly higher than that in autumn and in winter, while the CPUE in summer was significantly higher than autumn but not winter. There was no significant difference between CPUE in spring and summer. The CPUE of common wolffish in offshore waters was significantly higher than that inshore during the spring (P <0.001).

From the summer ground fish surveys carried out by CEFAS for 1977-1998, the CPUE for common wolffish was lowest in 1993 and 1998 (0.16 fish/hour) (Fig. 2.21). The trend of CPUE of common wolffish was significantly negatively correlated to the year (n = 22, Spearman's correlation = -8.35, $P < 0.001$). Averaging the CPUE data from 1977 to 1998 for each recording area, the values varied substantially between different areas (Fig. 2.22). Some areas had no catch records of common wolffish during the last two decades and were mainly located near the southern boundary for common wolffish in the North Sea. Using these data, there was no significant difference between inshore and offshore (one-way ANOVA, n = 67, df= 1,66; F= 1.664, P = 0.191). However, the CPUE of wolffish of some areas (e.g. 48E9, 50F1, 47F0, 44F4) were relatively high, and tended to be reliable capture areas over the 22 years of sampling.

2.4 Discussion

There are three species of the wolffish family distributed in the North Atlantic, but only the common wolffish has been found in the North Sea. This may be a reflection of the high bottom temperature (> 7°C) of the North Sea during the summer season that is too high for the spotted wolffish and northern wolffish to inhabit. Both of those species prefer temperatures between 1 and 7°C (Beese and Kändler, 1969). Common wolffish tolerate temperatures between 1 and 12°C, with a higher thermal maximum than the other two species. The temperature in the North Sea north of 54° N was between 5 to 12°C, while that south of 54° N was between 3 and 20°C. During the summer season, the temperature was too high for common wolffish to inhabit the southern part of the North Sea. The ICES ground surveys and commercial landing

Table 2.1 Comparion of mean CPUE values of North Sea common wolffish for 1996-1998 by season and by inshore (≤60 nm) or offshore (> 60 nm) area.

(a) Mean CPUE values

		Inshore		Offshore	
	N	CPUE	Std. Error	CPUE	Std. Error
Spring	72	0.36	0.07	1.88	0.28
Summer	25	1	0.18	1.87	0.49
Autumn	21	0.25	0.07	0.49	0.12
Winter	17	0.36	0.1	0.32	0.04

(b) Two-way ANOVA for Season and distance

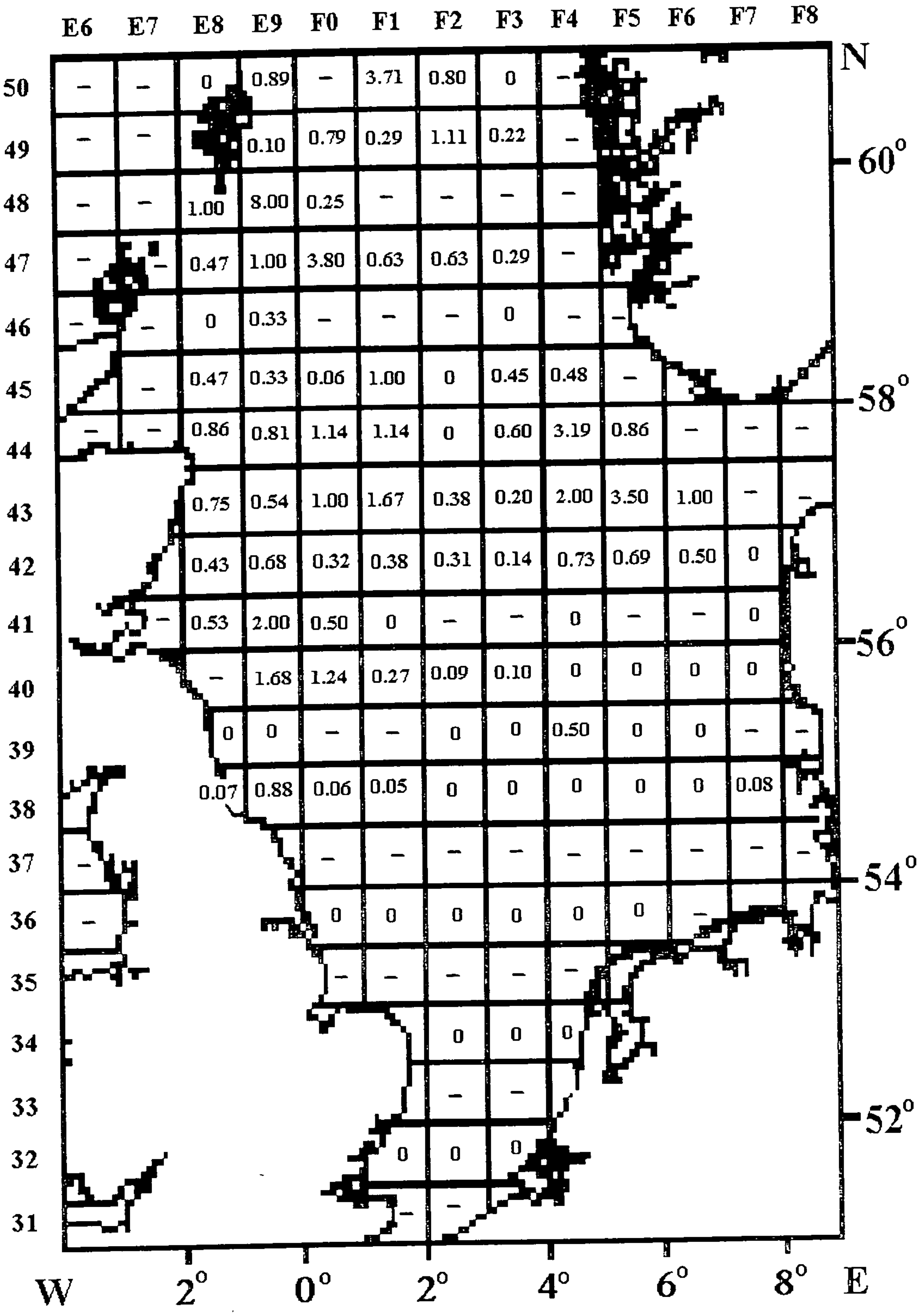
	df	*F*	Sig.
Season	3	4.201	0.007
Distance	1	6.478	0.12
Season*Distance	3	2.304	0.08

(c) Tukey test for Season

(I)	(J)	Mean Difference	Std. Error	Sig.
Autumn	Spring	-1.0153	0.3107	0.006
	Summer	-0.9932	0.3708	0.037
	Winter	0.000028	0.4087	1
Spring	Summer	0.022039	0.2908	1
	Winter	1.1053	0.3378	0.014
	Autumn	0.9932	0.3708	0.037
Summer	Winter	0.9932	0.3938	0.057

(d) one-way ANOVA for comparison of inshore/offshore CPUE in different seasons

	df	*F*	*Sig.*
Spring	1,70	15.69	<0.001
Summer	1,23	4.16	0.05
Autumn	1,19	3.1	0.095
Winter	1,15	0.21	0.65



	E6	E7	E8	E9	F0	F1	F2	F3	F4	F5	F6	F7	F8
50	–	–	0	0.89	–	3.71	0.80	0	–				
49	–	–		0.10	0.79	0.29	1.11	0.22	–				
48	–	–	1.00	8.00	0.25	–	–	–	–				
47	–	–	0.47	1.00	3.80	0.63	0.63	0.29	–				
46	–	–	0	0.33	–	–	–	0	–	–			
45		–	0.47	0.33	0.06	1.00	0	0.45	0.48	–			
44	–	–	0.86	0.81	1.14	1.14	0	0.60	3.19	0.86	–	–	–
43			0.75	0.54	1.00	1.67	0.38	0.20	2.00	3.50	1.00	–	–
42			0.43	0.68	0.32	0.38	0.31	0.14	0.73	0.69	0.50	0	
41		–	0.53	2.00	0.50	0	–	–	0	–	–	0	
40			–	1.68	1.24	0.27	0.09	0.10	0	0	0	0	
39			0	0	–	–	0	0	0.50	0	0	–	–
38			0.07	0.88	0.06	0.05	0	0	0	0	0	0.08	
37	–				–	–	–	–	–	–	–	–	–
36	–				0	0	0	0	0	0	–		
35					–	–	–	–	–				
34							0	0	0				
33							–	–					
32						0	0	0					
31						–	–						

Fig 2.22. The CPUE (fish/hour) of common wolffish in different areas of the North Sea. Data was calculated from the groundfish surveys (1977-1998) carried out by CEFAS. Each rectangle (0.5 degree latitude × 1 degree longitude) represents a fishing division in the UK alphanumeric code system. -, no data.

indicated that no common wolffish were caught south of 54° N in the North Sea. These results imply that 54° N is the current approximate southern limit for common wolfish in the North Sea. This temperature range for common wolffish in the North Sea is similar to that in the White Sea (Pavlov and Novikov, 1993) but is higher than that in Icelandic waters (Jónsson, 1982), northern Norwegian waters (Falk-Petersen *et al.*, 1990), west Greenland waters (Riget and Messtorff, 1988) and the Newfoundland area (Albikovskaya, 1982). Common wolffish do not appear to show shoaling behaviour and are dispersed over the seabed based on diving observation by Baruskov (1959) and Johannessen *et al.* (1993). The results from analysing groundfish surveys data indicated that the common wolffish were scattered both inshore and offshore on the bottom at different depths in the North Sea. The CPUE of common wolffish of the North Sea was very low compared with the main target species (ICES, 1993; Table 2.2). This implied that common wolffish are not very abundant and do not exhibit shoaling behaviour in the North Sea. This explains why common wolffish are taken as a by catch species in the North Sea demersal fishery. However, the catch rates of starry ray, dab and grey gurnard (*Eutrigla gurnardus*) have increased over last decade while the catch rates of spurdog (*Squalus acanthias*), cuckoo ray (*Raja naevus*), cod, haddock, whiting, and the common wolffish have declined (Heessen and Daan, 1996; Walker and Heesen, 1996; Pope and Macer, 1996). The main fishing grounds for common wolffish in the Northeast Atlantic are Icelandic waters, the Barents Sea and off Norwegian waters at higher latitudes than the North Sea, where common wolffish appear to be more abundant and comprise a larger proportion of fish community biomass (Jónsson, 1982).

The bottom substrates of areas in the North Sea inhibited by common wolffish were similar to other places where common wolffish are found, and included sand, gravel and stony areas (Barsukov, 1959). These substrates are usually good for trawler fisheries to operate over. Most common wolffish caught in the North Sea were taken by trawls. This was similar to other places such as in Icelandic waters (Jónsson, 1982), off west Greenland waters (Smidt, 1981), off Newfoundland waters (Riget and Messtorff, 1988) and in the Barents Sea (Pavlov and Novikov, 1993). Where observations are independent of fishing gear, e.g. diving, common wolffish are often

Table 2.2. Fishing hours, number of catch, and CPUE of some main target and non-traget fish species in the North Sea during the 1985-1987 ICES ground fish surveys.

Fish name	Hour	Catch	CPUE (fish/hour)
Lesser-spotted dogfish (*Scyliorhinus canicula*)	92	601	6.5
Spurdog (*Squalus acanthias*)	33	4951	150.0
Starry ray (*Raja radiata*)	774	9391	12.1
Cuckoo ray (*Raja naevus*)	120	748	6.2
Cod (*Gadus morhua*)	2021	114249	56.5
Haddock (*Melanogrammus aeglefinus*)	1556	1467718	943.3
Whiting (*Merlangius merlangus*)	2145	2313518	1078.6
Saithe (*Pollachius virens*)	460	78386	170.4
Norway pout (*Trisopterus esmarki*)	1015	2563567	2525.7
Dab (*Limanda limanda*)	1921	1239445	645.2
Grey gurnard (*Eutrigla gurnardus*)	1030	96565	93.8
Common wolffish (*Anarhichas lupus*)	267	601	2.3

observed in rocky areas (e.g. Barsukov, 1959; Keats *et al.*, 1986). Fishing gears used to capture common wolffish in these rocky areas are long-line fishing and drift nets. But these fishing gears were not important for catching North Sea common wolffish because these fisheries industries are less important in the North Sea. The purse seine, which was used to catch the pelagic species, has been reported to catch some common wolffish in the North Sea during the summer season. However, the common wolffish is considered as demersal species. Thus, it might be that the common wolffish caught by purse seine were fish which were active searching for food during the feeding season.

Worldwide, there is no specific fishery industry that captures the common wolffish as a primary target species. The common wolffish is usually described as by catch in fisheries statistics reports. At present, there is not established total allowable catch (TAC) for this species for EU countries, although Iceland and Greenland do have quotas for this species in their waters. In 1997, the quotas for the common wolffish in Icelandic waters and Greenland waters were 13,000 and 1,000 tonnes respectively.

The catch of common wolffish by UK boats in the North Sea increased from 1975 to 1992 while the catch of all demersal fishes by UK boats in the North Sea decreased. There are two reasons, which might explain this pattern: (1) The common wolffish were a by catch in the demersal fishery. This study shows that the UK catch of common wolffish increased with increasing UK fishing effort. The CPUE of the main demersal species in the North Sea has decreased since the 1970s (Cushing, 1975). Thus any increasing fishing effort to maintain a given level of yield in main target species would also increase the by catch of the common wolffish. (2) The value of the common wolffish increased sharply after 1980. Therefore, the fishermen would stop discarding them in order to earn more money while the yield of main species declined.

The quantity of North Sea common wolffish landed in the UK was over 80% of total catch of the North Sea after 1980. The main reason for this was that UK joined the EC and for a variety of fish species was offered a catch quota in the North Atlantic by the EC Commission. The North Sea became the most important fishing ground for the UK fishing fleet. The highest quotas of the main demersal species such as cod and haddock in the North Sea were given to the UK. Moreover, some countries were not allowed to catch some demersal species in the North Sea after the quota system was established. Therefore, the UK became the most important country that captured North Sea common wolffish as a by catch of its demersal fishing activities. Thus, studying the fisheries biology of common wolffish in the North Sea from analysing UK fisheries data only is appropriate. Although the amount of common wolffish landed at North Shields was low compared with that of Peterhead (Scotland), the biggest UK fish market for common wolffish, the pattern of variation in yield of North Shields was similar to that of Peterhead and the total UK catch. Therefore, the catch data of common wolffish from North Shields should reflect the same pattern for total UK landings. The fishing data of North Shields such as length distribution, age and growth, and CPUE can therefore be used to study the fisheries ecology of common wolffish in the North Sea. Moreover, the distribution of catches of the common wolffish in the North Sea, landed at North Shields, covered over 80% of the area of the North Sea inhabited by common wolffish.

Some authors have studied the movements of common wolffish by using tagging methods, and have suggested that common wolffish may exhibit seasonal short distance migration in many areas (Baruskov, 1959; Jónsson, 1982; Templeman 1984; Keats *et al.*, 1985; Pavlov and Novikov, 1993). This pattern of migration may be reflected in their reproductive behaviour. This study shows that the amount of landed common wolffish of North Shields exhibits seasonal variation. During the spring, both the amounts of landed common wolffish and CPUE were higher in deeper, offshore areas than in inshore areas, but a substantial amount of common wolffish were also caught in the inshore areas. Most common wolffish were captured in the inshore areas during the summer. However, the CPUE was not significantly different between inshore and offshore areas. Only small numbers of woffish were caught inshore during the autumn and winter seasons, but most were less than 50 cm in length. Most common wolffish do not mature at less than 50 cm (see section 4.3.3.4). Combining this information, it is suggested that the common wolffish begin to migrate into inshore waters in spring and are active this period. A number of common wolffish stay inshore during summer using these as a feeding ground. Only small numbers of wolffish were caught inshore and offshore in autumn and winter during the spawning (autumn) and tooth renewal (winter) seasons. They are presumed to be relatively inactive in this period; certainly males guard nests (Keats *et al.*, 1985). Thus, the catch rate could be reduced in this period. It is suggested then, that common wolffish have a migration pattern in the North Sea. However, some common wolffish, mostly immature, were caught in inshore in winter. This suggests that immature common wolffish might stay inshore during the spawning season. In this study, it is suggested that the larger common wolffish prefer to inhabit deeper water. This could reduce intraspecific competition between younger and older common wolffish. Moreover, many of the inshore areas near the eastern British coast side had rocky bottoms. Utilising these areas could allow younger common wolffish to increase their survival rates.

It has been reported that common wolffish spawn their egg masses in moderately deep waters between 70-300 m in many areas on the North Atlantic continental shelf such as Icelandic waters (Jónsson, 1982), the Barents Sea (Pavlov and Novikov, 1993), Norwegian waters (Baruskov, 1959) and off Greenland waters (Templeman 1984). However, spawning in shallow water at depths of up to 15 m along the Newfoundland coast has also been reported (Keats *et al.*, 1985). The length distribution of common wolffish in the North Sea indicated that juvenile common wolffish were mostly found in the depth range 90 m to 150 m. Therefore, common wolffish might spawn their egg mass in the deeper water in the North Sea. From a geographical view, the spawning ground of common wolffish might be located in the middle and upper areas of the North Sea. Although common wolffish spawned their egg mass in both shallow and deeper waters, Keats *et al.* (1986) suggested that the juvenile common wolffish lived only in the deeper waters whatever the depths they had spawned in.

The sex ratio of near 1:1 for common wolffish in the North Sea is common in many fish species (Castro and Huber, 1996). It has been reported that male common wolffish tend to be larger than females (Beese and Kändler, 1969; Jónsson, 1982). Most common wolffish larger than 85 cm in the North Sea were males. The biggest common wolffish found in this study (TL = 108 cm) was male. The mean total length of males was also larger than that of females. The pattern of length distribution and habitat depth for the common wolffish in the North Sea was similar to those found in Icelandic waters (Jónsson, 1982), Barents Sea (Baruskov, 1959, Pavlov and Novikov 1993), off west Greenland waters (Smidt, 1981), the Gulf of Main region (Nelson and Ross, 1992) and off Newfoundland (Albikovskaya, 1982). Common wolffish were found mostly at depths in the range of 70 m – 200 m. In other areas common wolffish are found at depths of up to 500 m whereas in the North Sea they are limited by water depth.

The patterns of length distribution of commercially landed individuals for 1996-1998 and from analysing 22 years of CEFAS ground survey data were similar. The high peak of length distribution was in the same group size. This suggests that overfishing, which causes the size distribution to shift to younger fish of smaller size, has so far not happened to a large degree in the North Sea for common wolffish (but see Chapter 5).

The CPUE of common wolffish varied between the different seasons. During the feeding season, both catch and CPUE increased simultaneously and were higher than those of autumn and of winter. Jónsson (1982) and Pavlov and Novikov (1993) also reported the same pattern in Icelandic waters and the Barents Sea. During the spring and summer season, the CPUEs of common wolffish in offshore areas were higher than those of inshore. However, larger catches of common wolffish were made in inshore areas during the summer, although higher CPUE occurred in offshore areas. This result was reflected in the vast majority of fishing effort in inshore areas (Greenstreet *et al.*, 1999a).

Catch per unit effort is a relative index of abundance used for many species when biomass is unknown (Cushing, 1957; Hilborn and Walters, 1992). The low CPUEs of the common wolffish in the North Sea suggest that they have low abundance but are widely distributed in this area. This is largely explained by the *K*-life cycle strategy of the common wolffish, characterised by relatively low fecundity, large eggs, low growth rate and long life. In general, the abundance of the common wolffish in the North Sea has decreased as have most other fish species in the North Sea over the last 10 years (Greenstreet *et al.*, 1999b). This result was reflected in the yield of the common wolffish for last 10 years. Moreover, the CPUE of common wolffish that was calculated from the data of summer ground surveys carried out at the same sites for the last 22 years showed a negative correlation with year. This also provided evidence that the abundance of common wolffish in the North Sea has declined. Increasing demersal fishing appears to have reduced the abundance of common wolffish as a result of it being taken as a by catch species for which there is no quota limit. However, whether the abundance of common wolffish in the North Sea has declined to a dangerous level could not be judged from only the catch data or CPUE. This requires consideration of other parameters such as age, growth and reproduction. These will be discussed in later chapters.

Catch per unit effort not only can be used to provide estimates of stock size or density in areas but also can be applied for estimating sustainable yield of target species, because fluctuations of CPUE reflect the changes of catch and stock structure (e.g. age composition, fish size) in relation to fishing intensity. Therefore, for fisheries management, CPUE provides a powerful information tool for pursuing MSY, by regulating the fishing intensity (e.g. fishing power, working hours, mesh size) depending on the increase or decrease in fishing success (Beverton and Holt, 1957). However, to follow this approach of maintaining sustainable yield, requires a long period of precise, yearly fishing data yearly including fishing gear (catchability), fishing effort, working hours, mesh size, fishing areas and catch in order to obtain reasonable CPUE estimates. There were sufficient commercial fishing data to calculate a reasonable CPUE of North Sea common wolffish for 1996-1998 in this study. However, three years of CPUE data might not be sufficient to allow calculations of abundance or estimates of sustainable yield for the long-lifed common wolffish in a high fishing-intensity area like the North Sea. In addition, CPUE calculated from data of 22 years of ground surveys carried out by CEFAS for North Sea common wolffish was precise, but these data were only available in late summer, a period that was close to the spawning season of North Sea common wolffish. Common wolffish could reduce their activities (e.g. feeding) in this period (Albikovskaya, 1983; Chapter 4) which may affect the catch rate. Furthermore, to use just a season's CPUE to represent the CPUE of the whole year may inflict a serious bias for estimating sustainable yield as significant seasonal variations in CPUE of common wolffish were found in this study. Consequently, CPUE presented in this thesis was not considered appropriate for estimating the abundance or sustainable yield of North Sea common wolffish. Length-frequency methods have been used to study age and growth successfully in a number of species (Pauly, 1994). However, these methods are affected by various factors such as width of the size class interval and sample size (Pauly, 1983; Mytilineou and Sardá, 1995). Pauly (1983) suggested that a total sample size in excess of 1,500 collected over a period of 4 months is required for using these methods (e.g. ELEFAN, MULTIFAN). The sample size in this study was insufficient to meet the requirements for the application of length-frequency methods, as was the existence of an extended sampling period. Also common wolffish are slow-growing fishes, for which clear size modes approximating to different ages are likely to be poorly defined if at all apparent. So far there have been no reports of age and growth studies of common wolffish using these methods. Therefore, in this study otoliths were used to examine age and growth.

Chapter 3 Metabolism of common wolffish

3.1 Introduction

3.1.1 General energy budget concept

Fish, like all animals, utilise food to provide nutrients and energy in order to live and produce offspring. Energy in the food is used to enable essential metabolism, including maintenance and tissue repairs, food digestion and locomotor activity, or is stored as energy for growth and reproduction. The study of fish energetics involves the partitioning of ingested energy into the major physiological components of the energy budget equation. This principle must obey the law of thermodynamics in that the exchange of energy between the input and output has to be equal and that as energy is used to do useful work some will be lost as heat (Wootton, 1992). Winberg (1956) provided a simple form for the equation as follows:

$$C = P + R + E$$

where C is ingested energy, P is the production, R is metabolism and E is the energy lost as waste products.

The equation is usually expanded to the more general form:

$$C = P + R + F + U$$

where F and U represent the energy losses in faeces and excretory products respectively.

The term $(P+R)/C$ could be considered as the efficiency by which consumed food is assimilated. Production can be expressed in terms of growth combined with reproduction: Metabolism may be subdivided to account for the energy losses in maintaining basic body function, activity and digestion. Brett and Groves (1979) suggested that for carnivores, the partitioning of energy from food is:

$$100C = 29P + 44R + 27E$$

The components of the energy equation display a dependent or competitive relationship. One very obvious metabolic conflict in fish is between using the same resources to produce biomass and paying the costs of activity. Calow (1985) provided a good review to describe the variable relationships between these factors. Trade-off in energy income and energy expenditure appears to have been strongly selected for in fish and a variety of other animals.

3.1.2 Growth

Growth depends on the quantity of food obtained, but as a fish grows it could choose a wider range of prey items. These variations in food consumption would influence the further growth of fish (e.g. body size, mature size etc.). Lucas (1996) provided a scheme to describe the relationship between the growth rate and food consumption rate (Fig. 3.1). This relationship is usually an asymptotic curve. The rate of growth (Q_G) is a function of food ration consumption (Q_C) and Q_G/Q_C indicates all possible values of growth rate at different levels of food consumption. A minimum quantity of food is required just to maintain body function where $Q_{CM} = 0$. A consequence of the shape of the relationship between growth rate and food consumption is that the maximum growth efficiency is gained at a ration, Q_{COPT}. Usually the fish cannot maximise its growth rate and growth efficiency at the same time (Brett, 1979).

The growth rate is also affected by the profitability of the food (Elliott, 1975). There is a range of food particle sizes that allow fish to digest them at minimum cost and achieve the highest growth rate. Temperature is another important factor in determining the growth rate. At the optimum temperature, fish have their highest growth rate if food supply is unlimited. However, high growth rate for fish is also accompanied by high mortality rate (Pauly, 1980).

For a long time fish growth has been expressed in various forms of the von Bertalanffy growth model (Elliott, 1979). Although the von Bertalanffy model has been widely used in the fisheries field and has been useful in modelling growth data, it is often still not satisfactory when combining several factors such metabolism and growth. Thus, the balance energy equation has been widely applied.

Initially, growth rate will increase with increasing body weight, will peak at a specific body size, and finally decline as the body weight continues to increase. Specific growth rate (SGR) is usually used as a measure of relative growth rate in experimental

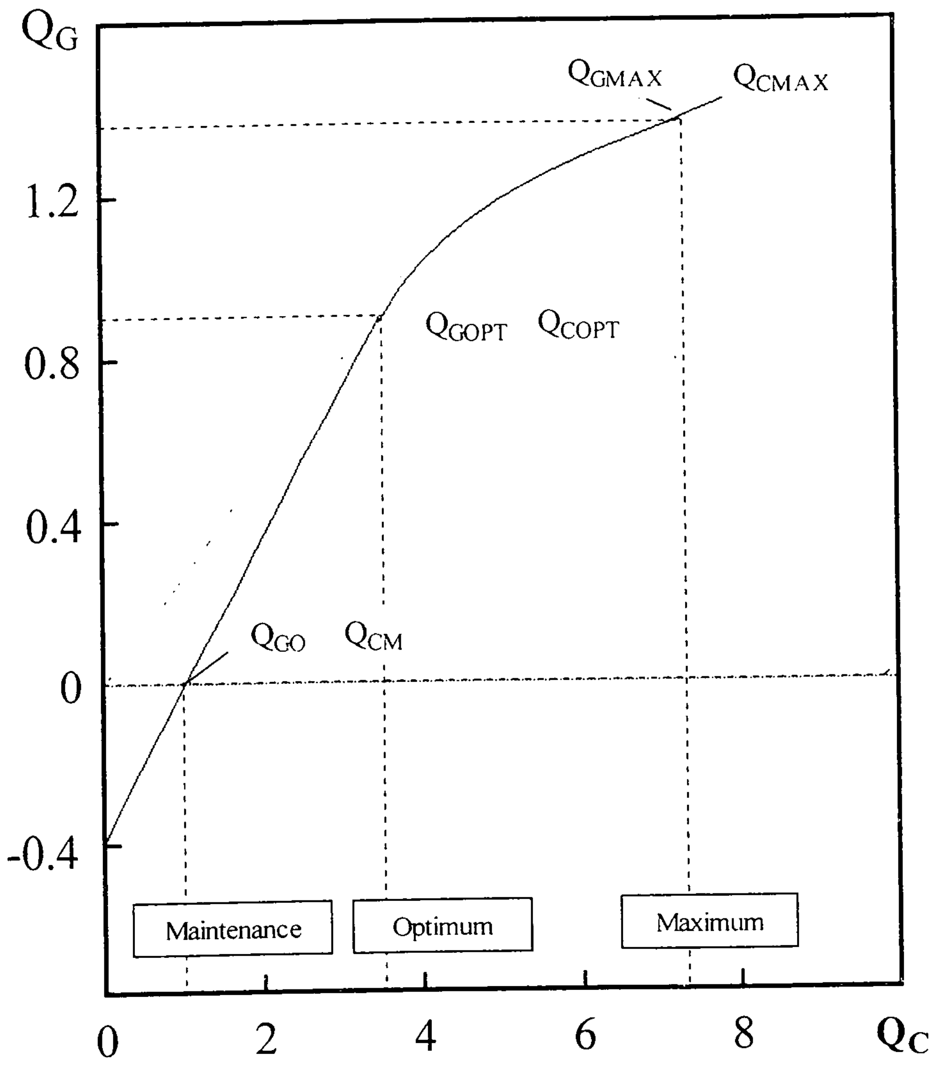


Fig 3.1. Interaction between food ration and growth for bioenergetics in fish. Q_C and Q_G are expressed as daily rates of food consumption and growth. Q_{CM}, the maintenance ration, provides the basic energy for survival where growth rate = 0 (Q_{G0}). Q_{COPT}, the optimal ration, gives the optimal growth rate and maximum growth efficiency (Q_{GOPT}). Q_{CMAX}, the maximum food availability, gives the maximum growth rate (Q_{GMAX}) but the growth efficiency will be lower than Q_{GOPT}. (Redrawn from Lucas, 1996)

studies. When food availability increases following a period of starvation or restricted food, the fish may increase their growth sharply. This phenomenon is usually termed compensatory growth (Wieser *et al.*, 1992). Another factor, which must be considered in studies of growth processes, is conversion efficiency. This efficiency normally declines with increasing body weight (Jobling, 1993).

3.1.3 Metabolism

Energy metabolism occurs by the oxidation of exogenous or endogenous materials to produce energy for maintenance, production, and activity (Waversveld *et al.*, 1989). Gaseous exchange by fish, principally through gill ventilation, provides oxygen for aerobic conversion of the energy contained in food to chemical energy and heat. Measurement of aerobic metabolism can often show us how a fish is responding to environmental conditions and what its physiological situation may be (Cech, 1990). Aerobic metabolic rate of fish is usually measured by quantifying oxygen consumption since dissolved oxygen levels are determined quite easily and reliably. Oxygen consumption rates can then be converted to energy units by using an appropriate oxycalorific equivalent (Gnaiger, 1983). .

Energy expenditure can be measured directly by measuring the total heat production (calorimetry). However, this is rarely used for fish because the metabolic rate and heat production rate of fish is generally low and the heat capacity of the surrounding water is large (Brett, 1970). Furthermore, the sensitivity of metabolic rate measurement by direct calorimetry is less than by indirect means such as oxygen consumption (Brett and Groves, 1979). There has been some success in direct calorimetry of fish (e.g. Smith *et al.*, 1978; Waversveld *et al.*, 1989). Respirometry is the most important and powerful method for estimation of metabolic rate of fish and has been used for more than 30 years.

Metabolic demands usually constitute a substantial proportion of the energy budget of a fish. These energy costs can be subdivided into the minimum costs required for maintaining basic body function, those related to the digestion and absorption of food and those associated with activity. These are usually expressed in the following format:

$$R = Rs + Rf + Ra$$

where R is total metabolism, Rs is standard metabolism, Rf is feeding metabolism and Ra is activity metabolism.

Standard metabolism (approximating to basal metabolism) represents a measure of the minimum energy required to sustain life, and is the heat production in the absence of muscular activity, food consumption and processing, and growth (Jobling, 1993). It can be difficult to measure the minimal metabolism from a quiescent fish in a post-absorptive state, because the measurement often includes some increase over the minimum rate due to the metabolic costs of low level spontaneous activity. Also the length of time without food affects metabolic rate, with increased periods of food deprivation leading to a reduction in metabolism apparently associated with decreased in rates of protein synthesis (Beamish 1964, Jobling 1980). Hence it has become common to calculate standard metabolism from data obtained on swimming fish. When a relationship between swimming speed and the metabolic rate is established, and the relationship is extrapolated to zero speed then the estimate of the metabolism at zero swimming speed can be defined as the standard metabolism of the fish. This method is useful for estimating the standard metabolic rate from active species, which do not remain quiescent in respirometry chambers. The development of tunnel type respirometry has been used widely to measure oxygen consumption at different levels of forced, steady swimming activity (Brett, 1964). For inactive, poorly-swimming fish species such as pike (*Esox lucius*), resting metabolic rate (RMR) provides an appropriate estimate of basal metabolism and is likely to be similar, though not necessarily the same as standard metabolism.

There are two major factors, which influence standard metabolic rate - body size and temperature. Although large fish usually consume more oxygen than small fish of the same species, on a per unit-weight basis, small fish consume more oxygen than larger fish (Schmidt-Nielsen, 1984). It is usually found that an increase in temperature leads to an increase in standard metabolic rate (Brett and Glass, 1973; Diana, 1983). Previous thermal environment may also influence the metabolic response to a change in temperature, so that if fish are transferred from one temperature to another, the results of metabolism measurement made immediately after transfer will usually be different from those obtained from temperature acclimated fish (Cossin and Bowler, 1987).

Feeding in fish is associated with increased heat production and an increase in the rate of oxygen consumption (Brett and Groves, 1979). This energy loss associated with feeding can be affected by several factors, such as locomotion and other incidental activity, the mastication, digestion and absorption of food in the gut, and the biochemical assimilation of the absorbed materials (Soofiani and Hawkins, 1982). After feeding, the rate of oxygen consumption increases steeply and typically peaks at two to three times the pre-feed level, then gradually declines to the resting level. This phenomenon had appeared in the literature was defined to by several names, including heat increment (Kleiber 1961), specific dynamic action (SDA), and apparent SDA (Beamish 1974). The mechanism of SDA is still not well known. It is generally assumed to be the result of the metabolism of protein and amino acid (Beamish, 1974), but also includes the release of energy accompanying lipid and carbohydrate metabolism (Soofiani and Hawkins, 1982). Jobling (1981) also suggests that SDA is directly related to protein synthesis and growth

Swimming is a very energy-demanding behaviour. Respiration rates usually increase with increasing activity or swimming speed (Brett, 1965; Farmer and Beamish, 1969). The aerobic energy expenditure of powerful swimmers such as salmonids and tuna swimming at maximum speeds can rise to 10-15 times that of a fish at rest (Graham and Laurs, 1982; Brett, 1972). The maximum aerobic metabolic rate is therefore often measured as the oxygen consumption during swimming at the maximum sustainable speed, usually termed active metabolic rate. However, for poor swimmers, maximum aerobic metabolic rate may occur following exhaustive activity, requiring oxygen debt repayment (Priede, 1985).

The extent to which measurements of oxygen consumption reflect the energetic costs of swimming activity varies with swimming speed, because anaerobic metabolism, leading to the production of lactate acid, increases with swimming speed (Jobling, 1993). Jobling also reported that in some species of typical sit-and-wait predator such as pike, anaerobic respiration begins in the muscle at low activity levels, whilst in actively foraging species higher speeds are reached before anaerobic respiration begins. On the basis of this, common wolffish would not be expected to achieve high-sustained aerobic swimming speeds.

Environmental conditions such as temperature, ambient oxygen level and salinity may act as controlling and limiting factors to oxygen consumption rate (Fry, 1971). The maximum rate of oxygen consumption typically increases as temperature increases but declines above some threshold (Brett, 1964; Wieser and Forstner, 1986; Kaufmann and Wieser, 1992). Salinity and oxygen effects are complicated by specific acclimation patterns and respiration rates may be dependent or independent of ambient oxygen levels (Neumann *et al.*, 1981).

The difference between the standard metabolic rate (Rs) and the maximum aerobic metabolic rate (Rmax) may be termed the scope for activity within which the animal must function (Fry, 1947) and is also known as metabolic scope. Most fish cannot sustain life for long outside the aerobic metabolic scope. It is therefore important for the fish to manage its metabolic processes within its power capacity. Generally speaking, active fish with high maximum metabolic rates and large metabolic scopes also have high standard metabolic rates. Priede (1985) suggested that the relative scope for activity of fish varies according to the species and stage of development and is also influenced by environmental factors, particularly temperature. According to Priede (1985) a normalised expression for use of metabolic scope is:

$$S = (R - Rs) / (Rmax - Rs)$$

where S is the metabolic rate normalised with respect to aerobic scope and R is the field metabolic rate.

In reviewing several studies Priede (1985) suggested that cod and brown trout (*Salmo trutta*) represented two different types of metabolism budgets. For cod, metabolism from SDA may be as more important in use of metabolic scope as metabolism from aerobic swimming activity. For trout, metabolic rate at maximum sustainable swimming speed corresponds to Rmax and occupies the whole of the metabolic scope. The SDA is less important than swimming activity. Hence, there is much less of a conflict between the needs of locomotion and SDA in trout than in cod. Nevertheless, this power budgeting problem is faced by all fish. This is especially so for fish with a low scope for activity, where a choice between swimming activity and food consumption must be made. In other words, reduced swimming activity may enable increased SDA costs, hence allowing more rapid growth.

Fisheries management needs data to quantify predator trophic demand and relative demand to prey supply. Ecological studies need quantitative tools to understand the complex biological and biophysical relationships in aquatic systems (Brandt and Hartman, 1993). Thus, bioenergetics models can be used as a powerful approach the problems of fisheries management and to examine ecological interactions (Stewart *et al.*, 1981; Hewett, 1989; Madon and Culver, 1993). These models are based on the mass energy balance equation, with which knowledge of growth, metabolism and waste may be used to predict consumption or vice versa, if the models are realistic.

Ney (1990) suggested that bioenergetics models closely link fish physiology and behaviour with environmental conditions. If combined with population dynamics, they can lead to ecosystem-level estimates of fish production and population (e.g. Hewett, 1989).

3.1.4 The aims of this chapter

Up to now, there have been some studies of common wolffish growth from laboratory experiments using larval and juvenile fish as well as studies of feeding regimes (Stefanussen *et al.*, 1993; Moksness, 1994) and protein synthesis (McCarthy *et al.*, 1999). There have also been studies of growth and food of wild fish (Falk-Petersen *et al.*, 1990; Nelson and Ross, 1992). However, there have been few attempts to study the respiratory energy budget, although Karamushko (1993) has done some measurements of post-feeding metabolic rates metabolic rates of this species. This information can help to provide an understanding of the energetic strategy that common wolffish use in the natural environment. Such information can also be applied to fisheries management and broader ecological studies. For aquaculture, the energy studies are also important in understanding the range of metabolism in relation to temperature and activity is important for determining likely stock densities and growth rates. Variation in metabolic scope in relation to temperature has been proposed as a way of establishing the optimum temperature for activity and feeding (Brett & Groves, 1979). Common wolffish are also a good model for sedentary benthic fish and therefore provide an interesting species for comparing metabolic strategies with other fishes.

3.2 Materials and Methods

3.2.1 Growth in relation to ration

Twenty-seven live adult common wolffish were obtained from North Shields in May 1996 by commercial trawls from along the Northumbrian coast (fishing division, 38E8). They were transported to Durham and moved into 7 tanks (1 × 1 × 1.5 m) in the departmental aquarium and acclimated for three weeks at 5 ± 0.5°C from the sea temperature of 7.5°C at a rate of 0.2°C per day. Each tank contained 3-4 individuals. Over this period no common wolffish died, but fish ate little, presumably due to the stress of being moved. After acclimation inspection showed no evidence of infection was found. However, two fish were blind in a single eye, two had bad damage to the caudal fin, and one had a bad scar near the dorsal fin. It is thought that these resulted from capture. To avoid experimental bias, these fish were removed and humanely killed.

After the acclimation period, ten common wolffish were chosen randomly and anaesthetised with ethyl-m-aminobenzoate methane sulphonate (MS-222). Total length and body weight was measured to the nearest millimeter and gram. Two individuals were placed in each of five tanks. Each tank contained 1200 L of seawater and was fitted with a filter pump and airstone. A plastic mesh running across the middle of each tank separated pairs of fish and enable the food consumption of each common wolffish to be measured accurately.

During the first experiment, temperature was controlled at 5 ± 0.5°C. A 12 hours day-12 hours night photoperiod was provided. The common wolffish were nominally fed 2% of their wet body weight of squid, obtained from Angel-Ocean Ltd. Canada, every two days continuing for 30 days and they were weighed and measured after 14 days and a further 16 days. Remaining food was removed after 12 hours. An analysis of food composition (fat, 4.4%; carbohydrate, 4%; protein, 14%; others (e.g. water, fibre) 77.6%) and energetic value (5.85 kJ g^{-1} wet weight) have been given by company. Fish showed a range of food consumption rates and the range of observed rations enabled prediction of maintenance ration from observed growth rates. The mean (±SE) weight of the ten fish was 1,494.8 ± 105.2 g at the start of experiment, was 1,506.7 ± 125.3 g after 14 days, and was 1,517.4 ± 124.1 g after 30 days.

Specific growth rate (SGR) was calculated according to the formula (Moksness *et al.*, 1989):

$$SGR = \{exp\ [ln\ (W_{t2}) - ln\ (W_{t1})] / (t_2 - t_1)] - 1\} * 100$$

where W_{t2} and W_{t1} are weights of an individual fish at days t_2 and t_1. Two measurements of specific growth rate in relation to ration were obtained for each fish (one from each of the experimental periods).

After finishing the growth experiment at 5°C, the same ten fish were acclimated to 10 ± 0.5°C for two weeks at a rate 0.5°C per day. During the acclimation period, fish were only fed once at 1% of body weight level. The protocols of growth experiments at 10°C were the same as at 5°C. The mean (±SE) weight of the ten fish was 1,429.5 ± 120.8 g at the start of experiment, was 1,418.3 ± 118.1 g after 14 days, and was 1,402.1 ± 109.4 g after 30 days.

3.2.2 Metabolism measurement

Oxygen consumption rates (MO_2) of common wolffish were examined by the use of a flushing, closed system respirometer in which individual fish was placed. Experiments were carried out at 5°C and 10°C, and the same fish were used at both temperatures. Fish were acclimated to the experimental temperature at a rate of 1°C per day, and held at the experimental temperature ± 0.5°C, for one month prior to experimentation. A 12h: 12h light-dark photoperiod was maintained throughout the acclimation and experimental period. Experiments were carried out during the growth and feeding period, rather than during the winter spawning / tooth-exchange fast (Jónsson, 1982; Albikovskaya, 1983).

To minimize the effect of size on metabolic rate (Brett & Groves, 1979), fish of a restricted weight range, 0.889-1.987 kg ($\bar{x}$ = 1.390 kg), were used. However, to further limit any effect of weight, standardised metabolic rates were also calculated using allometric scaling coefficients (see 3.2.5). Fish were starved for 5 days prior to introduction to the respirometer in order to avoid post-prandial artifacts (Karamushko, 1993). A total of six fish were used for the experiments. All fish were adult.

3.2.3 Respirometer design

The design of the respirometer system is shown in Fig. 3.2. The respirometer chamber was formed from a modified storage container constructed from polystyrene (0.64 × 0.30 × 0.28 m). The total volume of the respirometer system was 54 l. The chamber lid was secured by bolts and wing nuts and a foam rubber strip afforded an air-tight seal. A small airtight hatch (0.15 × 0.15 m) in the lid enabled fish to be inserted into or removed from the respirometer, and for air bubbles to be removed.

A centrifugal pump (Eheim 2025) was used to circulate water through the system. The respirometer system was submerged in an aerated water bath (1200L volume) at constant temperature maintained at the experimental temperature ± 0.1° C by the room's temperature control system. An oxygen electrode (Strathkelvin 1302) was installed in the circulation tubing and connected to an oxygen meter (Strathkelvin 781). Between measurements the respirometer was flushed with air-saturated water pumped from the water bath without disturbing the fish. Each oxygen consumption measurement was carried out over a 1 h period. No experimental run was allowed to reduce the oxygen content below 70 % of the air-saturated level. The oxygen electrode was calibrated at 0% and 100% air-saturation level at least once each day, correcting for barometric pressure.

The decrease in water oxygen content with time was recorded and the gradient of the trace was used to calculate oxygen consumption. Oxygen consumption rate ($mgO_2\,kg^{-1}h^{-1}$) was calculated in the following formula:

$$\dot{M}O_2 = [(O_{2i} \times c) - (O_{2f} \times c)] \times V_{net} \times W^{-1} \times t^{-1} \times 1$$

where:

O_{2i} = initial $\%O_2$ value

O_{2f} = final $\%O_2$ value

c = oxygen solubility constant ($mlO_2\,l^{-1}$)

V_{net} = volume of respirometer – volume of fish (l)

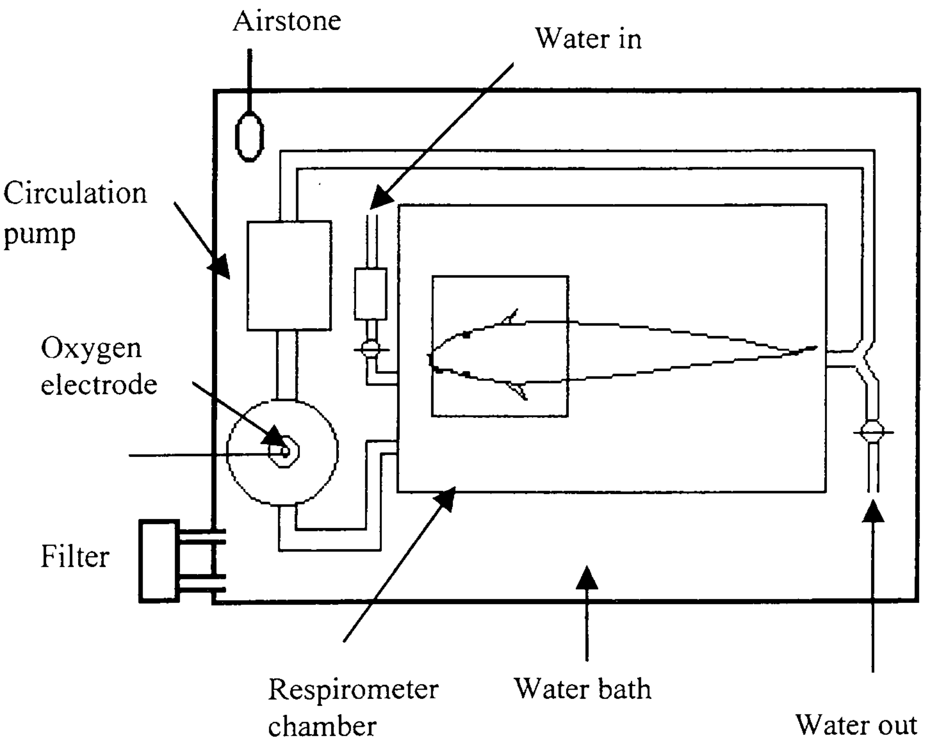


Fig. 3.2. The design and apparatus of the respirometer system used for common wolffish in this study. Oxygen consumption was determined from a flushing, closed flow-through system with an oxygen electrode (Strathkelvin 1302). The system consisted of a 54 L fish chamber which was submerged in an aerated water bath at constant temperature and controlled under a 12h L: 12h D regime.

W = weight of fish (kg)

t = time between O_{2i} and O_{2f} (h)

1.43 = constant for converting from mlO_2 to mgO_2. Oxygen solubility coefficients were read from a table of values (Parsons *et al.*, 1984) for the measured water temperature, salinity and barometric pressure.

3.2.4 Controls

Declines in oxygen partial pressure measured during experimental runs may not truly reflect real oxygen consumption by the animal, and may be influenced by microbial respiration or leakage in the system. To avoid this regular control runs, measuring MO_2 in chamber without fish, were carried out to measure and confirm that microbial respiration and system-leakage were insignificant.

3.2.5 Measurement of resting metabolic rate and maximum metabolic rate

Common wolffish are poor swimmers and estimation of *Rs* in swimming respirometers is likely to be difficult and inappropriate. Instead a better estimate of basal metabolism is likely to be achieved by measuring resting metabolic rate (RMR) of quiescent, post-absorption fish.

For measurements of RMR, fish were lifted by net from the tank and introduced to the respirometer immediately. Oxygen consumption rates were recorded for a period of 40 hours, with an interval of 2 h between the first five measurements and an interval of 4 h thereafter. A closed-circuit television camera mounted above the respirometer allowed fish activity to be monitored. Following acclimation to the respirometer, which took less than 5 hours at both temperatures, mean RMR was calculated for individual fish from those records for which the fish was quiescent. The data used for calculating RMR was characterized by activity occurring for less than 1% of the total experiment time, and comprising slow, repositioning movements.

In species with poor swimming abilities such as pike, maximum metabolic rate (MMR) occurs under circumstances of oxygen debt repayment following exhaustive exercise (Armstrong *et al.*, 1992). This method was used to measure MMR of common wolffish in the current study. Fish were followed with the net until they refused to swim further, and were then introduced to the respirometer, where measurements of oxygen consumption were made immediately. Maximum metabolic rates usually occurred within 1 h of introduction but measurement was continued until it was ascertained that the peak metabolic rate had been recorded. This measure of MMR is probably not sustainable for periods of > ~ 1h, but it probably represents a genuine metabolic ceiling for fish of this physiological type (Lucas & Priede, 1992).

Since the common wolffish used for oxygen consumption measurements were of varying sizes it was necessary to take account of allometric size effects on RMR and MMR. To remove the effects of body size on BMR and MMR, the values were adjusted and calculated from the equation (Soofiani and Priede, 1985):

$$\dot{M}O_{2adj} = (\frac{W_s}{W})^b \times \dot{M}O_{2\exp}$$

where MO_{2adj} is the corrected oxygen consumption in $mgO_2\,h^{-1}$ for a standard fish of weight W_s kg, W is the weight of the experimental fish in kg, b is the allometric scaling coefficient, and MO_{2exp} is the observed oxygen consumption of the fish in $mgO_2\,h^{-1}$. Allometric scaling coefficient b used in this study (0.8 for RMR, 1.0 for MMR) are based on values from Schmidt-Nielsen (1984).

The small sample sizes and relatively small weight range made determination of scaling coefficients from this data subject to substantial potential error. Therefore appropriate values from the literature were used.

3.3 Results

3.3.1 Growth rate and food ration to body size

Although common wolffish were fed at 1% W.B.W. day^{-1}, since not all food was eaten a range of rations was attained. There was a highly significant relationship between specific growth rate and ration (n = 20, $r^2 = 0.58$, $P < 0.001$). The result indicated a maintenance ration of about 0.5 % W.B.W. day^{-1}, for which zero growth was attained at 5 °C (Fig. 3.3). Therefore, a 1.5 kg common wolffish would need 7.5 g squid per day, equivalent to 43.8 kJ day^{-1}, to maintain its body tissue. A significant relationship was not obtained at 10° C, due to substantial variations in individual growth-ration responses (Fig. 3.3).

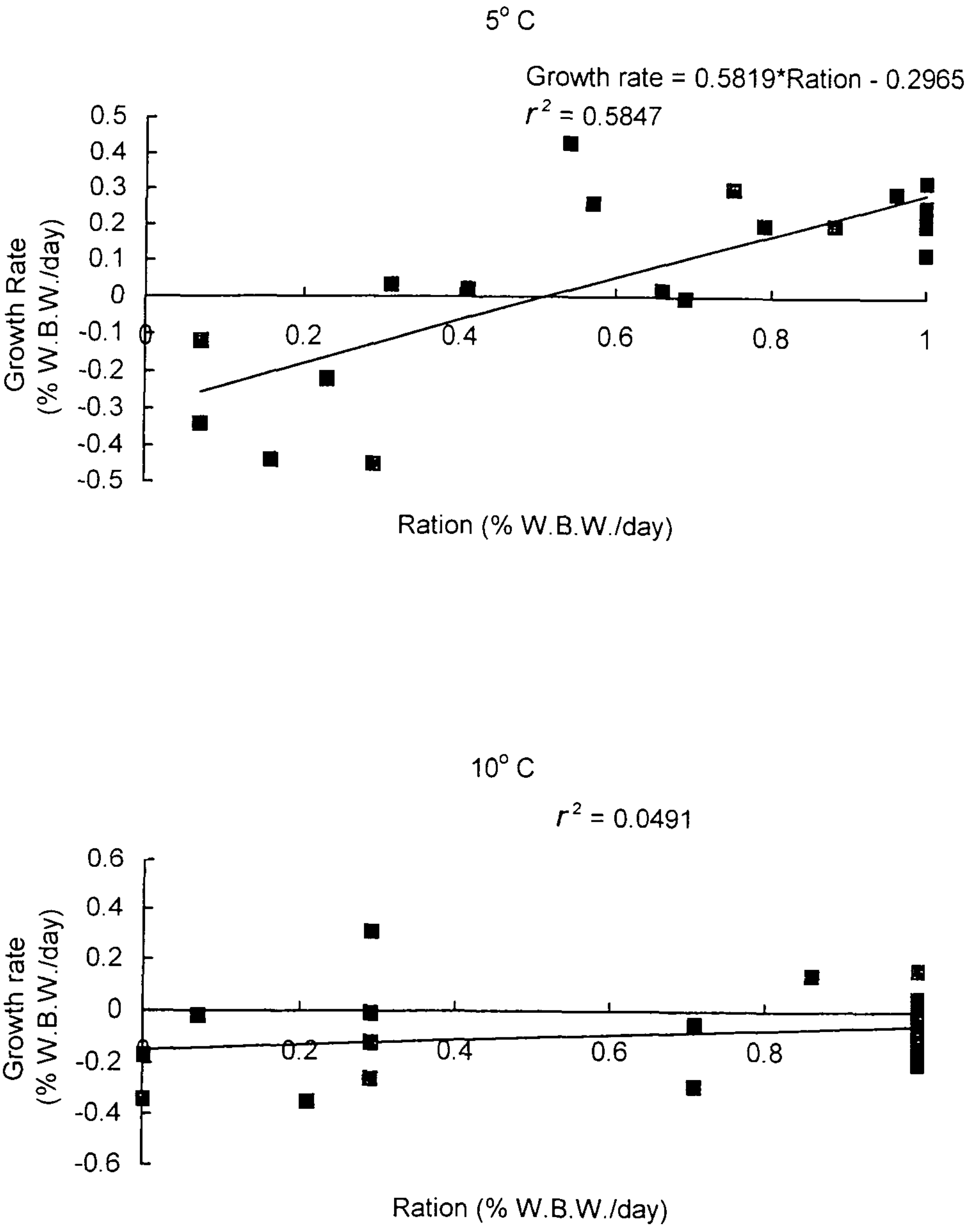


Fig. 3.3 Growth rate of ten individual common wolffish at different rations replicated over 14 and 16 day periods at 5° C and 10° C.

At 5°C the SGR for ten individuals throughout the experimental period (30 days) ranged from –0.36 to 0.30 %$\text{day}^{-1}\text{kg}^{-1}$ with a mean SGR ± SE was 0.28 ± 0.067 %$\text{day}^{-1}\text{kg}^{-1}$. Since there was no significant relationship in growth-ration at 10°C experiments, the SGR of common wolffish at 10°C was not available in this study.

3.3.2 Resting metabolic rate

Following introduction of minimally disturbed fish to the respirometer, oxygen consumption rates were relatively high at both 5°C ($\overline{x}$ = 62.7 mg $O_2\,kg^{-1}h^{-1}$) and 10°C ($\overline{x}$ = 88.2 mg $O_2\,kg^{-1}h^{-1}$), but declined to typical resting levels (20.40 mg $O_2\,kg^{-1}h^{-1}$ at 5°C; 27.18 mg $O_2\,kg^{-1}h^{-1}$ at 10°C) within 5 h (Fig. 3.4), indicating a rapid acclimation to the respirometer. Metabolic rate was low, as expected for large fish at low temperatures. Inside the respirometer, common wolffish mainly rested on the bottom, rarely moving around. Most activity was slow and tended to involve position changes, and during most measurements occurred for less 1% of the time. There were no statistically significant fluctuations in metabolic rate between day and night at both 5°C (*Z*-test, n = 60, P= 0.98) and 10° C (*Z*-test, n = 60, P = 0.35).

The mean ± SE of the weight-adjusted (1 kg) RMRs for all individual fish was 12.18 ± 1.60 mgO_2 $kg^{-1}h^{-1}$ at 5°C and 25.43 ± 1.31 mgO_2 $kg^{-1}h^{-1}$ at 10°C. Resting metabolic rate of common wolffish at 10°C was about twice that at 5°C. There were significant differences in RMR between individuals at 5° C (one-way ANOVA, df = 5,44, F = 30.64, $P < 0.001$), and at 10° C (one-way ANOVA, df = 5,44, F = 36.65, $P < 0.001$) (Fig. 3.5). The Q_{10} of RMR for this species over the temperature range 5-10°C was 3.2.

3.3.3 Activity in relation to oxygen consumption

Activity of individuals was recorded by CCTV during experimental periods. After an initial period of intense activity associated with introduction of fish to the respirometer, the behaviour of individual fish was similar. Fish rested for most of the time on the bottom of the respirometer. When a fish occasionally moved, it turned around in the respirometer chamber with the head held above the floor, usually at tail beat frequencies of <1 Hz. Oxygen consumption and spontaneous activity from three fish at each temperature were calculated (Fish 1,2,5 for 5°C and Fish 3,4,6 for 10°C).

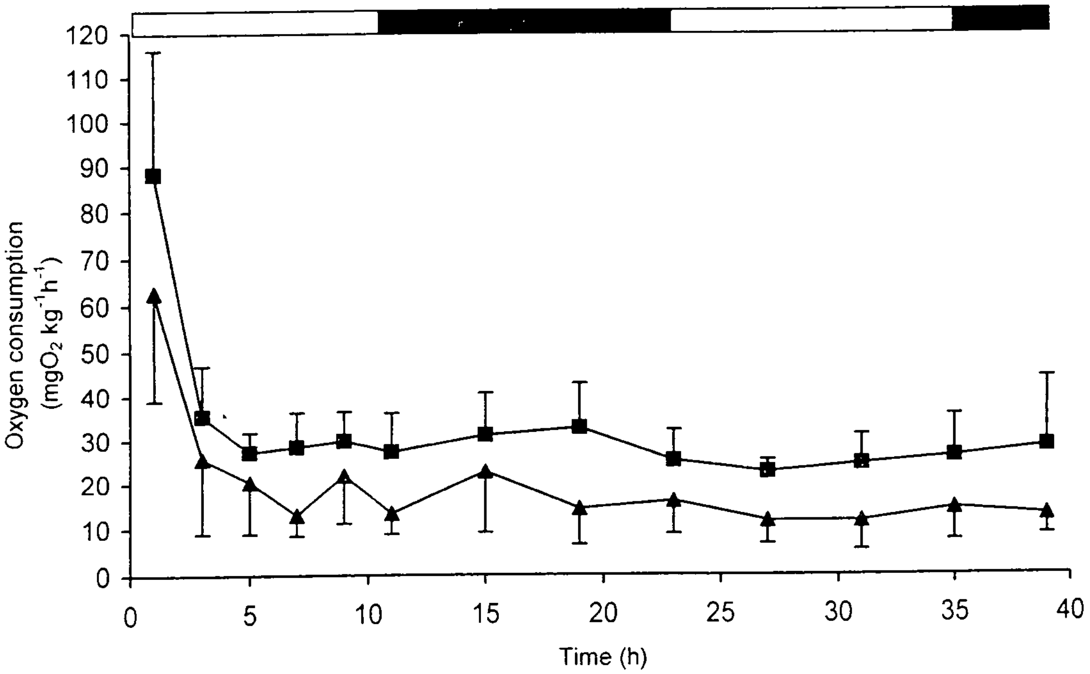
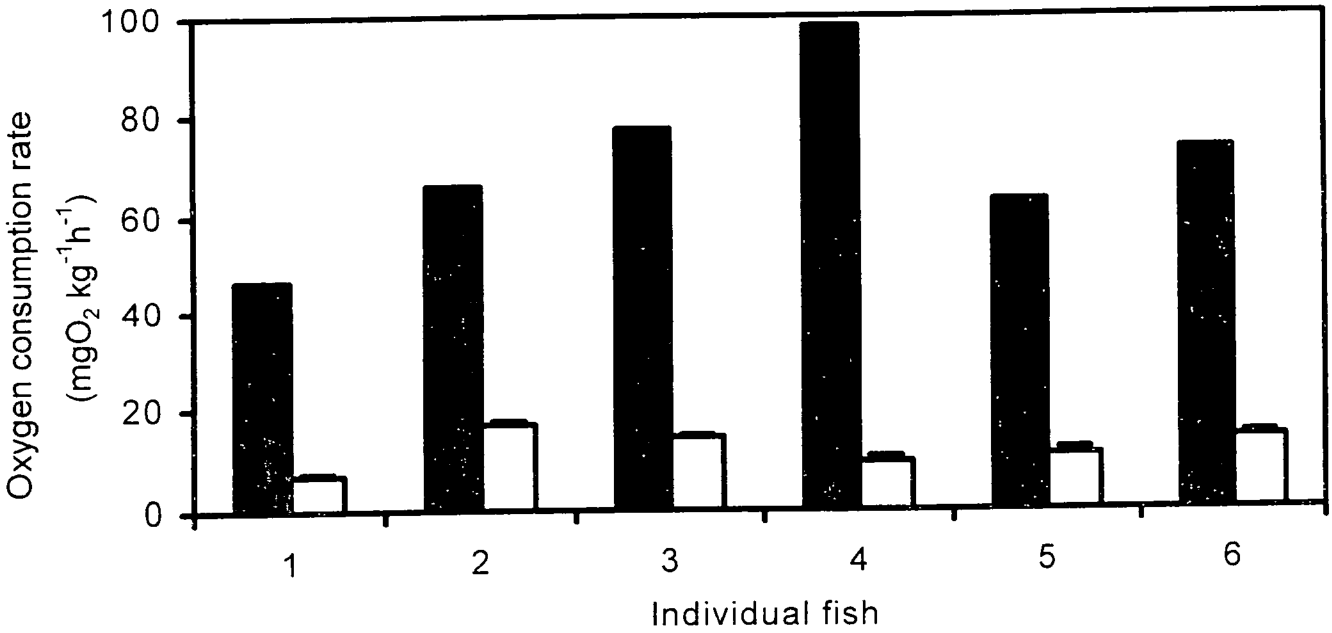


Fig 3.4. Resting metabolic rates (mean x ± SE) for wolffish at 5°C (▲) (N = 6) and 10°C (■) (N = 6), showing the rapid acclimation and the lack of significant diel rhythms. The shaded portion of the horizontal bar represents darkness.

(a)



(b)

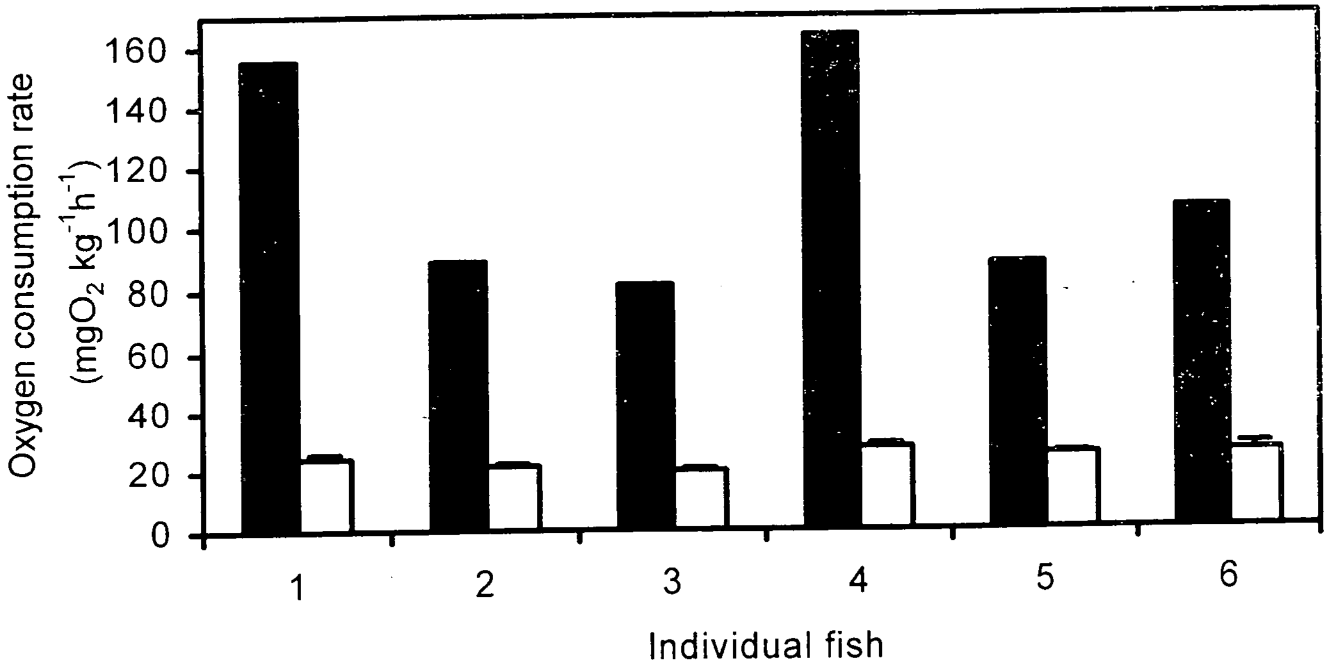


Fig. 3.5. Mean ± SE of resting metabolic rate (□) and maximum metabolic rate (■) for the same six individual wolffish at (a) 5°C and (b) 10°C. In each case the metabolic scope is given by the difference between resting and maximum metabolic rates.

The relationships between metabolic rate and total duration activity over a 1 h measurement of spontaneous of each fish at both temperatures are shown in Fig. 3.6a and Fig 3.6b. There were significant differences in the slopes of the metabolism-activity relationships between fish for both 5°C (ANCOVA, $F = 44.7$, $P < 0.001$) and 10°C (ANCOVA, $F = 9.96$, $P < 0.01$).

From extrapolation to zero activity it was possible to estimate the standard metabolic rate (Rs). The overall mean standard metabolic of common wolffish was 13.9 mg O_2 $kg^{-1}h^{-1}$ at 5°C and 30.5 mg O_2 $kg^{-1}h^{-1}$ at 10°C. The mean RMR for individuals was calculated as 12.18 mg O_2 $kg^{-1}h^{-1}$ at 5°C and 25.43 mg O_2 $kg^{-1}h^{-1}$ at 10°C. The Rs values were slightly higher than RMR values. A statistical comparison was not made due to the low sample size.

3.3.4 Maximum metabolic rate

Highest levels of oxygen consumption were observed soon after placement of the fish into the respirometer and declined rapidly as the fish recovered. The maximum aerobic metabolic rates, measured during recovery from exhaustive exercise were quite low by comparison to active species. Weight-adjusted mean ± SE maximum aerobic metabolic rates, measured during recovery from exhaustive exercise were 70.65 ± 7.63 mg O_2 $kg^{-1}h^{-1}$ at 5°C and 113.84 ± 16.26 mg O_2 $kg^{-1}h^{-1}$ at 10°C. The MMRs for individuals showed considerable variation between individuals at both 5°C and 10°C (Fig 3.5).

3.3.5 Metabolic scope and metabolic power budget

There appeared to be substantial variation in relative metabolic scope between individuals, with a range of 3.9-10.4 at 5°C and 3.5-6.4 at 10°C (Fig. 3.5). Mean absolute metabolic scope, calculated from scope measurements of individual fishes, increased from 58.47 ± 7.29 mg O_2 $kg^{-1}h^{-1}$ at 5°C to 88.9 ± 16.82 mg O_2 $kg^{-1}h^{-1}$ at 10°C.

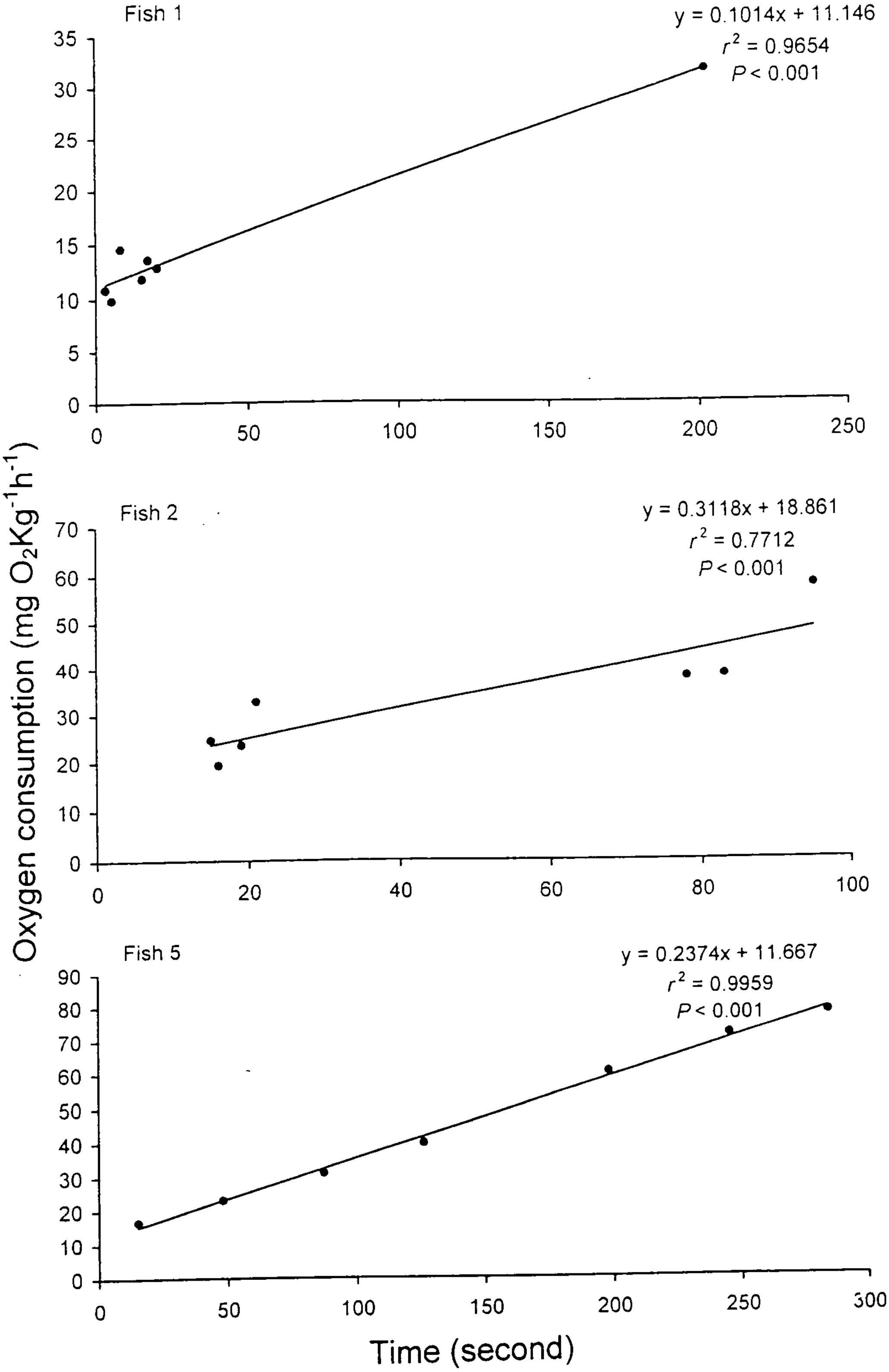


Fig. 3.6a. The relationship between metabolic rate and duration of movement for individual wolffish at 5° C.

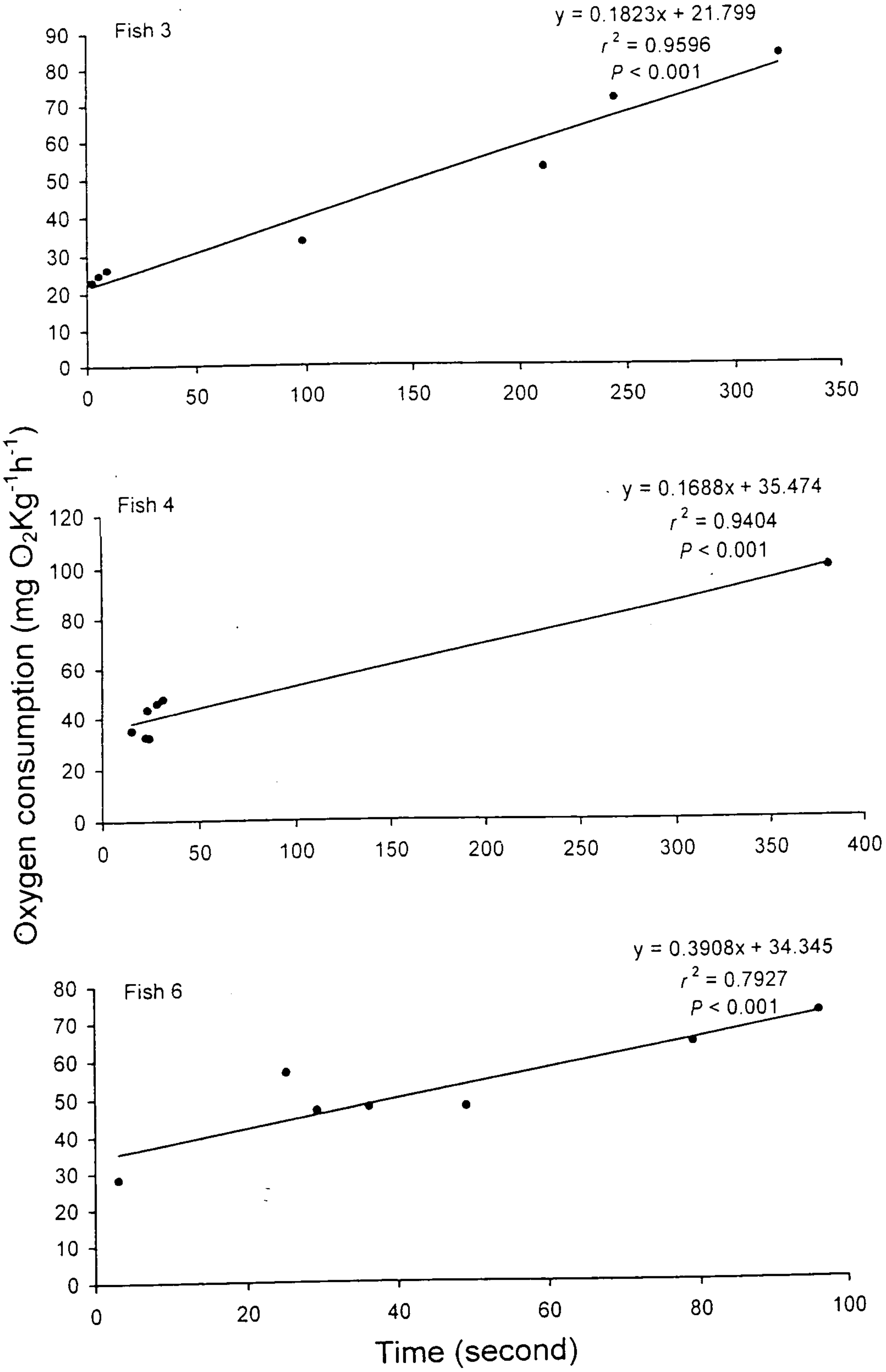


Fig. 3.6b. The relationship between metabolic rate and duration of movement for individual wolffish at 10° C.

In order to compare partitioning of the power budget in relation to metabolic scope for different metabolic parameters, the oxygen consumption data were converted to power units (W kg^{-1}) using Lucas' (1996) oxycalorific value of 13.6 J/ mg O_2. Data of post-feeding oxygen consumption rates used here were obtained from Karamushko (1993) who examined oxygen consumption of common wolffish after feeding meals of 2 % and 4 % W.B.W. Because data on SDA of common wolffish has been gathered by Karamushko, it was decided not to make such measurement. These data are shown in Table 3.1. The energy cost of SDA increased with meal size and temperature. However, the power budget showed that common wolffish fed moderately high rations appeared to have considerable remaining scope.

3.4 Discussion

3.4.1 Growth and maintenance ration

The specific growth rate (SGR) for adult common wolffish in this study averaged 0.28 % $day^{-1}kg^{-1}$ at 5°C. This value was slightly less than the value of 0.31 % $day^{-1}kg^{-1}$ at 6-14°C found by Moksness (1994). However, the weights of experimental fish used in Moksness's study were smaller than those in this study. This result follows the trend of decreasing growth with increasing body size found in all fish. The SGR of larvae common wolffish was about 2.1 to 3.8 % $day^{-1}kg^{-1}$ (Moksness *et al.* 1989, Pavlov and Novikov, 1993) and was much higher than that of adult common wolffish. Furthermore, Moksness *et al.* (1989) suggested that the optimum temperature for both larvae and adult common wolffish was between 8-10° C. The growth efficiency of the common wolffish is the highest at this range (Moksness, 1994; McCarthy *et al.*, 1999). Therefore, it seems likely that growth rate of the common wolffish increases with increasing temperature up to 10-11°C. Temperature seems to be one of the most important factors influencing the growth of common wolffish. Karamushko and Shatunovkiy (1994) suggested that adult common wolffish (1kg) achieve the maximum daily ration (g dry weight per day) at a value of 0.91% of body weight at a temperature of 6-7 °C with a full availability of food. This value of daily ration was less than the food fed to common wolffish in this study (1% wet body weight) at a similar temperature.

Table 3.1. Partitioning of metabolic power input. Karamushko (1993) provides estimates of the ratio of Rf peak/Rs for similar sized fish as in this study. These conversion factors have been applied to the weight standardised data here.

Parameter	Temp (°C)	Oxygen Consumption ($mgO_2\ kg^{-1}\ h^{-1}$)	Power Input ($W\ kg^{-1}$)	S
Rmax	5	70.7	0.27	1
Rr	5	12.0	0.045	0
Rr+ Rf (2% b.w.)	5	20.4	0.077	0.14
Rr+ Rf (4% b.w.)	5	26.2	0.099	0.24
Rmax	10	113.8	0.43	1
Rr	10	24.0	0.091	0
Rr+ Rf (2% b.w.)	10	44.4	0.169	0.23
Rr+ Rf (4% b.w.)	10	52.8	0.199	0.32

$$S = \frac{R - Rr}{R\ \mathrm{max} - Rr}$$

R= measured metabolic rate
Rmax = maximum metabolic rate
Rr = resting metabolic rate
Rf = peak post-feeding metabolic rate

The maintenance ration of common wolffish at 5°C was lower than found for flounder (*Platichthys flesus*) at similar temperatures (Duthie, 1982). Increasing temperature increases maintenance ration size and increasing body size decreases the maintenance ration (Johnson, 1966; Tyler and Dunn, 1976). It is likely that at 10°C, the maintenance ration for wolffish was higher than at 5°C, but the poor relationship prevented an estimate. The reason for the poor relationship is unclear. Fish were fed small rations because larger amounts of food damaged water quality. If is possible that at the lowest ration negative growth effects were masked by increases in tissue water content.

The growth-ration experiment in this study suggest that a 1kg common wolffish needs 29.7 kJ day^{-1} to maintain its body tissue at 5°C. This value was much higher than that obtained as RMR from respirometry experiments (3.9 kJ day^{-1}). The reasons for the difference between these results could be as follows: (1) Different techniques used to determine the maintenance ration could show different results. (2) The maintenance ration of common wolffish obtained from growth-ration experiments includes the energy used in SDA for digestion and losses in faeces and excretory products, as well as low levels of locomotor activity.

3.4.2 Partitioning of the metabolic scope and budget

The trend and duration of the acclimation response for individual fish was similar to that determined by other workers for a number of temperate fish species (e.g. Duthie, 1980; Armstrong, 1987). Resting metabolic rates of common wolffish were low, by comparison to other more active fish species of about the same size range (e.g. Atlantic salmon (*Salmo salar*), Lucas, 1994). In fact, common wolffish had among the lowest of reported RMRs, by comparison to other sedentary species, such as pike, cod, flatfishes although deep ocean species such as roundnose grenadier (*Coryphaenoides armatus*) (Smith, 1978) (Table 3.2) do exhibit lower metabolic rates. Antarctic icefish (*Notothenia neglecta*) at 0°C had similar rates to common wolffish at 5°C (RMR for a 1 kg icefish, summer, 18.1 mg O_2 kg^{-1}h^{-1}; winter, 13.5 mg O_2 kg^{-1}h^{-1}) (Johnston *et al*., 1991). This supports the view that common wolffish may be regarded as an energetically conservative species. The low RMR may reflect their apparently sedentary habits and provide a benefit for saving energy in basic maintenance costs as

Table 3.2. A comparison of mean standard (Rs), rest (Rrest) and maximum (Rmax) metabolic rates of common wolffish and other fish species, where appropriate allometric scaling coefficients for Rs, Rrest and Rmax have been used to calculatevalues for a 1 kg fish.

			$\dot{M}O_2$ ($mgO_2kg^{-1}h^{-1}$)					
Fish species	W (kg)	Temp	Rs	Rrest	Rmax	Scope	Relative Scope	Author
Roundnose grenadier, *Coryphaenoides armatus*	1.0	3		3.8				Smith (1978)
sockeye salmon, *Oncorhynchus nerka*	1.0	5.3	31.5		464	432.5	14.7	Brett & Glass (1973)
		10	~40		~600	~560	~15	
cod, *Gadus morhua*	0.65-1.5	5			~134.8			Tang *et al.* (1994)
	0.243	5	47.5		178.3	130.8	3.8	Schurmann & Steffensen (1997)
	0.371	10	62.4		227.4	165	3.6	
	~1.0	5		24.3†	134.8	117.8	5.5	Calculated based on above authors
pike, *Esox lucius*	0.68-1.28	5		16.9	52.8	35.9	3.1	Armstrong *et al.* (1992)
flounder, *Platichthys flesus*	~0.434	5		17.8	106.6	88.8	6	Duthie (1982)
common wolffish, *Anarhichas lupus*	1.0	5		12.2	70.7	58.5	5.6	This study
	1.0	10		25.4	113.8	88.9	4.5	

† Based on RMR of Schumann & Steffensen (1997), recalculated for 1kg fish using b= 0.82

suggested for flatfish (Duthie, 1982). Common wolffish undergo a tooth exchange in winter each year. During the spawning period and the following tooth exchange season, little food is taken by common wolffish, and the frequency of empty stomachs is about 60%-95% (Jónsson, 1982; Albikovskaya, 1983) to 34% (this study). This period occupies 3-4 months in a whole year. If a 1kg common wolffish does not consume any food over 4 months at 5°C (winter temperature), the costs for maintaining the basic body function are only about 713 kJ. This result was obtained based on the follow assumptions: 1) Assume no costs associated with food intake, digestion and faeces production; 2) Assume only minor locomotor activity occurrs over this period. The metabolic rate of minor activity of a 1 kg common wolffish could be estimated from low routine metabolic rates following acclimation to the respirometer (Fig. 3.4), and was 15.7 mg O_2 $kg^{-1}h^{-1}$. Therefore, the total energy cost of minor activity over 4 months was 614.9 kJ. 3) Assume low costs of urine production over this period. The energy cost of urine production was estimated to be about 16% of respiration costs based on the value from Lucas (1996). Hence, the total energy value of urine production over 4 month was 98.4 kJ. Considering the energy density of food taken by common wolffish (5.9 kJ g^{-1} (dry weight), Chapter 4), a common wolffish would only need to take about 345 g (34.5% of body weight) of food (dry weight: wet weight = 0.35:1, Chapter 4) to repay the energy loss over that period. It seems that the low RMR may act as an energy saving strategy to enable common wolffish to support maintenance physiological processes despite substantial energy losses during the reproductive period and little energy intake during the spawning and tooth exchange seasons. The significant between-individual variations in RMR reported here have been observed in other species such as Atlantic salmon (e.g. Metcalfe *et al.*, 1995). The reasons for this are unclearly known, but may relate to individual variations in physiological condition.

It is very difficult to measure the respiratory metabolism of animals in wild, especially marine fish, due to the complexity of equipment design and field techniques required. Most respirometry measurements of fish to date have been carried out under laboratory conditions. These results provided the basic estimates of metabolic costs for energetic studies of common wolffish. The differences between those results measured in the laboratory and those which might be obtained in the wild, might reflect more constant conditions of laboratory maintained fish. Those fish kept in the laboratory conditions, live typically at a constant temperature and photoperiod, saturated oxygen concentration, fixed food rations in a stable environment. Whilst the wild individuals undergo transient variations in temperature or dissolved oxygen, patchy food distribution and possible predation risks and may be expected to expend more energy in respiratory metabolism. In this study, all the individuals used to measure the metabolic rates were obtained during the summer season. The results obtained from the low temperature acclimation of 'summer' common wolffish to 'winter' temperature for comparison of metabolic rates or energey budget may not be a valid model of winter metabolic demands. The BMR measured from common wolffish in the winter may be lower than from 'summer' held at winter temperatures, since during the winter season common wolffish typically fast and undergo tooth exchange. Their body condition factors may be different between summer and winter. Moreover, it has been shown that there is a seasonal variation in the metabolic capacities of fish muscle (Thibault *et al.*, 1997). However, noting these limitations common wolffish are difficult to capture during the winter, and maintenance of wild fish until the winter season was also difficult, and compounded by the potential effects of long-term captivity on physiology.

Aerobic metabolic costs increase with swimming velocity and in most fish species occupy the whole metabolic scope at maximum sustainable speed. However, swimming at high speed (e.g. chasing prey, escape from predator) is achieved by use of anaerobically fuelled white muscle when oxygen supply is insufficient to meet the demands of aerobic metabolism. The evolution of fish body shape is closely associated with the eneregetic costs of swimming. Helfman *et al.* (1997) indicated that body shape and other morphological changes are important to the energetics of many benthic fishes. Facey and Grossman (1990) have shown that the shape of some cottid fish, with their large heads and tapering bodies, might help them remain on the bottom as water flowed over them. These body adaptations could help them hold position without a significant energetic cost. The tapering eel-like body shape of common wolffish is probably associated with crevice dwelling and a benthic mode of life. However, locomotion seems expensive, since fish active for only 5% of the time had metabolic rates closely approaching the MMR (Fig. 3.6). This suggests an inefficient locomotor system and likelihood that swimming cannot be sustained for long periods.

Longer distance movements that have been reported for common wolffish (Jónsson, 1982) may occur by swimming at very low velocities or by tidal stream transport (Arnold, 1981). In the central North Sea the tidal stream is relatively weak and so tidal stream transport may not be important. Common wolffish mainly consume molluscs and crabs for which the use of high speed to capture prey is unnecessary.

Maximum metabolic rate was relatively low by comparison to active species such as sockeye salmon and Atlantic salmon of a similar size and at a similar temperature (Brett and Glass, 1973; Lucas, 1994), and MMR was also lower than most other sedentary species except pike (Table 3.2). Although scope and relative metabolic scope for common wolffish was much smaller than in active fishes such as sockeye salmon of similar size, the relative scope was, by virtue of the low RMR, larger than for some sedentary species such as pike and cod, though similar to flatfish. For what purpose might relative metabolic scope of common wolffish be adapted? Soofiani & Priede (1985) found that for juvenile cod, metabolic scope was almost used up during digestion of large meals. Common wolffish are known to eat large meals, certainly up to 10% of body weight (section 4.3.1.2), and since much of their natural diet consists of decapods, molluscs and echinoderms (Albikovskaya, 1983; section 4.3.1.2), containing a high proportion of indigestible elements, the mechanical components of specific dynamic action (SDA) might be expected to be high (Tandler and Beamish, 1979). For relatively large meals of 6% body weight, Karamushko (1993) determined that the peak level of post-prandial oxygen consumption rate was 2.5 times the pre-feeding rate, and that the period of elevated metabolic rate increased with increasing meal size. This result is typical of other fish species (Jobling, 1981) (e.g. Muir and Niimi, 1972, aholehole (*Kuhlia sandvicensis*); Beamish, 1974, largemouth bass (*Micropterus salmoides*); Brett and Zala, 1975, sockeye salmon (*Oncorhynchus nerka*); Dabrowski, 1986, Atlantic salmon) and suggests that the relative metabolic scope of common wolffish is not adapted for especially high rates of feeding and digestion. These feeding strategies, combined with the available metabolic scope related to SDA, show that a spare metabolic capacity for locomotion remains in common wolffish.

It is true that the MMR of common wolffish may not be sustainable for such long periods of time as they are in salmonids swimming at maximum sustainable speeds, but it remains that relative metabolic scope was much greater for common wolffish than it was for species such as pike where metabolic rate was measured in a similar manner. It may be that under some circumstances common wolffish are more active swimmers than has been assumed; common wolffish are known to undergo spawning migrations of several hundred kilometers in Icelandic waters (Jónsson, 1982). It is also known that common wolffish are involved in aggressive encounters at spawning time, and that males guard their egg masses (Keats *et al.*, 1985). Goolish (1991) suggested that, for fish, anaerobic potential during activity was greater for inactive forager than for the active forager due to their larger white muscle masses. Perhaps the metabolic capacity of common wolffish enables rapid repayment of oxygen debt during intensive bouts of aggressive activity or foraging activity.

In the natural environment, there are several ways that the power budget conflict might influence natural selection processes on growth rate. Fish at high-risk of predation could be at a disadvantage when SDA is maximised leaving little scope for aerobic locomotion for escape from predator. Hence, fish should adopt a rate of energy flow that maximises the fitness benefits of growth and seeks to minimise the ratio of mortality risk to opportunity for growth (Conover and Schultz, 1997). The common wolffish of this study in the North Sea are at the southern limit of their boundary. They have a relatively long season for growth towards adult size and recovery from loss of energy during the spawning season. They may adopt a conservative activity strategy during summer, reserving a large proportion of metabolic scope for growth in an environment, which is rich in benthic food compared with other higher latitude areas. However, the significance of predation in such a relationship would seem limited, since common wolffish are unlikely to suffer high levels of predation except during the larval and early juvenile stages.

The absolute metabolic scope at 10°C was 53% higher than that at 5°C. This would suggest that common wolffish have more capacity for activities such as foraging, digestion, and growth at 10°C than 5°C. Houlihan (1991) has shown that much of SDA is accounted for by the costs of intermediary protein metabolism. The greater metabolic scope at higher temperature for common wolffish would allow them to consume more food although the SDA costs would also increase. Protein synthesis and protein growth are important elements of growth for all fishes (Houlihan *et al.*, 1995).

The protein synthesis rate reflects the growth rate of any ectotherm species and is influenced by temperature (Houlihan *et al.*, 1993). McCarthy *et al.* (1998, 1999) have shown that the optimum water temperature for growth and growth efficiency of common wolffish are between 8 and 11°C. They also suggested that the common wolffish is a sedentary species and that low aggression within the species would increase growth efficiency through reduced energy expenditure. Based on these laboratory studies, growth rate of common wolffish should be highest near the upper limit of its tolerance temperature (8-11°C), which is the similar to the bottom temperature occurring in summer in the North Sea basin above 54° N.

In the natural environment, common wolffish grow fastest during the summer and least in the winter season (Chapter 4). It seems that for the common wolffish, the relatively high summer temperatures allow more efficient growth while the greater absolute metabolic scope at higher temperatures offers them more capacity for feeding and digestion. This is a common approach for temperate fish species. Carrying out reproduction and tooth exchange during winter would allow them to survive the long period of no or reduced feeding by virtue of the very low RMR. While extended periods of starvation or low food intake are not uncommon in fish species (Wright and Martin, 1985; Jobling, 1993), the timing of reproduction and tooth exchange, and the very low maintenance metabolism do appear somewhat adaptive. The egg masses are laid down by females during the late autumn or winter period in the North Sea. The fry of common wolffish hatch after approximately 1000 day-degrees (Ringø and Lorentsen, 1987). The larvae of common wolffish hatch during the late spring plankton outburst and a number of fish species spawn during this period in the North Sea (Cushing, 1982). These abundant plankton, eggs and larvae would provide the relatively large common wolffish larvae with good food resources. Therefore, the common wolffish larvae are able to grow fast with high growth efficiency and minimise predation by other species during the first summer. The adult common wolffish achieve most growth in the summer as a compensation for the reduced growth or stopping growth during late autumn and winter season, and preserve energy for next period of reproduction and teeth exchange.

Chapter 4 Feeding, age and growth, and reproduction of common wolffish in the North Sea

4.1 Introduction

4.1.1 Feeding

All animals require energy for maintenance processes and somatic growth, and must obtain it through a balanced diet (Cowey and Sargent, 1979). Fish species consume a variety of foods. They can be classified as herbivores, carnivores or omnivores. In general, predation of fewer prey types occurs when the quantities of preferred prey are sufficient and stable. Conversely, fish tend to utilise more types of food when the food resources are unstable (Nikolskii, 1965). Specialisation for certain feeding modes has resulted in morphological distinction through long-term evolution (Balon, 1984). Different species have particular body shapes, sense organs, mouths and digestive system to meet the demands of feeding.

Because it is very difficult to observe fish feeding in their natural environments, their diets have to be determined by an examination of the stomach contents of a suitable number of individuals. This may require both qualitative and quantitative methods to analyse the diet composition. There are many factors that potentially influence both amount and type of food that fish consume. These include diel effects, seasonal effects, effects of fish size and territoriality and differential digestion rates (Bowen, 1992). Fish often stay in low predation risk environments during nonfeeding hours then move into places in which food is available during safe periods, and such diel changes in habitat and feeding intensity may have to be considered (Hobson, 1965; Bowen and Allanon, 1982). Food availability may be reflected in seasonal variation in stomach contents in many fish species (Angermeier, 1982). Fish may also vary their diets according to their size and sex (Bowen, 1992; Gerking, 1994). In general, as fish grow larger, they tend to choose larger and different prey compared with those in the juvenile stage. This may reduce intraspecies competition, but also reflects changes in optimal foraging of prey size (Townsend and Winfield, 1985). Digestion rate will also influence prey selection and feeding intensity by fish (Doble and Eggers, 1978). Digestion rate is influenced by the quantity and quality of food that fishes take (Pandian and Vivekanandan, 1985). All these dietary studies can enable us to understand how fish live and grow, how food might influence their distribution and abundance, and properties of trophic interactions (Joyce, 1996).

The diet composition of fish reflects food consumed as a result of scouting, approaching, selecting, capturing and ingesting these food items. As a result fish may favour some food items over other prey available in their ambient environments, because the favoured foods provide more energy and nutrients for its growth (Nikolskii, 1965; Townsend and Winfield, 1985). However, prey choice may be influenced by the fish's own morphological, ecological, and physiological characteristics and abiotic factors such as temperature and hydrological factors (Gerking, 1994). Optimal foraging theory has been developed to examine these situations. The hypothesis of optimal foraging theory considers that a series of morphological, ecological, behavioural and physiological characteristics during the foraging procedure have been decided by long-term evolution; these characteristics ensure that the feeding ecology of a fish is well adapted. That adaptability often allows fish to maximise its net energy gain (Pyke, 1984). This net energy gain is obtained from either seeking the maximal gain during the foraging process or by minimising the cost of capture. The food items and habitat selection will influence the foraging strategy for different species.

Research on feeding and diet provides important information in ecological studies of fish species in terms of interactions with prey and in terms of energy intake. Common wolffish have been reported as an important predatory fish, which can act as a important predator and significantly influence the structure of benthic communities (e.g. green sea urchin, *Strongylocentrotus droebachiensis*) in the Gulf of Maine (Witman and Sebens, 1992). Moreover, for fisheries employing longlines, development of efficient gear or better bait requires the knowledge about feeding behaviour. Longlines are a common capture method for common wolffish, although not in the North Sea (Smidt, 1981; Jónsson, 1982; Falk-Petersen and Hanssen, 1991). Knowledge concerning food or nutritional requirements of fish can also provide useful information for aquaculture industries.

4.1.2 Age and growth

Growth is commonly considered as a progressive increase with time in size and weight. It is the result of synthesis of new tissues through a continuous (though variable) process of metabolism. Growth characteristics of a fish species are the result of interaction between its genotype for potential growth and the ambient environment experienced (Wootton, 1992). Some species can live in an area where the food supply is limited because their growth rates are low and body sizes at maturity are small. They tend to have a high rate of potential mortality due to predation by other species, but compensate for this by higher than average fecundity (Garrod and Horwood, 1984). Species that grow fast and have larger body size will be less susceptible to predators (Cushing, 1968). But this mechanism will only occur in situations where the food supply is sufficient and the abundance of the population is limited (Nikolskii, 1965). Therefore, it is necessary to determine the relationship between growth of a given species and its living environment, because body size and mortality vary with different species (Conover and Schultz, 1997).

Rapid growth in length by immature fish speed enables them to reach maturity and reduce loss to predators. But unlike birds and mammals, fish will still grow in both size and weight after they have reached sexual maturity in spite of decreasing growth rate as they get larger (Pitcher and Hart, 1982). The adult fish shows a more rapid increase in body mass than length, because the energy previously available for body growth is redirected to developing gonads and stored for migratory processes (Jones, 1976).

The growth pattern of fish is indeterminate and flexible. Growth rates exhibit a greater variation within the same fish species than in mammals and birds (Schmidt-Nielsen, 1984). The age and body size at maturity of fish varies between areas and different breeding populations (Trippel *et al.*, 1997). Many authors have pointed out that food supply is the most important factor affecting the variability of growth, and may be considered in terms of the quality, quantity and size of prey items (Brett *et al.*, 1969). Temperature is another important factor, which can influence the growth of fish. The feeding intensity, behaviour and digestion rate will be affected by the metabolic rate of the fish (Pandian and Vivekanandan, 1985). The growth efficiency and metabolism of fish usually increases with increasing temperature within an appropriate range (Lucas, 1996). Temperature not only directly influences the growth rate but also indirectly influences other factors which effect growth. For example, changes in temperature may cause variation in abundance of prey items, the concentration of dissolved oxygen and salinity (Laevastu, 1993). Many temperate-water species exhibit a seasonal variation in growth rate because changes in temperature and photoperiod trigger other events of life history such as spawning, feeding, wintering and migration that share demands on energy uptake with growth (Jobling, 1993).

The growth rate of individual fish will also influence the population characteristics (Cushing, 1965; Rothschild, 1986). Individual growth may directly modify the numbers or biomass of a population and change the reproductive rate, in relation to environmental factors (Lucas, 1996). A strong year class usually tends to retard the growth of proceeding and subsequent ones (Nikolskii, 1965) through intraspecies competition effects.

A knowledge of the growth pattern of fish and the relative numbers of juvenile and adult ones in a stock is required in order to examine how fishing affects the stock (Jerald, 1992). Therefore, age determination is an important method in fisheries ecology. To study mechanisms such as growth, feeding, reproduction and migration without linking them with age would prevent an application of the linkage between biological activities and environment at each stage of the life history. Several mathematical growth equations have been established to describe the growth pattern of fish (e.g. von Bertalanffy equation (von Bertalanffy, 1938), Ricker equation (Ricker, 1975)). Age is an important parameter for these equations. Moreover, knowing the variation of the average size at each age over several years enables trends, which may reflect changes in the suitability of environment or fishing mortality, to be examined.

4.1.3 Reproduction

Fishes have evolved a huge variety of ways to produce progeny (Castro and Huber, 1996), with wide variation in gonad development, maturity, spawning, fertlisation and hatching (Wooton, 1984a). After the juvenile stage most fish divert a large proportion of energy to reproduction. They develop gonads, spawn, recover, and repeat this process until senescence and death. Fish species have distinct reproductive patterns, which are reflected in reproductive system, mode, time and cycle, as well as spawning ground, and behaviour patterns (Balon, 1984). The reproductive strategies of fish are the result of adaptive responses to their environments. The time and location of spawning represent adaptations to protect the eggs and juveniles from predators and to provide the young with food (King, 1995). These reproductive strategies help to ensure that a fish's genetic fitness is maintained through survival of its offspring (Wooton, 1984b).

The total volume of eggs that a fish can produce is constrained by the space available in the body cavity. The fecundity of fish species is modified by food availability via metabolism and by density dependent effects (Beverton, 1953, Cushing, 1975). In general, fecundity increases with body size and can be a related function of body length (Wooton, 1979). However, since the whole egg volume is defined by fecundity and the volume of a single egg, there is a tendency for a trade-off between fecundity and egg size (Elgar, 1990). The larger fry, which hatch from large eggs have a higher survival rate than fry from small eggs and this compensates for the reduced number of offspring produced (Ware, 1984). The fecundity also increases up to a certain age then declines and is often highest in those size or age classes representing greatest biomass (Nikolskii, 1965). Fecundity may be different between populations that live in different environments. At low latitudes there is usually greater fecundity than at high latitudes due to increased predation risk at low latitudes (Trippel *et al.*, 1997).

Endogenous and exogenous factors trigger gonad development and spawning. While environmental factors stimulate the fish to develop the gonads, there is also a premise that the fish has to reach a certain critical size or age (Pauly, 1994). The main factor that stimulates the development of gonads is sex hormones. They stimulate the maturation of gametes and cause changes in colour, shape and behaviour of fish (Stacey, 1984). This event may involve movement between different areas and show a rhythmic cycle. Fishes may migrate from adult feeding grounds to spawning grounds where eggs are spawned (Cushing, 1968). The gonad development is stimulated by exogenous factors such as photoperiod, food availability, salinity, moon phase and perhaps temperature (Hoar, 1970; Liley, 1970). Although a particular temperature or photoperiod is required to trigger gonad development, changes in temperature or photoperiod may also be important especially for temperate-zone species (Stacey, 1984; Bye, 1984). The reproductive cycle of temperate-water species is often that eggs are spawned in late winter so that larvae hatch in spring at the time of the spring plankton outburst (Hislop, 1984).

For fisheries, recruitment which may be defined as the number of fish of a single group entering the exploitable unit of a stock for fishing activities, is of special interest (Ricker, 1954), since it is integral to the sustainability of the fishery. The recruitment process is complex and is the result of a series of life history events involving survival by young over spawning, hatching, larval growth, and juvenile growth in the nursery ground. There may be interactions between the spawners and their progeny involving density dependent mortality (Cushing, 1973). Other environmental factors may also influence mortality. Therefore, the numbers of spawners and changes of environment will influence the level of recruitment yearly. The process of spawning is a crucial factor for enhancing recruitment. In fishes, the survival rate of larvae is strongly dependent on the time when the eggs are laid, with high larval survival and good subsequent recruitment occurring when spawning coincides with optimal survival conditions, according to the match-mismatch hypothesis (Cushing, 1973)

4.1.4 The aims of this chapter

The balance between body growth and gonad growth reflects a the trade-off between the energy that is obtained from food. The aims of this chapter are to determine the feeding ecology, age and growth pattern, and reproductive biology of common wolffish in the North Sea, and to examine the interactions among these life processes. Moreover, these studies on the North Sea common wolffish will be also compared with other studies of common wolffish over their geographic range to assess the effects of environmental variations on life history processes for this species.

4.2 Methods

4.2.1 Diet

4.2.1.1 Sampling and examination of stomach contents

The stomachs of 143 common wolffish were examined (spring, n = 64; summer, n = 50; autumn / winter, n = 29). Fish were obtained from the North Sea between 54 - 61 °N and 3 °W – 6 °E, in depths of 15 – 210 m. Fish were obtained between May 1996 and September 1998 from commercial trawls and during groundfish surveys by the FRS Marine Laboratory, Aberdeen and the CEFAS, Lowestoft Laboratory. The fish were measured and weighed to the nearest millimetre and gram respectively. The stomachs were removed and preserved in 10% formalin. No fish examined exhibited evidence of regurgitation. After opening, stomach contents were stored in a 90 % ethanol solution. All prey were identified to the lowest taxa, where possible to species, depending on the state of digestion. Since hermit crabs (Paguridae), which occupy empty gastropod shells, were an important food item care was taken to ensure that gastropod molluscs were recorded in the diet only when gastropod tissues were present. Fish were only recorded in the diet when they were partially digested, to eliminate the possibility of bias due to ingestion of fish during the trawl.

4.2.1.2 Indices for describing diets

Several indices were used to describe diets:

(1) Expression of diet in terms of numbers of prey items in stomachs, and percentage occurrence of prey items in stomachs.

(2) The diet breadth of common wolffish was calculated using Levin's standardized index *B* (Krebs, 1989) as follows:

$$B_i = [1/(n-1)][(1/\Sigma P^2_{ij}) - 1]$$

where Bi = Levin's index for predator i; Pij = proportion of guts of predator i containing prey item j (% occurrence); and n = number of prey categories. This index ranges from 0 to 1, low values indicating a diet dominated by few prey items (specialist predator) and high values indicating generalist diets.

(3) Calculation of a feeding index (FI) to assess seasonal variations in food intake (Hyslop, 1980) as:

$$\text{Feeding Index (FI)} = \frac{\text{Total stomach contents weight}}{\text{Total fish weight}} \times 100$$

4.2.1.3 Food item occurrence data from a ground survey

In order to make some comparison between the diet of common wolffish from the North Sea and the availability of different taxa of epibenthos, data on the relative abundance of epibenthos taxa were obtained from collections in ground survey trawls in August 1998 as part of monitoring by CEFAS. These data were used to make a crude comparison of the ingested and available epifauna for areas in which stomach-sampled common wolffish were captured. The fishing gear and method of use have been described in Chapter 2.

4.2.1.4 Measurement of energy content of food

The calorific values of major food items were determined with a ballistic bomb calorimeter (Gallenkamp, London). Fresh animals were collected from trawl samples in September 1998 and frozen. The samples were thawed, separated into digestible and indigestible (shell, exoskeleton) fractions and weighed to 0.01g. They were oven-dried at 45° C until constant dry mass was obtained and reweighed to calculate water content. Digestible material was ground into a powder, compressed into 0.25 – 0.45 g pellets, and the energy value was determined in the calorimeter.

Benzoic acid pellets were used as a thermochemical standard, against which experimental determinations were calibrated. In some cases it was necessary to combine several individuals of the same food category in order to obtain a sufficient sample for measurement. Measurements of calorific value were repeated at least five times for the same food category.

4.2.2 Age and Growth

4.2.2.1 Length weight relationships

Data from a total of 100 ungutted common wolffish were obtained between May 1996 to September 1998 (80 from the commercial fishery, 16 from FRS groundfish survey and 4 from CEFAS groundfish survey). In order to avoid shrinkage of body length or change in weight caused by freezing, common wolffish were measured as soon as possible after they were landed or were caught in survey trawls. Body weight was measured to 0.1 g and total length to 1 mm. The relationship between weight and length was described in the form-

$$W = aL^b$$

where W is the body weight (kg), L is total length (cm), and a and b are coefficients.

Similar measurements were made for the same fish after gutting. However, there were several additional gutted common wolffish obtained from North Shields during the study period, for which gutted weight and lengths were obtained to examine the relationship between gutted weight and length, giving a sample size of n = 104.

4.2.2.2 Age determination

Both sagittal otoliths were taken from a representative sample of 995 common wolffish between 1996 and 1998 for ageing and were stored in envelopes. The otoliths were firstly bathed in xylene mixed with glycerine, and then were read under a incident light at x20 magnification using a binocular microscope. Fish ages were determined by counting annual growth increments in otoliths. A small sample of 25 otoliths of a range of ages was independently read by M. Walsh (Marine Laboratory, Aberdeen) using the same method and gave close agreement with the results of this study.

Shallow-water temperate fish generally display a seasonal growth pattern, with one year of growth showing one opaque and one translucent zone termed the "annulus". To examine whether the one-year, one annulus hypothesis was appropriate for ageing common wolffish, the following growth increment (*GI*) formula was used to examine seasonal growth patterns of otoliths (Fig. 4.1):

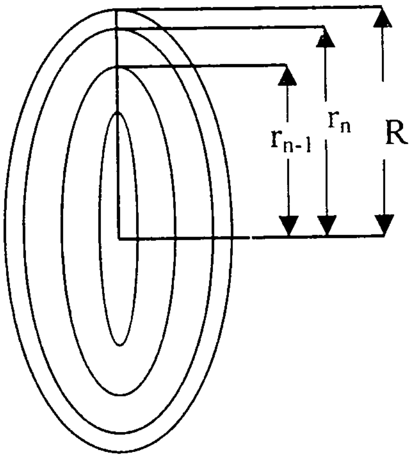
$$GI = \frac{R - r_n}{r_n - r_{n-1}}$$

where R = the radius measured from the nucleus to the edge of the anterior side of the otolith; r_n = the distance measured from the nucleus to annulus n; and r_{n-1} = the distance measured from nucleus to annulus $n-1$.

Growth was described by the von Bertalanffy growth equation (von Bertalanffy, 1938):

$$l_t = L_\infty(1 - e^{-K(t-t_0)})$$

where l_t = total length at time t; L_∞ = theoretical maximum total length; K = the constant rate of approach to L_∞ and t_o = theoretical age at which $l_t = 0$.



$$\text{Growth increment} = R - r_n \,/\, r_n - r_{n-1}$$

Fig. 4.1. Schematic representation of a sagittal otolith shows the measure method for calculating the marginal growth increment of otolith.

Growth equation parameters for the von Bertanlanffy growth model were calculated from length-at-age data by the Walford plot method (King, 1995).

4.2.3 Reproduction

4.2.3.1 Materials

A total of 797 common wolffish were randomly sampled from catches at North Shields monthly between January 1996 and November 1998 (Table 4.1). Some samples also were obtained from ground surveys by the FRS Marine Laboratory (n = 16), Aberdeen and the CEFAS Lowestoft Laboratory (n = 4) (Table 4.1). The total length (cm), sex, and gonad weight (0.1g) of each fish were recorded. Body weight (g) was also recorded where available. Gonads were removed and preserved in 10% formalin for further histological examination, fecundity assessment, and egg diameter measuring.

4.2.3.2 Histological determinations

After fixation, the mid-region portion of the right testis (n = 434) or right-hand limb of the ovary (n = 383) of all fish sampled (Table 4.1) were cut. This material was dehydrated in graded ethanol from 70% to 100%, cleared in Histo-clear solution (National Diagnostics Ltd, Georgia) and embedded in paraffin wax. The sections were cut at a thickness of 6-10 μm then were stained with Mayer's haematoxylin and eosin (Mahoney, 1971).

Histological identification of the maturity stages was judged according to the development of the gonads. These developmental stages were determined following terminology defined by Yamamoto (1956) and staging criteria modified from Marshall *et al.* (1993) (Table 4.2).

4.2.3.3 Morphological determinations

Gonadosomatic index (G.S.I) was used to assess occurrence of sexual maturity and the spawning season for the mature male and female common wolffish, defined according to Table 4.2. The G.S.I was calculated as follows:

$$G.S.I. = \frac{GW}{L^3} \times 10^3$$

Table 4.1. Numbers of male and female common wolffish sampled in the North Sea during 1996-1998 for the reproductive study.

Year	1996		1997		1998	
Month	Male	Female	Male	Female	Male	Female
January	0	0	9	8	0	1
February	20	20	3	9	11	17
March	17	17	45	48	15	10
April	23	45	25	26	11	9
May	34	20	35	28	9	10
June	23	18	0	0	21	13
July	24	15	0	0	9	10
August	6	7	0	0	3	0
September	0	0	16	8	10	3
October	16	3	11	8	2	1
November	0	0	6	4	0	1
December	19	14	11	10	0	0
Total	182	159	161	149	91	75

$\Sigma\Sigma = 817$

Table 4.2. Histological staging criteria used for common wolffish (adapted from Marshall *et al.*, 1993)

		Female	Male
Stage	Category	Histological criteria	Histological criteria
1	Immature	Oogonia: large nucleus with single nucleolus	Germs cells and spermagonia
2	Maturing	Chromatin nucleolar: spherical nucleus surrounded by a thin layer cytoplasm. Perinucleolar: homogeneous cytoplasm around a nucleus with several nucleoli	Spermatogonia and spermatocytes
3	Developing	Yolk vesicle: yolk vesicles formed in cytoplasm, increasing in size and number	Spermatogonia, spermatocytes and spermatids
4	Late developing	Yolk granular: uniform appearance of yolk vesicles, oil vesicles in cytoplasm. Peripheral nucleolus around neclear membrane	All stages present
5	Ripe	Nuclear migration and yolk fusion: coalescence of yolk granules to form uniform plate and dissolution membrane	Few spermatogonia; Mainly spermatozoa in sperm ducts
6	Spent	Occurrence of recent post-ovulatory follicles	Almost exclusively spermatozoa

where GW (g) is wet gonad weight, and L (cm) is total length of individual.. It was necessary to use this formula since body weight information was unavailable for a large proportion of common wolffish from which gonads were removed. In many studies, no significant differences in size distribution of eggs and number of eggs have been found between right and left ovaries (West, 1990; Marshall *et al.* 1993). However, average egg size may be different along with the length of ovary. To test for differences in egg size within the whole ovary, six sections from each of three ovaries were used for a presampling test. Because no differences were found among six portions of each ovary (ANOVA: Ovary 1, d.f. = (5, 447), $F = 1.17$, $P = 0.32$; Ovary 2, d.f. = (5, 582), $F = 0.86$, $P = 0.51$; Ovary 3, d.f. = (5, 573), $F = 0.43$, $P = 0.84$), all eggs were subsequently used from the central portion of the right-hand limb of the ovary in this study.

Size distributions of oocytes were studied from mature common wolffish only. Numbers of sampled fish varied according to the number collected each month (Table 4.3). However, numbers of ovaries examined were no more than 20 per month, giving a total sample size of 243 fish. Size distributions of oocytes from ovaries were obtained by teasing apart the ovarian lamella and mixing well in Gilson fluid (Falk-Petersen and Hansen, 1991). The frequency distributions of oocyte sizes were determined by randomly choosing 150 oocytes from the middle section of the above material under a dissecting microscope (×20) and measuring with a calibrated eyepiece graticule. The monthly variation in the diameters of oocytes, and the GSI were used to determine the spawning season.

Because of natural variability, size at first sexual maturity (L_{50}) is usually defined as the length at which 50% of all fish sampled reached maturity (i.e. median mature length, L_{50}). To estimate L_{50} for males and females, the proportion of mature fish in 2 cm intervals was fitted to the logistic function by nonlinear regression (Marquart method), by using the SAS software (SAS Institute Inc., 1992). Females were considered sexually mature when their ovaries reached stage 2 or higher. Males were considered mature only if their testes contained spermatozoa. A total of 432 male and 381 female common wolffish were used to determine length at sexual maturity. The logistic function used in this study was:

$$Y = \frac{1}{1 + a(e^{bX})}$$

Table 4.3. Numbers of mature male and female common wolffish used to determine G.S.I. and measure the size distributions of oocytes monthly for 1996-1998.

Year	1996		1997		1998	
Month	Male	Female	Male	Female	Male	Female
January	0	0	6	6	0	0
February	15	16	1	7	7	10
March	12	14	35	35	6	5
April	11	35	16	24	11	5
May	30	18	19	23	4	5
June	23	18	0	0	18	12
July	20	13	0	0	7	8
August	5	4	0	0	3	0
September	0	0	8	3	9	3
October	13	1	5	1	2	0
November	0	0	1	0	0	1
December	15	11	7	2	0	0
Total	144	130	98	101	67	49

$\Sigma\Sigma = 589$

where Y is proportion of mature fish, X is total length (cm), and a and b are constants (Lehodey *et al.*, 1997).

4.2.3.4 Fecundity

Only those ovaries that developed to stage 4 or higher were used to estimate the fecundity. The total fecundity was then estimated as (numbers of eggs > 0.2 mm in 2 g tissue) × (total gonad weight / 2 g gonad weight). The numbers of eggs were counted under a dissecting microscope at a magnification of × 20. The relative fecundity (i.e. weight-specific) fecundity was described as numbers of eggs per unit body weight.

4.3 Results

4.3.1 Diet

4.3.1.1 Size distribution of fish used for diet analysis

The length of common wolffish used in dietary analyses ranged from 11 to 105 cm and had a mean (± SE) length of 60.5 cm ± 14.4 (Fig 4.2). The distribution of size classes was similar to that of the North Shields catch data (Section 2.3.7). Most fish (85.4 %) were in the range of 41 to 75 cm.

4.3.1.2 Diet composition

Stomachs of 112 common wolffish contained food. Stomach contents weighed up to 10% of fish body weight reflecting the fact that common wolffish could eat large meals. Food consisted mostly of benthic organisms. Of the 27 families of prey items listed in Table 4.4, Paguridae (hermit crabs), Pectinidae (scallops) and Buccinidae (whelks) were the most important and together comprised 44% of food by relative occurrence. The most widely eaten groups of organisms were crabs, bivalves, gastropods, brittle stars and some polychaetes (Aphroditidae), together comprising more than 85 % of food by relative occurrence while hermit crabs were the most important single taxon (20.7% by number and 20.7% by relative occurrence). All cephalopods taken were young Loliginidae (< 6 cm). Sea urchins were also eaten by North Sea common wolfish and represented 4 % by number and 6.7 % by relative occurrence of all food items. The value of Levin's standardized index B = 0.68

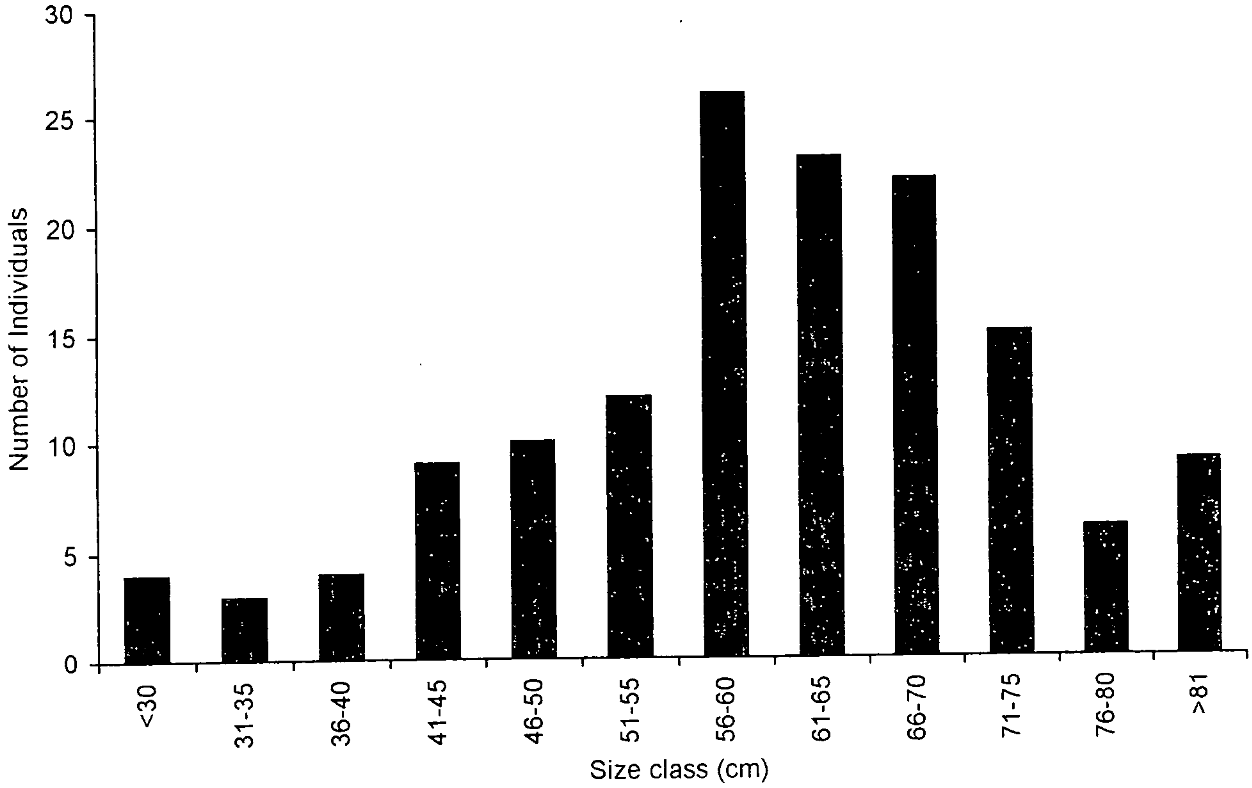


Fig. 4.2. The size distribution of 143 sampled common wolffish for the analysis of stomach contents.

Table 4.4. Diet of 112 common wolffish containing food, collected from the North Sea during 1996-1998.

Taxon	Number of prey items		Relative % occurrence	
Bivalvia	Total	85	Total	19.73
Arcticidae		27		3.43
Cardiidae		5		1.57
Mytilidae		5		1.57
Pectinidae		47		12.85
Unidentified		1		0.31
Gastropoda	Total	101	Total	11.59
Buccinidae		96		10.03
Littorinidae		1		0.31
Nassariidae		1		0.31
Naticidae		2		0.63
Turritellidae		1		0.31
Decapoda	Total	262	Total	38.56
Atelecyclidae		35		5.96
Corystidae		4		1.25
Majidae		35		5.96
Nephropidae		4		1.25
Paguridae		167		20.69
Portunidae		15		2.82
Unidentified		2		0.63
Cephalopoda	Total	42	Total	2.51
Loliginidae		42		2.51
Ophiuroidea		145	Total	7.21
Ophiolepidae		73		3.76
Ophiotrichidae		72		3.45
Echinoidea	Total	36	Total	6.90
Echinidae		34		6.27
Spatangidae		2		0.63
Polychaeta	Total	99	Total	8.15
Aphroditidae		99		8.15
Pisces	Total	33	Total	4.38
Cottidae		1		0.31
Clupeidae		6		0.31
Gadidae		21		2.51
Pleuronectidae		1		0.31
Triglidae		1		0.31
Unidentified		3		0.63
Others	Total	3	Total	0.94
Crisiidae		1		0.31
Opisthobranchia		2		0.63
	Total	806	Total	100%

indicates that the diet was not dominated by a few prey items, and that common wolfish in the North Sea may be regarded as generalist predators.

Chi-square analysis demonstrated no significant difference in the frequency with which Bivalvia ($\chi^2 = 0.13$, df = 1, $P = 0.72$) and Decapoda ($\chi^2 = 1.85$, df = 1, $P = 0.17$) occurred in the diet of small (≤ 55 cm, N = 34) and large common wolffish (> 55 cm, N = 78). However, for Ophiuroidea ($\chi^2 = 4.18$, df = 1, $P = 0.04$), Echinoidea ($\chi^2 = 6.8$, df = 1, $P = 0.008$), Polychaeta ($\chi^2 = 6.18$, df = 1, $P = 0.013$) and Gastropoda ($\chi^2 = 7.41$, df = 1, $P = 0.006$) there were significant differences in the frequency of occurrence of these prey in small and large common wolffish. Small common wolffish took relatively more sea urchins and brittle stars than large ones, while large common wolffish consumed gastropods and polychaetes (Aphroditidae) more than small ones (Fig. 4.3). Numbers of common wolffish taking fish and cephalopods were too low for chi-square analysis, but these prey were also selected by larger common wolffish.

The occurrence of food items that were found in the areas where common wolffish were captured is shown in Fig. 4.4. Paguridae (92.9% of sites) were widely found in the areas where common wolffish were caught in the North Sea. Echinoidea (64.3% of sites), Ophiuroidea (57.1% of sites), Buccindae (52.3% of sites) and Aphroditidae (50% of sites) were also commonly found in those areas.

Selection indices for these prey species were not calculated because the precision of prey availability data is probably too low for a detailed comparison. However, it would appear that prey were broadly chosen in relation to their availability with the probable exception of sea urchins which were under-represented in the diet.

4.3.1.3 Seasonal and inshore offshore variations of diet composition

Common wolffish exhibited relatively little seasonal variation in diet, with Decapoda remaining the most important food item over the whole year (Fig. 4.5). Bivalve molluscs were more important during the spring and summer while gastropods were more important in autumn / winter. However, some food items were only found in some seasons (Fig. 4.6a). Arcticidae (e.g. *Arctica islandica*) were only found in common wolffish stomachs in spring. Cardiidae, Corystidae and Mytilidae were not

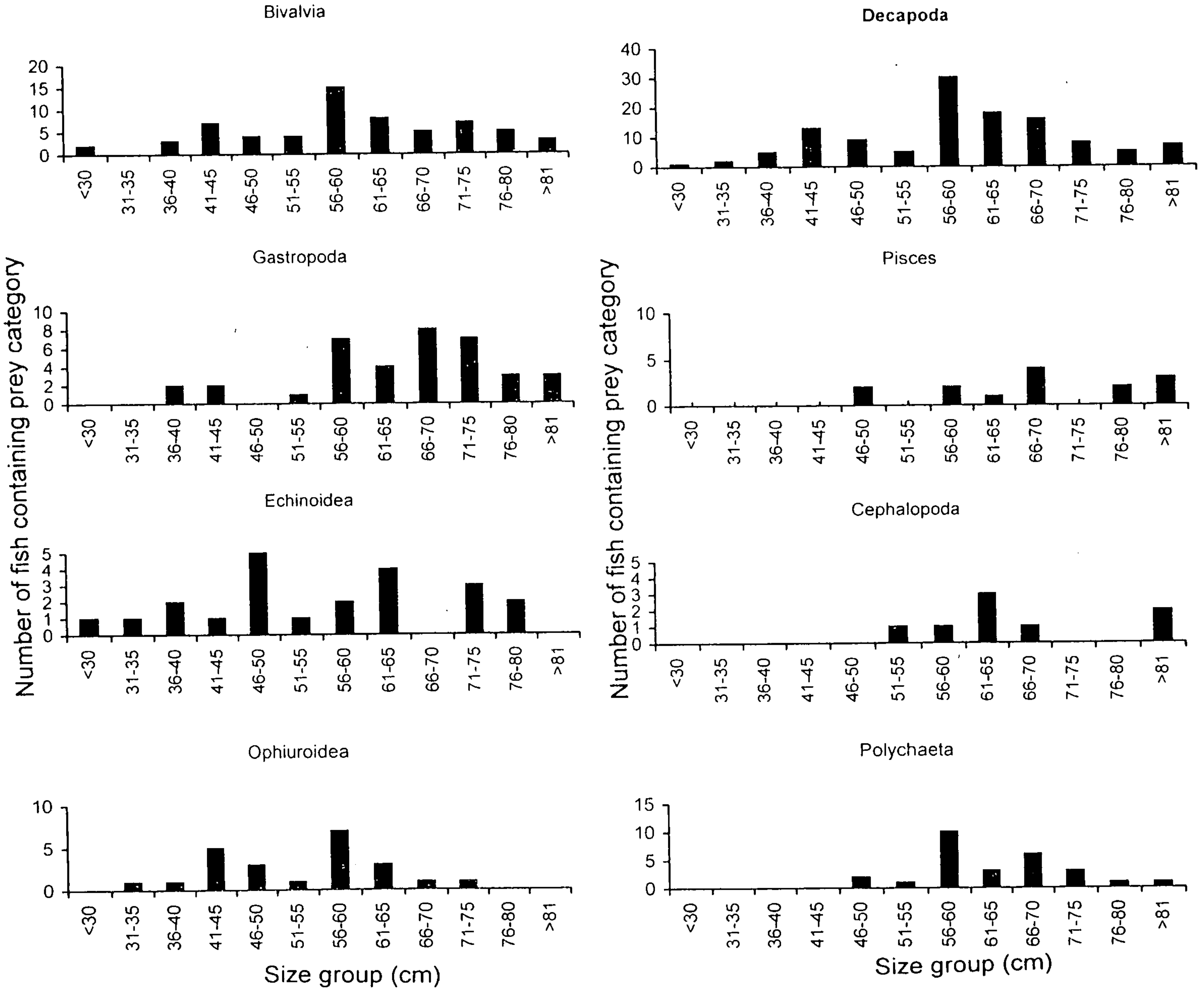


Fig. 4.3. Variation in frequency occurrence of prey categories in the diet of common wolffish in relation to fish length.

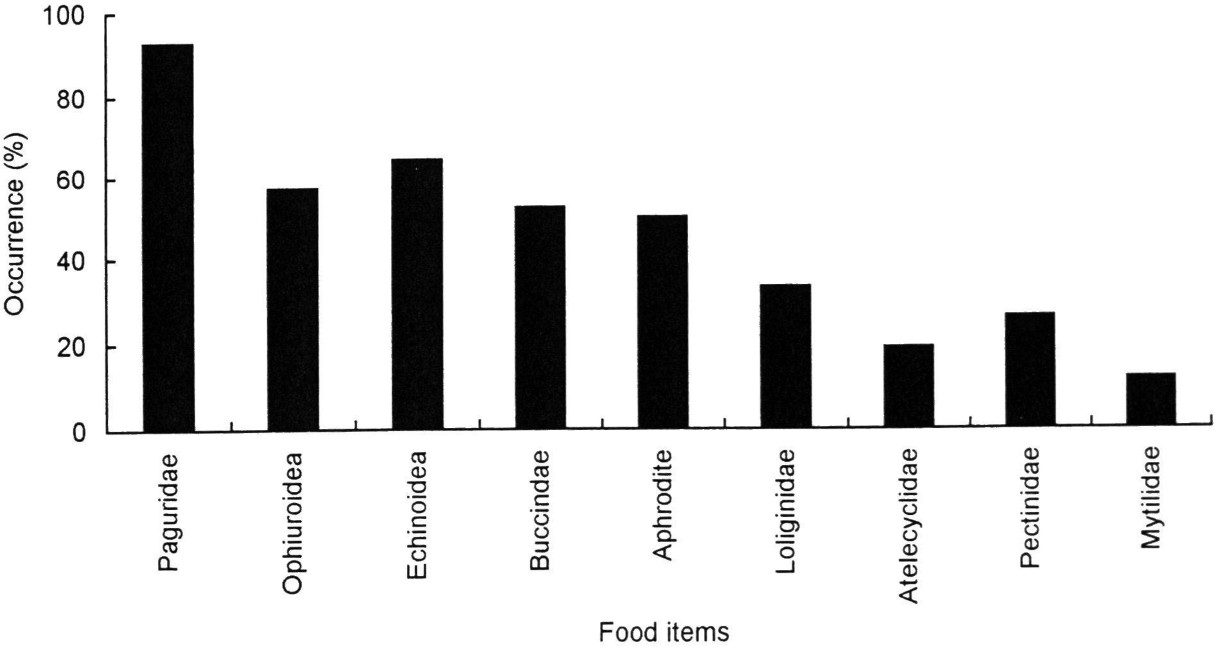


Fig. 4.4. The occurrence of food items found in areas where common wolffish were captured in the North Sea during 1996-1998, based on trawl samples in September 1998..

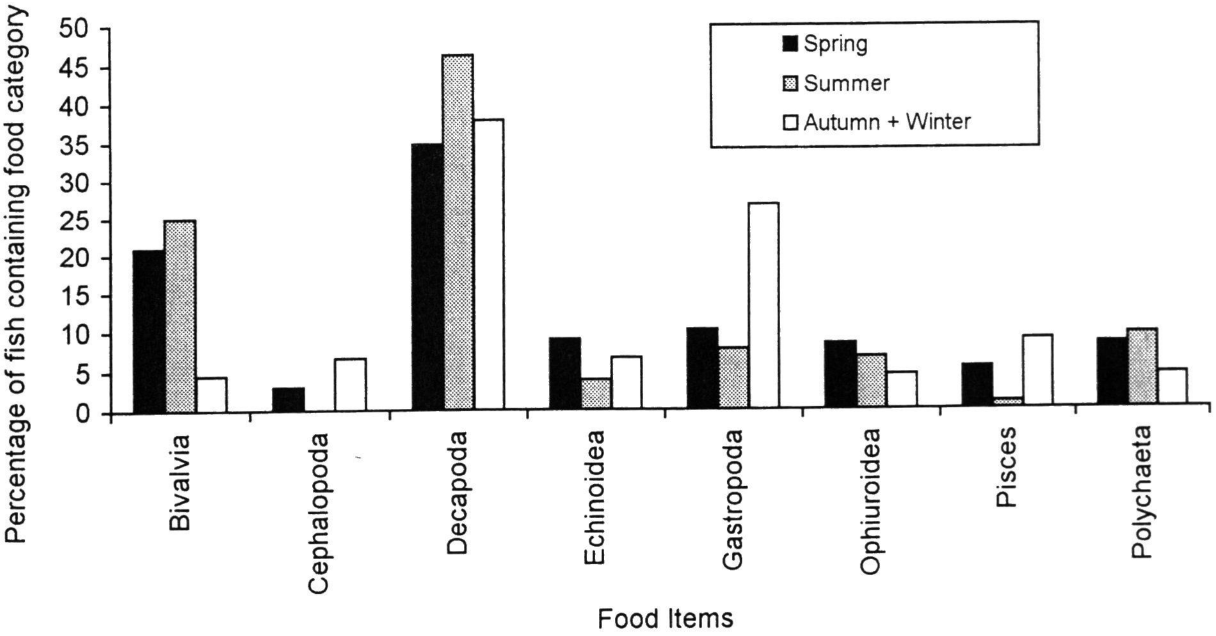


Fig. 4.5. Seasonal variation in relative occurrence of food categories in the diet of common wolffish from the North Sea.

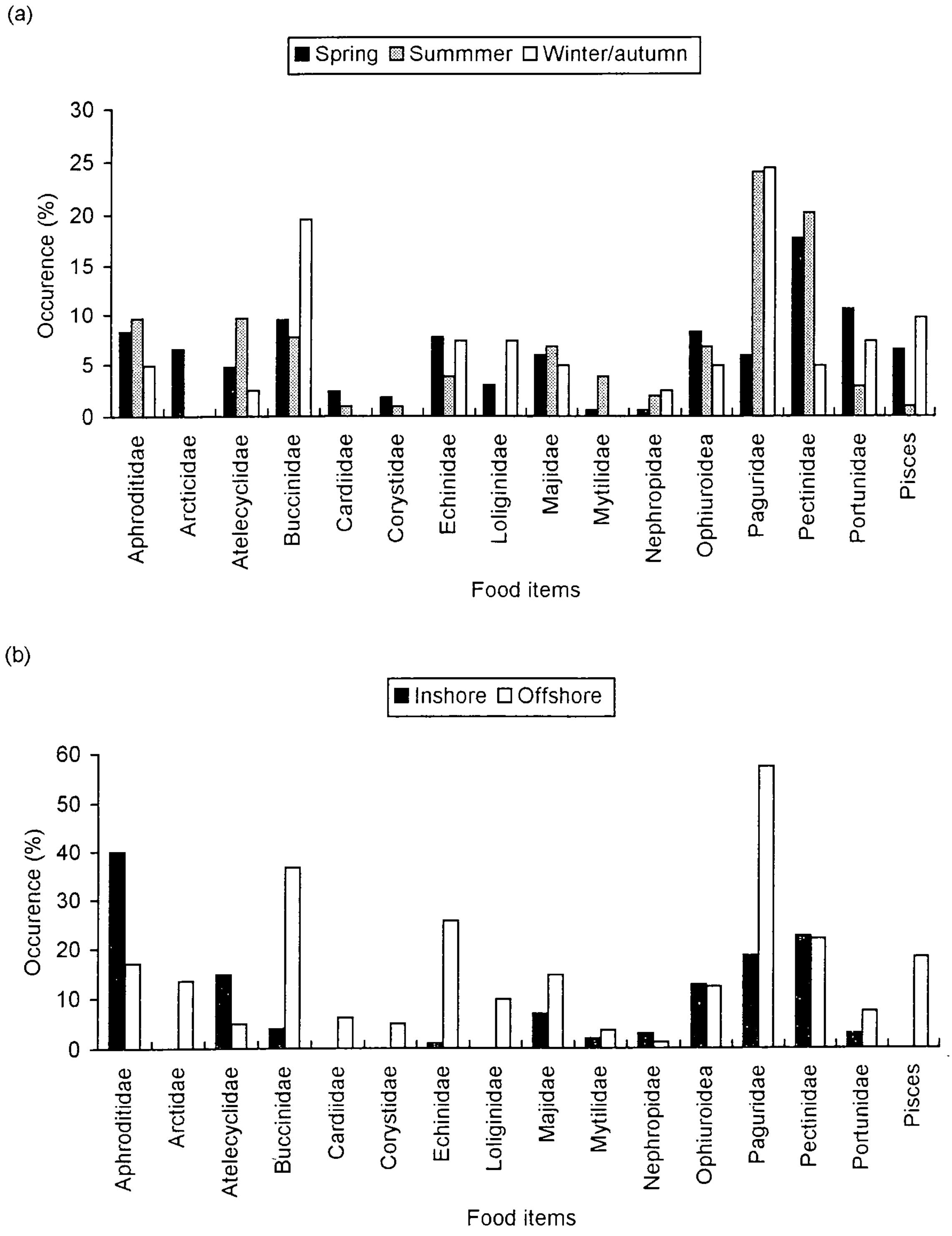


Fig 4.6. The occurrence of food items in the diets of common wolffish from the North Sea with variations of season and distance from UK mainland. (a) seasonal variation (b) inshore-offshore variation.

found in the autumn / winter season. Loliginidae (e.g. *Loligo forbesii*) were not found in summer. Pectinidae was the important food for common wolffish during spring and summer while Paguridae was more important in the summer and autumn / winter seasons. The variations of food items from fish taken in inshore and offshore areas (Chapter 2 definition) are shown in Fig. 4.6b. The Arctidae, Cardiidae, Loliginidae, Corytidae and Pisces were only found in stomachs of common wolffish from offshore areas. Aphroditidae, Atelecyclidae and Nephropidae occurred more in diets of common wolffish from inshore areas while Buccinidae, Echinidae and Paguridae occurred more in the stomachs of common wolffish caught in offshore waters.

Stomachs of 31 of the common wolffish (21.6 %) were empty. There was a significant difference in the frequency of empty stomachs between seasons ($\chi^2 = 11.71$, df = 2, $P < 0.001$) with significantly fewer empty stomachs in spring (7.8% empty) than in summer (34% empty) and autumn / winter (31% empty). The mean Food Index, a measure of feeding intensity, was lowest in the autumn / winter season (2.2) and higher in spring (3.4) and summer (3.0) (Fig 4.7).

4.3.1.4 The energy density of food items

The energy values of food items, which common wolffish consumed are shown in Table 4.5. These comprise data from this study as well as information from Cummins & Wuycheck (1971). When considered as digestible material only (i.e. discounting shells, calcified exoskeletons etc.) major prey such as Buccinidae and Paguridae exhibited high energy densities. The lowest energy densities were for sea urchins. A much greater differential was found when energy densities were expressed as values for total dry body weight including indigestible material, with sea urchins exhibiting 45% of the energy density of hermit crabs, and 61% of the energy density of whelks.

4.3.2 Age and growth

4.3.2.1 The relationship between weight and total length

The regressions between ungutted body weight (W, g) and total length (TL, cm), calculated separately for males, females, and combined sexes (Fig. 4.8a), were:

female: $W = 0.008\ TL^{3.02}$ ($n = 54$, $r^2 = 0.99$, $P < 0.001$)

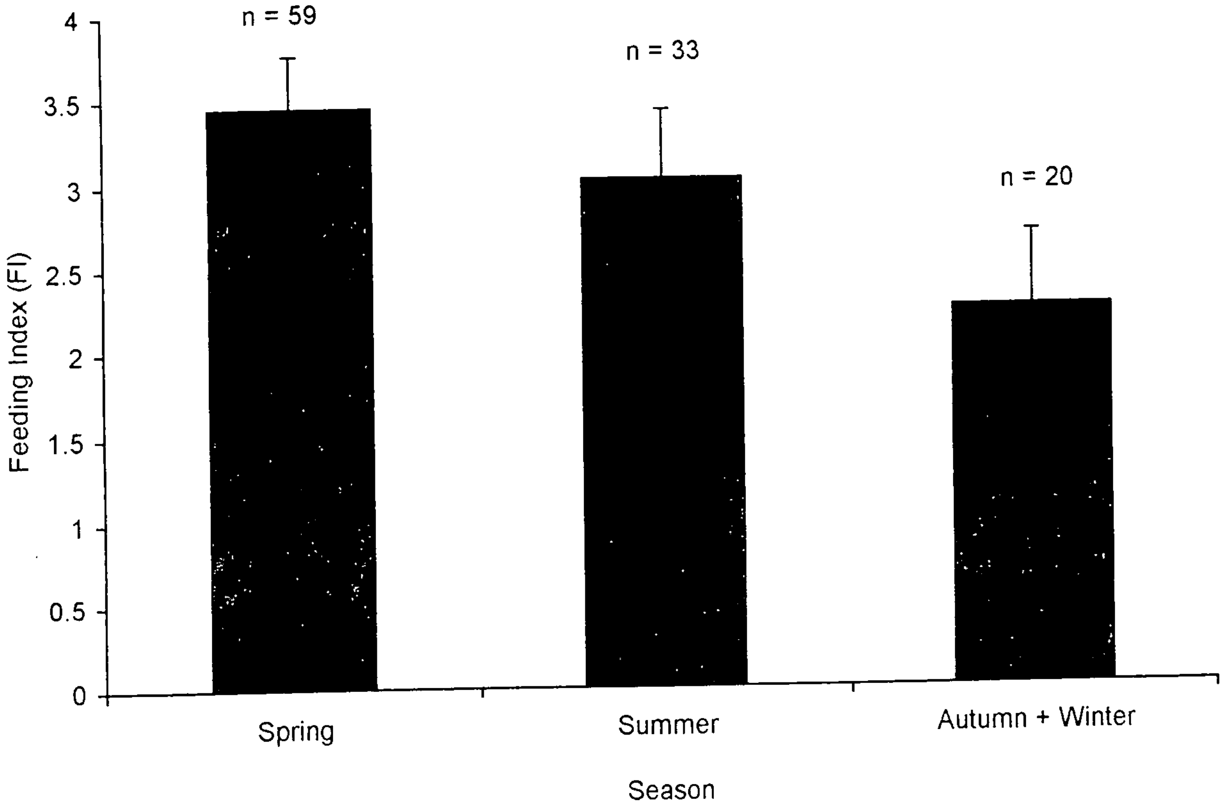


Fig. 4.7. Seasonal variation in the mean Food Index for North Sea wolffish. Bars represent the standard error.

Table 4.5. Mean energy density for prey items arranged by taxonomic category. 1 calorie = 4.186 J.

Prey Item	Dry weight kJ g^{-1}	Energy density kJ g^{-1} (dry)	% H_2O	Number of samples	Author
Cardiidae	18.92		92	3	Cummins & Wuycheck (1971)
Mytilidae	19.32			3	Cummins & Wuycheck (1971)
Buccinidae	22.77 ± 1.9	5.96	38	2	This study
Naticidae	18.45		82	2	Cummins & Wuycheck (1971)
Majidae	17.61		75	5	Cummins & Wuycheck (1971)
Paguridae	21.87 ± 0.5	7.97	69	5	This study
Echinidae	16.72 ± 1.34	3.61	72	17	This study
Aphroditidae	18.46 ± 0.4	5.98	84	2	This study
Cottidae	21.42		77	3	Cummins & Wuycheck (1971)
Clupeidae	26.42			1	Cummins & Wuycheck (1971)

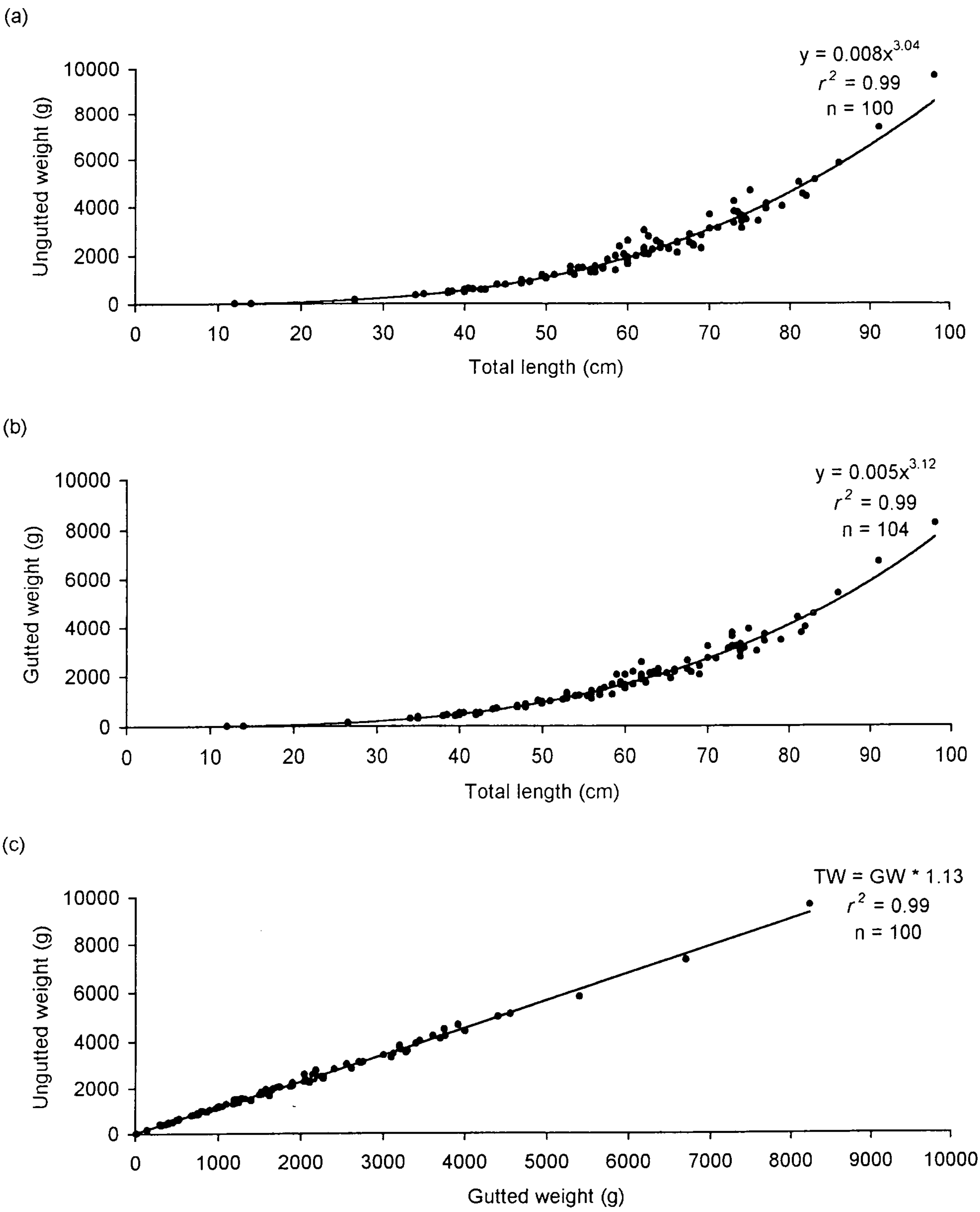


Fig. 4.8. The relationship between body weight and body length of North Sea wolffish, and the relationship for weight of same fish before gutting and after gutting. (a) ungutted (b) gutted (c) weight of the same fish before and after gutting. (TW = ungutted weight, GW = gutted weight).

male: $W = 0.007\ TL^{3.06}$ ($n = 46$, $r^2 = 0.99$, $P < 0.001$)
combined: $W = 0.008\ TL^{3.04}$ ($n = 100$, $r^2 = 0.99$, $P < 0.001$)

These regressions were calculated without considering the seasonal change in gonad size and fullness condition of stomach. The body weight of common wolffish exhibited a significant exponential relationship with increasing body length. The slopes of the TL-BW regressions exhibited significant differences between the sexes (ANCOVA; df = (1, 98), $F = 8.63$, $P < 0.004$), with males heavier than females at a given length.

The regressions between gutted body weight and total length for males, females, and combined sexes (Fig. 4.8b), were:

female: $W = 0.006\ TL^{3.06}$ ($n = 55$, $r^2 = 0.99$, $P < 0.001$)
male: $W = 0.004\ TL^{3.16}$ ($n = 49$, $r^2 = 0.99$, $P < 0.001$)
combined: $W = 0.005\ TL^{3.12}$ ($n = 104$, $r^2 = 0.99$, $P < 0.001$)

There were significant exponential relationships between gutted weight and total length for females, males and both sexes. The condition factor of males was still greater than that of females at the same total length.

The relationship between ungutted weight and gutted weight for the same fish of combined sexes is shown in Fig. 4.8c. There was a highly significant linear relationship between ungutted weight and gutted weight ($r^2 = 0.99$, $P < 0.001$). The ungutted weight was 17% greater than gutted weight.

4.3.2.2 Relationship between otolith radius and total length

The relationship between total length (TL, cm) and otolith radius (R, mm) of common wolffish was determined by regression analysis (Fig. 4.9):

$R = 1.823 + 0.059TL$ ($n = 985$, $r^2 = 0.565$, $P < 0.001$).

The regression between total length and otolith radius displayed a significantly linear form. Analysis of covariance applied to separate regressions of TL against R for male

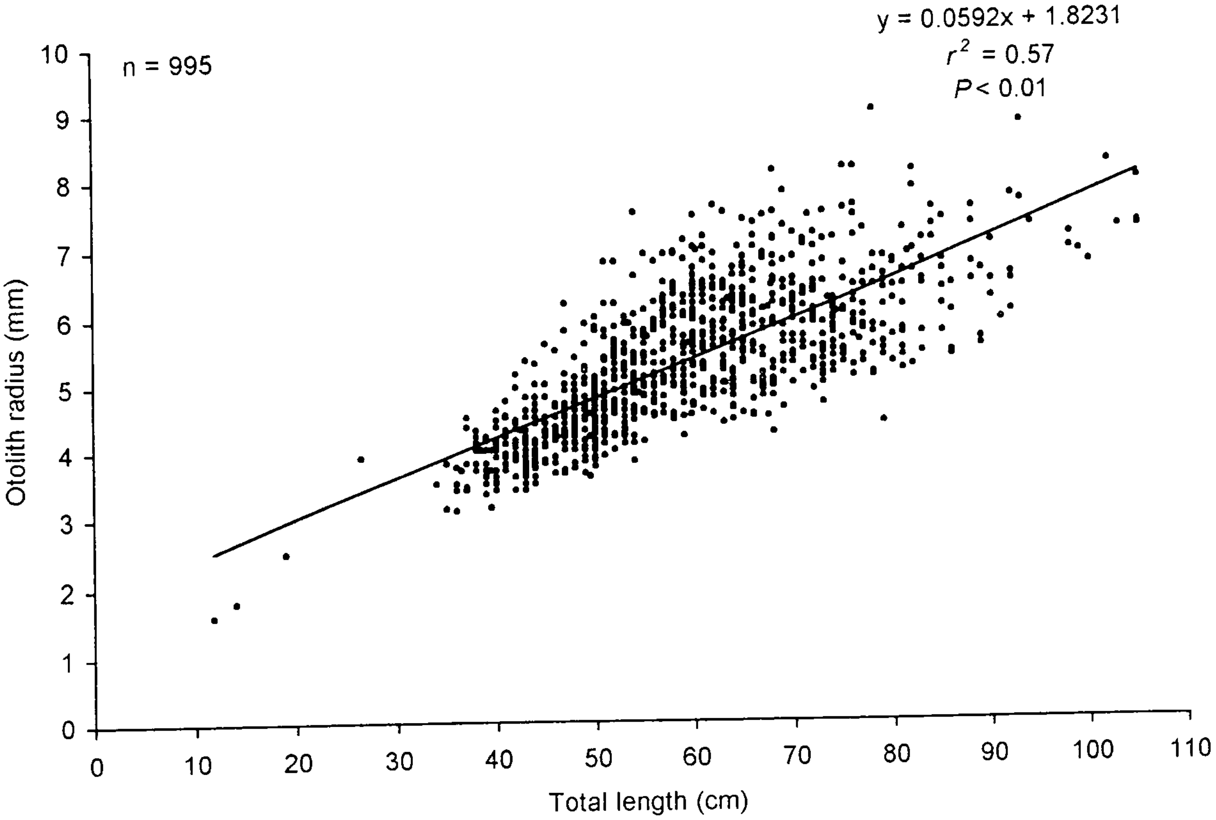


Fig. 4.9. The relationship between otolith radius and body length of North Sea wolffish.

and female common wolffish showed no significant difference in slopes ($F = 1.26$, df = (1, 875), $P > 0.05$).

4.3.2.3 Monthly variation of marginal increments of otoliths

Examination of seasonal changes in otolith marginal increments revealed that one opaque and one translucent zone were formed in a year (Fig. 4.10). The translucent zone was considered as an annual ring and was created at the end of the calendar year, when an opaque edge displayed a minimum value. Both the strong relations between TL and otolith radius, and annular ring formation provide verification for age and growth analyses. The monthly variations of marginal increments are shown in Fig. 4.11. The highest peak of otolith marginal increment occurred in August and September indicating that common wolffish grew faster during the summer season while the minimum value occurred in autumn and winter indicating that common wolffish reduced growth rate during these seasons. The periodicity of the marginal increment curve showed that only one cycle was produced in each year. Therefore, one year ring in an otolith represented one year old for this species in the North Sea. Based on the cyclic pattern of growth band deposition in otoliths, birth date was assumed to be 1 January.

4.3.2.4 Age composition

Common wolffish in the North Sea may be considered to be a relatively long-lived species. The oldest common wolffish sampled was estimated to be 18 years old. However, only one fish of this age was found, and the oldest of all other sampled fish were 15 years old. The age compositions for all commercially landed samples (from North Shields) are shown in Fig. 4.12. The majority of common wolffish ages were between the ages of 4 and 9 with a peak at age 4. The numbers of common wolffish of 11 years and older occupied only a small portion (5.7 %) of total catch. No age 1 or age 2 of common wolffish were sampled at North Shields despite there being no size limit, and despite specific requests to several boats to land any captured.

The age compositions of common wolffish landed at North Shields for each of the years 1996, 1997 and 1998 are shown in Fig. 4.13. The trend in age composition for each year was similar. The age compositions for males, females and combined sexes were mostly in the range of age 4 to age 10. Nevertheless, the frequencies of age 4 to

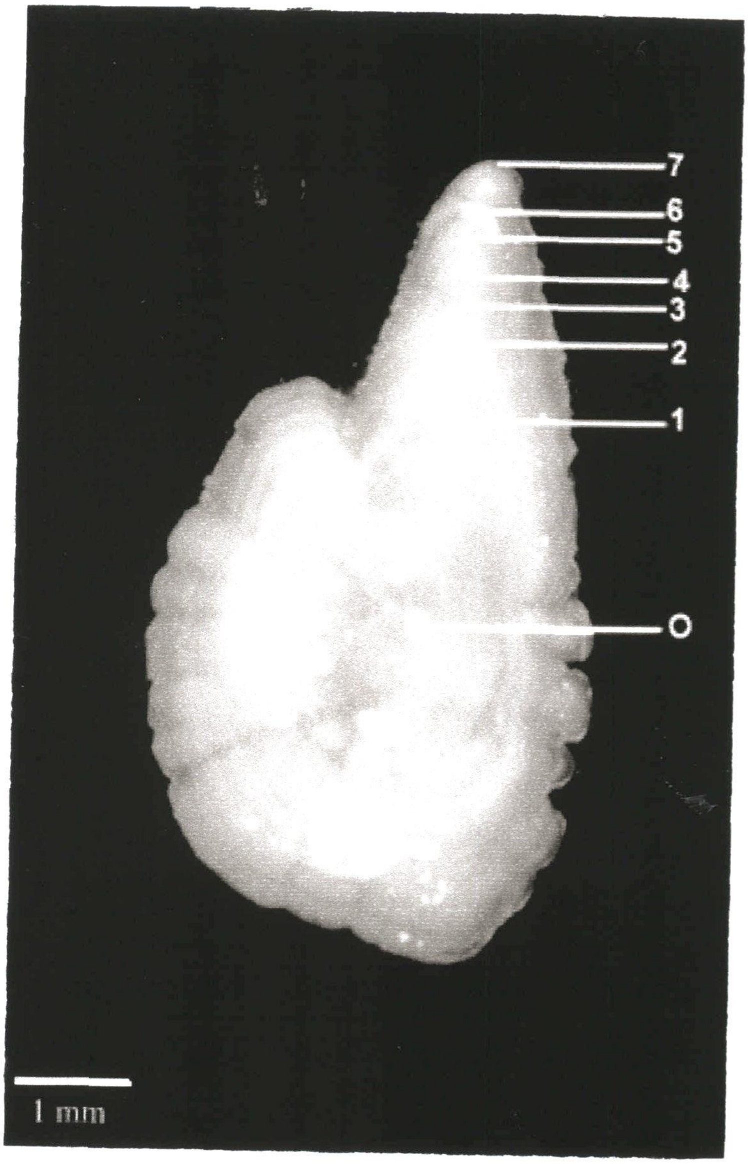


Fig. 4.10. Example of sagittal otolith from a common wolffish aged as 7. Lines show the positions of annuli. (O: centre).

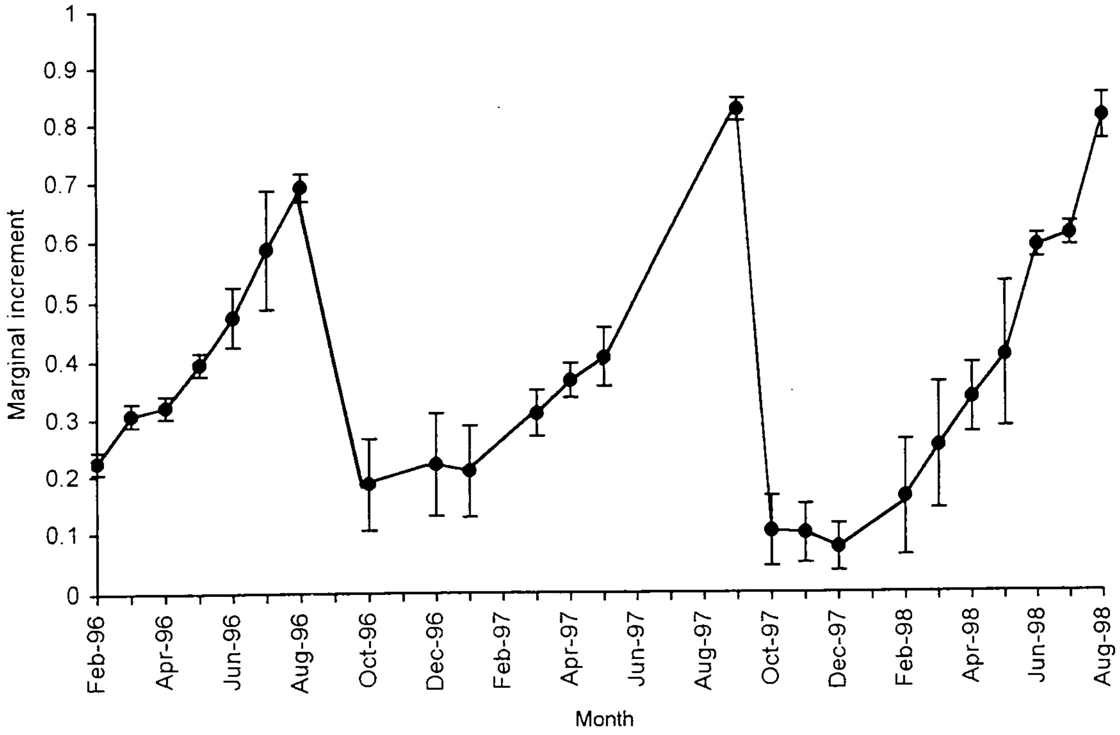


Fig. 4.11. The monthly variation in marginal increment of otoliths of common wolffish from the North Sea.

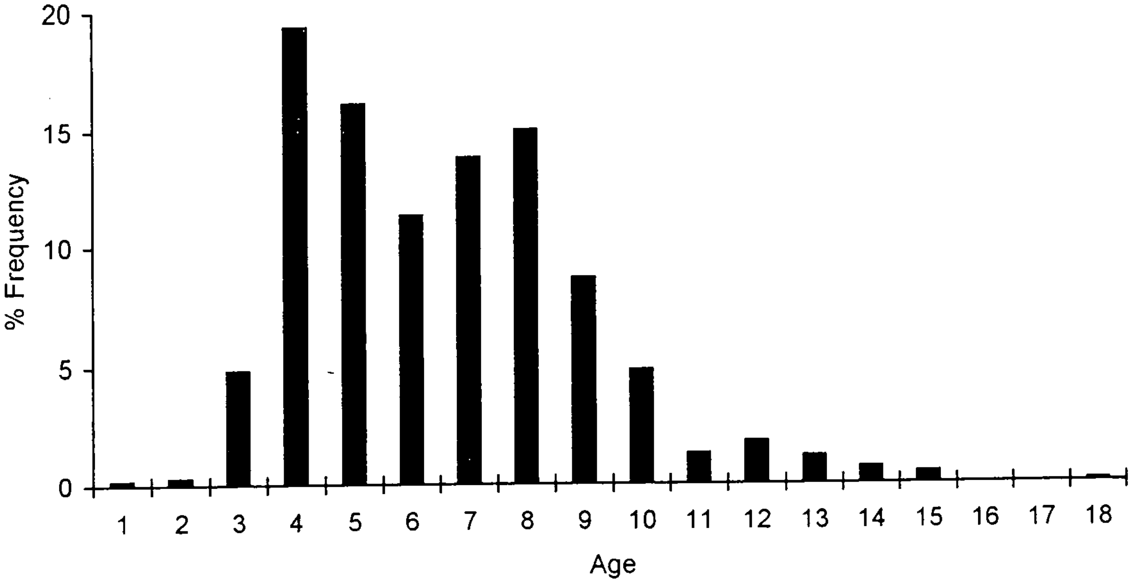


Fig. 4.12. Age distributions of common wolffish in the North Sea for 1996-1998.

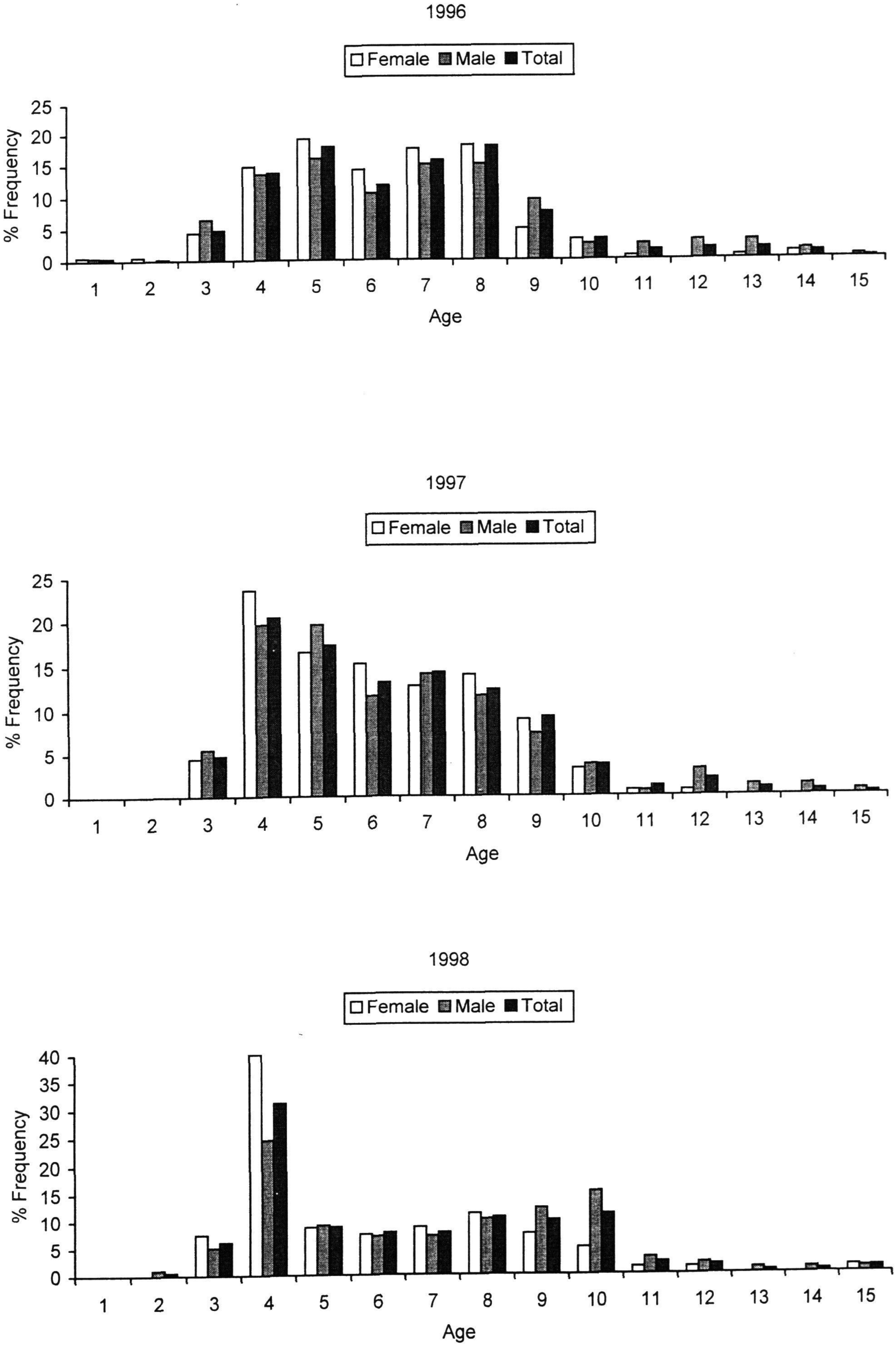


Fig. 4.13. Age distributions of North Sea wolffish for each year during 1996-1998 (one 18 year old fish for 1998 omitted).

age 8 had similar frequencies in 1996. In 1997 age 4 fish were most abundant with fewer fish in older age groups. The frequency of the age 4 group in 1998 was relatively more abundant than 1996 or 1997, while age 5 group to age 10 group had a similar level of frequency in 1998. The numbers of males were greater than of females for fish of over 11 years old.

4.3.2.5 The von Bertalanffy equation

Von Bertalanffy growth curves were estimated for male and female common wolffish and are shown in Fig. 4.14. The predicted von Bertalanffy growth curves provided a highly significant fit to the observed mean size for each age group for both female and male common wolffish in the North Sea (female, $r^2 = 0.92$; male, $r^2 = 0.96$). The slopes of growth curves for the age 1-5 fish were greater than that after age 6 for both sexes. Common wolfish in the North Sea grew faster up to 5 years old than at subsequent ages. The average growth was 9.8 cm per year for age 1 to age 5 years old common wolffish and 4.7 cm per year for age 6 to age 15. The equation parameters for males, females and both sexes combined were:

Male: $K = 0.12$, $t_0 = -0.43$, $L_\infty = 111.2$, $r^2 = 0.96$, $P < 0.001$
Female: $K = 0.11$, $t_0 = -0.39$, $L_\infty = 115.1$, $r^2 = 0.92$, $P < 0.001$
Combined: $K = 0.12$, $t_0 = -0.56$, $L_\infty = 114.9$, $r^2 = 0.95$, $P < 0.001$

The growth coefficient K was similar for males and females, at about 0.11. The mean total length within each age group was not significantly different between males and females in the North Sea (ANOVA, all $P > 0.05$).

The mean length of each age group for 1996-1998 is shown in Fig 4.15. The mean lengths of age 3 to age 8 fish were similar within the three years. However, the mean lengths of the age groups, which were older than 12 years old in 1997, were significantly less than those of the same age groups in 1996 (ANOVA, df = (1,27), $F = 7.94$, $P = 0.008$). The mean lengths of the age groups, which were older than 10 years in 1998, were significantly smaller than those of the same groups in 1997 (ANOVA, df = (1,58); $F = 34.03$, $P < 0.001$). Thus the mean lengths of older groups of landed common wolffish appear to have decreased gradually over the last three years, despite the small sample sizes.

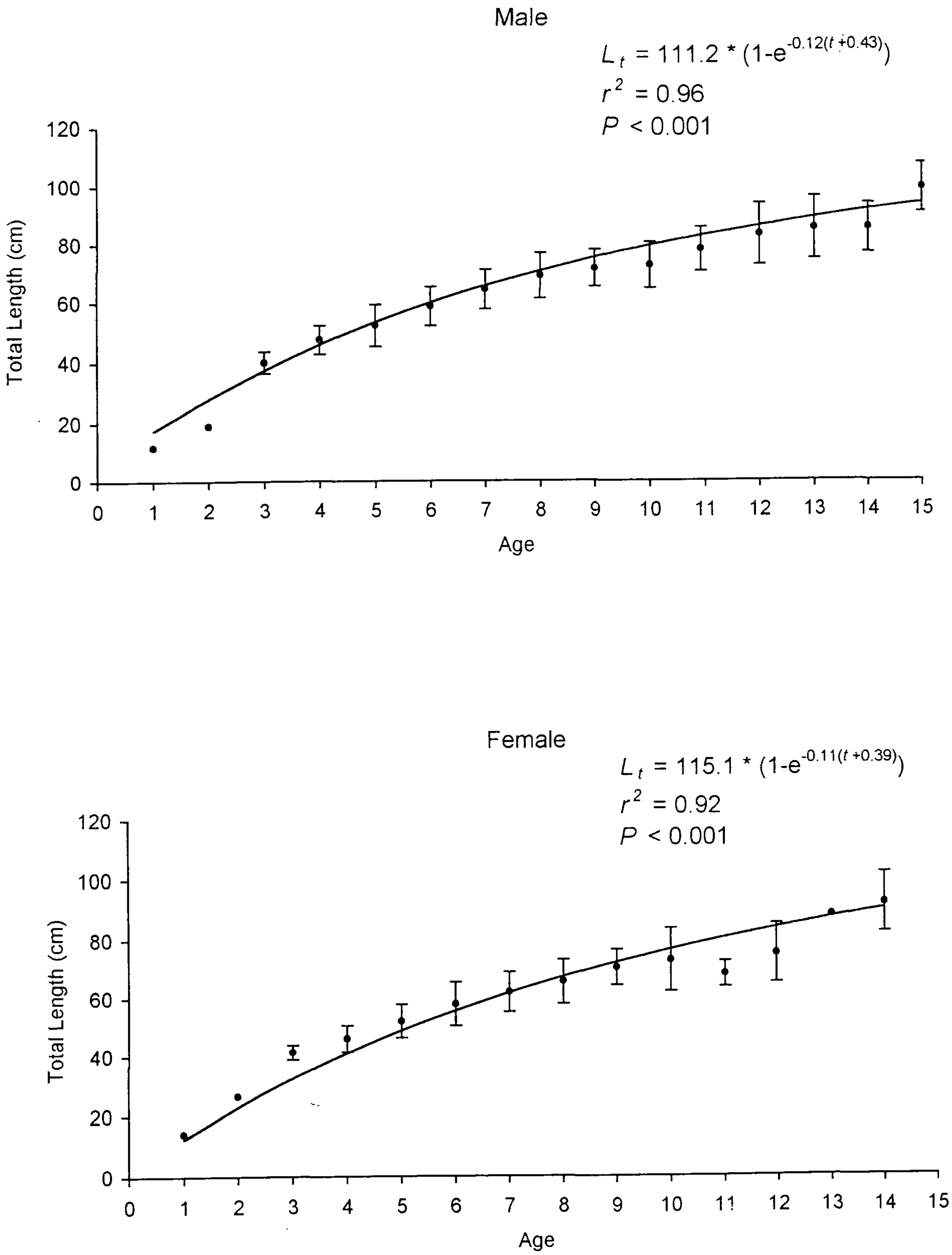


Fig. 4.14. Fitted von Bertalanffy growth curves and mean length-at-age for North Sea wolffish.

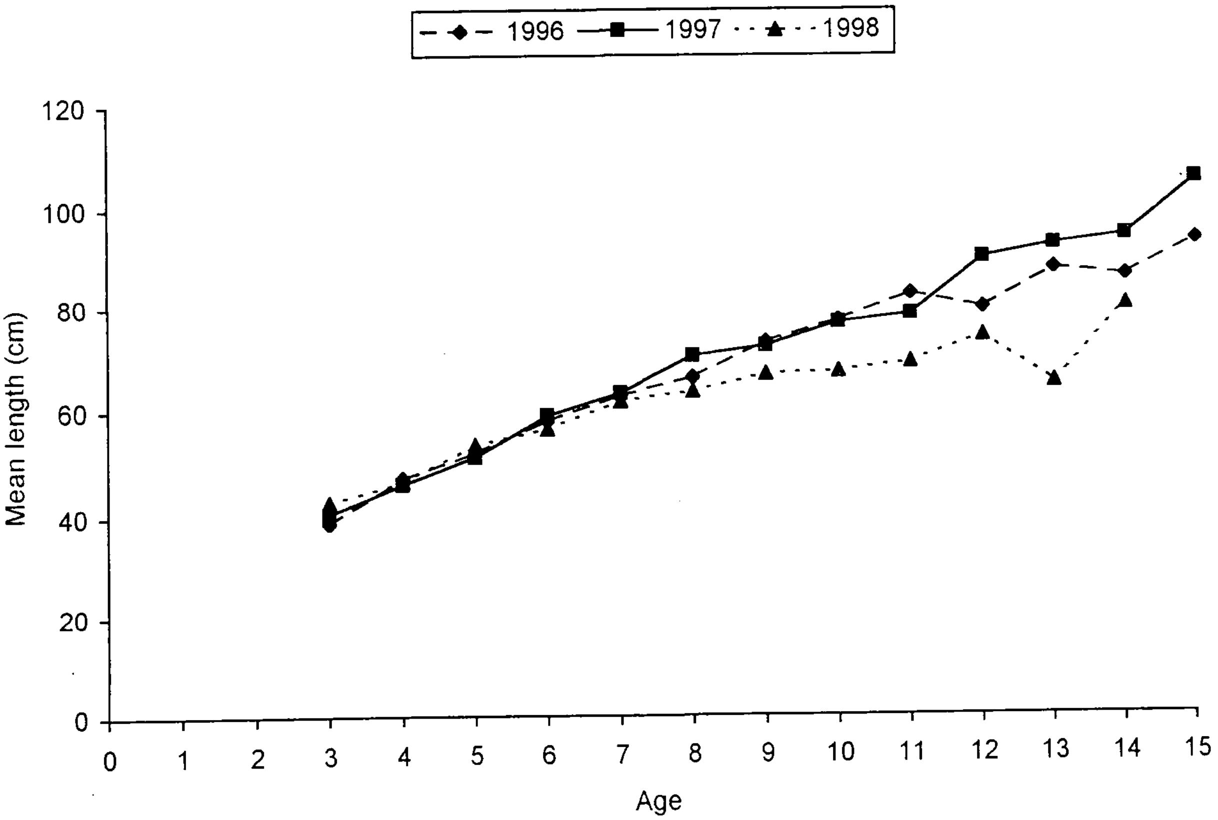


Fig. 4.15. The relationship between mean length and age for North Sea wolffish for each year during 1996-1998.

4.3.3 Reproduction

4.3.3.1 Histological studies of gonads

4.3.3.1.1 Females

The ovary of the common wolffish is an elongated-paired organ situated in the dorsal part of the abdominal cavity. It consists of a series of ovarian lamellae containing oocytes at different stages of development (Fig 4.16a). Most ovaries were identified as stage 1 and stage 2 (mainly October to May), stage 3 (February to July) and a few stage 4 (mainly June to October). A substantial proportion of mature individuals (50.7 %) had only reached stage 2 or later in the whole year (Table 4.6).

Oogonia (Fig 4.17a). The oogonia are spherical in shape and are sited on the periphery of the ovarian lamellae, isolated or forming nests with diameters from 20-80 µm. Each has a very large nucleus with single very prominent nucleolus.

Primary growth phase. This stage includes the chromatin nucleolus stage (Fig. 4.17b) and the perinucleolus stage (Fig. 4.17c) and is presented in the ovary throughout the entire annual cycle. The diameters of primary oocytes were between 70 µm and 280 µm. These oocytes were almost transparent. The nucleus was somewhat larger and the cytoplasm was stained dark purple through a strong affinity for haematoxylin. In the chromatin nucleolus stage, the large nucleus was only with a single nucleolus. In the perinucleolus stage, the nucleus had multiple nucleoli, which were generally prominent features towards the nuclear membrane. These oocytes usually had a thin layer of follicular epithelium surrounding them.

Yolk-vesicle stage (Fig 4.17d). The yolk-vesicle type oocytes were also found in ovaries through the entire annual cycle. These oocytes were slightly yellowish and had diameters in the range of 185 µm and 1050 µm. Yolk vesicles contained the intravesicular yolk. Vacuoles increased progressively in both volume and number with larger oocytes. The cytoplasm was stained a pink colour after fixation. The nucleus had multiple nucleoi close to the nucleus membrane. The follicular layer became visible at this stage.

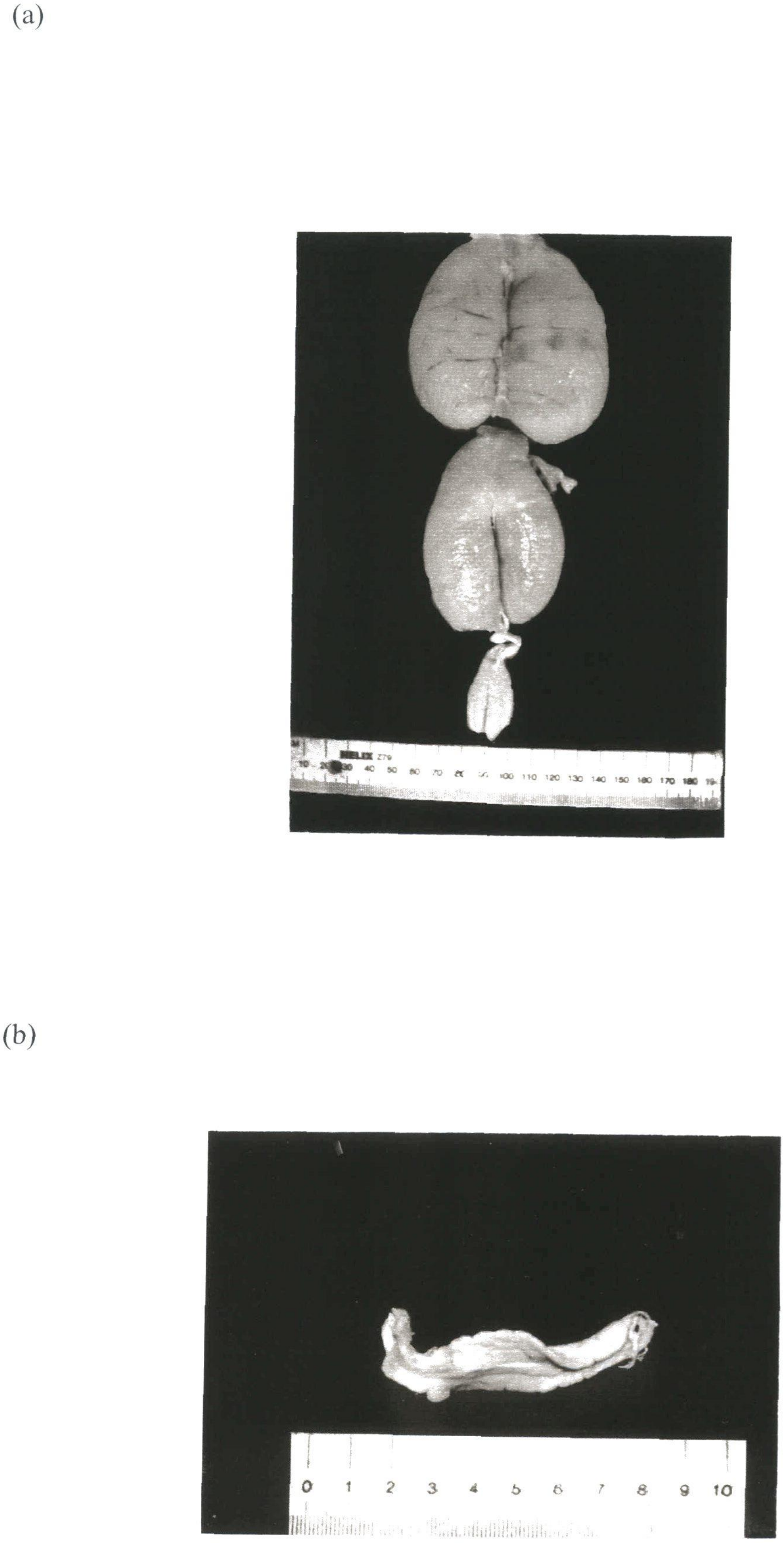
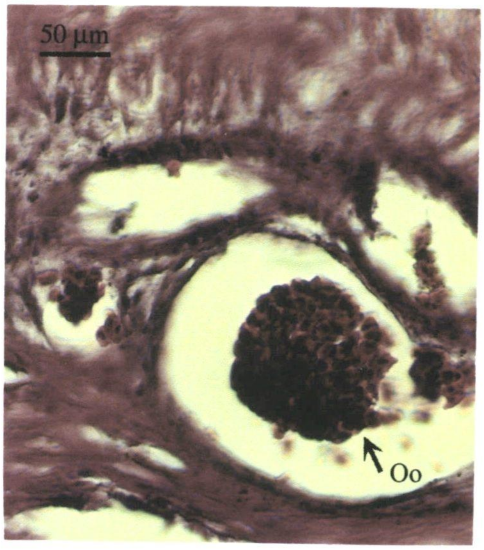


Fig. 4.16. Morphological features of gonads of common wolffish. (a) Macroscopic maturation stages of ovary from stage 2 (lower) to stage 4 (upper). (b) A mature testes. The spermiducts run longitudinally in the middle of elongated testes and transport sperm through a urinogenital papilla for internal fertlisation during the spawning period.

Table 4.6. The monthly variation of developmental stages of ovaries of mature female common wolffish, presented as % of ovaries in different stages.

	Stage						
Month	I	II	III	IV	V	VI	n
January	60	40	0	0	0	0	6
February	59.7	30.7	6.2	3.1	0	0.3	33
March	52.6	40.4	7	0	0	0	54
April	50.8	35.4	13.8	0.0	0	0	64
May	52.2	41.3	6.5	0.0	0	0	46
June	16.7	70	10	3.3	0	0	30
July	33.3	50	12.5	4.2	0	0	21
August	75	0	0	25	0	0	4
September	66	17	0	17	0	0	6
October	100	0	0	0	0	0	2
November	100	0	0	0	0	0	1
December	61.5	38.5	0	0	0	0	13

(a)



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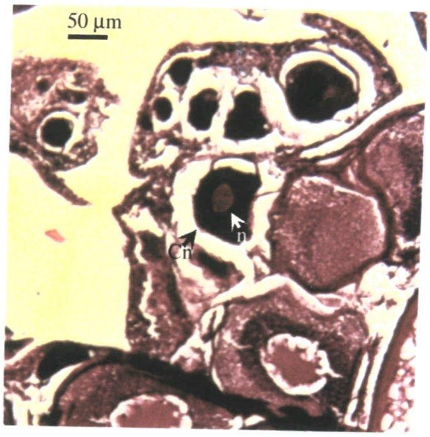


Fig. 4.17a,b. Photomicrographs showing the histological stage classification of developing oocytes. (a) Oogonia phase: nests of oogonia sited on periphery of ovarian lamellae. Oo: oogonia. (×100) (b) Primary growth phase- chromatin nucleolus stage: The ovary contain this stage oocytes with strongly basophilic cytoplasm and one nucleus. Cn: chromatin nucleolar oocyte, n: nucleus. (×50)

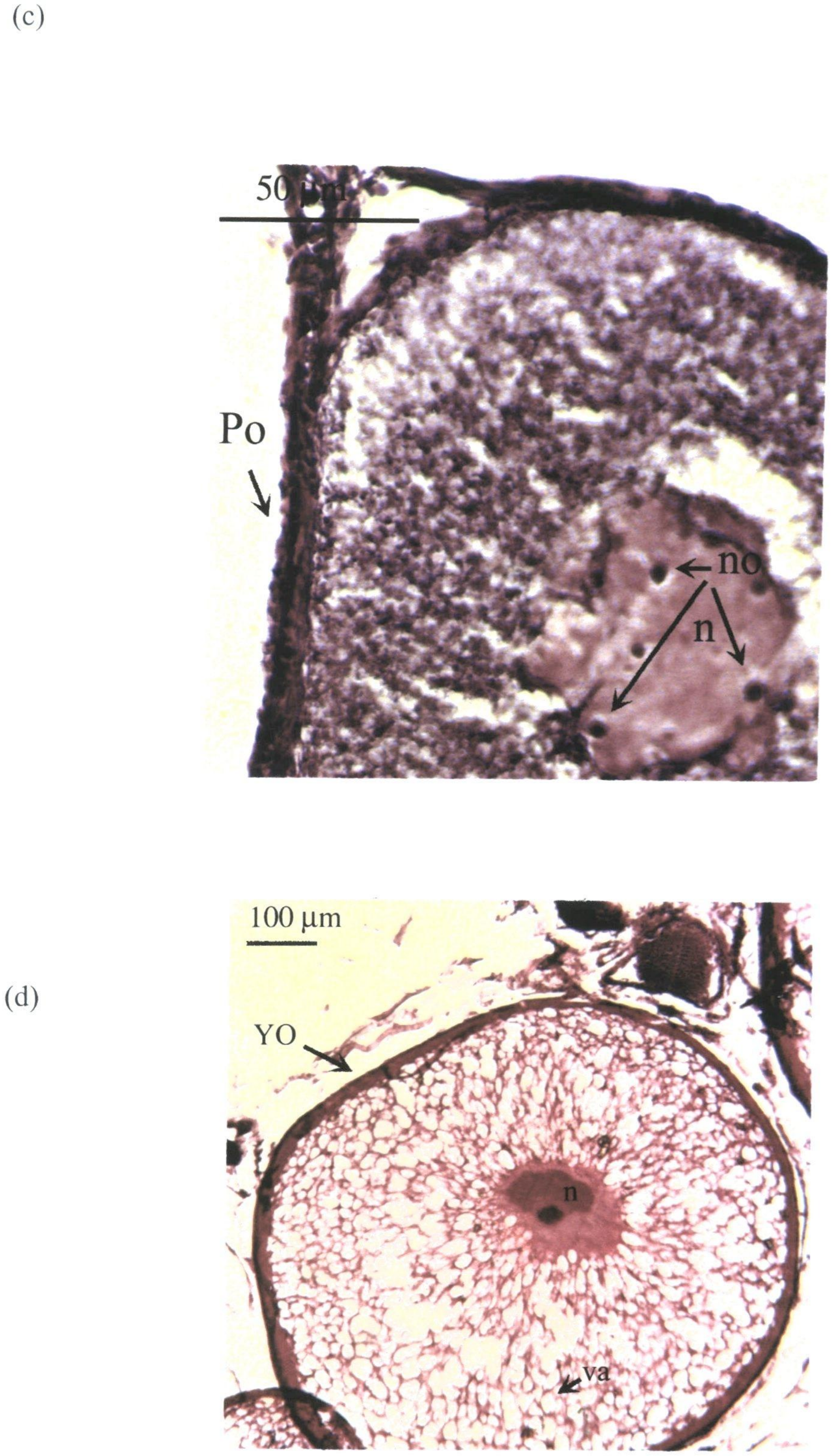


Fig. 4.17c,d. Histological stage classification of developing oocytes. (c) Primary growth phase- perinucleolus stage: oocytes with less baophilic cytoplasm and several nucleoli arranged along the nuclear wall. n: nucleus, no: nucleoli, Po: perinucleolar oocyte. (×100) (d) Secondary growth phase – yolk-vesicle stage: Vacuoles began to appear in the cytoplasm. As the oocyte grew, the vacuoles increased in number and volume rapidly. n: nuclear, va: vacuoles, YO: yolk veicle stage oocyte. (× 100). The cytoplasm stained a pale pink.

Vitellogenesis stage (Fig. 4.17e). The vitellogenic type oocytes commonly occurred from March to September, but larger ones were dominant from May. The diameters of this stage were between 820 µm and 4050 µm. Yolk vesicles increased in size and gravitated toward the periphery while the yolk granules expanded. The oocytes were filled with many large yolk globules. The yolk vesicles formed two layers in the periphery of the cytoplasm. These layers were dyed with eosin; the internal layer was light-pink and the external layer was dark pink.

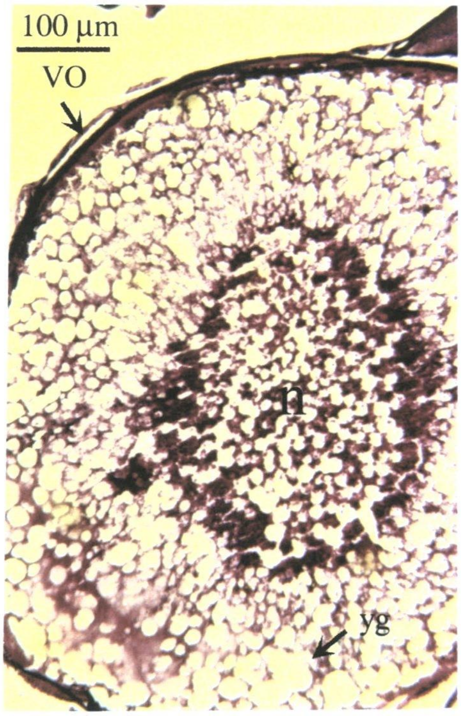
Ripe stage (Fig. 4.17f). The diameter of oocytes at this stage was about 5000 µm since only small samples have been observed. Yolk granules were fused in homogeneous and created the hyaline oocytes. These hyaline oocytes were found between June and September and were also noted in February. The oocyte envelopes became remarkably thick. The nucleus was not visible due to disintegration of the nuclear membrane and dispersion into the cytoplasm. When oocytes reached this stage, spawning was imminent.

4.3.3.1.2 Males

The testes of common wolffish were rather small and elongated. They were attached to the body wall by a mesentery and situated posterior to the kidney. The main sperm ducts ran longitudinally and united to form testes ducts (Fig. 4.16b). The testes of immature juveniles were mainly filled with germ cells and spermatogonia (Fig. 4.18a). Spermatogenic cells appeared in the interior of the seminiferous tubules with different stages during spermatogenesis. Five stages in the formation of spermatozoa could be determined and identified as spermatogonia (stage 1) (Fig.4.18a), primary spermatocytes (stage 2) (Fig4.18b), secondary spermatocytes (stage 3) (4.18b), spermatids (stage 4) (Fig. 4.18c) and spermatozoa (stage 5) (Fig. 4.18d). Each cyst was bounded by connective tissue and contained cells at the same stage of development. In mature testes, the seminiferous tubules were filled with spermatozoa.

All the developmental stages were present throughout the entire annual cycle. Spermatozoa were found in most sampled individuals. However the quantity of spermatozoa was highest during the summer and winter season.

(e)



(f)

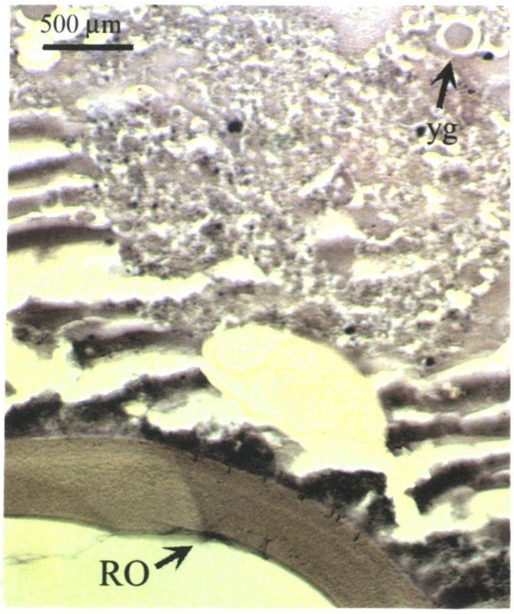


Fig. 4.17e,f. Histological stage classification of developing oocytes. (e) Secondary growth phase- vitellogenesis stage: Eosinophilic yolk granules began to appear and were further accumulated in the cytoplasm. yg: yolk granules, VO: vitellogenesis type oocyte. (×100) (f) Ripe stage: the oocytes were larger than 5000 µm. degraded the vitelline envelop and yolk granules. No nucleus was observed. RO: ripe oocyte (×50).

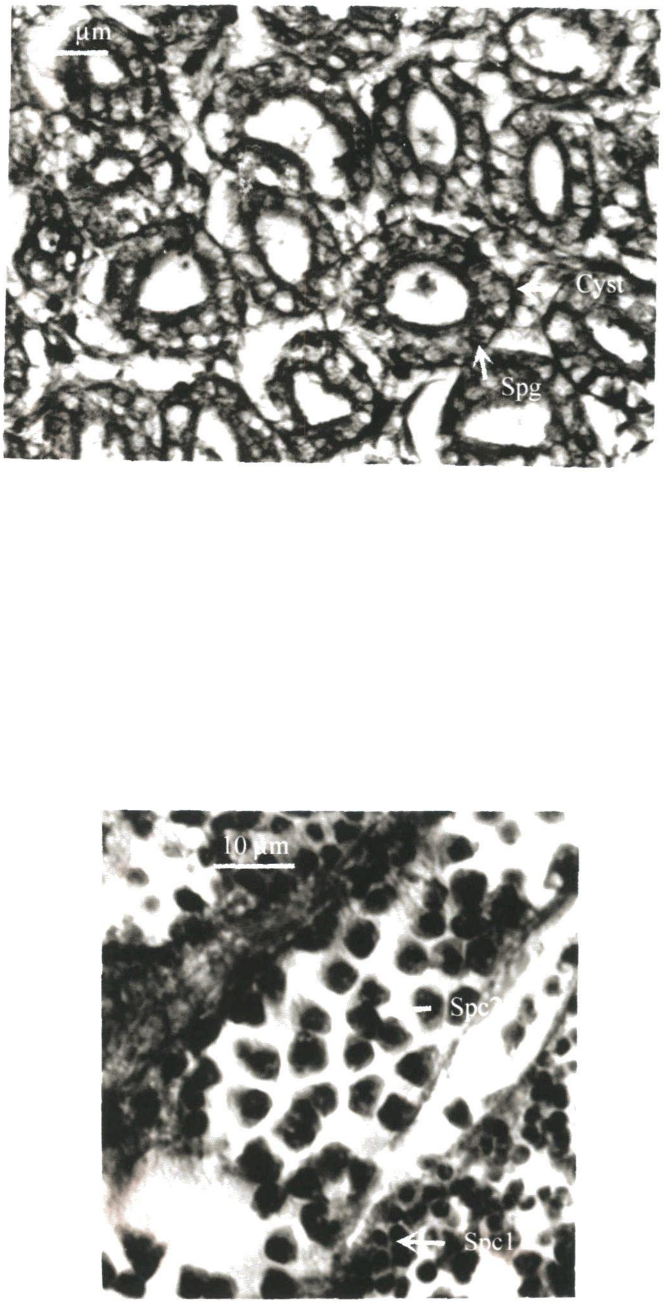
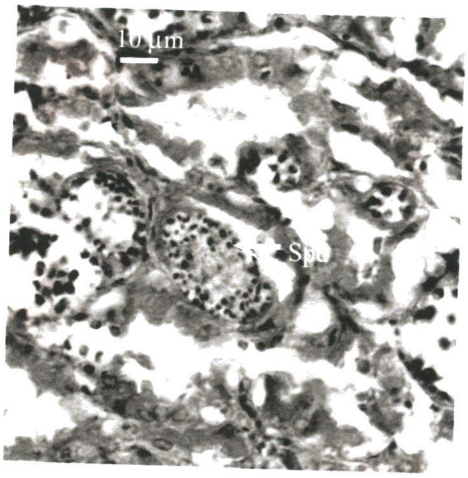


Fig. 4.18a,b. Histological stage classification of developing testes. (a) immature testes contained numbers of spermatogonia within the cysts. No spermatocytes were observed. Spg: spermatogonia, cyst: cyst (×100). (b) mainly cysts appeared the primary spermatocytes and secondary spermatocytes. Spc1: primary spermatocyte, Spc2: secondary spermatocyte (×200).

(c)



(d)

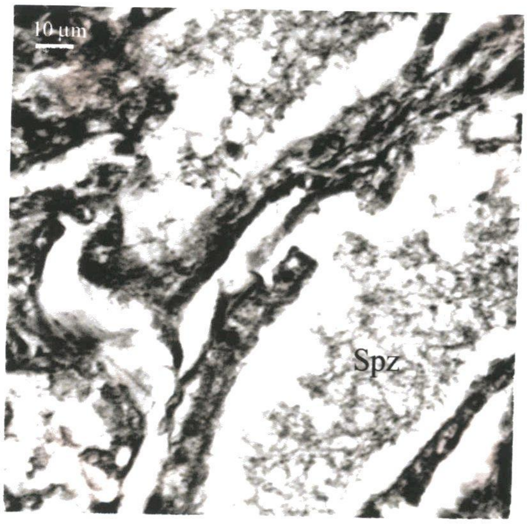


Fig. 4.18c,d. Histological stage classification of developing testes. (c) mainly cysts of spermatocytes with appearance of cysts of spermatids. Spd: spermatid, (×100). (b) Spermatozoa in sperm ducts during the spawning season. Spz: spermatozoa (×200).

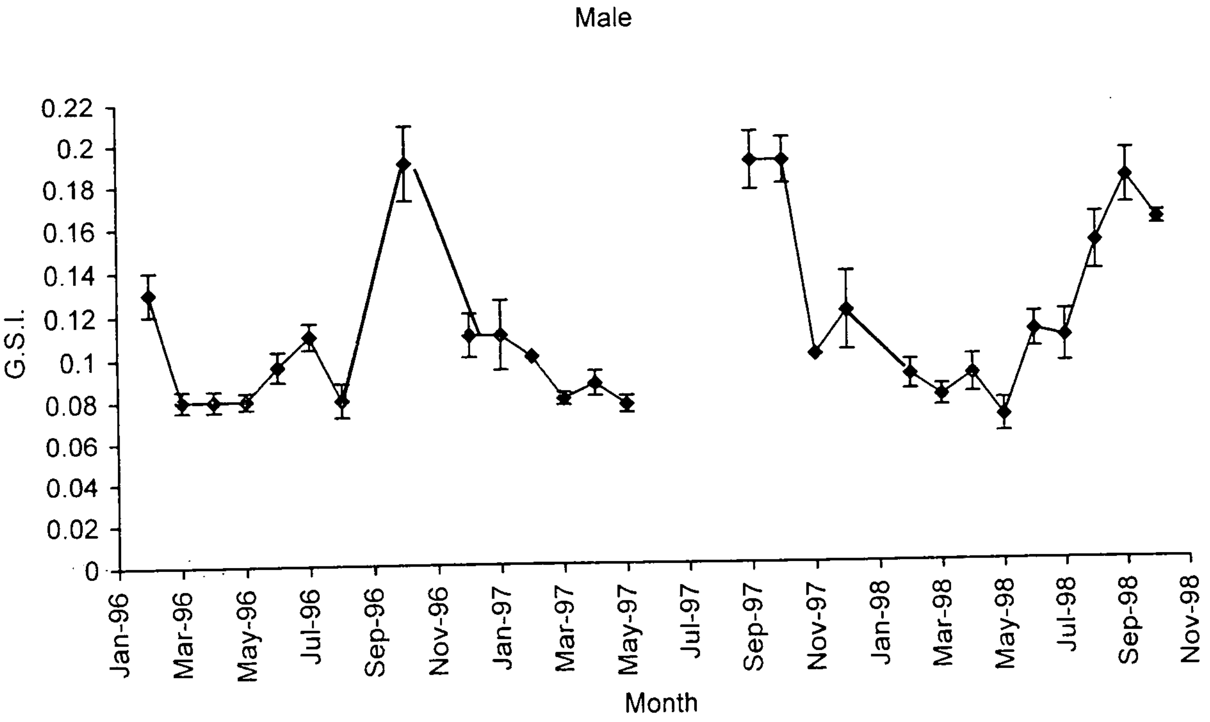
4.3.3.2 Spawning season

Seasonal changes in GSI for both sexes of common wolffish are shown in Fig 4.19. The weights of the testes were always low (means between 0.08 and 0.2). Although the spermatozoa were found in the testes of this species all year round, the seasonal changes in GSI for males indicated that the males increased their gonad weights from June to October, and they decreased rapidly after January and reached their lowest value during the March-May period. Although there is a gap between June and September in 1997 for female GSI data, the seasonal changes in GSI for females showed a pronounced pattern through the year. The values of GSI were lower from November to May and higher during June to October.

The frequency distributions of egg diameter by month are shown in Fig. 4.20. Eggs were not larger than 0.8 mm diameter during October to December and increased in size gradually after January with ripe eggs occurring in June. The proportions of different stages of ovary development by month (Table 4.6) also indicated that the percentage of eggs classified as stage 1 decreased from December to the lowest value in June while groups greater than stage 2 increased after December.

These results suggest that the spawning period of the common wolffish in the North Sea begins after the summer growth season. There was one female captured with ripe eggs in February 1998. This may represent a component of a late spawning group that has also been found in Icelandic waters and southern Norwegian waters. However, a female was also found in spent condition with loose ovary and a few ripe eggs in February 1997. Therefore, the spawning season of common wolffish in the North Sea is from October through to, but no later than February.

Most of the fish caught close inshore (38E8-38E9) during the spawning season were immature or resting stage one for both sexes (Table 4.7, Table 4.6). Almost all male common wolffish sampled from the offshore areas of North Sea were mature. The majority of immature common wolffish captured from the inshore areas of North Sea were caught between October and November for both sexes.



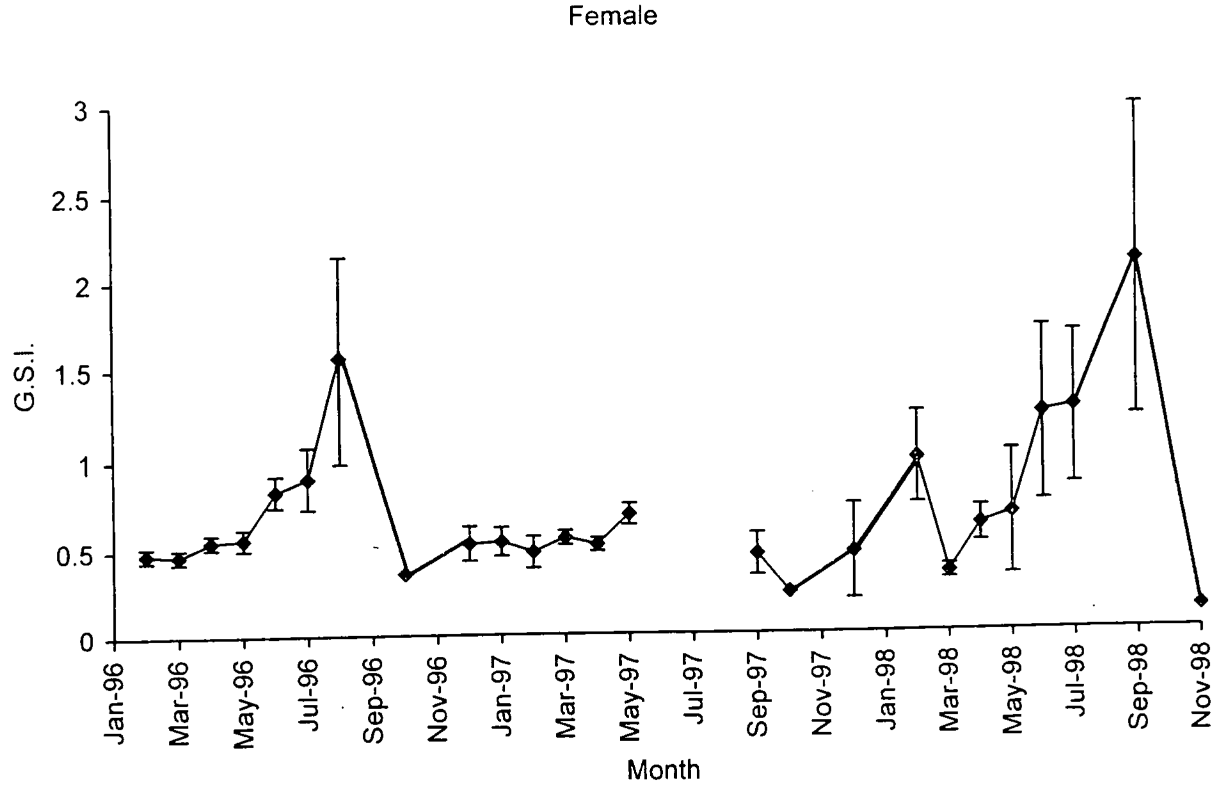


Fig. 4.19. Monthly mean G.S.I. for male and female common wolffish in the North Sea for 1996-1998.

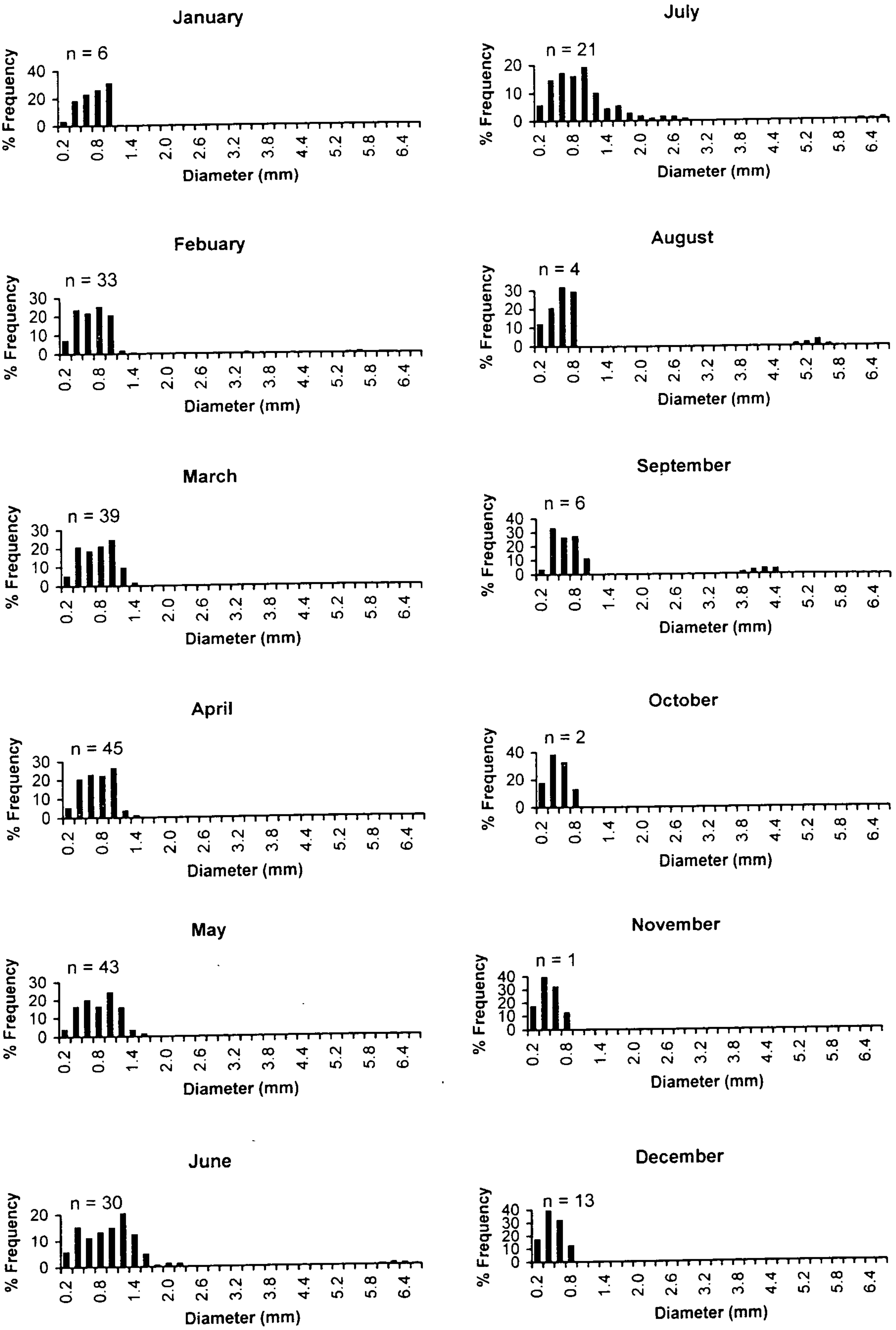


Fig. 4.20. Monthly oocyte diameter distributions during 1996-1998 for common wolffish in the North Sea. % frequency calculated from 150 randomly chosen oocytes from the middle section of the ovary of each sampled fish.

Table 4.7. Numbers of immature and mature common wolffish captured from the inshore or offshore areas of the North Sea during the spawning season, presented as percentage frequency.

Male

	Inshore			Offshore		
Month	Immature	Mature	n	Immature	Mature	n
October	33.3	66.7	27	0	100	2
November	83.3	16.7	6			
December	50.0	50.0	12	11.1	88.9	18
January	60.0	60.0	5	0	100	4
February	38.5	61.5	26	12.5	87.5	8

Female

	Immature	Mature	n	Immature	Mature	n
October	83.3	16.7	12			
November	80.0	20.0	5			
December	84.6	15.4	13	9.1	90.9	11
January	33.3	66.7	9			
February	29.5	70.5	44	0	100	2

4.3.3.3 Sex ratio

The sex structure of the sampled common wolffish is shown in Table 4.8. The frequency of males in samples was mostly not significantly different to that of females during the study period (Table 4.8). A chi-square tests showed no significant association between months (df= 25, $\chi^2 = 0.039$, $P > 0.05$). When all samples were pooled, the ratio of Male: Female was also not significantly different (1.16:1; χ^2, df= 1, $P > 0.05$).

The percentages of maturity of samples collected were mostly over 50 % monthly for both sexes (Table 4.8). However, there was some suggestion that the proportion of immature females in catches increased in autumn.

4.3.3.4 Size at first maturity

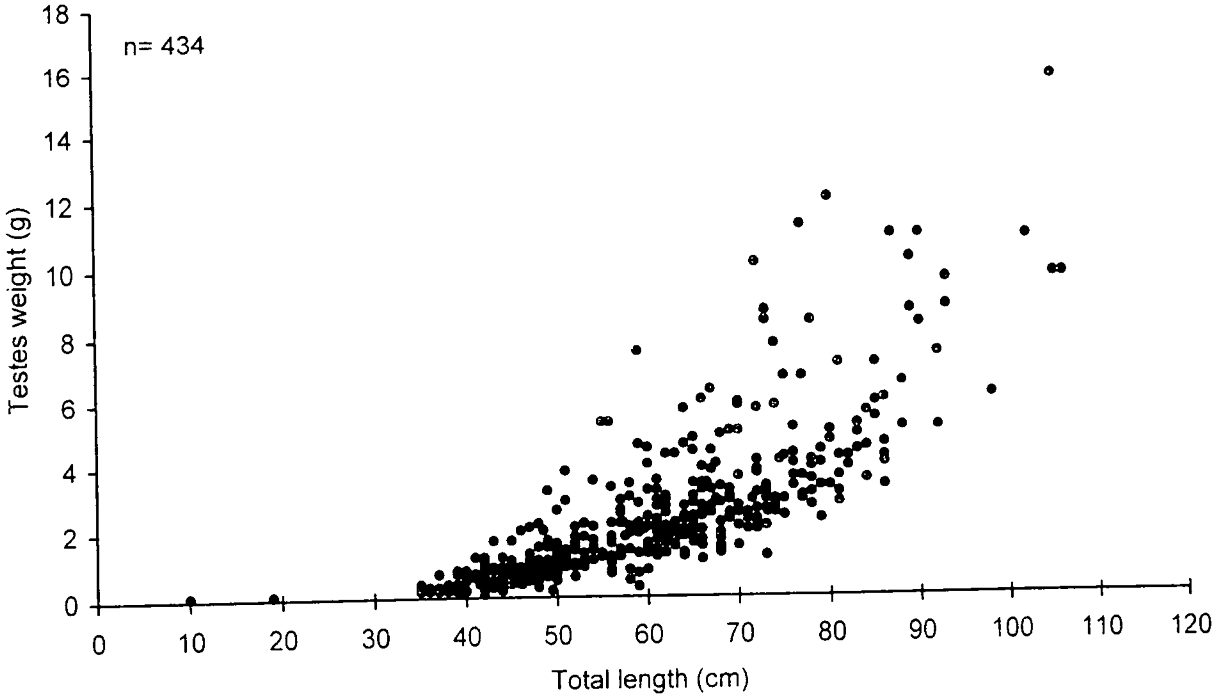
The minimum mature lengths for male and female North Sea common wolffish were 42 cm and 44 cm respectively since common wolffish developed their gonads rapidly after their body size reached this length (Fig. 4.21). At lengths greater than these the percentages of mature fish increased rapidly (Fig 4.22). The high values of the coefficients of determination ($r^2 > 0.98$) indicate a good fit of the regressions. Estimated median length at first maturity (L_{50}) was 51.9 cm for male common wolffish and 50.4 cm for female. All individuals greater than 70 cm were mature (Fig. 4.22). The age of median length at first maturity for both sexes was 4-5 years old.

4.3.3.5 Fecundity

Since most individuals were gutted quickly after capture by commercial vessels at sea, there were only three ovaries which had reached stage 4 that were collected during the study period. Another two stage 4 ovaries were obtained from groundfish surveys (one from FRS, August 1996; one from CEFAS, September 1998). Both female and male common wolffish near the spawning stage were obtained from offshore areas where they were fished all year round. The mature ovaries were collected between June and February. All stage 4 ovaries were collected from offshore areas where depths were over 90 m.

Table 4.8. The numbers and mature percentage of monthly sampled common wolffish.

	Male			Female		
Month	Immature	Mature	Mature%	Immature	Mature	Mature%
Feb-96	5	15	75.0	4	16	80.0
Mar-96	5	12	70.6	3	14	82.4
Apr-96	12	11	47.8	10	35	77.8
May-96	4	30	88.2	2	18	90.0
Jun-96	0	23	100.0	0	18	100.0
Jul-96	4	20	83.3	2	13	86.7
Aug-96	1	5	83.3	3	4	57.1
Sep-96	0	0		0	0	
Oct-96	3	13	81.3	2	1	33.3
Nov-96	0	0		0	0	
Dec-96	4	15	78.9	3	11	78.6
Jan-97	3	6	66.7	2	6	75.0
Feb-97	2	1	33.3	2	7	77.8
Mar-97	10	35	77.8	13	35	72.9
Apr-97	9	16	64.0	2	24	92.3
May-97	16	19	54.3	5	23	82.1
Jun-97	0	0		0	0	
Jul-97	0	0		0	0	
Aug-97	0	0		0	0	
Sep-97	8	8	50.0	5	3	37.5
Oct-97	6	5	45.5	7	1	12.5
Nov-97	5	1	16.7	4	0	0.0
Dec-97	4	7	63.6	8	2	20.0
Jan-98	0	0		1	0	0.0
Feb-98	4	7	63.6	7	10	58.8
Mar-98	9	6	40.0	5	5	50.0
Apr-98	0	11	100.0	4	5	55.6
May-98	5	4	44.4	5	5	50.0
Jun-98	3	18	85.7	1	12	92.3
Jul-98	2	7	77.8	2	8	80.0
Aug-98	0	3	100.0	0	0	
Sep-98	1	9	90.0	0	3	100.0
Oct-98	0	2	100.0	1	0	0.0
Nov-98	0	0		0	1	100.0



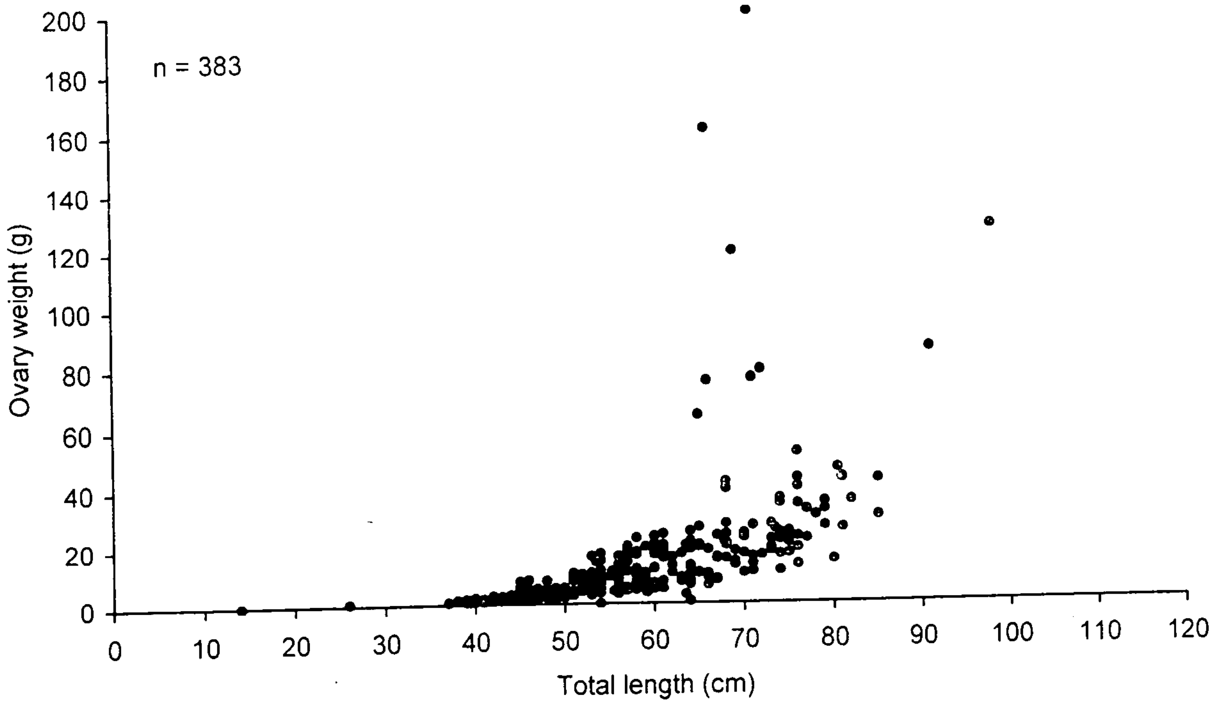


Fig. 4.21. The relationship between gonad weight and total length for common wolffish in the North Sea. Development of gonads increased rapidly after length reached 44 cm for both sexes.

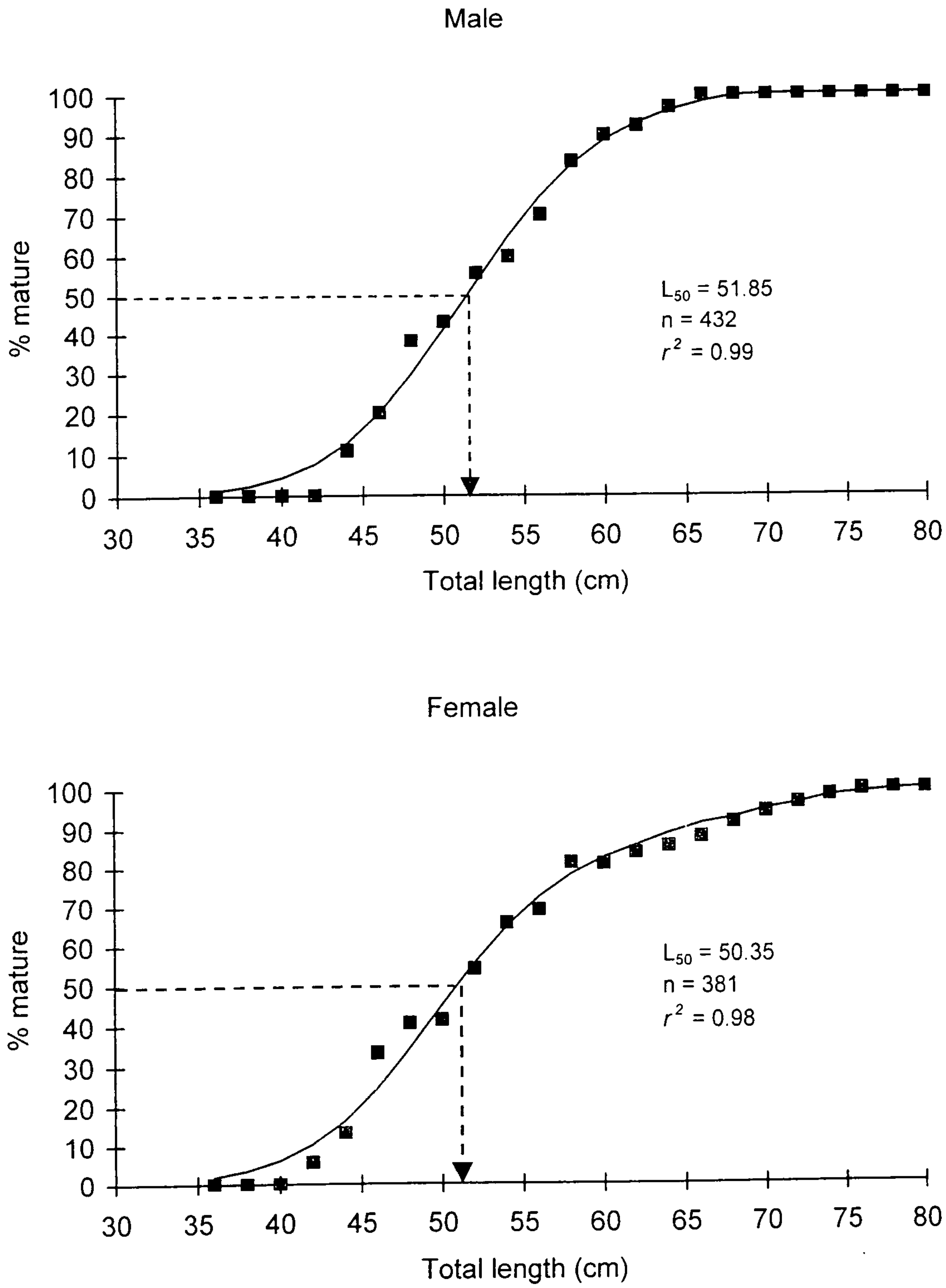


Fig. 4.22. Median size at first sexual maturity (L_{50}) of common wolffish in the North Sea. Parameters of logistic function estimated by non-linear regression. Arrows indicate median length at first maturity.

Common wolffish produced relatively large eggs (5-6.4 mm diameter) during the spawning season. When the ovary reached stage 4 or higher, there was still numbers of eggs smaller than 1.2 mm diameter (stage 1 and stage 2) remaining in the ovary. However, there was no intermediate size (1.5-4 mm) of eggs found in these running ripe ovaries. Therefore, the common wolffish would only lay one egg mass in each breeding season and are determinate rather than fractional spawners.

Although the sample sizes were small, there was a linear correlation observed between female body weight and absolute fecundity (Fig. 4.23). The fecundity could be obtained by the following regression:

$$F = 5357.6 + 866.48W \qquad r^2 = 0.91; P < 0.001, \mathrm{n} = 5$$

where F is fecundity, and W is the body weight of female (g).

The fecundity varied between a few thousand in small females to over 10,000 in the larger individuals. Based on this data the relative fecundity of this species for the North Sea is 3,132 ± 393 eggs per kg wet weight ($\bar{x}$ ± SE).

4.4 Discussion

4.4.1 Diet

The high value of Levin's standardized index indicates that common wolffish in the North Sea were generalist consumers. This reflects the view that common wolffish have flexible diets depending on various factors such as location, size of fish and time of year (Jónsson, 1982; Templeman, 1984). In the Gulf of Maine, scallops (62.2 % by occurrence), sea urchins (50.8%), whelks (21.3%) and hermit crabs (18%) were the main prey items of common wolffish (Nelson and Ross, 1992). Off Newfoundland waters, the species consumed mostly molluscs (e.g. whelks and scallops) and echinoderms (e.g. brittle stars and sea urchins (Albikovskaya, 1982; Templeman, 1985; Keats *et al.*, 1986). Decopoda were less important in this area. In Icelandic waters, the main prey items of common wolffish were hermit crabs, spider crabs, whelks and sea urchins (Jónsson, 1982). In the White Sea, the stomach contents of sampled individuals contained 72% of molluscs, 62% crustaceans and 37 % echinoderms (Barsukov, 1959). In the North Sea, the main prey items of this species

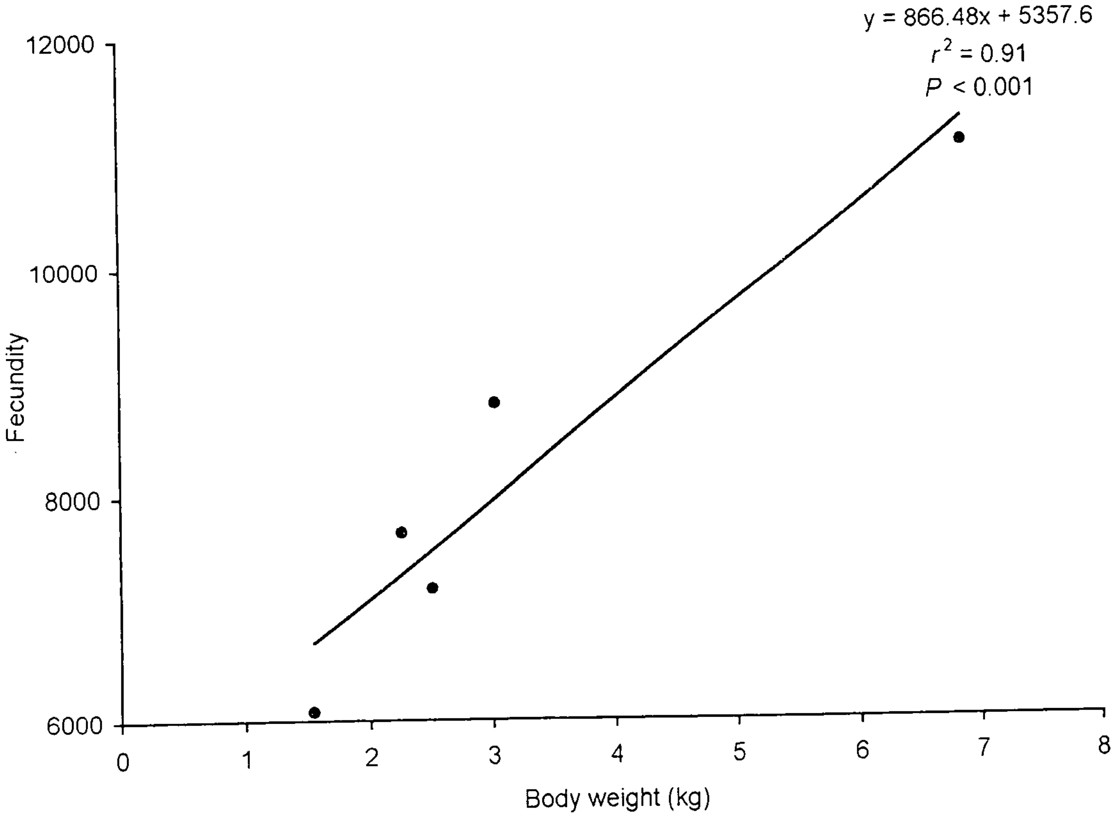


Fig. 4.23. The relationship between body weight and fecundity of female common wolffish from the North Sea.

were hermit crabs, scallops, whelks and sea mouse (Aphroditidae). These results broadly reflect the occurrence of prey items in the areas where common wolffish were caught in the North Sea. However, while sea urchins were eaten by common wolffish in the North Sea, they were less important than in other studies, even though sea urchins were the second most abundant group by occurrence in these areas of the North Sea.

Although common wolffish exhibited relatively little seasonal variation in diet, there were some species that they consumed only in some seasons. Common wolffish only consumed squid less than 6 cm during winter and spring season and this reflects the breeding period of *Loligo forbesii* in the North Sea, from December to May (Collins *et al.*, 1997). Arcticidae, Cardiidae and Corystidae were only found in the spring or summer season. However, the small samples collected in autumn and winter season may have biased results for infrequent prey during these seasons. The occurrence frequency of preys items that this species took also show the distance variations. The Arcticdae, Buccindae, Cardiidae, Echinidae are more abundant in offshore and deep water areas of the North Sea, while the Nephropidae and Atelecyclidae are more abundant in inshore and shallow waters (Hayward and Ryland, 1995). These results reflected the variety of food items consumed by common wolffish in inshore and offshore areas.

In this study there were significant differences in the frequency of occurrence of prey items in small and large common wolffish. Small common wolffish took more sea urchins and brittle stars than large ones, while large common wolffish consumed gastropods and polychaetes (Aphroditidae) more than small ones. It is possible that small common wolffish lack the mouth gape or jaw force to break open the shells of gastropods, which were mostly large Buccinidae, although this does not explain the lesser utilization of polychaetes by small common wolffish. Templeman (1985) also found similar results in the Northwest Atlantic, where small common wolffish (30-59 cm) consumed sea urchins and brittle stars more than larger ones, while large common wolffish took gastropods, bivalves, polychaetes and fish more than small ones.

There was a significant difference in the frequency of empty stomachs between seasons. Feeding activities in common wolffish seem to be correlated with the reproductive cycle. The autumn/winter period is associated with spawning, followed by tooth replacement, during which food intake decreases and may stop (Keats *et al.*, 1985), particularly during the tooth exchange period of several months over which fish lose condition (Jónsson, 1982; Albikovskaya, 1983). The low proportion of empty stomachs and high Feeding Index in spring in this study can be interpreted as a vigorous feeding episode during which time body condition is recovered. The feeding intensity also was higher in the summer season as body growth and gonad development proceeded at its fastest pace.

In this study crustaceans and molluscs accounted for more than 70% of the diet of common wolffish by relative occurrence, while sea urchins were rarely eaten, although they were often abundant in ground surveys samples throughout the study area. In other areas e.g. Newfoundland, Gulf of Maine and Iceland sea urchins may form an important component of the diet of common wolffish (Albikovskaya, 1983; Keats *et al*, 1986; Jónsson, 1982; Nelson and Ross, 1992), although diet is flexible (Albikovskaya, 1983; Templeman, 1986, this study). A high dependence on sea urchins with their low energy density would require increased rates of food intake to maintain high growth rates, with associated increased costs of foraging, handling and digestion (Brett & Groves, 1979). Therefore, it is probably more beneficial for the common wolffish in the North Sea to consume the higher energy prey e.g. gastropods, crabs to maximise energy intake with least cost, allowing higher growth rate, and recovery of energy lost during reproduction and the tooth exchange period.

4.4.2 Age and growth

The relationship between weight and total length for common wolffish in this study is similar to that found in previous studies in other areas where the coefficient *b* was greater than 3.0 (Beese and Kändler, 1969; Smidt, 1981; Pavlov and Novikov, 1993). Nevertheless, the North Sea common wolffish had a relatively larger body weight at a given length compared with the above studies for other areas. Moreover, the weight-at-age of North Sea common wolffish was much greater than elsewhere. These results reflect the fact that this species grows faster and has a higher condition factor in the North Sea than in other areas. The body weight calculated from the regression equation of this study at a given length was also greater than the result of other authors' study in the North Sea (Coull *et al.*, 1989). The significant regression for the relationship between ungutted and gutted weight of North Sea common wolffish will enable estimation of the original weight for a gutted fish obtained from a fish market.

Jónsson (1982) suggested that male common wolffish have faster growth rates in terms of length and are larger than females at a given age. However, in this study while males were generally larger than females, lengths at the same age were not significantly different between the sexes. Falk-Petersen and Hansen (1991) also found similar results to these for their work on common wolffish from off northern Norway. The adult males had small testes which occupied less than 0.3 % of total body weight all year round. Adult males put much less energy into reproductive effort than adult females, and therefore, males common wolffish probably have more energy to put into somatic growth.

Common wolffish otoliths are very small compared to fish size. Otoliths size was significantly linearly related to length of individuals with a similar relationship found by Beese and Kändler (1969) and Jónsson (1982). This implies that otolith size may provide a rapid and economic method of ageing. The growth of the otolith is associated with age but apparently also related to somatic growth. However, several authors (e.g. Templeman and Squires, 1956; Reznik *et al.*, 1989; Boehlert, 1985) suggest that growth of otoliths appears to be more or less decoupled from other somatic growth rate, and is more closely related to time and age, especially in old fish. Pawson (1990) and Fletcher (1991) indicated that otolith weight might provide a more accurate estimate of age than other parameters. In the present work, the results indicated that in the otoliths of common wolffish the opaque zones (annuli) were formed during the autumn and winter seasons while the translucent zones were formed during spring and summer seasons. Although the physiological basis for the formation of zones in otoliths has not been clearly established, their presence is generally believed to be influenced by variation of growth rate, temperature, photoperiod, feeding intensity, or reproductive cycle which influence microstructural characteristics of otolith composition (Casselman, 1990; Ferreira and Russ, 1994). Mosegaard *et al.* (1988) studied the effects of temperature, fish size, and somatic growth on otolith growth rate and suggested that metabolic activity is more important than somatic growth in determining otolith growth. Therefore, if the formation of the opaque zone in this species is associated with a period of reduced metabolic rates, the temperature could be the determining factor, as the lowest value occurs in the winter season for the North Sea. Annuli in otoliths of juvenile and adult common wolffish formed in the same period, suggesting that reproduction is not a necessary determining factor. The North Sea common wolffish have larger otoliths for a given length than individuals studied in other areas. This may be explained in terms of the North Sea common wolffish growing faster than common wolffish in other places during the feeding season, and the translucent zone of otoliths of North Sea common wolffish expanding faster during the same period.

Growth of common wolffish was principally confined to spring and summer, the time when temperature, nutrients, and primary and secondary productivity are at their peak in the North Sea (Cushing, 1968). Rapid growth of this species in summer has also been reported in the Barents Sea (Barsukov, 1959), Icelandic waters (Jónsson, 1982), off Greenland (Templeman, 1985), off Newfoundland (Keats *et al.*, 1984) and in the White Sea (Pavlov and Novikov, 1993). Reduced growth rates in the autumn and winter season may reflect the reducing foraging activity and enhanced gonadal development in this period.

The main criteria for a mathematical growth curve, which is chosen to describe a physiological growth process for fishery management depends on the quality of fit and convenience (Ferreira and Russ, 1994). In the present study the results indicated that the growth of common wolffish is well described by the von Bertalanffy growth curve. The curve was fitted to individual observations. Data showed that common wolffish growth rates reduced after they reached 5 years old. This result probably reflects the effect of gonadal maturation after this age for common wolffish in the North Sea when mature fish transfer substantial amounts of energy to gonad development rather than body growth. The K value for this species in the North Sea was 0.12, which was much greater than that found in other areas, such as 0.04 in the Gulf of Maine (Nelson and Ross, 1992), 0.03 in Icelandic waters (Jónsson, personal communication), and 0.02 from combined catches off Greenland and north Norwegian waters (Beese and Kändler, 1969). This reflects the fact that North Sea common wolffish grow faster than those in other areas to reach the asymptotic length. The largest body size of common wolffish, caught in the North Sea in this study was 108 cm, close to the estimated $L\infty=114$ of the von Bertalanffy equation for this study.

Most fishing gears are size selective, and smaller sizes of fish are usually not caught during fishing activities (Ricker, 1969). Therefore, it is possible that growth curves are fitted only to truncated data, which only represents part of the population. For the common wolffish, because of fishing gear selectivity, only fish of larger than 3 or 4 years were captured by commercial bottom trawls. However, the first three or four years of life represented the period of fastest growth, after which the growth rates changed considerably. As a result, large numbers of individuals with slower growth rates were obtained, and growth curves were fitted principally to those age classes that had recruited to the fishery. The estimated von Bertalanffy growth may therefore exhibit bias caused by the effects of different age ranges, and compromise comparisons of growth rates between populations (Knight, 1968; Mulligan and Leaman, 1992). Furthermore, one effect of size-dependent mortality is the removal of fast-growing individuals (Ricker, 1969). This seems to have happened in the older age groups of North Sea common wolffish for the last three years since observed lengths were well below the predicted lengths at age. A lack of data from younger ages under these situations may cause the underestimation of K, as well as overestimation of $L\infty$ (Mulligan and Leaman, 1992).

Growth rates of common wolffish found in this study are the fastest reported (Table 4.9). At five years of age North Sea common wolffish had a mean length of 52.1 cm and were 115%, 69%, 68%, 37%, 26 % and 22% longer than those from northern Norwegian waters, Icelandic waters, the White Sea, Gulf of Maine, Greenland / Barents Sea and the Barents Sea, respectively. Lengths at age 5 for the Skagerrak, White Sea and North Sea reported by Pavlov & Novikov (1993) were 42 cm, 31 cm and 27 cm respectively. The growth rates reported for the North Sea by Pavlov and Novikov disagree strongly with ours. However, these data were reported as a personal communication, and no further information was presented. Despite attempts to solicit the precise sources of information, these have failed. Recent research has suggested the possibility of different growth rates within a population with associated different levels of fishing mortality (Rijnsdorp and Beek, 1991; Rijnsdorp and Leeuwen, 1992). The fishing mortality of the North Sea has been very high for several decades (Jennings *et al.*, 1999; Greenstreet *et al.*, 1999). Such high fishing effort has caused some fish stocks to collapse (e.g. herring, mackerel) and decreased the populations of

Table 4.9. Age and mean length (cm) of common wolffish in this study compared with other areas.

Age	This study	Icelandic waters (Jonsson, 1982)	Barents Sea (Barsukov, 1959)	Green Land + Barents Sea (Beese & Kandler, 1969)	Northern Norwegian waters (Falk-Petersen & Hansen, 1991)	Gulf of Maine (Nelson & Ross, 1992)	White Sea (Pavlov & Novikov, 1993)
1	12.9	13.6	13.6			12	
2	22.8	18	17.4			14	
3	40.6	21.9	23.5			22	
4	46.6	25.8	28.7	21.8		31	26
5	52.1	30.8	42.8	24.2		38	31
6	58.1	35.6	48.6	28.6	46	46	38
7	63.1	44.9	59.4	36.7	51	60	42
8	67.2	56.8	66.4	42.4	56	66	44
9	70.9	61.7	66.3	45.5	58	71	50
10	72.6	65.9	71.8	48.6	59	75	54
11	74.9	69.6		55.7	62	82	55
12	82.1	72.1		56.9	64	89	58
13	85.6	75.2		62.9	66	87	60
14	86.9	78.6		67.1	69	85	52
15	99	82		70	70	92	57

many major roundfish, flatfish and pelagic fish (e.g. cod, haddock, plaice, sole) in the North Sea (Serchuk *et al.*, 1996; Rijnsdorp *et al.*, 1996)). These results have also altered the North Sea ecosystem and altered growth rates of many species. The growth rates of some demersal species (e.g. sole, plaice, lesser spotted dogfish, starry ray, dab) have increased in recent years. The CPUE of common wolffish has decreased gradually over the last 20 years (Section 2.3.8) although the catch rate increased in the 1980s. It is possible that differences in North Sea growth rates for common wolffish reflect reduced competition in the fish community. Therefore, the results of selective fishing mortality are an important effect of growth variability on population dynamics, and failure to consider such effects of different growth potentials can result in overestimation of optimal fishing intensity (Parma and Deriso, 1990).

Temperature is one of the most important environmental factors that regulate the growth rates of fishes (Brett, 1979; Jobling, 1994). From aquaculture experiments Pavlov & Novikov (1993), Pavlov & Moksness (1996) and McCarthy *et al.* (1999) suggested that optimum temperature of growth for common wolffish is between 7 and 11° C. This range of temperature is typical of the North Sea study area. Moreover, the winters of the North Sea have been warmer over the last decade (Becker and Pauly, 1996). Thus, North Sea common wolffish could grow faster in the North Sea than elsewhere in their geographical range.

Levels of mortality have the potential to directly affect growth rates of fish populations. Several studies have indicated that the numbers and diversity of the main target species have decreased in the North Sea over the last 30 years (Pope and Macer, 1996; Serchuk *et al.*, 1996; Rice and Gislason, 1996; Rijnsdorp *et al.*, 1996). These effects seem to have caused an increase in the abundance of non-target species (e.g. starry ray, bib, poor cod, dab, lemon sole) (Heessen and Daan, 1996; Walker and Heessen, 1996). In addition, beam trawling has been shown to increase food availability directly by damaging benthic animals in the trawl route (de Veen, 1976; Rijnsdorp and Leeuwen, 1996). It has also been shown that the abundance of zooplankton, characteristic of secondary production has increased over the last 20 years in Northumberland waters (Frid and Huliselan, 1996). Therefore, the faster growth of North Sea common wolffish might be due to increased food availability in the region for the young and adult fish as a result of fishing or because of less interspecific food competition due to the removal of large amounts of other species.

The higher absolute metabolic scope at 10°C (Chapter 3) indicates that common wolffish have more capacity for activities such as foraging, digestion, and growth at this temperature than at 5°C. From an energy budgeting view, this could explain how common wolffish grow much faster in the North Sea than in other areas. The typical bottom water temperature from where fish were caught in the summer feeding and growing season was 8 –10°C. This range of temperature would provide common wolffish with the greatest energetic capacity for foraging and digestion. Nevertheless, this temperature range is surprisingly close to the upper thermal limit for common wolffish. Although growth of common wolffish is highest in the North Sea, the lower abundance there suggests that factors other than somatic growth influence the success of this species. Common wolffish larvae are pelagic and in 0-group gadoid surveys in the North Sea they tended to be more abundant further north, and were not recorded south of 54° N (ICES, 1993). The prevailing currents are southerly, suggesting that most spawning of common wolffish in the North Sea occurs to the north of Scotland perhaps around Shetlands (see also Chapter 6). It seems plausible that despite lower rates of somatic growth, common wolffish compete more effectively at higher latitudes.

The high growth rates of common wolffish in this study were associated with shorter life expectancy by comparison with other areas (this study, maximum age 18 years; Iceland, maximum age 24 years (Jónsson, 1982); Gulf of Maine, maximum age 22 years (Nelson and Ross, 192); northern Norway, maximum age 23 years (Falk-Petersen and Hensen, 1991). The relationship between the growth rate and maximum age could result from a limit in energy resource availability because consumed food must be used for both somatic growth and other body functions (Jensen, 1997). For older fishes, where more energy is required for body maintenance and less energy is available for growth then *K* is smaller. The phenomenon of decreased life expectancy with increased growth rate in fishes is widely established (Beverton & Holt, 1959). However, maximum ages for North Sea common wolffish may have been underestimated because other studies have shown that otoliths of the oldest individuals of fish stop increasing in length but continue to increase in thickness with age for a wide variety of long-lived fish species (Templeman and Squires, 1956; Beamish, 1979; O'Gorman *et al.*, 1997). Moreover, the strong fishing intensity in the North Sea may have removed most of the oldest individuals of this species during recent decades. Although North Sea common wolffish grow faster than in other areas such as Iceland, Greenland and the Barents Sea they are on the edge of their range in the North Sea, and are less abundant by comparison to these other areas. Increasing growth rates of North Sea common wolffish may increase their survival rate since both predation intensity and the variety of predators variety increases with increasing temperature and decreasing latitude (Rice *et al.*, 1997).

4.4.3 Reproduction

The testes of common wolffish have spermatogonia cysts, which are randomly distributed within the testicular parenchyma. This unrestricted spermatogonial type is the typical pattern of the order Peciformes (Grier *et al.*, 1980; Rae and Calvo, 1996), of which the common wolffish is a member. Generally, the germ cells mature synchronically within the cyst in teleosts (Oven, 1977; Grier, 1981). However, in different tubules or cysts, the spermatogenetic process may or may not be synchronised. The testes of this species show a homogenous feature in the maturation process of the cysts. The maturation stages are defined in terms of the abundance of the different types of germinal cells (Selman and Wallace, 1986). Synchronisation of the development of different celluar types enables us to determine the five stages of spermatogenetic process. However, the common wolffish in the North Sea produced spermatozoa over the whole annual cycle with a high peak in autumn after they reached maturation size. Therefore it is difficult to illustrate the seasonal maturation stages for this species. Falk-Petersen and Hansen (1991) also observed this for common wolffish from northern Norwegian waters.

In common wolffish females, the histological analysis and diameter of oocytes show that they undergo total maturation in the ovaries, although there is still a small number of stage 1 and stage 2 oocytes remaining. The developing batch is completely laid during the spawning season. Consequently, ovaries are filled with post-ovulatory and a few residual oocytes after spawning. The GSI seasonal variations also agree with these results. Therefore, the common wollfish is a determinate spawner that spawns an egg mass in each spawning season.

Development of ovaries in common wolffish can divided into two phases as in other species (Wallace and Selman, 1981). During the pre-vitellogenic stages, the development of ovaries is relatively slow with few cytoplasmic changes from October to March during their resting stage (Falk-Petersen and Hassen, 1991) while the vitellogenic stage is characterised by faster growth with large amounts of yolk in the cytoplasm during the summer. Beese and Kändler (1969) suggested the development of the oocytes to ripe eggs in common wolffish take 2 years. However, it was found that 76 % of females repeatedly matured and spawned again the next year in captivity (Pavlov and Moksness, 1996). In this study, an average of 49.3 % of sexually mature females appear not to develop their ovaries in a year and do not spawn in that year based on the lack of over stage 2 and later oocytes in their ovaries during 1996 to 1998. Falk-Petersen and Hansen (1991) observed a similar situation. Therefore, it appears that common wolffish develop their oocytes to a ripe stage within one year but only a proportion of individuals produce eggs in a given year.

The macroscopic criteria, which were used to stage maturity for the sampled individuals were based on external morphological characteristics of the gonads. This method is simple but may be imprecise, particularly in deciding the size at first maturity or when the individuals were sampled in the rest period of reproduction. West (1990) pointed out that histological techniques are the most powerful method to study reproduction biology in spite of being expensive and time consuming. For mature common wolffish, the testes of males contained spermatozoa all year round, and in females ripe oocytes were large and covered a wide range in diameters for each developmental stage. Thus, for common wolffish histological techniques are useful in determining the degree of development in various stages of maturation that are not discernible on a macroscopic scale.

Analysis of seasonal variations in the diameter of oocytes, the percentage of different stage in ovaries, and the gonadosomatic index indicates a spawning season for common wolffish in the North Sea from October to February. These results on spawning season of common wolffish agree with previous studies for Icelandic waters

(Jónsson, 1982). However, this period is later than in other areas. The main spawning season of this species off Newfoundland was from mid August to October with peak in September (Keats *et al.*, 1985), off Greenland was from July to October with a peak in September (Beese and Kändler, 1969), in the White Sea was from July to September with a peak in August (Barsukov, 1959; Pavlov and Novikov, 1993), and off northern Norway was mainly in September (Falk-Petersen *et al.*, 1990). North Sea common wolffish have a relatively long and late spawning season compared with common wolffish in most other areas. García-Díaz *et al.* (1997) indicated that the spawning season of the same species in different areas generally increased in length with decreasing latitude. Carillo *et al.* (1989) and Pavlov and Moksness (1994) suggested that the photoperiod is the main factor influencing the maturation time. Temperature is another important factor for common wolffish (Tveiten and Johnsen, 1999). The North Sea has a lower latitude, a photoperiod which decreases less quickly after the summer solstice and is warmer than the above mentioned areas. Therefore, the later and longer spawning season for common wolffish in the North Sea is reasonable in terms of the direction of environmental cues.

The gonad development of fish usually alternates with body growth in life history. The spawning season is often after the somatic growing season and feeding season because a large amount of energy needs to be transformed into the gonads in the late developmental stages (Nikolskii, 1965). During this late developmental stage, the gonad has priority to take the energy contained in the fish's body even though the fish may stop feeding or begin to migrate. The spawning season of the common wolffish in the North Sea was in autumn and winter while the growing season was in summer, and therefore typical of the above strategy.

There are still few observations on the early life of common wolffish in the natural environment (Falk-Petersen *et al.*, 1990; Pavlov and Moksness, 1994) since it is difficult to obtain the larvae and only 15 egg masses have been obtained in natural environment over the last 50 years (Sokolov and Shevelev, 1994). Nevertheless, artificial hatching experiments (Johannessen *et al.*, 1993) have suggested that the hatch time is at least 700- 1000 day-degrees and that larvae are pelagic for several months before settling on the bottom when their body length reaches 5 cm.

Both female and male common wolffish near the spawning stage were obtained from offshore areas where they were fished all year round. All stage 4 ovaries were collected from offshore areas where depths were over 90 m in the study area. During the spawning season, the CPUE was lower in the inshore areas compared with offshore while the fishing intensity was stronger in the inshore areas during the winter season (Chapter 2). Moreover, during the spring season the CPUE and catch number was higher in the offshore areas (Chapter 2). These results suggest that reproduction in this species may involve a short range migration. These results support the studies of Keats *et al.* (1985) and Pavlov and Novikov (1993) that the numbers of common wolffish on inshore feeding grounds during the summer was mainly related to the availability of suitable shelters and the mature fish had to migrate into deeper water layers before the spawning season because the temperatures used for feeding were unsuitable for egg development and hatching. Furthermore, this study shows that the length-frequency distribution varies as a function of depth. Larger fish occupied the deeper or offshore waters in the North Sea. Most of the fish caught close inshore (< 60 nautical mile from the Northumbrian coast) during the spawning season were immature or resting stage one fish. Therefore, there would seem to be varying habitat use by North Sea common wolffish with inshore feeding zones inhabited by immature or resting stage common wolffish and offshore zones or reproductive zones (Chapter 6) occupied by mature individuals. In the northern North Sea the currents flow from the northwest or north to the south along the coasts (MAFF, 1981). Transport of pelagic juveniles between these zones might occur by drifting with currents.

Estimates of size at maturity for common wolffish in the North Sea from this study are generally larger than ones in other areas. In northern Norwegian waters, the species reached sexual maturity after 5-7 years old and at a length of 40 cm for both sexes (Falk-Petersen and Hansen, 1991). In the White Sea, maturity was at 5-7 years old and a length of 35 cm (Pavlov and Novikov, 1993), while in Greenland waters, it was 31-46 cm for females and 42-69 cm for males (Beese and Kändler, 1969). In Icelandic waters, the smallest mature female common wolffish was 25 cm (6 years old) (Jónsson, 1982) while the smallest one in this study was 42 cm (4 years old). However, the age of first maturity for this species in the North Sea is youngest among these areas. Generally, the sexual maturation of fish is a function of body size and less importantly of age (Trippel *et al.*, 1994). Since North Sea common wolffish have the fastest known growth rates, therefore, the larger size and younger age of first maturity for common wolffish in the North Sea is reasonable. In this study, the size at first maturity of females was smaller than that for males. This result agrees with the previous study of Beese and Kändler (1969).

The sex ratio of common wolffish in the North Sea was not significantly different during the spawning season. The common wolffish shows patterns of internal fertilisation, courtship behaviour and egg guarding by males during the spawning season (Keats *et al.*, 1985; Johannessen *et al.*, 1993; Pavlov and Moksness, 1994). Moreover, the milt volume of mature male common wolffish is only 2-3 ml, which is much lower than other species (e.g. twelve times lower than Atlantic salmon, *Salmo salar*) (Pavlov *et al.*, 1997). Therefore, a sex ratio near 1:1 for this internal fertilisation species is appropriate during the spawning season.

The fecundity results from this study aggrees with previous reports from other areas (Barsukov, 1959; Jónsson, 1982; Templeman , 1986; Falk-Petersen and Hansen, 1991). The common wolffish produce large oocytes (5-6.6 mm) and the fecundity varies between several thousands in small females to 20,000 in larger females. The females in the North Sea seem to produce more eggs than in other areas since common wolffish grow faster and have a larger weight at the same length in the North Sea by comparison to other areas. The bottom temperatures of the northern part of North Sea were between 5° C - 7°C which were near the temperature of higher egg production for common wolffish that Tveiten and Johnsen (1999) suggested from their study. Tveiten and Johnsen indicated that female common wolffish had a significantly higher egg production at 8° C than those at 4° C and at 12° C. However, this inference may be biased because only five ovaries were observed during this study.

Based on bioenergetic constraints, reproductive output is a result of the trade-off between survival, reproductive effort and growth. Therefore, if most surplus energy goes into reproduction after sexual maturation, early maturation implies reduced body size and higher mortality rate (Cushing, 1968; Beverton, 1992; Jensen, 1997). Reznick *et al.* (1990) have agreed with this view from their experiments. Gunderson (1997) reviewed 28 stocks of different species and also supported this assumption. The reproductive patterns of *K*-selected species may be characterised as: maturing later in life, putting less energy into reproduction, and living longer and were expected on the basis of life history theory. To decrease larval or juvenile mortality is more important than adult mortality for these *K*-strategists (Roff, 1992). The common wolffish has low fecundity, matures later in life and has a longer life and is therefore a typical *K*-strategist. They also show patterns of internal fertilisation, larger egg, and parental care behaviour which are again characteristics of *K*-strategists. Although common wolffish exhibit low abundance in the North Sea, these reproductive strategies can increase the survival rates of juveniles to maintain a safe level of population. Moreover, the younger common wolffish not caught by commercial fisheries and lower amounts of adult common wolffish caught in offshore waters during the spawning season due to lower fishing intensity in these areas, may enhance the survival rate of the common wolffish population in the North Sea.

Chapter 5 Stock analysis of common wolffish in the North Sea

5.1 Introduction

5.1.1 The concept of population dynamics

Studies of fisheries biology can be fundamentally divided into two categories: one is the life history of cohorts of target species, while the other is the variation of abundance of target species in spatial and temporal terms. The latter area is based on information from the former study area and has been termed "population dynamics". The aim of studying population dynamics is to fulfill the need to manage plant and animal populations that either harm or enhance human welfare (Rothschild, 1986). In the context of fisheries resources, the dynamics of these fish populations is a key area requiring understanding (Cushing, 1975).

The unit for consideration in fish population dynamics is termed a "stock", which has its unique characteristics in terms of spatial use, quantity and gene pool pattern (Cushing, 1968). In the natural environment, all species tend to show the existence of a "group" structure. These groups may possess the possibility for hybridism with each other. Thus it is often difficult to distinguish them by phenotypic characteristics. In contrast, they may also display a degree of reproductive isolation caused by geographical segregation. Each group would gradually develop its unique morphological, ecological and physiological phenotype for adapting to its ambient habitat. The group that combines all individuals of a species in a specific area has been called a "population" in terms of an ecological unit and a "stock" in terms of an exploited unit (Royce, 1996). According to Royce (1996), a stock has to obey the following criteria:

1. It has its own habitat range and limit. It is isolated from other stocks.
2. Individuals of the same stock have a similar life history. The stock may display characteristic variations in abundance in response to environmental fluctuations.
3. Within the stock there is unimpeded gene flow.

The ideal stock is that of a single interbreeding population, but this condition rarely exists in the natural world. For the study of population dynamics, the stock has to be more or less defined as dogmatic. Royce (1996) described a stock as a unit capable of independent exploitation or further management and contains as much of an interbreeding unit as possible. Therefore, a fish stock is a unit of exploitation defined for practical purposes.

Population dynamics models are either simple (Schaefer, 1954; Fox, 1975) or age-dependent (Deriso, 1980; Hilborn, 1990; Walker, 1992). Simple models are derived from direct assumptions about the total biomass dynamics of a fish population that relates its present biomass directly to its previous biomass. These models assume that we cannot measure certain age-dependent characteristics of a fish population. By contrast, age-dependent models associate the present biomass of a fish population with its previous biomass through its age structure (Xiao, 1997). These models provide a more precise representation of fish population dynamics, but they require the estimation of many parameters independently.

Many studies on population dynamics have tried to estimate the abundance of a stock and to forecast its abundance in order to maximise profit from fishing, especially during periods of high abundance. Additionally, these approaches can provide information about the options for managing fisheries. The first aim is normally to assess the abundance of the stock and to examine the responses of the fish population to natural and artificial manipulation. Stock assessment frequently involves the use of many statistical and mathematical calculations to examine the quantitative variation of fish populations and their responses to alternative management strategies. This assessment is examined in considerable detail and information on stock such as age structure, sex ratio, survival rate, mortality, growth, distribution and feeding behaviour are relevant.

There are many subtleties in the use of population dynamics models in fish stock assessment and management. However, all of the population dynamics models are derived from the following two concepts:

1. The logistic equation which was developed to describe the changes in number of an organism's population (Pearl, 1930):

   $$dN / dt = rN(1 - N / k)$$

where N is the number in the population; r is the instantaneous rate of increase and k is the carrying capacity of the environment. The population of organisms increases with time and approaches an asymptote as environmental pressure increases.

2. The production equation formulated by Russell (1931) which is:

$$P_2 = P_1 + (R + G) - (F + M)$$

where P_1 is the stock in the initial year and P_2 is that in the second year; R is the annual increment in recruitment; G is the annual increment in growth; F is the annual sum of deaths due to fishing pressure and M is the annual sum of deaths due to natural causes.

There are a number of more complicated stock assessment models, which have been developed in the last few decades. Gulland (1983), Rothschild (1986), and Hilborn and Walters (1992) provided detailed elaboration of these complex techniques. This chapter examines the use of some models to estimate the abundance of common wolffish in the North Sea.

5.1.2 Virtual population analysis (VPA)

The sum of catch numbers for each specific year class after recruiting to the fishery is called the virtual population. A development of the catch equation to estimate a virtual population or sum of catches throughout the life of a year class is called virtual population analysis.

Virtual population analysis calculates the number of fish alive in each year class for each past year. It uses the numbers of fish caught by commercial fishing to estimate pervious fishing mortality and stock numbers in a cohort of fish. It is also called cohort analysis because each cohort is analysed separately. This method avoids considering the problems related to recruitment estimation. It relies on a simple relationship for each cohort that is (Hilborn and Walters, 1992) the:

(number alive at beginning of this year) = (number alive at beginning of next year) + (catch this year) + (natural deaths this year).

If we know the number of fish at the oldest age (or that at some age there are none surviving) and we know the natural mortality, then we can use the above equation to calculate the number alive each year, beginning from the oldest age and moving backward to the youngest ages. This is the basic concept of VPA. In VPA, both the fishing and natural mortality must be considered carefully because they can cause bias in the estimated abundance of a cohort.

Virtual population analysis has successfully been applied to a wide number of species and geographic areas. It has been used to estimate the cohorts of sole (*Solea solea*) in the northeast Atlantic (Rijnsdorp *et al.*, 1992), cod in Newfoundland (Deyoung and Rose, 1993) and in Iceland (Thorarinsson and Johannesson, 1997), Pacific sardine (*Sardinops sagax*) in California (Jacobson and MacCall, 1995), black sea bass (*Centropristis triata*) in the southeastern U.S. (Vaughan *et al.*, 1995), king mackerel (*Scomberomorus cavalla*) in Mexico (Arreguinsanchez *et al.*, 1995), European hake (*Merluccius merluccius*) in the northwestern Mediterranean (Aldebert and Recasens, 1996) and gadoids in the North Sea (Patterson, 1998).

In the last few decades there has been increased interest in incorporating factors such as predator-prey interactions and effects of physical environment on stock dynamics assessment. For the North Sea, multi-species VPA has become an important tool for stock assessment and management advice (Rice and Gislason, 1996). It has been used both for predator and prey fish stocks to estimate the age-specific mortality rate of predation on each prey species for each predator. The common wolffish is a top predator in the North Sea but preys little on fish species. Therefore, single species VPA is appropriate. There have been no assessments of abundance of the common wolffish reported for the North Sea. Such assessments of common wolffish biomass would aid stock management and assist in the description of the North Sea ecosystem.

5.1.3 Yield per recruit

From the end of the last century, fishermen have asked fisheries scientists to provide an explanation of why their catches fluctuated, and especially, declined (Smith, 1994). These events encouraged several groups of scientists to begin a series of studies on population dynamics concentrating on questions such as: Why do fish populations fluctuate every year? What are the factors that influence recruitment? (Hjort, 1926). These researchers tried to establish models reflecting the factors influencing the survival of fish larvae in their early life (Pauly, 1994). However, the recruitment is very variable in most fish stocks (Cushing, 1975). It is very difficult to estimate precisely the annual recruitment of larvae into the stock. Therefore, modern developed models largely avoid the recruitment problem by dealing with a historical decline in catch rate in fisheries. After 1950 some scientists developed a number of useful models for such purposes. Beverton and Holt (1957) established a well known method, yield-per-recruit analysis, which offered a solution for making acceptable decisions even in the near absence of information on the variation of fish populations.

Beverton and Holt's model was developed fully from the Russell equation. This model was based upon the growth, age at first capture, and fishing mortality. It was assumed that mesh size selection by a trawl is knife-edged. Therefore, in theory all fish below a certain length are able to escape through the mesh of the net, while all fish above that length are assumed to be caught. That is, natural mortality is assumed to be a constant after the age at recruitment, and fishing mortality is constant after the age at first capture. This model also assumed that fish stock was in a steady state. That is, the total yield in any one year from all year classes is the same as that from a cohort over its whole life span (King, 1995). This equation was obtained by integrating the rate of change of weight of catch in time from recruitment to extinction for any year class. The yield per recruit is dependent on the amount of fishing mortality and changes in recruitment are ignored in this model.

With a lack of accurate catch and fishing effort data from commercial fisheries, it is difficult to estimate whether long-term fluctuations in catch represent changes in the population abundance or reflect historic changes in exploitation. There have been increasing concerns that declining landings may be related to the larger numbers of juvenile fish killed as by catch in trawl fishery (Barbieri *et al.*, 1997). Therefore, it is necessary to establish a minimum mesh size to ensure a reasonable amount of recruitment and to maximise the yield-per-recruit. The yield-per-recruit model could be a useful tool in defining fisheries management measures such as mesh size, closed season, etc. (Beverton and Holt, 1957; Ricker, 1975). There is a further advantage with this model. If we are able to obtain the values of yield or yield-per-recruit by this model under conditions of different fishing mortality and age at first recruitment, we could connect these values to plot an isopleth diagram. This approach can provide information for us to modify fishing effort and mesh sizes to gain maximum catches. This approach has been widely used in the management of the plaice, haddock and some other demersal fishes in the North Sea (Cushing, 1975).

5.1.4 Demographic analysis

Population changes can be described by a set of quantitative methods initially developed for human population analysis (Krebs, 1994). These methods were called demographic analysis, and are based on the Leslie matrix with the assumption of stable age-structure. The intrinsic rate of natural increase for any organism relies on its age-specific survival rate and its corresponding fecundity. These relationships can be drawn more clearly in a table, and this is called a life table. A life table is a powerful summary of age-specific mortality rates in a population, which can be used to show informative data such as survival rate (Gregory, 1997). Life tables are helpful, for example, when the mortality rate of fish is not equal for all ages, and often juveniles suffer high mortality.

Population dynamics are not only influenced by age-specific survival rate but also by growth rate and reproductive value. A fecundity table that summarises reproduction with respect to age can describe the reproductive value of population variation. Thus, combining the age-specific birthrate and the resulting life table, we can calculate the net reproductive rate, R_0. This is the average number of female offspring produced by an average female individual during its lifespan. The value is widely used as an index of the rate of change of a population size. It is a measure of potential growth of a population for given age-specific birth and death rates. Therefore, the intrinsic capacity for the increase of a population is determined by incorporating the life table with the fecundity table for particular environmental conditions. This is the basic concept for demographic analysis.

Krebs (1994) illuminated the principle of demographic analysis clearly as follows:
A population that is subject to a constant schedule of birth and death rates will:

(1) increase in numbers geometrically at a rate equal to the capacity for increase.
(2) assume a stable age distribution.
(3) maintain this age distribution.

The demographic approach has been used for a number of animal populations (e.g. Frazer *et al.*, 1991; Inverson, 1991; Woodley and Read, 1991). In fish, studies have included taxa such as brook trout (*Salvelinus fontinalis*) (McFadden *et al.*, 1967) and sharks (Hoenig and Gruber, 1990; Cailliet, 1992; Cortes, 1995; Cortes and Parsons, 1996). Although, demographic analysis is a useful tool to examine the increase of a population, it can only reflect the intrinsic rate of increase and generation time of a specific stock. It is difficult to compare the R_0 or generation time between different stocks or species.

5.1.5 Aims

The aim of this section was to analyse the state of the North Sea common wolffish stock in relation to fishing effort and demographic characteristics. In order to assess the stock abundance of the common wolffish in the North Sea, VPA and yield-per-recruit models were used. Most models need long term data such as landing data, fishing effort, age structure, and recruitment to estimate the abundance precisely. Although there are landings data of common wolffish during back more than 20 years, there is still a lack of fishing effort data due to this species mainly being a by catch in the North Sea. Thus, the VPA model is an appropriate method for the estimation of the abundance of common wolffish in the North Sea given the few years of data available. The yield-pre-recruit model was examined to show the present condition of common wolffish catches and suggest appropriate management conditions. Finally, the results of demography analysis under several scenarios were used to examine the increase or decrease of the common wolffish stock in response to environment and fishing factors.

5.2 Materials and Methods

5.2.1 Fish data

The data of total length (TL) of common wolffish were obtained monthly from the commercial fish market in North Shields for 1996 to 1998. All fish were caught by commercial boats. A total of 2,676 common wolffish were measured, of which 920 were examined in 1996, 1,492 were examined in 1997 and 264 were examined in

1998. The TL of common wolffish was measured in cm length classes. The length distribution of catches common wolffish was displayed in Fig. 2.14. The areas of capture were displayed in Fig. 2.2 and cover 80% of the area inhabited by common wolffish in the North Sea. Therefore, data should be representative of total catches.

5.2.2 Statistical analysis of catch data

The catch data of common wolffish for whole of the North Sea was obtained from the ICES database. The UK landings data of North Sea common wolffish were calculated from Sea Fisheries Statistics books published by MAFF. The amounts of common wolffish landed in North Shields, fishing hours, fishing areas, and the power of fishing boats were collected from the MAFF Fisheries Office, North Shields. The CPUE of common wolffish in the North Sea by North Shields fishing boats has been calculated and standardised, and shown in Chapter 2.

5.2.3 Age composition and growth coefficient parameters

The age composition of catches of common wolffish was shown in Fig. 4.13. The parameters of the von Bertalanffy growth equation were calculated using the results from chapter 4.

5.2.4 Estimation of the catches of common wolffish by number

Using the collected fishing data including lengths, numbers and weights of common wolffish landed in North Shields, mean weight of individual landed common wolffish could be calculated from the relationship between length and gutted weight (Chapter 4) each year for 1996 to 1998.

Catch at age j as number of common wolffish for year i ($C_{i,j}$) was obtained from catch in number of year i (Y_i/W_i) multiplied by proportion of each age class ($P_{i,j}$) which was estimated from the age composition of each year's landing data as follows:

$$C_{i,j} = (Y_i / W_i) \times P_{i,j}$$

where Y_i = catch of the wolffish in year i, and W_i = mean weight of the common common wolffish in year i.

5.2.5 Mortality rate

Total mortality rate (Z) for each year was calculated from Ricker's (1975) curve as the following:

$$\ln(U) = \alpha - Zx$$

where U = age-specific CPUE, which was obtained from the total CPUE multiplied by the proportion of each age class, and α is a constant obtained from the regression of $\ln(U)$ and x is age.

Instantaneous natural mortality (M) was estimated from Pauly's (1980) equation as follows:

$$\log M = -0.0066 - 0.279\log L_\infty + 0.6543\log K + 0.4634\log T$$

where L_∞ = asymptotic length, K = coefficient of growth, and T = mean temperature of the environment where this species is caught. For common wolffish the mean temperature of the North Sea was obtained from ground survey measurements made by ICES and CEFAS and was 8°C for the whole year during 1996 to 1998. Instantaneous fishing mortality (F) can be obtained from

$$F = Z - M$$

5.2.6 The VPA equations

The concept of VPA was based on Beverton and Holt's (1957) catch curve and was developed by Gulland (1965) as follows:

The basic assumption is that the survival of the cohort during a year is:

$$dN / dt = -N(F + M) \qquad (1)$$

where N = abundance

For the number surviving in the year this can be described as

$$N_{(i+1,j+1)} = N_{(i,j)} \times e^{-(F_{(i,j)}+M)} \qquad (2)$$

Fishing mortality can be calculated from

$$F_{(i,j)} = -\ln\left(\frac{N_{(i+1,j+1)}}{N_{(i,j)}}\right) - M \qquad (3)$$

Age-specific catch for year *i* can be expressed as

$$C_{(i,j)} = \frac{F_{(i,j)}}{F_{(i,j)} + M} \times (N_{(i,j)} - N_{(i+1,j+1)}) \tag{4}$$

where M = natural mortality, $F_{(i,j)}$ = fishing mortality for year *i* and age *j*, $N_{(i,j)}$ = abundance of age *j* in the beginning of year *i*, $C_{(i,j)}$ = catch in number for year *i* and age *j*.

Abundance of age *j* in the beginning of year *i* ($N_{(i,j)}$) can be calculated from the iterations of Newton's method with an assumption

$$X_{new} = X_{old} - \frac{f(x)}{f'(x)} \tag{5}$$

where X_{new} = a new $N_{(i,j)}$ estimated from (5), X_{old} = an old $N_{(i,j)}$ estimated from (3). Substituting (4) in (3) then

$$C_{(i,j)} = \left[1 - \frac{M}{\ln(N_{(i,j)}) - \ln(N_{(i+1,j+1)})}\right](N_{(i,j)} - N_{(i+1,j+1)}) \tag{6}$$

$$f'(x) = -1 - \frac{(\ln(N_{(i,i)}) - \ln(N_{(i+1,i+1)}))M - \frac{N_{(i,i)} - N_{(i+1,i+1)}}{N_{(i,i)}} M}{(\ln(N_{(i,i)} - \ln(N_{(i+1,i+1)}))^2} \tag{7}$$

where $f'(x)$ = derivative of $f(x)$.

The BASIC program of Gulland's VPA written by Hilborn and Walters (1992) was modified to estimate the year class abundance of common wolffish and fishing mortality for 1996-1998 (Appendix I). The mean natural mortality rate was obtained from the average of each year M from 1996 to 1998. The fishing mortality for the oldest age class of 1996-1998 and year-class abundance and fishing mortality in 1998 estimated by Pope's (1972) approximating method were used as parameters for VPA.

5.2.7 Yield per recruit equations

The Beverton and Holt (1957) model assumes that the stock is a steady state structure. The total yield in any one year from all age classes is the same as that from a single stock over its whole life span. The yield (in weight) of a single year class of fish at first capture (t_c) to maximum age (t_{max}) is an integral function of the fishing mortality (F), the abundance of fish present (*N*) and the mean weight of fish (*W*). The equation is as follows:

$$Y = \int_{t_c}^{t_{\max}} F_t N_t W_t \, dt \qquad (8)$$

The number of number of fish surviving, *N*, at any age (*t*) can be written as follows:

$$N_t = N_{tc} \exp[-(M+F)(t-t_c)] = R \ \exp[1 - M(t_c - t_r) - (M+F)(t-t_c)] \qquad (9)$$

where R = recruitment, t_r = the age of recruitment.

The fraction of the number of surviving recruits at age t is as follow:

$$N_t / R = \exp[-M(t_c - t_r) - (M + F)(t - t_c)] \qquad (10)$$

The von Bertalanffy growth equation in terms of weight can be modified as follow:

$$W_t = W_\infty \sum_{n=0}^{3} U_n (1 - \exp[-nK(t - t_0)] \qquad (11)$$

where $U_0 = 1$, $U_1 = -3$, $U_2 = 3$, $U_3 = -1$.

Substituting the above (11) into equation (8), then by integration, the yield per recruit can be expressed as follows:

$$Y/R = \{FW_\infty \exp[-M(t_c - t_r)]\} \sum_{n=0}^{3} \{U_n \exp[-nK(t_c - t_0)]/(Z + nK)\}$$
$$\{1 - \exp[-(Z + nK)(t_{\max} - t_c)]\} \qquad (12)$$

The maximum possible yield for a given year class usually occurs at the critical age t_{crit}, the age at which abundance of a stock is maximum in the absence of fishing. For comparison with the Beverton & Holt modelling results, t_{crit} was estimated for North Sea common wolffish following Deriso (1987), and Barbieri *et al.* (1997) as

$$t_{critic} = t_0 + \frac{1}{K} \ln(3K/M + 1)$$

where t_0, K and M are defined as in this chapter.

To estimate the proportion of the potential growth span (*P*) remaining when common enter the exploited phase of life (Beverton and Holt, 1957), we used Beverton's (1963) quantity equation:

$$P = (1 - l_c / l_\infty)$$

where l_c is the mean length at first capture, and l_∞ is the asymptotic length.

Parameter values used in the model are $K = 0.1\text{-}0.2$, $W_\infty = 13{,}800$ g (asymptotic weight), $t_0 = -0.56$, $t_r = 2$ yr (age at first recruit), $t_c = 2\text{-}5$ yr (age at first catch), $M = 0.1\text{-}0.4$ and $F = 0.1\text{-}2.0$. The calculations were with a computer program, which was written in BASIC language (Appendix II).

4.2.8 Demographic analysis equations

The life history parameters of North Sea common wolffish were considered from the best biological information possible. Age at maturity (L_{50}) for female common wolffish was estimated to be 5 years and the maximum age of caught common wolffish was estimated to be 15 years. The sex ratio of eggs was estimated to be 1:1 from our catch data. The age-specific fecundity of female common wolffish was estimated from the relationship between the number of ripe eggs and weight reported by Pavlov and Moksness (1996) to which the results in Chapter 4 were similar. The age-specific fecundity was further divided by two in the analysis because egg development data from this study (Chapter 4) showed that only a proportion (50.7 %) of females may produce eggs each year.

The survival rate of common wolffish between age 0-1 was assumed to be 3 ‰, this value being appropriate for demersal fish in the North Sea (Cushing, 1975). The natural mortality (M) from age 1 to age 15 was fixed at the same value, which was obtained from Pauly's equation (section 5.2.4). Therefore the survival rate (S) for age 1 to age 15 was e^{-M}.

Demographic parameters were calculated following Krebs (1985): net reproductive value per generation, $R_0 = \Sigma(1/2)m_x l_x$, generation length in years $G = \Sigma(1/2)x m_x l_x / R_0$, intrinsic rate of increase $r = (\ln R_0)/G$, population increase rate $\lambda = e^r$ where l_x is the probability at birth of being alive at age x, and m_x is the number of female eggs produced per year by a female at age x.

The first scenario considered that common wolffish died only due to natural causes, i.e. no fishing mortality. Therefore, this scenario could be seen as to obtain the natural net reproductive value. In the second scenario, the effect of fishing mortality rate on the demography of common wolffish was examined with varied values of F as a survivorship function. Fishing mortality of 0.1-0.6 and age at first-capture of common wolffish from age 3 was used in this scenario. The third scenario was to fix the fishing mortality at the present value 0.3, then change the age at first capture from 2 to 5 years old as a function. Proportion of survivors at an age was calculated from $l_x = N_0 e^{-(F+M)x}$, where N_0, and the initial population was set to 1 in all scenarios.

5.3 Results

5.3.1 Cohort analysis

5.3.1.1 Age composition

The length-frequency histograms for 1996 to 1998 were displayed in Section 2.3.8. The seven age classes 4+ to age 10+ were dominant in each year. They represent near normal distribution shapes over 1996 to 1998.

The relationship between common wolffish gutted weight and total length was expressed as $W = 0.005L^{3.12}$ for both sexes combined. Mean guttedweight of the individual common wolffish for each year was calculated from the regression of the relationship between weight and total length as 2.10, 2.85 and 1.87 kg for 1996-1998, respectively. Catch in number was then obtained from total catch divided by mean gutted weight. The peak of catch in number was in 1998 (534,759) and lowest value in 1997 (378,245) (Table 5.1)

5.3.1.2 Mortality rates

The total mortality (Z) was estimated from the Ricker (1975) catch curve (Fig. 5.1). The Z values for 1996 to 1998 were 0.47/yr, 0.48/yr and 0.44/yr respectively. Since the values of growth parameters were not significantly different, natural mortality (M) estimated from Pauly's (1980) equation was similar and for 1996 to 1998, were 0.16/yr, 0.18/yr and 0.16/y respectively. Fishing mortality (F) varied in a similar way and for 1996 to 1998, were 0.31/yr, 0.30/yr and 0.28/yr respectively.

Table 5.1 Estimated catch and proportion at age for common wolffish in the North Sea (1996-1998).

Year	1996		1997		1998	
Mean weight (kg)	2.1		2.85		1.87	
Catch (tonnes)	1,044		1,078		1,000	
Catch in number	497,143		378,245		534,759	
Age	%	Catch	%	Catch	%	Catch
3	10.13	50,361	12.64	47,810	9.17	49,037
4	18.95	94,209	20.93	79,617	21.67	115,882
5	25.33	125,926	19.79	74,855	13.89	74,278
6	18.20	90,480	20.57	77,805	16.39	87,647
7	9.01	44,793	11.21	42,401	11.94	63,850
8	9.01	44,793	7.71	29,163	13.89	74,278
9	4.88	24,261	3.21	12,142	5.00	26,738
10	1.50	7,457	1.21	4,577	5.28	28,235
11	1.13	5,618	1.36	5,144	1.11	5,936
12	0.56	2,784	0.43	1,626	0.56	2,995
13	0.38	18,89	0.43	1,626	0.28	1,497
14	0.56	2,784	0.21	794	0.28	1,497
15	0.38	1,889	0.29	1,097	0.56	2,995

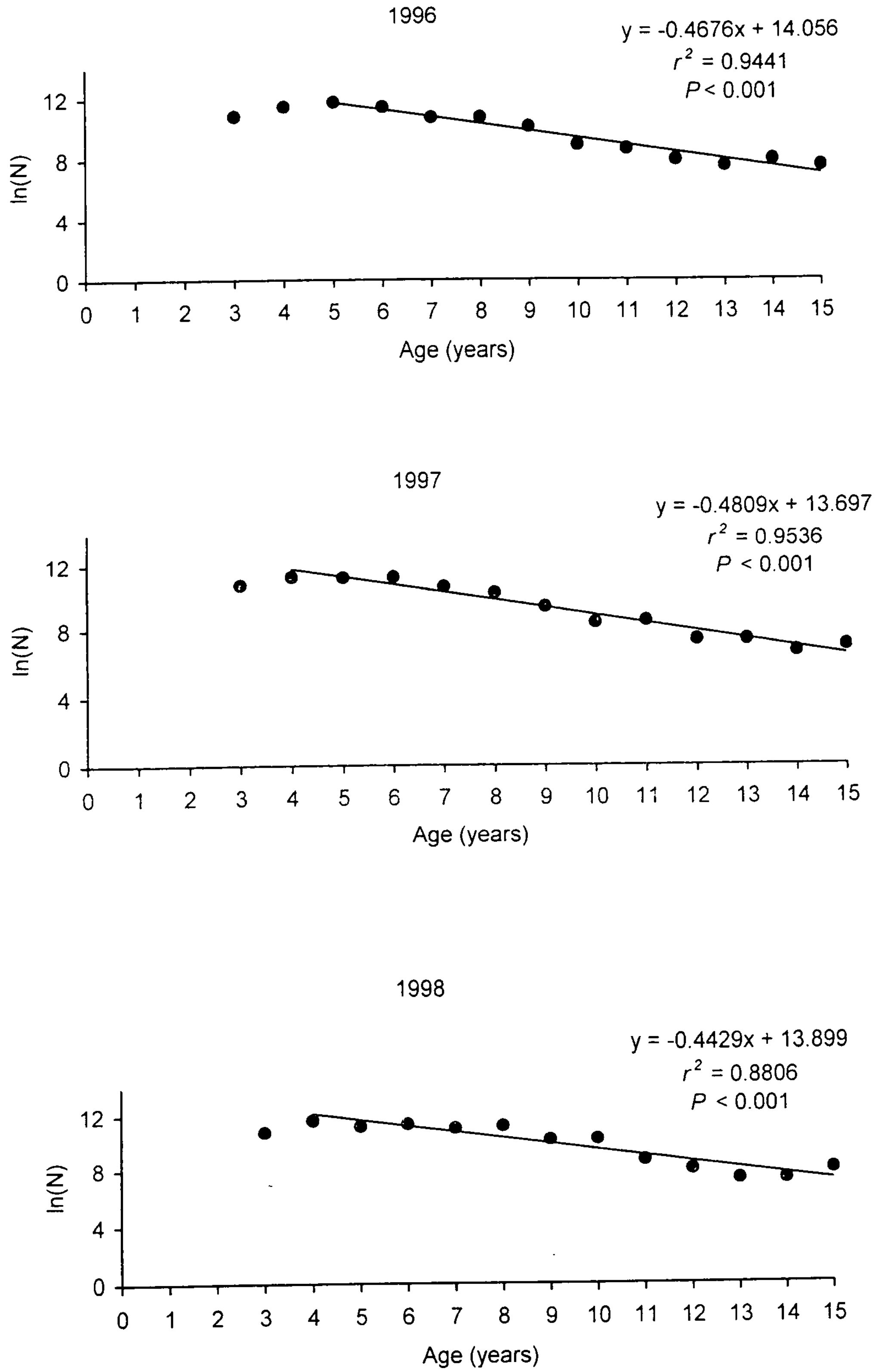


Fig. 5.1 Relationship between natural logarithm of the number of catch and age for common wolffish between 1996-1998.

5.3.1.3 Age-specific abundance and fishing mortality

The mean *M* value (0.17) for three years obtained from the above method was used for the VPA program to calculate the age-specific abundance. Estimated age-specific abundance is shown in Table 5.2. Age 1 and age 2 North Sea common wolffish are not caught commercially and are therefore not included in Table 5.2. The total abundance (age 3+ to 15+) of common wolffish increased from 1996 to 1998 (Table 5.2) from 3,822,436 to 4,035,184 in number. The age-specific abundance, which was estimated from VPA, showed that the abundance of age 3 year-class was highest in 1997 and the recruitment of age 3 in 1996 was the lowest (Table 5.2). Examination of age-specific abundance of the 1982-1993 year-classes indicated that the abundance of the stock decreased with increasing age for each year-class (Fig. 5.2). In 1997, the abundance of the 1987 year-class (age 9 to 10) decreased by 40.4 % from the previous year and the abundance of the 1982 year class (age 14 to 15) decreased by 45% as the two highest decreases in abundance (Fig. 5.2, Table 5.2). The abundance of 1991 year class decreased by 30.6 % (age 6 to 7) and that of 1989 year class decreased by 30.9 % (age 8 to 9), were the two lowest decreases in abundance of year classes.

Fishing mortality of 3+ common wolffish varied slightly and peaked in 1997. Common wolffish of age 6+ - 10+ endured higher fishing mortality in 1996-1998 with the age 8+ fish tolerating the highest average fishing mortality of 0.32 (Table 5.3). This result mirrored the higher proportion of these ages in total catches.

5.3.2 Yield per recruit

5.3.2.1 *M*, *K* and t_c simulation in Y/R model

Yield per recruit curves for the common wolffish in the North Sea based on population parameters are shown in Fig. 5.3. These curves provide several situations with different fishing mortalities, and provide a way of deriving the fishing effort which gives maximum yield from the stock. Fig. 5.3a indicates that independent of the level of *K* used in the model, yield per recruit values were consistently higher at $K = 0.15$ and decreased continuously with decreasing *K*. The value of Y/R at $K = 0.15$ is about 6 times compared with that at $K = 0.05$. This suggests that a high fishing effort is required to maximise yield. Fig 5.3b shows that increasing *M* will decrease the values of Y/R sharply. The value of Y/R will decrease by 56 % when *M* increases from 0.1 to

Table 5.2 Estimated abundance of common wolffish in the North Sea by year and age from VPA.

Year	Age													Total
	3	4	5	6	7	8	9	10	11	12	13	14	15	
1996	1,081,586	884,781	705,672	466,886	257,419	174,309	89,556	55,536	39,097	29,411	21,784	8,503	7,806	3,822,346
1997	1,116,980	865,440	659,480	479,642	310,815	176,008	106,029	53,343	39,985	27,813	22,239	16,631	4,625	3,879,030
1998	1,114,871	897,606	656,929	487,315	333,106	223,171	121,678	78,251	40,768	28,994	21,952	17,254	13,289	4,035,184
Total	3,313,437	2,647,827	2,022,081	1,433,843	901340	573,488	317,263	187,130	119,850	86,218	65,975	42,388	25,720	11,736,560

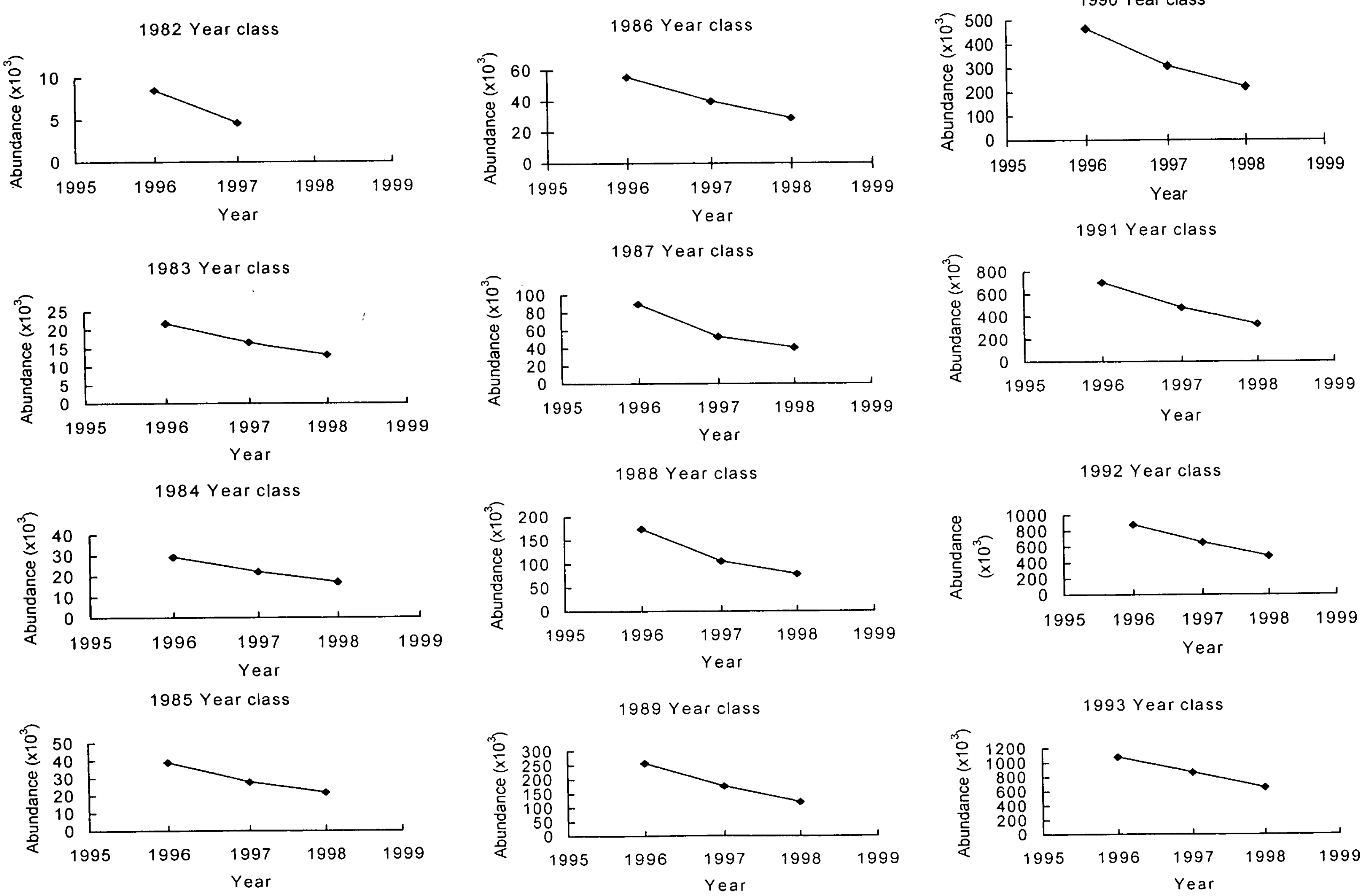


Fig. 5.2 Estimated abundance in number of each year class of common wolffish in the North Sea from 1982 to 1993 for 1996-1998.

Table 5.3. Estimated catchability coefficient and fishing mortality of common wolffish in the North Sea by year and age from VPA.

Year	Age 3	4	5	6	7	8	9	10	11	12	13	14	15	Average
	Catchability coefficient (q)													
1996	0.000013	0.000030	0.000052	0.000057	0.000050	0.000078	0.000083	0.000038	0.000041	0.000026	0.000024	0.000105	0.000073	0.000047
1997	0.000015	0.000033	0.000041	0.000060	0.000050	0.000062	0.000041	0.000031	0.000047	0.000021	0.000026	0.000017	0.000093	0.000017
1998	0.000031	0.000094	0.000082	0.000136	0.000146	0.000279	0.000170	0.000309	0.000108	0.000744	0.000048	0.000062	0.000175	0.000183
Average	0.000019	0.000052	0.000058	0.000084	0.000082	0.000140	0.000098	0.000126	0.000065	0.000264	0.000033	0.000061	0.000113	0.000082
	Instantaneous fishing mortality rate (F)													
1996	0.05	0.12	0.22	0.24	0.21	0.33	0.35	0.16	0.17	0.11	0.10	0.44	0.30	0.21
1997	0.05	0.10	0.13	0.19	0.16	0.20	0.13	0.10	0.15	0.07	0.08	0.05	0.30	0.13
1998	0.05	0.15	0.13	0.22	0.23	0.45	0.27	0.49	0.17	0.12	0.08	0.10	0.28	0.21
Average	0.05	0.13	0.16	0.22	0.20	0.32	0.25	0.25	0.16	0.10	0.09	0.20	0.29	0.19

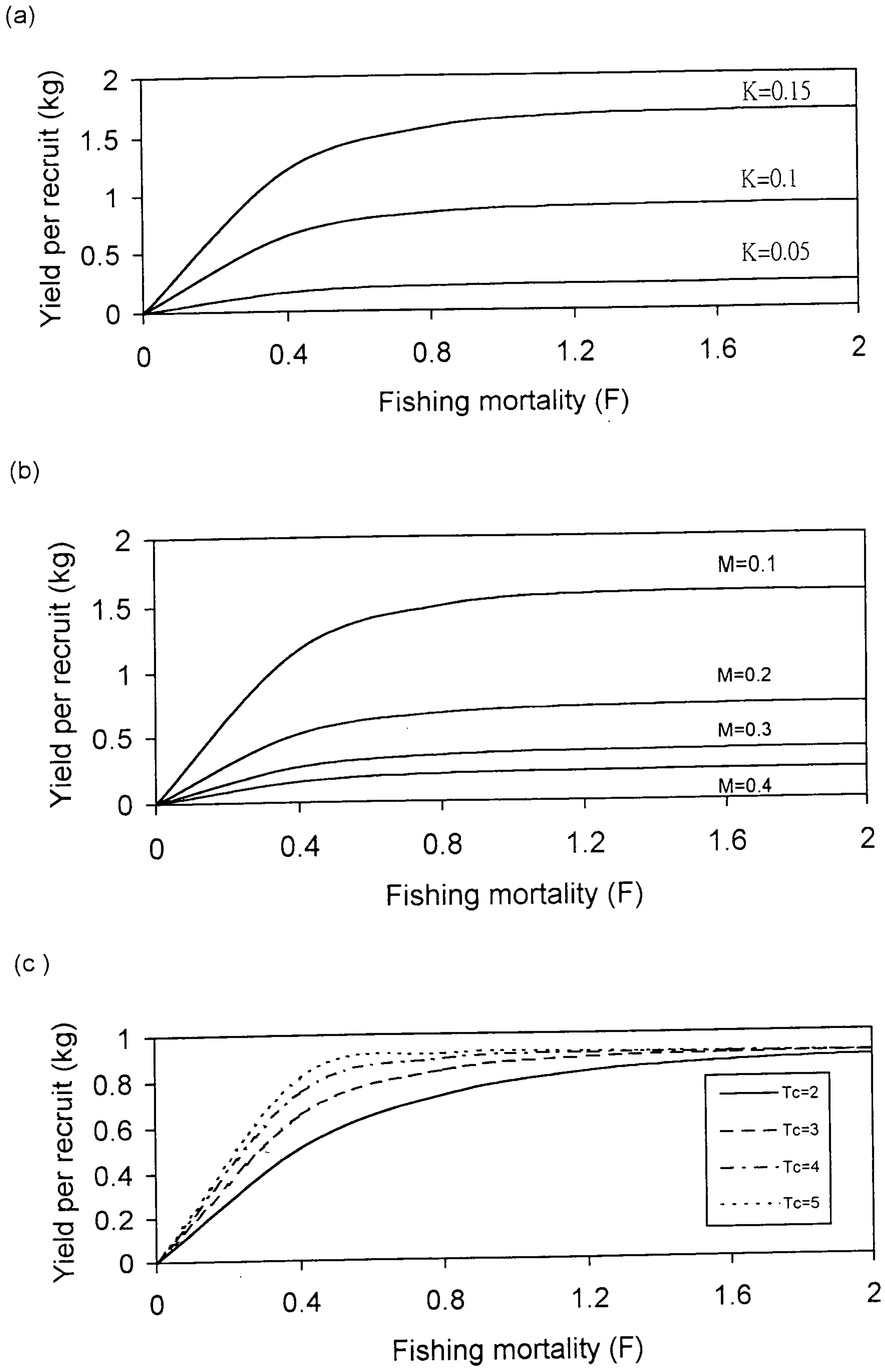


Fig. 5.3. Curves of yield-per-recruit on fishing mortality (*F*) for common wolffish in the North Sea for different: (a) growth rates, K=0.05 to 0.15; (b) mortality rates, M=0.1 to 0.4; and (c) ages at first capture, Tc=2 to 5.

0.2 for $F = 0.3$. This suggests that a fish stock with a high natural mortality will require more fishing effort to achieve a maximum yield than one with a small natural mortality. Fig. 5.3c shows that the yield of the common wolffish in the North Sea can be maximised by increasing the current level of $t_c = 3$ to $t_c = 5$ and will be decreased about 8 % when the t_c is 2 and when $F = 0.3$.

For all levels of K, M and t_c, yield curves increased rapidly in the range of fishing mortality between 0 and 0.5, then the curves were relatively flat thereafter. Although the yield per recruit values always increased with increasing fishing mortality, increases in yield beyond F = 0.5-0.6 were very small. This suggests that fishing mortality lower than 0.6 will give the best marginal yield for the common wolffish in the North Sea.

The values of t_{crit} estimated with different values of M were high for the common wolffish in the North Sea. The values of t_{crit} were 9.6, 8.0 and 6.9 for M equal to 0.15, 0.2 and 0.25, respectively. These values suggest that the maximum theoretical stock biomass without fishing mortality would be gained before the common wolffish reach age 9 for a range of M considered to be appropriate.

The estimated values of P for common wolffish in the North Sea were also relatively high. For the current estimated level of $t_c = 3$, the P value is 0.66. This value suggests that 66 % of its potential growth still remains when the common wolffish enters the exploitation phase at age 3.

5.3.2.2 The isopleth diagram of yield for common wolffish in the North Sea

Yield per recruit is a function of fishing mortality and the first age at entry to the exploited phase. Using the computer, it is easy to simulate the outcomes of yield with variable fishing effort and using different ages at first capture. Using these data a yield isopleth diagram was created for common wolffish in the North Sea (Fig. 5.4). The point T_p ($F = 0.30$, $t_c = 3$) represents the yield at the present level of exploitation for North Sea common wolffish and is about 500 g per recruit. A maximum value of yield is reached at a certain value of fishing mortality (F_{max}) or of age at first capture ($(t_c)_{max}$). Sections parallel to the F-axis (x-axis) at different levels of t_c indicate that

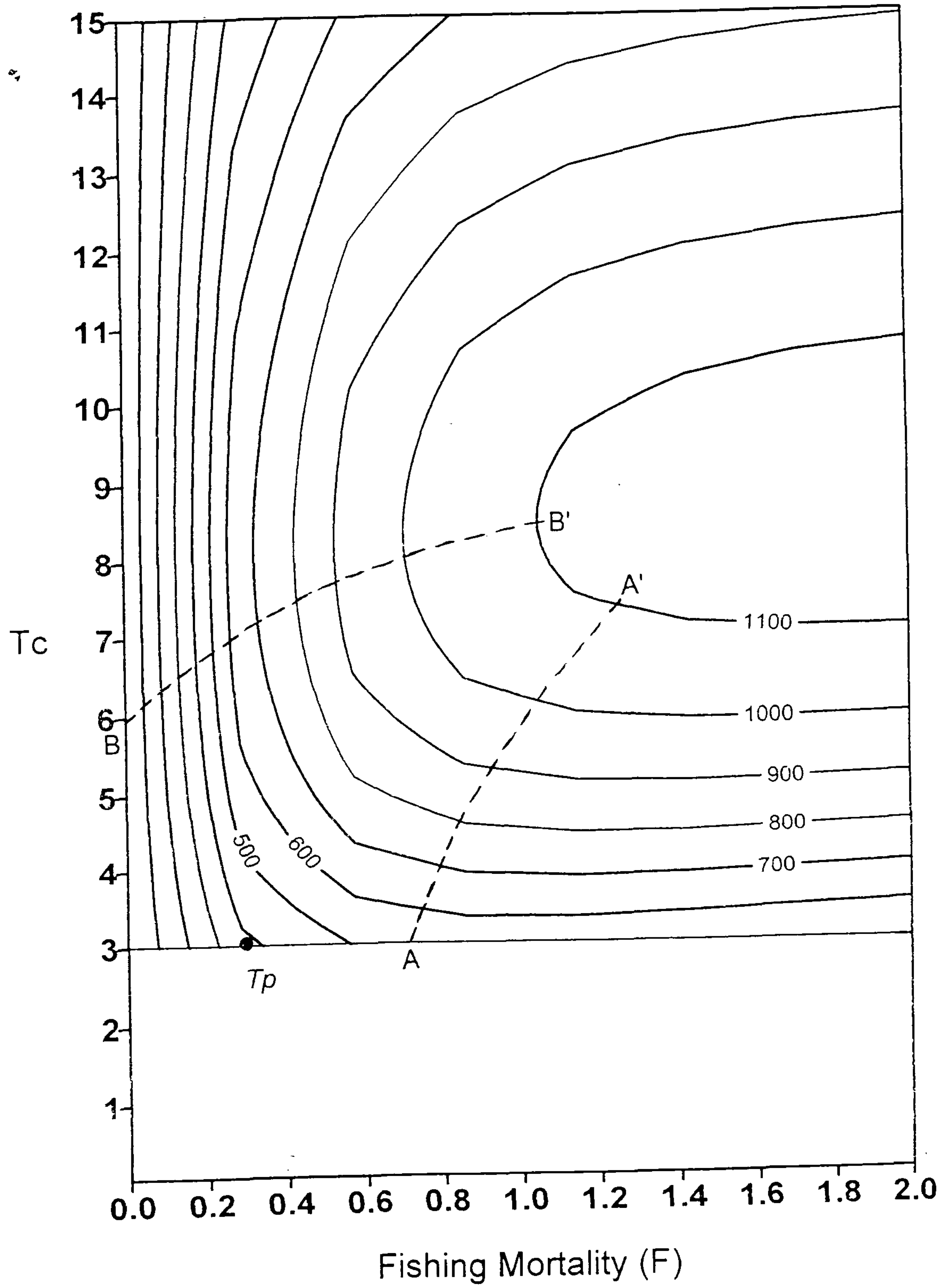


Fig. 5.4. Yield isopleth diagram showing average yield per recruit for any combination of fishing mortality (*F*) and age at entry (*Tc*) for common wolffish in the North Sea. Contours are of yield per recruit at intervals of 100 g. The line AA′ joins the locus of the horizontal tangents to the yield curves and represents the yields at those different minimum ages of first capture. The line BB′ joins the locus of the vertical tangents to the yield curves and represents the best yields generated by using the minimum fishing mortality. The point *Tp* indicates the present values of *F* and *Tc*.

F_{max} increases with increasing t_c. The change of F_{max} with various levels of t_c is shown by the dotted line A-A'. In the yield isopleth diagram, the line A-A' connects the locus of the horizontal tangents to the yield curves. For fisheries, the mesh size could be considered as the determining factor of age at first capture of recruit. Therefore, the point at which the line A-A' cuts each of the yield curves represents the minimum mesh size that can be allowed in a fishery for achieving that yield.

By contrast, sections parallel to the *Tc*-axis at various levels of F show that the value of $(t_c)_{max}$ increases with increasing F. The course of this increase is represented by the dotted line B-B'. The line B-B' joins the locus of the vertical tangents to the yield curves. The point at which the line B-B' cuts each of the yield curves indicates the minimum fishing mortality required to generate that yield. The line B-B' is also known as the 'best catch line' since it showed that the optimum fishing conditions occurred at lower levels of fishing mortality than line A-A'. Nevertheless, for fishing industries, the line A-A' might be considered as the preferred condition because a smaller mesh could produce a greater more yield (in the short term) than if fisheries pursued the B-B' option.

Any point occurring between the A-A' and B-B' lines indicates that the stock the yield represents is still in good condition. It is suggested that the condition of common wolffish stock is still above the minimum safe biomass at present levels of exploitation. However, the biomass of common wolffish is likely to decline when the fishing mortality is over 0.6 at the present t_c.

5.3.3 Demographic analysis

The outcome of scenario 1 (natural mortality only) suggested that common wolffish in the North Sea have a healthy and increasing population without human exploitation. The net reproductive value, R_0, was estimated to be 14.23 per generation, the mean generation time (G) to be 5.08 years, the intrinsic rate of natural increase (r) to be 0.52 and the population would increase at 68.2 % per year (Table 5.4). The population would double every 1.68 years.

Any increase of mortality would tend to cause the common wolffish population to

Table 5.4. Reproductive life table and demographic output parameters without exploitation for common wolffish in the North Sea.

x	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	1.00000		0.000	
1	0.00300		0.000	
2	0.00253		0.000	
3	0.00213		0.000	
4	0.00180		0.000	0.0000
5	0.00151	393.00	0.595	2.9746
6	0.00128	1071.00	1.366	8.1986
7	0.00108	1361.50	1.464	10.2483
8	0.00091	1639.50	1.486	11.8870
9	0.00076	1923.50	1.469	13.2233
10	0.00064	2064.75	1.329	13.2926
11	0.00054	2267.75	1.230	13.5352
12	0.00046	2994.00	1.369	16.4303
13	0.00039	3399.75	1.310	17.0349
14	0.00032	3559.75	1.156	16.1895
15	0.00027	5309.50	1.454	21.8055

$R_0 = 14.23$
$G = 5.08$
$r = 0.52$
$\lambda = 1.68$

decline unless offset by density dependent effects. When fishing mortality was added on scenario 1 at first capture age 3, R_0 decreased from 6.57 to 0.38 per generation, *G* decreased from 4.64 to 3.32, *r* decreased from 0.41 to –0.29 and the population increase rate decreased from +51 % to –25 % per year as *F* increased from 0.1 to 0.6 (Table 5.5). The population of common wolffish would tend to zero growth when the fishing mortality was 0.4. When the fishing mortality increased to 0.5, the population of common wolffish began to exhibit negative growth. Thus, fishing mortality had a substantial effect on R_0, *r and* λ but less effect on *G.*

When fishing mortality is included at the present level of $F = 0.3$,and age at first captured increased from 2 to 5, the population increased from 7% to 35% per year, R_o increasing from 1.32 to 3.26, *r* increased from 0.07 to 0.30 and the generation time was unchanged (Table 5.6). This output suggested that age at first capture has a great effect on the net reproductive value (Fig. 5.5). It would also greatly influence the population increase rate, but not the generation time. If fishing began at age 2, the population of common wolffish would decline at $F = 0.2$ or greater.

5.4 Discussion

5.4.1 VPA

The age composition and total mortality rate estimates influence the accuracy of abundance estimation by VPA. If older age classes were not determined carefully, the total mortality rate might be overestimated from Ricker's catch curve (King, 1995). Therefore, the sample size should be considered to affect the bias of age composition. In this study, the sample size was larger than 500 for each year except 1998 and so the effect of sample size is thought to be small. However, increased sample size would increase the ability of mode-slicing (MacDonald and Pitcher, 1979).

When the numbers of fish caught are not known, CPUE can be a reliable relative index of abundance for population (Cushing, 1968, Hilborn and Walters, 1992). Substituting the catch in number for CPUE to calculate the total mortality from the catch curve, the *Z* value ranged from 0.16 to 0.18, which was approximately that obtained from using catch in number as a parameter. This suggests that the CPUE could be a good index for

Table 5.5 Demographic parameters for common wolffish in the North Sea with various levels of *F* at age 3 of first capture. Age at maturity = 5 and longevity = 15.

F	R_0	G	r	λ
0.1	6.57	4.64	0.41	1.50
0.2	3.30	4.25	0.28	1.32
0.3	1.79	3.92	0.15	1.16
0.4	1.024	3.66	0.006	1.006
0.5	0.61	3.46	-0.14	0.87
0.6	0.38	3.32	-0.29	0.75

Table 5.6 Demographic parameters for common wolffish in the North Sea with *F*= 0.3 beginning at different ages. Age at maturity = 5, and longevity = 15.

t_c	R_0	G	r	λ
2	1.32	3.92	0.07	1.07
3	1.79	3.92	0.15	1.16
4	2.41	3.92	0.22	1.25
5	3.26	3.92	0.30	1.35

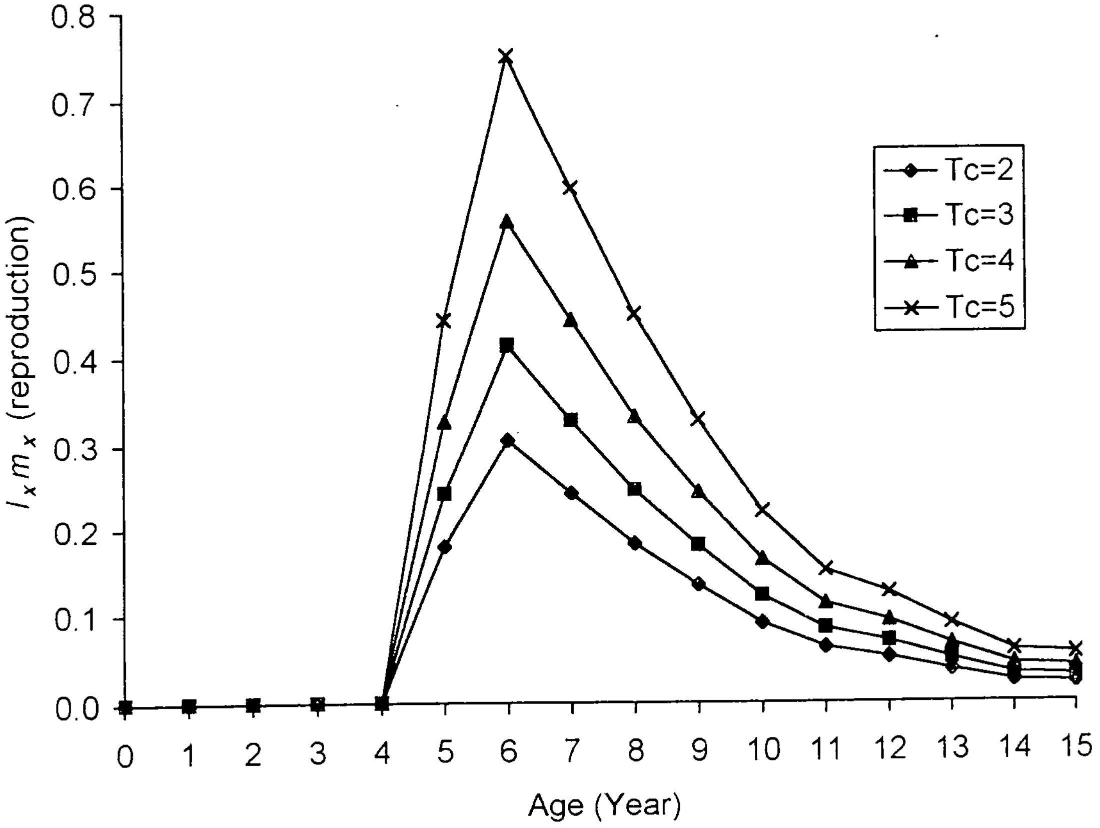


Fig. 5.5 Age-specific reproduction ($l_x m_x$) for common wolffish in the North Sea with M = 0.17 for ages 1-15 and F = 0.3 starting at different ages from 2 to 5.

estimating the abundance of North Sea common wolffish and be a parameter for estimating the total mortality. The mean weight of catch was lowest in 1998 when compared with that in 1996 and 1997. This result occurred because the body size of common was smaller at older ages and relatively high numbers of common wolffish were caught at age 3 and 4 in 1998. Thus, the CPUE for common wolffish was also lowest although the catch in number was highest in 1998. The CPUE was highest in 1997 due to both the highest mean weight of catch and total yield.

The most important and difficult parameter to obtain for stock dynamics is natural mortality (Beverton and Holt, 1957). A number of biological and environmental factors could affect the natural mortality of any fish. The two main factors are predation and temperature (Beverton and Holt, 1957; Pauly, 1980). Many studies use the Pauly's equation to calculate *M*. The average of natural mortality from Pauly's equation for wolffish was 0.17 in the North Sea. At present, there are still no reports of natural mortality values for common wolfish species from the literature. However, compared with demersal species such as plaice, haddock and cod in the North Sea that had similar *K* and maximum age, the *M* of common wolffish was similar at less than 0.2 (Beverton and Holt, 1957; Cushing, 1975; Myers and Doyle, 1983; Roff, 1984; Hilborn and Walters, 1992). Hence, the *M* value calculated from Pauly's equation for common wolffish would appear acceptable. However, this method could not account for variations of *M* at different ages since each age group of fish had a different natural mortality rate in a stock (Beverton and Holt, 1957; Hilborn and Walters, 1992). Although, Petersen and Wroblewski (1984) have developed an equation to estimate *M* from body size for pelagic teleosts, this equation appears inappropriate for common wolffish, since *M* for common wolffish, obtained from this equation was very high at 0.24. Since accurate estimation is essential in stock assessment, more studies are necessary to improve of natural mortality estimation for common wolffish in the future.

Both stable natural mortality and fishing mortality in 1996-1998 suggested that little variation occurs in total mortality. Fishing mortality was determined by the coefficient of catchability (*q*) and fishing effort (*E*). Since the fishing methods and mesh size used in the North Sea were the same for 1996-1998, the q would be similar in these years.

Therefore, fishing mortality was stable for 1996-1998 because the fishing efforts had not changed significantly. The fishing mortality rates of demersal species such as plaice and sole in the North Sea varied between 0.35 and 0.5 over the last decade (Rijnsdorp and Millner, 1996; Serchuk et al., 1996; Millner and Whiting, 1996). Since the common wolffish is a by catch species of the bottom trawl fishery in the North Sea, it is reasonable that the estimated fishing mortality of common wolffish in this study ($F = 0.3$) was lower than those of main target demersal species.

Virtual population analysis is a powerful technique which can be used to estimate the instantaneous rate of fishing mortality and the population surviving for a year-class (cohort) in each age separately. However, it has limitations as it requires the correct values of fishing mortality for each year, for a year-class and reasonable catch data at each age for a year-class (Pope, 1972). For example, there could be a significant bias in the estimation of abundance among the oldest age groups if the fishing mortality at the oldest age was overestimated by 100% (e.g. 68% bias for a year-class with an oldest age group of 12 years old if, $M< 0.3$, $F< 1.2$). Similarly, according to Pope's (1972) calculations, if the variance ratio of the catch data at each age was 10%, there would be a resulting 7% bias. VPA can provide reasonable estimates of fishing mortality on recent cohorts, even if the stock is heavily exploited, but the resulting estimates of F for the younger groups are relatively insensitive to the given initial value of F (Pope, 1972; King, 1995). Nevertheless, it is usually the older groups for which estimates are most important for fisheries management. Therefore, if one decides to manage a particular species, the use of VPA requires a long term catch-at-age data set (for at least one life cycle), to enable the variations of abundance of cohorts for a stock to accurately predict the acceptable yield for this species. This implies that it would need at least 15 years catch-age-data for the population management of common wolffish in the North Sea. In this study, just three years data were available to use VPA for estimating the abundance of common wolffish in the North Sea. This study can only indicate the abundance of North Sea common wolffish at present but is unable to show the long term variations of abundance for any year-class and better estimation of sustainable yield.

Virtual population analysis is a widely used method for estimating the abundance of fish population. But this method can estimate the stock precisely only if natural mortality, age structure and fishing mortality of the oldest fish are determined (Walters and Punts, 1994). If these parameters are incorrect, the abundance may be estimated unreasonably (Sims, 1982; Hilden, 1988). Myers and Cadigan (1995a) reported that fishing mortality of the oldest fish calculated from the commercial catch-at-age data had to be treated as a serious statistical problem because it would provide different results according to their model. Moreover, natural mortality is more sensitive to the model and strongly influences the estimated fishing mortality, year class strength and abundance (Ulltang, 1977). The overestimated M will cause the abundance to be overestimated whether the F value is over or underestimated. If correct estimation of M is made with an underestimated F, the abundance has to be adjusted upward. By contrast, the abundance has to be adjusted downward if the F value is overestimated. But the temporal trends of abundance would not change from those estimated by VPA. Ulltang (1977) suggested that the bias of abundance was 6%-7% at $M = 0.3$-0.4 per year with a level of $F = 1.2$ per year. Estimated natural mortality of common wolffish is lower than these values suggesting that less than 7% bias of abundance estimation might have occurred in this study.

In this study, VPA was applied by using data for both sexes combined. The result could be biased if the parameters of the growth equation between female and male were obviously different. Since there was no significant difference between sexes for common wolffish in the North Sea, this does not present a problem for the current analysis.

Fluctuations in abundance of fish population are influenced by a number of factors such as temperature, prey abundance, shift of current (Deyoung and Rose, 1993; Jacobson and MacCall, 1995;Gilbert, 1997). However, the mechanism of fluctuations of the common wolffish stock in the North Sea are unknown. A long term collection of data and further study is needed to provide likely explanations. Three years of data can not describe the fluctuations of each year class for a long-lived animal such as the common wolffish.

5.4.2 Yield per recruit

The strategies of fisheries management for any fish species rely on catch-at-age models to estimate abundance of fish stock using commercial data and survey research data. The M/K value of North Sea common wolffish was low, near to 1, and was similar to other temperate fish species (Pauly, 1994). Therefore, the curve of yield per recruit has a noticeable maximum, corresponding to a low fishing mortality, generating maximum yield per recruit. The models used in this study gave results which indicated that for a range of M and F used in the simulations, the value of yield per recruit would fluctuate intensely. It suggested that both yield and recruitment of common wolffish can be reduced visibly when the stock suffers poor environmental conditions. Typically fish stocks do not collapse when the natural mortality of fish is increased, but high fishing mortality may have catastrophic effects (Myers and Cadigan, 1995b). For a range of K, M and t_c input into simulations, the marginal increment of yield per recruit tended to be flat after F reached 0.5-0.6. Thus, there was no economic benefit for catching common wolffish in the North Sea using higher fishing effort than these values. Considering the age at first capture, the yield per recruit of common wolffish in the North Sea could be maximised by incorporating older age at first capture ($t_c = 5$) and higher fishing mortality ($F = 0.5$) than that at present ($F = 0.3$). Then the yield per recruit would increase by 63 % when the t_c increased from the present age 3 to age 5 and the F increased from the present 0.3 to 0.5. However, this might be not the most efficient management option for this species in the North Sea because raising the current level of F for common wolffish would almost certainly increase the overall rates of exploitation of other demersal species in the North Sea, which are captured by similar fishing gears. The low F for common wolffish probably reflects a different distribution and habits which make them less susceptible to capture than other demersal species.

The yield per recruit value of common wolffish in the North Sea increased very slowly with increasing F at lower levels of age at first capture, providing agreement with the high t_{critic} and P. This suggests that the maximum stock biomass of common wolffish in the North Sea is achieved in middle age (8-9) in life and there remains a high potential growth when fish enter the exploited phase at age 3.

Based on the isopleth analysis of yield per recruit, the abundance of the North Sea common wolffish stock still appears to be within the limits for a safe stock biomass. The historic catch data showed that the yield of the common wolffish in the North Sea has been low but stable for last decade (Chapter 2). These results suggest that the common wolffish stock in the North Sea has a positive but slow rate of increase. Serchuck *et al.* (1996) suggested that long term fishing mortality for demersal fish such as plaice and sole in the North Sea is between 0.28 and 0.33 considered on environmental and ecological conditions. Therefore, the present $F = 0.28\text{-}0.3$ for common wolffish seemed to approach the upper limit of sustainable fishing mortality. The pattern of moderately late maturation, long gestation period, long spawning season and relatively low fecundity in the common wolffish, suggests that reproduction would be harmed at a relatively low level of fishing mortality. Therefore, severe environmental impact or intense fishing mortality (> 0.5) would cause a decline in common wolffish stocks in the North Sea.

Yield per recruit models form only part of the tools used to make policy for fisheries management (Beverton and Holt, 1957; Gulland, 1983). They are best used in conjunction with other models such as spawning stock biomass per recruit (Barbieri *et al*., 1997) to estimate the effects of different strategies on egg production and biomass of the stock.

5.4.3 Demographic analysis

An important goal of ecological studies is to understand the role of processes that determine and control the abundance in a population (Hughes, 1990). The population size is strongly influenced by not only fecundity, but also ecological interactions (e.g. competition, predation). Weinberg *et al.* (1986) pointed out that the interactions between the number of life stages and their duration were of key importance in determining population growth. Demographic analysis was able to provide such information on population status and to realise how susceptible it might be for fisheries management. This study indicated that the common wolffish stock in the North Sea was in a positive growth condition without any fishing mortality, and might be vulnerable to intensive fishing mortality pressure at a younger age. However, the lack of survival rate data of age 0 group as well as egg hatching success, preclude a more detailed analysis at present. Trippel *et al.* (1997) suggested that egg size, production, hatching success, larval size and duration of spawning time could change the survival in early life. From the demographic analysis the net reproductive value of common wolffish was strongly influenced by the survival rate of early stages. The variation of survival rate in early life would strongly influence the R_0 value. Common wolffish exhibit parental care (egg mass guarding) and have large larval size (factors normally associated with high survival), but have relatively low fecundity. Pavlov (1994) pointed out that subtle temperature variation strongly affects the hatching success and spawning time. Therefore, more information is needed on the early life of common wolffish in order to assess survival during this critical part of the life cycle. In this study, increasing fishing mortality decreased the R_0 significantly. When F reached 0.5-0.6, the population of common wolffish in the North Sea might begin to decrease. The results of yield per recruit analysis of this study indicate that when F increases to 0.6-0.7 and beyond, the value of yield per recruit would increase very slowly. In addition, the historical catch data also showed that the catches of common wolffish were stable, and suggested that the population of common wolffish might be in a slow but positive growth condition. Therefore, the results of this demographic study combining fishing mortality seem reasonable.

The population of common wolffish in the North Sea had a capability of compensation when age at first capture was greater than two years old with $F = 0.3$/yr. However, the wolffish population would grow very slowly when fishing mortality ($F = 0.3$/yr) started at age 2 or less. This indicates that no extensive exploitation at a young age is desirable for population stability of North Sea wolffish..

Evaluation and correct estimation of net reproductive value, generation time and intrinsic rate of natural increase is difficult. Fenchel (1974) and Hennemann (1983) reported that the relationship between r (day^{-1}) and body size showed a positive correlation for most animals. The value of r calculated from the demographic analysis on common wolffish, when converted to daily rates ($r = 0.0014$ day^{-1}), fitted the Fenchel (1974) empirical curve well, suggesting that this estimate was reasonable.

It is difficult to compare the published data of demographic parameters because different authors use a variety of assumptions in their approaches. For common wolffish there have been no relevant studies against which to make comparisons. However, the demographic analysis provided useful information for further understanding the life history of common wolffish and for providing a framework for fisheries management of this species.

Chapter 6 General discussion

This chapter seeks to combine the studies in previous chapters and provides a framework of the life history and population dynamics of the common wolffish in the North Sea.

Common wolffish are moderately abundant but quite sparsely distributed in the North Sea north of 54° N. Catches of juvenile common wolffish (< 30cm) in the North Sea are not found in the landings from commercial fishing and are also quite rare from survey vessels (Chapter 2). The relatively low abundance and high dispersal of North Sea common wolffish prevents them from being a major target species in the trawl fishery. However, heavy fishing effort in the North Sea and removal of common wolffish as by catch have caused the CPUE of common wolffish to slowly decline. The population of North Sea common wolffish has been overexploited but the biomass is still above the safe level (Chapter 5). Since the 1980s the UK has become the most important country for landings of North Sea common wolffish. Nevertheless, the use of seine nets has decreased since the 1970s, particularly in the northwestern North Sea, while beam trawl fishing by UK boats has increased (Greenstreet *et al.*, 1999). The spatial distribution of demersal fishing effort is now also more widespread than in the 1960s. These factors may make the population of North Sea common wolffish more vulnerable to overfishing. Moreover, their increasing market value may encourage fishermen to put more fishing pressure on them.

Common wolffish show a very low energy expenditure in resting metabolism, which from an evolutionary perspective may be associated with extended periods of maintenance without feeding or periods interspersed with occasional feeding (Chapter 3). The greater metabolic scope at higher temperatures (e.g. summer season) provides both juvenile and adult common wolffish with more scope for food consumption under conditions when the food availability is higher in the North Sea.

A speculative scheme of the common wolffish's life history in relation to the North Sea environment is shown in Fig. 6.1. This scheme is based on information from this study and other authors' studies. The spawning ground of common wolffish in the

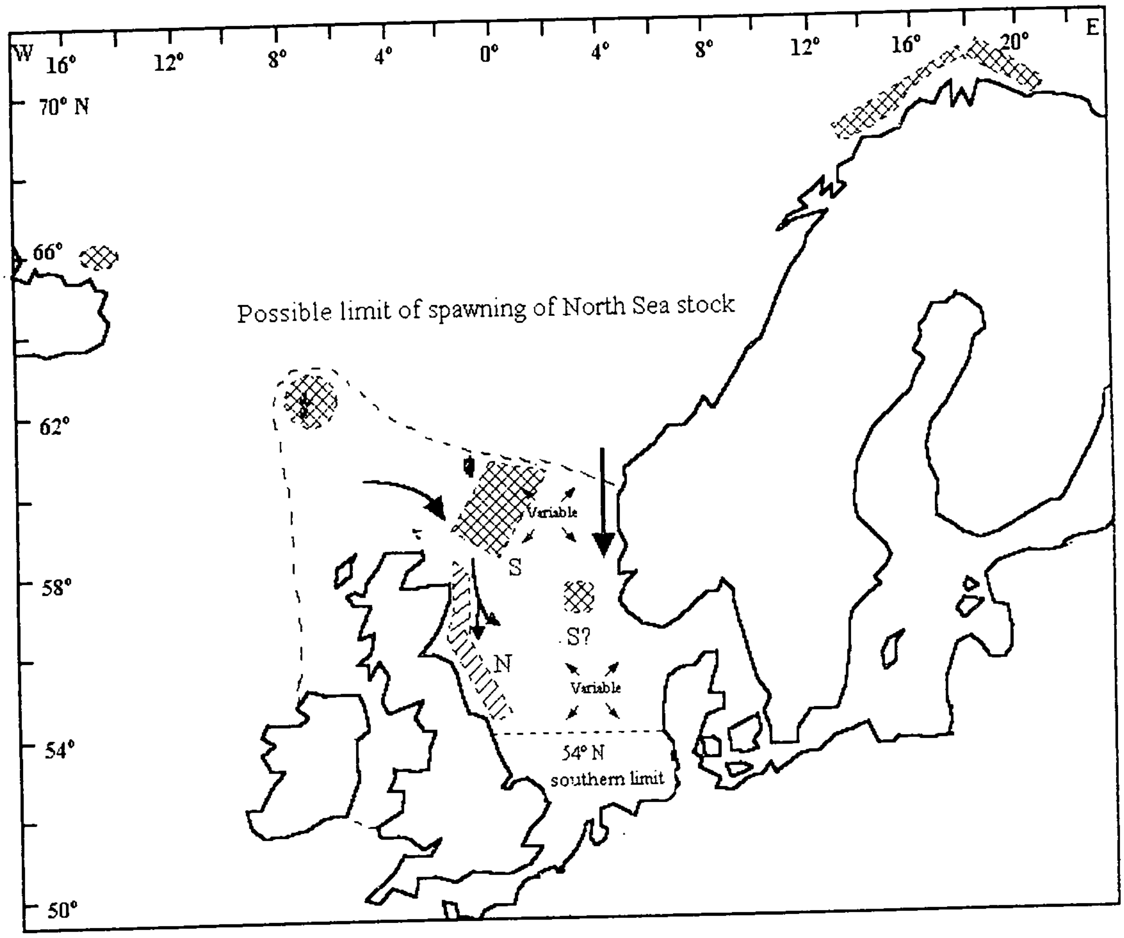


Fig. 6.1. Speculative scheme of common wolffish life history in relation to the North Sea stock. Larval common wolffish hatch in the spawning grounds (Shetland waters or off Faeroe Islands) and drift to the coasts of east Scotland and northeast England via coastal currents. Juvenile common wolffish (immature) stay in the nursery ground during the spawning season. The larger and mature common wolffish are widely distributed in the North Sea above 54° N, but are rarely found inshore during the spawning season. (S: spawning, N: nursery)

→ : Currents

▨ : Spawning ground

☐ : Nursery ground (mainly for juvenile/immature)

North Sea is still not clearly known because no egg masses have been found in this area. However, ICES 0-group survey data suggested that the main spawning ground of North Sea common wolffish might be east of the Shetlands since numbers of age-0 group common wolffish have been found in this area (ICES, 1978-1982). No age-0 group common wolffish were found in the areas south of 55° N from 0-group surveys data (ICES, 1978-1982). Informal discussion with coastal divers indicates that they have not found egg masses of common wolffish in the coasts of northeast England and east Scotland. Moreover, Pavlov and Moksness (1993, 1996) suggested that the temperatures for egg hatching of common wolffish in nature are under 8° C. Egg masses could also hatch at temperatures over 10° C in laboratory experiments, but were associated with increased rates of skeletal deformity (Pavlov and Moksness, 1996, 1997). Drift of common wolffish larvae would be in a southerly direction which concurs with results from ICES 0-group surveys (ICES, 1978-1982) There are another two possibilities for spawning grounds to which North Sea common wolffish might move. There are two strong currents that flow into the North Sea from west of Shetland waters (warmer Atlantic current) and Norwegian waters (deeper cold current). It has been reported that some egg masses of common wolffish have been caught in Faeroese waters (Jónsson, pers. comm.). Therefore, larval common wolffish, which hatched in Faeroese waters, might drift into the North Sea via current transportation. Another possibility is that larval common wolffish, which might hatch in southern Norwegian waters, could be transported by currents into the North Sea. Unfortunately, so far there is no information on common wolffish in southern Norwegian waters.

The coasts of northeast England and east Scotland seem to be an important nursery ground for the juveniles or immature common wolffish in the North Sea, while higher numbers of larger or mature common wolffish tend to be found in offshore areas. Several authors have indicated that common wolffish show a seasonal (spawning) migration pattern in different areas (Jónsson, 1982; Templeman, 1984; Keats *et al.*, 1985). The scheme in Fig. 6.1 requires some degree of migration within the North Sea also. During the period of this study, I hoped to use acoustic telemetry method to investigate local movements and residency of common wolffish on the coast of northeast England/southeast Scotland. However, this proved not to be possible because the live common wolffish could not be reliably obtained at appropriate sites such as Whitby or St. Abbs. However, in the future, mark and recapture of North Sea common wolffish (Templeman, 1984) or use of acoustic telemetry or data logging tags (Metcalfe and Arnold, 1997) would enable migration patterns of this species in the North Sea to be determined. The extent of stock mixing, and key routes of gene flow could also be determined by genetic techniques (Hoelzel, 1998).

Although the population of North Sea common wolffish is not high, their growth rates are faster than common wolffish elsewhere. Common wolffish are a stenothermal coldwater species, but their maximum growth/conversion rate occurs close to the upper critical temperature. The summer temperature of the North Sea near 54° N is the thermal limit for this species. Therefore, North Sea common wolffish, which are on the southern edge of their geographical range, may be expected to be sensitive to climate change. Any significant change in temperature would influence their distribution, abundance and or perhaps growth.

Temperature is generally considered one of the most important physical factors controlling the life of marine organisms. It influences geographic and bathymetric boundaries, reproduction periods, the period of larval occurrence in the plankton, recruitment, and metabolism (Bhaud *et al.*, 1995). The global environment is changing due to the effects of the increasing volume of carbon dioxide. Such global warming has impacted the global ecosystems significantly, including plants, animals, marine organisms and their communities (Graves and Reavey, 1996). Southward *et al.* (1995) provided a good example that warming since the early 1920s has significantly changed the plankton structure in the western English Channel and altered its ecosystem, and resulted in shifts of distribution of up to 2° latitude. If the warming of the seas around the UK including the North Sea continues, the distribution of common wolffish would be expected to retreat northwards and they would become rarer in the North Sea. However, other scenarios are possible. Wadhams (1990, 1992) indicated that ice thickness in the Greenland Sea has shown significant melting with downstream distance. If the global climate continues to warm, it will accelerate the melting rate of ice in the Greenland Sea. This could break the Atlantic Ocean pump due to large amounts of less-saline water implanting into the ocean (Pearce, 1994). If this happens, it might impede the warm north Atlantic gulf stream flowing into the North Sea. The temperature of the North Sea could decrease by several degrees C and the common wolffish population would expand southwards.

There are many factors which influence the distribution and abundance of fish, and clearly regional biogeography is one of the most important factor (Rogers *et al.*, 1999). Such biogeographic influences, which control fish population assemblage and diversity are subject to artificial changes, caused by human manipulation (Rice and Gislason, 1996). Heavy fishing efforts have impacted on the North Sea fish community significantly since the beginning of this century (Rijndorp *et al.*, 1996). Time-series data of the North Sea have shown large shifts in abundance of some major commercial fish species over several decades due to fishing mortality (Hempel, 1978). The relative abundance rank of some commercial fish species has significantly changed (ICES, 1993). The large and sudden increases in the population of gadoid species (e.g. cod, haddock, whiting and saithe) that occurred at the beginning of the 1960s while the herring stock declined (Cushing, 1980; Hislop, 1996) provides a good example. Cushing (1980) suggested that this 'gadoid outburst' might have resulted from either 'release of food' (food availability increasing as herring stocks declined) or from relaxed-predation (the decline in herring stocks increased the survival rates of gadoid larvae).

Beam and otter trawls are the two most widely used fishing gears in the North Sea (Jennings *et al.*, 1999) and have direct and indirect impacts on benthic fauna and habitats (Jennings and Kaiser, 1998). They remove a large proportion of the stocks of target and by catch fish species and can change the relative abundance of predators or their prey, and reduce biomass of vulnerable species. They may also have caused a shift in the benthic community from poorly-productive, long-lived species to highly-productive and short-lived species (Rijnsdorp and Leeuwen, 1996). Rice and Gislason (1996) analyzed North Sea survey data from the 1970s and showed significant changes in diversity and size composition of the exploited fish caused by the effects of fishing activity. A decline in the abundance of non-target species such as grey gurnard, spurdog, lesser-spotted dogfish (*Scyliorhinus canicula*) and thornback ray has been observed in the North Sea (Rijnsdorp *et al.*, 1996; Heessen and Daan, 1996; Walker and Heessen, 1996; Greenstreet and Hall, 1996). Some of the elasmobranchs are regarded as vulnerable to intense fishing mortality because of their low fecundity and sexual maturity at a high age (Walker and Heessen, 1996). The prey items of gurnard, spurdog, lesser-spotted dogfish, plaice, sole and some rays are similar to those of common wolffish at varying sizes (Ellis *et al.*, 1996, Kaiser and Spencer, 1994; Rijnsdorp and Leeuwen, 1996). Therefore, population growth of common wolffish might increase because of the decline in the populations of these food competitors of common wolffish, especially benthic elasmobranchs. There are some non-target fish species (e.g. starry ray, bib (*Trisopterus luscus*), dab) which have increased in abundance since the 1970s in the North Sea, probably due to declines in other demersal fish species (Heessen and Daan, 1996; Walker and Heessen, 1996). Commercial fishermen have given anecdotal reports that catches of common wolffish increased while catches of rays decreased. Certainly common wolffish are more fecund than elasmobranchs and so might be able to capitilise in a situation of competitive release as hypothesised. Moreover, the disturbance of the seabed by trawling activities would also provide increased food for scavenging common wolffish to increase their growth rates. However, analysis of North Sea ground-fish populations (Greenstreet and Hall, 1996) has shown that only small changes have occurred to the non-target species assemblage since the 1930s, and the evidence presented for common wolffish in this thesis is that they have not shown significant population increases, but to the contrary, have shown a decrease.

Fishing effort not only changes fish diversity in the community but also influences the length-frequency distribution of landed fish. A comparison of catch rates of demersal fish in the North Sea from the beginning of this century (Rijnsdorp *et al.*, 1996) has indicated that length-frequency distributions of roundfish and flatfish have shown a shift towards smaller-sized fish. North Sea common wolffish seem to not have shown a shift towards smaller size from the analysis of size distributions in Chapter 2, but sizes of old age groups have decreased (Chapter 4). The proportion of catch comprising young age group of common wolffish has increased gradually from the commercial data (Chapter 4). These results may indicate that North Sea common wolffish size and age distribution may change further in the future, but this requires further study.

The populations of common wolffish in the whole North Atlantic area have significantly decreased (Chapter 2). Historic data have shown that the length-frequency of distribution of common wolffish in Icelandic waters and west Greenland waters have shifted to smaller sizes (Jónsson, pers. comm.; Riget and Messtorf, 1988). However, the abundance and catches of common wolffish in Icelandic waters were the highest in the northeast Atlantic region over the last 30 years because Iceland established a quota for this species. The yields of common wolffish in the North Sea are much less than for other areas in the Northeast Atlantic (Chapter 2) and reflect the smaller population of common wolffish in the North Sea. The population of North Sea common wolffish may be more sensitive to fishing pressure compared with common wolffish in other areas. Therefore, if the UK established a quota and managed the North Sea common wolffish fishery, the yield and abundance of this species might remain sustainable, since it is the UK which captures the majority of common wolffish in the North Sea.

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Appendix I. Basic program for VPA (modified from Hilborn and Walters, 1992)

```
DECLARE SUB vector (n!, alist!(), x!(), lab$, lab2$, headfmt$, itemfmt$)
DECLARE SUB table (ny!, na!, iage!(), iyear!(), x!(), y!(), lab1$, lab2$, lab3$, rowfmt$, itemfmt$, lastfmt$)
DECLARE SUB vpainp ()
DECLARE SUB vpa ()
DECLARE SUB avbyag ()
DECLARE SUB avbyyr ()
DECLARE SUB blnkit (J!, I!)
DECLARE FUNCTION fcalc! (xnow!, xnext!, xm!)
DECLARE FUNCTION qcalc! (xnow!, xnext!, cat!, xm!, e!)
DECLARE FUNCTION calcn! (cc!, ff!, xm!)
DECLARE FUNCTION solve! (meth!, c!, xn!, xm!)
DECLARE SUB blank ()
DECLARE SUB InputMany (n!, x!())
COMMON SHARED label$, label2$, fmtcat$, fmtpop$, fmtq$, fmtf$
DIM SHARED iage(25), iyear(50), catch(50, 20), xn1(50, 20)
DIM SHARED xn2(50, 20), hr(50, 20), f(50, 20)
COMMON SHARED ny, na, xm, ipass, meth
DIM SHARED effort(50), q(50, 20), last(50, 20), xlast(50, 20)
DIM SHARED ifull, avgqa(20), avgfa(20), avgqy(50), avgfy(50)
DIM SHARED termfa(20), termfy(50)
COMMON SHARED yearfmt$, catchfmt$, effortfmt$, ffmt$, qfmt$, agefmt$, blnk$
'
'  this routine does VPA using the exact method
'
CALL vpainp
OPEN "wolffish.out" FOR OUTPUT AS #2

CALL table(ny, na, Iage(), Iyear(), catch(), effort(), label$, "Catch", "Effort", agefmt$, catchfmt$, effortfmt$)
CALL table(ny, na, Iage(), Iyear(), xlast(), avgfy(), label$, "Last ", " average", catchfmt$, catchfmt$, catchfmt$)
CALL vector(ny, Iyear(), termfy(), label$, "term f by year", yearfmt$, ffmt$)
CALL vector(na, Iage(), termfa(), label$, "term f by age", agefmt$, ffmt$)
CALL vector(ny, Iyear(), effort(), label$, "Effort by year", yearfmt$, effortfmt$)

CALL vpa

CALL table(ny, na, Iage(), Iyear(), xn1(), avgfy(), label$, "Numbers", "avg f", agefmt$, catchfmt$, ffmt$)
CALL table(ny, na, Iage(), Iyear(), q(), avgqy(), label$, "q value ", "average q", agefmt$, qfmt$, qfmt$)
CALL vector(na, Iage(), avgqa(), label$, "avg q by age", agefmt$, qfmt$)
CALL table(ny, na, Iage(), Iyear(), f(), avgfy(), label$, "Instant f", "average f", agefmt$, ffmt$, ffmt$)
CALL vector(na, Iage(), avgfa(), label$, "average f by age", agefmt$, qfmt$)

CLOSE (2)

SUB avbyag
'  get averages by age weighted by numbers at age
'
FOR I = 1 TO na
        lastyr = ny - na + I
        IF (lastyr > 1) THEN
                sumq = 0
                sumf = 0
                xn = 0
                FOR J = 1 TO lastyr
                        IF (catch(J, I) > 0 AND last(J, I) <> 1) THEN
                                sumq = sumq + q(J, I) * xn1(J, I)
                                sumf = sumf + f(J, I) * xn1(J, I)
                                xn = xn + xn1(J, I)
                        END IF
```

```
                NEXT J
                IF (xn > 0) THEN
                        avgqa(I) = sumq / xn
                        avgfa(I) = sumf / xn
                END IF
        END IF
NEXT I
END SUB

SUB avbyyr
'  get averages by year
'  include only ages reconstructed from fully complete
'  cohorts (lasta) and fully recruited (ifull)
'
FOR J = 1 TO ny
        lasta = na - ny + J    'last age from complete
        IF (lasta < ifull) THEN lasta = ifull
        sumq = 0
        sumf = 0
        xn = 0
        FOR I = lasta TO na
                IF (catch(J, I) > 0 AND last(J, I) <> 1) THEN
                        sumq = sumq + q(J, I) * xn1(J, I)
                        sumf = sumf + f(J, I) * xn1(J, I)
                        xn = xn + xn1(J, I)
                END IF
        NEXT I
        IF (xn > 0) THEN
                avgqy(J) = sumq / xn
                avgfy(J) = sumf / xn
        END IF
NEXT J
END SUB

SUB blank
'
'  blank estimates from incomplete cohorts
'  first go through last year and last ages
FOR I = 1 TO na
        CALL blnkit(ny, I)
NEXT I
'
'  now fill in the incomplete cohorts
'
FOR I = 1 TO na
        lastyr = ny - na + I
        IF (lastyr > 1) THEN
                FOR J = lastyr + 1 TO ny
                        CALL blnkit(J, I)
                NEXT J
        END IF
NEXT I
END SUB

SUB blnkit (J, I)
f(J, I) = -0
q(J, I) = -0
xn1(J, I) = -0
END SUB
```

```
FUNCTION calcn (cc, ff, xm)
z = ff + xm
calcn = (cc * z * EXP(-z)) / (ff * (1! - EXP(-z)))
END FUNCTION

FUNCTION fcalc (xnow, xnext, xm)
fcalc = -LOG(xnext / xnow) - xm
END FUNCTION

SUB InputMany (n, x())

  IF n > 16 THEN
       STOP
  END IF

SELECT CASE n

  CASE 1
    INPUT #1, x(1)
  CASE 2
    INPUT #1, x(1), x(2)
  CASE 3
    INPUT #1, x(1), x(2), x(3)
  CASE 4
    INPUT #1, x(1), x(2), x(3), x(4)
  CASE 5
    INPUT #1, x(1), x(2), x(3), x(4), x(5)
  CASE 6
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6)
  CASE 7
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7)
  CASE 8
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7), x(8)
  CASE 9
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7), x(8), x(9)
  CASE 10
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7), x(8), x(9), x(10)
  CASE 11
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7), x(8), x(9), x(10), x(11)
  CASE 12
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7), x(8), x(9), x(10), x(11), x(12)
  CASE 13
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7), x(8), x(9), x(10), x(11), x(12), x(13)
   CASE 14
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7), x(8), x(9), x(10), x(11), x(12), x(13), x(14)
  CASE 15
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7), x(8), x(9), x(10), x(11), x(12), x(13), x(14), x(15)
  CASE 16
    INPUT #1, x(1), x(2), x(3), x(4), x(5), x(6), x(7), x(8), x(9), x(10), x(11), x(12), x(13), x(14), x(15), x(16)
END SELECT
END SUB

FUNCTION qcalc (xnow, xnext, cat, xm, e)
qcalc = (xm * cat) / (e * (xnow - xnext - cat))
END FUNCTION

FUNCTION solve (meth, c, xn, xm)
'
'  get starting estimates using Pope's method
IF (meth = 2) THEN
```

```
        solve = xn * EXP(xm) + c * EXP(xm / 2!)
        EXIT FUNCTION
END IF
'  get estimates using Allen's method
start = xn * EXP(xm) + c * EXP(xm * .568)
IF (meth = 3) THEN
        solve = start
        EXIT FUNCTION
END IF
'

IF xn <= 0 THEN
  solve = start
  EXIT FUNCTION
END IF

FOR iter = 1 TO 100          'do Newtons method'
        xloss = start - xn
        IF (xn > 0!) THEN
                xlogs = LOG(start) - LOG(xn)
        ELSE
                xlogs = 1000000!
                        STOP
        END IF
        funct = c - ((1! - (xm / xlogs)) * xloss)
        deriv = -1! - (xlogs * xm - xloss * xm / start) / (xloss * xloss)
        start = start - funct / deriv
        solve = start
        IF (ABS(funct) < .01) THEN EXIT FUNCTION
NEXT iter
END FUNCTION

SUB table (ny, na, Iage(), Iyear(), x(), y(), lab1$, lab2$, lab3$, rowfmt$, itemfmt$, lastfmt$)
PRINT "Table of "; lab2$; " for stock "; lab1$
PRINT #2, "Table of "; lab2$; " for stock "; lab1$
PRINT blnk$;
PRINT #2, blnk$;
FOR I = 1 TO na
 PRINT #2, USING rowfmt$; Iage(i);
 PRINT USING rowfmt$; Iage(i);
NEXT I
PRINT "  "; lab3$
PRINT #2, "  "; lab3$
FOR J = 1 TO ny
        PRINT USING yearfmt$; Iyear(J);
        PRINT #2, USING yearfmt$; Iyear(J);
        FOR I = 1 TO na
          IF x(J, I) > 0 THEN
                PRINT USING itemfmt$; x(J, I);
                PRINT #2, USING itemfmt$; x(J, I);
          ELSE
                PRINT blnk$;
                PRINT #2, blnk$;
          END IF
        NEXT I
        PRINT USING lastfmt$; y(J)
        PRINT #2, USING lastfmt$; y(J)
NEXT J
END SUB

SUB vector (n, alist(), x(), lab$, lab2$, headfmt$, itemfmt$)
```

```
PRINT lab$; "   "; lab2$
PRINT #2, lab$; "   "; lab2$
FOR I = 1 TO n
  PRINT USING headfmt$; alist(i);
  PRINT #2, USING headfmt$; alist(i);
NEXT I
PRINT
PRINT #2,
FOR I = 1 TO n
  PRINT USING itemfmt$; x(i);
  PRINT #2, USING itemfmt$; x(i);
NEXT I
PRINT
PRINT #2,
END SUB

SUB vpa

FOR I = 1 TO na
'     use terminal f to calculate cohorts in year ny+1
'
        cc = catch(ny, I)
        ff = termfa(I)
        IF (ff <= 0!) THEN
                PRINT "Bad bad, terminal f <= 0 age ", I
        ELSE
                xn1(ny + 1, I + 1) = calcn(cc, ff, xm)
        END IF
NEXT I

'  use terminal f by year to calculate xn(year,last_age_in_catch)
 FOR J = 1 TO ny
FOR I = 1 TO na
IF (last(J, I) = 1) THEN
        cc = catch(J, I)
        ff = termfy(J)
        IF (ff <= 0!) THEN
                PRINT "Error: terminal f <=0 year ", J
        ELSE
                xn1(J + 1, I + 1) = calcn(cc, ff, xm)
        END IF
END IF
NEXT I
NEXT J
'
'  now that starting cohorts are set, do VPa
FOR I = na TO 1 STEP -1
        FOR J = ny TO 1 STEP -1
                xnext = xn1(J + 1, I + 1)
                IF (xnext > 0! OR catch(J, I) > 0!) THEN
                  tempcat = catch(J, I)
                  xn1(J, I) = solve(meth, tempcat, xnext, xm)
                END IF
                xnow = xn1(J, I)
                cat = catch(J, I)
                e = effort(J)
                lp = last(J, I) * ipass
                IF (xnext <= 0! OR lp = 1) THEN
                        f(J, I) = -0
                        q(J, I) = -0
```

```
                ELSE
                        f(J, I) = fcalc(xnow, xnext, xm)
                        q(J, I) = qcalc(xnow, xnext, cat, xm, e)
                END IF
        NEXT J
NEXT I
'  now do average q's and f's
'
CALL avbyag
CALL avbyyr
'  if ipass=1 then blank estimates for incomplete cohorts
IF (ipass = 1) THEN CALL blank
END SUB
'
SUB vpainp
DIM x(50)
INPUT "enter file for data "; file$
OPEN file$ FOR INPUT AS #1
LINE INPUT #1, label$
INPUT #1, ny, na, xm, ifull, ipass, meth
'  ny is number of years
'  na is number of ages
'  ifull is subscript for first fully recruited age
'  ipass = 1 means blank out non complete cohorts
'  meth is the method to use
'      1 = exact Newton's
'      2 = Pope's
'      3 = Allen's
'
INPUT #1, yearfmt$, catchfmt$, effortfmt$, ffmt$, qfmt$, agefmt$, blnk$
CALL InputMany(na, Iage())
FOR J = 1 TO ny
        'read in yer and catch for each age at this year
        CALL InputMany(na + 1, x())
        Iyear(J) = x(1)
        FOR i = 1 TO na: catch(J, i) = x(i + 1): NEXT i
NEXT J
CALL InputMany(na, termfa())   'terminal f by age
CALL InputMany(ny, termfy())   'terminal f by year
CALL InputMany(ny, effort())   'efforts
'  find out which are last catches from cohorts
FOR Jy = 1 TO ny
        FOR i = 0 TO na
          J = Jy - i
          I = na - i
          IF (J < 1) THEN J = 1
                IF (catch(J, I) > 0!) THEN
                        last(J, I) = 1
                        xlast(J, I) = 1
                        EXIT FOR
                END IF
        NEXT i
NEXT Jy
END SUB
```

Appendix II. Basic program for yield-per-recruit model

```
DIM M(10), K(10), WINF(10), T0(10), Xc(10), Tr(10), X(10), TC(10), Tx(10)
DIM F(20), LINF(10), YP(10, 20, 20), FMAX(10), FMIN(10), FINC(10)
DIM XMIN(10), XMAX(10), XINC(10)
30 CLS
  PRINT "1. YIELD PER RECRUITMENT ESTIMATION"
  PRINT "2. END"
100 PRINT "-->"; : INPUT MENU
  ON MENU GOTO 200, 400
  GOTO 100
  CLS : END

  '****************************************************************
200 CLS
  PRINT " ******************************"
  PRINT " YIELD PER RECRUIT ESTIMATION"
  PRINT " ******************************": PRINT
  PRINT "DATA ENTRY ": PRINT
  PRINT "  1. DISK "
  PRINT "  2. KEYBOARD ": PRINT
  PRINT "-->": INPUT SELT
  IF SELT = 2 THEN GOTO 250
  PRINT "FILE NAME"; : INPUT F$
  PRINT "HOW MANY DATA SET ?": INPUT N
  FOR I = 1 TO N
  OPEN F$ FOR INPUT AS #1
  INPUT #1, LINF(I), WINF(I), K(I), T0(I), Tr(I), Xc(I), M(I), F(I), Tx(I)
  NEXT I
  CLOSE #1
  GOTO 300
250 CLS
  PRINT "INPUT BIOLOGICAL DATA": PRINT
  PRINT "HOW MANY DATA SET ?": INPUT N
  FOR I = 1 TO N
  PRINT : PRINT "DATA SET NUMBER: "; I
  PRINT "LINF: "; : INPUT LINF(I)
  PRINT "WINF: "; : INPUT WINF(I)
  PRINT " K  : "; : INPUT K(I)
  PRINT "To  : "; : INPUT T0(I)
  PRINT "TXr  : "; : INPUT Tr(I)
  PRINT "NATURAL MORTALITY: "; : INPUT M(I)
  PRINT "Tx  : "; : INPUT Tx(I)
  NEXT I
300 CLS : PRINT "LIST OF DATA": PRINT
  PRINT "--------------------------------------------------"
  PRINT " LINF   WINF    K      T0    Tr     M      Tx"
  PRINT "--------------------------------------------------"
  FOR I = 1 TO N
```

```
   PRINT USING "####.# ####.### #.### #.### #.### #.###### ##.##";
LINF(I); WINF(I); K(I); T0(I); Tr(I); M(I); Tx(I)
   NEXT I
   PRINT "-----------------------------------------------"
   PRINT : PRINT "PRESS RETURN TO CONTINUE"; : INPUT M$

'*********************************************************************
   CLS
   FOR I = 1 TO N
   PRINT "MIN COUNT OF F   : ": INPUT FMIN(I)
   PRINT "MAX COUNT OF F   : ": INPUT FMAX(I)
   PRINT "INCR COUNT OF F  : ": INPUT FINC(I)
   PRINT "MIN COUNT OF XC  : ": INPUT XMIN(I)
   PRINT "MAX COUNT OF XC  : ": INPUT XMAX(I)
   PRINT "INCR COUNT OF XC : ": INPUT XINC(I)
   FOR LL = FMIN(I) TO FMAX(I) STEP FINC(I)
   FOR MM = XMIN(I) TO XMAX(I) STEP XINC(I)
'   L = LL * .1
   Z = LL + M(I)
   A = (1 - EXP(-Z * (Tx(I) - Xc(I)))) / Z
   X = MM + T0(I)
   B = (3 * EXP(-K(I) * X)) * (1 - EXP(-(Z + K(I)) * (Tx(I) - Xc(I)))) / (Z + K(I))
   C = (3 * EXP(-2 * K(I) * X)) * (1 - EXP(-(Z + 2 * K(I)) * (Tx(I) - Xc(I)))) / (Z + 2
* K(I))
   D = (EXP(-3 * K(I) * X)) * (1 - EXP(-(Z + 3 * K(I)) * (Tx(I) - Xc(I)))) / (Z + 3 *
K(I))
   P = LL * WINF(I) * EXP(-M(I) * (MM - Xr(I)))
   YP(I, LL, MM) = P * (A - B + C - D)
   PRINT USING "# ##.## ##.## ####.####"; I; LL; MM; YP(I, LL, MM)
   NEXT MM
   NEXT LL
   NEXT I
   PRINT "SAVE DATA TO DISK FILE (Y/N)"; : INPUT S$
   IF S$ = "N" OR S$ = "n" THEN GOTO 350
  OPEN "yield.out" FOR OUTPUT AS #2
   FOR I = 1 TO N
   FOR LL = FMIN(I) TO FMAX(I) STEP FINC(I)
   FOR MM = XMIN(I) TO XMAX(I) STEP XINC(I)
'   L = LL * .1
   Z = LL + M(I)
   A = (1 - EXP(-Z * (Tx(I) - Xc(I)))) / Z
   X = MM - T0(I)
   B = (3 * EXP(-K(I) * X)) * (1 - EXP(-(Z + K(I)) * (Tx(I) - Xc(I)))) / (Z + K(I))
   C = (3 * EXP(-2 * K(I) * X)) * (1 - EXP(-(Z + 2 * K(I)) * (Tx(I) - Xc(I)))) / (Z + 2
* K(I))
   D = (EXP(-3 * K(I) * X)) * (1 - EXP(-(Z + 3 * K(I)) * (Tx(I) - Xc(I)))) / (Z + 3 *
K(I))
   P = LL * WINF(I) * EXP(-M(I) * (MM - Tr(I)))
   YP(I, LL, MM) = P * (A - B + C - D)
   PRINT #2, USING "# ##.## ##.## ####.####"; I; LL; MM; YP(I, LL, MM)
```

```
   NEXT MM
   NEXT LL
   NEXT I
   CLOSE #2
350 STOP
400 END
```

Appendix III. Glossary of terms/abbreviations

CEFAS	Centre for Environment, Fisheries and Aquaculture Science
EC	European Community
EU	European Union
FAO	Food and Agriculture Organization
FRS	Fisheries Research Services
ICES	International Council for the Exploration of the Sea
MAFF	Ministry of Agriculture, Fisheries and Food
NAFO	Northwest Atlantic Fisheries Organization
SOAEFD	The Scottish Office Agriculture, Environment and Fisheries Department