

Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day

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Historic and current survey data are compared to describe the changes occurring in abundance, species richness and length–frequency of the rajid community in the central and north-western North Sea between the periods 1929–1956 and 1981–1995. Survey data show that some species have decreased in abundance (common skate and thornback ray), whilst others (starry ray) have increased. The length–frequency relationship is currently truncated at 70–79 cm, whilst individuals of up to and above 100 cm used to be common. Life-history characteristics show that the sensitivity of rays and skates to enhanced mortality is species specific. The sequence of the five most common species from most to least sensitive is: *Raja batis* (common skate) > *R. clavata* (thornback ray) > *R. montagui* (spotted ray) > *R. naevus* (cuckoo ray) > *R. radiata* (starry ray). This is also the order of commercial importance. The observed changes are discussed in relation to fishing.

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Key words: *Raja* spp., North Sea, length–frequency, abundance, life history.

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Introduction

Rays and skates are cartilaginous benthic fish, occupying the same spatial niche as teleost flatfish. Skates have traditionally been landed for consumption (Holden, 1973, 1974; Walker, 1996). Although they are mainly caught as bycatch, there is still a limited long-line fishery for skates off the British coast and in the past directed fisheries occurred off the European continental coast (Walker, 1996). All of the North Sea skate species have a commercial value, except for the starry ray (*Raja radiata*), which is landed incidentally in the Danish industrial fisheries. Commercial landings data on rays and skates have been collected by ICES since 1903. Landings started declining in the North Sea in the early 1920s and again in the mid-1950s, following a period of recovery during the Second World War, but have remained stable during the past 15–20 years (Fig. 1).

Recent trawl survey data show that the skate and ray species in the North Sea have quite discrete distributions

(Fig. 2). The starry ray is abundant offshore in the central North Sea, whereas the cuckoo ray (*Raja naevus*) occurs mainly in northern British coastal waters. Thornback rays (*R. clavata*) are found primarily in the coastal waters around the Thames estuary and spotted rays (*R. montagui*) off the east coast of Britain and around the Wash. The common skate (*R. batis*) is currently caught only off the Shetlands. However, in the past the distribution of thornback rays and common skates was considered to be extensive throughout the central/southern and central/northern North Sea, respectively (Walker, 1996). Two other species, the shagreen ray (*R. fullonica*) and the blonde ray (*R. brachyura*) are occasionally caught in small numbers in the North Sea.

The skate and ray species in the North Sea show a wide range in their age and length at maturity (Holden, 1973, 1974, 1975; Vinther, 1989) and it is to be expected that each species will be differently affected by fishing. Although only the largest individuals are landed, most length and age classes are caught in trawls due to their

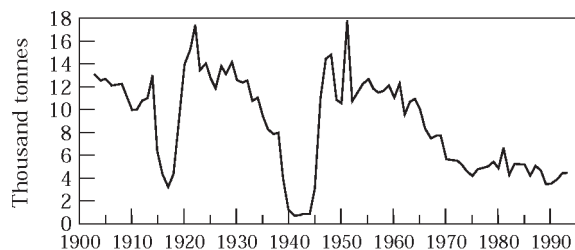


Figure 1. Annual landings of rays and skates from the North Sea. Data from ICES statistics.

large size at hatching (9–24 cm) and their morphology (large “wings” and the presence of sturdy spines). Since only mature individuals can contribute to the next generation, survival during the juvenile period is a key factor. Therefore, it is to be expected that those species with the lowest length and/or age at maturity have the highest chance of survival at increasing levels of exploitation. The limited evidence available suggests that in the past few decades the common skate has retreated to the very northern North Sea, the thornback ray is no longer caught in the south-eastern bight and the starry ray has replaced other species in the central North Sea (Rijnsdorp *et al.*, 1996; Walker, 1996; Walker and Heessen, 1996).

Demographic analysis of populations assumes constant age-specific rates of birth and death and a stable age distribution, with the population growing exponentially at an instantaneous rate r (Caswell, 1989; Krebs, 1989; Roff, 1992; Stearns, 1992). The basic equation of demography is the Euler-Lotka equation which is used to calculate the population growth rate (Caswell, 1989; Stearns, 1992). Brander (1981) used this equation to calculate the level of mortality at which growth rate (r) was zero (“replacement mortality”) for a number of skate and ray species, indicating the differences in species sensitivity to fishing mortality.

In this paper the changes occurring in skate and ray species composition in the central and north-western North Sea will be explained according to the species specific sensitivity to enhanced mortality as estimated using the Euler-Lotka equation. Sensitivity analyses will demonstrate the effect of changes in the input parameters (survival, fecundity and age at maturity) on the estimate of population growth rate. The relationship between life history traits and fitness will be discussed in relation to fishing exploitation.

Materials and methods

Survey data

Changes in abundance of demersal fish species between 1906–1909 and 1990–1995 have been analysed by

Rijnsdorp *et al.* (1996) for the south-eastern bight of the North Sea (Roundfish Area 6). Scottish trawl survey data for the central and northern North Sea are available for the periods 1929–1956 and 1981–1995 (Greenstreet and Hall, 1996). Data for eight skate and ray species have been analysed for this paper. Abundance estimates (catch rates) for the period 1929–1956 have been increased by 1.67 to compensate for changes in survey gear between the two periods (Greenstreet and Hall, 1996).

Leslie matrix

An age-structured Leslie matrix was used to estimate the population growth rate (r) at a given combination of year-class survival, fecundity and age at maturity (Caswell, 1989; Roff, 1992) according to the Euler-Lotka equation as follows:

$$1 = \sum_{x=\alpha}^{x=\omega} e^{-rx} l_x m_x$$

where X = age class; ω = age at last reproduction; α = age at first reproduction; r = instantaneous rate of natural increase; l_x = probability of surviving from birth to beginning of age class X ; m_x = expected number of offspring for a female in age class X . The population growth rate can be estimated from the dominant eigenvalue of the matrix (λ) by $\lambda = e^r$. It is also possible to estimate the theoretical value of year-class survival below which the population would decline, by setting r at 0. Converting this value of survival to mortality (mortality = $-\ln(\text{survival})$), gives the value of total mortality (Z = natural + fishing mortality) which should not be exceeded to ensure that the relevant population does not decline in numbers. This is referred to as replacement mortality.

The values for fecundity, age and length at maturity and growth, used as input for the life table to estimate r were taken from published data for ray and skate species in the North Sea (Holden *et al.*, 1971; Holden, 1972, 1975; Du Buit, 1976a,b; Stehmann and Bürkel, 1984; Walker and Witte, unpublished). See Table 1. These values were also used to calculate the replacement mortality.

Estimates of the current mortality on skates and rays have been made by a length-converted catch curve (Hilborn and Walters, 1992; ICES, 1997), using length–frequency data from the entire North Sea (area shown in Fig. 2). Lengths were grouped in 1-cm or 5-cm classes and the relative age corresponding to the midpoint of the class (L) was estimated as $-\ln(1 - L/L_\infty)$; this was plotted against \ln abundance in each length class and the descending slope is $1 - (Z/K)$, whereby Z can be estimated. The current growth parameters (L_∞ and K) were from unpublished data (Walker and Witte,

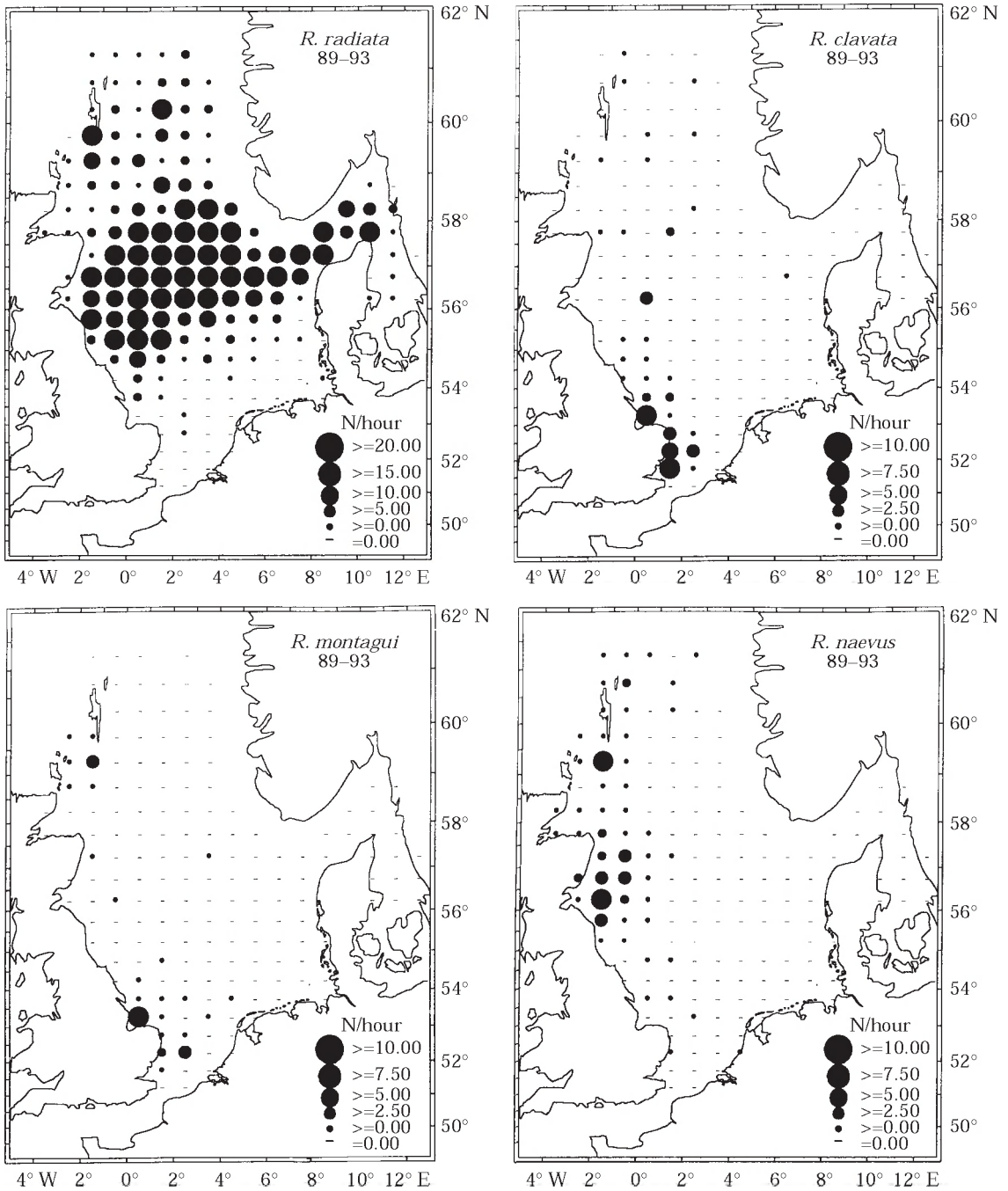


Figure 2. Distribution of *Raja radiata*, *R. clavata*, *R. naevus* and *R. montagui* in the first quarter of the year, derived from ICES International Bottom Trawl Surveys 1989-1993. (From Walker and Heessen, 1996.)

unpublished). This estimate represents the exploited part of the population. Although all size classes, even egg capsules, are caught in fishing gear, mortality of the early life stages (eggs and 0+ and 1+ individuals) is expected to be higher than that of the later stages, due to a higher predation risk. The mortality rate due to

predation of egg capsules of *R. radiata* in the North Sea has been estimated to be about 0.12 (Cox *et al.*, in press). This value is added to the above estimates for the transitions from egg to 0+ and 0+ to 1+.

The sensitivity of the estimate of population growth to changes in input parameters was

Table 1. Reproductive parameters for eight *Raja* species. Data on L_{∞} from Wheeler (1978) and Stehmann and Bürkel (1984); data on *R. batis* from Du Buit (1976a); *R. brachyura*, *R. clavata*, *R. montagui* from Holden (1972: 1975) and Holden *et al.* (1971); *R. naevus* from Du Buit (1976a, b); and *R. radiata* from Walker and Witte (unpublished). *=Wheeler (1978); **=estimated as 70% of L_{∞} ; ***=from Walker and Witte (unpublished).

Species	L_{∞} (cm)	Length at maturity F (cm)	Age at maturity F (yr)	Fecundity (eggs/yr)	Area
<i>R. batis</i>	237	180*	11	40	Celtic Sea
<i>R. brachyura</i>	113	92**		40–90	British west coast
<i>R. clavata</i>	85	72	10	60–140	Atlantic
<i>R. fullonica</i>	115	85**			Northern North Sea
<i>R. montagui</i>	75	58	8***	25–60	Bristol Channel/west coast
<i>R. naevus</i>	70	59	8***	90	Celtic Sea
<i>R. oxyrinchus</i>	156	120*			Northern North Sea
<i>R. radiata</i>	60	40	5	38	Central North Sea

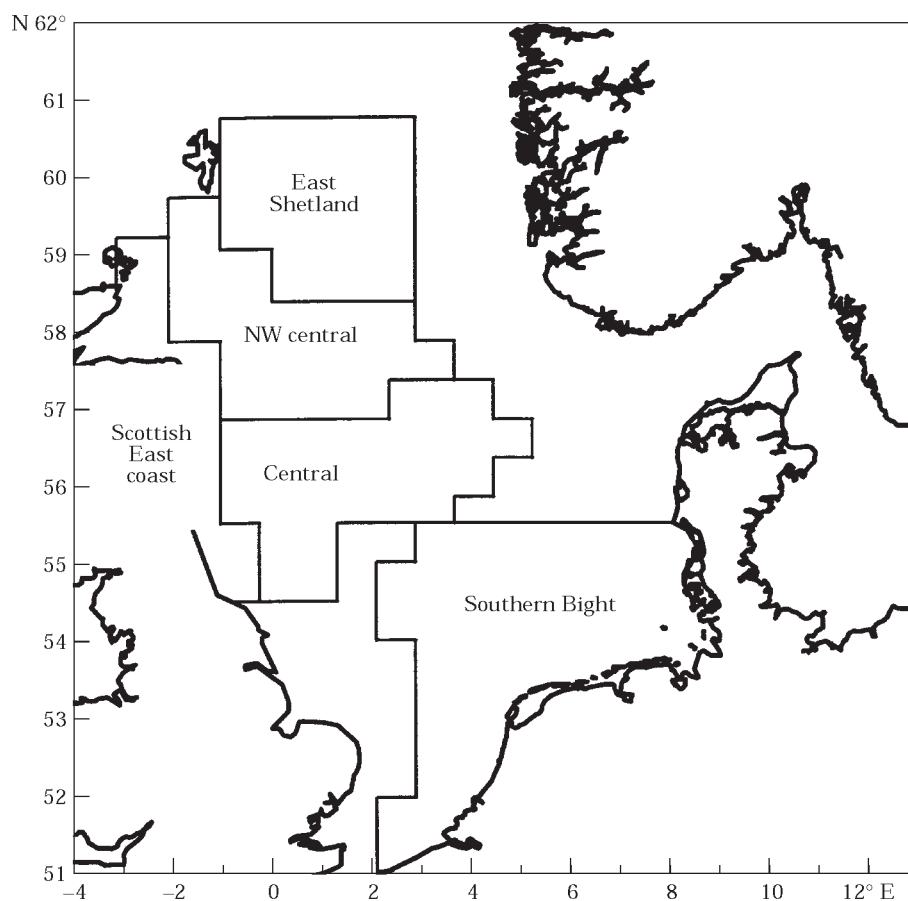


Figure 3. Areas of the North Sea sampled during the Scottish surveys (1929–1956 and 1981–1995) and the Southern Bight (Roundfish Area 6), sampled in 1906–1909 and 1990–1995.

estimated using an elasticity analysis (Caswell, 1989). Elasticity (e_{ij}) of a matrix element (a_{ij}) in row i and column j measures the proportional change in eigenvalue (λ) caused by a proportional change in mortality

or fecundity. This was calculated as follows (Caswell, 1989):

$$e_{ij} = \delta \ln \lambda / \delta \ln a_{ij}$$

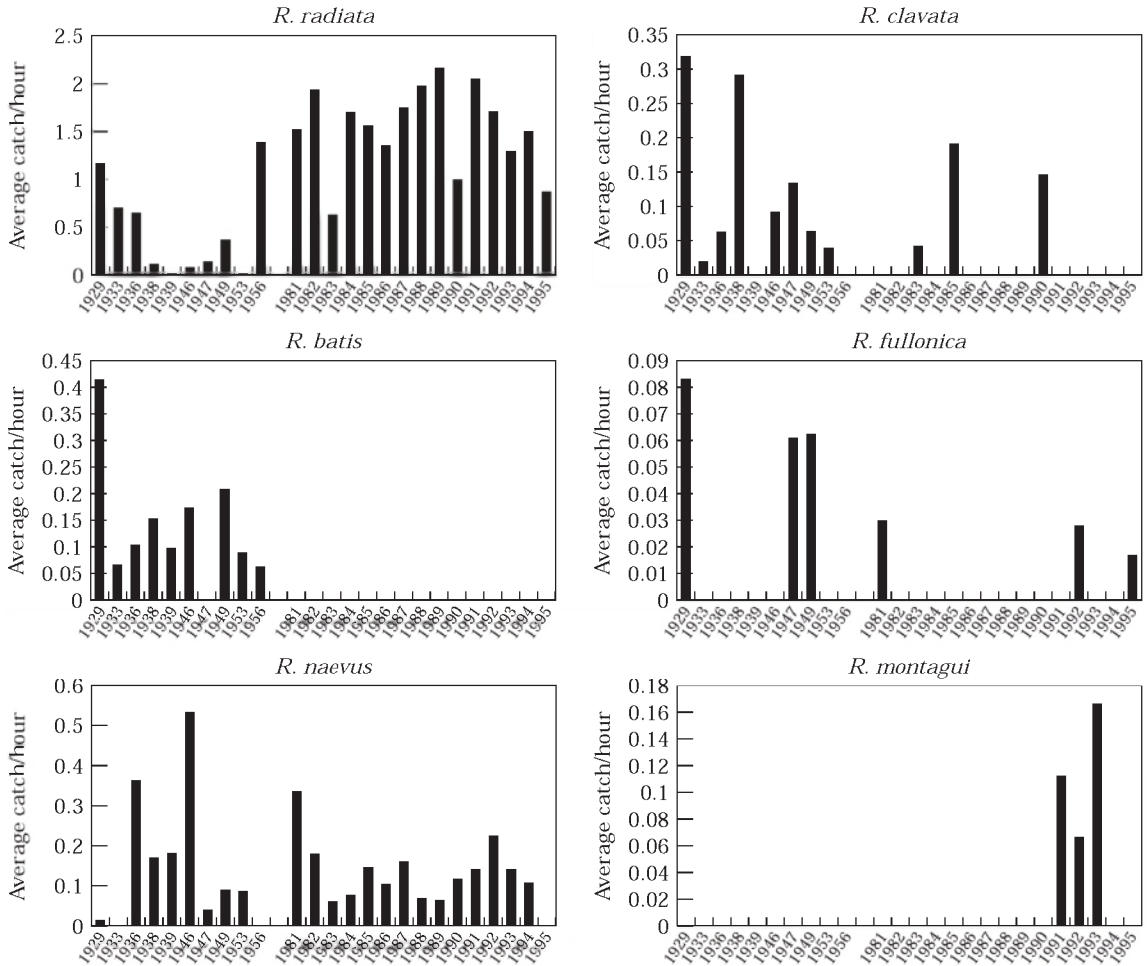


Figure 4. Annual catch/hour for six *Raja* species, averaged over the four areas covered by the Scottish surveys. Note that the data for the period 1929–1956 do not form a continuous time series.

Relative changes in population growth rate brought about by a change in age at maturity were calculated by subtracting the value of r at different ages from that at the estimated age at maturity.

Results

Survey data

The areas for which data were available are shown in Figure 3. Annual catch rates of six species taken in the Scottish surveys are shown in Figure 4. This shows that *R. batis* was caught regularly during the first period, but disappeared from the area between 1956 and 1981. The spotted ray, *R. montagui*, entered the north-eastern North Sea survey data in 1991 for the first time. The starry and cuckoo rays were caught throughout the two periods, but the thornback ray became less abundant

between 1981 and 1995 than it had been between 1929 and 1956. In Figures 5 and 6 the catches of all skates and rays in each of the four areas are shown separately for the periods 1929–1956 and 1981–1995. The overall abundance has increased in the two offshore areas (NW Central and Central) and decreased in the northern (East Shetland) area (Fig. 5). There has been a marked change in the species composition in all areas (Fig. 6). In the more northern and coastal areas, the common skate, the thornback ray and the cuckoo ray were also quite abundant in 1929–1956. However, by 1981–1995 the common skate and the thornback ray were no longer caught and the starry ray predominated in these areas. Data for the Southern Bight are shown in Table 2 (Rijnsdorp *et al.*, 1996). Although the estimate of abundance is dependent on the gear used, it is apparent that the thornback ray has decreased in numbers, whilst the common skate is no longer caught in the area.

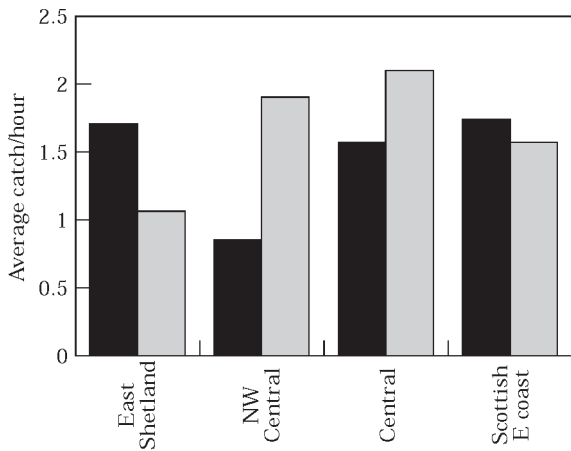


Figure 5. Average catch/hour of all rays and skates in each of the Scottish survey areas shown in Figure 3. 1929-1956 (■); 1981-1995 (□).

Changes in the length-frequency composition of the catches of the starry ray and all other species of skates and rays from the entire area are shown in Figure 7 for the two periods studied. The length-frequency of the starry ray was unchanged, but for the other species the largest size classes caught in the earlier period were no longer caught in the 1990s.

Leslie matrix and mortality

Estimates of replacement mortality (Z, y^{-1}) based on a rate of increase of the population $r=0$ are shown for five species in Table 3. The rank order is similar to that shown by Brander (1981) but the absolute values are different due to different input parameters. No estimate was made for the shagreen ray (*Raja fullonica*) due to lack of data. The level of total mortality which a species

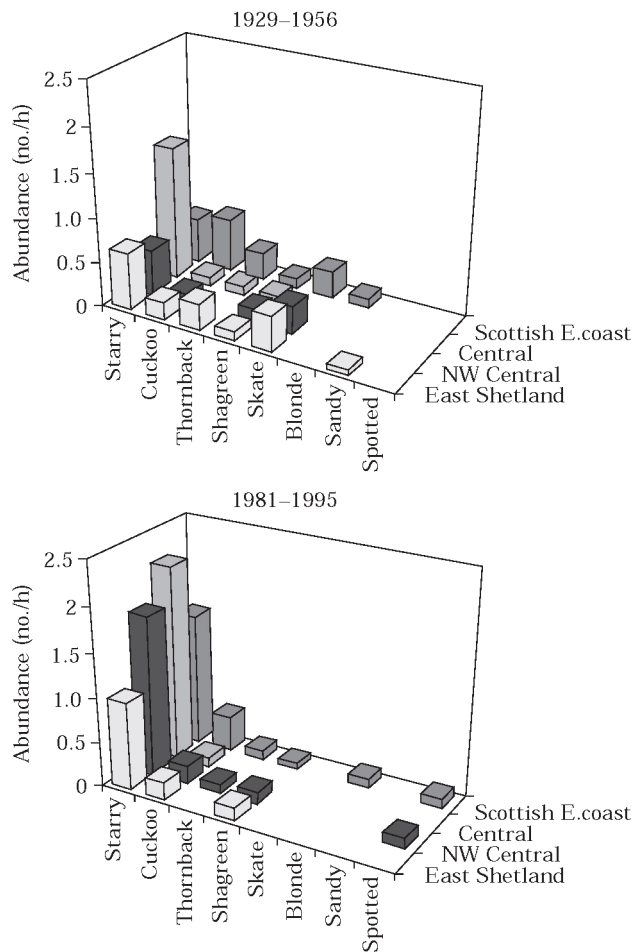


Figure 6. Average abundance (numbers/hour) per species. Sandy=*Raja circularis*; blonde=*R. brachyura*; skate=*R. batis*; shagreen=*R. fullonica*; thornback=*R. clavata*; cuckoo=*R. naevus*; starry=*R. radiata*; spotted=*R. montagui*.

Table 2. Standardized mean catch rate (numbers per hour fishing) for four *Raja* species in the Southern Bight (Roundfish Area 6). OT20 and OT90=20 and 86 foot otter trawl, respectively; BT13 and BT8=13 and 8 m beam trawl, respectively; GOV="chalut grande ouverture verticale". +=<0.05; NR=not recorded (Rijnsdorp *et al.*, 1996).

Fishing gear Species	1906–1909 OT20	1906–1909 OT90	1906–1909 BT13	1990–1995 GOV	1990–1995 BT8
<i>R. batis</i>	0	+	0.1	0	0
<i>R. clavata</i>	2.8	0.5	0.2	+	0.1
<i>R. montagui</i>	0	NR	NR	+	+
<i>R. radiata</i>	0	0.2	+	+	0.1

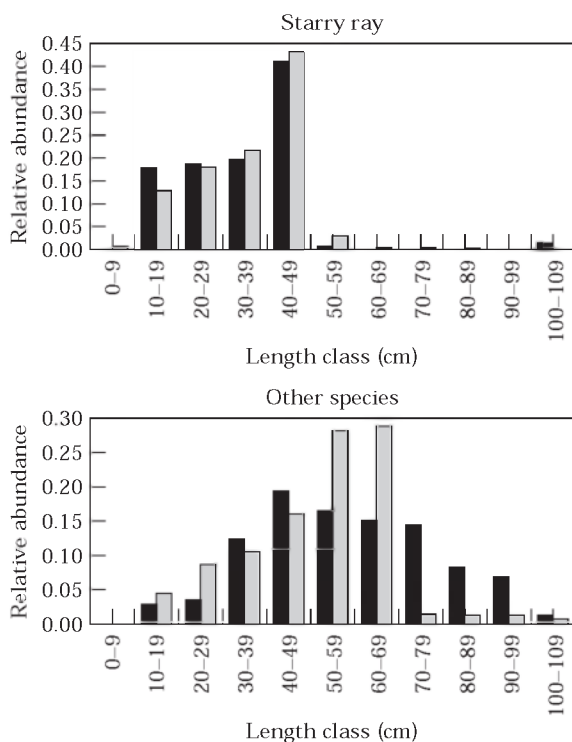


Figure 7. Proportional length–frequency relationship for all four areas covered by the Scottish surveys. Catches of other species represent *R. batis*, *R. brachyura*, *R. clavata*, *R. fullonica*, *R. naevus* and *R. montagui*. 1929–1956 (■); 1981–1995 (□).

can withstand before r drops below 0 has the following rank order:

R. batis<*R. clavata*<*R. montagui*<*R. naevus*<*R. radiata*

An increase in total mortality will lead to a decline in species abundance in the reverse order. The effect of a change in survival on population growth rate is greatest before maturity is reached (Fig. 8). Changes in fecundity are only effective after maturity and have a relatively small (*R. batis*, *R. clavata*) or similar (*R. radiata*, *R. naevus*) effect (on population growth rate) as compared

Table 3. Estimates of replacement mortality (Z , y^{-1}) for five *Raja* species. Data from Leslie matrix assuming a rate of increase of the population $r=0$.

Species	Common name	Replacement mortality ($r=0$)
<i>R. batis</i>	Common skate	0.38
<i>R. clavata</i>	Thornback ray	0.52
<i>R. montagui</i>	Spotted ray	0.54
<i>R. naevus</i>	Cuckoo ray	0.58
<i>R. radiata</i>	Starry ray	0.73

to survival. A decrease in age at maturity leads to an increase in population growth rate, if the other parameters remain the same (Fig. 9).

Length–frequency distribution and length-converted catch curves for starry and thornback rays are shown in Figure 10. Estimates of total instantaneous mortality on starry and thornback rays in the North Sea, based on these catch curves, are shown in Table 4, together with the estimates of rate of population increase or decrease. Estimates for cuckoo and spotted rays were not used, because p values for the regression were larger than 0.05. Using the estimates as an approximation for mortality in open sea (starry) and coastal waters (thornback), which is justified by looking at the species distribution (Fig. 2), gives a range of values for the rate of population growth for five species, shown in Figure 11.

Discussion

Species composition and exploitation

The role played by fisheries in bringing about the observed changes in the abundance and distribution of skates and rays in the North Sea is difficult to assess without direct observations. The available evidence seems to indicate that the skate species composition has changed in a way that could be predicted by an increase in total mortality. The observed changes in species composition show a shift to a situation in which the species with the lowest length and/or age at maturity, in this case the starry ray,

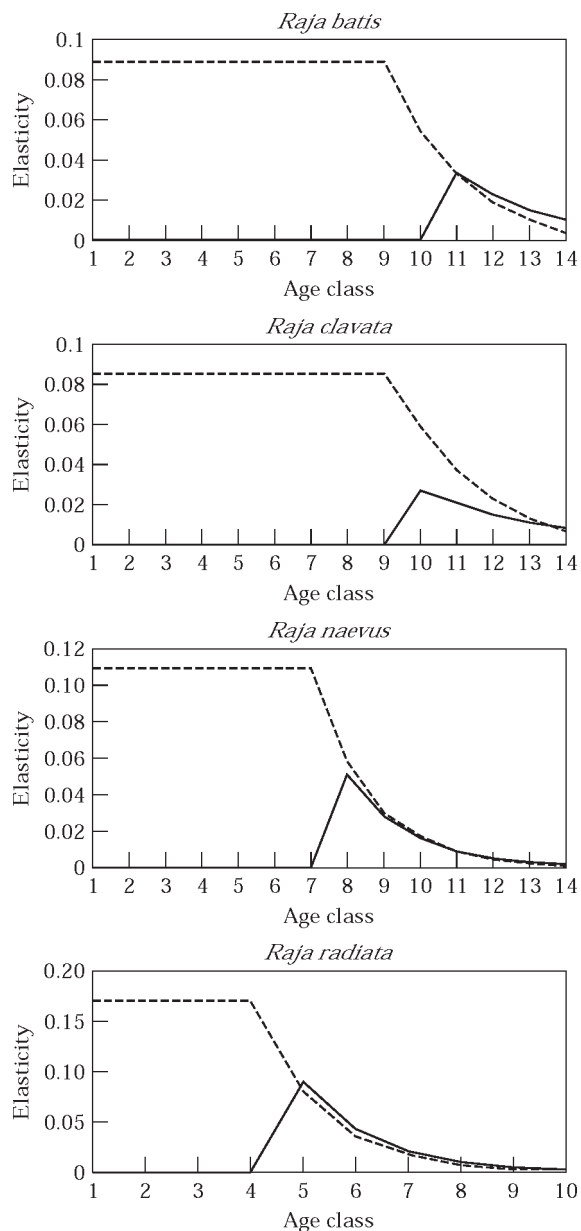


Figure 8. Elasticity analyses for four ray species. Elasticity=proportional change in λ caused by a proportional change in survival or fecundity. Survival (---); Fecundity (—).

dominates. The length–frequency patterns have changed accordingly and illustrate the paucity of individuals larger than 79 cm. This means that all the breeding females, and a large majority of the juveniles, of *Raja batis*, *R. fullonica* and *R. clavata* have disappeared, whilst the other species may have lost only the very largest individuals.

The observed decline of the common skate probably coincides with a decrease in total stock size, even

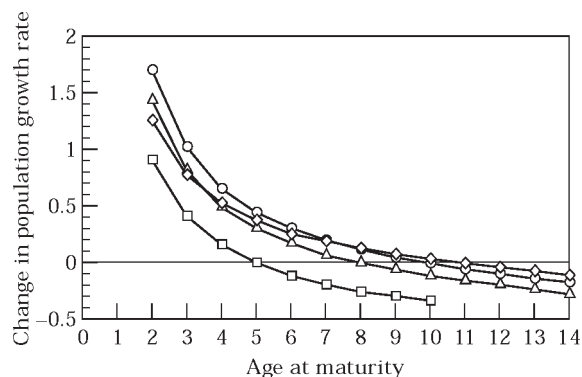


Figure 9. Changes in estimates of rate of population growth caused by changes in age at maturity. Starry (□); Cuckoo (△); Thornback (○); Skate (◇).

though the North Sea represents the eastern limit of the distribution of the species (Stehmann and Bürkel, 1984). In the past there were important skate fisheries in the North Sea, for example off the Scottish coast and on the Horn Reef off the Danish coast (Walker, 1996). However, in the past decades the species has changed from one which was relatively common and commercially important to one which is quite rare. Brander (1981) has described a similar situation in the Irish Sea.

Although the thornback ray is now caught very infrequently in the four areas covered by the Scottish surveys, it is still found off the south-east coast of Britain (Walker and Heessen, 1996). Between 1979 and 1993 the range of this species decreased. Whereas formerly it was distributed over the entire south-western, central and northern North Sea it is now caught predominantly off the coast of Britain and Scotland (Walker and Heessen, 1996). The sporadic catches of this species in the areas sampled could be due to movements up and down the British coast. The starry ray increased in abundance in the central North Sea between 1979 and 1993 (Walker and Heessen, 1996). The success of the starry ray, a Boreal species, in the central North Sea, rather than further north remains unexplained. Starry rays are known to be scavengers (Templeman, 1982) and might profit from high levels of discards from fishing vessels (although discards are not limited to the central North Sea). It is possible that there is less interspecific food competition due to removal of teleost flatfish. Moreover, there is plenty of opportunity for replenishment of the stock from the northern North Sea. The spotted ray, a Lusitanian species not caught in the historical surveys, has been regularly captured off the Scottish coast since 1991. The distribution of the species, around Orkney and off the north-east coast, suggests that it has entered the North Sea from the north. There appear to be two centres of distribution, one off the north-east coast of

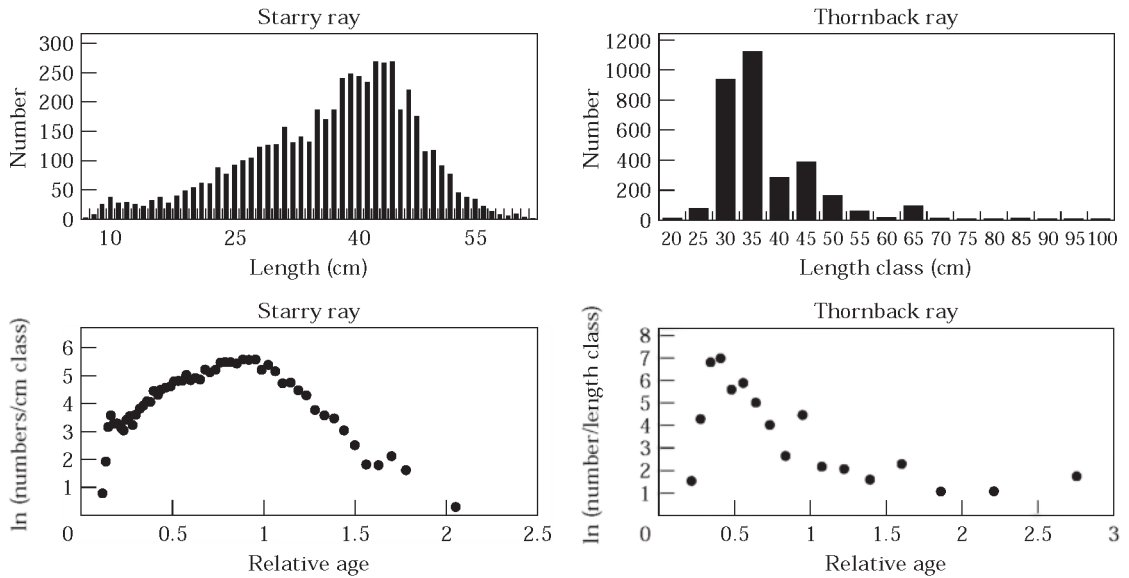


Figure 10. Length–frequency distribution (upper figures) and length-converted catch curves (lower figures), based on catches from the entire North Sea during ICES IBTS surveys, 1992–1995.

Table 4. Total mortality (Z) estimated from catch curves, with standard error of the estimate, and corresponding rate of increase or decrease of the population. n =number of age classes. Growth parameters L_{∞} and K from Walker and Witte (unpublished).

Species	L_{∞} (cm)	K	Mortality	n	r^2	p	Rate of population change
<i>R. clavata</i> thornback ray	109	0.155	0.588 (0.514–0.670)	12	0.98	<0.001	–0.073
<i>R. radiata</i> starry ray	68.7	0.125	0.700 (0.685–0.715)	17	0.97	<0.001	0.035

Scotland, and the other off the south-east coast of England (Walker and Heessen, 1996). In the latter region, large catches of juveniles were observed in the early 1990s (Walker and Heessen, 1996), following a series of warm winters in the late 1980s (Corten and van de Kamp, 1996). The spotted ray is a southerly species and it is likely that the northerly limits of its distribution are determined by water temperature. Recent analyses of beam trawl data from the coastal waters of Britain and north-western Europe, show that the mean catch weight of rays and skates is low in the central North Sea and English Channel, but higher in the shallow waters of the southern North Sea and highest off the south-western coast of the British Isles and in the Irish Sea (Rogers *et al.*, 1998).

The patterns of exploitation have changed in the past decades. For example, although Scottish demersal fishing effort doubled in the areas north-west central and east Shetland between 1960 and 1995, it diminished in the coastal area (Greenstreet and Hall, 1996). The

common skate and thornback ray are landed if caught, but the starry ray is almost always discarded. Although the survival rate of the discarded fish is unknown, it is thought to be quite high (ICES, 1995). The species and size classes landed commercially will change in response to changing patterns of demand. For example, in the past ten years the cuckoo ray began to be landed commercially in Scotland and juveniles of all species are often landed if larger fish are unavailable (P. Walker, pers. obs.).

The change in the distribution of fishing effort from coastal waters to open sea in the past 60 years (Greenstreet and Hall, 1996; Rijnsdorp and Millner, 1996) is important when taking fisheries effects into account. The spatial distribution of the individual species is especially significant and current mortality estimates, which are based on the exploited part of the population, are probably overestimates. For example, true survival rates would be higher if there were unfished (and unsampled) sources of rays; or nursery areas where

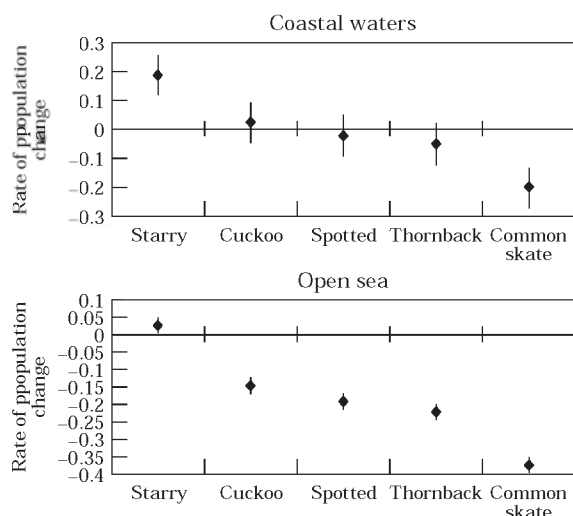


Figure 11. Rates of change of the population of five skate and ray species at current estimates of mortality in open sea and coastal areas.

juveniles could grow, and be exempt from the high (fisheries) mortality; or if there was immigration of individuals from less exploited areas. The idea of strongholds, or sources, within the North Sea, where mortality (or emigration) is lower than natality (or immigration) (Pulliam, 1988) is an appealing one from the point of view of replenishment of exploited stocks. The topography of the North Sea is highly heterogeneous and there are areas that are difficult to fish. Thornback rays, for example, are still found between the banks off the east coast of Britain and in deep, stony pits (i.e. Silver Pit). These and similar areas could function as sources of recruitment to the more exploited areas, but the very characteristic of a source (birth rate > death rate) makes it difficult to identify with classical methods. There is a real need to identify the spatial distribution of the different stages of the life cycle of the North Sea rays and skates and to make reliable estimates of fishing and discard mortality of all these stages in order to fully understand the impact of fisheries on these species.

Life history parameters

The use of fixed values in a life table for life-history parameters such as fecundity and length and age at maturity, which may have been estimated under different circumstances, can lead to an unreliable estimate of rate of population increase, and thus replacement mortality. Changes in abundance can lead to changes in life-history parameters. For example individual growth rate can increase at lower density, resulting in changes in length and age at maturity and fecundity, which may lead to a higher net reproductive rate (Roff, 1992;

Gotelli, 1995). Thus density-dependent feedback can influence population size, as is implied by the logistic growth model (Krebs, 1989; Roff, 1992; Gotelli, 1995). Moreover, the traits measured at a particular moment are themselves the result of past selection pressures. It is also unknown how reliable the published data are for most of the skate and ray species, as many studies were limited by numbers of individuals, area or season. The sensitivity analysis illustrates how important the estimates of juvenile survival and age at maturity are to the outcome of the matrix analysis.

Changes in age and/or length at maturity and fecundity as a result of changes in growth patterns is a subject of ongoing research. Initial results indicate that thornback rays have a higher length at age now than in the past (Holden, 1972) and reach maturity sooner (Walker and Witte, unpublished). In order to be effective any such compensatory changes should ultimately result in an increase in juvenile survival, regardless of species. However, if fishing is the major selective pressure in operation, then only those species which can exhibit a fast enough compensatory response will survive. From Figures 9 and 10, it is apparent that, in theory, the compensatory change necessary for the starry ray to be able to withstand an increase in total mortality is smaller than for the other species. Whether compensation actually occurs is unknown and without experimental evidence, it is speculative to compare the responses made by the individual species to fishing.

Although there have been temporal and spatial shifts in species composition, the ray and skate trophic and spatial niche remains occupied. It is likely that there have been changes in predator-prey relationships resulting from the observed changes in the size composition of the populations, i.e. the marked reduction in the number of large skates and rays in the North Sea. However a detailed analysis of such goes beyond the scope of this paper.

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