Predicting Extinction Vulnerability in Skates

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Abstract: *Relatively few marine fishes have been assessed under World Conservation Union criteria, yet it is believed that marine fish extinction rates have been underestimated by one order of magnitude (McKinney 1999). Given the paucity of data required for traditional assessment methods, we explored the use of potential correlates of extinction vulnerability to prioritize species for conservation assessment. We focused on the world's 230 species of skates and rays (Rajidae) because they have been identified as one of the most vulnerable groups of marine fishes. We searched for all documented cases of local extinction and compiled a database of body size and latitudinal and depth ranges for all species for which data were available. We found that species that have disappeared from substantial parts of their ranges ("locally extinct") have large body sizes compared with all other skates, but that latitudinal and depth ranges were similar to those of other species. The body size correlate may be due to higher mortality rates and correlations with life-history parameters such as late age at maturity. We used the locally extinct species that had the smallest size or ranges as benchmarks to generate lists of other species that may be vulnerable. Body size generated the smallest species list (7), excluding the known local extinctions, compared with lists generated by size of latitudinal (150) or depth range (63). Body size was the only trait that correctly identified the known local extinctions, suggesting that it is more useful than range sizes for identifying potentially vulnerable fishes. This provides a simple, objective method of prioritizing species for further assessment, which complements direct methods that are more data-intensive and time-consuming.*

Predicción de la Vulnerabilidad de Extinción en Rayas

Resumen: *Pocos peces marinos han sido evaluados según los criterios de la UICN, sin embargo se cree que las tasas de extinción de peces marinos han sido subestimadas por un orden de magnitud (McKinney, 1999). Dada la escasez de los datos requeridos por los métodos de evaluación tradicional, exploramos el uso de correlaciones potenciales de vulnerabilidad de extinción para priorizar especies para la valoración de su conservación. Nos enfocamos en las 230 especies de rayas del mundo (Rajidae) puesto que han sido identificadas como uno de los grupos de especies marinas más vulnerables. Buscamos todos los casos documentados de extinción local y recopilamos una base de datos de tamaño corporal y rangos latitudinales y de profundidad para todas las especies de las que existen datos disponibles. Encontramos que las especies que han desaparecido de partes sustanciales de sus rangos de distribución ("localmente extintas") han tenido cuerpos grandes comparadas con las otras rayas, pero sus rangos latitudinales y de profundidad fueron similares a los de las otras especies. La correlación del tamaño del cuerpo puede ser debida a tasas de mortalidad más altas y a correlaciones con parámetros de la historia de vida como lo es la edad avanzada al madurar. Usamos las especies localmente extintas que tenían los tamaños más pequeños o los rangos más pequeños como referencias para generar listas de otras especies que pueden ser vulnerables. El tamaño corporal generó la lista más corta (7), excluyendo las extinciones locales conocidas, comparada con la lista generada por el tamaño del rango latitudinal (150) o el tamaño del rango de profundidad (63). El tamaño corporal fue la única característica que identificó correctamente las extinciones locales conocidas, sugiriendo que es mas útil que los tamaños de los rangos para identificar peces potencialmente vulnerables. Esto provee un método simple y objetivo para priorizar especies para evaluaciones futuras, lo cual complementa métodos directos que requieren datos intensivos y consumen mucho tiempo.*

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Introduction

Marine fishes present unique challenges for conservation assessment (Vincent & Hall 1996; Roberts & Hawkins 1999). Fisheries have caused severe declines in many species, but there are still no documented cases of complete extinction, and there is considerable debate as to whether marine species could become extinct (Roberts & Hawkins 1999; Hutchings 2001; Jennings et al. 2001). Many species are thought to be safe due to large geographical ranges and long-range dispersal mechanisms (Malakoff 1997; McKinney 1998), although this will not be true for all taxa (Vincent & Sadovy 1998; Roberts & Hawkins 1999; Reynolds & Jennings 2000). It has also been argued that biological extinction by exploitation is unlikely because economic extinction would occur first, causing a decline in exploitation and allowing population recovery (Beverton 1990, 1992). Again, this orthodoxy has exceptions. For example, prices of southern bluefin tuna (*Thunnus maccoyii*) have soared as high as U.S. $178,000 per fish as stocks have declined (Watts 2001). This value makes it economically viable to use airplanes to direct boats to single individuals. Species caught as bycatches are another exception because they can continue to decline as an indirect effect of fisheries aimed at more valuable species (Brander 1981; Casey & Myers 1998; Roberts & Hawkins 1999; Dulvy et al. 2000).

Uncertainty about the theoretical likelihood of extinctions in marine ecosystems is compounded by practical difficulties in identifying species at risk (Mace & Hudson 1996; Vincent & Hall 1996). It is difficult to conduct sampling with sufficient power to determine rates of decline, how many individuals are left, or whether the last individual has disappeared (Roberts & Hawkins 1999). Fisheries biologists pay more attention to valuable targeted species, but because the majority of fishes are not managed, we know little about them. Consequently, local extinctions of marine fishes and invertebrates tend to be overlooked until long after they have occurred (Brander 1981; Casey & Myers 1998; Carlton et al. 1999; Dulvy et al. 2000). As a result of these problems, the conservation status of <5% of approximately 24,600 fish species has been assessed according to the World Conservation Union's Red List of Threatened Species (Hilton-Taylor 2000). Given the current situation, it seems timely to devise rules of thumb to allow the rapid, objective assessment of the conservation status of marine fishes (e.g., Musick 1999*a*). This is particularly true for elasmobranchs such as skates and sawfishes (Camhi et al. 1998), which are believed to be highly vulnerable to exploitation due to their large body size and associated large offspring size, slow growth, late maturation, and low fecundity relative to bony fishes (teleosts) (Holden 1973, 1974; Compagno 1990; Hoenig & Gruber 1990; Stevens et al. 2000; Goodwin et al. 2002).

One approach to prioritizing species for conservation is to use life-history traits correlated with declining or extinct taxa (Reynolds et al. 2001). The most obvious biological feature to examine is body size. In a wide variety of taxa, large-bodied species are consistently more prone to declines or extinction (Lessa & Farina 1996; Bennett & Owens 1997; McKinney 1997). Larger fish species are usually more valuable and hence targeted more extensively. They are also more prone to being caught by many types of fishing gear. Large-bodied species have correlated life-history characters that render populations less resilient to exploitation; for example, late maturity leads to low intrinsic rates of population increase (reviewed by Musick 1999*b*; Smith et al. 1999; Reynolds et al. 2001). These expectations have been borne out by recent comparative studies showing that larger-bodied species, including skates, tend to suffer greater declines than smaller ones (Jennings et al. 1998, 1999*a*; Dulvy et al. 2000; Stevens et al. 2000). Additional features linked to high extinction vulnerability in other taxa are small geographic range size (Jablonski & Chaloner 1994; Gaston 1996; Gaston & Blackburn 1996; Purvis et al. 2000) and ecological specialization, including feeding modes, habitats, and migration (Carlton et al. 1991; McDowall 1992; Bibby 1994; Angermeier 1995).

Although species can be ranked along these gradients of vulnerability, it is helpful to have benchmarks for determining how vulnerable a given species is apt to be and hence what priority the species deserves for protection or further assessment. Choices of dividing lines will always be rather arbitrary, whether based on ecology (Stobutzki et al. 2001), life histories (e.g., Musick 1999*a*), or population changes and range size (Mace 1995; Purvis et al. 2000). We explored a potential way forward that involves the use of species whose vulnerable status has been well documented as benchmarks for comparison with other species with similar life histories. We suggest that exploited species beyond the benchmark for the relevant extinction correlate should be given high priority for conservation attention because they could face a similar fate. Testable hypotheses derived from this reasoning are that species larger than a body-size benchmark should be more vulnerable, as should species with smaller geographic ranges.

We searched for documented local extinctions of all 230 known skate species and compared the body sizes and two measures of geographical range size, latitude and depth, of the known locally extinct species to those of all other species to qualitatively test the hypotheses. The known locally extinct species were used as benchmarks to identify additional species that may be at risk on the basis of body size and range and that therefore deserve high priority in conservation assessments.

Methods

Locally extinct species are defined as those that have undergone severe population declines and have disap-

peared from a substantial part of their geographical range. To determine which of the world's described skates have become locally extinct, we searched the literature and questioned people on ELASMO-L, an electronic elasmobranch discussion group of approximately 675 subscribers (J. G. New, personal communication).

For each species, where available, we collated information on body size (109 species), latitudinal range (202 species), and depth range (147 species). Total length (in centimeters) was used as a measure of body size, latitudinal range was measured in degrees, and depth range was measured in meters. Data were compiled from FishBase (Froese & Pauly 2000), primary literature, and regional checklists. The data set is available on request from the authors. Relative geographical ranges were calculated from the residuals of a least-squares regression model of each range size on body size.

Through a two-step approach, we asked how useful body size and both measures of range size were for identifying vulnerable species. First, we compared the body size and ranges of species exhibiting evidence of extirpation to all other species to see at which end of the trait spectrum the locally extinct species lie. Second, we used the results of this analysis to provide a benchmark for identifying additional species that may have been at risk, but for which data on their status were not yet available. As a precautionary approach, we searched our database for all species that met any of the following three criteria: (1) larger body size than the smallest known locally extinct species, (2) smaller latitudinal range size than the locally extinct species with the smallest latitudinal range, and (3) narrower depth range than the locally extinct species with the narrowest depth range. We used the locally extinct species with the smallest body and range size as benchmarks to search for species facing the double jeopardy of large body size and small range size.

We tested for relationships between body size and the two measures of range size using both cross-species regression, in which each species contributed one data point to the analyses, and phylogenetically based comparative analyses (Felsenstein 1985; Harvey & Pagel 1991; Martins 1997; Rickman et al. 2000; Reynolds et al. 2001). The latter method addresses the fact that common ancestry usually precludes species from being treated as if they are statistically independent. Statistical and phylogenetic independence can be achieved by calculating paired independent contrasts (PICs) or differences in life history and biogeographical traits between closely related pairs of species. The use of contrasts also reduces the Type 1 error rate by controlling for spurious differences among unrelated taxa. We calculated contrasts using CAIC (Purvis & Rambaut 1995), based on the most detailed and recent genus-level skate phylogeny (McEachran & Dunn 1998). Information on the branch lengths between species was unavailable, so we set them to zero. Data were $\log_{10}$-transformed to achieve normality, and the raw contrasts were standardized by the square root of their expected variance to meet the assumptions of regression analysis (Purvis & Rambaut 1995; Freckleton 2000).

Results

To the best of our knowledge, there is evidence for the local extinction of only four species of skate: barndoor skate, common skate, long-nose skate, and white skate (Table 1 [contains scientific names]; Fig. 1). We compared the distribution of the traits of the locally extinct species with those of all other species (Fig. 2). The locally extinct species were all on the large end of the body-size spectrum, the smallest of which was the barndoor skate, and it was therefore used as a benchmark for this trait (Fig. 2). The locally extinct species exhibited intermediate to large latitudinal ranges and intermediate depth ranges compared with the other species (Fig. 2). The white skate had both the smallest latitudinal range and smallest depth range; it was therefore used for a benchmark for these traits in later analyses. Overall, large-bodied species had larger latitudinal ranges than smaller species (cross species, $F_{1,94} = 11.9, p = <0.001$; phylogenetic contrasts, $F_{1,27} = 26.2, p = <0.001$), and they occupied greater ranges of depth (cross species, $F_{1,93} = 3.7, p = 0.057$; phylogenetic contrasts, $F_{1,25} = 4.85, p = 0.037$) (Fig. 3).

In addition to the known local extinctions, seven species had larger body sizes than the barndoor-skate benchmark (Table 2; Fig. 4). Many species had smaller latitudinal (150) and depth (63) ranges than the white-skate benchmark. Fewer species had smaller relative latitudinal ranges (29) and smaller relative depth ranges (20) than the benchmark white skate when body size was controlled for. Three species had both larger body sizes and smaller relative latitudinal ranges than the benchmarks: Richardson's ray, spinetail ray, and smooth skate. Only one species, the roughbelly skate, had both larger body size and smaller relative depth range than the benchmarks. The only trait that correctly identified the other known local extinctions, apart from those used as benchmarks, was body size (Fig. 4). Contrary to the hypothesis linking vulnerability to range size, all three of the nonbenchmark local extinctions involved species occupying larger ranges and living in deeper water than the benchmarks. Four of the 7 species identified as potentially vulnerable, based on their body size, have shallow continental shelf and slope distributions. Three others—pale ray, Richardson's ray, and the roughbelly skate—inhabit abyssal plains (Table 2).

As an additional test of the value of body size compared to range size for predicting vulnerability, we reanalyzed correlates of population trends of five exploited

Table 1. Documented local extinctions of skates.

Species	*Population trend*	*Range reduction*	*Conservation status*[a]	*Habitat*	*Distribution*	*References*[b]
Barndoor skate (*Dipturus laevis*)	~96% decline between 1963–1965 and 1997–1999	extinct in six of nine statistical areas of the North Atlantic Fisheries Organisation	vulnerable	benthic on shelf and slope, now mostly on deep slope	northwest Atlantic	1–5
Common skate (*D. batis*)	92% decline in landings to Concarneau, France between 1969 and 1979	almost gone from Irish Sea, only six individuals caught between1988 and 1997 in government surveys; locally extinct in southern and central North Sea, West Baltic, and western Mediterranean	endangered	benthic on shelf and slope	eastern Atlantic & Mediterranean	4, 6–14
Long-nose skate (*D. oxyrhinchus*)	unknown	present in Irish Sea catches during 1880s; absent from recent government surveys; severe decline in North Sea	not assessed	deep slopes, previously known from shelves	eastern Atlantic	6, 8, 9, 13–15
White skate (*Rostroraja alba*)	unknown	present in Irish Sea catches during 1880s; absent from recent government surveys; concern raised for Mediterranean stock	not assessed; protected under Annex II of the Bern Convention	benthic	northwest Atlantic & southwest Indian ocean	4, 8, 9, 13–16

[a] *Based on World Conservation Union Red List data.*
[b] *References: 1, Leim & Scott (1966); 2, Scott & Scott (1988); 3, Casey & Myers (1998); 4, Froese & Pauly (2000); 5, Northeast Fisheries Science Center (2000); 6, Wheeler (1969); 7, Brander (1981); 8, Stehmann & Bürkel (1984); 9, Stehmann (1990); 10, Walker & Heessen (1996); 11, Walker & Hislop (1998); 12, Fahy (1989); 13, Dulvy et al. (2000); 14, Walker & Ellis (1998); J. R. Ellis personal communication; 15, Bruce et al. (1963); and 16, Anonymous (1999b).*

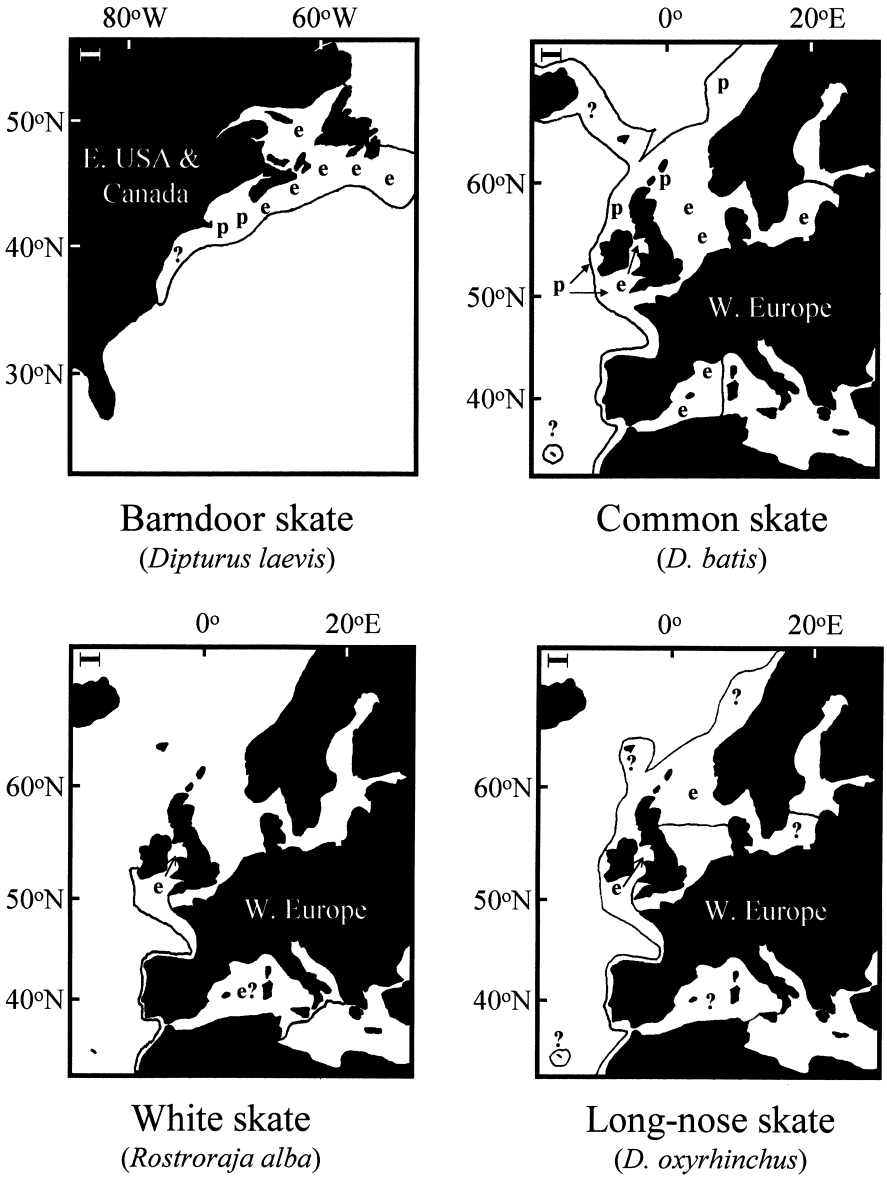

Figure 1. Historical distribution of four locally extinct skates in the northwest and northeast Atlantic, from Table 1. Key: e, area of local extinction; p, present in recent fisheries surveys; ?, no knowledge of status; e?, possible local extinction. Scale bar represents 150 km.

Irish Sea skates (based on Dulvy et al. 2000). There was a significant negative relationship between body size and both measures of abundance (numerical abundance, $F_{1,4} = 18.8$, $p = 0.023$; biomass, $F_{1,4} = 10.5$, $p = 0.048$), whereas no significant relationship was found between global geographical range size and either measure of abundance, suggesting that global range is not very helpful in predicting vulnerability at smaller scales.

Discussion

Prioritizing Species for Conservation

Our study highlights seven species of skate that may be vulnerable to extirpation if exploited in a manner similar to that of the four species that we consider to have undergone local extinction (i.e., disappearance from substantial parts of their geographical ranges). None of these species lives solely on the continental shelf, so they may be able to survive in deep-water refuges. This factor has been implicated in limiting the decline of other skates (Brander 1981; Casey & Myers 1998). Such a refuge may not be available to the smooth skate (*Dipturus innominatus*) because it is occasionally captured by deep-water fisheries (Francis 1997; Hurst & Bagley 1997). This species is endemic to New Zealand and has the least productive suite of life-history traits known for any skate, maturing at 13 years old and reaching at least 24 years of age (Francis et al. 2001). It is the only shallow-water species facing the double problem of large body size and small latitudinal range, and it deserves the greatest conservation attention of the seven

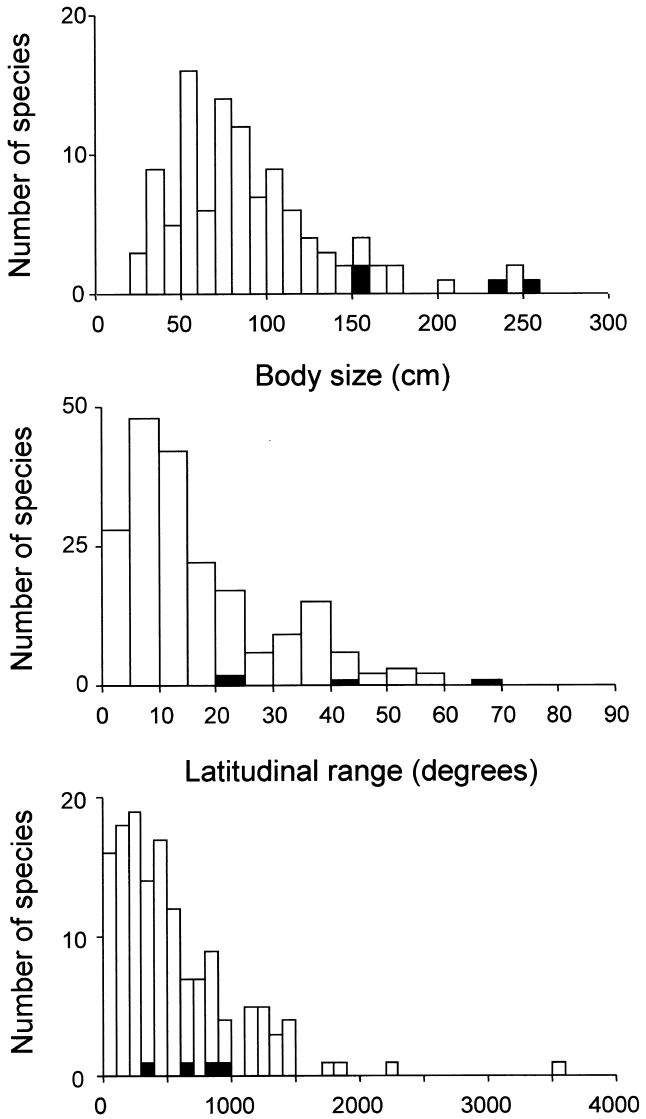

Figure 2. Frequency distribution of skate body size, latitudinal range, and depth (m) range. Locally extinct species are shaded.

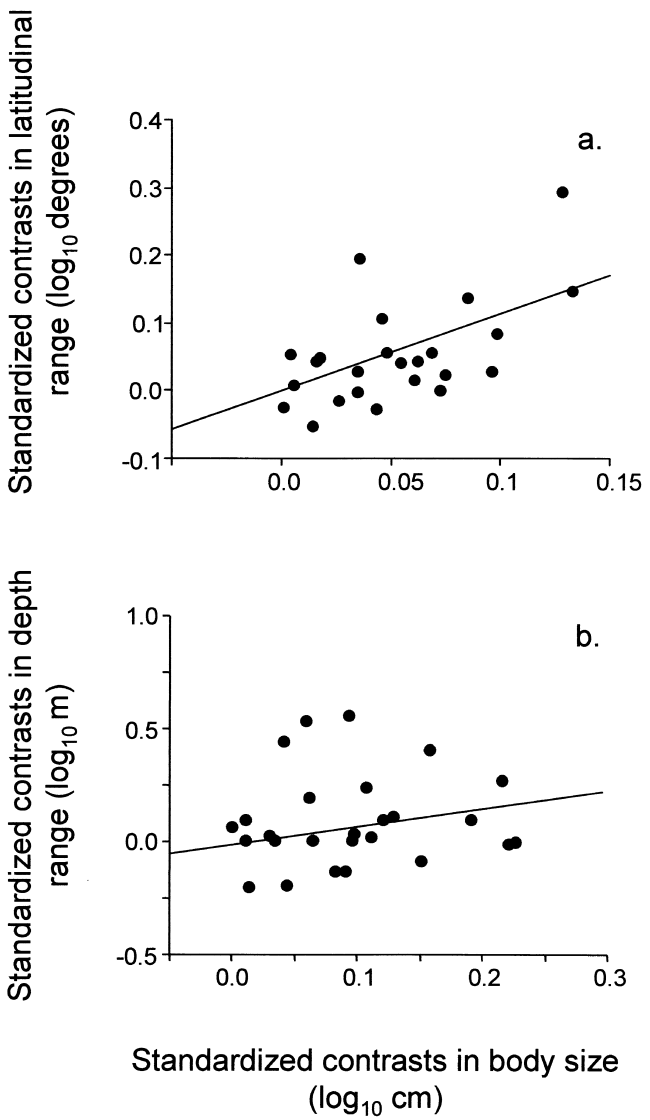

Figure 3. Relationships between phylogenetically independent contrasts in skate body size and (a) contrasts in skate latitudinal range size and (b) contrasts in skate depth range. A contrast is the trait difference between two related taxa (see methods).

species identified here. The three deep-water species may not require immediate prioritization because they live beyond the depth of most fishing gear, but they should not be forgotten if new deep-water fisheries are planned.

The choice of benchmark for any method of conservation assessment is arbitrary. In our study, the thornback ray (*Raja clavata*) might be included under our definition of locally extinct and used as a benchmark. This species is smaller than our current benchmark, the barndoor skate (112 cm vs. 152 cm). It has disappeared from the southeast (Dutch) coast of the North Sea, and it has undergone an approximately 45% decline in abundance in the Irish Sea between 1988 and 1997 (Dulvy et al. 2000). It is present in the southwest (Thames) coast of the North Sea, however, and it is the most abundant skate species in the Irish Sea (Walker & Heessen 1996; Walker et al. 1997; Dulvy et al. 2000). We believe this species should be watched carefully.

Body Size and Range Size as Predictors of Vulnerability

Our analyses suggest that body size is more useful for detecting species at risk than any measure of global geographic range size. Body size generated a manageably small number of species, but—more importantly—it was the only trait that correctly identified the other locally extinct skates.

Body size is useful for several reasons, both practical and theoretical. Body-size data can be easily collected

Table 2. Skate species identified as potentially vulnerable to extinction.

Species	*Habitat*	*Total length (cm)*	*Distribution*	*Fishery*	*Conservation status*[a]	*References*[b]
Pale ray (*Bathyraja pallida*)	benthic, deepwater	160	eastern Atlantic	unknown	very rare, known from only three specimens; not assessed	1
Richardson's ray (*B. richardsoni*)	benthic, deepwater	175	northern Atlantic & southwest Pacific	unknown	rare; not assessed	1, 2
Spinetail ray (*B. spinicauda*)	benthic	152	northern Atlantic	unknown	unknown; not assessed	1–7
Smooth skate (*Dipturus innominatus*)	benthic on shelf and slope	240	New Zealand	commercial landings are aggregated; captured using trawls and long-lines	endemic; not assessed	7–12
Norwegian skate (*D. nidarosiensis*)	benthic on shelf and slope, mainly around 200 m	156	northeast Atlantic	commercially exploited, landings of 19–393 t (1982–1993)	unknown; not assessed	1, 6, 7, 13
Roughbelly skate (*D. springeri*)	benthic, deepwater	160	southeast Atlantic & western Indian Ocean	unknown	rare; not assessed	14,15
Big skate (*Rostroraja binoculata*)[c]	benthic on shelf	244	northwest Pacific	commercially exploited throughout range	unknown; low risk (near threatened)	7, 16–23

[a]*The categories of "not assessed" and "low risk" are based on World Conservation Union Red List data.*
[b]*References: 1, Stehmann & Bürkel (1984); 2, Scott & Scott (1988); 3, Andriyashev (1964); 4, Leim & Scott (1966); 5, Robbins & Ray (1986); 6, Stehmann (1990); 7, Froese & Pauly (2000); 8, Paulin et al. (1989); 9, Cox & Francis (1997); 10, Bonfil (1994); 11, Francis (1997); 12, Francis (1998); 13, Anonymous (1997); 14, Hulley (1986); 15, Compagno et al. (1991); 16, Anonymous (1979); 17, Hubbs (1916); 18, Hitz (1964); 19, Hart (1973); 20, Lamb & Edgell (1986); 21, Allen & Smith (1988); 22, Teshima & Wilderbuer (1990); and 23, Zeiner & Wolf (1993).*
[c]*North Pacific assemblage.*

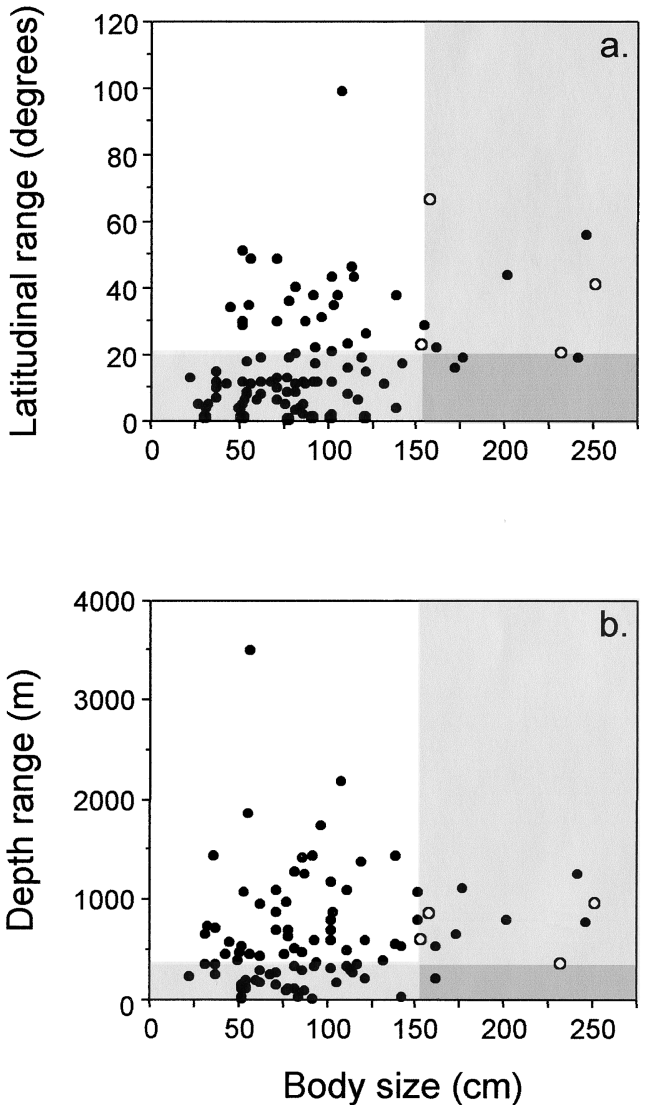

Figure 4. Relationships between skate body size and (a) latitudinal range and (b) depth range. The benchmark species for body size is the barndoor skate and for latitudinal or depth range the white skate. Locally extinct species are represented by the open symbols. Light shading represents the domain of species theoretically vulnerable due to either large body size or small range, according to the benchmarks (see text). Dark shading represents the domain of species potentially vulnerable due to both small range size and large body size.

from the literature, and size is intimately linked to life histories and demography via life-history invariants and tradeoffs involving individual growth rate and natural mortality (Roff 1992; Charnov 1993; Reynolds et al. 2001). Individual growth rates are tied to age and size at maturity, and the intrinsic rate of population increase is determined largely by age at maturity in sharks (Smith et al. 1999). It is therefore not surprising that body size is a reasonable predictor of vulnerability, particularly where the threat is from fishing. Most fisheries are biased toward larger individuals and species (Jennings et al. 1999*b*). Indeed, there is a negative correlation between skate body size and population trend (Walker & Hislop 1998; Dulvy et al. 2000). From a demographic perspective, it would be more satisfying to be able to calculate r, the intrinsic rate of population increase, but the required estimates of age-specific fecundity and survival are rarely available, and the value of r calculated for wild populations depends on population density (Reynolds et al. 2001; Sutherland & Gill 2001). This makes it a slippery parameter to pin down, because its measurement will change as populations change.

Skates, like other marine and terrestrial species, exhibit a positive relationship between body size and global geographical range size (Gaston & Blackburn 1996; Pyron 1999). Consequently, it is not immediately apparent why our measures of geographic range size did not correctly identify locally extinct skates in addition to the benchmark. This failure was also shown by the quantitative analysis of the population trends of five skate species in the Irish Sea between southwest Britain and Ireland.

For three reasons, we believe that skates are not buffered by large geographic distributions. First, the geographic scale of mortality is often large, with fisheries covering large areas, especially in shallow-water continental-shelf regions. Second, population recovery is hampered by the continuing mortality of these fishes as bycatches of fisheries targeting more valuable species. Third, even if fishing pressures decrease, skates may have little capacity for dispersal and recolonization of depleted areas. Skates lay benthic eggs and tend to be philopatric, exhibiting only limited seasonal movement (<50–100 miles) (Wheeler 1969; McEachran & Musick 1975; Walker et al. 1997; Anonymous 1999a). In support of the second and third factors, there is little evidence for recolonization of the Irish Sea by the common skate, despite the presence of a nearby population off western Scotland. Only six individuals were captured in government surveys of the Irish Sea between 1988 and 1997 (Dulvy et al. 2000). Although there is insufficient empirical evidence to quantitatively examine the vulnerability of skates with restricted ranges, the undescribed Port Davey skate has been listed as endangered because it is known only from two Tasmanian estuaries and because range restrictions suggest that a number of Mediterranean species may be vulnerable (Notarbartolo di Sciara 1998; Hilton-Taylor 2000). Unusually for fishes, the skate family includes a large proportion of species confined to a single zoogeographic locality, approximately 55% (McEachran 1990; McEachran & Miyake 1990). As more data become available, future studies should investigate the interaction between body size and geographic

range size in predicting the vulnerability of fishes (e.g., Purvis et al. 2000).

Our approach is a first step toward an objective means of prioritizing species for conservation assessment in data-poor situations. This method is not a substitute for demographic analyses, if they can be done, but the data required for such quantitative approaches are unlikely to become available except for fishes of the highest economic value. The American Fisheries Society has recently proposed a method that requires information on both life histories and population trends (Musick 1999*a*). This is being used for assigning threat status, rather than for making an initial decision about which species should be examined, as we have emphasized here. Although we agree with the theoretical motivation for this approach, its data requirements still make it impractical for most marine fish species, including most of those studied here. Thus, many regions of the world lack the data necessary to know which species should be examined. We hope comparative approaches such as those used here will point researchers in the right direction.

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