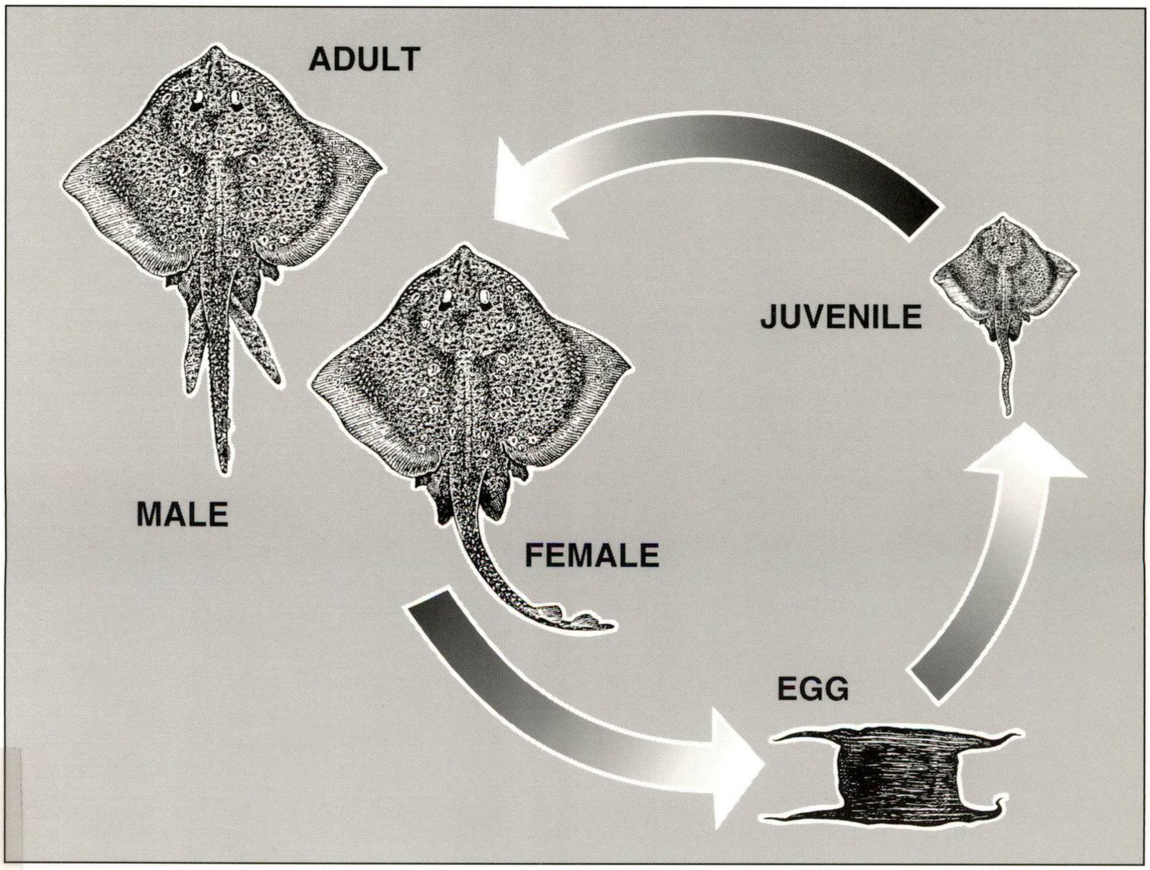
NIOZ-RAPPORT 1994 - 9

REPRODUCTIVE STRATEGIES OF *RAJA RADIATA*, *RAJA NAEVUS*, *RAJA MONTAGUI* AND *RAJA CLAVATA* IN THE NORTH SEA

J.J. van Steenbergen



Nederlands Instituut voor Onderzoek der Zee

Kustsystemen

Beleidsgericht Wetenschappelijk Onderzoek NIOZ (BEWON)

Netherlands Institute for Sea Research (NIOZ)
P.O. Box 59, 1790 AB Den Burg, Texel
The Netherlands

ISSN 0923 - 3210

Cover design: H. Hobbelink

REPRODUCTIVE STRATEGIES OF *RAJA RADIATA, RAJA NAEVUS, RAJA MONTAGUI* AND *RAJA CLAVATA* IN THE NORTH SEA

J.J. van Steenbergen

NETHERLANDS INSTITUTE FOR SEA RESEARCH

Kustsystemen
Beleidsgericht Wetenschappelijk Onderzoek NIOZ (BEWON)

NIOZ-RAPPORT 1994 - 9

SAMENVATTING

Dit rapport vergelijkt de reproduktieve strategieën van de sterrog (*Raja radiata* Donovan 1808), de koekoeksrog (*R. naevus* Müller & Henle 1841), de gladde rog (*R. montagui* Fowler 1910) en de stekelrog (*R. clavata* Linnaeus 1758) met elkaar, in relatie tot verspreiding en biomassa in de Noordzee. De onderzochte roggen zijn gevangen in de Noordzee in 1992. De gonaden van zowel de mannelijke als de vrouwelijke roggen ontwikkelen zich en worden volwassen bij de kleinste disk breedte in *R. radiata* gevolgd door *R. naevus, R. montagui* en *R. clavata.* De gonado/somatische index, het gewicht van de nidamentaal klieren, het totale aantal gele eieren en de lengte van de rechter clasper laten dezelfde volgorde van ontwikkeling zien voor de vier soorten. Vrouwelijke roggen zijn volwassen of bijna volwassen als er gele eieren in hun ovaria aanwezig zijn. De eerste vrouwtjes met gele eieren zijn in *R. radiata* aanwezig in disk breedte klasse 20-24 cm (lengte klasse 31-37 cm), in *R. naevus* in disk breedte klasse 28-32 cm (lengte klasse 49-55 cm), in *R. montagui* in disk breedte klasse 40-44 cm (lengte klasse 58-64 cm) en in *R. clavata* in disk breedte klasse 56-60 cm (lengte klasse 77-82 cm). *R. radiata* is waarschijnlijk het minst kwetsbaar voor visserij van de 4 soorten, omdat deze soort sneller volwassen wordt dan de andere drie soorten. *R. radiata* is tegenwoordig de meest algemeen voorkomende soort in de Noordzee en de relatief gezien lage leeftijd waarop deze soort volwassen wordt, is waarschijnlijk de sleutel factor voor het "succes" van deze soort in de Noordzee.

Reproduktie en opslag van energie tussen twee groepen van *R. radiata*, gevangen in de Noordzee in 1992, zijn vergeleken met elkaar. De indeling in twee groepen (twee gebieden) is gebaseerd op verschillen tussen de gemiddelde bodem temperatuur in augustus over de periode 1902-1952. De gonado/somatische index en de lengte van de claspers van de mannelijke roggen gevangen in kwartaal 3 (augustus/september) zijn significant hoger in het warme gebied (9±2°C) dan in het koude gebied (7±2°C). Van de vrouwelijke roggen gevangen in hetzelfde kwartaal was de gonado/-somatische index hoger en het gewicht van de lever en de hepato/somatische index lager in het warme gebied dan in het koude gebied. Deze verschillen worden waarschijnlijk veroorzaakt door verschillen in temperatuur tussen de gebieden waar deze twee groepen roggen werden gevangen. Er waren geen significante verschillen in reproduktie en opslag tussen de twee groepen die zijn gevangen in de kwartalen 1 (januari/februari) en 2 (mei). In deze kwartalen was dee gemiddelde bodem temperatuur hetzelfde tussen de twee gebieden.

SUMMARY

This paper compares the reproductive strategies of the starry ray (*Raja radiata* Donovan 1808), the cuckoo ray (*R. naevus* Müller & Henle 1841), the spotted ray (*R. montagui* Fowler 1910) and the thornback ray (*R. clavata* Linnaeus 1758), in relation to differences in their distribution and abundance in the North Sea. The investigated rays were caught in the North Sea in 1992. The gonads of males and females begin to develop and become mature at the lowest disc width in *R. radiata* followed by *R. naevus, R. montagui* and *R. clavata.* The gonado/somatic index, the weight of the nidamental glands, the total number of yellow eggs and the length of the right clasper show the same sequence in development for the four species. Female rays are mature, or close to maturity, when yellow eggs are present. The first females with yellow eggs are present in *R. radiata* at disc width class 20-24 cm (length class 31-37 cm), in *R. naevus* at disc width class 28-32 cm (length class 49-55 cm), in *R. montagui* at disc width class 40-44 cm (length class 58-64 cm) and in *R. clavata* at disc width class 56-60 cm (length class 77-82 cm). *R. radiata* probably has the highest tolerance to fishery of the four species, because this species reaches maturity sooner than the other three species. At present *R. radiata* is the most abundant species in the North Sea and the relative low age-at-maturity of this species is probably the key-factor for the "success" of this species in the North Sea.

Reproduction and storage of energy between two groups of *R. radiata* caught in the North Sea were compared. The two groups (two areas) were divided on the basis of the mean bottom water temperature in August from 1902-1952. For males caught in quarter 3 (August/September) the gonado/somatic index and the length of the claspers were significantly higher in the warmer area (9±2°C) than in the colder area (7±2°). For females caught in the same period the gonado/somatic index was significantly higher in the warmer area than in the colder area; whereas the weight of the liver and

hepato/somatic index were significantly lower in the warmer area than in the colder area. These differences are probably caused by differences in temperature between the areas in which the groups were caught. There were no significant differences in reproduction and storage between the two groups of *R. radiata* caught in quarters 1 (January/-February) and 2 (May). The mean bottom water temperature in these quarters was the same in both areas.

1. INTRODUCTION

The elasmobranchs belong to the Chondrichthyes (cartilaginous fish) and have been evolving independently for at least 450 million years. Rays and skates (Rajiformes) and sharks (Squaliformes) belong to this group of fishes. The elasmobranchs have developed a life-history pattern that is different from that most of teleosts (bony fish; Osteichthyes). The main life-history characteristics of the elasmobranchs are slow development, large adult size, low fecundity and late age-at-maturity (HOLDEN, 1973; HOENIG & GRUBER, 1990). On the contrary most teleosts have rapid development, small adult size, high fecundity and early age-at-maturity (HOENIG & GRUBER, 1990). According to the r/K selection theory of MCARTHUR & WILSON (1967) the life-history characteristics of the elasmobranchs makes them K-strategists, compared with the teleosts which are mostly r-strategists.

In the past some species of rays and skates in the North Sea were caught commercially for human consumption, while nowadays they are usually a by-catch. Only the bigger rays are taken for their flesh and the smaller rays are thrown back as discards (ANON., 1989a; ANON., 1989b). The International Council for the Exploration of the Sea (ICES) has collected catch statistics of North Sea fishes since the beginning of the century. These are published annually in the Bulletin Statistiques. Analysis of the data shows that the landings of rays and skates declined between 1910 and 1975, with periods of recovery during World Wars I and II, when fishing was virtually stopped (see also HOLDEN, 1978). The catches have been relatively stable during the past 15 years, but are much lower than at the beginning of this century (Fig. 1). This decline in catches of rays and skates and the recovery periods during World Wars I and II, suggests that rays and skates are vulnerable to fisheries exploitation. In shark fisheries initial exploitation is often followed by a rapid decline in catch rates and sometimes a complete collapse, suggesting the same vulnerability to fishery (HOLDEN, 1974a; WOOD *et al.*, 1979). The life-history characteristics of the elasmobranchs in terms of the slow development, large adult size, low fecundity and late age-at-maturity are probably the main reasons for their vulnerability to fishery (HOLDEN, 1973; HOLDEN, 1974a; FOGARTY *et al.*, 1989; HOENIG & GRUBER, 1990). It has been inferred that these species generally have little capacity to compensate for the effect of harvesting (FOGARTY *et al.*, 1989). Low reproductive output and the extended time required to reach maturity are the dominant factors resulting in low resilience to exploitation in the elasmobranchs (FOGARTY, *et al.*, 1989). The relationship between stock and recruitment in the elasmobranchs is quite direct, because of the low fecundity and low numbers of well developed eggs and offspring. Therefore a decrease in adult population will lead directly to a decrease in recruitment (HOENIG & GRUBER, 1990). For species with low fecundity, the natural mortality rate is assumed to be low and the conclusion suggested from fisheries which have collapsed is that these species can withstand, at the most a small increase in fishing mortality, on top of the fishing mortality already present, before recruitment is reduced below the replacement level (HOLDEN, 1973). Not all the elasmobranchs have the same vulnerability to fishery, because of differences in the reproductive strategies between species. The tolerance to fishery is probably higher for a species that has a faster development, smaller adult size, higher fecundity and lower age (size)-at-maturity (lesser K-strategist) than another ray species. The species with the smallest adult size, highest fecundity and the lowest age-at-maturity can probably withstand the highest exploitation pressure and will therefore increase in abundance relative to the species which have a larger adult size, lower fecundity and a higher age-at-maturity. According to BRANDER (1981) the net survival to maturity is probably more important than the fecundity of the ray species. The longer it takes for a female ray to mature, the higher the chance that she will be caught before she can reproduce, assuming there are no differences in the catchability of different ray species. A shift in distribution area and abundance in favour of the lesser K-strategists could indicate a higher tolerance to fishery for these species, which is probably caused by differences in reproductive strategies. The age-at-maturity is probably a key-factor in the difference in tolerance to fishery between ray species (BRANDER, 1981).

There are also differences in life-history parameters from (sub)populations of the same species in elasmobranchs. For example: the maximum size of *R. radiata* is much smaller in the North Sea (about 66 cm; VINTHER, 1989) than in the North Atlantic (about 90 cm; TEMPLEMAN, 1984; WHITEHEAD *et al.*, 1984) and the egg-cases are smaller in the North Sea than in the North Atlantic

(TEMPLEMAN, 1984), suggesting differences in the age and size-at-maturity. Differences in growth parameters have been observed between populations from different locations of female spiny dogfish (*Squalus acanthias*; FAHY, 1989b). In the North Sea the maximum length, age-at-maturity and life-expectancy of the spiny dogfish is lower than that of populations from relatively colder areas (Canadian Pacific and New Zealand Pacific). These differences suggest some latitudinal influence in which temperature could play an important role. Observations of reproduction and storage of food in two thermally differentiated groups of a ray species could offer some insight into the energy requirements of the species.

This paper compares the reproductive strategies of the starry ray (*Raja radiata* Donovan 1808), the cuckoo ray (*Raja naevus* Müller & Henle 1841), the spotted ray (*Raja montagui* Fowler 1910) and the thornback ray (*Raja clavata* Linnaeus 1758) in relation to distribution and abundance between these species. Secondly, reproduction and storage of energy (food resources) between two thermally differentiated groups of *R. radiata* will be compared with each other. In Chapter 2 an introduction on the biology of the family *Rajidae* and the *Raja* species treated in this paper will be given.

2. BIOLOGY OF RAYS IN THE NORTH SEA

The ray species of the family Rajidae occurring in the North Sea are opportunistic in their feeding habits. They feed on various kinds of bottom animals and the larger individuals also have a substantial amount of fish in their diets (HOLDEN & TUCKER, 1974; TEMPLEMAN, 1982; WHITEHEAD *et al.*, 1984; VINTHER, 1989). They are all oviparous, laying horny egg-cases that are formed by the nidamental glands (HOBSON, 1930). The egg-cases are deposited on the sea bottom or become attached to stones, rocks or vegetation (CLARK, 1926; HOBSON, 1930; DU BUIT, 1976; RYLAND & AJAYI, 1984). There is clear sexual dimorphism. The males have claspers (mixopterygia) which are inserted (probably one at a time) into the cloaca of the female to transfer the spermatophores (STEVEN, 1934; HOLDEN, 1975). About sixteen species occurred in the English Channel and the North Sea in the 1920's (CLARK, 1926). Nowadays about ten species occur in the English Channel and the North Sea (WHITEHEAD *et al.*, 1984; KNIJN *et al.*, 1993; DAAN *et al.*, 1990), of which *R. radiata* is the most abundant. Maximum length, age-at-maturity, maximum age and the average annual production of egg-cases of the four most abundant species (*R. radiata*, *R. naevus*, *R. montagui* and *R. clavata*) in the North Sea are presented in Table 1.

***Raja radiata* Donovan 1808: starry ray or thorny ray**. Size to about 60 cm at lower latitudes and moderate depths, to about 90 cm at higher latitudes and deeper water (arctic and boreal latitudes up to 1000 m deep) (WHITEHEAD *et al.*, 1984). The smallest egg-cases are reported from the North Sea and females probably reach maturity at a lower size than in the North-west Atlantic (TEMPLEMAN, 1982). No seasonal changes in the distribution pattern were observed and there are no indications for the existence and location of spawning grounds in the North Sea (KNIJN *et al.*, 1993). No information about the fecundity of this oviparous species is known for the North Sea. The main spawning season is probably between February and June, but mature females in the North-west Atlantic with well developed eggs occur throughout the year (TEMPLEMAN, 1982). Starry ray is a by-catch species in the trawl, seine and longline fisheries. It is usually discarded because it is too small for human consumption (KNIJN *et al.*, 1993). The mean biomass of the starry ray in the North Sea from 1977 to 1988 was estimated at 100,000 ton, making it the most abundant ray species in the North Sea (SPARHOLT & VINTHER, 1991). Migration in the Newfoundland area occurred across deep water channels in which temperatures were close to zero, but not if temperatures where higher (TEMPLEMAN, 1984). Both male and female become sexually mature at 4-6 years and reach a maximum length of 66 cm in the North Sea (VINTHER, 1989; Table 1). Distribution: whole northern Atlantic, southward to the English Channel, all (except southern part) of the North Sea, western part of the Baltic. Elsewhere, north-western Atlantic southward to South Carolina; also reported from western side of South Africa, in deep water (WHITEHEAD *et al.*, 1984).

***Raja naevus* Müller & Henle 1841: cuckoo ray**. The presence of egg-cases throughout the year in the Celtic Sea suggests that in this area there is no distinctive peak spawning season (DU BUIT, 1976; WHITEHEAD *et al.*, 1984). Catches in the North Sea are largely confined to the north-western part. Some seasonal migration may take place in the North Sea (KNIJN *et al.*, 1993). Maximum length for this species caught off the Brittany coast is about 92 cm, the age-at-maturity is about 9 years, maximum age is about 13-14 years and the females produce an average of 71-90 eggs a year, (CLARK, 1922; HOLDEN, 1974A; DU BUIT, 1975; DU BUIT, 1976; Table 1). The mean biomass of the cuckoo ray in the North Sea from 1977 to 1986 was estimated at 45,000 ton (DAAN *et al.*, 1990). Distribution: Atlantic coast northward from northern Morocco to Ireland and Britain and northern part of North Sea, to Kattegat; western part of Mediterranean, to Tunisia and western Greece, rare in eastern part. Elsewhere reported from Senegal (WHITEHEAD *et al.*, 1984).

***Raja montagui* Fowler 1910: spotted ray.** Catches of this species in the North Sea are presently limited to two well separated areas, one in the north-western part of the North Sea and the other one in the south-western part of the North Sea (VINTHER & SPARHOLT, 1988; KNIJN *et al.*, 1993). Peak spawning in the Bristol Channel is from February to June (RYLAND & AJAYI, 1984). Maximum length for this species caught in the Irish Sea and Bristol Channel is about 69-73 cm (HOLDEN, 1972) and in Carmarthen Bay, off the Welsh coast, 98 cm (RYLAND & AJAYI, 1984). The age-at-maturity is about 11 years, maximum age is about 18 years and the females produce an average of 24-61 eggs a year (HOLDEN *et al.*, 1971; HOLDEN, 1972; HOLDEN, 1974a; RYLAND & AJAYI, 1984; FAHY, 1989a; Table 1). The mean biomass of the spotted ray in the North Sea from 1977 to 1986 was estimated at 16,000 ton (DAAN *et al.*, 1990). Distribution: Atlantic coasts from Morocco northward to the Shetlands, southern North Sea and Baltic Sea, also western part of Mediterranean (to Tunisia and to western Greece) (WHITEHEAD *et al.*, 1984).

***Raja clavata* Linnaeus 1758: roker or thornback ray.** There appears to be spawning migration and mating aggregation by this species. Spawning occurs between March and September in inshore areas, which probably serve as nursery grounds for the immature individuals (CLARK, 1922; CLARK, 1936; STEVEN, 1936; HOLDEN, 1975; RYLAND & AJAYI, 1984; ROUSSET, 1990; KNIJN *et al.*, 1993). Maximum length for this species is about 86-120 cm, the age-at-maturity is about 7-12 (females 9-12) years, maximum age is about 20 years and the females produce an average of 62-140 eggs a year (CLARK, 1922; STEVEN, 1936; HOLDEN *et al.*, 1971; HOLDEN, 1972; HOLDEN, 1975; RYLAND & AJAYI, 1984; Table 1). The mean biomass of the thornback ray in the North Sea from 1977 to 1986 was estimated at 11,600 ton (DAAN *et al.*, 1990). Distribution: Atlantic coasts from Madeira and Morocco northward to Iceland and Norway (south of Arctic Circle), as well as North Sea and western Baltic (rare); also whole Mediterranean and western part of Black Sea. Elsewhere, southward to South Africa and south-western Indian Ocean (WHITEHEAD *et al.*, 1984).

3. MATERIAL & METHODS

3.1. FIELD SAMPLING

3.1.1. FISHING METHODS

Males and females of the starry ray (*Raja radiata* Donovan, 1808), the cuckoo ray (*R. naevus* Müller & Henle, 1841), the spotted ray (*R. montagui* Fowler, 1910) and the thornback ray (*R. clavata* Linnaeus, 1758) were measured and investigated on the research vessels or in the laboratory. These rays were caught in the North Sea throughout 1992. For the determination of the species the drawings and descriptions in Whitehead *et al.* (1984) were used. Two methods of fishing were used, a GOV-trawl (average distance between trawl doors 72 m; average distance between wing ends 21 m; headline height 5 m; stretched mesh 200-20 mm) and a beamtrawl (5.5 m; 50 mm mesh at the cod end; two tickler chains), respectively used by the RV Tridens from the Netherlands Institute for Fishery Investigations (RIVO) and the RV Pelagia from the Netherlands Institute for Sea Research (NIOZ). The catch statistics of these caught rays are presented in Table 2.

3.1.2. MEASUREMENTS

The total weight (g), length (mm) and disc width (mm) were measured on board of research vessels or in the in laboratory (after thawing the frozen rays). No correction has been made for freezing because only small differences were present between the length and disc width of *R. montagui* and *R. clavata* (Table 3). Length (tip of snout to end of tail) of a ray is sometimes impossible to measure, because a part of the tail is missing. Disc width can always be measured and has been chosen to describe the size of the rays. The disc widths of the rays are divided into classes of 4 cm (0 to 4 cm, 4.1 to 8 cm, 8.1 to 12 cm etc.). Male rays have cartilage appendages called claspers (mixopterygia) which are used (probably one at a time) to implant the spermatophores into the cloaca of the female. The length (mm) of the right clasper was measured as the distance between the tip of the clasper and its point of emergence from the skin of the inner side (STEVEN, 1934).

The gonads and the liver were investigated and measured after opening the abdominal cavity (ventral side). The egg-cases are formed by the nidamental glands of the female. The weight of the oviducts were included in the weight (mg) of the nidamental glands. Egg-cases were not included in the weight of the nidamental glands. The eggs in the ovaries were divided into three different classes.

1. Eggs with a diameter from 1 to 4 mm; eggs usually white or white/translucent.
2. Eggs with a diameter from 4 to 5 mm; eggs usually white/pale yellow or white/translucent/-pale yellow.
3. Eggs with a diameter of 5 mm or higher; eggs usually yellow or yellow/red. Only the eggs in this egg class were counted (both ovaries) and are called "yellow eggs" throughout this paper.

For the males weight (mg) of the gonads consists of the weight of the testes and the weight of the vas deferens (the part rostral to the kidneys). Weight of the gonads for females consists of the weight of the ovaries and the weight of the nidamental glands (including the oviducts). Egg-cases were not included in the weight of the gonads.

3.1.3. ANALYSIS

In literature disc width (DW) or length (L) is used to describe the size of a ray. The parameters a and b of the following formula have been estimated to make these two size measurements exchangeable:

$$L_{(cm)} = a + b * DW_{(cm)}$$

The relationship between total weight (TW) of a ray and disc width (DW) was calculated. Parameters a and b of the following formula have been estimated:

$$TW_{(g)} = a * DW_{(cm)}^{b}$$

The estimate of the parameters was performed with the Quasi-Newton method (non-linear least squares method, minimizing the squared deviations of the dependent variable data values from values estimated by the function at the same independent variable points. Numeric estimates of the first and second derivatives of the loss function are made to seek a minimum).

The gonado/somatic index (GSI) is the weight of the gonads (TWG) divided by the total weight (TW) of the ray. This index describes how much energy is put into reproduction.

$$GSI = TWG_{(g)} / TW_{(g)}$$

The hepato/somatic index (HSI) is the weight of the liver (LW) divided by the total weight (TW) of the ray. This index describes how much energy is put into fat storage.

$$HSI = LW_{(g)} / TW_{(g)}$$

The analyses were performed with SYSTAT version 5.0.

3.2. DISTRIBUTION

The numbers of rays caught per hour fishing (catch per hour) have been calculated for the starry ray (*R. radiata*), the cuckoo ray (*R. naevus*), the spotted ray (*R. montagui*) and the thornback ray (*R. clavata*) in 1974, 1981, 1986 and 1991 per ICES rectangle (quadrant). No distinction in the calculation of the catch per hour has been made between males, females, immature, adolescent or mature individuals. The size of each dot in the various North Sea maps in this paper corresponds with the size of the mean catch per hour made in that quadrant. The calculation of the mean catches per hour per quadrant are based on catches made by research vessels of different countries, joining the February surveys (quarter 1) in the North Sea (including Skagarak/Kattegat) of the International Council for the Exploration of the Sea (ICES) and the International Young Fish Survey (IYFS). Some of the cooperating research vessels used other gears than the standardized GOV-trawl, because of a continuation of existing national surveys. The catches per hour of other gears were recalculated to make them comparable with the catch per hour of the GOV-trawls (KNIJN *et al.*, 1993).

4. RESULTS

4.1. FIELD SAMPLING

4.1.1. ANALYSIS

Only the catches of *R. radiata* contained individuals smaller than 20 cm. In the catches of *R. naevus*, *R. montagui* and *R. clavata* individuals of the disc width classes (4-20 cm) were virtually absent. Individuals of *R. clavata* were the largest caught, followed by *R. montagui*, *R. naevus* and *R. radiata*. These four species were the only ones caught during the surveys. Most of the caught rays were *R. radiata* (Table 2).

The relationship between disc width and length for the caught males and females of *R. radiata*, *R. naevus*, *R. montagui* and *R. clavata* is presented in Table 4

The total weight (TW) of the males and females of *R. radiata* (Figs. 2a and 2b), *R. naevus* (Figs. 3a and 3b), *R. montagui* (Figs. 4a and 4b) and *R. clavata* (Figs. 5a and 5b) is plotted against disc width (DW).

The relationship between total weight and disc width for the caught males and females of *R. radiata*, *R. naevus*, *R. montagui* and *R. clavata* is presented in the Figs. 2, 3, 4 and 5.

4.1.2. MATURATION STAGES

The investigated individuals of *R. radiata*, *R. naevus*, *R. montagui* and R.clavata can be divided into three development stages.

1. Immature rays

The claspers of the **males** do not exceed the pectoral fins. The testes are very small, white and not differentiated. The vas deferens is narrow and the part just rostral of the kidneys is not coiled. The rostral part of the vas deferens is not swollen.

The ovaries of the **females** are very small and when they contain eggs (white/translucent), these have a diameter smaller than 1 mm. The nidamental glands are small and not differentiated. The oviducts are narrow.

2. Adolescent rays

The tip of the claspers of the **males** exceeds the pectoral fins, but the cartilaginous parts are not ossified and hard. Small white/translucent globules can be seen in a part of the testes, but the greater part of the testes is still not differentiated. The vas deferens is still thin, but slightly coiled in the caudal part of the abdominal cavity. The rostral part of the vas deferens is slightly swollen.

The eggs in the ovaries of the **females** are developing. The eggs are small white/translucent to white/yellow with a diameter lower than 5 mm. The nidamental glands become kidney shaped, but are not differentiated completely. The oviducts are developing but are still narrow.

3. Mature rays

The tip of the claspers of the **males** exceed well beyond the pectoral fins and the cartilaginous parts are partially ossified and hard. The testes are well differentiated and in a large part of the testes well developed translucent globules are present. The vas deferens is thick and heavily coiled in the caudal part of the abdominal cavity. The rostral part of the vas deferens is swollen.

The ovaries of the **females** contain yellow or yellow/red eggs with a diameter greater than 5 mm. The nidamental glands are kidney shaped and fully differentiated. The oviducts are wide.

4.1.3. REPRODUCTION OF THE FOUR RAY SPECIES

There are clear differences in gonad development between *R. radiata, R. naevus, R. montagui* and *R. clavata*. The gonads of males and females begin to develop and become mature at the lowest disc width in *R. radiata* followed by *R. naevus*, *R. montagui* and *R. clavata* (Figs. 6a and 6b). The gonads of the males of *R. montagui* and *R. clavata* begin to develop and become mature at a lower disc width than the gonads of the females. The gonads of the males of *R. radiata* and *R. naevus* mature at about the same disc width as the gonads of the females. The gonado/somatic index (Figs. 7a and 7b), the weight of the nidamental glands (Fig. 8), the total number of yellow eggs (Fig. 9) and the length of the right clasper (Fig. 10) show the same sequence in size for the four species. The gonado/somatic index for males and females of *R. radiata* and *R. naevus* is higher than that for *R. montagui* and *R. clavata.* Female rays are mature, or are close to maturity, when yellow eggs are present (Fig. 9). Yellow eggs are present in *R. radiata* at disc width class 20-24 cm (length class 31-37 cm; see Table 4), in *R. naevus* at disc width class 28-32 cm (length class 49-55 cm), in *R. montagui* at disc width class 40-44 cm (length class 58-64 cm) and in *R. clavata* at disc width class 56-60 cm (length class 77-82 cm).

4.1.4. REPRODUCTION AND STORAGE IN TWO GROUPS OF *RAJA RADIATA*

The starry rays (*R. radiata*) caught in 1992 in the North Sea are divided into two thermally differentiated groups. Reproduction and the weight of the liver (storage of energy) of the rays of the two groups are compared with each other, taking into account the sex and the quarter of the year in which they were caught (quarter 1; January/February, quarter 2; May and quarter 3; August/September, Table 2). The two groups (areas) were defined by looking at the thermoclines of the mean bottom temperature of January, May and August from 1902 to 1952 (TOMCZAK & GOEDECKE, 1962) and by taking into account the number of specimens available for each group. The mean bottom water temperature of the month August from 1902 to 1952 shows the highest temperature difference between the areas in which groups 1 (9±2°C) and 2 (7±2°C) of the starry rays (*R. radiata*) in 1992 in the North Sea were caught (Fig. 11). The border that was drawn to divide the rays into two groups is therefore mainly based on this month. ANOVA was used to see if the differences between groups 1 and 2 of quarter 3 are significant. Only rays with a disc width larger than 20 cm were tested with ANOVA.

The males of group 1 have a significantly higher gonado/somatic index (Fig. 12a; ANOVA, p=0.027) and length of the claspers (Fig. 16; ANOVA, p=0.021) than the males of group 2. No significant differences between the males of groups 1 and 2 could be detected for the weight of the gonads (Fig. 13a; ANOVA, p=0.248), although it appears that the values between disc width 20 and 28 cm are slightly higher for group 1 than for group 2.

The females of group 1 have a significantly higher gonado/somatic index (Fig. 12b; ANOVA, p=0.002) than the females of group 2. No significant differences between the females of groups 1 and 2 could be detected for the weight of the gonads (Fig. 13b; ANOVA, p=0.070), the weight of the nidamental glands (Fig. 14; ANOVA, p=0.063) or the total number of yellow eggs (Fig. 15; ANOVA, p=0.198), although it appears that the values between disc width 20 and 32 cm are slightly higher for group 1 than for group 2.

No significant differences between the males of groups 1 and 2 of quarter 3 could be detected for the weight of the liver (Fig. 17a; ANOVA, p=0.070) or the hepato/somatic index (Fig. 18a; ANOVA, p=0.177), although it appears that the values between disc width 20 and 36 cm are slightly lower for group 1 than for group 2.

The females of group 2 have a significantly heavier liver (Fig. 17b; ANOVA, p<0.001) and a higher hepato/somatic index (Fig. 18b; ANOVA, p<0.001) than the females of group 1.

There were no differences in overall mean bottom water temperature in January and May from 1902-1952 between the areas in which groups 1 (6±1.5°C) and 2 (6±1.5°C) of *R. radiata* were caught (TOMCZAK & GOEDECKE, 1962) and no differences in reproduction and weight of the liver could be detected between groups 1 and 2 (males and females) in these quarters (1 and 2).

4.2. DISTRIBUTION

To see if there have been changes in the distribution areas and abundance of *R. radiata*, *R. naevus*, *R. montagui* and *R. clavata* in the North Sea during the past 20 years, the catches per hour per ICES quadrant, made during the ICES February surveys were calculated for the years 1974, 1981, 1986 and 1991. These catches per hour per quadrant are presented in Fig. 19 (*R. radiata*), Fig. 20 (*R. naevus*), Fig. 21 8 (*R. montagui*) and Fig. 22 (*R. clavata*).

In 1974 ***R. radiata*** was only caught in a few quadrants. No differences in distribution area between 1981, 1986 and 1991 could be detected. It appears that between 1974 and 1981 this species became more abundant in the North Sea. The highest catches per hour in 1981, 1986 and 1991 have been made in the central North Sea. The southern boundary for this species is about the same in 1981, 1986 and 1991, situated approximately between the central and the southern North Sea (Fig. 19).

No clear differences in the distribution area of ***R. naevus*** could be detected between the years 1974, 1981, 1986 and 1991. The catches were largely confined to the north-western part of the North Sea. It appears that the distribution area has not changed during the past 20 years (Fig. 20).

In 1974 only one specimen of ***R. montagui*** was caught in quadrant 46E7, during the ICES February surveys. In 1981 no specimens where caught. Important information from the southern North Sea and south of the Shetlands is lacking for 1974 and 1981. It appears that the spotted ray has slightly increased its distribution area and its abundance between 1986 and 1991. In 1991 a high mean catch rate of 129 individuals per hour fishing occurred during two hauls made in quadrant 35F0. Two separate distribution areas can be distinguished in the year 1991. The first one in the southern North Sea and the second one south of the Shetlands (Fig. 21).

It appears that the distribution area of ***R. clavata*** has changed from 1974 to 1991. In the years 1974 and 1981 this species was caught, although in low numbers, in the northern and central North Sea. Unfortunately no hauls were made around the Shetlands and in the southern North Sea during 1974 and 1981. In 1986 and 1991 almost all the specimens were caught in the southern North Sea. It appears that the distribution area of this species has moved southward. In 1991 an exceptionally high mean catch rate of 2887 individuals per hour fishing occurred during two hauls made in quadrant 35F0. The dot in this quadrant has been resized to a catch per hour of 200 (Fig. 22).

5. DISCUSSION

5.1. SIZE COMPOSITION

Individuals of the width classes (4-20 cm) were virtually absent in the catches of *R. naevus*, *R. montagui* and *R. clavata*. Most of the individuals of all disc width classes of *R. radiata* were caught by the RV Pelagia (beamtrawl), but the RV Pelagia fished primarily in areas were *R. radiata* is abundant. All the individuals of *R. naevus* were caught by the RV Tridens (GOV-trawl; Table 2). Individuals of *R. montagui* and *R. clavata* were caught with the beamtrawl as well as with the GOV-trawl. Two explanations for the absence of small individuals of *R. naevus*, *R. montagui* and *R. clavata* in the catches are:

1. The smaller rays have a lower chance of being caught by the gears used than the bigger rays, especially the GOV-trawl.
2. The smaller rays do not have the same distribution area as the bigger rays.

The hauls made in 1992 in the North Sea to catch the rays were all quite a distance from coastal waters (Table 2). It is possible that there is migration of the mature individuals to shallow waters where the eggs are spawned and the young rays grow up. It appears that there are spawning migrations (also mating aggregations) of mature individuals in at least certain populations of *R. clavata* (STEVEN, 1936; HOLDEN, 1974b; HOLDEN, 1975; RYLAND & AJAYI, 1984) and *R. montagui* (HOLDEN, 1974b; RYLAND & AJAYI, 1984; KNIJN *et al.*, 1993). The bay of Douarnenez (Brittany) serves as a nursery area for the young of *R. clavata* in their first years of life (ROUSSET, 1990; KNIJN *et al.*, 1993). Some seasonal migration of *R. naevus* may take place in the North Sea (KNIJN *et al.*, 1993). There are no indications for the existence and location of spawning grounds of *R. radiata* in the North Sea (KNIJN *et al.*, 1993) and surveys with the RV Pelagia showed that in areas where individuals of *R. radiata* have been caught, there were usually a lot of egg-cases of this species in the catches. Most egg-cases were empty, but some of them contained eggs or even young rays in different stages of development. So, it is possible that the immature and adult stages of *R. radiata* have a similar distribution.

5.2. REPRODUCTION OF THE FOUR RAY SPECIES

The estimates of the lengths-at-maturity (based on the presence of yellow eggs) obtained in this study for the four species can be transposed to age with the use of mean lengths-at-age data of different authors (based on rays caught in different areas and different ageing methods, see below). It is then possible to estimate the age at which the females are mature orclose to maturity. See below.

R. radiata	2-3 yr	(VINTHER, 1989; central North Sea)
R. naevus	2-3 yr	(FAHY, 1989a; Irish waters)
	6-7 yr	(DU BUIT, 1975; Celtic Sea)
R. montagui	4-5 yr	(FAHY, 1989a; Irish waters)
	4-7 yr	(RYLAND & AJAYI, 1984; British Isles)
	8-11 yr	(HOLDEN, 1972; British waters)
R. clavata	6-7 yr	(FAHY, 1989a; Irish waters)
	6-7 yr	(RYLAND & AJAYI, 1989; British Isles)
	6-8 yr	(BRANDER & PALMER, 1984; Irish Sea)
	9-11 yr	(HOLDEN, 1972; British waters)

These estimates of first age-at-maturity for female *R. radiata*, *R. naevus*, *R. montagui* and *R. clavata* are, therefore, derived from the results of this paper and the mean lengths-at-age calculated by different authors (HOLDEN, 1972; DU BUIT, 1975; BRANDER & PALMER, 1984; RYLAND & AJAYI, 1984; FAHY, 1989a; VINTHER, 1989). The presence of yellow eggs (diameter > 0.5 cm) was used as an indication that the female rays are mature or close to maturity. VINTHER (1989) estimated the first age-at-maturity of *R. radiata* between 4 and 6 years, but the estimate in this paper, based on the presence of yellow eggs, is between 2 and 3 years, which is probably too low. For *R. naevus* the first age-at-maturity derived from mean lengths-at-age of FAHY (1989a) is estimated between 2 and 3 years. This estimate is probably also too low. This could be due to:

1. The yellow eggs are present before a ray reaches maturity.
2. The published age-at-maturity values are based on observations of fish, which have external evidence of maturity. These fish could have been mature for some time.
3. The area in which the rays have been caught seems to have an influence on the growth rates and therefore the mean lengths-at-age (FAHY, 1989a). HOLDEN (1972) also suggested there were possible differences between the growth rates of different populations of *R. clavata*.
4. The methods (usually by counting the number of opaque and translucent bands in calcified structures in the vertebrae) used by the different authors to calculate the mean lengths-at-age are often different and according to WALKER (pers. comm.), in some of the methods the bands are not easy to distinguish. This could also be a reason for the inconsistency between the mean lengths-at-age of the same species calculated by different authors. The material used for this project will be aged in the near future, which will clarify this point.

The different reproductive characteristics used in this paper for *R. montagui* and *R. clavata* are probably on the low side due to seasonal variation in reproductive activity. For example, the number of yellow eggs (diameter > 0.5 cm) counted in females of these two species could be influenced by the season in which they have been caught. Egg-laying in *R. clavata* caught in British waters starts in February, reaches a peak rate in June and ceases by September (HOLDEN, 1975). Peak spawning in *R. montagui* caught in the Bristol Channel is from February to June (RYLAND & AJAYI, 1984). The rate of egg-laying in rays is apparently temperature dependent (HOLDEN *et al.*, 1971). The individuals of these two species used for this paper were all caught in December in the southern North Sea. The reproductive activity (rate of egg-laying) of the caught individuals is probably low in this month.

Although there are differences in the published mean lengths-at-age of the same species, it appears that *R. radiata* reaches maturity at the lowest age, followed by *R. naevus*, *R. montagui* and *R. clavata*. According to BRANDER (1981) the net survival to maturity is probably more important than the fecundity of the ray species to maintain recruitment. The longer it takes for a female ray to mature, the higher the chance that she will be caught before she can reproduce, assuming there are no differences in the catchability of *R. radiata*, *R. naevus*, *R. montagui* and *R. clavata*. If we take this into account than *R. radiata* has the highest tolerance to fishery of the four species. *R. radiata* is the most abundant species in the North Sea nowadays and the relatively low age-at-maturity for this species is probably the key-factor for the "success" of this species in the North Sea. No differences in the distribution area could be detected in the past 20 years for *R. naevus* and *R. montagui*. However, it appears that the distribution area of *R. clavata* has moved southwards (Fig. 22). According to BRANDER (1981), *R. clavata* has the lowest tolerance of the four species studied to fishery, because the females of this species mature at a very high age. This high age-at-maturity is probably the key-factor in the shift of the distribution area of this species from the central and the southern North Sea to the southern North Sea. Fishery pressure in the southern North Sea is higher than in the central and northern North Sea (ANON., 1992), but in the areas in which *R. clavata* is abundant fishery pressure is relatively low, because of the stony sea bottom. Changes in food abundance, natural mortality, temperature or changes in other biotic or abiotic factors could also play an important role. *R. batis*, a ray species that reaches maturity at an even higher age than *R. clavata*, has disappeared from the Irish Sea, although it was very common in these waters in the past and it is suggested by BRANDER (1981), that this is due to fishery. Although *R. radiata* is the most abundant species in the North Sea at present (VINTHER & SPARHOLT, 1988;

SPARHOLT & VINTHER, 1991), the overall landings of rays and skates from 1910 to 1992 has declined rapidly (Fig. 1, see also HOLDEN, 1978). Species with a very high age-at-maturity will probably suffer most from fisheries and will be the first species to disappear. Therefore, future exploitation of rays and other elasmobranchs has to be done with extreme care.

5.3. REPRODUCTION AND STORAGE IN TWO GROUPS OF *RAJA RADIATA*

No differences could be detected in reproduction and storage of energy between groups 1 and 2 of *R. radiata* caught in quarters 1 (January/February) and 2 (May), but there were almost no differences in the overall mean bottom water temperature of January and May from 1902-1952 between the two areas in which in two groups have been caught (both areas in both months 6±1.5°C).

For males there are significant differences in the gonado/somatic index and the length of the claspers between groups 1 and 2 caught in quarter 3. For females there are significant differences in gonado/somatic index, weight of the liver and hepato/somatic index between groups 1 and 2 caught in quarter 3. The overall mean bottom water temperature of August from 1902-1952 (TOMCZAK & GOEDECKE, 1962) was higher in the area in which group 1 was caught (9±2°C), than in the area in which group 2 was caught (7±2°C). The gonado/-somatic index of males and females of group 1 is higher than the gonado/somatic index of males and females of group 2. Therefore, the investment in reproduction relative to body weight is higher when the temperature is higher. A higher rate of egg-laying of *R. clavata* has been observed in the warmer months of the year (HOLDEN, 1975; RYLAND & AJAYI, 1984). The hepato/somatic index and the weight of the liver are higher in females of group 2 than in females of group 1. This suggests that relatively more energy is stored by females at lower temperatures than at higher temperatures. No difference was found between the weight of the liver and the hepato/somatic index in males of the two groups. It is possible that in the summer months (quarter 3) the females store more energy to enable the production of reproductive tissue than during the winter and spring (quarters 1, 2 and 4). The hepato/somatic index is relatively high in the elasmobranchs, because of the fatty liver, which has a higher mass of adipose cells than glandular tissue (OGURI, 1990). The fatty liver is probably used for static lift, because rays, skates and sharks do not have a swim bladder. In addition the storage of high energy fatty acids in the liver may act as a lipid nutrient reservoir for the adult fishes during hard times (shortage of food or low temperature, causing problems in catching food, because of slower movement) and egg development (OGURI, 1990). HOENIG & GRUBER (1990) believe that a large liver is an adaptive characteristic for predators that live under feast-or-famine regimes.

Growth, movement and metabolism in ectotherms is probably also higher when temperature is higher. To what extent these other energetic processes contribute to the differences found in reproduction and storage between the two thermally differentiated groups of *R. radiata* is difficult to say. Temperature differences will not only affect the physiology of the fish but will also determine the abundance of food. It is assumed, however, that food is not a limiting factor to growth.

TEMPLEMAN (1982) found differences in the size of the egg-cases and the size-at-maturity in *R. radiata*. The smallest egg-cases of *R. radiata* were found in the North Sea and these rays probably reach maturity at a lower size than in the more northern waters. In the North Sea the maximum length, age-at-maturity and life-expectancy of the spiny dogfish (*Squalus acanthias*), a member of a closely related family, are lower than that of populations elsewhere (FAHY, 1989b), suggesting latitudinal influence in which temperature could play an important role. This appears to be the case for *R. radiata*. Two thermally differentiated groups of *R. radiata* caught in the North Sea in August and September in 1992 show differences in reproduction and storage, probably caused by differences in temperature between the areas in which the groups were caught. The group of *R. radiata* that lived in the "warmer" area developed their gonads and reached maturity at a lower size than the group that lived in the "colder" area. The group of female *R. radiata* that lived in the "colder" area stored more energy in the liver than the group that lived in the "warmer" area.

ACKNOWLEDGMENTS

I am very grateful to Paddy Walker (NIOZ) for her support and cooperation during the time needed to collect the data and to complete this paper. I am also very grateful to Paddy and Henk van der Veer (NIOZ) for their useful comments on previous drafts of this paper. I wish to express my thanks to Henk Heessen of the Netherlands Institute for Fisheries Research (RIVO) for providing me the ICES data used in this paper and the manuscript of the Atlas of North Sea Fishes, Jacques van Alphen (RUL) for his helpful comments and support, Frans Hovenkamp (NIOZ) for his advice in processing the data. Further I wish to thank Hans Witte, Jaap van der Meer and the crews of the RV Pelagia (NIOZ) and Tridens (RIVO). The Netherlands Institute for Sea Research (NIOZ) provided most of the facilities to carry out the investigations presented in this paper.

REFERENCES

ANONYMOUS, 1989a. Fisheries for Ray (Batoidei) in Western statistical division VIIA, investigated through the commercial catches. ICES Working Document for ICES study group on Elasmobranch Fisheries, April 1989: 1-26.

ANONYMOUS, 1989b. Report of the study group on elasmobranch fisheries. ICES C.M. Pelagic Fish Committee 1989/G: 554: 1-37.

ANONYMOUS, 1992. Report of the ICES Study group on tagging experiments for juvenile plaice. ICES, C.M. 1992/G: 10.

BRANDER, K., 1981. Disappearance of common skate *Raja batis* from Irish Sea. Nature **290**: 48-49.

BRANDER, K. & D. PALMER, 1985. Growth rate of *Raja clavata* in the Northeast Irish Sea. J. Cons. perm. int. Explor. Mer **42**: 125-128.

BUIT, M.H. DU, 1975. Age et croissance de *Raja batis* et de *Raja naevus* en Mer Celtique. J. Cons. perm. int. Explor. Mer **37**: 261-256

BUIT, M.H. DU, 1976. The ovarian cycle of the cuckoo ray, *Raja naevus* (Muller and Henle), in the Celtic Sea. J. Fish Biol. **8**: 199-207.

CLARK, R.S., 1922. Rays and Skates (Raiae). No. I - Egg capsules and young. J. Mar. Biol. Assoc. U.K. **12**: 577-643.

CLARK, R.S., 1926. Rays and Skates. A revision of the European species. Fish. Bd. Scot. Sci. Invest. 1926. No. **1**: 1-66.

DAAN, N., P.J. BROMLEY, J.R.G. HISLOP & N.A. NIELSEN, 1990. Ecology of North Sea fish. Neth. J. Sea Res. **26**: 343-386.

FAHY, E., 1989a. Growth parameters of rays (Batoidei) in Irish waters, from material examined in commercial catches. ICES Paper C.M. 1989/G: **59**: 1-12.

FAHY, E., 1989b. The value of alterations in fecundity to an exploited shark population, illustrated by *Squalus acanthias* (L.). ICES C.M. 1989/Mini, No **2**: 1-11.

FOGARTY, M.J., J.G. CASEY, N.E. KOHLER, J.S. IDOINE & H.L. PRATT, 1989. Reproductive dynamics of elasmobranch populations in response to harvesting. ICES, ICES Mini-symposium: Reproductive Variability, The Hague, Netherlands, 1989: 1-21.

HOBSON, A.D., 1930. A note on the formation of the egg case of the skate. J. Mar. Biol. Ass. U.K. **16**: 577-581.

HOENIG, J.M. & S.H. GRUBER, 1990. Life-history patterns in the Elasmobranchs: Implications for fisheries management. In: H.L. PRATT, S.H. GRUBER & T. TANIUCH. Elasmobranchs as living resources: Advances in the biology, ecology, systematics and the status of the fisheries. NOAA Technical Report NMFS **90**: 1-15.

HOLDEN, M.J., 1972. The growth rates of *Raja brachyura, Raja clavata* and *Raja montagui* as determined from tagging data. J. Cons. perm. int. Explor. Mer **34**: 161-168.

HOLDEN, M.J., 1973. Are long-term sustainable fisheries for elasmobranchs possible? Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, 164: 360-376.

HOLDEN, M.J., 1974a. Problems in the rational exploitation of elasmobranchs populations and some suggested solutions. In: F.R. HARDEN-JONES. Sea fisheries research, Elek Science, London: 117-137.

HOLDEN, M.J., 1974b. Ray migrations - do bigger eggs mean better dispersal? Proc. Challenger Soc. **4**: 215.

HOLDEN, M.J., 1975. The fecundity of *Raja clavata* in British waters. J. Cons. perm. int. Explor. Mer **36**: 110-118.

HOLDEN, M.J., 1978. Long-term changes in landings of fish from the North Sea. Rapp. P.-v. Réun Cons. perm. int. Explor. Mer **172**: 11-26.

HOLDEN, M.J. & R.N. TUCKER, 1974. The food of *Raja clavata* Linneaus 1758, *Raja montagui* Fowler 1910, *Raja naevus* Muller and Henle 1841 and *Raja brachyura* Lafont 1873 in British waters. J. Cons. perm. int. Explor. Mer **35**: 189-193.

HOLDEN, M.J., D.W. ROUT & C.N. HUMPHREYS, 1971. The rate of egg laying by three species of ray. J. Cons. perm. int. Explor. Mer **33**: 335-339.

KNIJN, R.J., T.W. BOON, H.J.L. HEESSEN & J.R.G. HISLOP, 1993. Atlas of North Sea fisheries based on bottom trawl survey data from the years 1985-1987. ICES, Cooperative Research Report No. **194**, ICES, Denmark: 268 pp.

MCARTHUR, R.H. & E.O. WILSON, 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

OGURI, M., 1990. A review of selected physiological characteristics unique to Elasmobranchs. In: H.L. PRATT, S.H. GRUBER & T. TANIUCHI. Elasmobranchs as living resources: Advances in the biology, ecology, systematics and the satus of the fisheries. NOAA Technical Report NMFS **90**: 48-55.

ROUSSET, J., 1990. Population structure of thornback rays *Raja clavata* and their movements in the Bay of Douarnenez. J. Mar. Biol. Ass. U.K. **70**: 261-268.

RYLAND, J.S. & T.O. AJAYI, 1984. Growth and population dynamics of three *Raja* species (Batoidei) in Carmarthen Bay, British Isles. J. Cons. perm. int. Explor. Mer **41**: 111-120.

SPARHOLT, H. & M. VINTHER, 1991. The biomass of starry ray (*Raja radiata*) in the North Sea. J. Cons. perm. int. Explor. Mer **47**: 295-302.

STEVEN, G.A., 1934. Observations on the growth of the claspers and cloaca in *Raja clavata* Linneaus. J. Mar. Biol. Ass. U.K. **19**: 887-899.

STEVEN, G.A., 1936. Migration and growth of the thornback ray (*Raja clavata* L.). J. Mar. Biol. Ass. U.K. **20**: 605-614.

TEMPLEMAN, W., 1982. Development, occurrence and characteristics of egg capsules of the Thorny Skate, *Raja radiata*, in the Northwest Atlantic. J. Northw. Atl. Sci. **3**: 47-56.

TEMPLEMAN, W., 1984. Migrations of thorny skate, *Raja radiata*, tagged in the Newfoundland area. J. Northw. Atl. Fish. Sci. **5**: 55-63.

TOMCZAK, G. & E. GOEDECKE, 1962. Monatskarten der Temperatur der Nordsee, dargestellt für verschiedene Tiefenhorizonte. Deutschen Hydrographischen Zeitschrift, Ergänzungsheft Reihe B (4°), nr. **7**.

VINTHER, M., 1989. Some notes on the Biology of the starry ray *Raja radiata*, in the North Sea. ICES Working document for ICES study group on Elasmobranch fisheries, April 1989: 1-20 .

VINTHER, M. & H. SPARHOLT, 1988. The biomass of skates in the North Sea. ICES C.M. 1988/G: 48: 1-26.

WHITEHEAD, P.J.P., M.-L. BAUCHOT, J.-C. HUREAU, J. NIELSEN & E. TORNONESE, 1984. Fishes of the North-eastern Atlantic and the Mediterranean. In: M. STEHMANN & D.L. BÜRKEL. United Nation Educational, Scienticic and Cultural Organisation: 163-196.

WOOD, C.C., K.S. KETCHEN & R.J. BEAMISH, 1979. Population dynamics of spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Board Can. **36**: 647-656.

APPENDICES

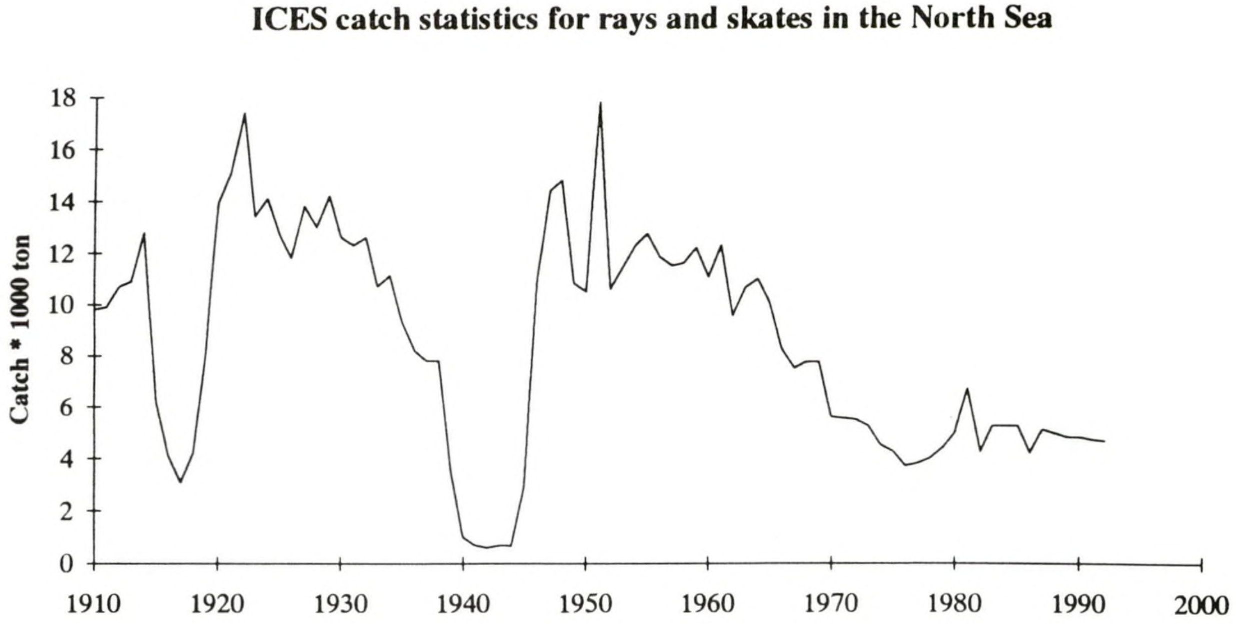


Fig. 1. ICES catch statistics for rays and skates in the North Sea from 1910 to 1992. Data from Bulletin Statistique (1910-1990).

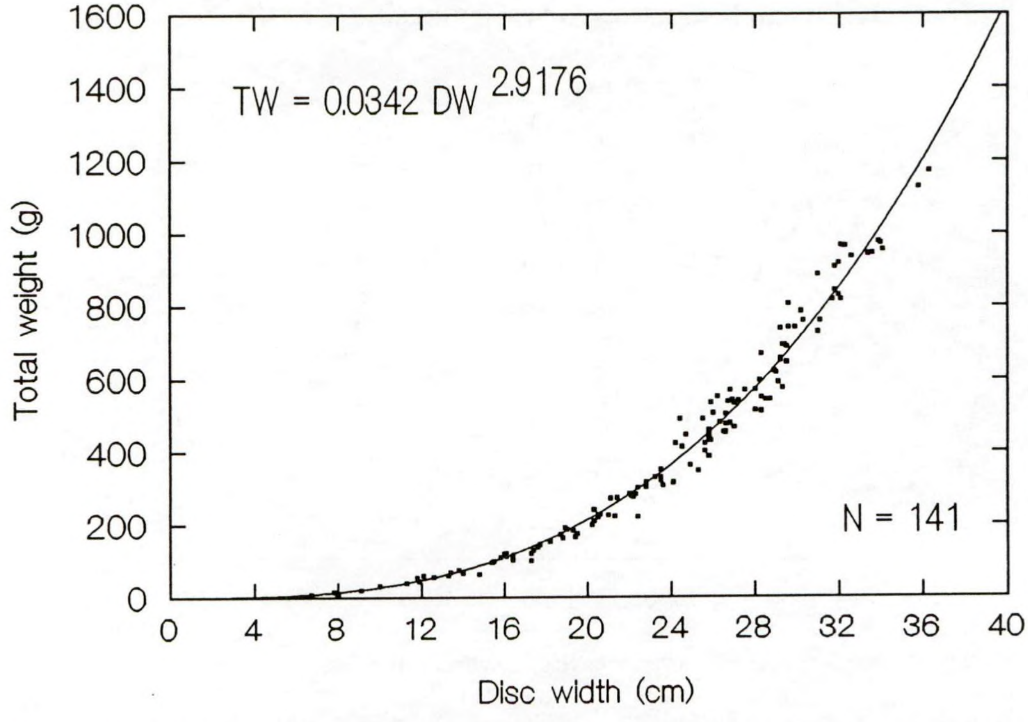


Fig. 2a. Relationship between total weight and disc width of male *Raja radiata* caught in the North Sea in 1992.

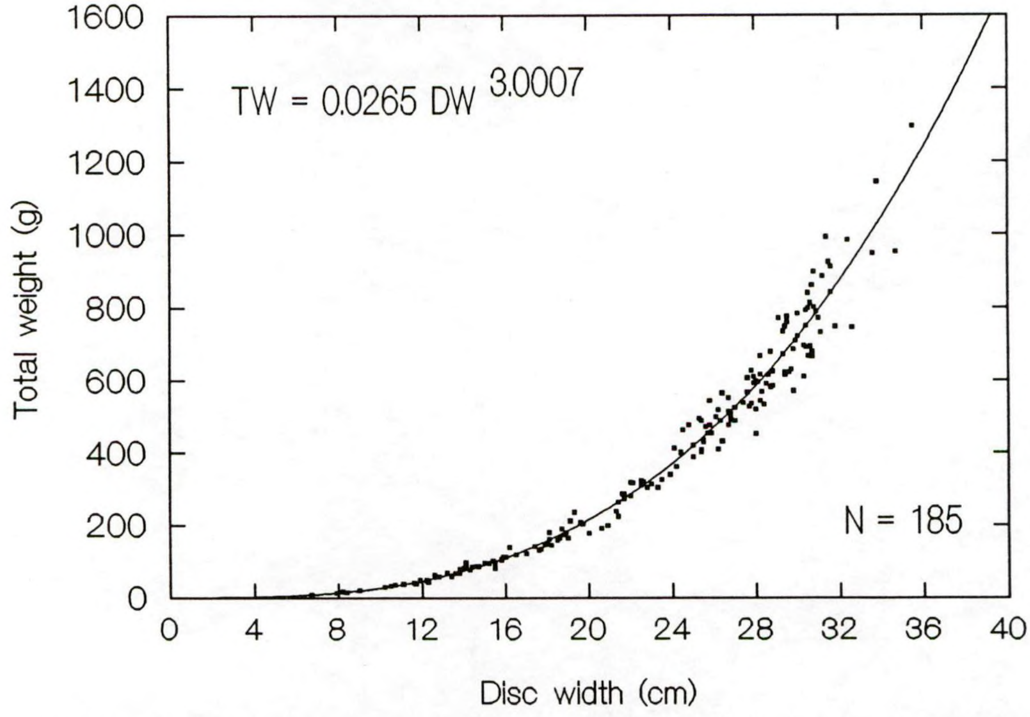


Fig. 2b. Relationship between total weight and disc width of female *Raja radiata* caught in the North Sea in 1992.

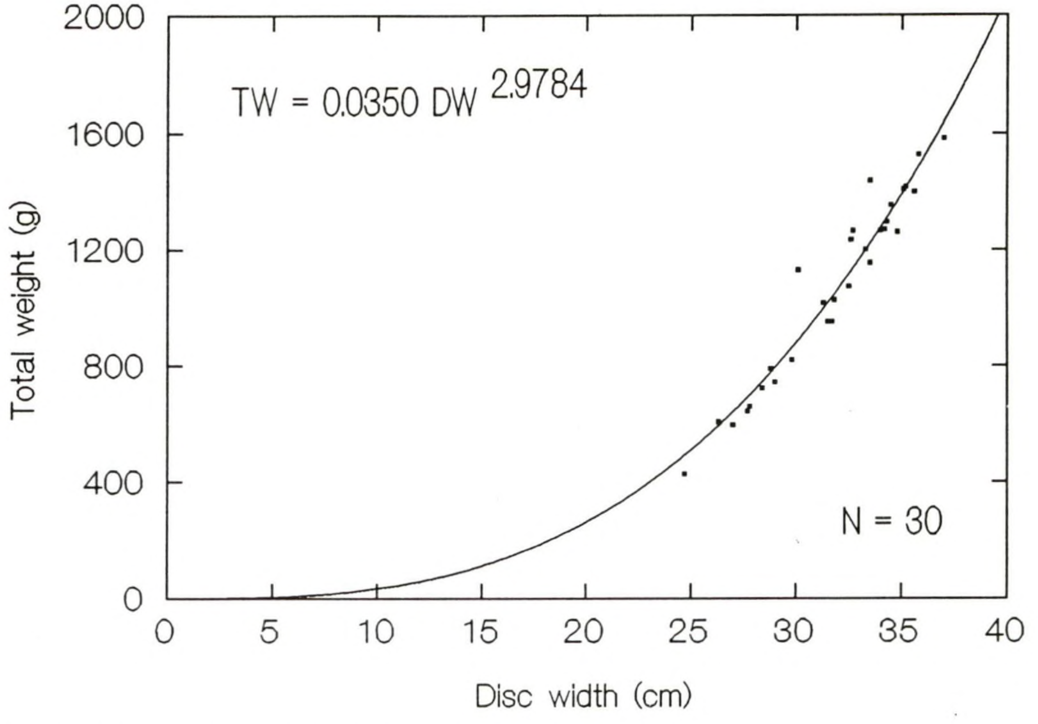


Fig. 3a. Relationship between total weight and disc width of male *Raja naevus* caught in the North Sea in 1992.

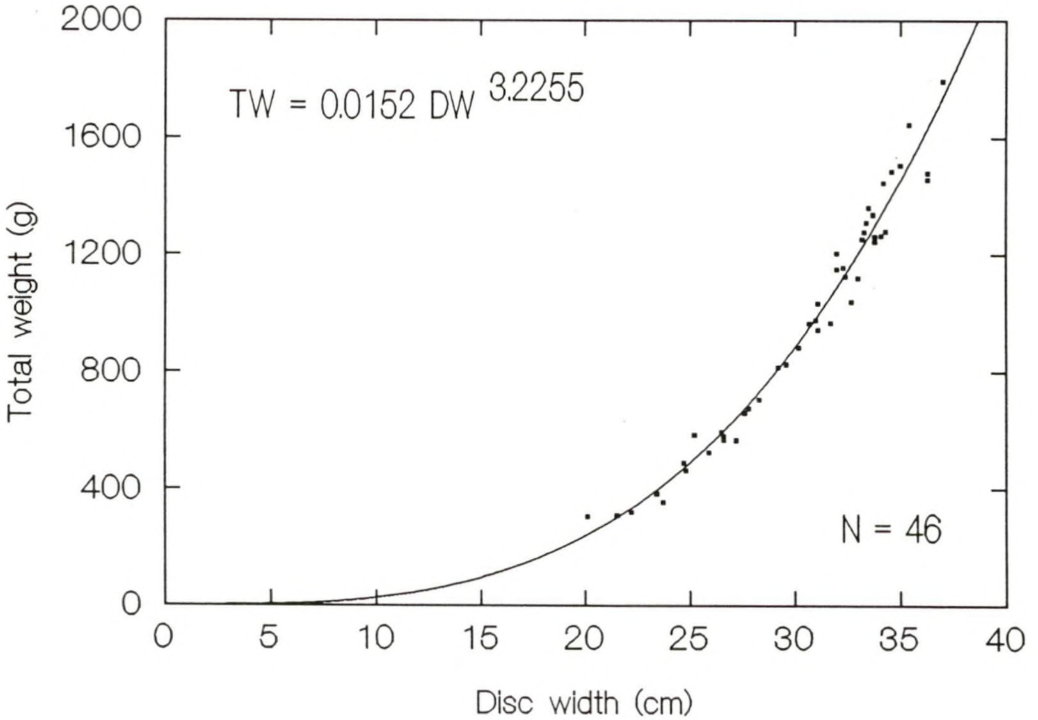


Fig. 3b. Relationship between total weight and disc width of female *Raja naevus* caught in the North Sea in 1992.

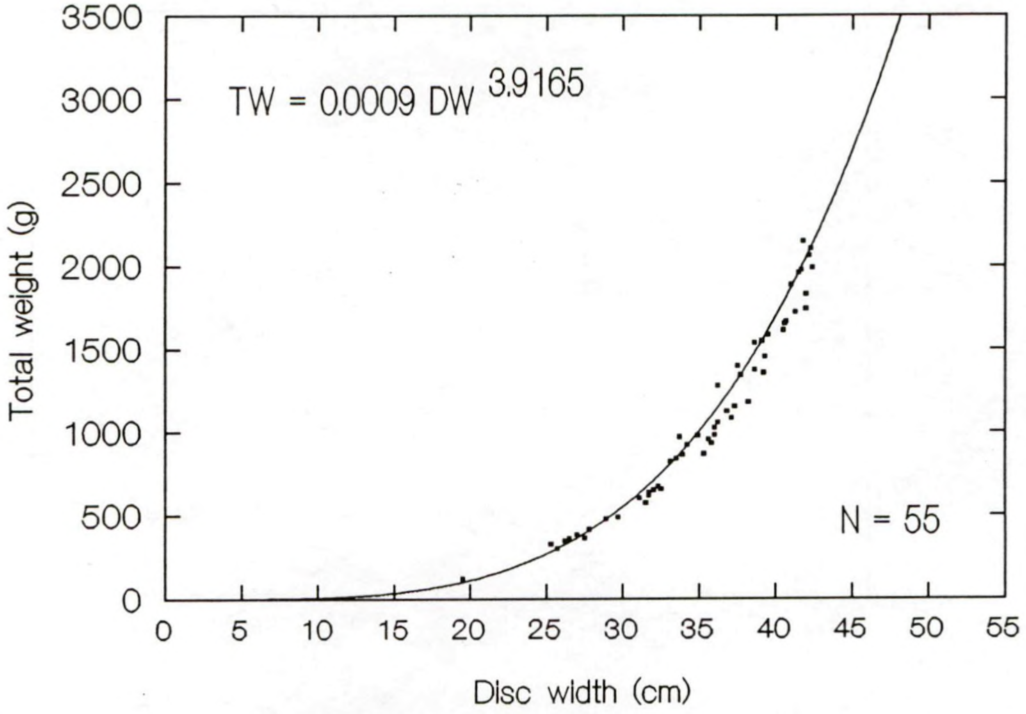


Fig. 4a. Relationship between total weight and disc width of male *Raja montagui* caught in the North Sea in 1992.

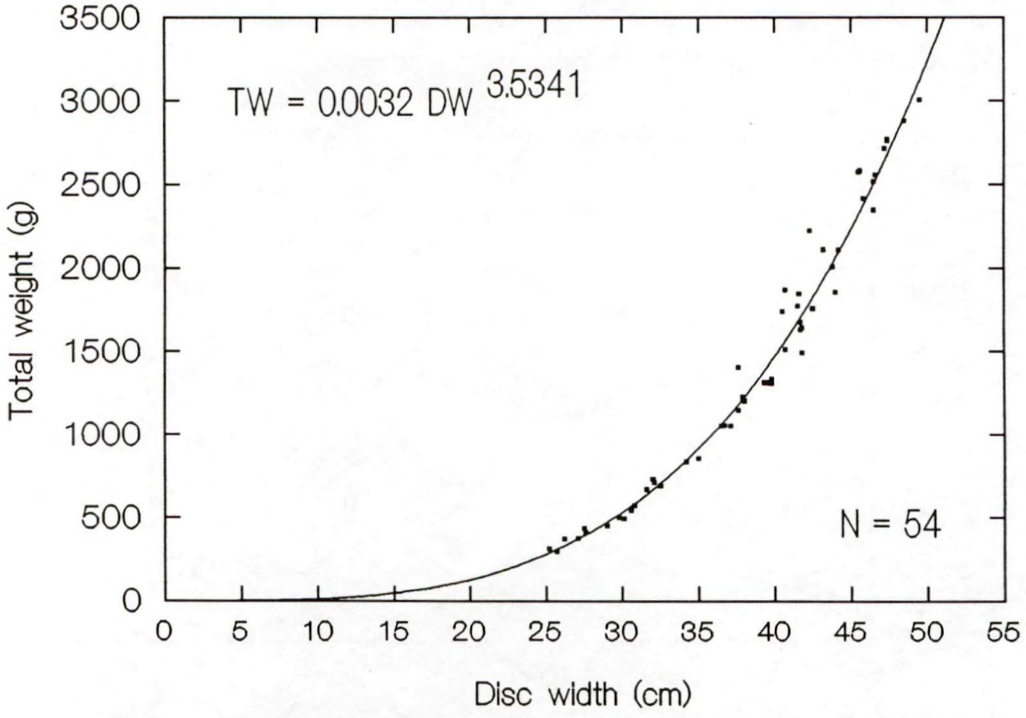


Fig. 4b. Relationship between total weight and disc width of female *Raja montagui* caught in the North Sea in 1992.

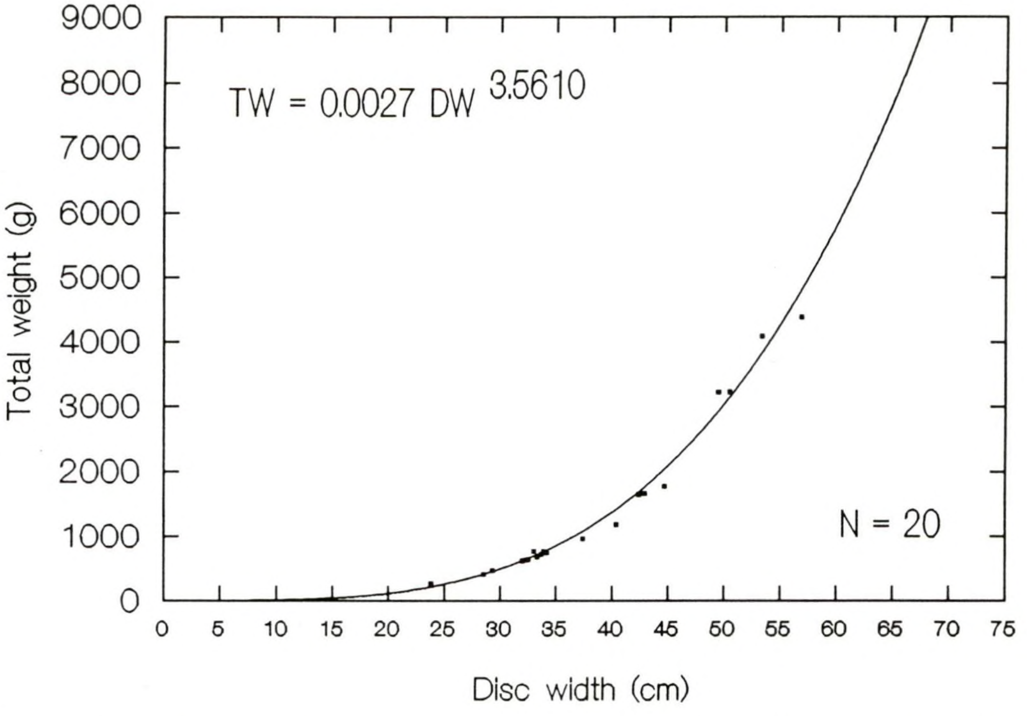


Fig. 5a. Relationship between total weight and disc width of male *Raja clavata* caught in the North Sea in 1992.

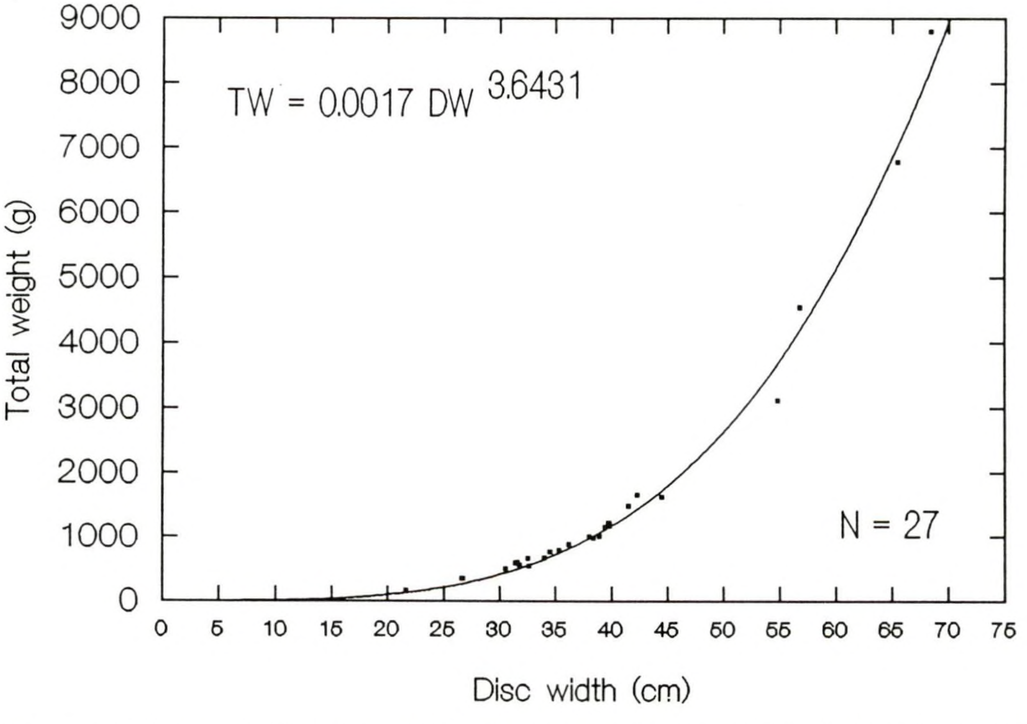


Fig. 5b. Relationship between total weight and disc width of female *Raja clavata* caught in the North Sea in 1992.

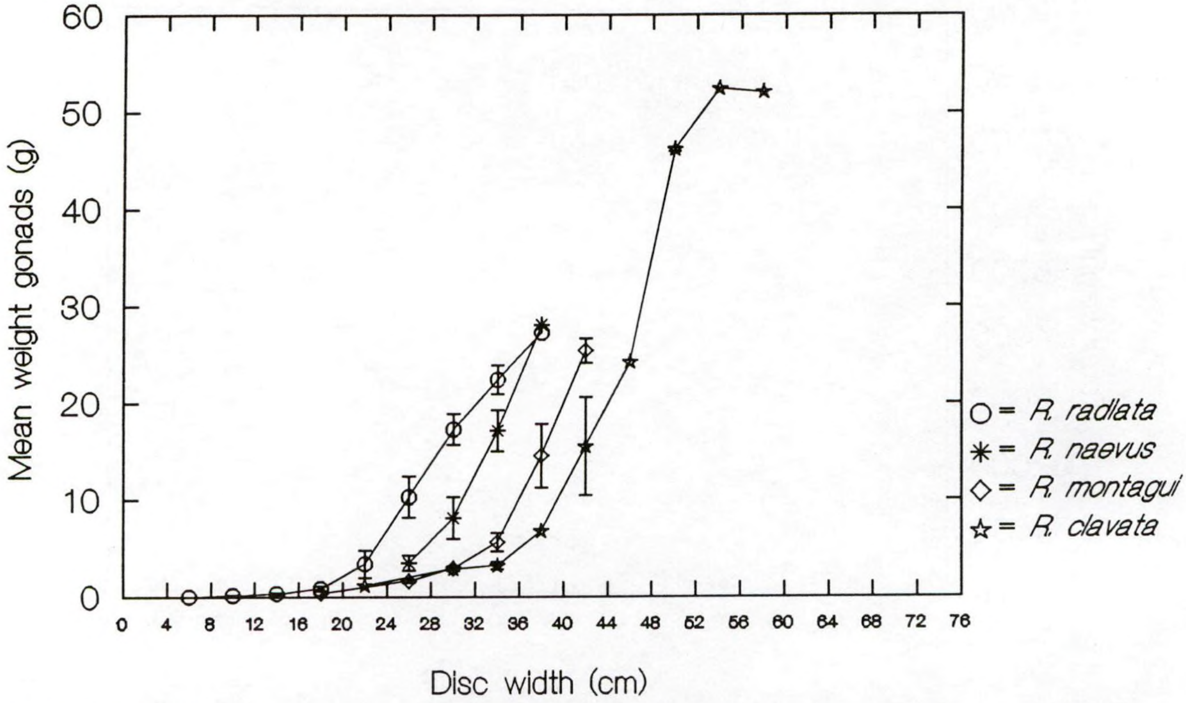


Fig. 6a. Mean weight of the gonads per disc width class of male *Raja radiata*, *R. naevus*, *R. montagui* and *R. clavata* caught in the North Sea in 1992. The values and standard deviation are plotted in the middle of each disc width class.

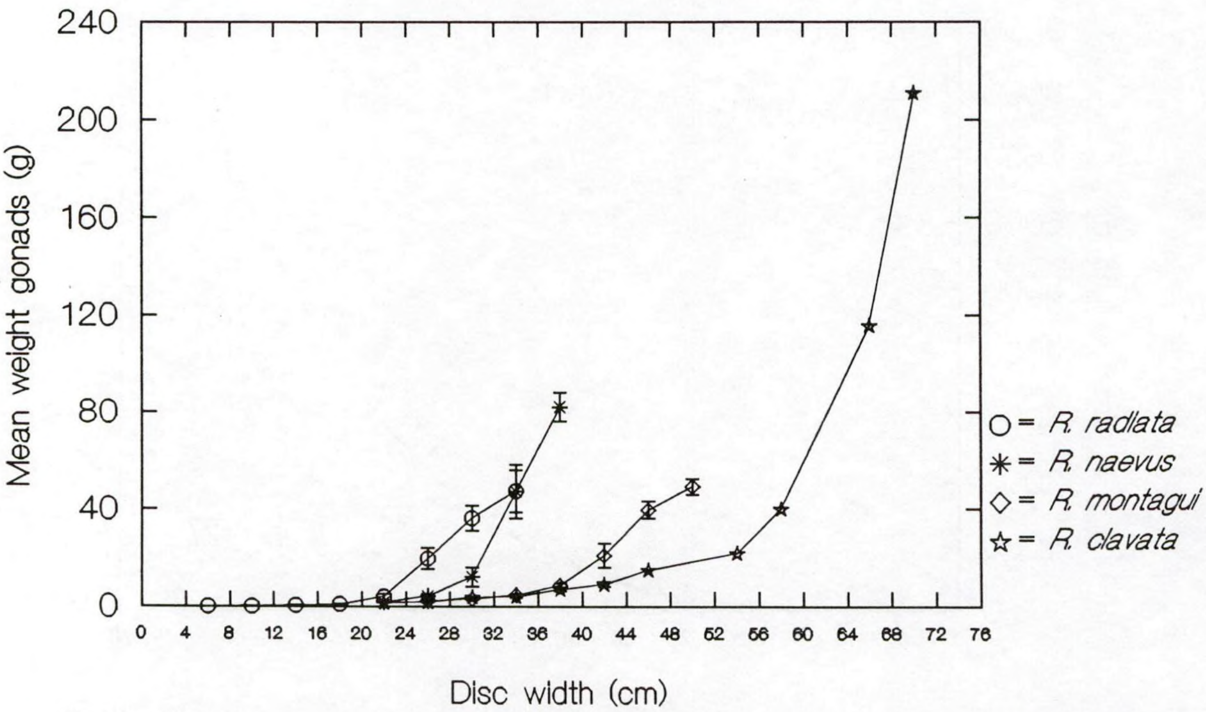


Fig. 6b. Mean weight of the gonads per disc width class of female *Raja radiata*, *R. naevus*, *R. montagui* and *R. clavata* caught in the North Sea in 1992. The values and standard deviation are plotted in the middle of each disc width class.

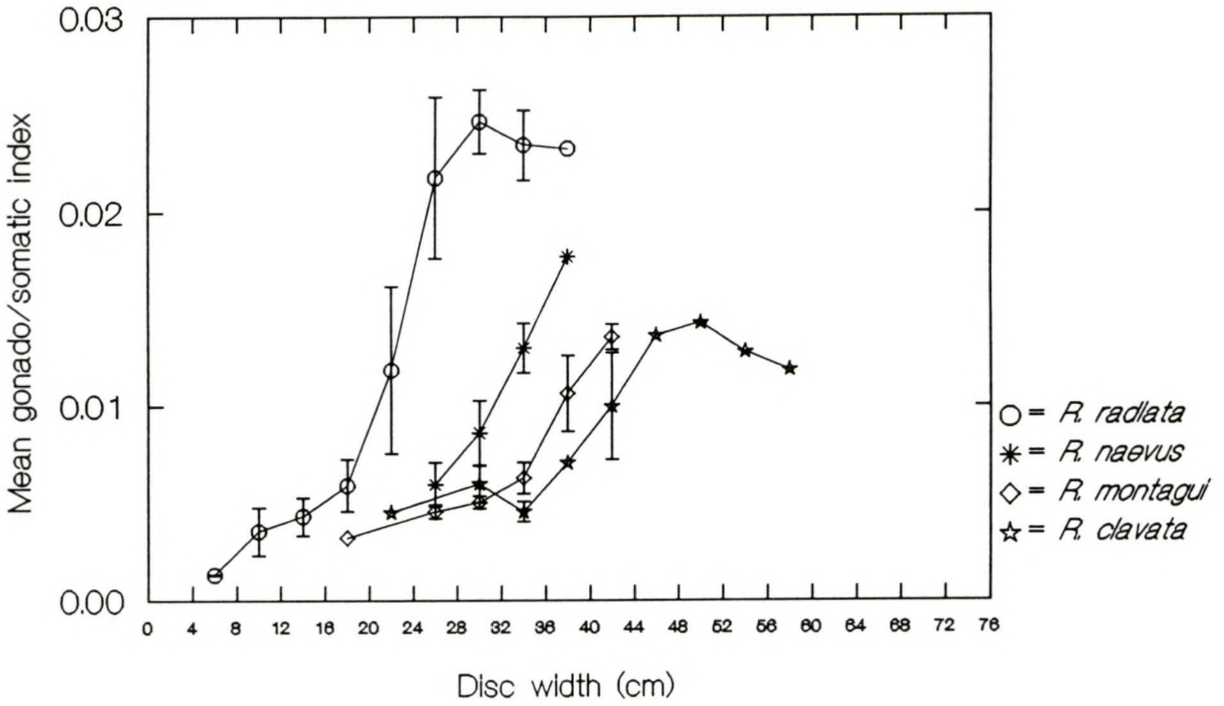


Fig. 7a. Mean gonado/somatic index per disc width class of male *Raja radiata*, *R. naevus*, *R. montagui* and *R. clavata* caught in the North Sea in 1992. The values and standard deviation are plotted in the middle of each disc width class.

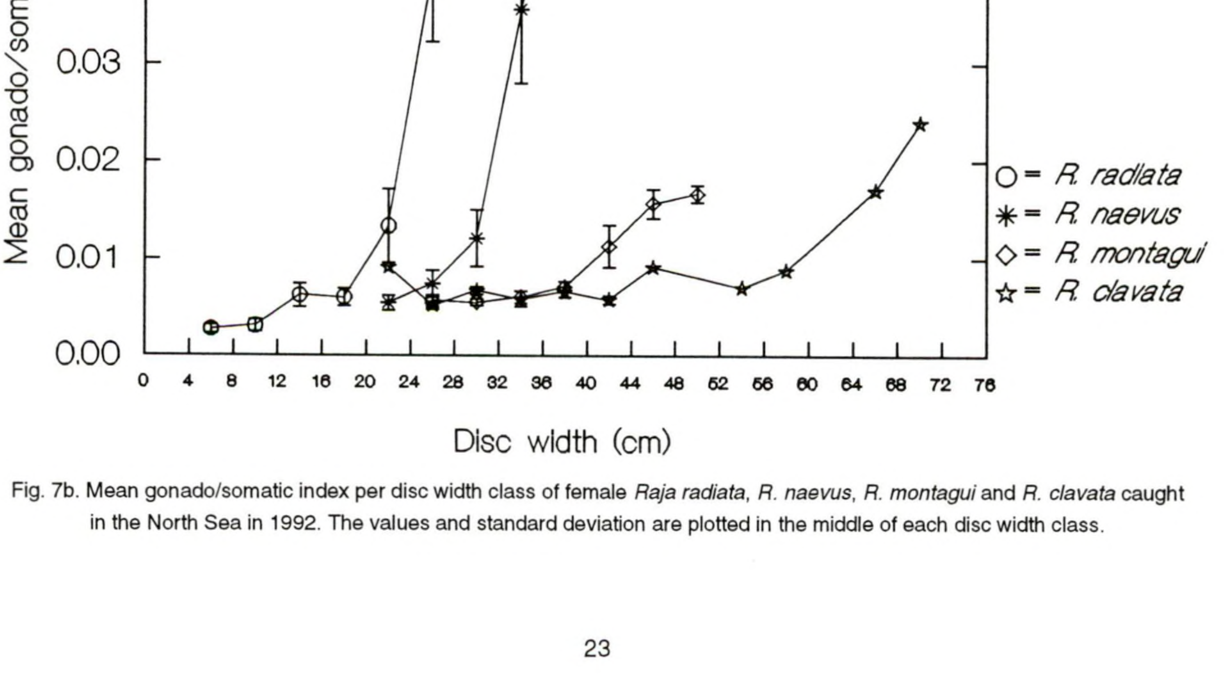


Fig. 7b. Mean gonado/somatic index per disc width class of female *Raja radiata*, *R. naevus*, *R. montagui* and *R. clavata* caught in the North Sea in 1992. The values and standard deviation are plotted in the middle of each disc width class.

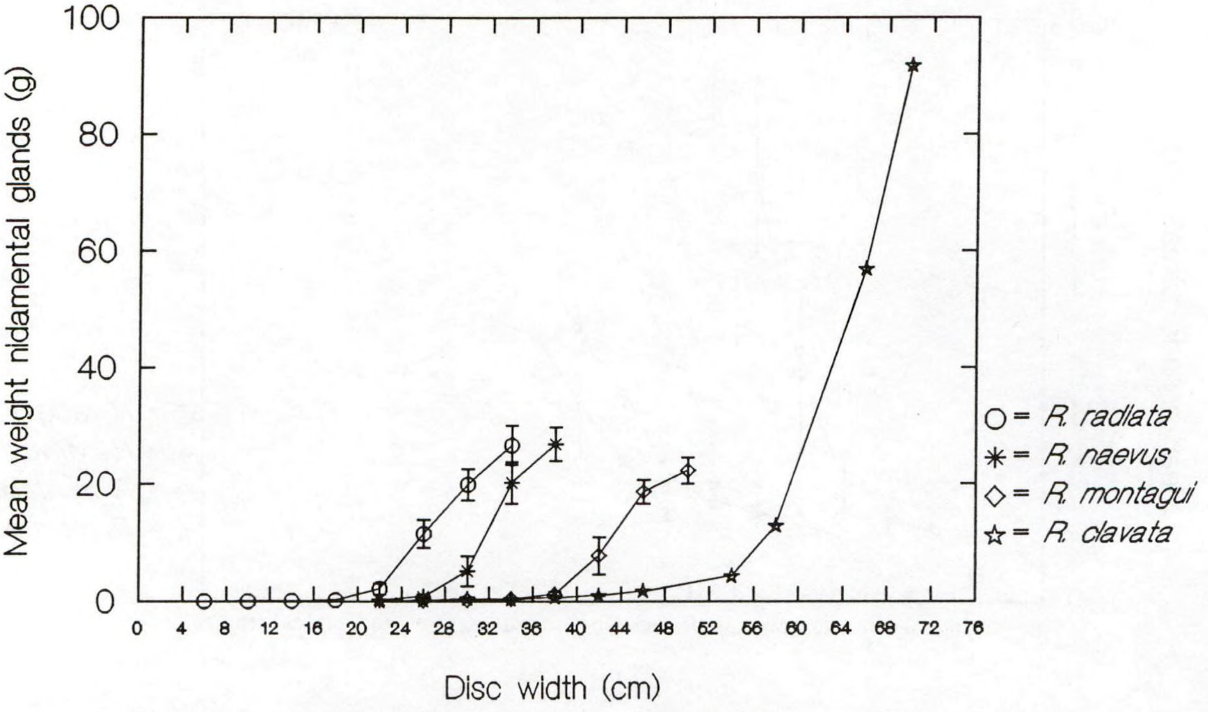


Fig. 8. Mean weight nidamental glands per disc width class of female *Raja radiata*, *R. naevus*, *R. montagui* and *R. clavata* caught in the North Sea in 1992. The values and standard deviation are plotted in the middle of each disc width class.

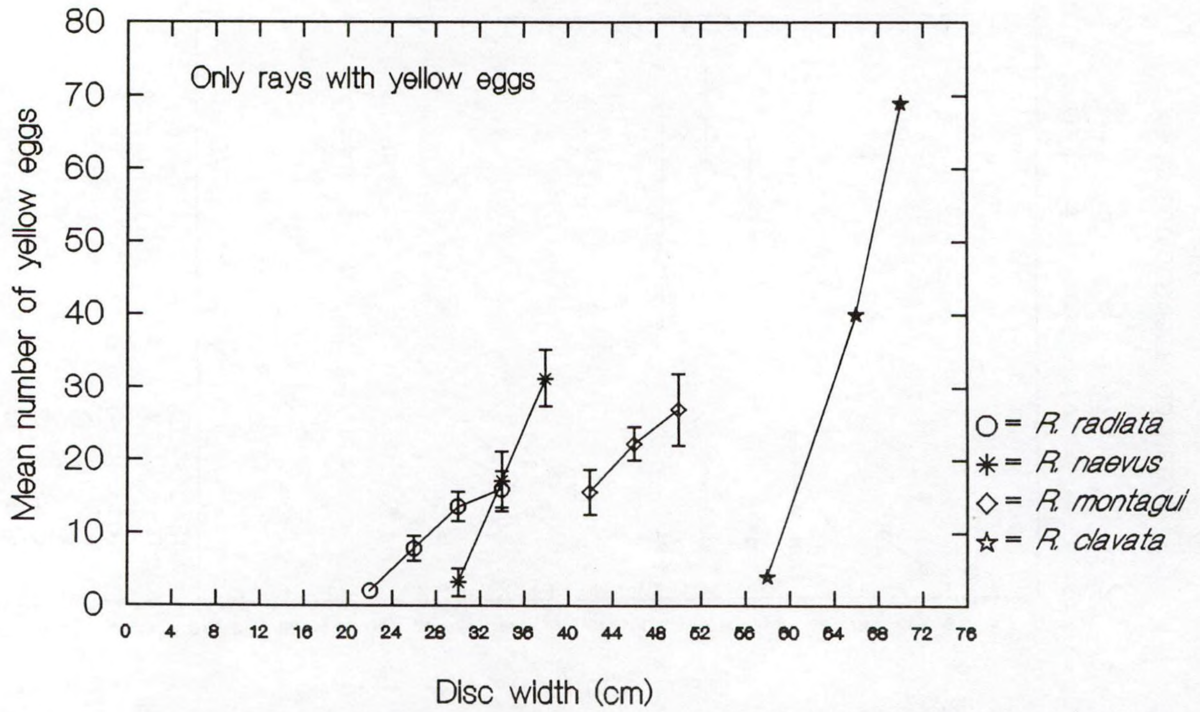


Fig. 9. Mean number of yellow eggs per disc width class of female *Raja radiata*, *R. naevus*, *R. montagui* and *R. clavata* caught in the North Sea in 1992. The values and standard deviation are plotted in the middle of each disc width class.

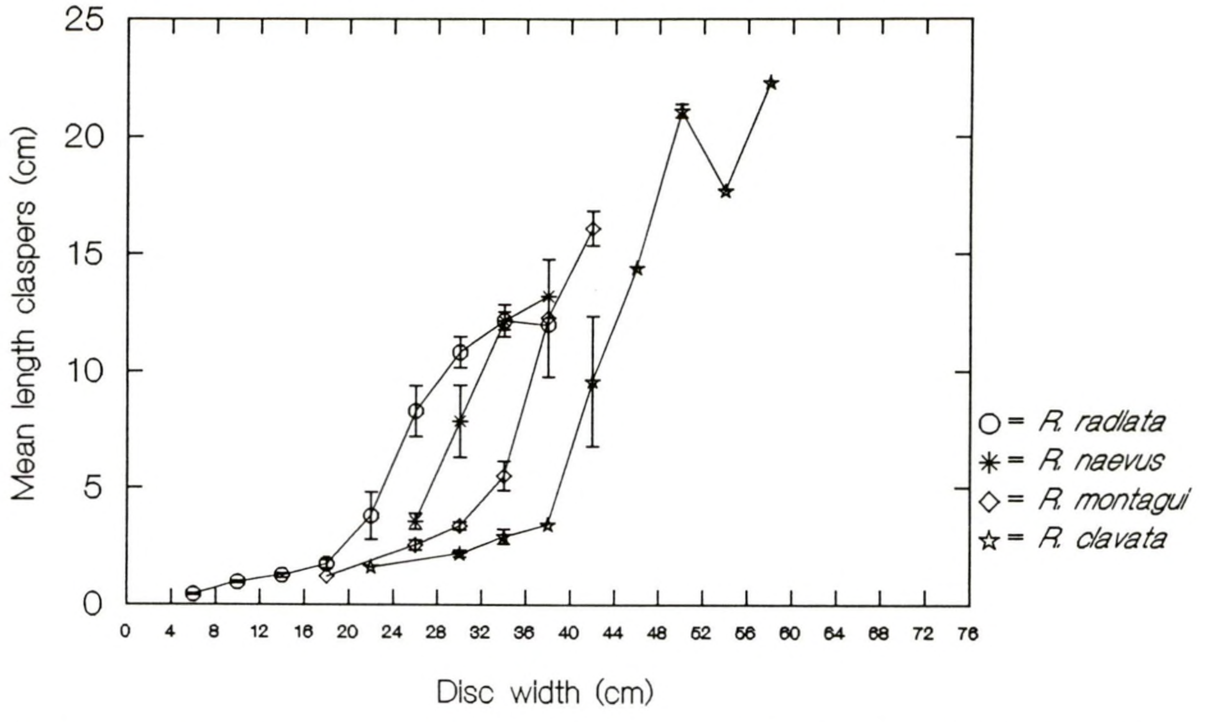


Fig. 10. Mean length of right claspers per disc width class of male *Raja radiata*, *R. naevus*, *R. montagui* and *R. clavata* caught in the North Sea in 1992. The values and standard deviation are plotted in the middle of each disc width class.

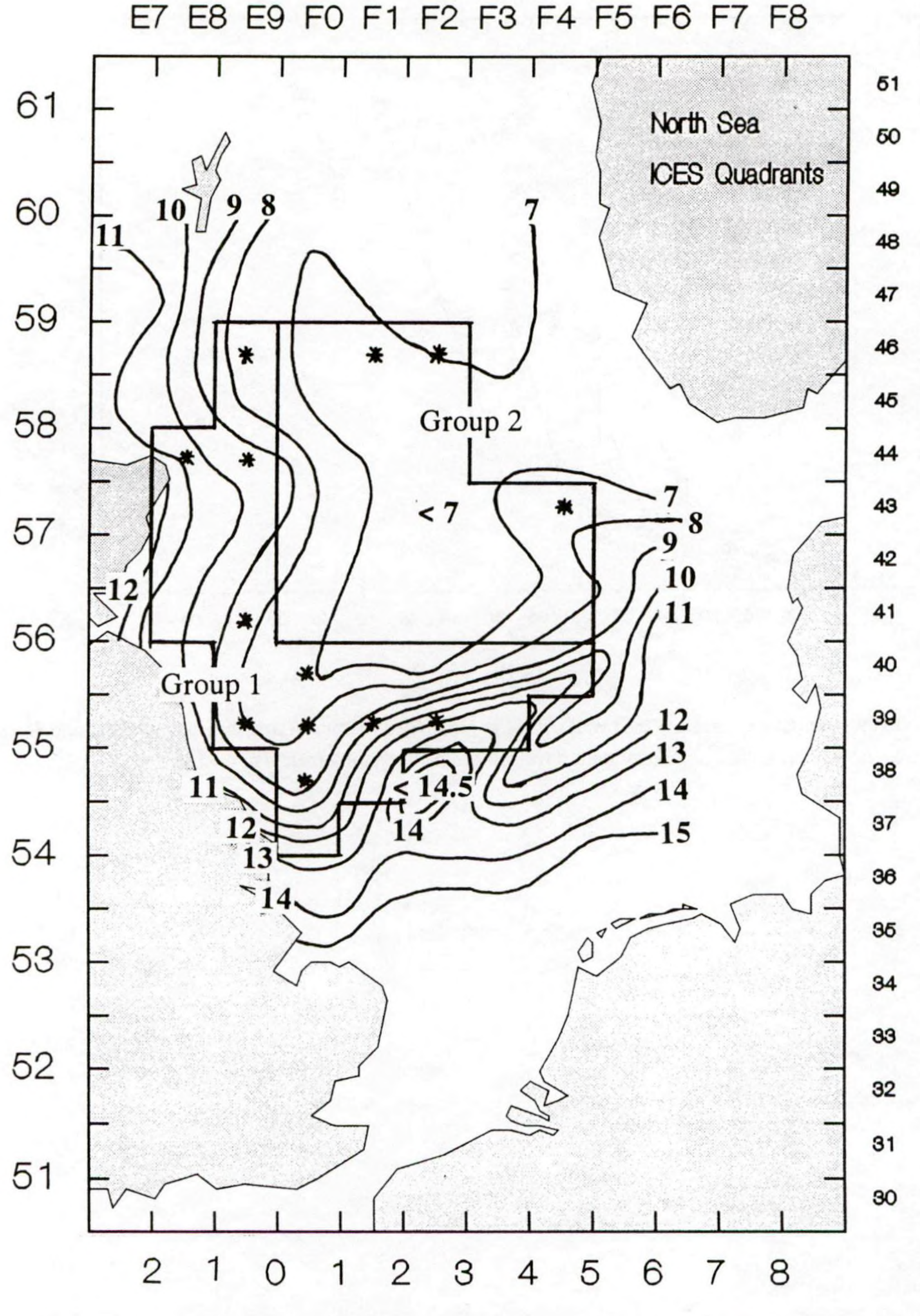


Fig. 11. Mean bottom water temperature in August from 1902-1952 (redrawn from TOMCZAK & GOEDECKE, 1962). Stars represent the ICES quadrants in which individuals of group 1 and 2 of *Raja radiata* were caught in the North Sea in August/September in 1992 (see Table 2). The division in group 1 and 2 is based on overall difference in mean bottom water temperature of August.

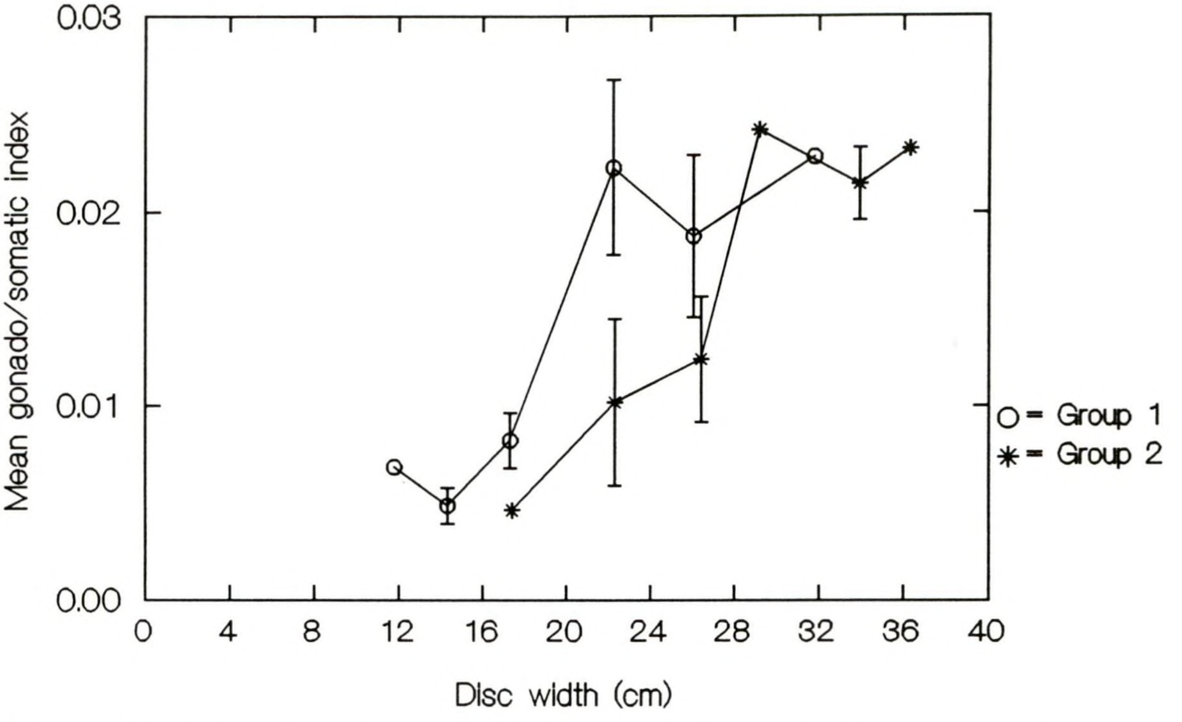


Fig. 12a. Mean gonado/somatic index (mean and standard deviation) per disc width class of male *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

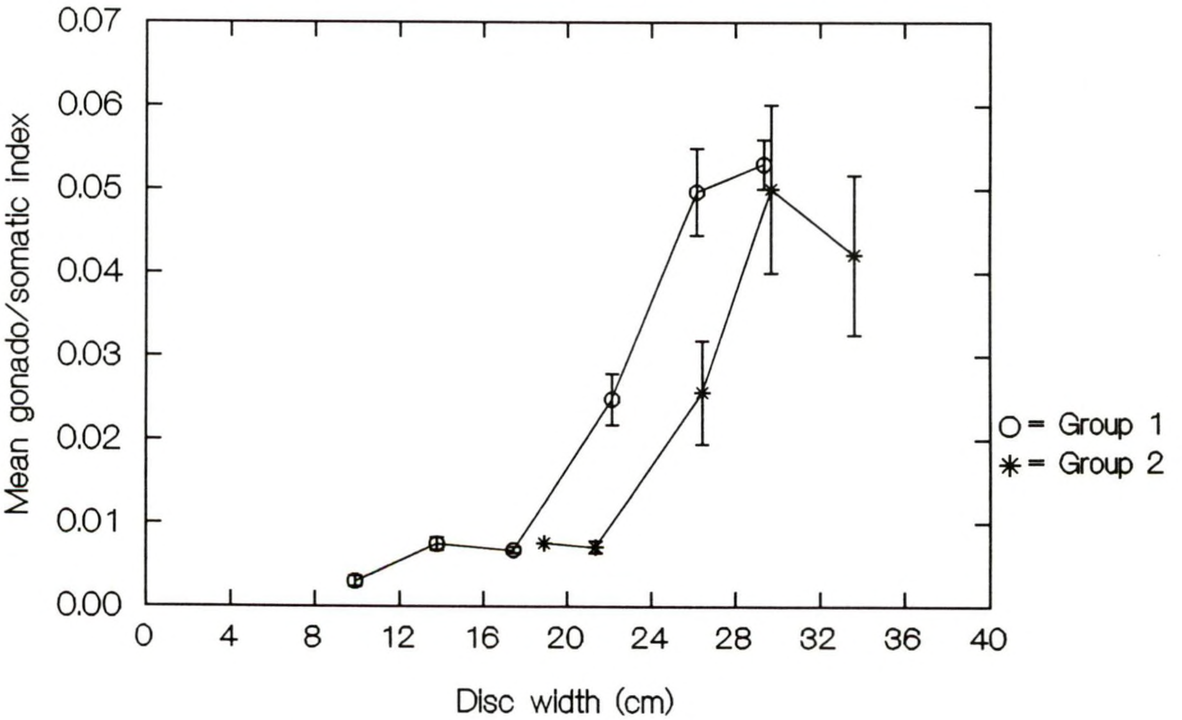


Fig. 12b. Mean gonado/somatic index (mean and standard deviation) per disc width class of female *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

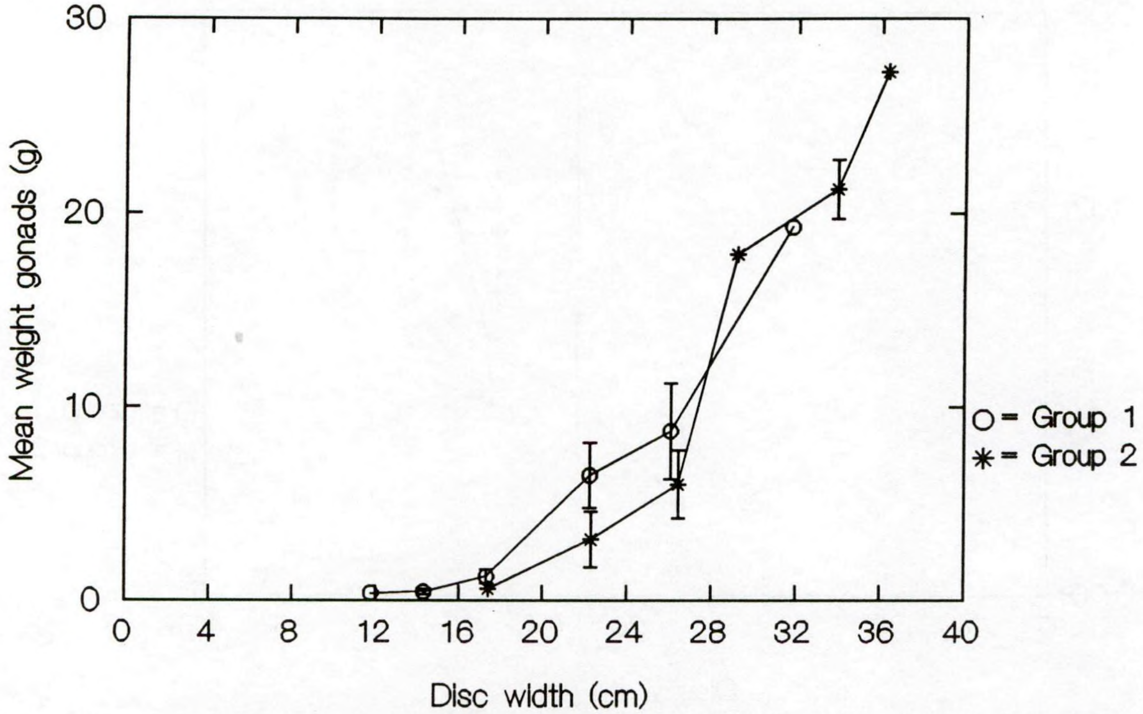


Fig. 13a. Mean weight of the gonads (mean and standard deviation) per disc width class of male *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

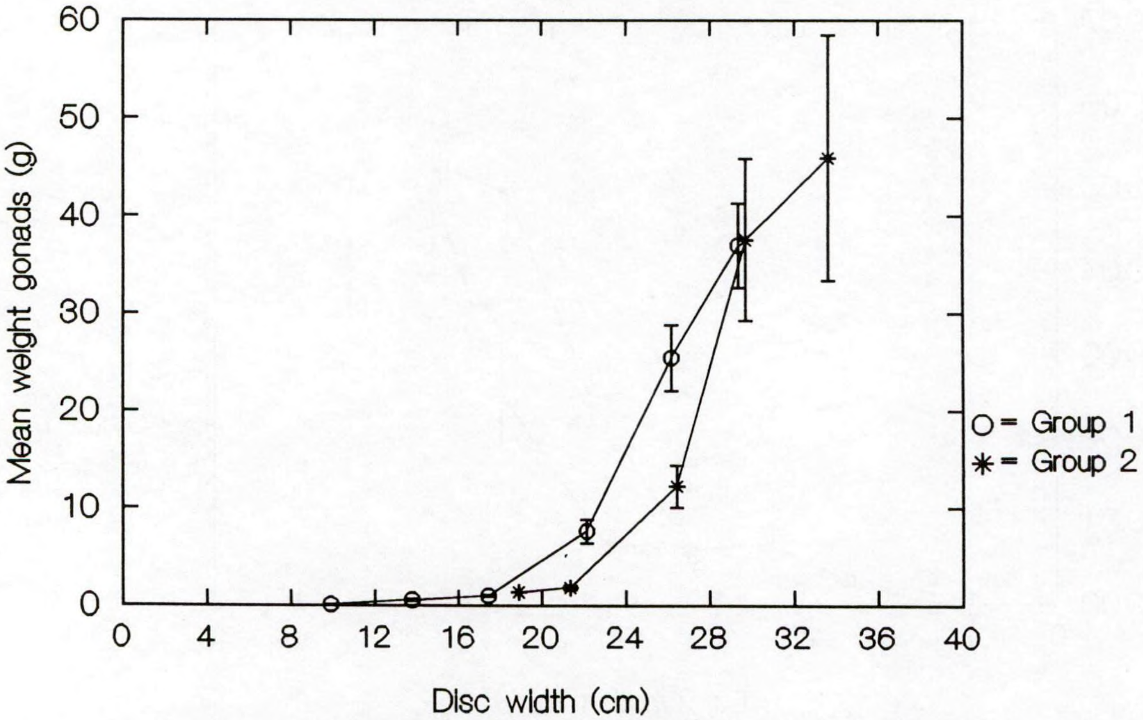


Fig. 13b. Mean weight of the gonads (mean and standard deviation) per disc width class of female *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

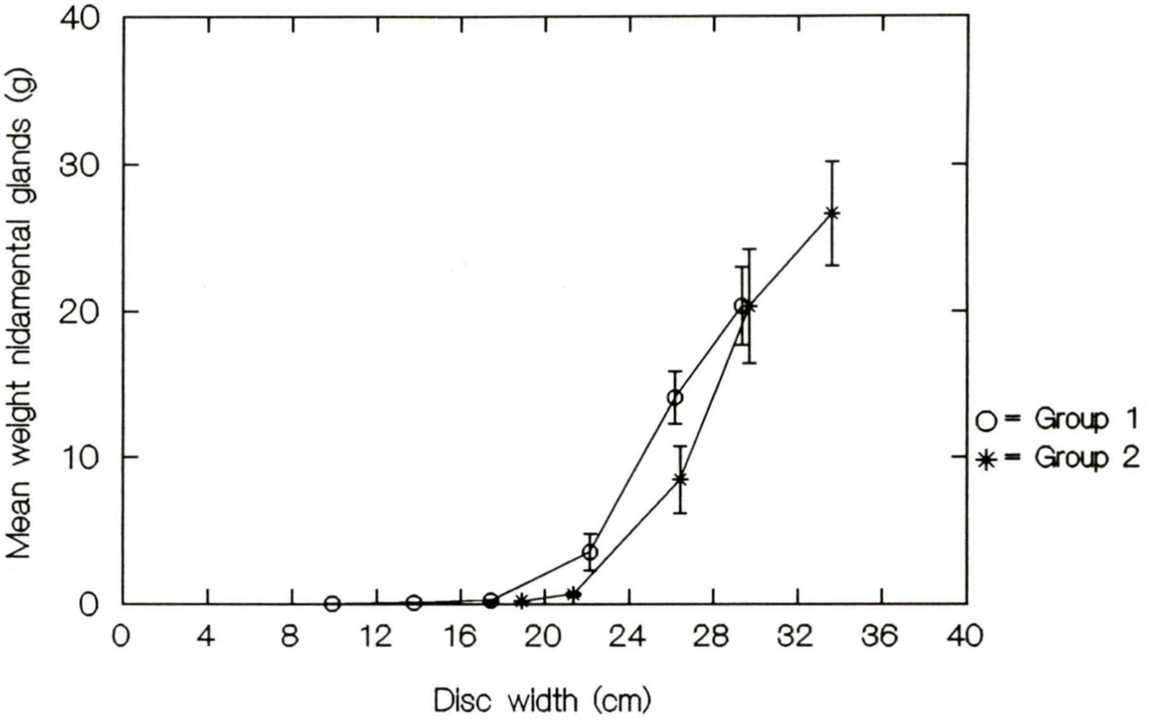


Fig. 14. Mean weight of the nidamental glands (mean and standard deviation) per disc width class of female *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

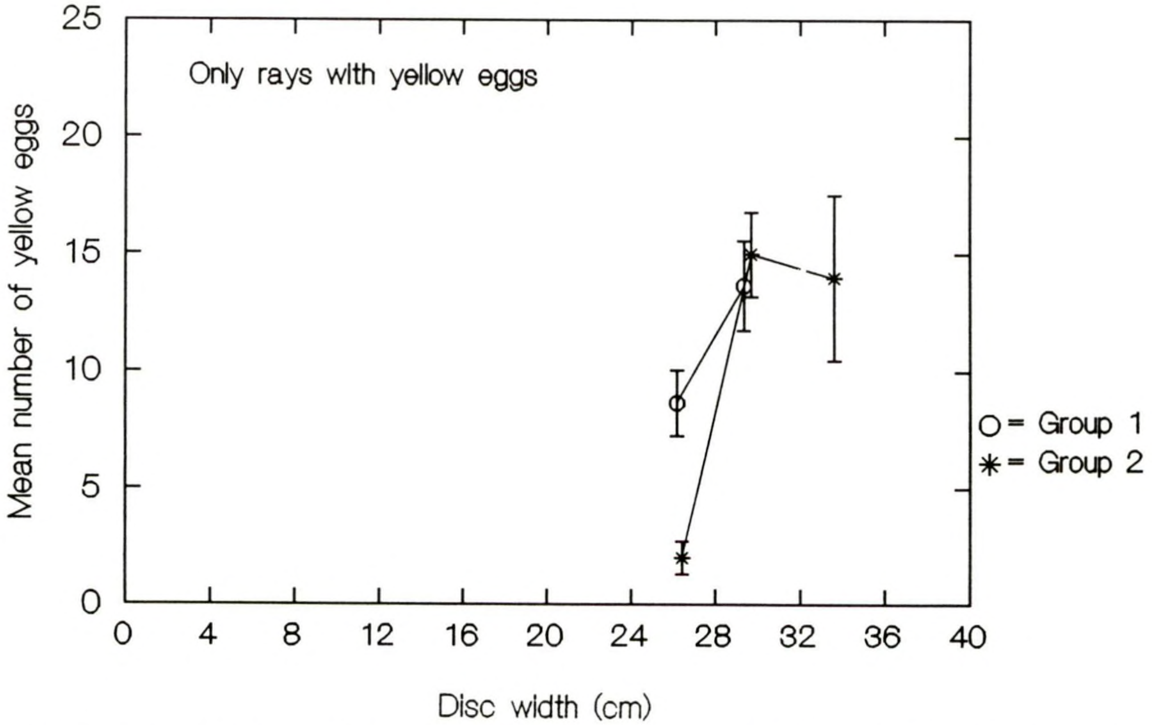


Fig. 15. Mean number of yellow eggs (mean and standard deviation) per disc width class of female *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

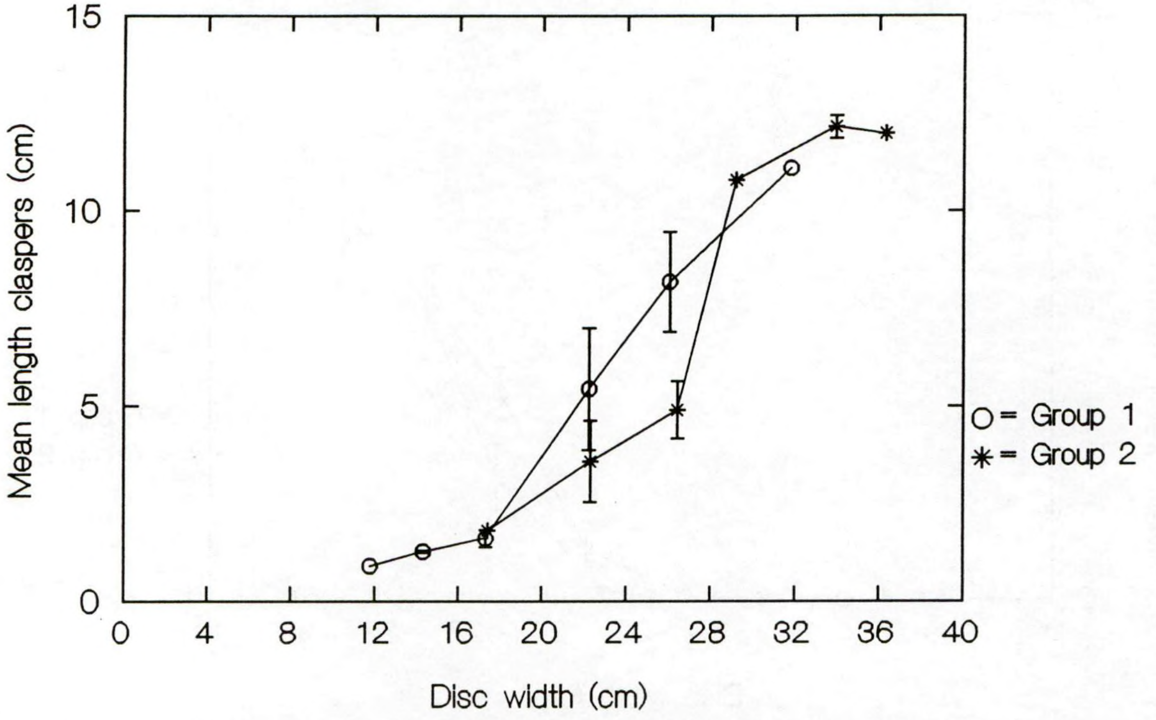


Fig. 16. Mean length of the right claspers (mean and standard deviation) per disc width class of male *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

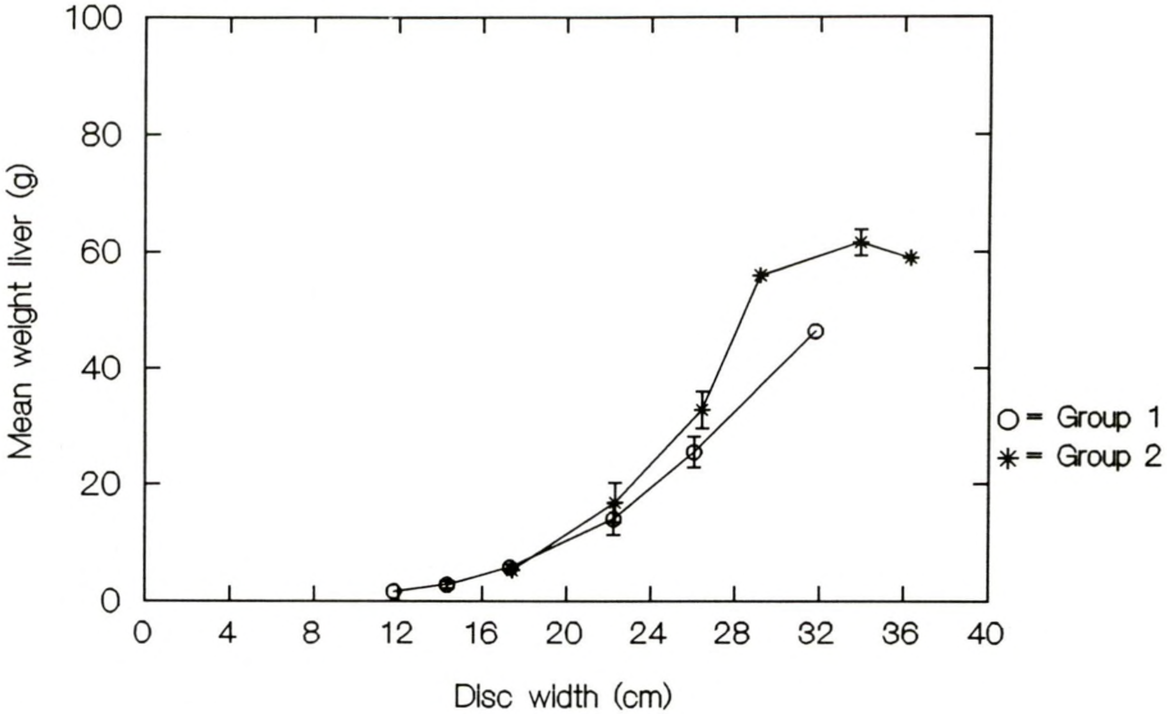


Fig. 17a. Mean weight of the liver (mean and standard deviation) per disc width class of male *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

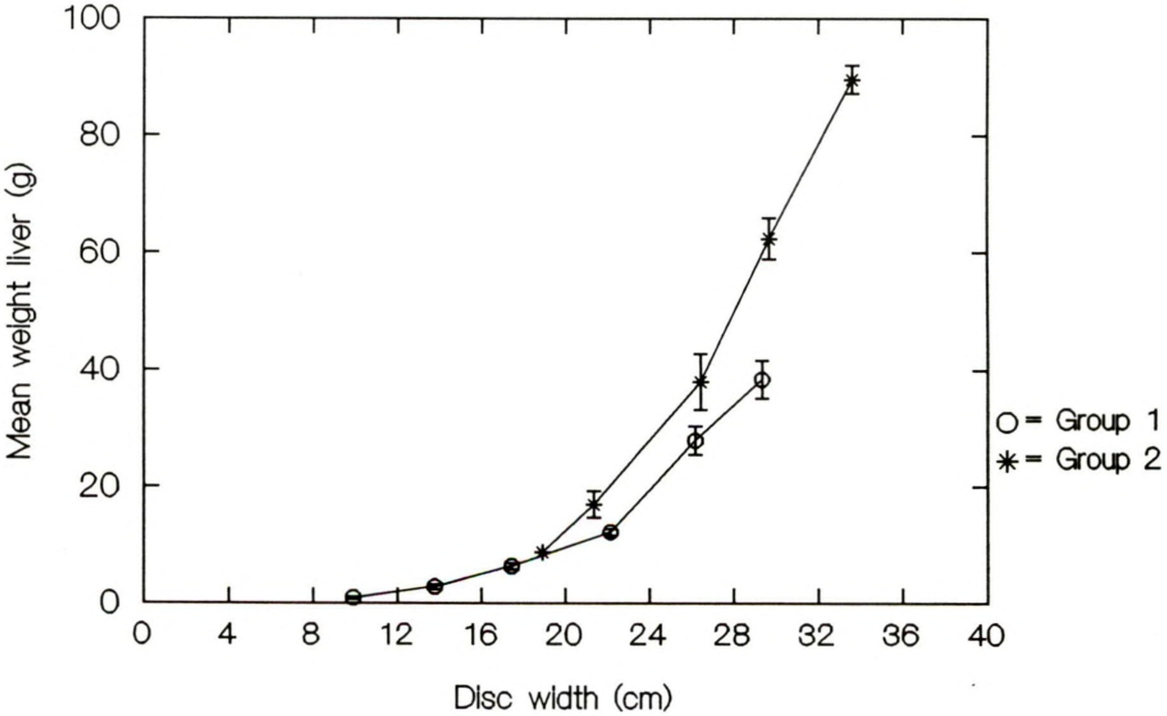


Fig. 17b. Mean weight of the liver (mean and standard deviation) per disc width class of female *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

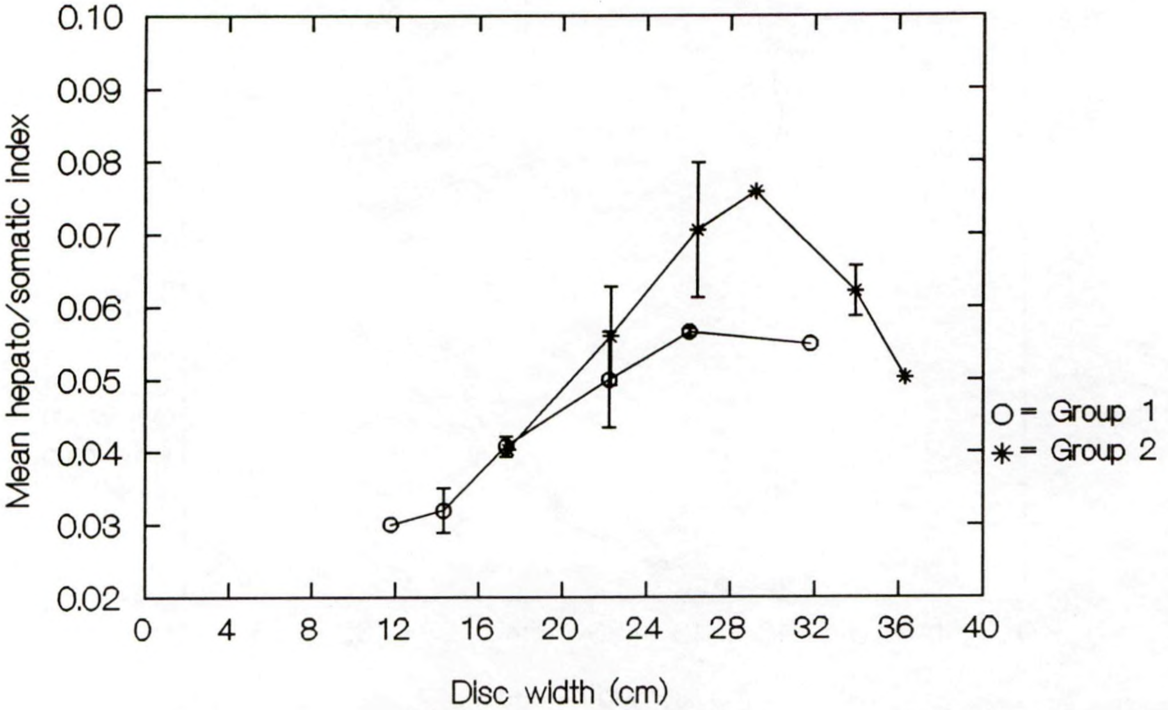


Fig. 18a. Mean hepato/somatic index (mean and standard deviation) per disc width class of male *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

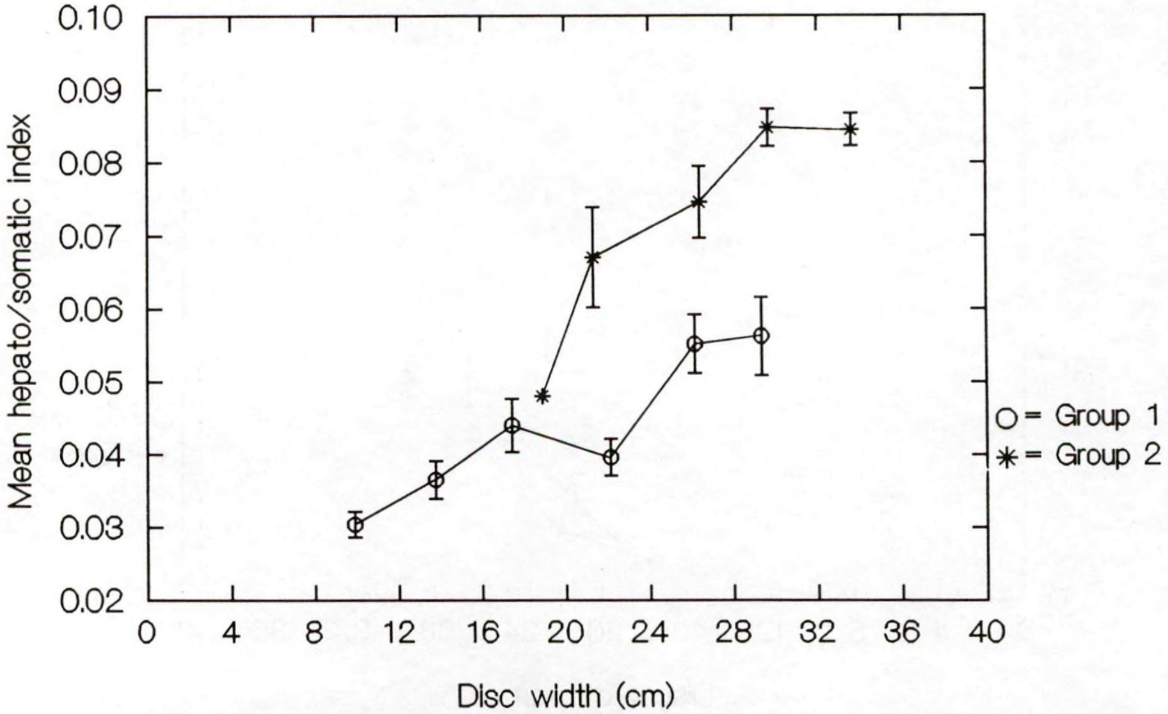


Fig. 18b. Mean hepato/somatic index (mean and standard deviation) per disc width class of female *Raja radiata* of group 1 and 2 caught in the North Sea in August-September 1992.

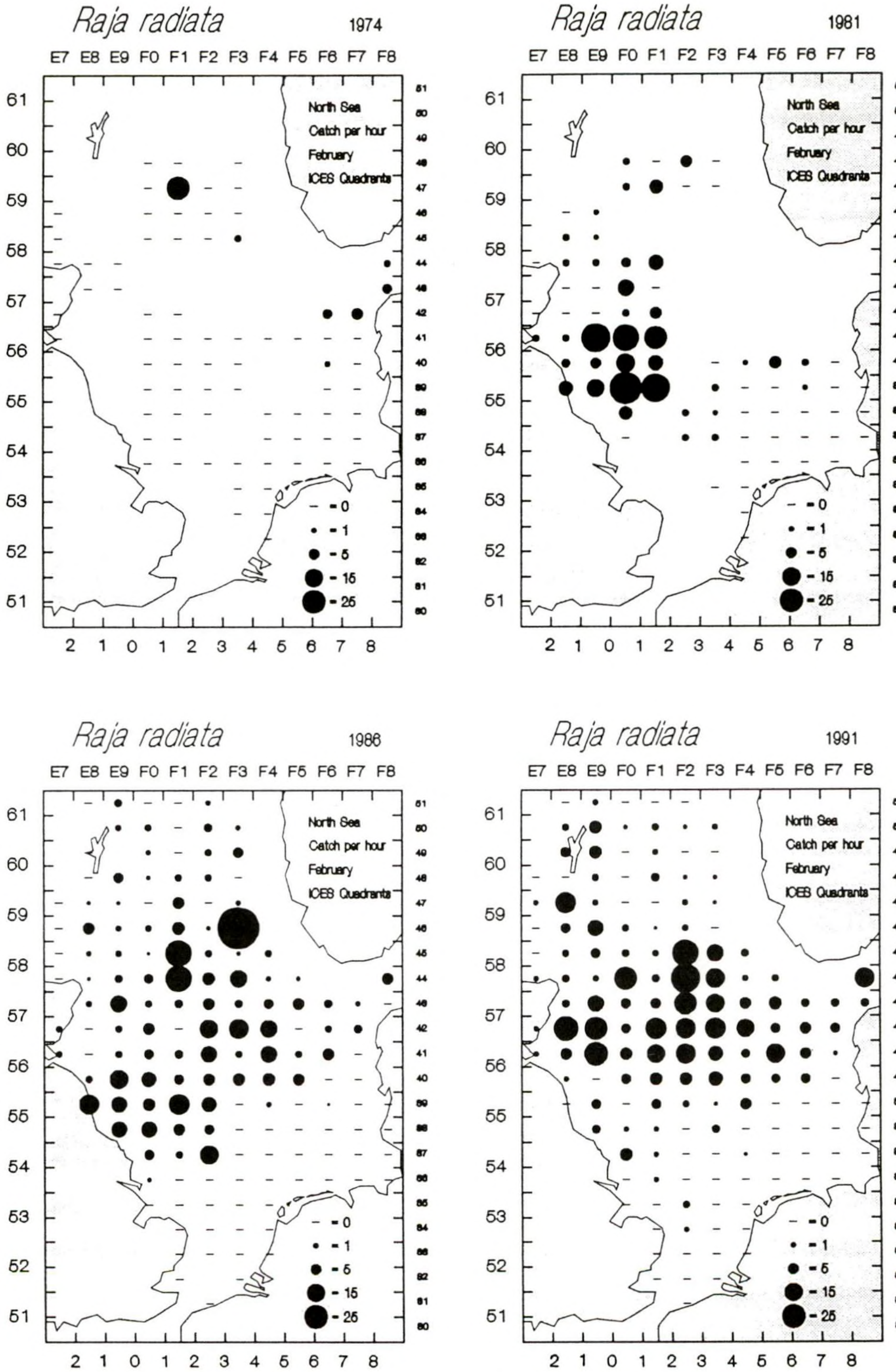


Fig. 19. Distribution area and abundance of *Raja radiata* in the North Sea in 1974, 1981, 1986 and 1991, based on catches made by the February surveys of the ICES and the IYFS. Each dot represents the mean number of rays caught per hour fishing per ICES quadrant.

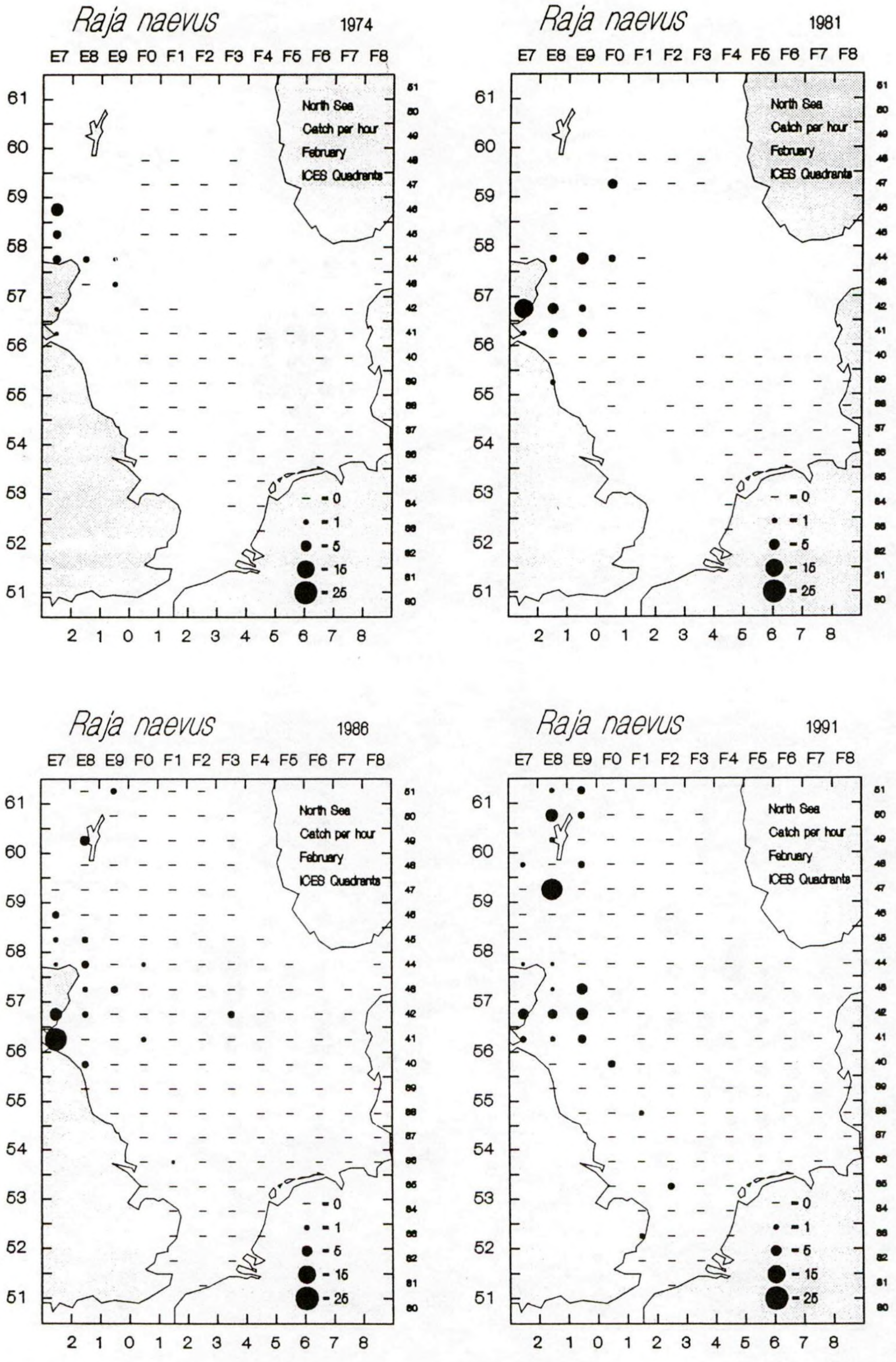


Fig. 20. Distribution area and abundance of *Raja naevus* in the North Sea in 1974, 1981, 1986 and 1991, based on catches made by the February surveys of the ICES and the IYFS. Each dot represents the mean number of rays caught per hour fishing per ICES quadrant.

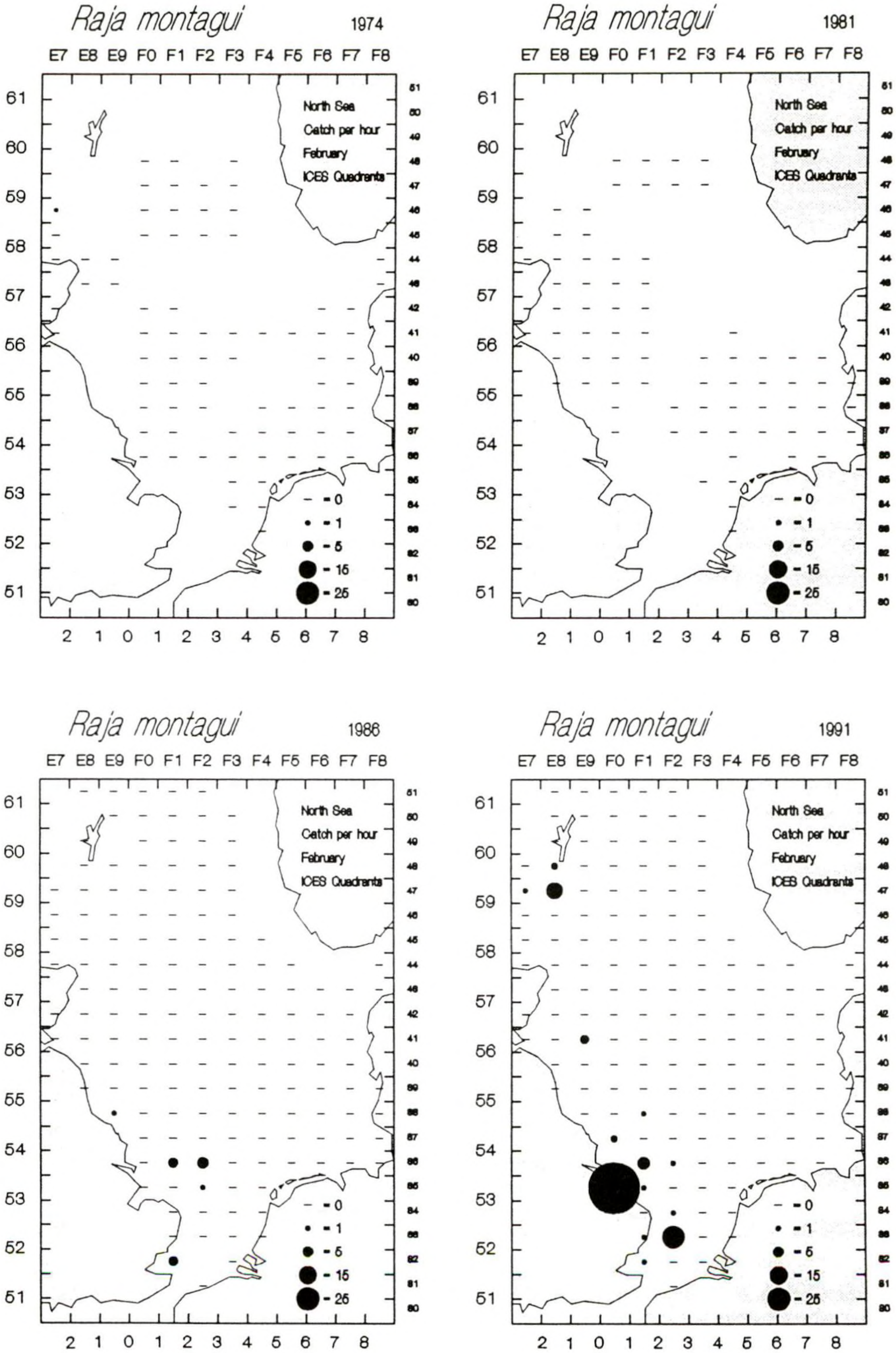


Fig. 21. Distribution area and abundance of *Raja montagui* in the North Sea in 1974, 1981, 1986 and 1991, based on catches made by the February surveys of the ICES and the IYFS. Each dot represents the mean number of rays caught per hour fishing per ICES quadrant.

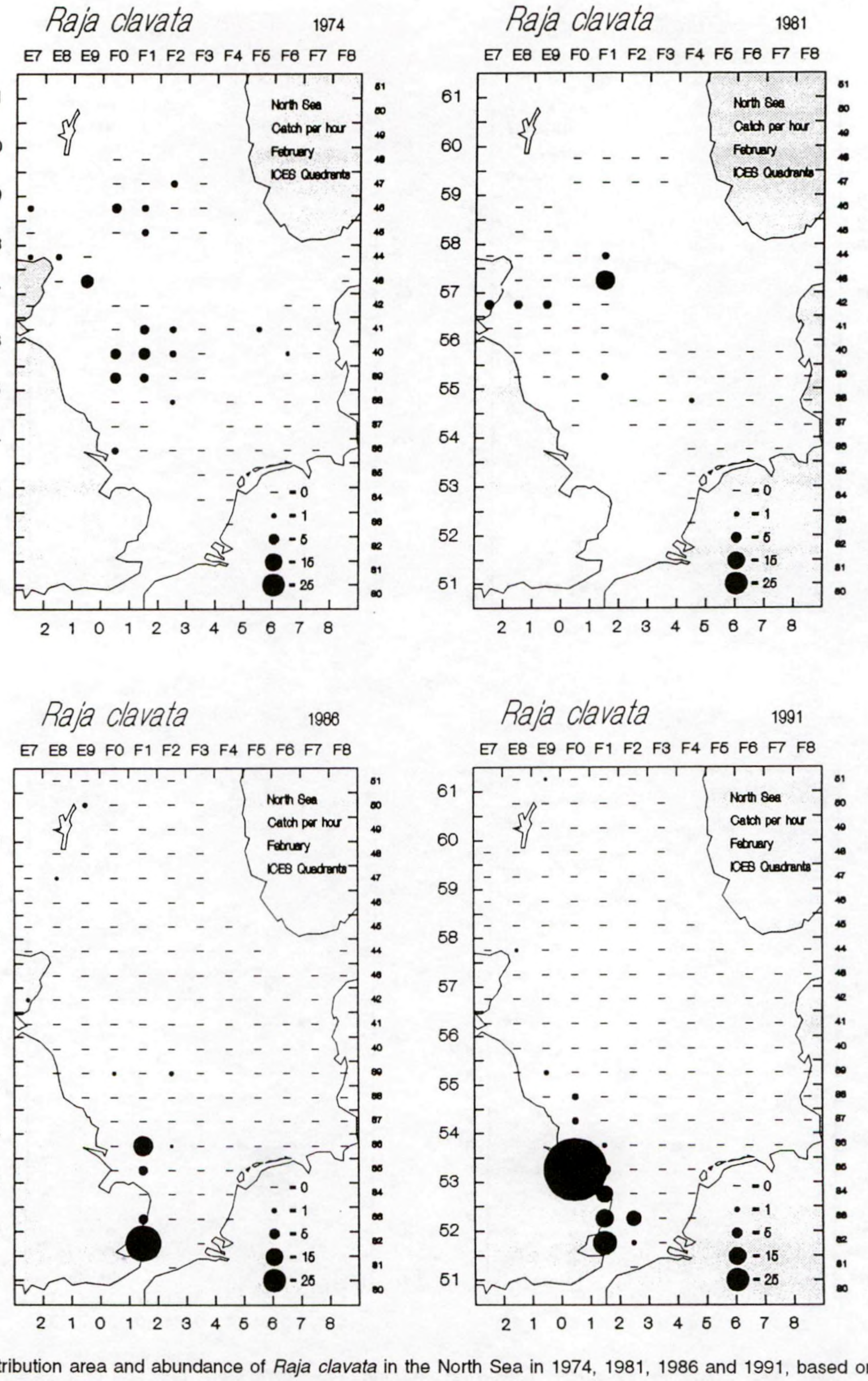


Fig. 22. Distribution area and abundance of *Raja clavata* in the North Sea in 1974, 1981, 1986 and 1991, based on catches made by the February surveys of the ICES and the IYFS. Each dot represents the mean number of rays caught per hour fishing per ICES quadrant.

TABLE 1

Growth parameters and fecundity of male and female *R. radiata*, *R. naevus*, *R. montagui* and *R. clavata* from different sources.

Literature summary

Growth parameters and fecundity

Species	Maximum length (cm) males	Maximum length (cm) females	Age at maturity males	Age at maturity females	Max. age males and females	Eggs/year average	Source
R. radiata	66	66	4-6	4-6			VINTHER, 1989
R. naevus	92	92	9	9	13-14	71-90	CLARK, 1922 DU BUIT, 1975, 1976
R. montagui	69-98	73-98	11	11	18	24	HOLDEN *et al.*, 1971 HOLDEN, 1972; 1974 RYLAND & AJAYI, 1984 FAHY, 1989
R. clavata	86	107	7-12	9-12	20	52	CLARK, 1922; STEVEN, 1936; HOLDEN *et al.*, 1971;HOLDEN, 1972 RYLAND & AJAYI, 1984

TABLE 2

Catch statistics of male and female *R. radiata*, *R. naevus*, *R. montagui* and *R. clavata* caught in the North Sea in 1992.

1992 Date	Survey	Quarter	*R. radiata* Groups	ICES Quadrant	Depth (m)	*R. radiata* # Females	*R. radiata* # Males	*R. naevus* # Females	*R. naevus* # Males	*R. montagui* # Females	*R. montagui* # Males	*R. clavata* # Females	*R. clavata* # Males
08-Jan-92	RV Pelagia	1	Group 1	39F0		2	2					1	
15-Jan-92	RV Pelagia	1	Group 1	39F3		2	1						
25-Jan-92	RV Pelagia	1	Group 1	37F0		4	4						
20-Feb-92	RV Pelagia	1	Group 1	40F4	50	6	6						
24-Feb-92	RV Pelagia	1	Group 1	38F1	58	6	3						
26-Mar-92	RV Pelagia	1	Group 1	39F0		1	3						
					Total	21	19	0	0	0	0	1	0
20-Jan-92	RV Pelagia	1	Group 2	42F2		5	4						
21-Jan-92	RV Pelagia	1	Group 2	45F1		9	9						
21-Jan-92	RV Pelagia	1	Group 2	46F1		18	8						
					Total	32	21	0	0	0	0	0	0
06-May-92	RV Tridens	2	Group 1	39F2	32	1							
07-May-92	RV Tridens	2	Group 1	41E9	73	4	2	1					
07-May-92	RV Tridens	2	Group 1	39F0	77	2	6						
07-May-92	RV Tridens	2	Group 1	39E9	67	7	3						
07-May-92	RV Tridens	2	Group 1	41E8	53	2	2		1				
08-May-92	RV Tridens	2	Group 1	44E8	81	1	1		1				
08-May-92	RV Tridens	2	Group 1	44E9	107	2	4		2				
08-May-92	RV Tridens	2	Group 1	43E8	82	2	4	18	14				
08-May-92	RV Tridens	2	Group 1	43E9	77	2	1	4	1				
14-May-92	RV Tridens	2	Group 1	37F0	56	7							
					Total	30	23	23	19	0	0	0	0
11-May-92	RV Tridens	2	Group 2	43F0	81		1						
11-May-92	RV Tridens	2	Group 2	43F1	91	2	4						
11-May-92	RV Tridens	2	Group 2	43F2	77	7	5						
11-May-92	RV Tridens	2	Group 2	43F3	59	4	6						
13-May-92	RV Tridens	2	Group 2	41F4	55		1						
13-May-92	RV Tridens	2	Group 2	41F1	78	6	3						
13-May-92	RV Tridens	2	Group 2	41F3	63	1	1						
13-May-92	RV Tridens	2	Group 2	41F0	75	6	2						
13-May-92	RV Tridens	2	Group 2	41F2	74		2						
					Total	26	25	0	0	0	0	0	0
27-Aug-92	RV Tridens	3	Group 1	46E9	123	2	1						
28-Aug-92	RV Tridens	3	Group 1	44E9	109	1	1						
28-Aug-92	RV Tridens	3	Group 1	44E8	85	1		8	8				
31-Aug-92	RV Tridens	3	Group 1	41E9	70		1	1					
01-Sep-92	RV Tridens	3	Group 1	39E9	76	1							
01-Sep-92	RV Tridens	3	Group 1	39F0	75	2	2						
01-Sep-92	RV Tridens	3	Group 1	39F2	30	1							
02-Sep-92	RV Pelagia	3	Group 1	38F0	62	3							
02-Sep-92	RV Pelagia	3	Group 1	39F1	63	1							
02-Sep-92	RV Pelagia	3	Group 1	39F0	63	1							
02-Sep-92	RV Pelagia	3	Group 1	40F0	90	23	13						
					Total	36	18	9	8	0	0	0	0
26-Aug-92	RV Tridens	3	Group 2	43F4	54	10	11						
26-Aug-92	RV Tridens	3	Group 2	46F1	104	3	1						
26-Aug-92	RV Tridens	3	Group 2	46F2	105	5	4						
					Total	18	16	0	0	0	0	0	0

TABLE 2 CONTINUED

1992 Date	Survey	Quarter	*R. radiata* Groups	ICES Quadrant	Depth (m)	*R. radiata* # Females	*R. radiata* # Males	*R. naevus* # Females	*R. naevus* # Males	*R. montagui* # Females	*R. montagui* # Males	*R. clavata* # Females	*R. clavata* # Males
14-May-92	RV Tridens	2		35F0	80	1							
14-May-92	RV Tridens	2		35F1	27								
20-May-92	RV Pelagia	2				2							
28-Aug-92	RV Tridens	3		43E8	78			9	3				
31-Aug-92	RV Tridens	3		41E8	53			4					
31-Aug-92	RV Tridens	3		41F1	80			1					
02-Sep-92	RV Tridens	3		35F1	26					7	7	3	
26-Oct-92	RV Tridens	4		39F1	34	3							
26-Oct-92	RV Tridens	4		39F2	35	1							
27-Oct-92	RV Tridens	4		38F0	75	3	6						
27-Oct-92	RV Tridens	4		36F0	95						1		2
27-Oct-92	RV Tridens	4		39F0	77	13	10						
27-Oct-92	RV Tridens	4		37F0	69		3						
28-Oct-92	RV Tridens	4		35F1	27					11	5	2	4
28-Oct-92	RV Tridens	4		36F1	80					3	9	4	4
28-Oct-92	RV Tridens	4		35F2	31					2	7		1
28-Oct-92	RV Tridens	4		36F2	28					8	7		
07-Dec-92	RV Pelagia	4		35F2	35					1			
08-Dec-92	RV Pelagia	4		36F1	88					1	1		
08-Dec-92	RV Pelagia	4		35F1	30								1
08-Dec-92	RV Pelagia	4		36F1	80					2	2		1
08-Dec-92	RV Pelagia	4		36F1	86					10	8	2	1
08-Dec-92	RV Pelagia	4		36F1	90					2		1	2
08-Dec-92	RV Pelagia	4		36F1	87					2	2	9	4
09-Dec-92	RV Pelagia	4		37F1	74					2	1	1	
09-Dec-92	RV Pelagia	4		36F2	33					1	1	1	
09-Dec-92	RV Pelagia	4		37F1	72					1	2		
09-Dec-92	RV Pelagia	4		37F1	75					1	1	1	
					Total	23	19	14	3	54	55	26	20
					All	186	141	46	30	54	55	27	20

TABLE 3

Difference in length and disc width between fresh and thawed male and female *R. montagui* and *R. clavata*.

Difference in length and disc width between fresh and thawed rays		***R. montagui* Females**	***R. montagui* Males**	***R. clavata* Females**	***R. clavata* Males**
Number		23	18	15	9
Mean fresh length	(cm)	48,33	51,47	56,24	52,66
Mean thawed length	(cm)	47,78	50,79	55,49	52,14
Range fresh length	(cm)	36.3-62.9	36.9-65.3	37.7-94.2	45.2-75.7
Overall percentage thawed/fresh		98,8%	98,7%	98,7%	99,0%
Overall difference fresh-thawed	(cm)	0,56	0,68	0,75	0,51
L(fresh)=a+b*L(thawed)	a=	0,5616	-0,1605	0,362	0,6532
L(fresh)=a+b*L(thawed)	b=	0,9999	1,0165	1,0069	0,9973
Mean fresh disc width	(cm)	33,61	34,3	40,2	40,2
Mean thawed disc width	(cm)	33,28	34,09	39,86	39,86
Range fresh disc width	(cm)	25.2-43.8	25.3-41.8	26.6-68.4	32.0-49.5
Overall percentage thawed/fresh		99,0%	99,4%	99,2%	99,6%
Overall difference fresh-thawed	(cm)	0,33	0,21	0,34	0,14
DW(fresh)=a+b*DW(thawed)	a=	0,2111	-0,3225	0,5558	-0,2141
DW(fresh)=a+b*DW(thawed)	b=	1,0036	1,0155	0,9946	1,01

TABLE 4

Length / disc width relationship of male and female *R. radiata*, *R. naevus*, *R. montagui* and *R. clavata*.

Length = a + b * Disc width				
Species	**Sex**	**a**	**b**	**Number**
R. radiata	Females	1.014	1.479	179
	Males	0.600	1.476	134
R. naevus	Females	3.211	1.630	45
	Males	1.460	1.688	30
R. montagui	Females	-2.620	1.522	54
	Males	-7.441	1.717	55
R. clavata	Females	2.254	1.331	27
	Males	-7.108	1.654	20

CONTENTS