Predicting species vulnerability with minimal data to support rapid risk assessment of fishing impacts on biodiversity

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Summary

1. Large-bodied species are especially vulnerable to fishing in mixed fisheries. Their effective conservation requires predictions of sensitivity and exposure to fishing mortality, but such predictions are hard to make when the population dynamics of most of these species have not been described.

2. We present a method for assessing sensitivity and conservation management reference points using widely available life-history data. The method allows the sensitivity of all fish species in a community to be assessed in relation to conservation- and yield-based fishery reference points.

3. Knowledge of sensitivity is used to (i) rank species by sensitivity, (ii) conduct a risk assessment to identify species potentially vulnerable to current fishing pressure and (iii) examine potential trade-offs between fishery catches and the conservation status of sensitive species.

4. The method is applied to the Celtic Sea bottom-dwelling fish community. For the species present, conservation threshold fishing mortalities ranged from 0.05 per year for the most sensitive large elasmobranchs to over 1 per year for small teleosts. The assessment predicts that current levels of fishing mortality may place all the elasmobranchs and over a quarter of the teleosts below conservation reference points.

5. Depending on the relative mortality rates affecting commercially targeted species and species of conservation concern, up to 65% of the potential yield-per-recruit of commercially important species may have to be forgone to reduce fishing mortality below conservation limit reference points for the most sensitive species.

6. *Synthesis and applications*. The method presented provides a clear objective procedure to construct ranked species sensitivity lists that can inform management, monitoring and research. The Celtic Sea case study demonstrated that limiting fishing pressure on key commercial stocks to meet fisheries production targets may be insufficient to guarantee the persistence of more sensitive species. Management actions that effectively decouple the mortality rates on commercial species and 'conservation' species are likely to be required to make progress in relation to conservation objectives. The method would support rapid assessment of sensitivity to fishing in many regions around the world as only taxonomic lists and estimates of body size are required.

Key-words: biodiversity, conservation, fisheries, population dynamics, threatened species, trade-offs

Introduction

Central to implementing an ecosystem approach to fisheries is the need to achieve an acceptable balance between the social and economic benefits of fish production and the ecological impacts of fishing (FAO 2003). One impact of fishing that can compromise existing international policy commitments to biodiversity conservation (e.g. CBD 2010) is the local and regional extinction of vulnerable species (Dulvy, Sadovy & Reynolds 2003). To identify and manage trade-offs between fish production and the conservation of vulnerable species, it is necessary to know the sensitivity of species to fishing and the levels of fishing mortality they can sustain. As the ecology and population dynamics of many species of conservation

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concern are poorly known compared to target species, methods for assessing vulnerability based on relatively simple considerations can help to ensure that they can be applied to a wide range of species in a given management region (e.g. Stobutzki, Miller & Brewer 2001; Hobday *et al.* 2011).

The persistence of an exploited population largely depends on its capacity to replenish through recruitment; if recruitment is maintained, then the risk of population collapse is reduced. However, owing to the difficulties in establishing a relationship between spawner abundance and numbers of recruits, even in data-rich situations (Myers & Barrowman 1996), the alternative approach of managing to targets based on reproductive output has been used (Mace & Sissenwine 1993). Strictly, the reproductive output necessary to achieve replenishment of a population should be determined from knowledge of the spawner-recruit relationship at low stock sizes. In practice, reference points for reproductive output are typically calculated using 'per-recruit' models and expressed as the % spawningper-recruit (%SPR) achieved under a given fishing rate, i.e. the reproductive output-per-recruit at that fishing rate relative to the reproductive output-per-recruit in the absence of fishing (Goodyear 1993; Mace & Sissenwine 1993; Thompson 1993).

Large-bodied fish are particularly sensitive to exploitation owing to their low intrinsic rates of increase (Adams 1980; Myers, Bowen & Barrowman 1999; Denney, Jennings & Reynolds 2002; Reynolds *et al.* 2005); large-bodied elasmobranchs are of additional concern as they typically have life histories that render them more sensitive to a given rate of mortality than equivalent size teleosts (Walker & Hislop 1998; Frisk, Miller & Fogarty 2001).

The theory of life-history trade-offs (Charnov 1993), and empirical observations (Beverton 1963; Charnov 1993; Jensen 1996; Frisk, Miller & Fogarty 2001; Gislason et al. 2010), demonstrates that life-history traits are related within and among species. The existence of these relationships allows 'per-recruit' population models to be set up using widely available information on life history and taxonomic affiliation (e.g. teleost or elasmobranch). This allows the relationship between %SPR and fishing mortality (F) to be calculated and thus conservation limit reference points (e.g. to avoid extinction) can be estimated for the majority of species in any management region. If the fishing mortality applied to sensitive species is known directly, this can be compared with threshold %SPR values. If, however, fishing mortality is not known, a rapid preliminary assessment of the potential risks to species can be conducted by invoking 'Pope's postulate' and assuming that the fishing mortality affecting nontarget species is unlikely to exceed the fishing mortality affecting assessed target species (Pope et al. 2000). Pope's postulate is expected to hold in many circumstances because the assessed species are usually the main target species in a fishery. If Pope's postulate does hold, the F applied to assessed commercial species can be taken as a precautionary upper limit for the F on nontarget species. This approach can be extended to examine the potential trade-offs between conservation and fishing by comparing the conservation limit reference points for sensitive species with the target fishing mortalities for the main commercially exploited species.

Here, we develop and apply a method for estimating conservation thresholds and sensitivity with minimal data to support rapid risk assessment of fishing impacts on biodiversity. First, a method was developed to describe and rank the sensitivity of all bottom-dwelling species in a fish community, and the conservation limit fishing mortalities of individual species were compared with the known fishing mortality rates for the main target populations to provide a preliminary assessment of species vulnerability. Secondly, potential future trade-offs were examined by comparing the fisheries and conservation reference points of the main commercial species and species of conservation concern. For the purposes of this analysis, fisheries reference points are associated with achieving high and sustainable yields, while conservation limit reference points are associated with avoiding extinction (although some sectors of society would argue that conservation limit reference points should be more conservative). Sensitivity analyses were conducted to assess the effects of uncertainty in the life-history relationships used in the analyses. Although the methods developed are widely applicable, we focused on the Celtic Sea shelf ecosystem in the northeast Atlantic Ocean as an example.

Materials and methods

To support the assessment of potential fishing impacts on biodiversity, we (i) identified the species and their maximum body sizes in the Celtic Sea, (ii) developed an age-structured population model based on life-history invariants to establish reference points and thus the sensitivity of these species to fishing mortality (F) and (iii) compared reference points with realized rates of F to assess vulnerability.

The species list for the Celtic Sea [defined as International Council for the Exploration of the Sea (ICES) areas VII f, g and h] included all bottom-dwelling fish species recorded in either of two bottom trawl surveys that covered the region (English quarter 4 western ground fish survey and French quarter 4 Evhoe ground fish survey from 2005 to 2009) and in the English and Welsh Catch and Discard sampling programme (Enever, Revill & Grant 2007). Some caution is required when compiling the species list as data from trawl surveys can contain misidentifications, especially for noncommercial fish taxa (ICES 2007). The L_{max} of each species was defined as the length of the largest recorded individual in any data set, apart from Dipturus cf. intermedia and Dipturus cf. flossada which were taken from Iglésias, Toulhoat & Sellos (2010). Although they did not occur in the above records, white skate Rostroraja alba Lacepède and angel shark Squatina squatina (Linnaeus) were also included in the analysis because (i) they were common in the region prior to fishery development, (ii) they are included in the Oslo and Paris Commission (OSPAR) list of declining or threatened species in OSPAR area III (Celtic Seas) and (iii) very occasional specimens are still encountered in the Celtic Sea (R. alba, Iglésias, Toulhoat & Sellos 2010; S. squatina, J. Ellis, personal communication); L_{max} estimates were taken from reports in Fishbase (http://www.fishbase.org) when data for the Celtic Sea were unavailable. Each species on the list was categorized as an elasmobranch or teleost. Pelagic species and species with a regional L_{max} of < 20 cm were excluded from the analysis as they do not form a significant part of demersal fisheries.

Relationships between L_{max} and other life-history parameters were used to parameterize age-structured per-recruit models (Table 1), where production was measured as yield-per-recruit (YPR). Two separate measures of reproductive output were calculated; spawning

22 W.J.F. Le Quesne & S. Jennings

	Unit	Relationship	Source		
Function					
Asymptotic length	cm	$Log_{10}(L_{\infty}) = 0.044 + 0.9841 \times Log_{10}(L_{max})$	Equation 5 in Froese & Binohlan (2000)		
Weight	g	$W_t = 0.01 \times L_t^3$	Equation 14 in Gislason <i>et al.</i> (2008)		
Natural mortality rate	per year	$\dot{M_t} = \exp(0.55 - 1.61 \times \ln(L_t) + 1.44 \times \ln(L_\infty) + \ln(k))$	Equation 2 in Gislason et al. (2010)		
Relative reproductive output		$R = L_t^{3.75}$	See Appendix S1 in Supporting Information		
Teleosts		0. <i>11</i>			
Von Bertalanffy K	per year	$K = 2.15 \times L_{\infty}^{-0.46}$	See text		
Length at first maturity	cm	$L_{\rm mat} = 0.64 \times L_{\infty}^{0.95}$	Table 1 for demersal species inGislason et al. (2008)		
Elasmobranchs					
Von Bertalanffy K	per year	$K = -0.17 \times \ln(L_{\max}) + 0.97$	Equation in caption for Fig. 6 in Frisk, Miller & Fogarty (2001)		
Length at first maturity	cm	$L_{\rm mat} \ 0.7 \times L_{\rm max} \ + \ 3.29$	Equation in caption for Fig. 1 in Frisk, Miller & Fogarty (2001)		

Table 1. Life-history relationsh	ips used to define the parameterizatio	n of the age-structured p	opulation models from L_{max}

stock biomass (SSB)-per-recruit as a percentage of the SSB-perrecruit expected in the absence of fishing (%SPR), and the % reproductive output-per-recruit (%RPR) which is based on a similar calculation but includes a term to represent increases in relative reproductive output with size and age, thus giving more weight to the reproductive contribution of older individuals. The rate of increase in relative reproductive output with size was estimated from the mean exponent of the relationship between fecundity and length, as determined from fecundity–length relationships in the literature (see Appendix S1 in Supporting Information). Species from many regions were included in the fecundity–length analysis because very limited data were available for the species and region considered in this study.

The conservation limit reference point for reproductive output, measured as %SPR or %RPR, was set at 10%, and $F_{\rm conS}$ and $F_{\rm conR}$ were defined as the fishing mortality rates that reduced a population to the 10% %SPR and %RPR reference limits, respectively. This reference level was selected on the basis of a meta-analysis of replacement %SPR that found the 5-10%SPR class to be the modal class (Mace & Sissenwine 1993), where, following Sissenwine & Shepherd (1987), the replacement SPR refers to the year class sizes that, on average, replace the spawning biomass of the parent population. Thus, species fished above $F_{\rm conS}$ and $F_{\rm conR}$ are considered at risk of regional extirpation. The sensitivity of the analysis to the assumption of a 10% conservation limit reference level was examined by running parts of the analysis for a range of different conservation limit reference %SPR levels.

Two reference points were considered as targets for fisheries productivity. First, the maximum YPR irrespective of reproductive output (YPR_{max}), which is achieved with a fishing mortality of F_{max} ; beyond this level, a stock would be considered to be growth-overfished. Second, owing to concerns that fishing at F_{max} is likely to lead to recruit limitation (Deriso 1982) and reduced fisheries productivity, F_{40} was also applied (Clark 2002). This is the fishing mortality that reduces %SPR to 40% and corresponds to a yield of YPR₄₀. Although a number of alternative target %SPR values have been proposed, depending on the biology and level of compensatory recruitment shown by a population (e.g. Mace 1994; Walters & Kitchell 2001; Caddy 2004), F_{40} is considered to be a reasonably aggressive fishing strategy that leads to high sustainable yields from typical widespread and productive demersal fish stocks and has been adopted by some fisheries management agencies. Although F_{40} is considered the more pertinent reference point for applied fisheries management, F_{max} was kept in the analysis as an upper bound to target *F*s that might be applied in the case of the few highly resilient stocks where recruit limitation occurs at $F > F_{\text{max}}$ (Mace & Sissenwine 1993; Mace 1994).

Species were defined by their L_{max} and taxonomic affiliation (teleost or elasmobranch); L_{max} was used rather than L_{∞} (a modelled estimate of maximum length based on growth trajectory) as L_{max} is readily available information that can be directly accessed from data sets and because sufficient data to model growth were not available for all species. Model parameterization was based on the life-history relationships available from literature (Table 1), apart from the von Bertalanffy k relationship for teleosts. Here, the parameter values for the relationship with L_{∞} were calculated by fitting a power relationship to 168 pairs of L_{∞} and k estimates for teleosts reported by Gislason et al. (2010, in their Supporting Information Table S1). The parameter values are not statistically different from the values calculated for North Sea stocks presented in Gislason et al. (2008), but as the parameters calculated from Gislason et al. (2010) were based on a more comprehensive compilation, they were considered preferable for this study. When a required relationship was based on length, rather than age, this was converted to an age-based relationship by calculating length at age from the von Bertalanffy growth equation, where the age was taken as the mid-point in the age class. The parameter calculations and subsequent model simulations were based on 'decimal years' with 10 pseudo monthly time steps per year.

Population models were set up for both teleost and elasmobranch 'species' with L_{max} ranging from 20 to 250 cm, incrementing in 1-cm-length steps. For each species, simulations were run under a range of *F*s ranging from 0 to 1 per year, incrementing in 0.01 steps, and the conservation and fisheries reference points and associated YPR calculated. Knife-edge selection by the fishery was assumed and was set at 1 year, unless stated otherwise. The sensitivity of reference points to the assumed age of selection was assessed, and additional sensitivity analyses were used to assess how the life-history relationships affected F_{conS} .

To conduct the vulnerability ranking, and to identify species potentially at risk, F_{conS} was compared with the *F* reported by ICES for assessed stocks in 2007 in ICES areas VII f, g and h. For demersal stocks occurring in VIIf-h, ICES provided assessments for cod *Gadus morhua* Linnaeus in VIIe-k (F = 0.67 per year), sole *Solea solea* (Linnaeus) (F = 0.27 per year) and plaice Pleuronectes platessa Linnaeus (F = 0.41 per year) in VIIf, g, and hake *Merluccius* merluccius (Linnaeus) (F = 0.25 per year) in IIIa, IV, VI, VII and VIIa, b (ICES 2010a,b). The 2007 values were selected for this illustrative analysis as the 2007 cod assessment was the last assessment accepted by ICES.

The potential costs and trade-offs associated with meeting conservation limit reference points were assessed by calculating the potential lost YPR. This was calculated by comparing the YPR taken from the main commercial stocks when fishing at a rate equivalent to F_{conS} of the species of conservation concern, with the YPR obtained from the main commercial stocks when they were fished at their own F_{max} or F_{40} .

The list of species of primary conservation concern used for the analyses was made up of the demersal shelf dwelling fish species included in the OSPAR list of declining or threatened species in OSPAR area III, the Celtic Seas. The common skate Dipturus batis Linnaeus is named on the OSPAR list but has recently been shown to be two species based on genetic, morphological and life-history considerations (Iglésias, Toulhoat & Sellos 2010). These species, the flapper skate D. cf. intermedia and the blue skate D. cf. flossada. were therefore included in our 'OSPAR list' in place of D. batis. The most commercially important species in the Celtic Sea were identified by ranking total first sale value of demersal fishes landed in 2009 from ICES areas VIIf-h by the England and Wales fleet, where catch and price data were obtained from the England and Wales fishing activity data base. The 10 most valuable species were considered in our analysis and accounted for over 80% of the total value of demersal fish landed by the English and Welsh fleet in the study area.

Results

The vulnerability analysis of demersal fish in the Celtic Sea included 124 species, of which 95 are teleosts and 29 elasmobranchs (see Table S1 in Supporting Information). $F_{\rm conS}$ ranged from 0.05 per year for flapper skate and white skate to > 1 per year for teleosts with an $L_{\rm max} < 38$ cm. $F_{\rm conS}$ showed greater sensitivity to the age of first capture for teleosts than for elasmobranchs (see Fig. S1a,b). As the age of first capture was increased from 1 to 3 years, there was a 0.38 per year for an elasmobranch, with the change in $F_{\rm conS}$ declining as $L_{\rm max}$ increases. Similarly, $F_{\rm max}$ for teleosts increases with increasing age of first capture (see Fig. S1c).

There was little difference between conservation limit reference points based on SSB (F_{conS}) or reproductive output (F_{conR}) (Fig. 1 and see Table S1). As the maximum difference between F_{conS} and F_{conR} was 0.01 per year for elasmobranchs, and 0.08 per year for teleosts, only F_{conS} was considered in subsequent analyses.

Given the assumption that the F for nontarget species was the same as for assessed species, current levels of F have the potential to drive many non-assessed species below conservation limit reference points (Fig. 2). Irrespective of the assessed species considered, over 79% of elasmobranchs (23 species) are potentially fished to below their conservation limit reference point, and all elasmobranchs are potentially driven to below this reference point given the F for cod. In the case of teleosts, no species are considered at risk given the F applied to hake,

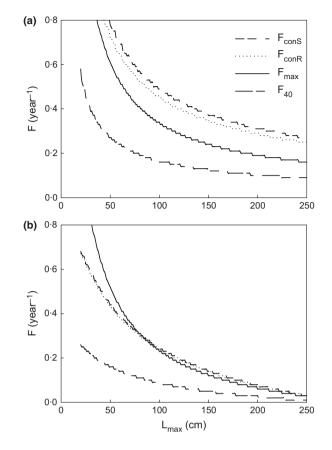


Fig. 1. The modelled relationship between L_{max} , and conservation and fishery reference points for (a) teleosts and (b) elasmobranchs.

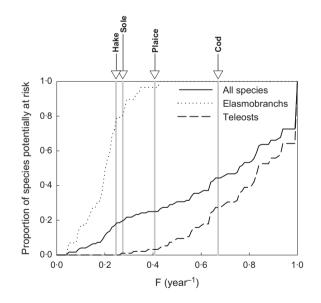


Fig. 2. The relationship between the proportion of species potentially at risk (10%SPR limit reference point) and *F*. Estimated *F*'s for assessed stocks is shown as vertical grey bars. SPR, spawning-per-recruit.

rising to over 27% (26 species) for the *F* applied to cod. However, estimates of F_{conS} are sensitive to the choice of the threshold conservation %SPR (see Fig. S2), and the proportion of species at risk depends on this choice.

24 W.J.F. Le Quesne & S. Jennings

The most valuable commercial species in the Celtic Sea are teleosts, and, apart from cod, all the species of conservation concern are elasmobranchs (Table 2). Accordingly, fishery-conservation trade-offs were examined by comparing the relationships between teleost YPR and elasmobranch %SPR with F (Fig. 3). In all cases, teleosts would have to be fished below F_{40} to ensure that a 230-cm elasmobranch subjects to the same F remained above 10% SPR. However, as the length of the 'conservation' species considered declines, it would be possible to fish some of the main commercial species at F_{40} without compromising conservation objectives.

Hake currently has the lowest *F*. Under the assumption of Pope's postulate, at this level of fishing, all the species on the OSPAR list, apart from spotted ray and cod, are fished to below 10% SPR (Fig. 4). Cod has the highest *F*, and at this mortality rate, all the species of conservation concern are overfished in relation to F_{conS} . If the main commercial species are exposed to the *F* applied to cod, they are all overfished in relation to F_{max} and F_{40} . However, if they are exposed to the *F* applied to hake, then only monkfish is overfished in relation to F_{max} , but all are still considered overfished in relation to F_{40} (Fig. 4).

These relationships demonstrate trade-offs between the objectives of maintaining sensitive species above conservation thresholds and maximizing YPR from the main commercial species (Fig. 5). If the management target was to reduce F below the conservation limit for the most sensitive species in the system, white skate and flapper skate, 64% or 59% of the

potential maximum sole yield and 44% or 38% of the potential maximum monkfish yield would have to be foregone compared to fishing each species at F_{max} or F_{40} , respectively. If, however, the target was to reduce F below the conservation limit for blue skate, the smaller of the two skate species recently reclassified by Iglésias, Toulhoat & Sellos (2010), 25% or 15% of the sole yield and 5% or 0% of the monkfish yield would have to be foregone compared to fishing at F_{max} or F_{40} , respectively.

This analysis was based on the assumption of equal mortality applied to target and nontarget stocks, and that all species had knife-edge selection to the fishery at age 1. When the mortality applied to nontarget species was reduced to 0.75 of the *F* applied to targets, the potential loss in sole yield relative to yield at F_{40} was reduced from 69% to 53% to conserve flapper skate and white skate and was reduced from 15% to 3% for blue skate (see Fig. S3a). The estimated cost, in terms of foregone yield, of meeting conservation limit reference points is sensitive to the assumption of the age of first capture, with the estimated costs of conservation increasing with the age of first capture (see Fig. S3b).

The sensitivity analysis of the life-history relationships used in the population model shows that the results were most sensitive to the assumed L_{max} -k relationship and L_{max} - L_{mat} relationships (see Fig. S4). In no case, did the predicted F_{cons} vary by more than 0.04 in response to a $\pm 10\%$ change in the life-history relationships. In general, the sensitivity of conservation limit reference points decreased with increasing L_{max} .

Table 2. Fishing mortality conservation and fisheries reference points for the main commercial species and species of conservation concern.Commercial species are ranked by value of landings, and conservation species by L_{max}

Common name	Latin name	Code	L_{\max} (cm)	Teleost∕ elasmobranch	$F_{\rm conS}$	$F_{\rm conR}$	F _{max}	F_{40}
Commercial specie	es							
Monk*	Lophius piscatorius Linneaus	MON	149	Т	0.38	0.35	0.24	0.13
Sole	Solea solea (Linneaus)	SOL	67	Т	0.64	0.59	0.47	0.22
Lemon sole	Microstomus kitt (Walbaum)	LEM	67	Т	0.64	0.59	0.47	0.22
Pollack	Pollachius pollachius Linneaus	POL	98	Т	0.50	0.46	0.34	0.17
Megrim	Lepidorhombus whiffiagonis (Walbaum)	MEG	67	Т	0.64	0.59	0.47	0.22
Turbot	Psetta maxima (Linneaus)	TUR	86	Т	0.54	0.50	0.38	0.18
Plaice	Pleuronectes platessa Linneaus	PLE	69	Т	0.64	0.59	0.46	0.22
Brill	Scophthalmus rhombus (Linnaeus)	BLL	71	Т	0.61	0.57	0.45	0.21
Haddock	Melanogrammus aeglefinus (Linnaeus)	HAD	81	Т	0.56	0.52	0.40	0.19
John Dory	Zeus faber Linnaeus	JOD	63	Т	0.66	0.61	0.50	0.23
Conservation spec	ies							
White skate	Rostroraja alba Lacepède	RJA	230	Е	0.05	0.05	0.04	0.01
Flapper skate [†]	Dipturus cf. intermedia	SKI	229	Е	0.05	0.05	0.04	0.01
Angle shark	Squatina squatina (Linnaeus)	ALS	183	Е	0.10	0.09	0.08	0.03
Blue skate†	Dipturus cf. flossada	SKF	143	Е	0.15	0.15	0.13	0.05
Cod	Gadus morhua Linnaeus	COD	122	Т	0.43	0.40	0.28	0.14
Spurdog	Squalus acanthias Linnaeus	DGS	120	Е	0.20	0.19	0.18	0.07
Spotted ray	Raja montagui Fowler	RJM	98	Е	0.25	0.25	0.24	0.09

*Landings data combine *L. piscatorius* and *L. budegassa* into a single category, over 75% of the landings are *L. piscatorius* so they are treated as *L. piscatorius*.

[†]The OSPAR-listed *Dipturus batis* has recently been identified for reclassification as *D*. cf. *flossada* and *D*. cf. *intermedia* (Iglésias, Toulhoat & Sellos 2010), although at the time of writing, the OSPAR listing had not been updated; our analysis was conducted using the proposed species identities.

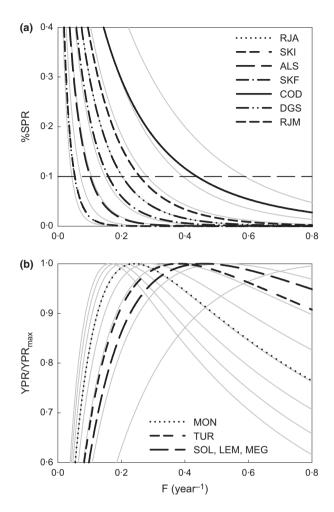


Fig. 3. The relationship between conservation status and fishery yields; (a) %SPR, grey lines are for elasmobranch species with L_{max} of 30–240 cm increasing in 30 cm increments and black lines show OSPAR-listed threatened and/or declining species; (b) YPR/YPR_{max}, grey lines for teleosts with L_{max} of 30–240 cm increasing in 30 cm increments and black lines for selected commercially important species. YPR, yield-per-recruit; SPR, spawning-per-recruit. Species codes as per Table 2.

Discussion

Advising on the management of fisheries to meet biodiversity conservation objectives can be challenging when the life histories and dynamics of species vulnerable to fishing are not well known. We show that information on body size, coupled with life-history relationships and some basic taxonomic information, can be used to determine conservation limit reference points for all recorded species in a regional sea. The assessment of sensitivity to fishing mortality does not provide a complete assessment of vulnerability, but it does highlight species of conservation concern and the expected trade-offs between fishing and biodiversity conservation. In the event that actual Fs can be estimated, then these can be compared with the conservation limit reference points to explicitly define vulnerability. However, given the challenges of estimating Fs for rare species, it is likely that proxies for F such as the Fs for commercial species in the same region and invoking Pope's postulate will need

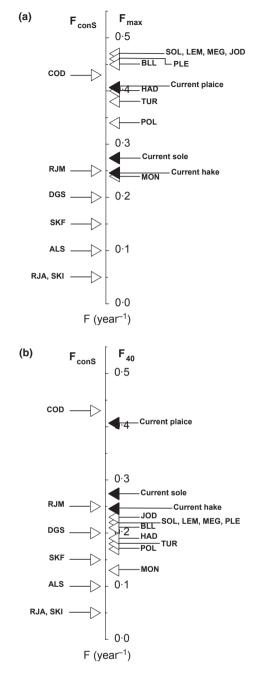


Fig. 4. Relationship between conservation *F* reference points for species of conservation concern (left of line) and target reference point *F* for commercial species (right of line); (a) F_{conS} of conservation species and F_{max} target levels, (b) F_{conS} of conservation species and F_{40} target levels for commercial species. The solid arrows indicate the current *F*s for assessed species, cod (F = 0.67 per year) not shown. Species codes as per Table 2.

to be accepted in many cases. The challenge is even greater in regions where no assessments of commercial stocks are conducted.

Although this was a regionally based analysis, the use of generic life-history relationships to parameterize the models and thus estimate conservation limit reference points means that the approach can be widely applied. Clearly, there is scope to refine the life-history relationships to improve the accuracy

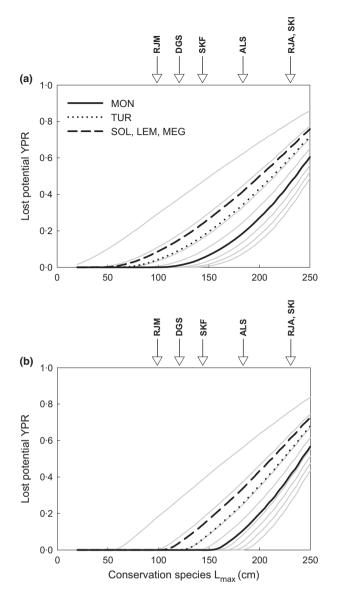


Fig. 5. Lost potential yield for teleosts with different L_{max} when *F* is maintained below F_{conS} for elasmobranchs of increasing L_{max} . Grey lines indicate lost potential YPR for teleosts with L_{max} ranging from 30 to 240 cm, increasing in 30-cm increments, and black lines for selected commercially important species. The L_{max} for OSPAR-listed species is shown on the top axis, species codes as per Table 2. Lost potential yield compared to fishing at (a) F_{max} and (b) F_{40} . YPR, yield-per-recruit.

of predictions and to further account for phylogenetic effects, and we hope that this work will catalyse activity to attempt such refinement. The F_{conS} values calculated for the 124 species included in the analysis ranged from 0.05 to > 1.00 per year. This analysis included seven species from the OSPAR list of threatened and/or declining species in OSPAR area III, the Celtic Seas. The F_{conS} values for the elasmobranchs considered on the OSPAR list ranged from 0.05 per year for white skate and flapper skate to 0.25 per year for spotted ray. The F_{conS} value of cod, the only teleost considered on the OSPAR list, was 0.43 per year. When ranked by sensitivity, 31 species were ranked above cod and considered more sensitive to mortality; these species should be prioritized for further assessment of their conservation status.

The extension of this approach to give a full assessment of vulnerability requires that realized Fs can be compared with the conservation limit reference points. The standard approach for estimating F at age in population assessment requires knowledge of natural mortality and abundance at age, both of which are challenging variables to estimate. However, accurate calculation of F is important as estimated %SPR is sensitive to assumed F, particularly for larger species at lower values of F. For example, if an F of 0.10 per year was calculated with an accuracy of ± 0.05 , the estimated %SPR of flapper skate could vary between 11% and <1% (i.e. varying from safe to high risk). Piet, van Hal & Greenstreet (2009) applied the swept area method to calculate mortality at age for the majority of species in the North Sea demersal fish assemblage. Their model predictions showed reasonably good agreement with observed discards and landings for some of the main commercial species. However, for a few species, predictions suggested that approaching 100% of the standing-stock biomass was removed annually, even in the case of slow-growing species where annual growth could not account for such a high rate of biomass removal. While Pope et al. (2000) concluded that they had generated plausible estimates of beam trawl fishing mortality on nontarget dab Limanda limanda (Linnaeus) and grey gurnard Eutrigula gurndardus (Linnaeus) in the North Sea, their result is of little consolation in the present context because common nontarget species show closer agreement with the assumptions of homogeneous distribution than rare and patchily distributed species. The challenge of generating reasonable estimates of mortality, even in the well-studied North Sea, illustrates the challenges of trying to directly calculate mortality across whole-species assemblages in less well-studied regions.

Given the difficulties of generating accurate estimates of F for nontarget species, as also substantiated for the Celtic Sea by a preliminary analysis of available data and comparison with landings records, Pope's postulate was invoked here. Our approach was precautionary to the extent that the Fs for target species were taken to be the upper limit of Fs applied to nontarget species. Although Pope's postulate is likely to be acceptable for many species, there are reasons that it may not hold (Pope et al. 2000). For example, it may be violated for species with a morphology that leads to relatively high catchability and species that occupy a limited area within fishing grounds for target species. This can occur if distribution-abundance relationships lead to range contraction with decreasing abundance (Fisher & Frank 2004). With estimates of F for the rarer nontarget species so difficult to obtain, a rigorous test of Pope's postulate, although desirable, would be difficult to achieve. As such, it is difficult to predict whether any additional level of precaution is warranted; although an initial appraisal might be conducted by comparing distributions of vulnerable species and the main species targeted by the fishery.

Our analysis showed that significant reductions in mortality may be needed to meet conservation limit reference points for the more sensitive species. Ongoing management actions to increase long-term yields for the main commercial species are

expected to reduce F and provide conservation benefits for a limited proportion of the species deemed to be vulnerable. However, if mortality rates for the most sensitive species cannot be decoupled from those on commercial species, then meeting conservation limit reference points for these species would lead to significant 'lost' yield. If losses of 20% of potential yield were accepted within the management system, this would improve the conservation status of more sensitive species and provide for more precautionary management of the commercial species in a region where the potential yield of commercial species has already been 'lost' for many years owing to exploitation beyond F_{max} . However, to meet conservation limit reference points for all species, up to 65% of the potential YPR of some commercial species would be lost.

Minimizing the losses of fisheries yield while improving the prospects for biodiversity conservation would require management actions that decouple the F on fisheries and conservation species, allowing greater fishing pressure to be applied to commercial stocks without simultaneous increases in the fishing pressure applied to conservation species. There are many existing management tools that might be used to achieve this, the use of which can be informed by the analysis of relative distribution, catchability and other factors that influence mortality rates. Alternatively, a critical analysis of Pope's postulate may conclude that Fs applied to commercial and conservation species are already decoupled and therefore the perceived costs and need for management interventions are less than those predicted in this analysis.

Estimates of F_{conS} , and thus the costs of achieving conservation objectives, are sensitive to the choice of %SPR reference limit and increase with the reference limit %SPR. Selection of the %SPR limit is inevitably a slightly contentious issue as accurate selection of the limit requires knowledge of the gradient at the origin of spawner-recruit relationships. However, SPR has to be used as the reference limit because spawnerrecruit relationships are not available for a majority of species. The choice of the 10% limit applied in this study was predominantly based on Mace & Sissenwine's (1993) meta-analysis of replacement SPR levels which found that the 5-10% %SPR class was the model value. This may be an underestimate as the overall mean replacement %SPR was 20%, and for some stocks of small pelagics was as high as 60%. Conversely, the analysis of replacement %SPR assumes that the descending limb of spawner-recruit relationships is linear and does not show compensation at very low stock sizes close to the origin. If compensation does occur, the selection of the %SPR limit may be an overestimate. Issues relating to the selection of appropriate SPR reference limits have been considered by a number of authors (e.g. Clark 1991, 2002; Goodyear 1993; Mace & Sissenwine 1993; Mace 1994; Williams & Shertzer 2003; Brooks, Powers & Cortes 2010), and the most promising solution for defining more accurate SPR reference levels is to conduct an updated meta-analysis of S-R time series that are ever increasing in length and are now available for a greater number of stocks.

of body size are required. By applying generic life-history rela-

Fishing impacts on fish biodiversity 27

tionships, the analysis essentially considers the question of trade-offs in terms of 'average' species. In reality, problems often occur in exceptional cases that deviate from the norm, and these exceptional cases will not be picked up in this analysis. However, implementation of the ecosystem approach to fisheries may necessarily demand generalizations of this nature, and they are helpful in assessing the broad consequences of setting different Fs for the main commercial species.

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28 W.J.F. Le Quesne & S. Jennings

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Variation in teleost F_{conS} , elasmobranch F_{conS} , and teleost F_{max} with age of first capture.

Fig. S2. Variation in the conservation limit fishing mortality rate for elasmobranchs depending on the %SPR conservation reference level.

Fig. S3. The lost potential yield for teleosts with different L_{max} when the objective is to maintain F below F_{conS} for elasmobranchs of increasing L_{max} .

Fig. S4. The response of F_{conS} to a $\pm 10\%$ change in life-history relationships.

 Table S1. Ranked vulnerability for demersal fish of the Celtic Sea shelf.

Appendix S1. Data and data sources used to calculate exponent for the relative reproductive output to length relationship.

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