Distribution and feeding ecology of *Raja radiata* in the northeastern North Sea and Skagerrak (Norwegian Deep)

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The distribution and feeding ecology of *Raja radiata* in the deeper parts of the northeastern North Sea and Skagerrak (i.e. the Norwegian Deep) are described from data obtained from research cruises in 1984–1987 and 1995–1996. *R. radiata* was found in the entire area but was particularly abundant in the Skagerrak. The larger individuals were most abundant in waters less than 300 m but there were indications of a movement towards deeper waters in winter. The comparatively shallow areas off the west coast of Norway are probably used as nurseries. Maturity was attained from a total length of 45 cm onwards in both males and females. The diet of juveniles and adolescents consisted mainly of polychaetes and crangonid shrimps. Upon reaching maturity, a major diet shift to fish, larger shrimps and squat lobsters (Munida) occurred.

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Introduction

In the Northeast Atlantic three genera and at least 36 species of skates (Rajidae) occur (Stehmann and Bürkel, 1984), and several species are characteristic of fish communities found in soft-bottom areas of the continental slope and shelf (Andriyashev, 1954; Bakken *et al.*, 1975; Knijn *et al.*, 1993; Daan *et al.*, 1990, 1993; Bergstad, 1990; Walker and Heessen, 1996; Walker, 1998). In the North Sea, six Rajidae species are common (Knijn *et al.*, 1993; Bergstad, 1990; Walker, 1998), typically in deep sandy or muddy habitats. These are: *Raja clavata* L. (1758), *Raja montagui* Fowler (1910), *Raja naevus* Müller and Henle (1841), and *Raja radiata* Donovan (1808), all of which primarily inhabit the relatively shallow North Sea plateau (e.g. Knijn *et al.*, 1993; Walker, 1998), and *Raja fyllae* Lütken (1888) and *Raja lintea* Fries (1839), which are largely restricted to the deeper northeastern areas (Bergstad, 1990). Of these, *Raja radiata* is the most abundant and the one with the widest depth range (Knijn *et al.*, 1993; Walker, 1998).

R. radiata lives on sandy and muddy bottoms, where its diet usually consists of a variety of polychaetes, crustaceans and fish prey (McEachran *et al.*, 1976; Robichaud *et al.*, 1991). It is common on both sides of the Atlantic (Templeman, 1982, 1984a,b, 1987; Stehmann and Bürkel, 1984) and seems to have increased in numbers in the North Sea in recent years (Heessen and Daan, 1996; Walker and Heessen, 1996).

Estimates of total biomass of *R. radiata* in the North Sea are of the order of 100 000 t (Sparholt and Vinther, 1991). These estimates were based on data from the area sampled during major international and national trawl surveys coordinated by the International Council for the Exploration of the Sea (ICES). The sampling effort was restricted by depth and area, hence the results were not representative of the deeper northeastern part of the North Sea and the Skagerrak, i.e. the Norwegian Deep (Fig. 1). As an element of the ICES coordinated 1991 International Stomach Sampling Project for the North Sea, 3201 *R. radiata* stomachs were sampled and examined (Daan *et al.*, 1993). This data set significantly enhanced our understanding of the ecological role of *R. radiata*, but was again primarily representative of conditions in those parts of the North Sea shallower than about 200 m.
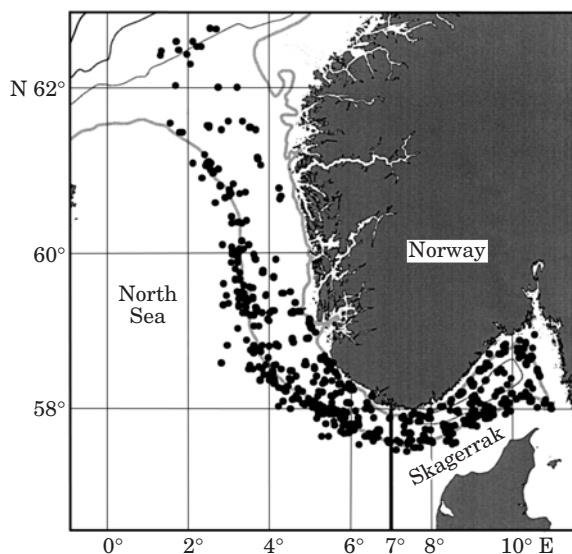
Figure 1. Sampling locations (bottom trawl stations) in the Norwegian Deep in the northeastern North Sea and Skagerrak on cruises listed in Table 1. The 200, 500, 1000 and 1500 m isobaths are indicated. The 200 m isobath delineates the Norwegian Deep running along the coast of Norway into the Skagerrak.

In and along the Norwegian Deep, *R. radiata* is very common and is the most abundant skate species (Bergstad, 1990). Here, we supplement the knowledge gained from previous studies by presenting new information on the species' distribution, size structure, biology and feeding ecology in the deep northeastern areas of the North Sea.

Material and methods

The study area is a deep channel running along the Norwegian coast from the inner Skagerrak to the shelf edge bordering the Norwegian Sea (Fig. 1). At around 200 m depth there is a faunal transition zone, and the fish community in the Norwegian Deep proper differs from that in surrounding areas (Daan *et al*., 1990; Bergstad, 1990). The change in species composition coincides with a transition from relatively course to finer sediments, i.e. sand and silt, which characterize the lower slope and bottom of the channel (van Weering *et al*., 1973; Longva and Thorsnes, 1997). The deepest parts of the Norwegian Deep are in the central Skagerrak where the maximum depth is about 710 m (Longva and Thorsnes, 1997). An important characteristic of the Norwegian Deep is the inflow of comparatively saline and warm Atlantic water from the Norwegian Sea along its western slopes (Otto *et al*., 1990).

Sampling

The data originated from research vessel cruises conducted in two periods, 1984–1987 and 1995–1996

(Table 1). The cruises were either general fish community surveys or special surveys for *Pandalus borealis* (all October cruises). The sampling strategy and trawl gears used on the cruises in 1984–1987 were described in detail by Bergstad (1990). From that period, catch data by numbers and weight, length compositions, and occasional stomach contents samples were available. The trawl positions are shown in Figure 1. In 1995–1996 the collection of *R. radiata* samples was also supplementary to other investigations. Most of the stomach samples and biological data used in this study came from the 1995–1996 cruises. However, the rather limited catch data from this period were not used in the analyses of distribution and abundance.

The processing of samples varied by period and cruise. For all trawls, the catch in terms of weight and numbers was recorded. For most catches total length (TL) from the snout to the endpoint of the caudal fin was measured. On selected cruises, more detailed data on individual specimens were collected, i.e. TL, ungutted weight (W), sex, and stage of maturity, based on macroscopic examination of gonads and claspers. The maturity scale used was that proposed by Stehmann (1987). A maturity ogive in terms of length was derived by logistic regression, i.e. Proportion mature $= \exp(a + b \times TL)/1 + \exp(a + b \times TL)$. Estimates of the coefficients a and b of the relationship $W(g) = a \; TL(cm)^b$ were obtained by linear regression of logarithmic values. Stomachs were either extracted at sea and frozen, or extracted from specimens brought frozen to the laboratory. Only contents of the section of the gut from the oesophagus to the pyloric sphincter were sorted and included in the analyses. After sorting and blotting on paper tissue, each prey category was weighed. Whenever possible, the prey were measured and counted. In cases where only body fragments were found, the highest number of individuals from which these body parts could have originated was recorded.

Analyses of distribution and abundance

Input to analyses of distribution and abundance was the weights and numbers of the individual catches in 1984–1987. The catches were adjusted to a standard 1 h tow. The catch data were in some cases analysed by two sub-areas, i.e. North Sea and Skagerrak, defined as areas to the west and east of 7°E, respectively, i.e. the border between ICES Divisions IVa and IIIa. There are no physical barriers limiting migration between these two sub-areas, but there are environmental differences that may influence distribution and ecology. The former sub-area is the shallower and is more strongly influenced by the Atlantic Inflow along the western slope (Furnes *et al*., 1986). The Skagerrak is considerably deeper (720 m), and the deep water shows a steady cyclonic basin-wide circulation (Rohde, 1996). Hauls were

Table 1. Research vessel cruises that provided data and material for the study of *Raja radiata*. Data on gears used in 1984–1987 were given in Bergstad (1990). In 1995–1996, RV ''Michael Sars'' used the Campelen 1800 sampling trawl with rockhopper ground gear (Engås and Godø, 1989), and the ''G. M. Dannevig'' used a smaller shrimp trawl. IBTS-ICES coordinated International Bottom Trawl Survey, Quarter 1 (supplementary tows made in addition to regular survey trawls).

Vessel	Time period	Data on catch and length	Data available Other biological data	Feeding data
IBTS (F/F Eldjarn)	8–19/2 1984	*		*
F/F Håkon Mosby	31/3–9/4 1984	*		*
F/F Håkon Mosby	3–9/8 1984	*		
F/F Michael Sars	5–19/10 1984	*		*
F/F Håkon Mosby	12–19/3 1985	*		
F/F Håkon Mosby	9–13/4 1985	*		
F/F Håkon Mosby	26/7–2/8 1985	*		
F/F Michael Sars	12–27/10 1985	*		
IBTS (F/F Eldjarn)	28/1–6/2 1986	*		
F/F Håkon Mosby	8–26/3 1986	*		
F/F Håkon Mosby	4–10/8 1986	*		*
F/F Michael Sars	22/10–8/11 1986	*		
IBTS (F/F Eldjarn)	31/1–18/2 1987	*		
F/F Håkon Mosby	24/2–13/3 1987	*		
F/F Håkon Mosby	8–14/9 1987	*		
F/F Michael Sars	20/10–9/11 1987	*		
F/F Michael Sars	13–30/10 1995	*	*	*
F/F Michael Sars	May 1996	*	*	*
F/F G. M. Dannevig	13–20/6 1996	*	*	*
F/F G. M. Dannevig	20/8–2/9 1996	*	*	*

further stratified by the four depth strata <180 m (1), 180–239 m (2), 240–300 m (3), and >300 m (4). These four strata were adopted on most of the 1984–1987 cruises. In analyses of seasonal distribution and abundance, summer was defined as the months July–September, autumn as October–November, and winter as January–April.

When comparing catch levels between pairs of strata, only positive catches were used. In cases where one of the strata contained over twice as many catches as the other, a random sample of the catches in the stratum with the highest number of observations was used. Pairwise tests were only conducted if at least 10 catches had been made in each of the strata.

Diet analyses

The diet was characterized in terms of percentage by weight (%W) and in some cases numbers (%N), i.e.:

$$\%W = \frac{W_i}{W_{tot}} \times 100 \quad \text{or} \quad \%N = \frac{N_i}{N_{tot}} \times 100$$

where W_i, N_i=weight or numbers of prey category i, and W_{tot}, N_{tot}=weight or numbers of all prey items of all non-empty stomachs considered. In addition, the percentage frequency of occurrence (%F) of different prey categories in non-empty stomachs was calculated.

Dietary overlap was assessed by Schoener's (1970) index:

$$C_{jk} = 1.0 - 0.5 \sum_{i=1}^{m} (|P_{ij} - P_{ik}|)$$

where P_{ij} and P_{ik} is the contribution of prey item i in the diet of predatory j and k, respectively, and m is the number of prey categories. This index ranges between 0 and 1, indicating totally different and identical diets, respectively. The degree of overlap between different predator groups was classified as low ($C_{jk} < 0.30$), medium ($0.30 < C_jk < 0.60$) and high ($C_{jk} > 0.60$) (Langton, 1982). Proportions by weight were used in these analyses since the numeric results were considered too uncertain in many instances. Overlap indices were only calculated in cases where at least 20 stomachs containing food were available in both predator groups compared.

Results

Distribution and abundance

R. radiata was caught in 269 of a total of 639 trawls in the study area (41%). In Figure 2, the catches from individual stations from the 1984–1987 period are plotted with symbol size proportional to the numbers in
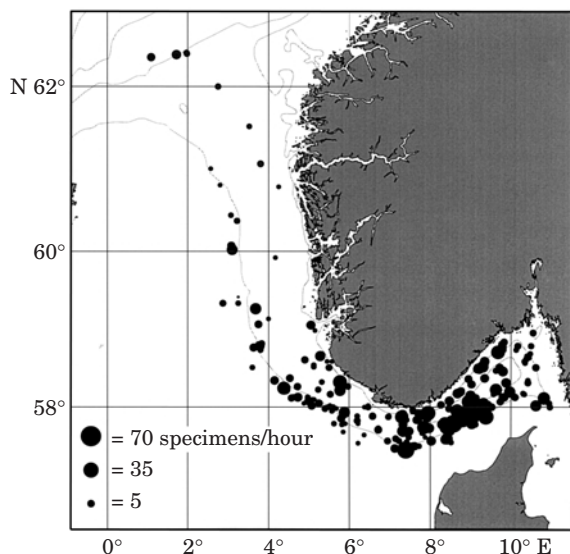
Figure 2. Catch rates of *Raja radiata* on cruises in the period 1984–1987, all seasons. Sampling locations are given in Figure 1.

the catch. Catches of *R. radiata* occurred in the entire area sampled, but there was a concentration of relatively big catches in the Skagerrak. This difference in abundance was also reflected in the frequency distributions of the catches by numbers in different depth strata of the two subareas (Fig. 3). The frequency of zero catches was higher in the North Sea in both seasons and all depth strata, and no catches exceeded 30 specimens. In the Skagerrak, the catches were larger, and the biggest catch (at 510 m) contained 70 individuals.

In the North Sea there was no significant difference between the positive catches in different seasons (Pairwise Mann-Whitney U, p>0.05). In winter there seemed to be slightly fewer zero catches in the deeper parts. In the Skagerrak, there was a seasonal difference in catch level at depths exceeding 300 m (Mann-Whitney U test, p<0.001); catches in winter were higher. At depths less than 240 m no such difference was found.

In the Skagerrak there seemed to be an increase in abundance with increasing depth. In comparing the catches in summer in Skagerrak, there was a significant difference between the depth strata 3 (240–300 m) and 4 (>300 m) (Fig. 3, Mann-Whitney U test, p<0.003), but not between any of the other depth strata. In winter there was so few hauls in depths less than 300 m that depth strata 1–3 were combined and compared with stratum 4. The catches in the deepest area (>300 m) were then found to be significantly higher (Mann-Whitney U test, p<0.0001).

Comparisons in terms of weight gave similar results (Table 2).

Size distribution

The size (TL) of *R. radiata* caught in the Norwegian deep ranged from 8 to 72 cm. The smallest individuals were thus rather smaller than the range 9–11 cm reported for newly hatched juveniles by Walker (1998). There was no difference between the size distributions of males and females (Fig. 4). Catches from the North Sea sub-area had a significantly larger proportion of small individuals in both seasons (Fig. 5). Within each sub-area, there were no significant differences between seasons. The difference in size between sub-areas and depth strata is also expressed in terms of mean individual weight in Table 2. The average individual weight was three to six times higher in the Skagerrak than in the North Sea. In the Skagerrak, the mean weight of the *R. radiata* from depths less than 300 m was significantly higher than of those caught deeper, both in summer and winter (Mann-Whitney U test, p<0.05 in summer and p<0.02 in winter).

The length–weight relationship $W(g)=0.004\ TL(cm)^{3.164}$ was calculated based on measurements of 157 *R. radiata* ($R^2=0.97$).

Maturity and reproduction

Data on maturity were recorded for 83 females and 74 males collected in summer and autumn. In both seasons about 15% of the adult females appeared to be reproductively active (Stage 4 and higher). Both sexes appeared to become mature from a length of 30 cm TL onwards, and a logistic regression fitted to the data suggested that 50% of the fish had attained maturity at a length of 44 cm (Fig. 6). The coefficients a and b of the logistic equation were -12.67 and 0.29 for females, and -16.97 and 0.38 for males, respectively.

Diet

The bulk of the stomachs used in the diet analyses came from the area of highest abundance off southern Norway and in the southwestern Skagerrak (Fig. 2). A total of 175 stomachs were examined for food, and 56 prey categories were identified (Table 3). Since some categories were almost completely digested, this is an underestimate of the actual number of prey species. In particular, polychaetes, small crustaceans and fish were often unidentifiable.

Three prey categories contributed about 90% to the wet weight of the stomach contents. These were decapod crustaceans (30%), polychaetes (11%) and bony fish (48%). The large fraction of fish was partly attributable to a few large fish specimens eaten by large *R. radiata*. A single witch flounder (*Glyptocephalus cynoglossus*) and a whiting (*Merlangius merlangus*) contributed 4.9% and 7.4% respectively in terms of wet weight. The most
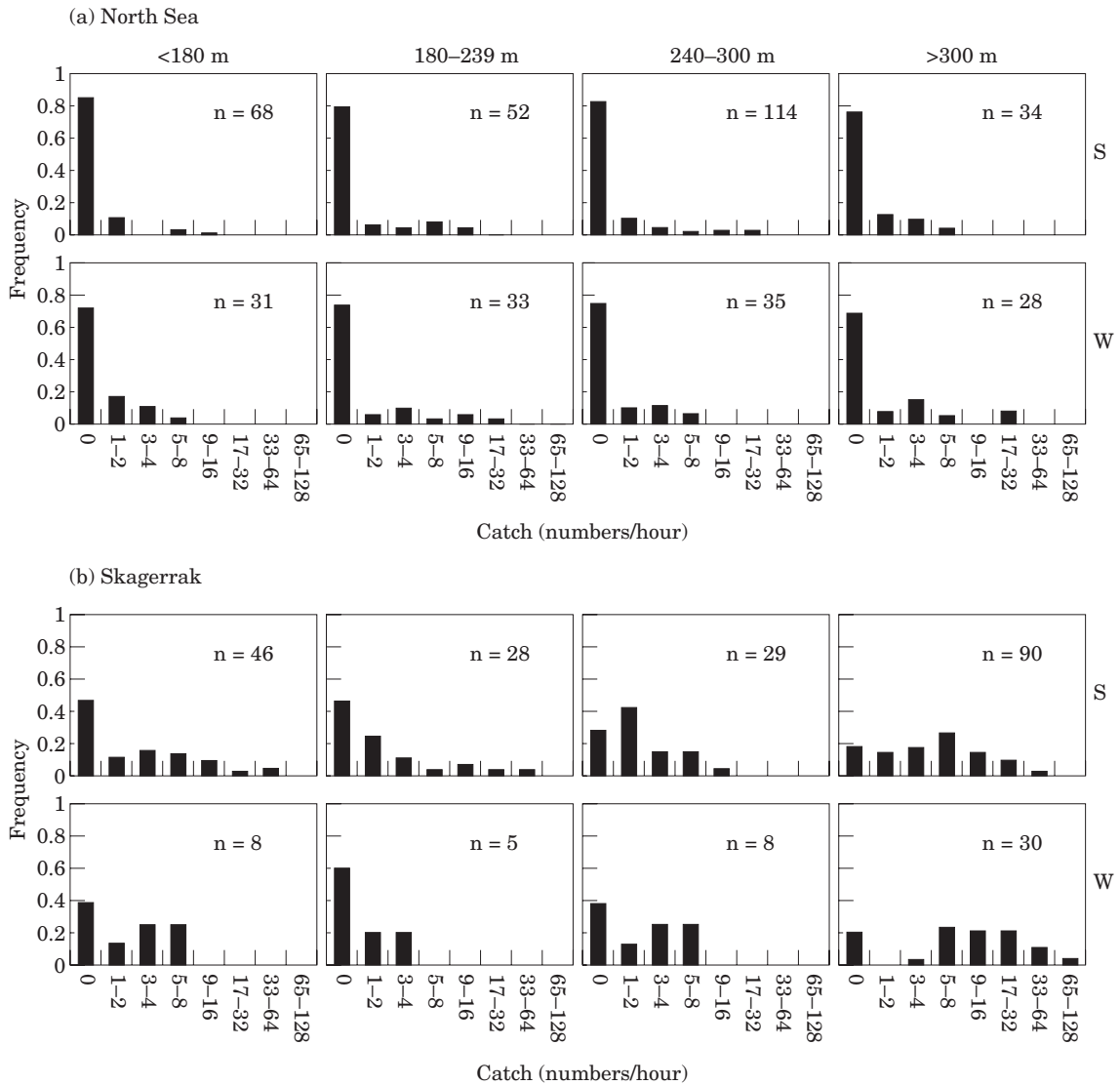
(a) North Sea

Figure 3. Frequency distributions of catch rates of *Raja radiata* in bottom trawls in the Norwegian Depth by depth zone and season in the two subareas; (a) the North Sea (west of 7°E), (b) the Skagerrak (east of 7° east). Data from 1984–1987. S, summer—autumn; W, winter; n, number of tows.

common fish prey was gadids, while the bulk of the decapods consisted of crangonids (5.6%) and *Pandalus borealis*. The polychaetes that could be identified belonged to three families, the Polynoidae, Sigalinoidae and Ophellidae.

The most common food item was polychaetes which occurred in 37% of the stomachs, followed by shrimps, isopods, and fish. In terms of numbers, gammarid amphipods were highly significant, contributing 27%. These were followed by shrimps (unidentified) and the crangonid *Pontophilus norvegicus*. The stomach seldom contained many food items. In 41% of the stomachs four or more categoreies were found. In 19% of the cases,
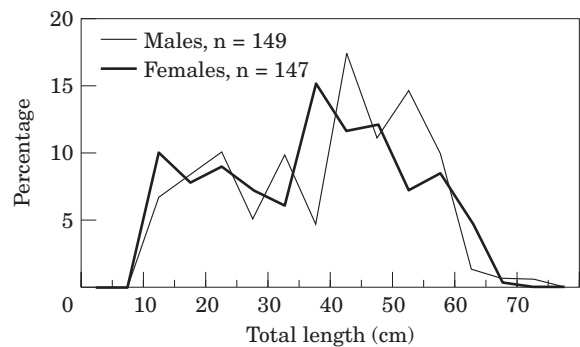

Figure 4. Length–frequency distributions of male and female *Raja radiata* in the Norwegian Deep. Data from all years and seasons. n, number of specimens measured.
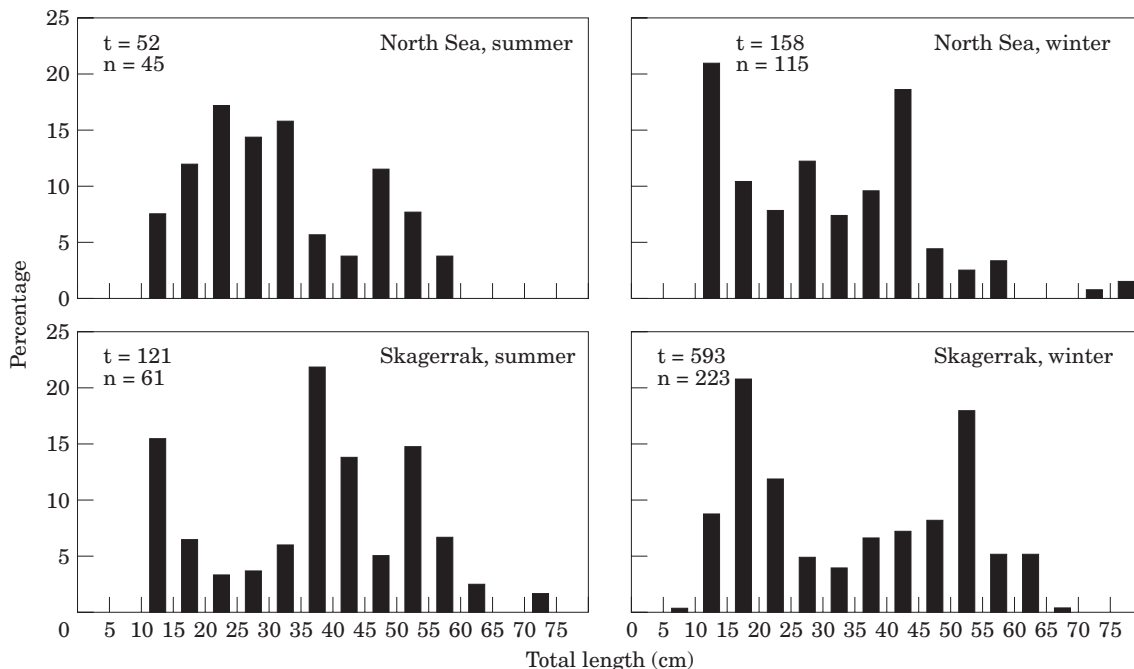
Figure 5. Length–frequency distributions of *Raja radiata* from all depths of the Norwegian Deep, by subarea and season. t, total number of fish in the catches where length was recorded; n, number of fish measured. Data from 1984–1987.

only one food item was found, while 13% of the stomachs were empty.

The diet composition for the length classes <25 cm, 26–40 cm and 41–70 cm, approximating to juvenile, adolescent and mature specimens, respectively, is shown in Figure 7. The diet of the smallest group consisted largely of polychaetes and shrimps. Among the shrimps

crangonids, especially *Pontophilus*, were very common. *Calocaris macandreae* was also common. Amphipods and isopods also occurred regularly.

The adolescent skates had a diet very similar to the juveniles. In terms of weight polychaetes, amphipods and decapods were the most important groups. A single hagfish (*Myxine glutinosa*) that contributed 22% to the wet weight was omitted from all analyses. The Schoener's index was 0.52, indicating moderate overlap between the diets of juveniles and adolescents. The main differences were that polychaetes seemed somewhat

Table 2. Mean catch in terms of weight and mean weight of individual *R. radiata* by sub-area, season and depth zone. Data from 1984–1987.

| Sub-area	Season	Depth zone (m)	Mean catch (kg)	Mean individual weight (kg)
North Sea	Summer	− 180 m	0.16	0.24
	Summer	181–239	0.58	0.35
	Summer	240–300	0.17	0.23
	Summer	>300	0.18	0.26
	Winter	− 180 m	0.22	0.31
	Winter	181–239	0.34	0.19
	Winter	240–300	0.33	0.48
	Winter	>300	0.38	0.15
Skagerrak	Summer	− 180 m	3.57	0.82
	Summer	181–239	5.59	0.81
	Summer	240–300	3.66	0.87
	Summer	>300	4.60	0.61
	Winter	− 300	2.36	1.15
	Winter	>300	8.57	0.56
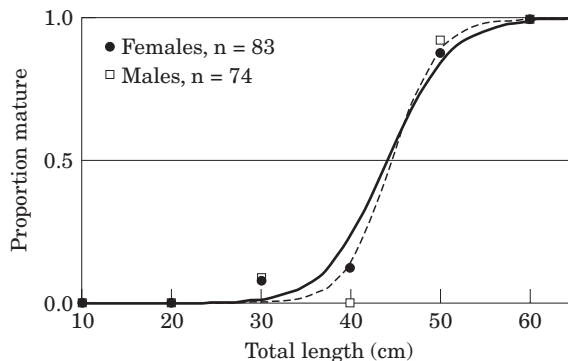
Figure 6. Proportion of mature male and female *Raja radiata* in different length groups. Lines represent logistic regression fits for females (continuous line) and males (broken line).

Table 3. Composition of the stomach contents of juvenile adolescent and adult *R. radiata* in the Norwegian Deep. % W, percentage by weight; % N, percentage by numbers; and % F, frequency of occurrence. Values <0.1% are given as +, and cases where the prey item could not be counted are indicated by —.

| Prey item	Stomach contents by predator size class								
	1–25 cm (juveniles)			26–40 cm (adolescents)			41–70 cm (adults)		
	% W	% N	% F	% W	% N	% F	% W	% N	% F
Polychaeta	27.2	0.8	58.8	9.6	2.6	45.2	2.6	—	25.6
Polynoidae	3.5	—	2	20.8	2.6	16.7	4.4	3.7	12.2
Sigalinoidae				2.8	1.3	2.4	2	1.5	3.7
Opheliidae				2.0	1.3	9.5	0.2	—	1.2
Crustacea	2.8	—	17.6	3.4	+	16.7	1.5	—	8.5
Copepoda	+	2.5	2						
Calanoida	0.6	11.7	21.6	0.2	12.8	16.7	+	1.5	2.4
Cyclopoida	+	0.8	2						
Malacostraca				0.7	1.3	2.4	2.0	1.5	4.9
Mysida				+	1.3	2.4	+	1.5	1.2
Mysis sp.	0.1	—	2						
Isopoda	2.9	10.8	47.1	0.7	2.6	35.7	+	—	1.2
Anthuridea	+	—	2						
Flabellifera				0.2	2.6	2.4			
Cirolana borealis							0.5	6.6	2.4
Valvifera	0.8	5.8	5.9						
Idoteidae	0.7	0.8	5.9	0.2	5.1	7.1	+	2.2	3.7
Asellota	0.6	3.3	7.8	0.1	1.3	9.5			
Epicaridea	+	—	2						
Amphipoda	2.2	5.8	19.6	2.2	3.9	21.5	0.3	0.7	7.3
Gammaridea	3.5	10.8	15.7				+	2.9	3.7
Gammaridae	4.7	26.7	19.6	2.9	26.9	19	+	6.6	1.2
Hyperidea				0.1	1.3	2.4			
Caprellidea				0.9	+	2.4			
Caprellidae				2.1	1.3	4.8	0.1	—	1.2
Eucarida							+	2.2	1.2
Decapoda	2.7	—	3.9	0.4	+	9.5	0.3	0.7	8.5
Sergestes arcticus				+	+	2.4			
Caridea	19.6	10.8	37.3	11	15.4	38.1	3.8	12.4	29.3
Spirontocaris sp.	+	0.8	2						
Pandalus sp.	0.5	—	2				0.5	1.5	6.1
Pandalus borealis							8.1	4.4	7.3
Pandalus propinquus							0.2	0.7	1.2
Thoralus cranchii	0.5	—	2						
Crangonidae	15.1	2.5	19.6	0.4	1.3	4.8	4	0.7	8.5
Crangon sp.	+	—	2						
Crangon allmani							0.2	0.7	1.2
Pontophilus norvegicus	3.9	3.3	13.7	3.4	5.1	7.1	1.3	13.1	11
Calocaris macandreae	7.7	1.7	5.9	5.8	2.6	7.1	2.2	3.7	9.8
Paguridae				0.3	1.3	2.4			
Pagurus sp.							0.5	0.7	2.4
Munida sp.							0.1	0.7	1.2
Munida sarsi							8.6	15.3	4.9
Brachyura				5.3	+	7.1	0.4	—	3.7
Macropipus sp.							+	0.7	1.2
Cephalopoda							+	—	1.2
Myxine glutinosa				21.6	1.3	2.4	0.9	2.2	26.8
Teleostei	+	—	2	2.8	5.1	11.9	25.8	5.8	1.2
Clupea harengus				0.1	+	2.4	3.9	0.7	1.2
Trisopterus esmarki							1.7	0.7	1.2
Merlangius merlangus							8.4	0.7	1.2
Micromesistius poutassou							4.3	0.7	1.2
Merluccius merluccius							3.8	0.7	1.2
Lycodes vahli							1.4	0.7	1.2
Glyptocephalus cynoglossus							5.6	0.7	1.2
Unidentified	0.1		3.9	0.3	+	4.8	+	0.7	4.9
Number of stomachs with contents		45			36			70	
Number of empty stomachs		6			6			12	
Average weight of content (g)		0.56			1.46			8.11	
Number of stations with samples		13			19			41	
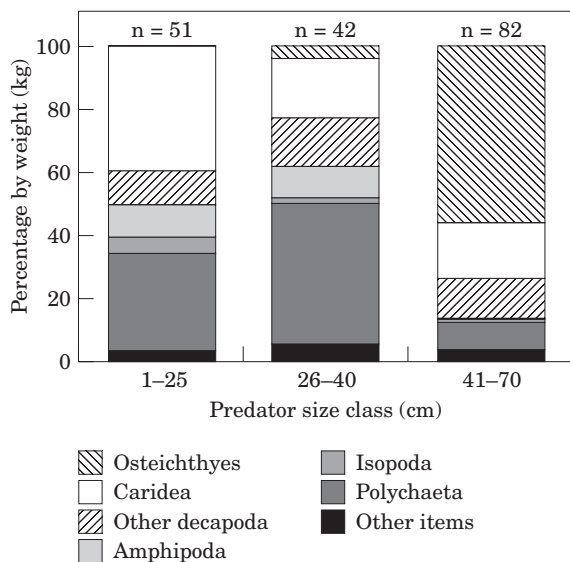
Figure 7. Composition of the stomach contents of three different size groups of *Raja radiata* from the Norwegian Deep. Data from all seasons. n, number of stomachs examined.

more important to adolescents, and no juveniles had eaten fish prey.

The mature skates had a significantly different diet from those of the two smaller groups. Fish prey were most important in terms of weight (Fig. 7). Large decapods other than shrimps became increasingly

important, and *Munida sarsi* contributed 12% to the wet weight. Crangonids was replaced by the larger *Pandalus borealis*. Decapod shrimps occurred most frequently, followed by fish and polychaetes. The Schoener's index for adults and juveniles (0.20) and adults and adolescents (0.24), respectively, suggest little overlap. The sizes of prey items eaten were also different between the size groups. The size distributions of caridean shrimps consumed are shown in Figure 8. The mature skates took a wider range of prey sizes than the smaller ones. There seemed to be no clear difference between the sizes of shrimps eaten by juvenile and adolescent fish but this result is uncertain because few shrimps from these groups were measured.

The study of seasonal differences was limited by the low number of samples from winter (20 stomachs). The winter sample consisted mostly of large specimens (Table 4), and the composition of the stomach contents was furthermore strongly influenced by a single stomach that contained 18 specimens of *Munida sarsi*, and by a single large fish in one stomach that contributed 10% to the contents in weight. However the comparatively large proportion of empty stomachs (9/20 stomachs) in winter is noteworthy.

In summer, the weight of the stoach contents was higher than in winter and autumn (Table 4). This was caused by a comparatively large fish fraction and a low percentage of empty stomachs compared with the winter samples. Prey compositions for summer and autumn by predator size classes are shown in Figure 9. In summer,
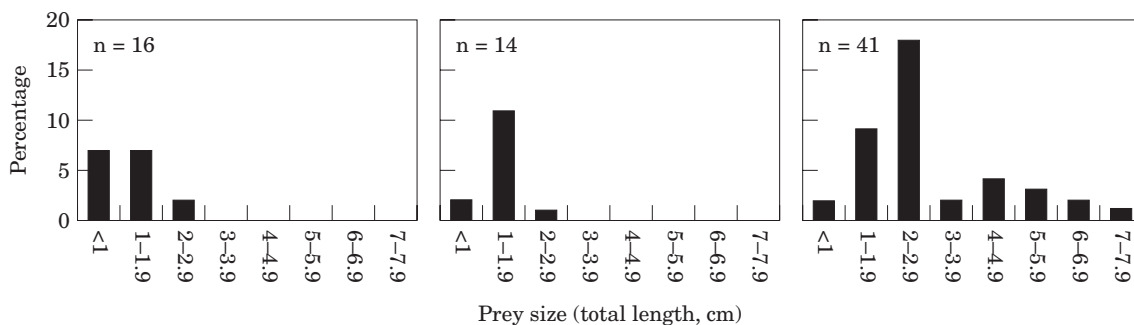

Figure 8. Size distributions of caridean shrimps in the stomachs of *Raja radiata* of the size classes <25 cm (left), 26–40 cm (middle), and 41–70 cm (right).

Table 4. Average ungutted weight, and data on stomach contents of *R. radiata* in Norwegian Deep in different seasons.

Season	No. of specimens	Ungutted weight (g)	No. of prey categories	Average weight of stomach contents (g)	Percentage of empty stomachs
Winter	20	1035	12	4.1	45
Summer	48	745	27	6.1	15
Autumn	107	465	47	3.6	7

(a) Summer (May–early September)

(b) Autumn (October)

Osteichthyes
Caridea
Other decapoda
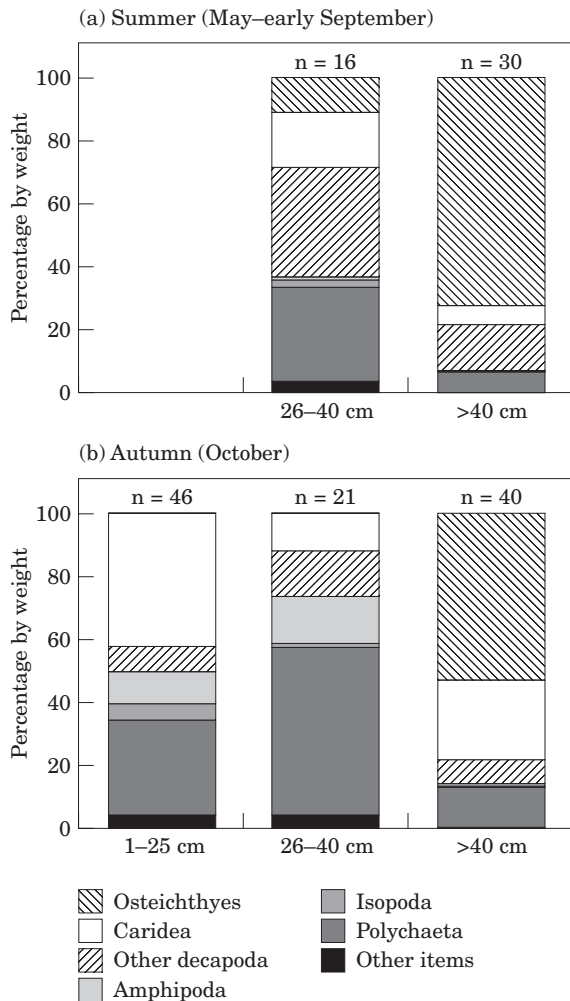Amphipoda
Isopoda
Polychaeta
Other items

Figure 9. Composition of the stomach contents of *Raja radiata* in (a) summer 1996 and (b) autumn 1995. All samples were from areas east of 4°40′E and south of 59°58′N. n, number of stomachs examined.

a long rough dab, *Hippoglossoides platessoides*, and a whiting, *Merlangius merlangus*, that comprised 13 and 20%, respectively, of the wet weight of the pooled stomach contents were not included in the analyses. No summer data for juveniles are shown due to low sample size.

Size-related differences in prey composition seemed more pronounced than seasonal differences. In summer the fish and decapod shrimp fraction seemed higher than in autumn for both adolescents (26–40 cm) and adults (>40 cm), whereas the polychaete and amphipods appeared to have their highest contributions in autumn. The seasonal difference appeared strongest for adolescents but this may partly be a result of the lower sample size for this size class. Schoener's indices comparing the diets of adolescents and adults between

seasons were 0.61 and 0.73, respectively, suggesting rather a high level of similarity between the sampling periods.

Discussion

Distribution and biology

Information on distribution and abundance of *R. radiata* was collected opportunistically as part of more comprehensive fish community studies and stock-assessment surveys. The trawl gear was not optimal for skates, and it is uncertain how the catch rates were related to the absolute abundance of *R. radiata* in the area. The new data on relative abundance within the study area may nevertheless be valid and suggest some features of particular interest. The most striking pattern observed was the elevated abundance of *R. radiata* on the Skagerrak slope and on the slope off the south-western tip of Norway. The catches increased with increasing depth, particularly in the Skagerrak. In a wide area further north *R. radiata* was much less abundant. Only at the northernmost end of the sampling area, where the Norwegian Deep opens towards the Norwegian Sea, did some rather large catches occur.

There is no directed fishery for *R. radiata* or other skates in the study area. There are, however, unreported by-catches in the industrial trawl fisheries for Norway pout *Trisopterus esmarki* and blue whiting *Micromesistius poutassou*, and also in the shrimp (*Pandalus borealis*) fishery. The by-catches in the industrial fisheries are monitored routinely (e.g. ICES, 1998), but the skate fraction is small and included among "other species". The by-catches in both fisheries combined are likely to be too limited to influence the distribution and abundance patterns of *R. radiata*. The patterns observed rather reflect responses to environmental factors. *R. radiata* generally prefers soft fine substrates (Stehmann and Bürkel, 1984; Robichaud *et al.*, 1991) as found in the deeper parts of the Norwegian Deep (Basford *et al.*, 1993). In the southern areas of greatest abundance the sediments at depths greater than about 150 m tend to be sand-silt-clay, silt or clay, and the sedimentation rates are higher than in areas west of Norway (van Weering *et al.*, 1987; Longva and Thorsnes, 1997). The southern Skagerrak slope is less steep and the depth range wider (100 to 500–700 m) compared with the western slope west of Norway (100 to 275–350 m) and this creates more living space for *R. radiata*. Because of the generally stronger influence of the Atlantic inflow off western Norway compared with the Skagerrak (e.g. Furnes *et al.*, 1986; Svendsen and Magnusson, 1992; Danielssen *et al.*, 1996) current strength and temporal variation in salinity and temperature may be lower in the southern than the northern areas of the Norwegian Deep. There are thus differences in the physical environment between

the areas with and without high abundance of *R. radiata*. There may also be spatial variation in biotic factors such as the distribution of preferred prey types but there is not enough information to analyse this further.

The area of concentration of *R. radiata* off the southern tip of Norway may be considered to be a continuation of the area of distribution illustrated by Knijn *et al*. (1993) for the shallower parts of the North Sea. The species is found over wide areas of the northern and central North Sea, but adults appear to be most abundant at the rim of the Norwegian Deep off southern Norway. Also in the shallower areas of the North Sea, *R. radiata* of all sizes are mostly confined to areas with fine sediments.

The comparatively large proportion of zero catches, even at greater depths, suggested that *R. radiata* were unevenly distributed. This could be linked to patches of suitable bottom substrate but also to temporal and spatial variation in the availability of food. From marking experiments Templeman (1984a) and Walker *et al*. (1997) found that *R. radiata* seldom migrated great distances, although Templeman (1984a) showed that they were capable of considerable movement in relatively short periods of time. Migration and aggregation could be linked to spatial and temporal variation in prey concentration or mating behaviour. If it is the case that *R. radiata*, in common with many other skates, lay their egg capsules in relatively shallow water (Holden, 1975; Rydland and Ajayi, 1984; Cox and Koob, 1993), migration onto the North Sea plateau would seem likely and might cause temporal variation in abundance of adult skates. In our study, some indications of seasonal variation in distribution were found in the Skagerrak sub-area, but this seemed to be restricted to limited bathymetric movement. The apparent movement into deeper water in winter could be a response to winter cooling in the shallower waters and perhaps a reduction in food supply (Bergstad, 1990). We found no indications of immigration from or emigration to the Norwegian Deep, but the distribution by time of our sampling effort would not be sufficient to detect short-term changes associated with mating or egg deposition. Lack of a distinct breeding season, which seems to be a characteristic of *R. radiata* (Templeman, 1982), would also obscure such a migration, since this would not significantly change the number of mature individuals in the northern parts of the Norwegian deep at any particular time of the year. From our observations and those of Knijn *et al*. (1993) of juveniles, it appears that shallower northern parts of the Norwegian Deep and wide areas of the central and northern North Sea plateau provide nurseries for *R. radiata*.

No significant difference was found between the size distributions of males and females in the Norwegian Deep. This is in agreement with Walker's (1998) results

for *R. radiata* from the shallow parts of the North Sea. Templeman's (1987) investigations along the east coast of Canada also showed no significant size difference between males and females within a given area, although significant differences could be found between areas. Both the length frequency distributions and the average individual weights showed that there was a larger fraction of small fish in the North Sea part of the Norwegian Deep than in the Skagerrak part. The most likely explanation of this observation is that there is a gradual ontogenetic movement from relatively shallow areas to deeper parts within the study area.

Compared with the shallower parts of the North Sea (Walker, 1998; Walker and Hislop, 1998), the size distributions from the Norwegian Deeps were wider, primarily because they contained higher proportions of fish bigger than 50 cm. It has been argued that a truncation of the size-frequency distribution seen for other Rajidae in the shallower parts of the North Sea may reflect heavy exploitation by trawling (Walker and Hislop, 1998). The trawling activity in our study area is quite restricted to the depth band 150–250 m, and the trawling activity in the Norwegian Deep as a whole is probably much lower than in the shallower parts of the North Sea. The differences in the length frequency distributions of *R. radiata* may thus be an indication that the fishing mortality is less in the Norwegian Deep than in the shallower areas to the west. However, for *R. radiata*, Walker and Hislop (1998) found no change in the length distributions within the time period 1929–1995, i.e. within a period when trawling effort certainly increased. The differences between the Norwegian Deep and other areas may thus rather reflect a tendency for bigger fish to inhabit deeper sub-areas within its total area of distribution than effects of exploitation.

In the Skagerrak sub-area the biggest individuals tended to occur at intermediate depth, in waters less than 300 m. This could reflect differences in feeding and be related to prey distribution. We showed that mature *R. radiata* had a significantly different diet from the immature *R. radiata*. Whereas the mature *R. radiata* feed on benthopelagic animals like gadid fishes and *Pandalus borealis*, which are most abundant at intermediate depth (Bergstad, 1990), the immature *R. radiata* appear to prefer benthic animals such as polychaetes, amphipods and crangonids. Although the numerical abundance of benthic macrofauna declines with depth, these prey type are probably relatively abundant across a wider depth range than demersal gadids and *Pandalus* (Rosenberg *et al*., 1996).

The material available for biological studies was rather limited. The macroscopic examination of gonads indicated that most *R. radiata* matured from a length of 30 cm onwards and that the length when 50% of the fish were mature was 44.0 and 44.6 cm for females and males, respectively. These values for the 50% length at

maturity are somewhat higher than the 39.5 and 39.6 cm, reported by Walker (1998) from the shallower parts of the North Sea.

Diet

There was a higher frequency of empty stomachs in winter than in summer and autumn, and this suggested that the feeding activity was somewhat reduced during the winter. The stomach contents consisted mainly of polychaetes, decapod crustaceans and fish. This corresponds with other observations both from the North Sea (Rae and Shelton, 1982; Daan *et al.*, 1993) and other areas, e.g. the Barents Sea (Dolgov, 1997) and West Greenland (Pedersen, 1995). Cephalopods (Ellis *et al.*, 1996) and holothurians (Ebeling, 1988) that were considered important prey items in some areas, were not recorded or insignificant in our collection.

The fish species that predominate in the diet vary between studies and study areas and this suggests that *R. radiata* is a rather opportunistic feeder. As in this study, Daan *et al.* (1993) and Dolgov (1997) found juvenile gadids to be the most important prey in the North Sea and Barents Sea, respectively. Unfortunately, only a minor fraction of the gadid prey could be identified to species. In the shallower parts of the North Sea, sandeel (*Ammodytes* sp.) is also significant (Rae and Shelton, 1982). Off West Greenland, Pedersen (1995) found juvenile redfish (*Sebastes* sp.) to be most important.

Juvenile and adolescent *R. radiata* were predominantly benthivorous, whereas benthopelagic food items became important to larger fish. Similar size-related changes were observed by others (Ajayi, 1982; Daan *et al.*, 1993; Pedersen, 1995; Dolgov, 1997). *Pontophilus norvegicus* and *Calocaris macandreae* were typical prey of juvenile *R. radiata*, again in line with other findings (Ellis *et al.*, 1996). The size attained at the pronounced shift from a benthic to a benthopelagic diet apparently varies between areas. McEachran *et al.* (1976) found this switch to occur at a size of 40 cm, as in our study, while both Daan *et al.* (1993), Pedersen (1995) and Dolgov (1997) recorded a major diet shift at about 30 cm. This geographical variation may simply reflect differences in prey availability (McEachran *et al.*, 1976; Robichaud *et al.*, 1991; Pedersen, 1995). Templeman (1987) found that mature *R. radiata* had a significantly larger body disc relative to the tail width and length than immatures. This may enhance mobility and enable bigger skates to catch pelagic prey.

The occurrence of highly mobile fish like whiting (*Merlangius merlangus*) and blue whiting (*Micromesistius poutassou*) suggested that *R. radiata* may to some extent feed on carcasses. This was also noted by Pedersen (1995). We had no means of assessing the significance of this feeding mode.

Seasonal comparisons of prey composition could only be made for the two larger size classes and only between summer and autumn. There were indications of minor changes in the relative importance of prey categories, but the ontogenetic patterns were retained. Seasonal changes appeared minor compared with ontogenetic diet changes.

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