Fishery Stability, Local Extinctions, and Shifts in Community Structure in Skates

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Abstract: *Skates are arguably the most vulnerable of exploited marine fishes. Their vulnerability is often assessed by examining fisheries catch trends, but these data are not generally recorded on a species basis except in France. Aggregated skate catch statistics tend to exhibit more stable trends than those of other elasmobranch fisheries. We tested whether such apparent stability in aggregated catch trends could mask population declines of individual species. We examined two time series of species-specific surveys of a relatively stable skate fishery in the northeast Atlantic. These surveys revealed the disappearance of two skate species, long-nose skate (*Dipturus oxyrhinchus*) and white skate (*Rostroraja alba*) and confirmed a previously documented decline of the common skate (*D. batis*). Of the remaining five skate species, the three larger ones have declined, whereas two smaller species have increased in abundance. The increase in abundance and biomass of the smaller species has resulted in the stability of the aggregated catch trends. Because there is significant dietary overlap among species, we suggest the increase in abundance of the smaller species may be due to competitive release as the larger species declined. A consequence of this kind of stability is that declining species cannot be detected without species-specific data, especially in taxa exhibiting competitive interactions. This may explain why previously documented disappearances of two species of skates went unnoticed for so long. The conservation of skates and other elasmobranchs requires species-specific monitoring and special attention to larger species.*

Estabilidad de la Pesquería, Extinciones Locales y Cambios en la Estructura de Comunidades de Rayas

Resumen: *Las rayas son presumiblemente los peces explotados más vulnerables. Su vulnerabilidad es frecuentemente evaluada mediante el examen de tendencias de capturas pesqueras; sin embargo, con la excepción de Francia estos datos generalmente no son obtenidos a nivel de especie. Las estadísticas de las capturas agrupadas de rayas tienden a exhibir tendencias estables en comparación a otras pesquerias de elasmobranquios. Evaluamos si esta aparente estabilidad en las tendencias de las capturas agrupadas podría encubrir una disminución poblacional de las especies a nivel individual. Examinamos dos series de tiempo de estudios especie-específicos en una pesquería de rayas relativamente estable del Atlántico nororiental. Estos estudios revelaron la desaparición de dos especies de rayas, la raya nariz larga (*Dipturus oxyrhinchus*) y la raya blanca (*Rostroraja alba*) y confirmaron un declive previamente documentada de la raya común (*D. batis*). De las cinco especies restantes, las tres más grandes disminuyeron, mientras que las especies pequeñas incrementaron en abundancia. El incremento en abundacia y biomasa de las especies más pequeñas resultó en la estabilidad de las tendencias de las capturas agrupadas. Debido a que existe una sobreposición dietética entre especies, el incremento en abundancia de las especies pequeñas resultó en la estabilidad de las tendencias de las capturas agrupadas. Debido a que existe una sobreposición dietética entre especies, el in-*

cremento en abundancia de las especies pequeñas posiblemente es ocasionando por una liberación competitiva al disminuir las especies más grandes. Una consecuencia de este tipo de estabilidad es que las especies en disminución no pueden ser detectadas sin datos especie-específicos, especialmente en los taxa que exhiben interacciones competitivas. Esto podría explicar el porqué las desapariciones previamente documentadas de dos especies de rayas pasaron desapercibidas por tanto tiempo. La conservación de rayas y otros elasmobranquios requiere de monitoreos especie-específicos y de especial atención hacia las especies más grandes.

Introduction

The conservation of marine species has received less attention than that of terrestrial species (Norse 1993; Irish & Norse 1996; Vincent & Hall 1996; Vincent & Sadovy 1998; Reynolds & Jennings 2000; Roberts & Hawkins 1999). The low conservation priority of marine species can be attributed to two causes. First, it is debated whether marine species could be driven to extinction, because they typically exhibit large geographic ranges and long-distance dispersal strategies (Malakoff 1997; McKinney 1998; Roberts & Hawkins 1999). Second, short-term economic interests in the relatively few commercial species tend to prevail over long-term conservation interests in nontargeted species and ecosystem health (Earll 1994; Vincent & Clarke 1995; Dayton 1998; Mace & Hudson 1999). These conflicting economic and conservation goals were highlighted by the controversy surrounding the listing of Atlantic cod (*Gadus morhua*) and halibut (*Hippoglossus hippoglossus*) in the IUCN Red List (World Conservation Union 1996; Mace & Hudson 1999). The first evidence that the conservation status of exploited marine fishes should be considered seriously came 19 years ago with the disappearance of the common skate (*Dipturus batis*) from the Irish Sea (Brander 1981). Since then another skate species, the barndoor skate (Casey & Myers 1998), has been driven to near extinction throughout its large geographic range. Also, four North Sea skates have undergone severe declines and now exist only in localized pockets (Walker & Heessen 1996; Rijnsdorp et al. 1997; Walker & Hislop 1998).

The worrisome aspect of the local extirpations of these species is that, unlike declines in other marine species, such as whales, they were not discovered until years after they occurred (Brander 1981; Casey & Myers 1998). The barndoor skate has not even been assessed under IUCN criteria (World Conservation Union 1996). Clearly, it is important to understand why disappearances of marine taxa can go unnoticed and to predict beforehand which species may be vulnerable.

As members of the Elasmobranchii, skates are thought to be particularly vulnerable to exploitation because of their large size, slow growth rate, late maturity, low fecundity, and large size at birth. These life-history traits translate into low rates of reproduction and low potential rates of population increase (Holden 1973; Hoenig &

Gruber 1990; Walker & Hislop 1998; Smith et al. 1999). Indeed, elasmobranch life histories and demographics are more similar to those of large mammals than other fishes, with the exception of higher fecundity in skates (40–150 eggs produced per year) (Hoenig & Gruber 1990; Ellis & Shackley 1995; Smith et al. 1999). There is evidence that links between life histories and population dynamics can be used to prioritize species for conservation (Jennings et al. 1998, 2000; Sutherland & Reynolds 1998).

Elasmobranchs typically exhibit rapid declines in catch rates (boom and bust yields), with fisheries collapsing soon after the initiation of exploitation (Holden 1973; 1977; Anderson 1990; Bonfil 1994). Despite this, elasmobranchs tend to receive cursory conservation and fisheries assessment because of their relatively low economic value and the paucity of species-specific data (Compagno 1990; Manire & Gruber 1990; Bonfil 1994; Rose 1996). Consequently, fishery assessment tends to be limited to examining trends in numbers caught, particularly for skates (e.g., Holden 1973; Compagno 1990; Taniuchi 1990; Bonfil 1994; Rose 1996). Unfortunately, skate capture data are not usually recorded on a species-specific basis by nations, with the exception of France (Anonymous 1997). There is a tendency to collect fisheries capture statistics by aggregated categories that can include several species, for skates as well as for other elasmobranchs (Compagno 1990; Bonfil 1994; Rose 1996). Compared to those of other elasmobranch fisheries, aggregated catch statistics for skates exhibit stable patterns of catches and tend to be overlooked in favor of taxa exhibiting more perilous trends (e.g., Holden 1973; International Council for Exploration of the Seas 1989; Taniuchi 1990; Bonfil 1994; Rose 1996).

We examined species-specific abundance patterns of skates to determine whether such apparent stability in aggregated fisheries statistics masks declines in individual species. The skate fishery in the Irish Sea of the northeast Atlantic is currently unmanaged, and all skate species have been exploited for human consumption since at least the 1880s (Anonymous 1889; Holden 1973; Fleming & Papageorgiou 1996). We determined life-history correlates of vulnerability to exploitation for each species. Such correlates could be used for a priori identification of vulnerable species sharing life histories similar to those of other skate species, thereby aiding conservation prioritization (Jennings et al. 1998, 2000).

Methods

Nomenclature and Study Sites

The Rajidae are correctly known by the common name of skates, whereas the term rays is reserved for tropical myliobatoid taxa (Nelson 1994). In European waters, long-nosed rajid species are colloquially known as skates and short-nosed species as rays (Hayward & Ryland 1990). These common names for individual species are used throughout this paper, but we refer to skates when discussing the family Rajidae.

Both historical and recent surveys have been conducted in the Western Seas area of the northeast Atlantic. This area includes the Irish Sea and Bristol Channel and part of the northeast Celtic Sea, corresponding to divisions VIIa, VIIf, and VIIg, respectively, of the International Council for the Exploration of the Seas (ICES; Fig. 1). For international statistical purposes, each division was divided into areas or statistical rectangles, each 0.5° latitude and 1° longitude in size. The study site encompasses 27 such rectangles.

Fishery Statistics

Data on annual yield to the fishery (tonnes), fishing effort (vessel days spent at sea), and catch value of the skate and ray fishery in the Irish Sea and Bristol Channel were extracted from sea fisheries statistics of Her Majesty's Stationary Office (HMSO; Anonymous 1996). Technically, these are landings, because unknown numbers of individuals may be caught and discarded at sea. The lengths of the time series differ because of changes in availability of data. Species-specific data from the commercial fishery are not available because species are aggregated into the category of skates and rays in fisheries statistics. Only data on fishing effort by towed (trawl) and static (long-line) fishing gear were extracted because few skates are captured by seine nets (for the North Sea, see Walker et al. 1997). Data from the Irish Sea and Bristol Channel were combined for statistical analyses. No data were available for the Celtic Sea.

Historical and Recent Data Sources

Historical data on skate community structure were obtained from four research cruises between 1959 and 1965 (Table 1). The aim of these surveys was to tag all individuals and species of skates encountered. It is possible that juveniles of each species are underrepresented. The records of fish released during this survey provide a historical measure of community composition. Surveys were conducted by means of an otter (Lowestoft) trawl with 70-mm mesh. The size of the net mouth is unknown. This gear was towed along the seabed. Records of tow time for the 1959 cruises were not available, so we calculated estimates based on mean tow times of the later Platessa cruises. Six species were captured, including common skate (*Dipturus batis*), blonde ray (*Raja brachyura*),
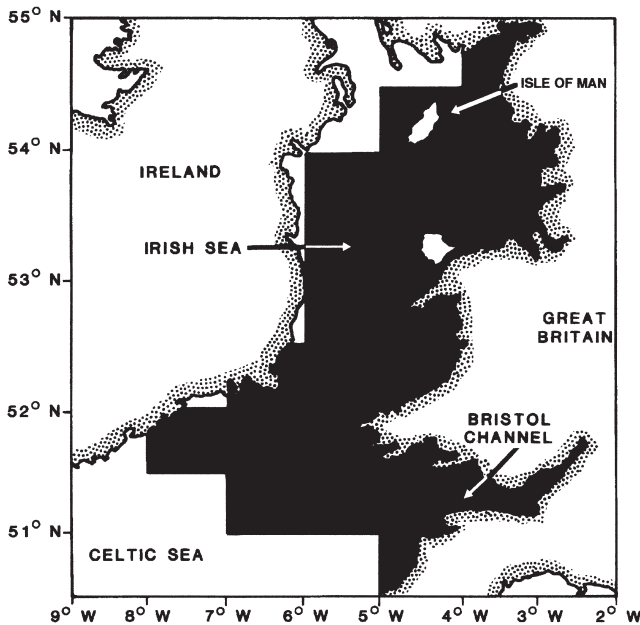

Figure 1. The coast of the United Kingdom and Ireland showing the survey area (shaded) encompassing the Irish Sea, Bristol Channel, and northeastern part of the Celtic Sea.

Table 1. Sampling effort of historical and recent surveys in the Western Seas area of the northeastern Atlantic Ocean.

Year	Vessel name and cruise number	Cruise date (day/month)	Season	Number of tows	Total time towed (hours)
	Platessa				
1959	12	14/7–12/7	summer	42	52.5–61.5*
1959	13	22/7–27/7	summer	38	47.5–55.6*
1964	7	13/5–28/5	spring	74	92.6
1965	7b	2/6–11/6	summer	47	68.8
	Corystes				
1993	3	4/3–29/3	spring	117	58.5
1994	3	3/3–29/3	spring	119	59.5
1996	4	15/3–10/4	spring	78	39
1997	3a	26/2–19/3	spring	115	57.4
1988	7	20/9–13/10	autumn	79	19.8
1989	9	5/9–27/9	autumn	78	19.5
1990	10	6/9–27/9	autumn	108	32
1991	9	10/9–1/10	autumn	106	39.7
1992	10b	28/8–21/9	autumn	158	66.6
1993	10	2/9–27/9	autumn	142	71
1994	10	26/8–19/9	autumn	121	60.3
1995	9	24/8–17/9	autumn	119	59.5
1996	11	23/8–16/9	autumn	121	60.5
1997	10a	15/9–6/10	autumn	110	54.5

*Estimated.

thornback ray (*R. clavata*), painted or small-eyed ray (*R. microocellata*), spotted ray (*R. montagui*), and cuckoo ray (*Leucoraja naevus*).

Recent catch rates of each species were determined from surveys in September–November of 1988–1997 conducted by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) of the Ministry of Agriculture, Fisheries and Food of the United Kingdom. Data were also available for surveys in March–April of 1993–1997, except for 1995. This time series was too short to detect any trends and was used solely for comparison with historical community structure. Although surveys were conducted prior to 1988, they used an incomparable fishing gear, the Granton trawl. The post-1988 data set was chosen because of the comparability of fishing gear and thus of catches over the time period. Surveys were conducted by means of a 4-m beam trawl with 40-mm mesh. This gear is also towed over the seabed but can have higher catch rates than a conventional trawl because of the faster towing speed. The number of fishing tows per year varied from 78 to 158, and the total time towed varied between 19.5 and 71 hours (Table 1). Each fish caught was identified to species, measured (total length in centimeters from the tip of the rostrum to the end of the tail), and weighed (wet and ungutted) to the nearest 10 g.

Surveys between 1989 and 1991 used 15-minute tows, whereas later surveys used 30-minute tows. To determine the effect of the change in tow duration on catch rate and the mean size distribution of fish captured, we tested for differences using a data set consisting of 18 paired tows (15-minute vs. 30-minute). Each pair of tows was conducted in the same area, and the sequence of the tows was randomized. There was no significant difference in catch rate or mean length of individuals caught (mean number of individuals caught: 15-minute tow = 8.7 ± 1.7 standard error of the mean (SEM), 30-minute tow = 6.3 ± 1.4 SEM; paired t = 1.8, df = 17, p = 0.090; mean length of individuals: 15-minute tow = 38.7 ± 1.2 SEM cm, 30-minute tow = 39.4 ± 1.2 SEM cm;

paired t = -0.404, df = 17, p = 0.686). Because both tow durations caught similar quantities and sizes of fish, they were treated as equivalent, and catch rates were calculated as catches per tow (equivalent to 15-minute tow). To ensure that our results were robust to tow duration, we performed two alternative sets of analyses. First, we scaled the 30-minute tows to the 15-minute tows according to the difference in the mean catch rates of the paired tow trial. Second, we scaled the catch rates according to the difference in tow time by halving the catch rate of the 30-minute tows. Neither of these alternative corrections changed the patterns, except the latter data set changed a nonsignificant life-history correlation to significant; therefore, we retain the more conservative unstandardized data throughout. The abundance of all species appears consistently higher in 1991; this is likely to be a survey artefact.

Data on Life Histories and Fishing Mortality

Life-history parameters and estimates of fishing mortality for each species were gathered from published sources and unpublished CEFAS survey data (Table 2). Estimates of fishing mortality from the literature had been derived by means of catch curves and mark-and-recapture methods. To the best of our knowledge, these tables include every published estimate. Fishing mortality (*F*) is expressed as annual mean instantaneous fishing mortality, which is related to survivorship(*S*):

$$S = e^{-(F+M)},$$

where *S* is the survival rate per unit time (1 year) and *M* is natural mortality. Growth rate and body size of each species were described by *K* and L_∞ of the Von Bertalanffy growth equation

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

where L_t is length at age *t* (in years), L_∞ is the asymptotic length, *K* is the rate of growth toward the asymptotic length, and t_0 is the time at which length is zero

Table 2.   Fishing mortality and life-history parameters for all Western Seas species, ranked in descending order of body size (±SE).[a]

Species	Mean F	K (per year)	L_∞	L_{max}	$L^{1st\ m}$ (cm)	$L^{50\%\ m}$ (cm)	References[b]
Common skate	no data	0.057	253.7	220 ± 30	no data	no data	1–4
Blonde ray	0.71 ± 0.16	0.220 ± 0.013	123.3 ± 3.2	96.7 ± 4.4	no data	90 ± 5	4–7
Thornback ray	0.58 ± 0.10	0.188 ± 0.013	107.5 ± 3.4	96.7 ± 3.5	51.7 ± 2.5	62.7 ± 2.9	5–15
Shagreen ray	no data	no data	95	89.5 ± 9.7	56.2	53.3	1, 3
Painted ray	0.57 ± 0.04	0.074	no data	80.0 ± 0.9	44.3 ± 5.7	no data	1, 14
Cuckoo ray	0.7 ± 0.06	0.223 ± 0.064	78.2 ± 6.8	68.0 ± 0.6	57.3	53.9	2, 6
Spotted ray	0.59 ± 0.10	0.218 ± 0.032	76.3 ± 5.5	68.0 ± 1.0	58.5 ± 0.8	70	5–7, 14

[a]F, *instantaneous fishing mortality*; K, *growth rate, from the von Bertalanffy equation*; L_∞, *asymptotic (maximum) length*; L_{max}, *maximum length recorded*; $L^{1st\ m}$, *length at first maturity*; and $L^{50\%\ m}$, *length at which 50% of the population are mature.*
[b]*References: 1, Wheeler (1969); 2, Du Buit (1977); 3, Whitehead et al. (1984); 4, Fahy (1991); 5, Holden (1972); 6, Fahy (1989); 7, Pawson & Nichols (1994); 8, Steven (1947); 9, Williams et al. (1965); 10, Lesser (1967); 11, Jardas (1973); 12, Fitzmaurice (1974); 13, Nottage & Perkins (1983); 14, Ryland & Ajayi (1984); and 15, Brander & Palmer (1985).*

(Beverton & Holt 1957). We also used an alternative body size parameter, L_{max}, defined as the largest individual recorded for each species, because L_∞ is particularly sensitive to sample size.

Analyses

Historical data (1959–1965) on percent community composition of each skate species were averaged across 12 statistical rectangles and compared to percent community composition of groundfish surveys (1989–1997) averaged across the same statistical rectangles. Standard-error bars represent spatial variability among sites during each survey period. Percent community composition was used for relative comparisons because differences in catch rates of historical and recent fishing gears are unknown.

To examine short-term community changes, catch rates were summed by ICES statistical rectangle and expressed as means for each year. Standard errors thus represent spatial variability within each year. Regression coefficients of species trends in numerical abundance, biomass, and mean size were determined using least-squares regression on transformed ($\log_{10} + 1$) abundance and biomass against time. This linear model provided a suitable short-term description of trends. We controlled for differences in fishing mortality (F) by taking residuals from regressions between mean fishing mortality and population trend (abundance and biomass).

To determine life-history correlates of short-term population trends, we conducted a cross-species study. A phylogenetically explicit analysis is preferred because species are not strictly statistically independent (Felsenstein 1985; Harvey & Pagel 1991; Martins 1997). Electrophoretic species-specific data suggest that *R. clavata* and *R. montagui* can be grouped together, as can *R. brachyura* and *L. naevus* (Blake 1972). These pairings are supported by a morphological phylogeny that suggests *R. brachyura* is basal to the other *Raja* species, thus allowing a comparison to be made between it and *L. naevus* (McEachran & Dunn 1998). Thus, two phylogenetically independent comparisons can be calculated from these pairs.

Results

Stability of the Skate Fishery

Generally there has been a gradual decline in catches (technically, landings) except between 1978 and 1987, when catches increased slightly (Fig. 2a). There has been no change in fishing effort over time, although it has varied considerably between 8000 and 13000 days at sea per year. As a result, catch per unit of fishing effort of skates and rays has declined over time, but there have been two periods during which it increased, 1958–1965 and 1972–1989 (Fig. 2b). There has been an increase in
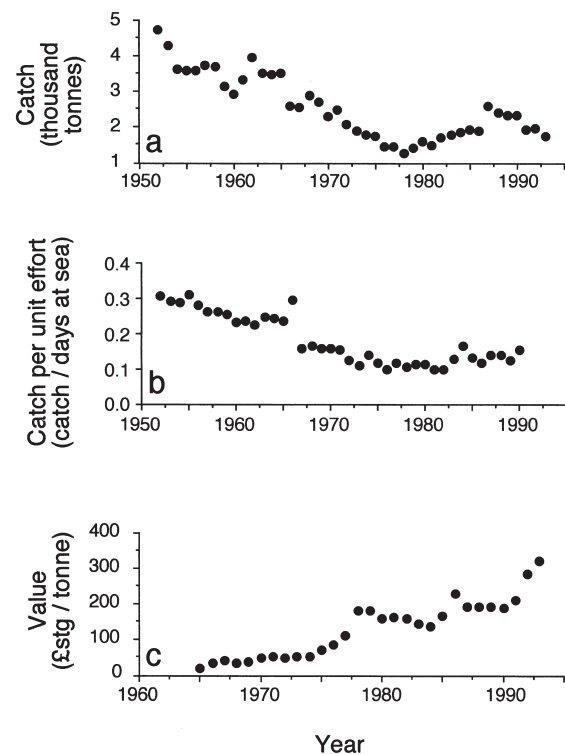

Figure 2. Skate and ray catches: (a) combined for the United Kingdom fleet in the Irish Sea and Bristol Channel (1952–1993), (b) catch per unit fishing effort (1952–1989), and (c) monetary value of catches in the Irish Sea and Bristol Channel (1965–1993).

the value of these fish over time (Fig. 2c). The fishery catches exhibited a slight decline during the groundfish survey period (1988–1997).

Changes in Community Structure

Comparison of present community structure with that of the 1959–1964 period showed that, with one exception, the larger species declined in abundance, whereas the smaller species increased in abundance (Fig. 3). The dominant species, the thornback ray, declined from 52.8% to 42.8%. The largest species in the community, the common skate, declined from 2% to 0.2%. In contrast, the smaller cuckoo ray has increased from 4.8% to 21.3%. The more southerly distributed painted ray increased in relative abundance from 0.6% to 7.6%. There was little change in the relative abundance of one large species, the blonde ray (3.8% to 4.4%), and a smaller species, the spotted ray, exhibited a decline in relative abundance (36% to 23.7%).

The numerical abundance and biomass of all skates combined showed slight declines during 1988–1997 (Fig. 4a & 4b), reflecting the gradual decline in fisheries catches over the same period (Fig. 2). There were declines in both the numerical abundance and biomass of
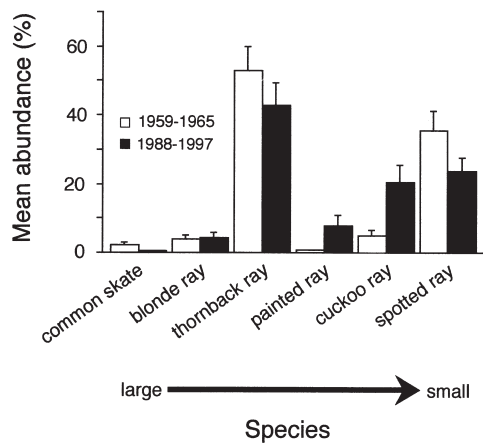
Figure 3. Relative abundance of skates (Rajidae) between 1959–1965 and 1988–1997. Species are ranked according to body size with the largest species on the left.

the three largest species: blonde, thornback, and painted rays (Fig. 5a & 5b). The most marked change was in the relative abundance of thornback ray, which declined from 64.4% at the beginning of the survey to 44.7% at the end (Table 3). In contrast, both smaller species exhibited increasing trends in numerical abundance and biomass throughout the time period (Fig. 5a & 5b). This pattern was particularly marked in the spotted ray, which increased in numerical abundance from 13.5 % to 28.4%.
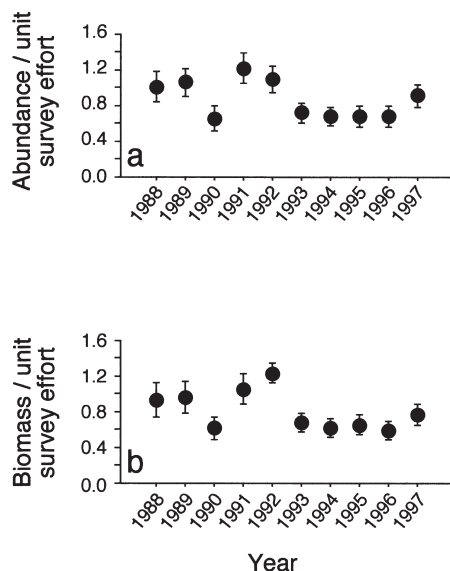

Figure 4. Trends in (a) numerical abundance (log_{10} +1 numbers per tow) and (b) biomass (log_{10} +1 kg per tow) of five skate species (Rajidae) combined between 1988 and 1997, as determined by the autumn groundfish survey conducted by the Centre for Environment, Fisheries and Food of the United Kingdom.

The cuckoo ray exhibited a dome-shaped pattern of numerical abundance and biomass, suggesting an initial increase followed by a decline. Such a fluctuating pattern of abundance and biomass is apparent to a lesser extent in all species trends. The rank order of species in the community in terms of a mean of both numerical abundance and biomass was as follows: thornback ray > spotted ray > cuckoo ray > painted ray > blonde ray (Table 3).

The only additional species encountered were the common skate (*D. batis*, 6 individuals) and shagreen ray (*L. fullonica*, 10 individuals). No white skates (*Rostroraja alba*) or long-nose skates (*Dipturus oxyrhinchus*) were recorded in either of these data sets. Both species are documented as having been targeted by long-line fisheries operating from the Isle of Man, in the center of the Irish Sea during the late 1880s (Bruce et al. 1963). This suggests they are now locally extinct in the Irish Sea and Bristol Channel areas.

Life-History Correlates of Response to Exploitation

Larger species (>85 cm, based on either body size measure) declined, whereas smaller species increased during the 9-year study period, 1989–1997, independently of differences in fishing mortality (Fig 6a & 6b). A significant relationship was found between L_{max} and response to exploitation, but this was not significant when L_∞ was used as a measure of body size (Table 4), probably because there are no L_∞ data for the painted ray. We found no significant relationship between either measure of population trend and other life-history traits (Table 4), but caution is warranted due to the paucity and variable quality of trait estimates other than body size, such as painted ray growth rate (*K*) and spotted ray length at 50% maturity ($L_{50\%}$). The hypothesis that larger species are more vulnerable to exploitation is supported by a phylogenetic analysis. Of the two pairs of taxa, the larger of each pair declined, whereas the smaller related species increased in abundance and biomass. The use of the first alternative method for scaling between 15- and 30-minute tows resulted in significant relationships between L_∞ and both measures of abundance. The use of the second scaling method did not affect the results.

Discussion

Aggregated Abundance Trends and Conservation Issues

Our data suggest that the stability exhibited by this multispecies skate community masks serious conservation issues, notably the local disappearance of three species—common, long-nosed, and white skates—and declines in three of the remaining five species. This kind of aggregated stability may explain why large species such as the
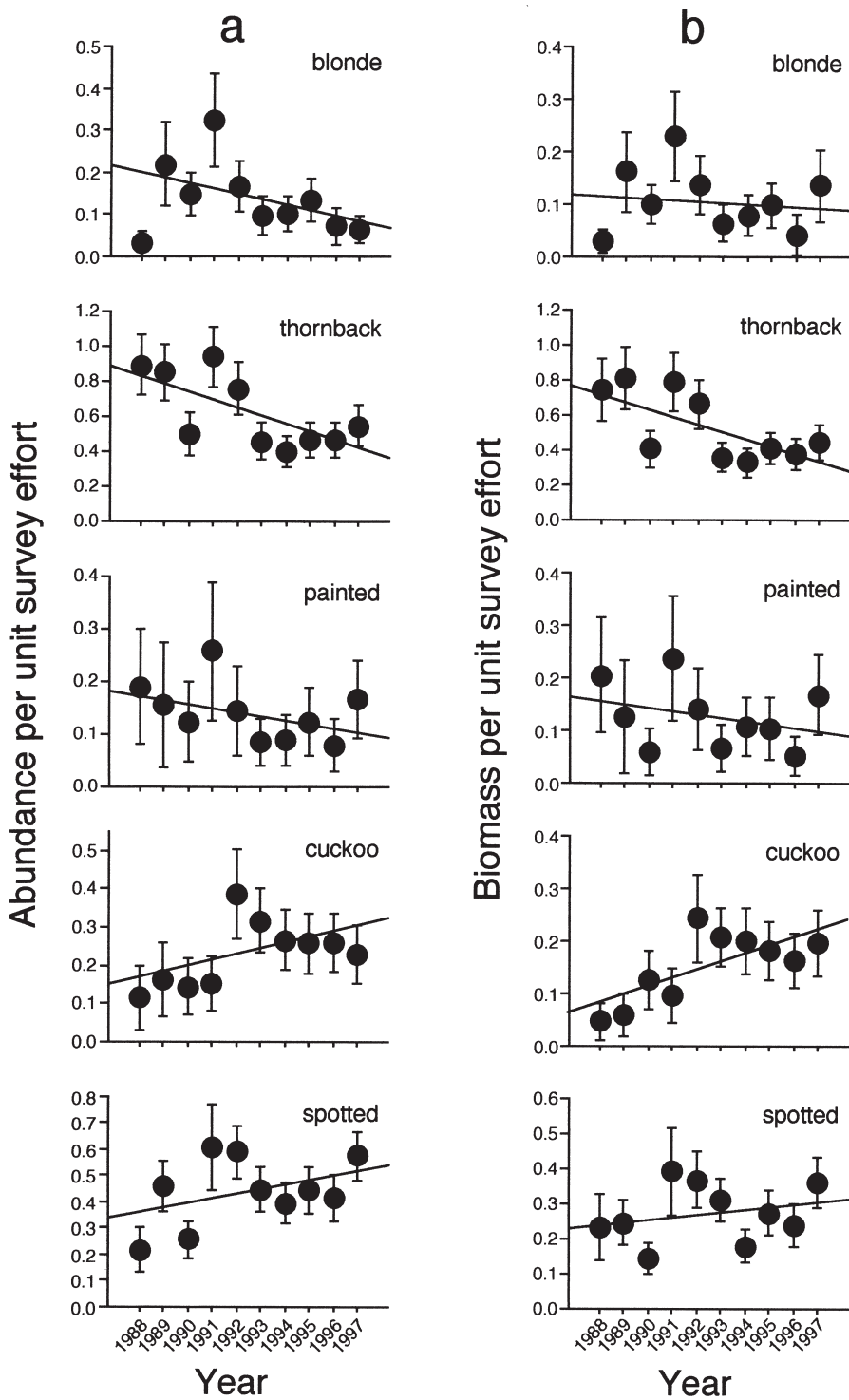
Figure 5. Change in (a) numerical abundance (log_{10} + 1 numbers per tow) and (b) biomass (log_{10} + 1 kg per tow) of five skate species (Rajidae) between 1988 and 1997. Graphs are ranked in order of body size, with largest species at the top and smallest at the bottom. Trend lines were fitted by least squares regression.

common and barndoor skates disappeared unnoticed (Brander 1981; Casey & Myers 1998). In most cases there are either too few data to allow accurate assessments or such data are aggregated among different species, potentially masking important trends and crypto-extinctions (Carlton et al. 1991; Bonfil 1994; Rose 1996; Roberts & Hawkins 1999).

Some fisheries managers might assume that skate fishery stability is analogous to the stability of teleost fisheries, which is regarded as a measure of successful management (Holden 1992; Garcia & Newton 1995). This could explain why skate fisheries have been overlooked more readily than fisheries exhibiting more perilous trends (e.g., Holden 1973; International Council for Exploration of the

Table 3.   Population trends for exploited skates (Rajidae), 1988–1997, in the Western Seas area of the northeastern Atlantic Ocean.

| Species*	Abundance trends regression coefficient	Biomass trends regression coefficient	Mean abundance (%)		Mean biomass (%)	
			1988–1990	1994–1997	1988–1990	1994–1997
Blonde ray	−0.009	−0.003	5.0	4.0	4.0	6.8
Thornback ray	−0.047	−0.045	64.4	44.7	76.0	46.0
Painted ray	−0.008	−0.007	10.0	8.4	6.8	5.1
Cuckoo ray	+0.015	+0.016	7.1	14.4	6.1	13.3
Spotted ray	+0.018	+0.006	13.5	28.4	13.9	28.8
All species	−0.033	−0.034	—	—	—	—

Species are listed in descending order of body size.

Seas 1989; Taniuchi 1990; Bonfil 1994; Rose 1996). That there is stability at all is remarkable because these skates have been exploited at extremely high rates (43–50% of all individuals killed per year). This level of mortality is higher than that faced by the nearly extinct barndoor skate, is almost as high as that of the IUCN Red-Listed cod, and is 3–20 times higher than the sustainable exploitation rates of some mammals (van Dyne et al. 1980; Casey & Myers 1998; Jennings et al. 1998). This level of skate exploitation is also similar to the maximum sustainable hunting rates of elephant (*Loxodon africana*), red deer (*Cervus elaphus)*, and reindeer (*Rangifer tarandus*) (Beddington & Basson 1994). We suggest that effective conservation of skates, and possibly other elasmobranch species, requires species-specific monitoring of abundance and rates of mortality caused by exploitation.

Community Shifts under Exploitation

Declines in larger skate species have been accompanied by increases in smaller species in the community. This is apparent in both the long-term comparison of relative abundance (1959–1965 vs. 1988–1997) and especially in the more detailed short-term comparison of absolute abundance (1988–1997). Neither data set is perfect, given the differences in sampling equipment in the long-term comparison (1959–1965 vs. 1988–1997) and the limited time series available for the short-term comparison (1988–1997). Yet both approaches yield consistent results. Indeed, the three species that have been almost completely depleted from the Irish Sea since the turn of the century have all been large. The common skate, long-nose skate, and white skate are 250, 150, and 200 cm maximum length, respectively (Stehmann 1990). Of the remaining species,, those >85 cm declined, whereas smaller species increased in abundance. Similar shifts in skate community composition have been observed in the North Sea (Walker & Hislop 1998). Declines were recorded for the largest species (common skate, thornback ray, blonde ray, and shagreen ray), accompanied by increases in the abundance of the smaller species (the cuckoo ray and starry ray [*R. radiata*], which is absent from the Irish Sea) (Walker & Heessen 1996; Rijnsdorp et al. 1997; Walker & Hislop

1998). Furthermore, a small species, the spotted ray, appears to have invaded the area recently (Walker & Heessen 1996; Walker & Hislop 1998). Although the authors of the North Sea studies were unable to control for the level of fishing mortality for each species, their results are similar to ours.

A key question is why the smaller species of skates in our study increased in abundance? Because the population trends were independent of fishing mortality (*F*), we suggest that these species—cuckoo and spotted rays—have undergone competitive release. Skates are generalist benthic predators that feed predominately on crustaceans and fishes, as well as polychaetes and molluscs (Holden & Tucker 1974; Ajayi 1982; Ellis et al. 1996). Dietary data
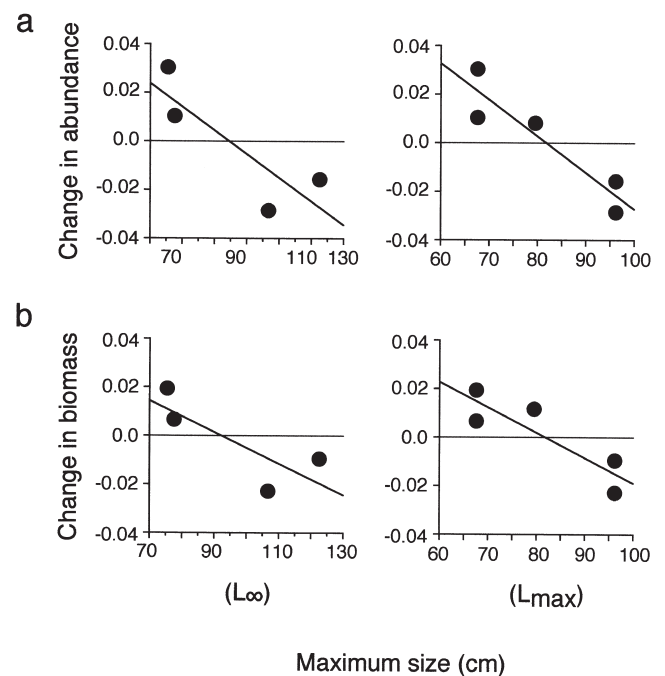
Figure 6. Body-size correlates of response to exploitation measured as (a) numerical abundance trend and (b) biomass trend (controlling for fishing mortality) (L_∞*, asymptotic length in the von Bertalanffy equation, *L_{max}*, maximum length documented.)*

Table 4.   Relationships between life-history traits and population trends (abundance and biomass) of skates.

Life-history trait	Population trend	Regression coefficient	r^2	n	F	p^a
Bodysize[b]						
L_{max}	abundance	−0.001	0.863	5	18.83	0.023*
L_{max}	biomass	−0.001	0.778	5	10.51	0.048*
L_∞	abundance	−0.001	0.723	4	5.22	0.149
L_∞	biomass	−0.001	0.650	4	3.714	0.194
Growth rate, K	abundance	−0.007	0.003	4	0.001	0.975
Growth rate, K	biomass	−0.049	0.033	4	0.102	0.770
Size at first maturity	abundance	0.001	0.146	4	0.341	0.619
Size at first maturity	biomass	0.001	0.034	4	0.071	0.815
Size at 50% maturity	abundance	0.001	0.078	4	0.085	0.820
Size at 50% maturity	biomass	0.001	0.061	4	0.065	0.841

[a] Significant results at $p < 0.05$ are marked with an asterisk.
[b] L_{max}, largest individual documented; L_∞, asymptotic length of the Von Bertalanffy growth equation.

collected from the same recent survey series (1988–1997) show significant dietary overlap between large and small skates, including blonde and spotted skates, juvenile thornback and spotted and cuckoo rays, and adult thornback and spotted rays (Ellis et al. 1996). Thus, the removal of the larger skates may have led to the increase of smaller species through increased food availability. This competitive release mechanism has also been suggested to explain the increase in starry ray abundance in the North Sea (Walker & Heessen 1996). Such competitive release, mediated by dietary overlap, has been proposed to explain the phase shift from a teleost-dominated to an elasmobranch-dominated community in the Georges Banks area of the northwest Atlantic (Grosslein et al. 1980; Murawski & Idoine 1992; Fogarty & Murawski 1998). Although there is evidence of indirect effects of exploitation, such as prey release and trophic cascades, there appear to be few examples of the type of strong species interaction or competitive release that we have shown here (Jennings & Lock 1996; Jennings & Kaiser 1998).

Predicting Vulnerability to Exploitation

Our results match those of recent studies of temperate and tropical teleost (bony) fishes, suggesting that larger species are more vulnerable to exploitation (Jennings et al. 1998; Russ & Alcala 1998; Jennings et al. 2000). These studies showed that the most vulnerable species have larger maximum sizes, and later maturation, and lower rates of potential population increase. Large body size is one of the most cited correlates of extinction vulnerability (Brown 1995; Hunter 1996; McKinney 1997; Meffe & Carroll 1997). This pattern is found in a wide range of both fossil and extant taxa, from corals to birds and mammals (Lessa & Farina 1996; Bennett & Owens 1997; Lessa et al. 1997; McKinney 1997). The only taxa that do not exhibit a relationship of body size to extinction risk are marine molluscs and freshwater fishes (Angermeier 1995; Parent & Schriml 1995; Jablonski

1996). A re-analysis of Walker and Hislop's (1998) sensitivity index shows that replacement rate is related to body size, suggesting that body size is a surrogate of demography (regression coefficient $= -0.2$; $r^2 = 0.769$; $F^{1,4} = 10$; $p = 0.051$). In mammals there is also a negative relationship between body size and intrinsic rate of population increase, r (Sinclair 1996). Although body size appears to be a reasonable predictor of intrinsic rate of population increase, other traits such as reproductive lifespan and fecundity are also important in determining r (Smith et al. 1999). This generalization could be used in a predictive manner, however, to prioritize skate species for assessment of their conservation status, because larger species in assemblages are likely to be most vulnerable to exploitation due to their lower intrinsic rates of natural increase.

Our results indicate that conservation or management assessment based on aggregated population trends of several species may be misleading. Such aggregated abundance statistics mask local disappearances and declines of individual species. It appears that larger skates are more vulnerable to exploitation than are smaller species. We suggest that future conservation efforts focus on collection of species-specific abundance statistics and prioritization of larger species of skates and other elasmobranchs for conservation assessment.

Acknowledgments

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