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What is a "large fish"? - taking a species perspective.

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Abstract

OSPAR has decided to elaborate on the proportion of large fish in survey catches as an Ecological Quality Objective (EcoQO). 'Large fish', as defined from the human perspective, is clearly an elastic concept and a theory that might be used to identify suitable reference levels and to turn the available metrics into a management objective is lacking. I take a species perspective and use a 'functionally large' criterion that relates the size of individuals caught to the reported maximum size of the species (L_{max}), a metric that can be linked to changes in the reproductive potential of the total fish community. Also, the fraction surviving to a particular size is affected by total mortality. Therefore, at least in principle, reference levels might be set for unexploited conditions. Using North Sea IBTS data, the annual fractions of individuals larger than 50% of their L_{max} as well as the fraction larger than length-at-50% maturity were calculated. Although the overall results for these two criteria were similar, responses (levels and slopes) within species were sensitive to the cut-off point selected. The fractions, averaged over all species, declined significantly and consistently (by approximately 15% over a 28-year period). This negative trend significantly affected 24 of the 30 species included in the analysis. Only one species (spurdog) showed a significant positive trend. No progress could be made in defining reference levels, because trends derived from surveys for four commercial roundfish species were not correlated with ratio's of spawning-stock-biomass/total-biomass based on stock assessment. The evidence for declining fractions of functionally large fish should be viewed in the context of other significant changes observed in the North Sea fish community. The complexity of what is going on should warn against a premature setting of a community EcoQO based on simple-minded metrics that cannot yet be fully understood.

Keywords: EcoQO, fish community, large fish, maturity, North Sea, reference level, trend analysis.

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Introduction

The Oslo-Paris Commission (OSPAR) is developing a comprehensive set of Ecological Quality Objectives (EcoQO) that should guide management to maintain a healthy North Sea ecosystem (OSPAR, 2005). An EcoQO is defined as a desired level of an ecological quality, preferably set in relation to some reference level. Fish communities have been identified as a key issue for describing the quality of the ecosystem and one of the elements proposed for measuring the health of communities is "changes in the proportion of large fish and hence the average weight and average maximum size of fish in the community". In response to requests from OSPAR, recent reports of the Working Group on Ecosystem Effects of Fishing (WGECO) and the Working Group on Fish Ecology (WGFE) have provided many analyses based on research vessel surveys showing that significant changes

in these metrics have occurred in the North Sea over the last century (e.g. ICES, 2006a, 2006b). However, it is less clear what has caused these changes and, although restriction of fishing activities in general might help to reverse these trends, it is not at all clear to what extent fleet activities have to be reduced to stop the trend or achieve a specific increase.

More generally, there is a large body of theoretical and empirical evidence that size-based metrics are responsive to changes in the exploitation of the fish community (review by Shin *et al*., 2005). However, using these metrics for setting objectives in a legally binding management framework is a different matter, because different surveys may show different responses and from any survey an infinitely large number of metrics may be derived that all show deviating responses depending on arbitrary choices of for instance the size range included and the cut-off point for 'large' fish used. Also, there is no theoretical basis for setting reference levels that might be considered

as appropriate for defining management targets. To cope with this problem, Jennings and Dulvy (2005) proposed to use reference directions instead (stop the decline and reverse the trend), although they note that it may take 5-10 years before a reversed trend may be identified statistically.

The large-fish element selected by OSPAR for further development of an EcoQO addresses two fundamentally different issues: changes in the size composition irrespective of species (proportion of large fish and average weight) and changes in the species composition in terms of their maximum attainable size. The proportion of large fish may be thought of as some measure of the availability of large predators relative to their prey (ICES, 2006a). Obviously, this proportion will critically depend on the selected cut-off point. Calculating the average weight of fish caught in a survey requires no arbitrary choices, but this metric does not relate specifically to changes in the presence of large fish. The average maximum size is also a straightforward measure, but tells us more about the potential within the fish community to grow to a large size than about the actual presence of large fish.

An important point to make here is that these metrics largely reflect changes in those species dominating in the catches rather than providing a balanced index for the entire community. Consequently, they are likely to be affected largely by the mortality on specific stocks rather than reflecting the overall exploitation of the fish community.

The main problem with the proportion of large fish is the human perspective involved: where to draw the line between large and small? Greenstreet and Rogers (2006) advocate a statistical boundary such as 95% of the cumulative frequency distribution, but such a statistical criterion would change itself if size compositions change! Also, the presence of many large fish may be considered healthy, but an ecological rationale for such a value judgement is largely lacking.

During a recent meeting of WGFE (ICES 2006a), the idea emerged to define 'functionally large fish' from the perspective of an individual species. A suitable biological criterion in this context would be the size-at-maturity (L_{mat}), because the proportion of large fish then becomes a relative metric of assemblage reproductive capacity. This approach has a few advantages. First, this fraction should reflect the total mortality within a species. Thus, averaging fractions over all species should be indicative of the exploitation rate of the entire fish community. Secondly, estimates of the ratio of spawning stock biomass (SSB) relative to total biomass are available from routine stock assessment and it may be possible to relate these to the reference levels of SSB and fishing mortality used in formulating management advice. By linking survey estimates of the fraction mature to stock assessment data for commercial species, it might, at least in theory, be possible to develop suitable reference levels.

This approach hinges on the availability of L_{mat} data for a wide variety of species or on the application of life history invariants (Charnov, 1993; Beverton, 1992; Froese and Binohlan, 2000). I present an explorative analysis of existing trends in the fraction of functionally large fish by using, and comparing, both actual maturity-at-length data and approximations based on invariants. As Beverton (1992) notes, life history parameters reported in the literature may have been derived using a variety of methods and thus may not be strictly comparable. This may lead to bias in the estimates of the invariants, but using invariants may also remove some of the bias present within the actual estimates. Therefore, when combining data from different sources, using actual estimates may not always be better than using estimates from invariant approaches.

Methods

Fractions of functionally large fish

The analysis is based on data from the annual North Sea International Bottom Trawl Survey (IBTS) in February (Heessen et al., 1997; ICES, 1999). For reasons given elsewhere (Daan et al., 2005), only data from 1977 onwards have been used.

Extensive data on size- and/or age-at-maturity are available for most commercial fish species . Maturation may vary over the years and these variations are commonly taken into account in stock assessment. However, in using L_{mat} in the context of community metrics, we are not interested in annual variations but rather in an easy and commonly applicable rule of thumb that roughly defines the mature component among stocks. According to Beverton (1992), first maturity is on average reached approximately at a size that corresponds to 50% (pleuronectids), 60% (gadoids) and 80% (clupeids) of L_∞, (the theoretical average maximum length of an individual according to the Bertalanffy growth equation). In practice, L_∞ is poorly known for many of the non-commercial species, while information on the maximum attainable size (L_{max}) is readily available for all species. Therefore, a life history invariant that expresses L_{mat} in terms of L_{max} would be preferable. Froese and Binohlan (2000) provide a general relationship for both $\log(L_{mat})/\log(L_\infty)$ and $\log(L_\infty)/\log(L_{max})$. However, these relationships are less useful here, because the estimated log-transformed

functions lead to criteria that vary with changing L_{max}. Figure 1 plots estimates of L_{mat} against L_{max} for North Sea species, based on information provided by Jennings *et al.* (1999), with some adjustments based on Knijn *et al.* (1997) and Walker (1999). These estimates refer to size-at-50% maturity, but the methods by which these have been calculated may not always have been exactly the same. Despite considerable scatter around the line, on average maturity appears to be reached at approximately $0.5*L_{max}$. Given that L_{max} exceeds average asymptotic length, this criterion to separate mature from immature fish would not be inconsistent with the values given by Beverton (1992). In a parallel exercise, the actual estimates of L_{mat} have also been applied.
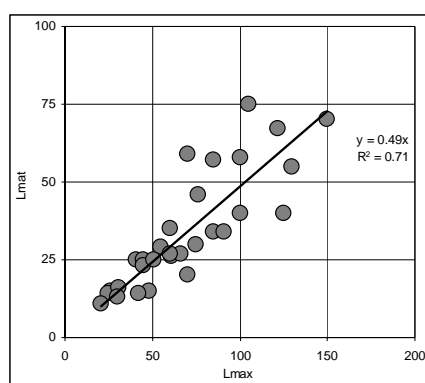

Figure 1. Plot of estimates of L_{mat} versus L_{max}, with the regression line forced through the origin.

The data base provides information on the total numbers by size class (Lclass; with class width 0.5, 1 or 5cm, depending on species and/or size) and species. By adding information on L_{max} and L_{mat} for each species, it becomes straightforward to calculate the numbers of small and large individuals within each haul. However, a fish close to L_{max} contributes considerably more to the mature biomass and to the reproductive potential of a population than a fish that has just passed L_{mat}. Therefore, weight fractions are likely to be more sensitive to varying exploitation rates than number fractions. Because the weight distributions of individual fish in the catches are not available, a common isometric length-weight relationship ($W = a*L^3$, where L is given in cm, W in g and a=0.01), corrected for class width (L = Lclass+0.5*Class), was used to calculate the total weights of small and large fish within each species.

The IBTS is a stratified survey, with statistical rectangles serving as strata. Therefore, numbers (n) and weights (w) were first averaged by rectangle and these means were averaged by species over all rectangles. To obtain the overall ratio of functionally large fish in the catch, all numbers and weights were summed over all species. These total catch ratio's (TCR) are largely determined by those species that are most abundant (in case of n ratio) or reach the largest size (w ratio). Because these TCR seem less informative as community metrics, the average of the ratio's observed within species (ASR) in numbers and weight were also calculated as a potentially more sensitive metric of the functionally large fish at the community level (note that in this case the value for coefficient a in the length-weight relationship is trivial).

Regressions of the various metrics against time were tested for significance (Pearson correlation coefficients) for individual species, for species groups (roundfish, flatfish, elasmobranchs, and 'other demersal') and for all species combined.

Selection of species
IBTS data suffer from species identification problems that have to be addressed before they can be used for community analysis (Daan, 2001; ter Hofstede and Daan, 2006). Because uncertainty about the appropriate species id leads to uncertainty about the appropriate L_{max}, all taxa that have been identified as problematic were removed. For this specific analysis, the following taxa were also excluded: (1) all pelagic species, because the survey typically samples demersal fish; (2) species that were not consistently reported in at least 90% of the surveys, because rarer species may easily yield extreme ratio's (0 or 1), depending on whether these individuals happened to be immature or mature; (3) species that proved to represent only one of the two size classes distinguished, because the information content of the metric is zero in that case; (4) species with $L_{max}<20cm$, because the catches of the category 'small' would refer to fish<10cm, which are likely to be strongly affected by the selectivity of the gear.

The remaining 30 demersal species included in the analysis, with the relevant information on life history parameters, are listed in Table 1. The total numbers of fish caught by species are also given to indicate their relative numerical dominance. Only 4 species (Norway pout, whiting, haddock and dab) account for 93% of the total, while grey gurnard, long rough dab and cod are responsible for an additional 5%.
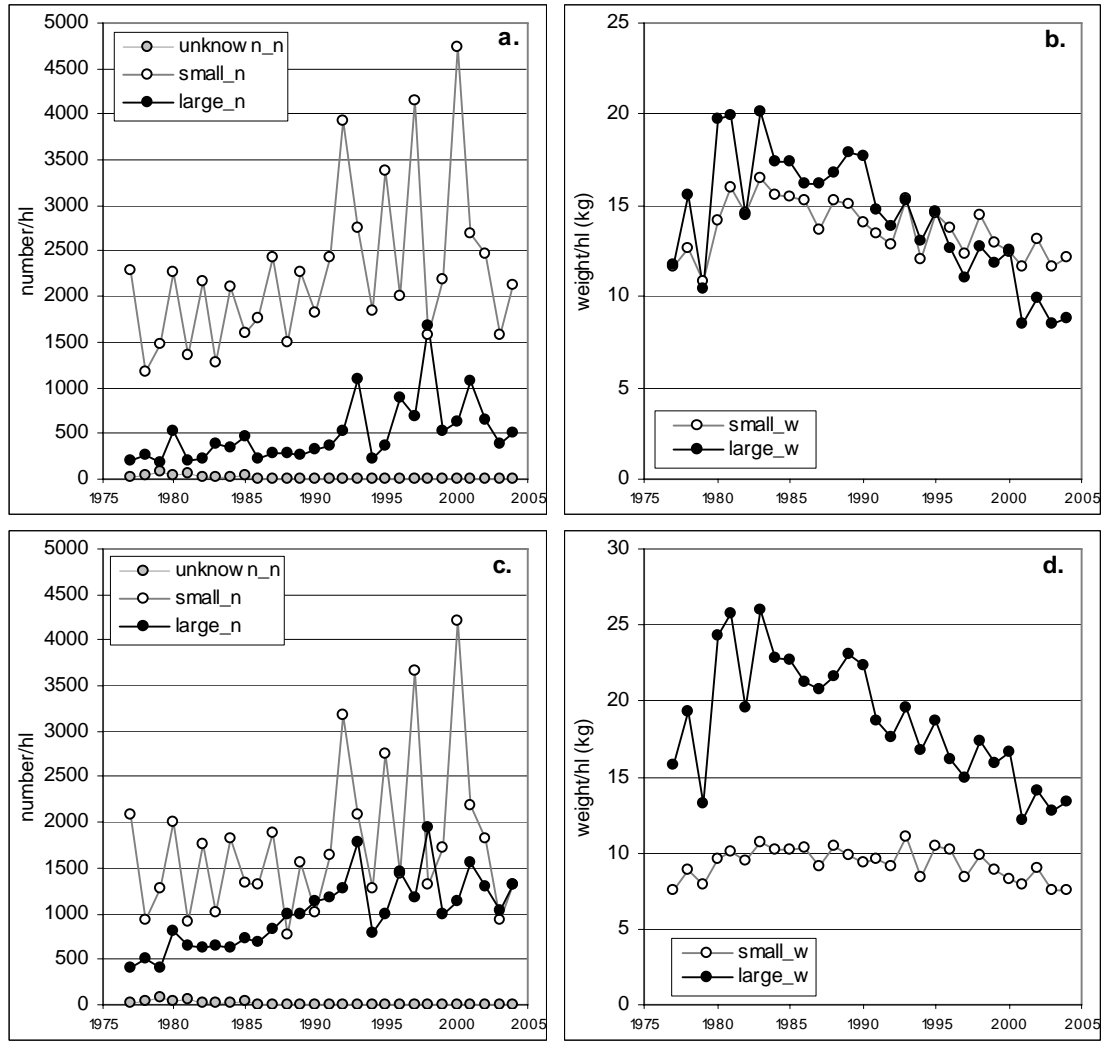
Figure 2. Average (a, c) number and (b, d) weight per haul per rectangle of small and large fish according to (a, b) the $0.5*L_{max}$ criterion and (c, d) available L_{mat} information (number of fish of unknown size indicated in a, c; source DATRAS).

Reference levels

The ASR_w for individual species represents a metric for the fraction of mature fish in the population that can be directly compared with the ratio of spawning stock biomass (SSB) to the total biomass (TB) based on stock assessment. Such estimates are available for four commercial roundfish species (cod, haddock, whiting, saithe). In this case, a somewhat longer IBTS time series may be used than the one described previously, because these species have been a target species from 1970 onwards and have been sampled consistently since. ASR_w and SSB/TB should exhibit similar trends over time, even though actual levels might be different because of differences in the method of calculation. On theoretical grounds, these ratio's should also be correlated with the exploitation rate and therefore the correlations with estimated fishing mortality based on stock assessment were also tested.

Results

Comparison of various metrics

Figure 2 compares the average number of small and large fish per haul according to the 50% of Lmax criterion and those according to the actual information on Lmat. Although the levels differ, the long term patterns are essentially similar. The numbers of both small and large fish have shown an increasing trend over time, but the annual fluctuations are huge, especially within the category small (left panels). In terms of weights, catches of small and large fish have been much more stable and both groups show a highly significant, decreasing trend, at least from the early 1980s onwards (right panels). The implication of these opposing trends between numbers and weights is that also the
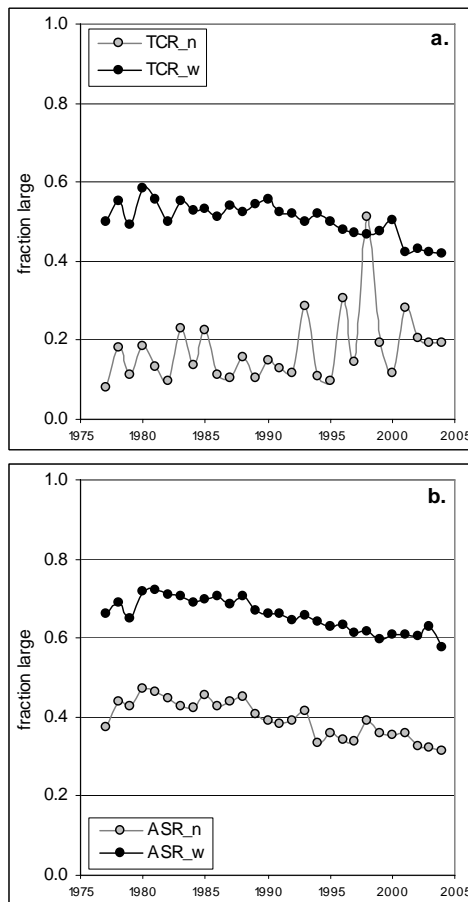
average weights within both groups have decreased.

Figure 3. Time series of fraction of large fish (0.5* L_{max}) in numbers (n) and weights (w) expressed as (a) total catch ratio (TCR) and (b) average species ratio (ASR).

It seems remarkable that the large variations in numbers of small fish become damped to such a large extent when weights are used instead. However, this can be explained by recruiting year classes: the numbers of the numerically most abundant species may vary widely among years, but their weights are negligible compared to those of the older but still immature fish.

Figure 3 provides estimates of the four primary metrics for the fraction of large fish (TCR and ASR in both numbers and weights), but only for the 0.5*L_{max} criterion because trends for L_{mat} were virtually indistinguishable. The TCR_n has increased (r=0.36), while the TCR_w has decreased over time (-0.75). In contrast, trends in both ASR_n and ASR-w are negative (-0.82 and -0.84, respectively).

The relative overall contribution of the four most dominant species within each size category to the TCR is indicated in the text table below:

Numbers		
Small	0.98	N. pout, whiting, haddock, dab
Large	0.97	N. pout, dab, grey gurnard, poor cod
Weights		
Small	0.78	cod, haddock, whiting, saithe
Large	0.62	cod, saithe, haddock, spurdog

It appears that by taking overall fractions, we are actually dividing apples by oranges, different species being largely responsible for trends within size categories. This is a good reason not to pursue this approach further and to concentrate on the ASR. Given the similarity observed between ASR_n and ASR_w with the higher variance explained by the latter, ASR_w was selected as probably the most informative metric.

Trends in ASR_w
The species-specific information is summarized in table 1 for both the 0.5*L_{max} criterion and the actual information on L_{mat}. In both sets, significant negative regression coefficients (P<0.05) predominate and only one is significantly positive (spurdog). Seventeen species show a significant decline in both sets, while six species show no trends in either set. For the remaining seven species, trends are significant only in one set. However, the average fractions of large fish and the estimated slopes vary considerably depending on the criterion used, both within and among species. Although these results appear to reflect a common response of most species to some external variable, the results for individual species vary considerably, both in terms of average fraction observed and in slope, but also in terms of annual variations (Figure 4). For instance, among the flatfish, the lemon sole has probably shown the steadiest and most severe decline of all species, turbot and brill show a decline superimposed on large annual variations, while dab and flounder have remained virtually constant.

Figure 5 shows the average trend within each of the four groups considered. The trends for roundfish, flatfish and 'other demersal' were highly significant (p<0.01) and rates of change were comparable (slopes of -0.006, -0.006 and -0.004, respectively), while the trend for elasmobranchs was not significant. However, closer inspection of Figure 5 suggests that, after an initial increase, the ratio of large elasmobranchs has declined as well from the late 1980s onwards and in fact the trend based on L_{mat} was also significant (Table 1).
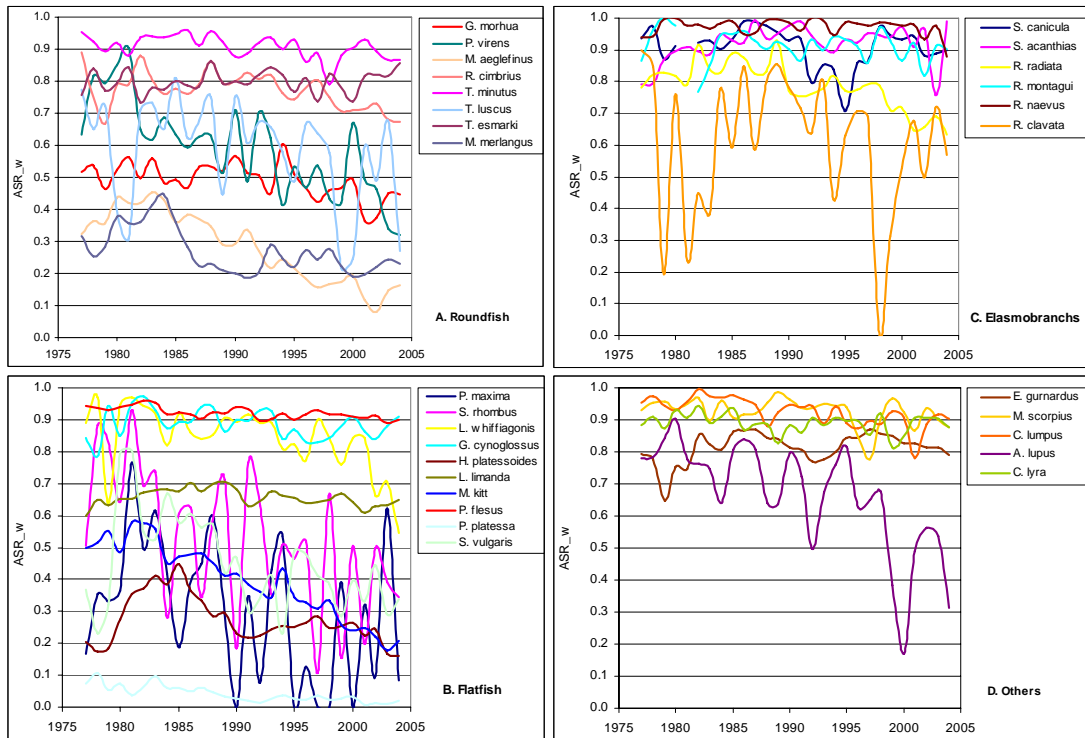
Figure 4. Time series of weight ratio of functionally large fish by species (0.5*L_{max}; source DATRAS).
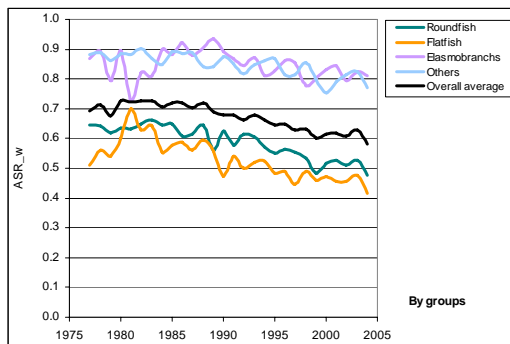

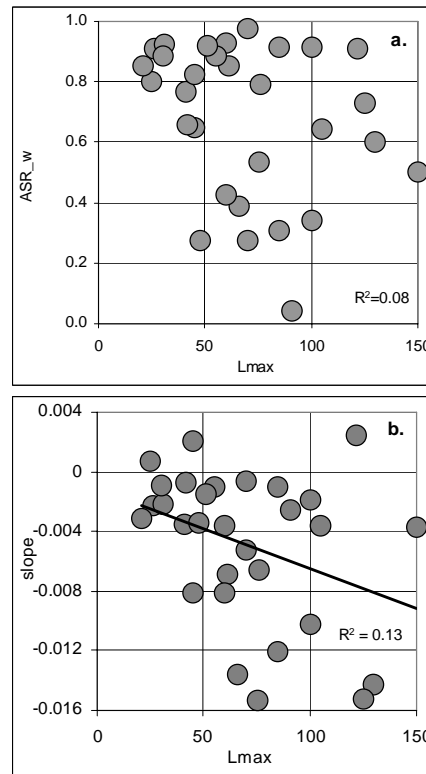Figure 5. Time series of average species ratio (weight) of functionally large fish by group (50% of L_{max} criterion).

Figure 6. Plot of (a) the average ratio of large fish (0.5*L_{max}) and (b) the slope of the temporal trend in this ratio against L_{max} for individual species.

To investigate whether these metrics may be directly influenced by life history characteristics, Figure 6 provides plots of average ASR_w (0.5*L_{max}) over all years and the slope of the temporal trend against L_{max}. Both the average ASR_w decreases and the slope becomes steeper with increasing L_{max}, but only the latter regression is significant (p<0.05). The corresponding correlations for the L_{mat} set were slightly lower and not significant (R2=-0.07 and 0.11, respectively).

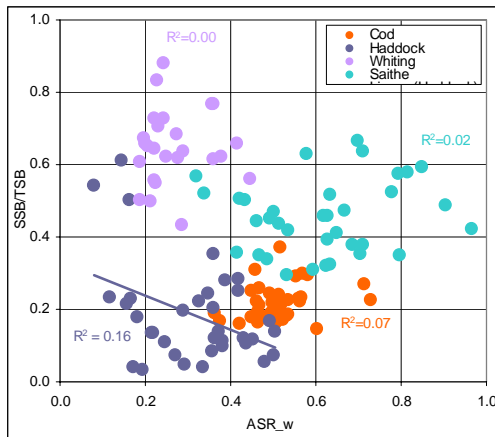Figure 7. Plot of SSB/TSB ratio's from stock assessment against ASR_w (0.5*L_{max}) from IBTS (1970-2004) for 4 roundfish species.

Figure 7 compares the SSB/TB ratio from stock assessment and the ASR_w from IBTS for four roundfish stocks. For cod, whiting and saithe the slope is slightly positive but the correlations are not significant. However, for haddock the correlation is negative and significant, indicating that the assessment shows no match with the survey data!
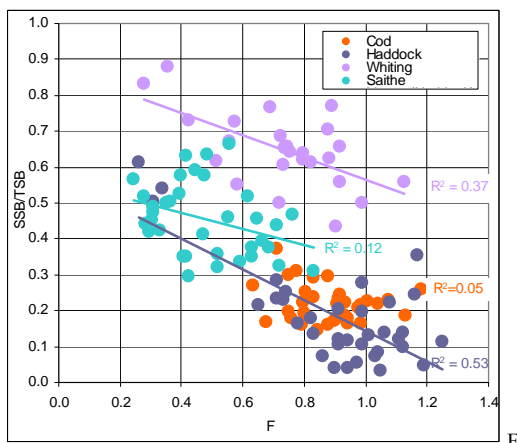

igure 8. Relationship between SSB/TB ratio and estimated F from stock assessment for 4 roundfish species.

The SSB/TB ratio for haddock and whiting was significantly correlated with the estimated fishing mortality (p<0.01) and marginally so for saithe (p<0.05) (Figure 8). For cod, the

correlation was not significant. None of the correlations between ASR_w derived from the two sets and F were significant, except for positive correlations for haddock.

Discussion

The approach taken here deviates fundamentally from earlier analyses of proportions of large fish (Piet and Jennings, 2005; Greenstreet and Rogers, 2006) that have chosen an arbitrary and fixed limit to distinguish between large and small fish, irrespective of species. The difficulty with a fixed size limit is that the two size classes will be dominated by different sets of species, and these groups will vary when a different boundary is selected. This may result in totally different responses observed and it should be virtually impossible to determine an appropriate reference level for management for any arbitrary choice of boundary. Jennings and Dulvey (2005) have argued to use a reference direction as a more appropriate management target rather than absolute reference levels. but even the direction of change in response to management action may be unpredictable in this case. Similar arguments apply for the functionally large fish approach when summing size distributions over species (TCR). However, at least all species contribute to this metric to some extent and therefore more consistency in the response may be expected, if the criterion is changed. The situation becomes greatly improved, when averaging the species-specific responses (ASR), because all species in the community contribute equally and there should be a good deal of autocorrelation among trends derived from varying the criterion.

Indeed, using actual maturity information or 0.5*L_{max} does not make a great deal of difference for the response of ASR_w at the community level, even though the responses for individual species vary, both in terms of level and of slope. Differences in level among species might be expected if total mortalities differ. The significant relationship between slope and L_{max} supports that this may be a factor involved because L_{max} and natural mortality are correlated (Charnov, 1993). However, such differences might also originate from differences in catchability among small and large fish or differences in distribution relative to survey coverage. For instance, species with coastal nurseries (e.g., many flatfish species) should necessarily exhibit a different ratio from those with overlapping distributions (e.g., haddock).

The quality and consistency of the input values for L_{max} and L_{mat} are also a concern. For instance, the L_{max} for plaice is 91cm, leading to a cut-off point of 45cm for the 0.5*L_{max} criterion. This value is unrealistically high

compared to a length-at-50% maturity of 34cm for females and 22cm for males (Rijnsdorp, 1989). However, even when using 34cm, a large part of the mature male biomass is excluded. Sex dimorphism is clearly an important factor affecting the estimated ratio.

The patterns seen for the four commercial roundfish species in the ASR_w deviate considerably from those appearing in the SSB/TB ratio from routine stock assessment. Changes in age-at-maturity introduced in the latter over time could have masked trends that would have been present when age-at-maturity had been fixed. However, this explanation seems unlikely because this should also have affected the correlations between SSB/TB ratio and F and these were significant for three out of four species, whereas those between ASR_w and F were not. Another possibility is that the discrepancy between surveys and assessment indicate shortcomings in the latter. Whatever the reasons, the consequence is that no progress could be made in determining suitable reference levels for the survey metrics.

Despite the apparent limitations of the approach, the evidence from the IBTS that the demersal fish community as a whole appears to have suffered a marked decline of ca 17% over the 28-year period in the ratio of functionally large individuals, with some 70% of the species affected, appears to signify a major change in the community. This change should be viewed in the context of other changes that have been documented, such as increases in the absolute abundance of small fish and the shift to higher abundance of low-L_{max} species (Daan et al., 2005), increases in species richness for both southerly and northerly species (Daan, 2006) and many other community metrics (Jennings et al., 1999; Piet and Jennings, 2005; Greenstreet and Rogers, 2006). Many of these trends are undoubtedly related and may just be expressions of complex changes caused by a restructuring of the community in response to anthropogenic as well as natural forces (Jennings et al., 1999, 2002; Heath, 2005).

In conclusion, the proportion of large fish as formerly formulated from a human perspective (number or weight of fish above some absolute size limit divided by the total; OSPAR, 2005) may tell us more about changing proportions of the species dominating the community than about the response of the community itself. In contrast, taking a species perspective and calculating the average proportion of functionally large fish provides a much clearer interpretation of what has happened, because overall less fish appear to contribute to the reproductive potential within the entire fish community. Based on first principles should be related to increased exploitation or to a delayed

response to long-term overexploitation. However, this still has to be shown. As yet, we do not understand how all changes observed in the North Sea fish community are interrelated, what their exact causes are, what the metrics convey, and how trends might be reversed. While overexploitation of the North Sea ecosystem appears to have played a major role (Greenstreet and Rogers, 2006), potential effects of climate change on the distribution and dynamics of individual species cannot be excluded (Heath, 2005). We may only hope that trends would become reversed if fishing effort is effectively reduced throughout all demersal fisheries. Therefore, I feel it would be premature to single out a specific metric at this stage as being appropriate for developing management objectives in the EcoQO context and provide advice to OSPAR accordingly.

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Table 1. Species included in the analysis with their L_{max}, L_{mat}, total number recorded (#) and results: mean average species ratio's (ASR_w), regression coefficients (R) and slopes of the temporal trends and significance for the two criteria for setting limits for what is considered a large fish ($0.5*L_{max}$ and L_{mat}).

Latin name	English name	L_{max}	L_{mat}	#	$0.5*L_{max}$				L_{mat}			
					ASR_w	R	slope	p	ASR_w	R	slope	p
Scyliorhinus canicula	Lesser-spotted dogfish	100	58	1705	0.91	-0.25	-0.002	n.s.	0.79	-0.44	-0.008	<0.05
Squalus acanthias	Spurdog	122	67	4943	0.92	0.35	0.002	n.s.	0.84	**0.48**	**0.006**	**<0.01**
Raja radiata	Starry ray	76	46	11453	0.79	**-0.72**	**-0.007**	**<0.01**	0.43	-0.43	-0.012	<0.05
Raja montagui	Spotted ray	85	47	489	0.91	-0.17	-0.001	n.s.	0.68	-0.34	-0.009	n.s.
Raja naevus	Cuckoo ray	70	59	1076	0.97	-0.18	-0.001	n.s.	0.37	-0.45	-0.032	<0.05
Raja clavata	Roker	105	75	2962	0.61	-0.13	-0.004	n.s.	0.36	-0.44	-0.028	<0.05
EL - Elasmobranchs					0.85	-0.26	-0.002	n.s.	0.58	**-0.50**	**-0.012**	**<0.01**
Gadus morhua	Cod	150	70	141753	0.49	**-0.55**	**-0.004**	**<0.01**	0.57	**-0.48**	**-0.005**	**<0.01**
Pollachius virens	Saithe	130	55	36078	0.59	**-0.79**	**-0.014**	**<0.01**	0.76	**-0.76**	**-0.016**	**<0.01**
Melanogrammus aeglefinus	Haddock	85	34	2584839	0.28	**-0.90**	**-0.012**	**<0.01**	0.65	**-0.78**	**-0.013**	**<0.01**
Rhinonemus cimbrius	Four-bearded rockling	41	25	6009	0.77	**-0.51**	**-0.004**	**<0.01**	0.46	-0.35	-0.007	n.s.
Trisopterus minutus	Poor cod	26	15	69442	0.91	**-0.51**	**-0.002**	**<0.01**	0.81	**-0.54**	**-0.005**	**<0.01**
Trisopterus luscus	Bib	45	25	7776	0.59	-0.40	-0.008	<0.05	0.56	*-0.52*	*-0.024*	**<0.01**
Trisopterus esmarki	Norway pout	25	14	7638907	0.80	0.18	0.001	n.s.	0.72	0.13	0.001	n.s.
Merlangius merlangus	Whiting	70	20	3459747	0.27	**-0.61**	**-0.005**	**<0.01**	0.91	-0.04	0.000	n.s.
RF - Roundfish					0.59	**-0.90**	**-0.006**	**<0.01**	0.67	**-0.84**	**-0.009**	**<0.01**
Eutrigla gurnardus	Grey gurnard	45	23	363284	0.814	0.36	0.002	n.s.	0.82	0.36	0.003	n.s.
Myoxocephalus scorpius	Bullrout	31	16	4911	0.925	-0.41	-0.002	<0.05	0.92	-0.41	-0.002	<0.05
Agonus cataphractus	Hooknose	21	11	7601	0.863	**-0.57**	**-0.003**	**<0.01**	0.85	**-0.57**	**-0.004**	**<0.01**
Cyclopterus lumpus	Lumpsucker	60	35	1319	0.926	**-0.68**	**-0.004**	**<0.01**	0.78	**-0.54**	**-0.009**	**<0.01**
Anarhichas lupus	Wolffish	125	40	555	0.666	**-0.72**	**-0.015**	**<0.01**	0.98	**-0.52**	**-0.002**	**<0.01**
Callionymus lyra	Dragonet	30	13	9576	0.890	-0.26	-0.001	n.s.	0.96	-0.38	-0.001	<0.05
OT – Other demersal					0.847	**-0.80**	**-0.004**	**<0.01**	0.88	**-0.72**	**-0.003**	**<0.01**
Psetta maxima	Turbot	100	40	378	0.30	-0.38	-0.010	<0.05	0.59	-0.41	-0.019	<0.05
Scophthalmus rhombus	Brill	75	30	323	0.52	**-0.57**	**-0.015**	**<0.01**	0.87	**-0.63**	**-0.008**	**<0.01**
Lepidorhombus whiffiagonis	Megrim	61	26	2242	0.84	**-0.55**	**-0.007**	**<0.01**	0.95	**-0.51**	**-0.003**	**<0.01**
Glyptocephalus cynoglossus	Witch	55	29	4824	0.89	-0.18	-0.001	n.s.	0.86	-0.28	-0.002	n.s.
Hippoglossoides platessoides	Long rough dab	48	15	321527	0.27	**-0.38**	-0.003	<0.05	0.90	-0.37	-0.001	n.s.
Limanda limanda	Dab	42	14	1358446	0.66	-0.22	-0.001	n.s.	0.96	-0.07	0.000	n.s.
Microstomus kitt	Lemon sole	66	27	22652	0.40	**-0.95**	**-0.014**	**<0.01**	0.72	**-0.94**	**-0.017**	**<0.01**
Platichthys flesus	Flounder	51	25	20311	0.92	**-0.70**	**-0.002**	**<0.01**	0.95	**-0.75**	**-0.002**	**<0.01**
Pleuronectes platessa	Plaice	91	34	86048	0.04	**-0.81**	**-0.003**	**<0.01**	0.40	**-0.95**	**-0.031**	**<0.01**
Solea vulgaris	Sole	60	27	2448	0.45	-0.44	-0.008	<0.05	0.59	-0.40	-0.009	<0.05
FF - Flatfish					0.53	**-0.78**	**-0.006**	**<0.01**	0.78	**-0.85**	**-0.009**	**<0.01**