



MARINE STRATEGY FRAMEWORK DIRECTIVE

Task Group 4 Report

Food webs

APRIL 2010

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Joint Report

**Prepared under the Administrative Arrangement between JRC and DG ENV
(no 31210 – 2009/2010), the Memorandum of Understanding between the
European Commission and ICES managed by DG MARE, and JRC's own in-
stitutional funding**

Editor: H. Piha

EUR 24343 EN - 2010

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JRC 58110
EUR 24343 EN
ISBN 978-92-79-15656-4
ISSN 1018-5593
DOI 10.2788/87659

Luxembourg: Office for Official Publications of the European Communities

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Printed in Italy

PREFACE

The Marine Strategy Framework Directive (2008/56/EC) (MSFD) requires that the European Commission (by 15 July 2010) should lay down criteria and methodological standards to allow consistency in approach in evaluating the extent to which Good Environmental Status (GES) is being achieved. ICES and JRC were contracted to provide scientific support for the Commission in meeting this obligation.

A total of 10 reports have been prepared relating to the descriptors of GES listed in Annex I of the Directive. Eight reports have been prepared by groups of independent experts coordinated by JRC and ICES in response to this contract. In addition, reports for two descriptors (Contaminants in fish and other seafood and Marine Litter) were written by expert groups coordinated by DG SANCO and IFREMER respectively.

A Task Group was established for each of the qualitative Descriptors. Each Task Group consisted of selected experts providing experience related to the four marine regions (the Baltic Sea, the North-east Atlantic, the Mediterranean Sea and the Black Sea) and an appropriate scope of relevant scientific expertise. Observers from the Regional Seas Conventions were also invited to each Task Group to help ensure the inclusion of relevant work by those Conventions. A Management Group consisting of the Chairs of the Task Groups including those from DG SANCO and IFREMER and a Steering Group from JRC and ICES joined by those in the JRC responsible for the technical/scientific work for the Task Groups coordinated by JRC, coordinated the work. The conclusions in the reports of the Task Groups and Management Group are not necessarily those of the coordinating organisations.

Readers of this report are urged to also read the report of the above mentioned Management Group since it provides the proper context for the individual Task Group reports as well as a discussion of a number of important overarching issues.

Contents

Executive Summary	1
1. Definition of terms, and scientific understanding of the key concepts associated with Food Webs	1
2. Good Environmental Status of food webs	1
3. How should “scale” be addressed	2
4. Key Attributes of the Descriptor	2
4.1. Attribute 1; Energy flows in food webs	2
4.1.1. Description of attribute and why it is important	2
4.1.2. Indicators of the attribute	3
4.2. Attribute 2; Structure of food webs (size and abundance)	3
4.2.1. Description of attribute and why it is important	3
4.2.2. Criteria: characteristics of the attribute with respect to GES	3
4.2.3. Indicators of the attribute	4
5. Method for aggregating indicators within the Descriptor to achieve an overall assessment, if available	4
6. Emergent messages about monitoring and research, and Final Synthesis	4
Report	5
1. Definition of terms	5
1.1. Definition of key terms in descriptor	5
1.2. Glossary of key terms in descriptor	5
1.3. What is covered and what is outside scope	6
2. Scientific understanding	7
2.1. Good Environmental Status of Food Webs	7
2.2. Pressures acting on food webs	7
2.3. Patterns in food webs	8
2.4. What is special about marine food webs	8
2.5. Current considerations of food webs in management	9
2.6. Existing approaches to monitoring Food Webs	9
2.7. Ecosystem Models	9
3. Relevant spatial and temporal scales	10
4. Key attributes of the descriptor	10
4.1. Attribute 1: Energy flows in food webs	10
4.1.1. Criteria 1a) Production or biomass ratios that secure the long term viability of all components	11
4.1.2. Criteria 1b) Predator performance reflects long-term viability of components	14
4.1.3. Criteria 1c) Trophic relationships that secure the long-term viability of components	18
4.2. Attribute 2: Structure of food webs (size and abundance)	21
4.2.1. Size based	21
4.2.2. Criteria 2a) Proportion of large fish maintained within an acceptable range	22
4.2.3. Abundance /distribution	23
4.2.4. Criteria 2b) Abundance /distribution maintained within an acceptable range	24

5.	How are the indicators aggregated to assess GES for the descriptor?	25
5.1.	Aggregation of assessments across Attributes	26
6.	Emergent messages about monitoring and research and final Synthesis.....	27
7.	References.....	28
8.	Task group members.....	39
	Annex 1. The role and merits of ecosystem models.....	41
	Annex 2. Shellfish Production requirement ratio to support eider ducks (<i>Somateria mollissima</i>) in the Wash, UK.....	47
	Annex 3. Changes in the food web of northwestern Atlantic shelf seas as a result of collapse in cod stocks	48
	Annex 4. Ratios of fishery landings (or derivatives of landings) to production of lower trophic levels.....	50
	Annex 5. Background information on the Marine Trophic Index (MTI).....	51
	Annex 6. Abundance of species	54

EXECUTIVE SUMMARY

The 2008 European Marine Strategy Framework Directive (2008/56/EC) includes a requirement for EU Member States to report on the environmental status of the seas under their jurisdiction and to work to achieve Good Environmental Status (GES). This is defined by eleven qualitative descriptors, and one of them deals with 'Food Webs'.

The Task Group 4 'Food Webs' descriptor reads: *All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity.*

This report defines the terms used in this descriptor (section 2), describes the scientific understanding (section 3) and the relevant spatial and temporal scales (section 4). A framework to describe attributes of GES for food webs is provided in section 5.

1. DEFINITION OF TERMS, AND SCIENTIFIC UNDERSTANDING OF THE KEY CONCEPTS ASSOCIATED WITH FOOD WEBS

Food webs are networks of feeding interactions between consumers and their food. The species composition of food webs varies according to habitat and region, but the principles of energy transfer from sunlight and plants through successive trophic levels are the same. This descriptor addresses the functional aspects of marine food webs, especially the rates of energy transfer within the system and levels of productivity in key components.

'All elements.' All components of food webs have been considered, i.e. all trophic and functional groups, comprising either one or several species. This potentially includes all living organisms and non-living organic components.

'..to the extent that they are known..' While examination of food webs should in principle include 'all elements', for practical purposes it would include only those food web components that can effectively be sampled by established robust methods of monitoring.

'..normal abundance and diversity and at levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity.' This provides guidance on the reference points and/or target values selected to correspond to good environmental status. Full reproductive capacity refers to the maintenance of fertility and avoidance of reduction in population genetic diversity.

2. GOOD ENVIRONMENTAL STATUS OF FOOD WEBS

The interactions between species in a food web are complex and constantly changing, making it difficult to identify one condition that represents 'good' status. However, changes in species relative abundance in an ecosystem will affect interactions in several parts of a food web, and may have an adverse effect on food web status. There is, however, a significant lack of understanding to assess the ecosystem consequences of such change, or the value that society should attribute to it. As all marine food webs have already been adversely affected by humans, a judgement will need to be reached by Member States to identify regional limit reference points.

Good Environmental Status of Food Webs will therefore be achieved when the indicators describing the various attributes of the descriptor reach the thresholds set for them. These should ensure that populations of selected food web components occur at levels that are within acceptable ranges that will secure their long-term viability. Components must be selected carefully to avoid use of large numbers of species for which abundance / biomass

trends are required (i.e. avoid use of general terms such as ‘predators’ or ‘prey’). Assessment of food webs will need to include;

- (i) biological groups with fast turnover rates (e.g. phytoplankton, zooplankton, bacteria) that will respond quickly to system change;
- (ii) groups that are targeted by fisheries;
- (iii) habitat-defining groups; and
- (iv) charismatic or sensitive groups often found at the top of the food web.

3. HOW SHOULD “SCALE” BE ADDRESSED

Attributes of food webs can in principle be applied on any spatial scale or time scale, however, there are clear interpretational and practical limitations. The fundamental time scale over which ecosystem assessments might be required is annual. The temporal scale necessary to assess growth, mortality and feeding fluxes between food web components should be annual to integrate over seasonal variability at the lowest trophic levels. More frequent assessments, for example those that could be undertaken monthly, are operationally difficult to undertake and maintain, and their interpretation becomes complicated by seasonal dynamics. For the higher trophic levels, some smoothing of annual rates may be required to eliminate inter-annual variability. For longer lived species such as piscivorous fish, mammals and birds, assessments on an annual basis may be too frequent since variability at this scale becomes more influenced by unexplained processes such as recruitment variability, and less by internal population processes.

Similar issues apply to considerations of appropriate spatial scales: at small spatial scales, such as parts of a MSFD Sub-Region, immigration and emigration by advection and migrations become important components of change. For large, long-lived taxa, spatial scales which integrate over migration ranges may be appropriate, but these scales may span fundamentally different habitats and communities for lower trophic levels, for example plankton or benthos, to the point that a synthesis at this scale becomes questionable.

4. KEY ATTRIBUTES OF THE DESCRIPTOR

The effects of fishing are the most important pressures which directly affect target species, and indirectly affect other non-target components of food webs. While these effects respond to management action, the components which they influence are also subject to climate variation and other natural drivers making precise attribution of cause and effect difficult. It is also likely that other pressures will need to be considered in the development of measures, and particularly the cumulative effects of multiple activities.

4.1. Attribute 1; Energy flows in food webs

4.1.1. Description of attribute and why it is important

The food web is a fully interconnected system, so pressures on one part of the system may have impacts elsewhere which are not easily predictable. For example, harvesting of sandeels in the North Sea, where they are a key species in the food web, will remove food for birds, mammals, piscivorous fish, and release predation pressure on zooplankton. There may also be indirect consequences for a range of other species. Managing human activity to achieve a desired balance between species in the system is therefore a major challenge. Energy flows through the food web are an attribute which allows us to diagnose the state of the system.

4.1.2. *Indicators of the attribute*

We identify three criteria of energy flows in the food web which are feasible to measure and apply at a regional scale: a) ratios of production at different trophic levels, b) the productivity (production per unit biomass) of key species or groups, and c) trophic relationships. Many indicators within each criterion require further elaboration to become operational, and it is not yet possible to robustly define thresholds or limit reference points, or the full extent to which climate change may affect the metrics.

a) Production or biomass ratios that secure the long term viability of all components. Ratios of production or biomass between different trophic levels in the food web provide measures of the pattern of energy flow, and the efficiency of energy transfer through the web. It is proposed that a ratio indicator is developed, specific to each marine Regions or Sub-Regions, and based on either ratios of pelagic to demersal fish biomass and/or production, or benthos to fish production, or the proportions of plankton and benthos production required to support fisheries.

b) Predator performance reflects long-term viability of components. Some species, or groups of species, may act as guides to change in the ecosystem. The performance of these species, as measured by their productivity, effectively summarises the main predator-prey processes in the neighbourhood of the food web that they inhabit. The basis for such measures is already established in OSPAR EcoQO, for example in terms of the fledging success of kittiwakes, which relates to the availability of sandeels. Following the same principle, we propose indicators based on the nutritional status of marine mammals or seabirds.

c) Trophic relationships that secure the long-term viability of components.

The diet composition of a group of species is dependent on the consumption by each component species and can be a valuable measure of the relative abundance of prey in a food web and the degree of connectivity in the food web. The diet of some single species, particularly top predators, can provide similar insights. For group-level assessment, the Marine Trophic Index has been used to calculate the mean feeding level of a group from species composition data, assuming a particular diet for each species. At the species level, changes in stomach contents (which indicate the trophic level of diet) can also be diagnostic of underlying change in the food web.

4.2. **Attribute 2; Structure of food webs (size and abundance)**

4.2.1. *Description of attribute and why it is important*

Size structure of food webs is an important attribute and integral to the maintenance of predator prey relationships. Most life history traits are correlated with size, which constrains metabolic rate and controls growth, reproduction and survival, so body size is also a proxy for trophic level. Fishing is usually size-selective within species, so larger individuals generally suffer greater rates of mortality. Exploited populations and communities therefore contain relatively fewer large fish and mean size is reduced. This may in turn have an indirect impact on their prey populations as a result of size-dependent predation and changes in density-dependent growth. The abundance (and distribution) of carefully selected indicator populations (e.g. jellyfish, plankton, etc) can describe food web status and/or levels of human perturbation.

4.2.2. *Criteria: characteristics of the attribute with respect to GES*

Changes in the mean size of fish and the proportion of large species in the community can be detected by indicators of the mean size and size distribution. It is, however, difficult to determine reference values for size-based community indicators. Attempts to do so have

been based on modelling the expected community structure in the absence of fishing, or by selecting a time in the past when the community structure was judged to have been acceptable.

Changes in absolute or relative abundance can be assessed in relation to reference directions and limit reference points, rather than specific targets. For many species, minimum viable populations can be inferred from ecosystem models.

4.2.3. *Indicators of the attribute*

Monitoring the rate of change of functionally important species to highlight rapid increased or decreased abundance will help to identify where future management action may be required. The following two criteria are proposed;

- a) Proportion of large fish maintained within an acceptable range. This criterion describes the changes in the proportion of large fish, and hence the average weight and average maximum length of the fish community in a Region or Sub-Region. The OSPAR EcoQO (Proportion of large fish), provides a protocol that can be applied in other regional seas.
- b) Abundance maintained within an acceptable range; To make this criterion operational requires an assessment of the most suitable species in a Region or Sub-Region to represent food web integrity, based on key biological groups present. Indicators should describe regional abundance trends to identify changes in population status that may have implications for food web status.

5. **METHOD FOR AGGREGATING INDICATORS WITHIN THE DESCRIPTOR TO ACHIEVE AN OVERALL ASSESSMENT, IF AVAILABLE**

TG4 identifies two main attributes of food webs, ‘Energy flows in food webs’ and ‘Structure of food webs (size and abundance)’. It is necessary that both attributes must be addressed for an assessment to be acceptable. Within each attribute TG4 suggests a number of promising criteria, but there may be others. To overcome the burden of proof within an attribute, it will be necessary to address the entire spatial extent of the assessment Region or Sub-Region. This can be achieved using a suite of localised indicators which together cover the domain, or a single spatially comprehensive indicator. More work is required to understand the practical implications of this requirement for Member States or Regional Seas Conventions.

6. **EMERGENT MESSAGES ABOUT MONITORING AND RESEARCH, AND FINAL SYNTHESIS**

There are several operational indicators already in use that are relevant to this descriptor of GES, and that can contribute to the assessment of food web dynamics. It is encouraging to note that these are coherent with other international activities to ensure sustainable fisheries and maritime strategy in European waters, therefore allowing coordinated activity by Member States. While it is therefore possible to begin work now, some further development is required for indicators that cover all the criteria identified in TG4.

The practical process for achieving GES for this descriptor is not well defined. The completion of monitoring programmes and delivery of food web indicators for a Regional Sea in which several Member States have a stake will require substantial levels of coordination. This will have a major influence on successful implementation of the Directive.

1. DEFINITION OF TERMS

1.1. Definition of key terms in descriptor

‘All elements of the marine food webs,..’

The structure of food webs is generically the same as they all involve predator prey interactions and energy transfer between levels, but the species composition of food webs varies according to the environment in which they occur. Food webs in different regions are therefore distinguished by interactions between key species, but the processes of energy transfer are the same. This description defines the spatial scale of food webs used in this report.

We interpret all ‘elements’ as all food web components, i.e. all trophic and functional groups, which could be made up of one or several species. This includes living organisms (from higher predators such as birds and marine mammals to bacteria and viruses) and non-living components (detritus and dissolved nutrients).

‘..to the extent that they are known..’

This includes all food web components that can be sampled by established methods of monitoring.

‘..occur at normal abundance and diversity and at levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity.’

Normal abundance should be interpreted as the reference point / target values selected to correspond to good status. In the MSFD this represents a sustainable state of use from an ecosystem perspective. For living organisms this is an abundance that can recover from perturbation caused by human induced pressures within a reasonable time frame. A ‘Normal’ assemblage is also interpreted as having a functional diversity that would be typical for the marine region and under the prevailing conditions of climate to ensure the overall functioning of the ecosystem.

Full reproductive capacity is not interpreted in the way that is defined in ecology (which is the maximum lifetime reproductive output of a species). Full reproductive capacity refers to the maintenance of fertility and avoidance of reduction in population genetic diversity. Full reproductive capacity sustains the functions of the species in the assemblage.

1.2. Glossary of key terms in descriptor

A food web is a “Representation of feeding relationships in a community that includes all the links revealed by dietary analysis” (Begon *et al.* 1995) (Figure 1-1). In other words it describes those organisms that are eaten by other organisms. Parasitism and disease is in principal a predator-prey interaction, but by smaller organisms (e.g. bacteria or virus) on larger (e.g. phytoplankton or fish).

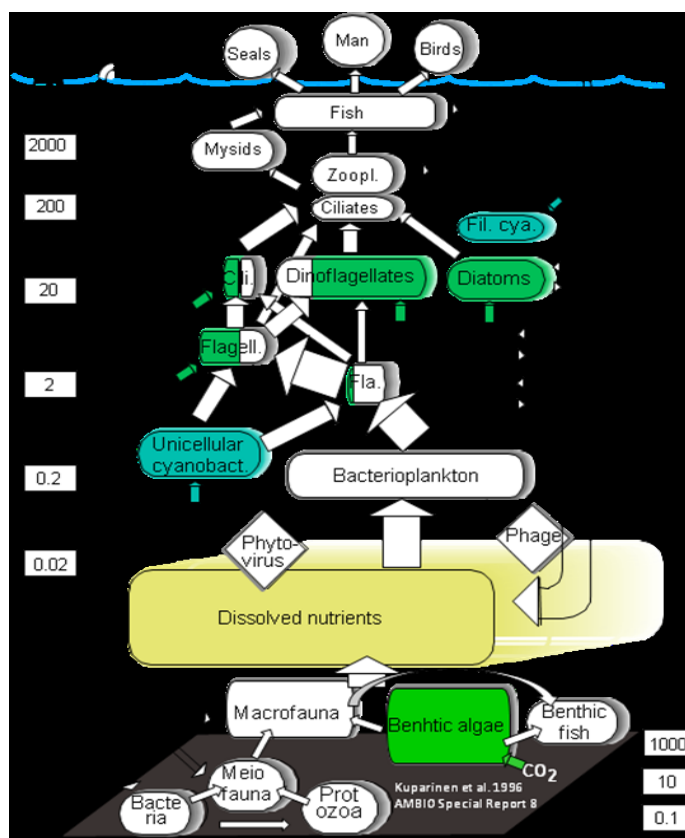


Figure 1-1 Simplified model of a marine food web. Size ranges of organisms indicated by the numbers. Major trophic interactions are shown by arrows, as well as sedimentation of particulate matter and excretion of nutrients. Groups with auto-, hetero- and mixotrophic organisms are shown by green and white boxes. Cili.=ciliates, Flag.=flagellates, Fil. Cya.=filamentous cyanobacteria.

Trophic group; refers to a category of organisms within a trophic structure, defined according to their mode of feeding.

Functional Group; a group of organisms that are using the same type of prey.

1.3. What is covered and what is outside scope

This report will deal with only the functional aspects of marine food webs, especially the rates and directions of energy transfer within the system and levels of productivity in key components. This descriptor will generally not address structural indicators of biodiversity for common benthic or pelagic communities using, for example, metrics of species relative abundance or biomass. It is intended that the Biodiversity Task Group (TG 1) will deal with these along with other measures of diversity relating to threatened, declining and charismatic species. However the abundance and distribution of some key species or functional groups (top predators, jellyfish etc) can be representative of substantial parts of food webs, so where they are considered sufficiently important they will be included in this descriptor. Abundance of non-indigenous species will be dealt with by TG 2, commercial fish and shellfish stock status will be dealt with by TG 3, and the description of benthic communities and biotic structure, substrate and habitat structure will be dealt with by the group addressing sea-floor integrity (TG 6).

2. SCIENTIFIC UNDERSTANDING

2.1. Good Environmental Status of Food Webs

This descriptor is one of three which addresses marine biodiversity. It is also one of the most difficult to implement. The food webs descriptor deals with the functional aspects of species interactions, especially the rates and directions of energy transfer within the system and levels of productivity in key components. Metrics to describe food web status should consider both the extent of bottom-up controls on marine ecosystems, as well as highlighting top-down controls.

Such assessments will take account of the pressure exerted by top predators on prey communities, using, for example, estimates of productivity, reproductive success and size-based measures of population change. There has been recent progress to develop indicators for some of these processes, including the development of OSPAR Ecological Quality Objectives for seabirds and fish communities in the North Sea, and other applications elsewhere in Europe. The productivity of primary and secondary producers has not been included elsewhere in the GES descriptors yet is important to describe the functioning of marine ecosystems. Thus the extent of plankton productivity using both field and remote observation will be used to generate metrics that describe the food supply available for dependent predators. The contribution of ecosystem and food web modelling will provide useful insights into future scenarios of ecosystem change.

Attributing the cause of change in food web structure or function is complex, and will be the result of pressures which act both directly and indirectly on different components of the ecosystem. It will therefore be necessary, wherever possible, to develop metrics that respond to a manageable activity, so that the assessment of good environmental status can lead to specific monitoring requirements and appropriate thresholds or reference levels.

One of the most valuable contributions that can be made by the descriptor 'Food webs' is to provide an overview of broad scale ecosystem status, integrating across a number of different trophic groups, and usually at a broad scale. This is a distinguishing feature of the descriptor, and compliments those also focussing on biodiversity issues (descriptors 1, 2 and 6). The spatial scale at which food web status is monitored is likely to reflect local or regional environmental conditions, and be dependent on the availability of data for key components.

The interactions between species in a food web are complex and constantly changing, making it difficult to identify one condition that represents 'good' status. However, changes in species relative abundance in an ecosystem will affect interactions in several parts of a food web, and may have an adverse effect on food web status. There is, however, a significant lack of understanding to assess the ecosystem consequences of such change, or the value that society should attribute to it. As all marine food webs have already been adversely affected by humans, a judgement will need to be reached by Member States to identify regional limit reference points.

Good Environmental Status of Food Webs will therefore be achieved when the indicators describing the various attributes of the descriptor reach the thresholds set for them. These should ensure that populations of selected food web components occur at levels that are within acceptable ranges that will secure their long-term viability.

2.2. Pressures acting on food webs

Patterns in the structure and function of marine ecosystems can be substantially affected by both environmental changes (e.g. through interannual and interdecadal climatic variation and change) and the pressures of human activities such as fishing effects (e.g. through

overexploitation of large predatory or forage fishes) (Cury *et al.*, 2003). Different types of controls can therefore be exerted on marine ecosystems and can lead to alternate states.

The effects of fishing are the most important pressures which directly affect target species, and indirectly affect other non-target components of food webs. While these effects respond directly to management action, the response time can be slow and variable, and recovery can be impeded by the influence of other natural drivers, making precise attribution of cause and effect difficult.

2.3. Patterns in food webs

Bottom-up control is the conventional trophic flow control that seems to dominate most ecosystems, where the regulation of food-web components derives from change in the abundance of primary producers which is itself strongly influenced by environmental conditions. Literature documenting the relationship between the abundance of different trophic levels and environmental variability is widely available. This has been documented for example in the North Atlantic where parallel long-term trends across four marine trophic levels, ranging from phytoplankton, zooplankton and herring to marine birds, have been related to environmental changes in the North Sea (Aebischer *et al.*, 1990).

Top-down control is the regulation in abundance that is exerted by predators on their prey. A large reduction in predator abundance can cause an increase in prey that cascades downward in the food chain, a phenomenon known as a trophic cascade. Trophic cascades can therefore be thought of as reciprocal predator–prey effects that alter the abundance, biomass or productivity of a population or trophic level across more than one link in a food web, resulting in alternate trends between different trophic levels. The decline in top predator abundance has been demonstrated to cascade down several marine food webs. Recent studies reveal that reduced abundance of large fish predators (e.g. cod) had profound effects on the abundance of small pelagic fishes which in turn affect plankton dynamics in the Black Sea, the NW Atlantic ecosystems and the Baltic sea (Casini *et al.*, 2008). Substantial reductions in marine mammal, shark, and piscivorous fish abundance have led to increased abundances of mesopredators and invertebrate predators. Predation has also inhibited recovery of depleted species, sometimes through predator–prey role reversals.

Top-down and bottom-up processes are not mutually exclusive within ecosystems. In fact, both ways of ecosystem control may act in concert and their relative strength can vary in response to ecosystem alterations (Litzow and Ciannelli, 2007; Casini *et al.*, 2009).

In several productive upwelling ecosystems (e.g. Canary, Benguela, California and Humboldt currents), there is an intermediate trophic level, occupied by a limited number of species of small, plankton-feeding pelagic fish, comprising substantial populations that are exploited intensively and vary considerably in abundance (Cury *et al.*, 2000). Examples are capelin in the Norwegian Sea, anchovy or sardine in some upwelling systems. Pelagic fish can exert a major control on energy flows in productive ecosystems, and this has been termed ‘wasp-waist’ control as those forage fish resources can affect trophic levels both downwards and upwards (i.e. a bottom-up control of top predators by small pelagic fishes, and top-down control of plankton by Small pelagic fishes). The collapse of small pelagic fish populations in the northern Benguela had profound effects on top predators such as marine bird and mammals as well as on lower trophic levels such as jelly-fish (Cury and Shannon, 2004).

2.4. What is special about marine food webs

The structure of marine food webs is not inherently different from terrestrial or freshwater ecosystems, so classical food web theory also applies to marine systems. This theory is

most relevant for conservation biology, specifically related to biodiversity issues (May, 2009) rather than the management of exploited populations. Marine food webs are, however, characterised by many weak links between species and relatively short average path lengths (Link, 2002). This high level of connectance in most marine food webs makes them relatively robust to the secondary effects of species declines or local extinction. Short average path lengths between species suggest that perturbations such as fishing or climate change will be transmitted more widely throughout marine ecosystems compared to their terrestrial or freshwater counterparts (Dunne *et al.*, 2004). Furthermore, body size is an important structuring variable in marine communities and consequently size spectra have been much studied in marine systems, though the implications for food web functioning have been less well studied (Jennings *et al.*, 2001; Raffaelli *et al.*, 2005).

2.5. Current considerations of food webs in management

Food web issues are of increasing importance in European marine management and legislation, though there are few tools or frameworks in current use that focus on food webs or relationships between species. The main approaches use multi-species models for determining maximum sustainable yield values (multi-species MSY). These developments have been driven by criticism of the long-standing single-species approach to European fisheries management which take no account of the state of prey and predator populations.

Worm *et al.* (2009) analyzed current trends in multi-species exploitation rates and biomass in a range of well studied fisheries ecosystems using Ecopath/Ecosim and 'Atlantis' models. In 5 of 10 well-studied ecosystems, the average exploitation rate has recently declined and is now at or below the rate predicted to achieve maximum sustainable yield for seven systems. Yet 63% of assessed fish stocks worldwide still require rebuilding, and even lower exploitation rates are needed to reverse the collapse of vulnerable species. Crucially, the sum of single-species *MSY* was generally a poor predictor of multi-species *MSY*. This is thought to be because of difficulty in deciding *a priori* whether compensatory or compensatory responses to fishing will occur as a result of food web interactions. Each response will lead to divergence between yields at the system level and those predicted by single-species assessments. Similar results were found for the Eastern Bering Sea/Gulf of Alaska (Mueter and Megrey, 2006), and the North Sea (Mackinson *et al.*, 2009). Overall, the sum of predicted single-species *MSY* differed from system-level *MSY* by more than 20% in 42% of the systems and by more than 50% in 18% of the systems analysed by Worm *et al.* (2009).

2.6. Existing approaches to monitoring Food Webs

The extent to which communities function normally depends on the trophic structure and size structure of their component taxa. A number of metrics have been proposed for monitoring these functions in marine communities (e.g. Rochet and Trenkel, 2003; Cury *et al.*, 2005). The metrics fall into several categories: a) assessment of the biomass/abundance of trophic groups or ratios of groups (total/mean weight/abundance or mean trophic level of piscivores, planktivores, benthivores), b) metrics derived from size structure (slope of size spectrum, mean length), and c) metric describing linkages or networks (consumption ratio, number of cycles in food web, mean number of trophic links). No reference points with a theoretical basis exist currently for any of these metrics, though Link (2005) proposed limit and warning values for some of them, and other authors have suggested the use of reference directions (Jennings and Dulvy, 2005, Rochet *et al.*, 2005).

2.7. Ecosystem Models

The multitude of links and processes that make up a real food web mean that the consequences of change will probably be much wider than expected and, because of non-linear

relationships between species, may even lead to counterintuitive outcomes. Trophic ecosystem models are an important component of the tools that will be needed to advise on the state of food webs and the extent of impacts. However, these models are still in an early stage of development and the strengths and weaknesses of the various alternatives are difficult to understand, though there have been some important reviews (Fulton et al., 2005). In general, there seems to be a humped relationship between the detail included in a model, and its effectiveness. Too little detail is ineffective because the model is too abstract. Too much detail is ineffective because the model tries to capture all known processes but at the expense of requiring detail for too many poorly understood parameters. Between these extremes is a set of models that can be parameterised and will effectively at represent the key properties of the system. An important recommendation from reviews is that the use of a single ecosystem model is ill-advised. The comparative and confirmatory use of multiple ‘minimum-realistic’ models is strongly recommended. More detailed information in the role and merits of ecosystem models is given in Annex 1.

3. RELEVANT SPATIAL AND TEMPORAL SCALES

Attributes of food webs can in principle be applied on any spatial scale or time scale, however, there are clear interpretational and practical limitations. The fundamental time scale over which ecosystem assessments might be required is annual. The temporal scale necessary to assess growth, mortality and feeding fluxes between food web components should be annual to integrate over seasonal variability at the lowest trophic levels. More frequent assessments, for example those that could be undertaken monthly, are operationally difficult to undertake and maintain, and their interpretation becomes complicated by seasonal dynamics. For the higher trophic levels, some smoothing of annual rates may be required to eliminate inter-annual variability. For longer lived species such as piscivorous fish, mammals and birds, assessments on an annual basis may be too frequent since variability at this scale becomes more influenced by unexplained processes such as recruitment variability, and less by internal population processes.

Similar issues apply to considerations of appropriate spatial scales: at small spatial scales, such as parts of a MSFD Sub-Region, immigration and emigration by advection and migrations become important components of change. For large, long-lived taxa, spatial scales which integrate over migration ranges may be appropriate, but these scales may span fundamentally different habitats and communities for lower trophic levels, for example plankton or benthos, to the point that a synthesis at this scale becomes questionable. Ultimately, it seems likely that the appropriate spatial scale at which to assess food webs will be set by the purpose for which the assessment is required rather than any ecological considerations. Other practical considerations, such as the availability and spatial extent of monitoring data for key taxa, are also likely to influence the scale at which assessments are made.

4. KEY ATTRIBUTES OF THE DESCRIPTOR

Based on current understanding of food web trophodynamics and the key components that are available for study, it was agreed that fundamental attributes of food webs related to the flow of energy (as carbon) through the system, and the structural features of components, specifically their size and abundance. The following section introduces each of these attributes and suggests criteria that might be applied to determine their status.

4.1. Attribute 1: Energy flows in food webs

Meta-analyses of marine ecosystems show a generic relationship between primary production (standardised to sea surface area), and production at successively higher trophic lev-

els, for example fish (Nixon 1988; Iversen, 1990; Chassot *et al.*, 2007). This relationship is an expression of the efficiency with which the energy captured by primary production is transferred up the food web. Within individual regions this efficiency may change over time depending on a variety of human interventions and climatic factors. The aim of the approach described in this section is to summarise the energy flow by means of a set of metrics which allow an assessment of efficiency, and ultimately to allow an assessment of whether there is unacceptable damage by human activity.

At some levels in a food web, energy flow may pass through a large number of predator-prey linkages, whilst at others the flow may be focused through only a small number of species and/or developmental stages or ‘bottlenecks’ in the web. In some cases, bottlenecks in the web may lead to a so-called ‘wasp-waist’ food-web - one in which a single species acts as a conduit between the lower and upper trophic levels. Such systems are especially sensitive to changes in mortality of the key bottleneck species (Cury 2000), which are thus key components for monitoring the state of the food web.

Metrics which aim to summarise energy flow through the system must incorporate, implicitly or explicitly, data from a number of different trophic levels. Absolute levels of primary production, plankton, fish or seabird production, cannot in themselves be diagnostic of flows. However, we can identify three generic types of measures that can be diagnostic of energy flows and patterns: i) ratios of production at different trophic levels, ii) the productivity (production per unit biomass) of key species or groups, and iii) the trophic level of the species or group of species.

- i) The concept of ratios of production is straightforward. The ratio of, for example, benthic to planktonic secondary production is a clear statement of the proportion of primary production which is diverted to the benthic seabed food web as opposed to the planktonic water column food web.
- ii) The diet of individual species in the food web will be largely determined by the abundances of suitable prey taxa to which they have access. Some predator species, or groups of species, may play a significant part in food web dynamics and thereby act as indicators of change in the system as a whole. The performance of these species, as measured by their productivity, effectively summarises the main predator-prey processes in the neighbourhood of the food web that they inhabit.
- iii) The diet composition of a group of species is dependent on the consumption by each component species and can be a valuable measure of the relative abundance of prey in a food web and the degree of connectivity in the food web. The diet of some single species, particularly top predators, can provide similar insights. For group-level assessment, the Marine Trophic Index has been used to calculate the mean feeding level of a group from species composition data, assuming a particular diet for each species. At the species level, changes in stomach contents or isotopic compositions (which indicate the trophic level of diet) can also be diagnostic of underlying change in the food web.

4.1.1. *Criteria 1a) Production or biomass ratios that secure the long term viability of all components*

The purpose of applying ratios of production or biomass for assessing GES is to detect gross structural changes in the energy flow through a food web which may have been caused by, for example, removal of key species by harvesting, or disruption of distributional overlap between predators and prey through climatic factors. Examples of the type of change which ratios of production would be intended to detect are: a) dominance of jellyfish as planktivores in a system as a result of over-harvesting of small pelagic fish or

removal of top predators, or b) increased abundance of benthic invertebrates due to over-harvesting of benthivorous demersal fish.

Fishing is an important pressure in most if not all shelf ecosystems, but not necessarily the only factor which may shift energy flow between major pathways through the food web. Hence it is important to remember that production ratios are snapshots summarizing multiple cumulative effects on the system. For example, trends in the ratio of macrobenthos to demersal fish production in the North Sea imply top-down control of the benthos by fish predation (Heath, 2005a) and explain the emergence of *Nephrops* fisheries as cod and other gadoid species have been depleted by harvesting. However, both environmental and fishery changes have been suggested to be responsible for recently observed shifts in benthic invertebrate to groundfish dominance and the emergence of shrimp fisheries in the Gulf of Alaska (Anderson and Piatt, 1999; Bailey, 2000).

Many investigators have examined ratios between fishery yield/landings from an ecosystem and the underlying primary production. Comparing across ecosystems, some consistency in this ratio certainly exists (Nixon 1988; Iverson, 1990; Chassot *et al.*, 2007; Gaichas *et al.*, 2009). However, ratios of bulk fishery yield to primary production take no account of the species or functional group composition of catches. This is clearly important since harvesting of high trophic level piscivore species accounts for more primary production than harvesting low trophic level planktivores. For this reason, a more logical approach is to compare the Annual Production Requirement of fishery catches resolved to a given trophic level, with total production at that level. This ratio expresses the proportion of production removed by fisheries. Annual Production Requirement is equivalent to the term Primary Production Requirement (PPR) as defined by Pauly and Christensen (1995), but not necessarily resolved to level of phytoplankton. The concept of an Annual Production Requirement ratio can be applied in other ways than to fishery catches. For example, the prey production required to support a given population of a predator can be derived from an energetic model of that predator, and compared to the measured production of prey in the environment. In this case the ratio expresses the contribution of the predator to total utilisation of the prey. An example of this application of Production requirement ratios is given in Annex 2.

Production or biomass ratios have been used effectively to identify fundamental characteristic differences between ecosystems (Gaichas *et al.*, 2009; Pranov and Link, 2009), however, setting management thresholds or limits to such ratios within a system is difficult. The pelagic to demersal fish biomass ratio was considered to be one of the most robust ecosystem indicators of fishing effects by Fulton *et al.* (2005). Based on experience in the Georges Bank and in other heavily exploited systems, Link (2005) suggests that a warning threshold has been crossed when pelagic fish biomass exceeds 75% or drops below 25% of total fish biomass. However, other results are somewhat counter intuitive with respect to the effect of fishing. For example, the pelagic to total fish biomass ratio in the Norwegian Sea was found to be 0.85, despite the fact that fishery catch is low in this system relative to others in the North Atlantic (Gaichas *et al.*, 2009).

Assessments of fishery yield to primary production are typically undertaken on higher predators for which sampling is relatively simple (Nixon 1988; Gaichas *et al.*, 2009). A similar promising indicator for food web efficiency at the base of the food web measures the relative flow of biomass in the food web through the microbial heterotrophic component, (Turley *et al.* 2000). This indicator has relevance for fish yield, sediment flux and thereby also benthic production. It is therefore proposed for further development and evaluation, and to be considered in future recommendations. Methods can be used in routine monitoring programs at reasonable cost and with good spatio-temporal coverage. The measure is based on bacterial community biomass production (e.g. ^3H -thymidine uptake) relative to

autotrophic planktonic primary production (e.g. $^{14}\text{HCO}_3^-$ uptake method) (Turley *et al.* 2000).

4.1.1.1. Recommended production or biomass ratios

It is recommended one region-specific indicator is developed based on one of the following examples;

Ratio of pelagic to demersal fish production or biomass. Annex 3 provides an example of the application of pelagic to demersal fish biomass ratios to diagnose changes in the food web of northwestern Atlantic ecosystems following the collapse of cod stocks. The ratio has been identified as a robust indicator of food web status. Preliminary thresholds have been suggested.

Ratio of macrobenthos invertebrate to demersal fish production or biomass. Annex 3 also provides an example of the application of benthic invertebrate to demersal fish biomass ratios to diagnose changes in the food web of northwestern Atlantic ecosystems following the collapse of cod stocks. The ratio has also been identified as an indicator of major food web impacts due to harvesting of demersal fish in the North Sea. No indicative thresholds have been identified.

Ratio of zooplankton production requirement of landings to zooplankton production as a measure of pressure on the food web due to fishing. An application of this ratio in the North Sea, Celtic Sea and west of Scotland is given in Annex 4. The ratio indicates increasing and more intense fishing pressure in the North Sea and west of Scotland area compared to the Celtic Sea. Fishing pressure in the Celtic Sea appears lower than the other area due to the lack of large scale industrial fisheries for small pelagic species.

Ratio of benthos requirements of landings to benthos production as a measure of pressure on the food web due to fishing. An application of this ratio in the North Sea, Celtic Sea and west of Scotland is given in Annex 4. The ratio indicates more extreme fishing pressure in the west of Scotland area compared to the others. Pressure in the Celtic Sea appears to be increasing due to escalating removals of high trophic level species and Horse Mackerel. The latter has a benthic component of diet and has increased in abundance in the region due to a move towards the poles in its' geographic range.

4.1.1.2. Technical evaluation of production of biomass ratio indicators

Ease of understanding

The overall concept is easy to understand and communicate.

Data availability

Much of the data required to derive ratios of abundance or production across a wide range of trophic levels are already collected from fish assessment surveys, fishery landings, plankton assessment surveys using e.g. the Continuous Plankton Recorder, and potentially also remote sensing programmes.

The task of assembling data sets spanning a range of trophic levels or groups of species would be a departure from the current working practices of scientific assessments for most EU waters. For example, all ICES fish stock assessments are carried out on a species-by-species basis, with no overview of the total pelagic or demersal fishery or survey data, or of data from other trophic levels. Derivation of food web production or biomass ratios will require the science community to take a wider view of data gathering and synthesis.

Technical methodology

Production ratio indicators will require some degree of modelling or further analysis methodology to convert observations of abundance to measures of production. Technical methods are described in the examples used in Annex 2 to 4, and the references cited therein. In some cases, the use of ecosystem analysis and modelling software such as Ecopath may be appropriate, but this is not necessarily the case for all ratio measures.

Sensitive to a manageable human activity

Production or biomass ratios at different trophic levels provide a snapshot of the state of the food web, given the underlying assumptions used in the calculations. It is not possible to conduct future scenario analyses from such snapshots to evaluate the potential implications of management measures, but these can be done with some available models, using system snapshots as initial conditions. Comparative analyses of the same ecosystem in different time periods, performed using e.g. Ecopath, show that production ratio metrics are sometimes correlated with changes in human activity.

Relatively tightly linked in time to that activity

It is not clear that responses at the scale of an entire food web could be tightly linked in time to changes in human activity at all. In fact, the reverse is likely to be true - when long-lived species are important in the system we can expect considerable lag-times in response to human activity.

Responsive primarily to a human activity, with low responsiveness to other causes of change

We cannot expect the status of marine food webs to respond primarily to human activity. It is clear that they will also respond to environmental changes.

Relevance to Food webs

Ratios of trophic level biomass or production are unambiguously descriptors of the state of food webs.

Current and historic levels

Ecopath analyses have been carried out for a number of marine regions that will be covered by the MSFD. However, these have not been performed to a common standard or based on common criteria for selecting the species or groups to be included, or using universally accepted parameters. Hence we cannot currently define historic levels that are valid across regional seas. There is an urgent need for a concerted action to develop the common standards needed for Ecopath analyses for MSFD regions.

Recommendations for reference levels / limit points

Tentative threshold levels of pelagic: demersal fish biomass have been suggested by some authors studying food web interactions in specific regional seas, but appropriate levels cannot be specified at present for all marine regions, or for other ratios.

4.1.2. Criteria 1b) Predator performance reflects long-term viability of components

The abundance of species in the food web will generally be determined by the abundance of suitable prey taxa on which they can feed. Some species, or groups of species, may play a significant part in food web dynamics and so their population status will effectively summarise the main predator-prey processes in the part of the food web that they inhabit.

This metric therefore quantifies the performance of predators through direct population counts and measurements, which to a large extent are already collected as part of national

monitoring programmes, and/or planned to support existing and planned programmes (e.g. OSPAR EcoQOs).

The quantity of food is important as predators that prey upon forage species are sensitive to fluctuation in prey abundance and can suffer from lack of food resulting from overexploitation or/and environmental changes (e.g. starvation, breeding failure) (Frederiksen *et al.* 2007). Food quality is also recognized as critical to the survival of many marine species including birds (Wanless *et al.* 2005), mammals (Soto *et al.* 2006) and fishes (Litzow *et al.* 2006). For marine birds and marine mammals that are highly dependent on their fish prey for survival and are keystone predator species in ecosystems (Boyd *et al.* 2006), the required prey abundance to quantitatively and qualitatively sustain viable populations of predators should constitute a threshold value. This minimum abundance level of prey necessary to sustain predators can be calculated from existing ecosystem models and could represent a limit reference point for predator prey interactions within marine ecosystems.

Several studies have shown a connection between seabird survival or breeding success and the availability (abundance and/or distribution) of key prey species, which mainly are small pelagic fish (see review by Durant *et al.*, 2004). A particularly relevant example is the influence of a sandeel fishery in the Firth of Forth, northwestern North Sea, on fledging success of the black-legged kittiwake, which has been developed into an OSPAR EcoQO. The breeding success of kittiwakes is calculated using local counts at selected colonies in Scotland and NE England. The indicator uses the black-legged kittiwake as an indicator species for the community of predator species that depends on sandeels as an important food resource. The indicator assumes that if black-legged kittiwakes are unable to breed successfully for several years in succession, then it is likely that sandeel abundance is low, representing a serious risk of adverse effects on many animal species. The effect on breeding success is reflected on a yearly basis; the indicator is only triggered after three years, and benefits of management actions will accrue only in subsequent years. The breeding productivity at colonies within foraging range of the fishery zone was reduced during the period when the fishery was active (Frederiksen *et al.* 2008), and recovered relative to control areas when the fishery was closed. However, environmental factors, especially sea temperature were also very influential on fledging success. In terms of ecosystem management, the results demonstrate that Marine Protected Areas, in this case a fishery closure, can benefit short-lived pelagic fish stocks and their avian predators. However, such positive effects require that the regulations of the MPA exclude or restrict all human activities with negative impacts on the critical resource.

OSPAR has selected the seal population trends indicator for Grey seals (*Halichoerus grypus*) (declines of less than 10% in pup production) to achieve its ecological quality objective (EcoQO). Grey seals give birth in terrestrial habitats and are best counted as numbers of pups produced per year, while harbour seals give birth in intertidal habitats and are best counted as one-year-old or older seals during the period that they haul-out terrestrially to moult. This EcoQO would be triggered rather often due to the interannual variations in numbers of seals (both pups counted or numbers on haul-outs). The probable level of “alarms” is felt to be too high, and thus a five-year running mean might be applied to these figures. Such an approach would detect long-term changes in pup production of grey seals or haul-out numbers of harbour seals. The disadvantage of this is that mortality events, such as caused by epizootics, would not trigger the EcoQO. ICES felt that this was not a major disadvantage as large mortality events are already investigated in depth, whereas more subtle long-term changes might be easily overlooked. The EcoQO as stated in the Bergen Declaration does not differentiate between sub-units of the North Sea and it is unclear whether the EcoQO applies to the whole North Sea population or only to parts of it. It is not scientifically possible or valid to assess trends for the whole North Sea as there is a variation in counting methods depending mostly upon the habitat in which the seals are

giving birth or hauling out. Scientifically consistent trends can be derived for sub-units of the North Sea, but it should be noted that these sub-units are not necessarily biologically separate.

There are other potential metrics that could be useful to determine predator performance, but which are under-developed at this stage. One such metric relates to shifts in the food web and consequently prey availability, which have been shown to affect body condition and health of cetaceans and other predator species (e.g. Harwood *et al* 2000, Bluhm and Gradinger 2008). For humans and domestic animals it has been shown that a reduction in nutritional status can lead to reduced reproductive success, affecting age of onset of puberty, fertility, and success in maintaining pregnancies (Gerloff and Morrow 1986) as well as immune suppression (Landgraf *et al.* 2005). Reduction in prey availability of marine mammals and seabirds is also likely to lead to similar adverse effects on health, in particular causing greater susceptibility to endemic pathogens and increased occurrence of diseases. The health of predators could therefore be used in some circumstances to identify adverse changes in food webs. Information on the nutritional status of marine mammals and seabirds can be gained from dead specimens that are collected through stranding networks, that have been incidentally by-caught in fishing operations or that can be sampled live (e.g. seals). It is important to consider if the animals are a representative sample of a population, as stranded animals alone might have a high proportion of diseased animals (Murphy *et al.* 2009). Standard measurements are routinely used to determine body condition indices of marine mammals and seabirds (Pitcher *et al* 2000, Read 1990). However, morphometric indices alone may not be sensitive indicators to changes in condition in phocid seals and other physiological indices, such as blood variables, have been suggested (McLaren and Smith 1985, Rea *et al* 1998).

Another example of a potential index that could be applied to fish is the use of the liver condition index of Northeast Arctic cod (*Gadus morhua*) as an indicator of composition of capelin (*Mallotus villosus*) and herring (*Clupea harengus*) in the Barents Sea. Temporal variation in the liver condition index (LCI) of five length classes of Northeast Arctic cod was described and compared to the abundance and availability of capelin and herring in the Barents Sea Yaragina & Marshall (2000). On inter-annual time scales, large and rapid fluctuations in LCI occurred which were synchronous across length classes. For all length classes the annual mean LCI was non-linearly related to capelin stock biomass such that LCI decreased rapidly when capelin stock biomass was below one million tonnes. Liver condition index and the frequency of occurrence of capelin in cod stomachs were positively associated. Neither the abundance of juvenile herring in the Barents Sea nor the frequency of occurrence of herring in cod stomachs were positively correlated with LCI. However, a significant, inverse relationship between the frequency of occurrence of capelin in cod stomachs and total stock biomass of herring was observed suggesting that herring influence cod LCI via predation on capelin. On seasonal time scales, LCI values for February through July were significantly higher in years of high capelin biomass compared to years having low capelin biomass. In years of high capelin biomass the proportion of capelin in the stomach contents of cod showed a peak in March and (or) April.

Both these latter examples (body and liver condition) could be used in the future to develop potential indicators for population status of fish and marine mammals.

4.1.2.1. Recommended indicators of predator performance:

Seal population size and pup production in the North Sea (OSPAR EcoQO (OSPAR, 2005)). Declines in the population size of the harbour seal (*Phoca vitulina*) or pup recruitment of the grey seal (*Halichoerus grypus*) indicate poor food supply to seal colonies. The purpose of the indicator is to maintain healthy populations of seals by triggering management actions when needed. Although developed only for the North Sea, the principles can

be applied to all other European marine waters, and methodological standards are well documented.

Seabird breeding population size and breeding success in the North Sea (OSPAR EcoQO (ICES, 2008)). Changes in population sizes are an indicator for important changes in community structure. Seabird populations may be affected by a range of human activities although it may take years before these impacts become evident because of the long life-span and slow reproduction in some seabird species. A change in population trends might trigger further research to investigate the causes of change, and management might formulate "species recovery" or "species action plans". The aim is to maintain a healthy seabird community. Although developed only for the North Sea, the principles provide valuable information of food web status and can be applied to all other European marine waters, and the methodological standards are well documented.

4.1.2.2. Technical evaluation of predator performance indicators;

Easy to understand

Productivity and condition factors of marine animals are easy to understand and to communicate.

Data Availability

Data on productivity, condition factors as well as diets of major marine birds and mammals have been collected routinely in some parts of Europe. Thus, where data are available, the proposed indicators could be easily and accurately measured using data from monitoring of seabirds, or stranded and by-caught animals as well as data from breeding colonies.

Technical methodology

Aerial surveys and counts as well as counts from shore are easy to implement and are undertaken routinely by many countries.

Sensitive to a manageable human activity

Marine birds and mammals are typically closely tied to specific geographical locations. Either because of the location of breeding colonies or their reliance on predictable concentrations of prey, they may not be buffered against the effects of longer-term fluctuations in prey resources. Commercial fishing within the foraging arena of birds and mammal populations can potentially affect availability of food and have detrimental effects on colonies.

Relatively tightly linked in time to that activity

Seabirds and marine mammals are long-lived species and consequently at the population level tend to buffer any adverse conditions. Breeding success as well as pup production is highly sensitive to the local production of food and sometimes induce mass-mortality in offspring.

Easily and accurately measured

Standard methods in the open sea through line transects have been long developed and provide accurate estimates, although are not currently available in all marine regions. Seals can be counted easily while they are on land as well as seabirds on breeding colonies.

Responsive primarily to a human activity, with low responsiveness to other causes of change

Distribution and abundance of prey, such as pelagic fish, vary substantially with environmental changes and strongly affect survival of seabirds and marine mammals. Fishing ef-

fects and environmental variability can act in synergy and appear to be difficult to tangle.

Relevance to Food webs

Top predators are important and emblematic indicators of the overall functioning of the food-web. They are representative of the general ecosystem state.

Current and historic levels

Historical levels of populations for seals and seabirds are well documented but only few data are available for marine mammals.

Recommendations for reference levels / limit points

For marine birds and mammals that are highly dependent on their fish prey for survival, the required abundance to sustain viable predator population of predators should constitute a threshold value. Minimum viable population sizes are often available for marine birds and mammals, and represent limit reference points below which populations should not be driven. Large population increases in seabird and marine mammal populations can also be detrimental to other components of the food webs and maximum population size can be defined below which populations should be kept.

4.1.3. Criteria 1c) Trophic relationships that secure the long-term viability of components

The trophic level (TL) expresses the position of an organism in a food web, and is estimated using diet data. In marine ecosystems, The TL averaged across size/age of a species population can take any value ranging from 1, for primary producers and other taxa at the bottom of the food chain, to 5.5, for specialized predators of marine mammals (e.g. the polar bear) (Pauly *et al.*, 1998). The temporal changes in trophic level of a species or group of species can indicate progressive changes in prey and can be used to highlight adverse effects on food web status.

Information about trophic relationships and current prey of species can be obtained through examination of the diet. Dietary changes can be estimated through isotopic, fatty acid, stomach content, contaminant analyses and visual observation (e.g. Burek *et al.* 2008). For marine mammals, this is usually undertaken using stranded or by-caught animals or in some cases through non-lethal sampling of live animals (e.g. biopsy darting) (e.g. Krützen *et al.* 2002). Such an approach can be used to study shifts in prey use of a species or functional group (e.g. the shift in prey of North Sea harbour porpoise from herring to gadoid species; Santos and Pierce, 2003).

A number of methods which highlight feeding relationships of species in food webs are in development or are currently applied in some circumstances. There was no consistent agreement within the Task Group on the extent to which these methods were suitable for immediate application in EU marine regions. Further evaluation within Regions or Sub-Regions will be necessary.

In February 2004 the Marine Trophic Index (MTI) was adopted by the Conference of the Parties to the Convention on Biological Diversity (CBD) as one of eight indicators to monitor achievement by 2010 of a significant reduction in the current rate of biodiversity loss. The MTI can be calculated from the commercial landings of exploited species (i.e., algae, invertebrates, fish, marine mammals) (Pauly *et al.*, 1998), as the mean weighted TL of fisheries landings for a cut-off TL (i.e., TL > value 3.25) (Pauly and Watson, 2005). The MTI can also be calculated from any measure of biomass or abundance derived from routine fishery-independent surveys (e.g. data collected from the shelf seas by research vessels: Pinnegar *et al.*, 2002), for different spatial and temporal scales, for example from

localised ecosystems such as enclosed bays, to larger areas such as the Large Marine Ecosystems or wider oceanic areas, using annual or seasonal data. Also, the index could be applied to any assemblage (not just fish) for which there is abundance data for species at known TL. If the MTI is calculated using fishery landings instead of information from assemblages, then it will be necessary to interpret the results by investigating changes in fisheries regulations, technical measures and exploitation strategies. One method to assist with this task is the Fishing in Balance (FiB) index (for details see Annex 5). Before recommending that this indicator is applied operationally throughout European Regional Seas, further work is necessary to agree generic TL values of fish species (such as those already provided by FishBase www.fishbase.org) and those for other components (such as benthic invertebrates) which may also be available.

The dominant prey in diets can be used as a potential index to show temporal shifts in the main prey consumed. For example, some assessments of diets are already routinely completed, including stomach content analyses of higher predators (fish, birds and marine mammals). Additional analyses of diet and associated trophic pathways can be done by standardizing sample protocols and analysis for isotopic, fatty acid and contaminants for animals caught, bycaught or stranded. Marine mammal species range from opportunistic to specialized feeders and the trophic level of their prey also varies. Baleen whales such as the bowhead or right whale feed on prey such as copepods with a low trophic level. Some of the toothed whales, such as the Killer Whale, not only feed on squid or fish, but include higher trophic levels such as other cetaceans or pinnipeds in their diet. Shifts in the food web and consequently prey availability can have an effect on a number of population parameters including reproductive success, abundance, distribution, body condition, health, and mortality. Existing sampling protocols, e.g. within marine mammal stranding networks, could be extended for a potential indicator of changes in trophic level of prey, but this indicator needs more development work before it can be made operational.

4.1.3.1. Technical evaluation of indicators of trophic relationships

Easy to understand

The trophic level of species in a food web describes the level at which a population feeds, averaged across life-history stages and habitats. Although conceptually relatively simple the TL varies between individuals in a species and with time, so care must be taken when applying the concept to time-series data or broadly across eco-regions.

Data Availability

Data describing annual fluctuations in fish population size, either from commercial landings or from fishery-independent surveys, are widely available in European marine waters. Data quality is dependent on the methods used (such as the gear type and mesh size) and the accuracy with which landings are recorded. Data for other components (such as marine mammals, seabirds or benthos) are less frequently available, but can in principle also be used to track changes in prey (and thereby mean TL of the population).

Technical methodology

The MTI can be easily calculated because it uses a simple measure of abundance (i.e., landings, biomass) weighted by the TL value. The quality and reliability of the analysis and results depend entirely on the accuracy of the TL value. Although such values available from online databases such as FishBase, www.fishbase.org, for fishes and SeaLifeBase, www.sealifebase.org, for other organisms, these make assumptions about the size/age range of the target populations, and their seasonal feeding ecology. Further work is necessary to provide reliable TL estimates of species that are applicable in all European

seas. The methods used to quantify stomach contents to infer TL can be complex and costly when relying on isotopic analysis.

Sensitive to a manageable human activity

The TL of a species in a food web can be influenced by adverse human impacts on prey items, especially for top predators. The MTI, when based on commercial landings, is sensitive to fishing strategies and market values, putting emphasis on the effects of fishing on the relative abundances of the high-TL organisms (mainly fish), which are generally more threatened than low TL ones. A strong trend in a long MTI time series is generally affected by fishing activities whereas year-to-year variability can be the result of both fishing practices and other causes (e.g. environmental factors, population dynamics).

Relatively tightly linked in time to that activity

The response of the index is on a multi-annual scale.

Easily and accurately measured

It can be easily measured because it uses only a measure of abundance (i.e., landings, biomass) for an array of species and their trophic levels. The estimation of MTI is based on some assumptions and has drawbacks. Firstly, when using commercial landings data it is calculated only for the exploited fraction of the ecosystem (i.e., algae, invertebrates, fish, marine mammals) resulting from fishing strategies and availability and does not take into account other important biotic components of the food web (i.e., bacteria, viruses, phytoplankton, micro-zooplankton, various marine mammals, marine birds and turtles). Thus, its use assumes that the exploited fraction is representative of wider marine biodiversity. Secondly, the TL of fish usually changes as fish grow and some species occupy different trophic levels as they get older. TL can also change from year to year. Thus the use of a constant TL value might adversely affect the MTI value and the significance and sign of the trend. Finally, the MTI is sensitive to the TL values used for different species (e.g. Cury *et al.* 2005), it might partially reflect changes in the way fishers target different species, and does not include discards or illegal landings (which however can be included should data or estimates become available).

Responsive primarily to a human activity, with low responsiveness to other causes of change

The strong trend in a long MTI time series based on landings is mainly affected by fishing activities whereas year-to-year variability can be the result of both fishing practices and other causes (e.g. environmental factors, population dynamics).

Relevance to Food webs

The feeding relations of marine species, especially those of higher predators, are of direct relevance to issues related to food web integrity and ecosystem functioning.

Recommendations for reference levels / limit points

The MTI can be linked to a reference point if information is available for periods before the major industrialization of fisheries. A potential reference point is the mean MTI of landings (or biomasses) at a time when most stocks were considered to be exploited sustainably.

Despite the availability of some indicators to track rate of change of trophic relationships in food webs, the development of reference values or reference directions, and acceptable deviation from these, is complex and needs further work.

4.2. Attribute 2: Structure of food webs (size and abundance)

One of the simplest means of describing the complex relationships within food webs takes account of the relative abundance and size distribution of the component species. As food webs tend largely to be structured by predator prey interactions, the body size of predators, and the abundance of their prey, will determine the strength and direction of energy flow through the system. In this section these structural measures are used to identify criteria for good environmental status of food webs, and suggest simple indicators to record their rate of change. This attribute links closely with comparable metrics developed to support descriptors related to biodiversity (TG 3) and sea floor integrity (TG 6).

4.2.1. Size based

The concept of body size as an indicator of structure for food webs encompasses all marine organisms. However, most research has been carried out for fish, hence the following text draws from the results obtained for fish and considers fishing as the dominant human pressure.

Body size (length, weight) is a structuring variable for both individuals and their interactions. Most life history traits are correlated with size, which constraints metabolic rates and energy assimilation, thus controlling growth, reproduction and survival of individuals (Reiss, 1989). On average, larger species and individuals feed at higher trophic levels. As a result, changes in community size structure will result in changes in trophic structure. The so-called ‘fishing down the food web’ (Pauly *et al.*, 1998) is the result of disappearing from the ecosystem due to overexploitation and fishing exploitation individuals at lower and lower trophic level.

Fishing is usually size-selective, both within and among species, so larger individuals and larger species often (though not always) suffer greater rates of mortality but have less capacity to sustain it. The net result is that exploited populations and communities contain relatively fewer large fish and mean size is reduced (Rochet *et al.* 2005; Methratta and Link, 2006). Moreover, the proportion of large species in the community will fall and the slope of the size spectrum increase (Pope and Knights, 1982, Pope *et al.* 1988; Rice and Gislason, 1996).

Fisheries can also have an indirect impact on the body size of non-target fish (e.g. prey fish), when the fishery alters the abundance and/or size-structure of the targeted fish (e.g. large predators). These responses can be a result of the size-dependent predation of the predators on their prey, or by density-dependent growth (e.g. weight-at-age) of the prey.

Size-based indicators have been shown to be suitable for monitoring the trophic structure of exploited fish communities (Shin *et al.*, 2005). They have the advantage over trophic level derived indicators that; a) the relationships between size and trophic level within individual species are often stronger than relationships among species and, b) trophic level is not a life history trait that determines the response of a species to mortality, but a consequence of feeding relationships. The second point is demonstrated by the vulnerability to fishing of some of the larger bodied species feeding on lower trophic levels, such as big plaice eating polychaetes. Thus, since trophic level is not a strong measure of vulnerability and changes in mean trophic level are a consequence of changes in species and size composition, it may be more logical to use size and species composition directly to measure the impacts of fishing.

The size-based structure of food webs is variable on a range of spatial scales and depends on species distribution and developmental stage. For example, small fish will generally dominate the community in coastal nursery areas while larger individuals are often found in deeper waters. Therefore, the pertinent spatial scale for size-based indicators must take

these factors into consideration and ensure that they integrate fully across all spatial scales to provide a comprehensive representation of the food web.

Persistent temporal changes in the complete size structure of food webs are expected to occur on a multiannual scale. This is related to the generation time of marine species. However, some indicators might react over a shorter time scale.

4.2.2. *Criteria 2a) Proportion of large fish maintained within an acceptable range*

The proportion of large individuals captures the state of an assemblage. Heavily fished assemblages will have fewer large fish compared to when they were more lightly fished (or not at all). Thus, a large proportion of large fish is a good sign. However, the size to which individuals grow does not only depend on mortality but also on species composition and general environmental conditions. For example, individuals of the same fish species are generally smaller in the Mediterranean compared to the North Sea. The proportion of large individuals in a given assemblage, is calculated by estimating the proportion of individuals in weight above a certain size threshold (large/all). This threshold should be system and assemblage dependent, and so far has been estimated only for the North Sea fish assemblage.

The proportion of large fish when calculated as a proportion by weight has the advantage over average size in that it should be less influenced by recruitment variations. As a consequence, the indicator is expected to be more reactive to changes in fishing pressure rather than changes in recruitment due to global change (which would influence the denominator of the proportion).

It is impossible to determine a global reference value for the proportion of large fish. Attempts to derive regional reference values were based on modelling expected community structure in the absence of fishing or to use its value obtained at a time in the past where the size-structure was judged to have been satisfactory (see example). Others have derived expected directions of change under the impact of fishing (Shin *et al.*, 2005), i.e. a decrease in the proportion of large fish with increasing fishing pressure.

4.2.2.1. Recommended indicator for proportion of large fish:

OSPAR has selected the large fish indicator (proportion by weight) to achieve its ecological quality objective (EcoQO) for the demersal fish assemblage in the North Sea (ICES, 2007; OSPAR, 2008). The large fish indicator is calculated using quarter 1 International Bottom Trawl Survey (IBTS) survey data, excluding pelagic species. Based on analysis of the available time series, the size limit for large individuals was set at 40 cm. At the start of the time series in 1983 the proportion of fish in the survey above 40 cm was 0.3 and decreased thereafter. It was judged that a proportion of 0.3 was a suitable limit reference value. Hence the objective is to re-establish the size-structure of the North Sea demersal fish assemblage such that at least 30% by weight of fish are larger than 40 cm.

4.2.2.2. Technical evaluation of proportion of large fish

Easy to understand

Yes

Sensitive to manageable human activity

The proportion of large fish is sensitive to fishing as these large fish are the target of directed fisheries in all ecosystems. The indicator is also somewhat sensitive to indirect effects due to density reduction and resulting enhanced growth and predation relaxation making smaller fish increase in biomass (increase in denominator of indicator).

Relatively tightly linked in time to that activity

In addition to being sensitive to direct impacts of removal of large fish, in the short term, the indicator can also be sensitive to environmental changes leading to increased recruitment, which will increase the denominator. However, eventually the small fish will grow large and become part of the numerator of the indicator.

Easily and accurately measured

For calculating the proportion of large fish, estimates of biomass by size group and a size limit for each ecosystem is required. For fish, the bottom trawl surveys for fish funded under the EU Data Collection Framework provide estimates of numbers at length on an annual basis for wide areas. Similar surveys exist in the Mediterranean. If only numbers are available biomass can be estimated using available length-weight relationships.

4.2.3. Abundance /distribution

This criterion describes the abundance and spatial distribution of major species which represent key community and or/ecosystem properties. In some cases, when representative species cannot be evaluated, functional groups can be considered. In the ideal case, a set of species representing different communities or habitats (benthos, plankton, fish, top predators) should be selected, in this way covering a large part of the ecosystem. However, typically, ecosystems are characterized by few strong links and many weak links among species or trophic levels (Wootton and Emmerson 2005). Therefore, one (or few) indicator populations could also serve as broader indicator of ecosystem state and/or human perturbation (e.g. fishing activity, Link 2005) if the chosen indicator is strongly linked to the other trophic levels. This might be particularly the case in low-diversity systems (Casini *et al.*, 2008).

Criteria for selecting the groups/species that could be included in this category are (see Fulton *et al.*, 2005):

- i) groups/species with **fast turnover rates**, responding quickly to any change in the system. Such species may cause false alerts, but are potentially useful as early warning indicators (e.g. phytoplankton, bacterioplankton, microzooplankton, mesozooplankton, jellyfish, short-living pelagic fish)
- ii) groups/species that are **targeted by fisheries**, responding to fishing impact (e.g. pelagic and demersal fish), and plankton-feeding pelagic fish exerting control on energy flows in productive ‘Wasp-Waist’ ecosystems (see Section 3.1).
- iii) **habitat-defining** groups/species (e.g. benthic fauna)
- iv) groups/species at the **top of the food web** and charismatic indicator species, providing indications about the underlying ecosystem state and how heavily it has been impacted by fishing (e.g. tuna, sharks, marine mammals, seabirds and turtles)
- v) groups/species that are **tightly linked** (via food web linkage) to other trophic levels

Abundance and spatial distribution should be representative of the territorial seas, continental shelf, and deeper waters present in each region. For all variables, integrated annual values are recommended as a basic temporal unit. For seasonally migrating species (e.g. fish) local season-specific monitoring could also provide important information (e.g. to describe the seasonal immigration of emigration of spawning fish in rivers and estuaries). Several existing monitoring programs are performed only once a year, so they will reflect a particular phase of the populations’ annual cycle.

4.2.4. Criteria 2b) Abundance /distribution maintained within an acceptable range

We recommend monitoring the abundance and distribution of representative species/groups (based on the selection criteria listed above) and evaluating these in the context of sub-regional reference values. It is recommended that these focus on key groups, rather than be generically applied to large numbers of species, to target specific issues related to food web status. These will be specific to European regional seas and cannot be further developed here. Organisms maintained within normal abundance range are further indirect evidence that their reproductive capacity is maintained.

Seven phytoplankton indices have been proposed for the southern Baltic Sea (Sagert *et al.* 2008). Among these are total phytoplankton biovolume, the percentage of diatoms, and the biovolume of different size ranges of diatoms and one indicative species (*Woronichinia compacta*). This analysis was based on 1163 data sets from 15 sites covering salinities between 5-10 psu and 13 years of data. The proposed indices were shown to properly classify 3 environments with different trophic status. A decrease in Diatom abundance, accompanied by an increase in Dinophytes and Cryptophytes, was also in accordance with observations from other marine areas. Further examples of species and communities that may be used as indicators based on abundance are shown in Annex 6.

Jellyfish are involved in some spectacular modifications of the food web structure and ecosystem functioning such as in the Black Sea (Daskalov *et al.*, 2007), and these data suggest there are indications of increased abundance (Gibbons and Richardson, 2009). Jellyfish are likely to provide an important indicator species in this category for some regional seas.

Mesozooplankton play a key pivotal role in marine food webs. Besides responding to bottom-up forcing, the zooplankton community responds indirectly to top-down (fishing) forcing (e.g. Frank *et al.*, 2005 in the western North Atlantic; Casini *et al.*, 2008 in the Baltic Sea; Daskalov *et al.*, 2007 : in the Black Sea), so in this way acts as an indicator of human impact on ecosystems.

4.2.4.1. Recommended indicator for abundance/distribution:

The abundance and distribution of representative groups/species, to be selected by regional seas conventions or as appropriate in regions or sub-regions. Groups/species that could be included here are those with fast turn-over rates and those targeted by fisheries, habitat defining groups, top predators which are often also charismatic, and those tightly linked to other trophic levels. The food web coverage for each indicator should be established, preferably with a clear understanding of the relationships to other food web components based on peer-reviewed literature. Threshold values should be selected and evaluated in the context of sub-regional reference values.

4.2.4.2. Technical evaluation

Easy to understand

Yes.

Sensitive to a manageable human activity

The sensitivity to human activity will depend on the selected indicator.

Higher trophic levels (top predators) and nutrients are both directly sensitive to human pressure and therefore generally responsive to management action. Also plankton groups are indirectly influenced by human drivers, responding to important changes in trophic status of the ecosystem (Cole *et al.*, 1988, Thingstad and Sakshaug 1990). Waste water

discharge, agricultural practices and atmospheric nutrient deposition may also directly influence plankton abundance.

Relatively tightly linked in time to that activity

The timing between disturbance and response may vary among species, from rapid for plankton (e.g. in case of anthropogenic nutrient emission) to slow for top-predators (e.g. fishery or bottom-up processes). However, in case of indirect effects (e.g. through trophic cascades) the response of lower trophic levels may be also slow.

Easily and accurately measured

Abundance of organisms is often relatively easily and accurately measured. In some cases, standardized monitoring programmes exist, often internationally coordinated (e.g. fish surveys). Applying spatial distribution as a criterion will, however, require substantial and consistent spatial coverage in the data sets. Standardized methods and regular inter-laboratory calibrations are needed to avoid inaccuracies in both taxonomic determination and abundance estimates.

Responsive primarily to a human activity, with low responsiveness to other causes of change

The abundance and distribution of organisms is typically not only responding to human pressure but also hydrographical, meteorological and climate variation. Therefore, effort should be made to disentangle the anthropogenic causes from natural forces.

Relevance to Food webs

Currently there is little scientific understanding of the relevance of species or communities as indicators of food web quality (as compared with their structural integrity). More research and evaluation is needed to select and recommend specific species as good (appropriate) indicators. In the appendix there are some examples of species and communities that may be used as indicators based on abundance.

Current and historic levels

Current abundances are known for several marine species that are candidates as indicators. The understanding of historic levels is available only for a few species further than 20 years back in time.

Recommendations for reference levels / limit points

It is strongly recommended to develop a common approach to derive acceptable reference limits including allowance for natural variability.

For commercially important fish species there are single-species reference levels for abundance (ICES biological reference points), but these levels are not set taking into consideration the effects on the ecosystem. Therefore, they are not suitable in a food web context. There are no reference values for spatial distributions.

5. HOW ARE THE INDICATORS AGGREGATED TO ASSESS GES FOR THE DESCRIPTOR?

TG4 identifies two main attributes of food webs, ‘Energy flows in food webs’ and ‘Structure of food webs (size and abundance)’. It is necessary that both attributes must be addressed for an assessment to be acceptable. Within each attribute TG4 has identified a number of criteria (listed below);

Attribute 1; Energy Flows in Food Webs

The food web is a fully interconnected system, so pressures on one part of the system may have impacts elsewhere which are not easily predictable. For example, harvesting of sandeels in the North Sea, where they are a key species in the food web, will remove food for birds, mammals, piscivorous fish, and release predation pressure on zooplankton. There may also be indirect consequences for a range of other species.

Criteria;

- a) Production or biomass ratios that secure the long term viability of all components.
- b) Predator performance reflects long-term viability of components.
- c) Trophic relationships that secure the long-term viability of components.

Attribute 2; Structure of Food Webs (size and abundance)

Most life history traits are correlated with size, which constrains metabolic rate and controls growth, reproduction and survival. The abundance (and distribution) of carefully selected indicator populations (e.g. jellyfish, plankton, etc) can also describe food web status and/or levels of human perturbation.

Criteria;

- a) Proportion of large fish maintained within an acceptable range
- b) Abundance/Distribution maintained within an acceptable range

To overcome the burden of proof within an attribute, it will be necessary to address the entire spatial extent of the assessment Region or Sub-Region. This can be achieved using a suite of localised indicators representing one or more of the criteria which together cover the domain, or a single spatially comprehensive indicator. More work is required to understand the practical implications of this requirement for Member States or Regional Seas Conventions.

Indicators have been identified for some of the criteria listed above, often based on those already developed by Regional Seas Conventions or through other ongoing Institutional activities. While this report has been able to suggest some promising indicator classes it has not been possible to select the specific group of taxa that would be most suitable for each Region or Sub-Region. The examples and literature provided will, however, be sufficient for all Member States to apply the principles described to their own region.

In some regions, while we have been clear about the attributes of Food Webs, it has not been possible to recommend the most suitable indicators for generic application. Further work will be necessary to agree a full suite of indicators, particularly to confirm the correct methodological standards for use in criteria c) (trophic relationships) and e) Abundance / Distribution changes.

5.1. Aggregation of assessments across Attributes

As described above, TG4 expects that evaluation of both the two main attributes of food webs, 'Energy flows in food webs' and 'Structure of food webs (size and abundance)' must be undertaken for an assessment of Food Web status in marine waters to be complete. In addition, it will be necessary to develop one or more indicators for these attributes which together provide comprehensive spatial coverage of each region or sub-region, as appropriate. However, further work needs to be undertaken to agree how a number of assessments can be combined to achieve an overall assessment of GES for the descriptor.

Several methods have been proposed to combine assessments, ranging from those (such as in the Water Framework Directive) which requires all assessments to be acceptable before agreeing a final status assessment ('one out all out'), to those which provide weightings to give priority to some ecosystem components or attributes over others. Each individual assessment will also be subject to uncertainty in determining the metric and the reference point value. The 'fuzzy set' approach has been suggested by Silvert (1997; 2000) as a way of including uncertainty when combining a range of specific ecological assessments. The method relies on scoring assessments based on a combination of their achievement of assessment criteria and certainty of knowledge. However, there is currently no agreed method for aggregating the assessments of Food Web status across attributes and within Regional Seas. Further discussion should take place to review the proposals for the other 'biodiversity' descriptors, and derive a pragmatic process that is suitable across, rather than within, descriptors.

6. EMERGENT MESSAGES ABOUT MONITORING AND RESEARCH AND FINAL SYNTHESIS

Food webs are networks of feeding interactions between marine organisms. The species composition of food webs varies according to habitat and region, but the principles of energy transfer from sunlight and plants through successive trophic levels are the same. This descriptor addresses the functional aspects of marine food webs, especially the rates of energy transfer within the system and levels of productivity in key components.

The interactions between species in a food web are complex and constantly changing, making it difficult to identify one condition that represents 'good' status. However, changes in species relative abundance in an ecosystem will affect interactions in several parts of a food web, and may have an adverse effect on food web status. There is, however, a significant lack of understanding to assess the ecosystem consequences of such change, or the value that society should attribute to it. As all marine food webs have already been adversely affected by humans, a judgement will need to be reached by Member States to identify regional limit reference points.

The time scale over which ecosystem assessments might be required is at least annual. More frequent assessments are operationally complex and their interpretation is affected by seasonal dynamics. For longer lived species such as piscivorous fish, mammals and birds, annual assessments may be more influenced by unexplained processes such as recruitment variability, rather than by internal population processes. Variability between habitats suggests that appropriate spatial scales will be based on the purpose for which the assessment is required rather than ecological considerations.

The effects of fishing are the most important pressures which directly affect target species, and indirectly affect other non-target components of food webs. While these effects respond to management action, the components which they influence are also subject to climate variation and other natural drivers making precise attribution of cause and effect difficult. Managing human activity to achieve a desired balance between species in the system is therefore a major challenge.

There are several operational indicators already in use that are relevant to this descriptor of GES, and that can contribute to the assessment of food web dynamics. It is encouraging to note that these are coherent with other international activities to ensure sustainable fisheries and maritime strategy in European waters, therefore allowing coordinated activity by Member States. While it is therefore possible to begin work now, some further development is required for indicators that cover all the criteria identified in TG4.

The practical process for achieving GES for this descriptor is not well defined and requires further work. Even once indicators are agreed in principle, the completion of monitoring programmes and delivery of food web indicators for a Regional Sea in which several Member States have a stake will require substantial levels of coordination. This will have a major influence on successful implementation of the Directive.

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8. TASK GROUP MEMBERS

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ANNEX 1. THE ROLE AND MERITS OF ECOSYSTEM MODELS

The following text comprises extensive quotations and modified extracts from the following publication:

Elizabeth A. Fulton, Anthony D. M. Smith and Craig R. Johnson (2003). Effect of complexity on marine ecosystem models. *Marine Ecology Progress Series* 253: 1–16.

Ecosystem rather than species management has become an explicit part of policies that feature in international treaties and national legislation. Many of the tools that will be needed to fulfil the requirements of these policies are still in an early stage of development. One such tool is trophic ecosystem modelling. These models have been put forward to aid system-level understanding and provide insight into the potential impacts of human activities. Despite this, there are many gaps in knowledge of their strengths and weaknesses. In particular, little is known about the effect of the level of detail in a model on its performance. There has been some consideration of the effects of model formulation, as well as the effects of the physical, biological and chemical scope of multispecies and ecosystem models on their performance. A review of existing research indicates that there is a humped relationship between model detail and performance for these models, and that there are some guiding principles to consider during model development. Other reviews give some insight into which model structures and assumptions are likely to aid understanding and management, and which may be unnecessary. A key criterion is the determination of whether a model can capture properties of real systems that other models cannot. The main recommendation from such analyses is that the use of a single ‘ultimate’ ecosystem model is ill-advised, while the comparative and confirmatory use of multiple ‘minimum-realistic’ models is strongly recommended.

During the last 30 yr, with every push to understand entire ecosystems rather than isolated components, ecosystem models have become a popular tool (Watt 1975, Halfon 1979, Walters *et al.*, 1997, Sainsbury *et al.*, 2000). However, complex general models have often acquired a poor reputation (Jørgensen *et al.*, 1992), primarily because of 2 factors. First, these models are often so large and complex that they may not be cost efficient, with the majority of the modelling resources spent in development and maintenance rather than on their application (Watt 1975). Second, complexity introduced for the sake of completeness accomplishes nothing if the resulting model is actually of poor quality (O’Neill 1975, Silvert 1981, DeCoursey 1992). While modern computing power makes ecosystem models attractive, as computational restraints are lifted (Beck 1999), this does not solve the problems of uncertain model specification, parameterisation and system understanding, or the effects of model structure and detail on model performance (Silvert 1981, Jørgensen 1994). These areas of modelling still require much attention and the need becomes more urgent with increasing pressure on scientists and managers for ‘whole system’ approaches, predictions and policies.

The evolution of ecosystem models has often seen a tendency to incorporate increasingly detailed process formulations and model structure. The mixed success and potentially large computational demands of early attempts at highly detailed reductionist ecosystem models (Hedgpeth, 1977; Platt *et al.*, 1981) lead to a return to ‘simple’ models during the late 1970s through to the mid-1990s. With advances in computing power and the growth of ecosystem and ecological theory large models that are flexible enough to be applied in a range of locations, and that account for a large amount of the system, are becoming attractive again. For instance, over 130 ECOPATH with ECOSIM models have been published (Christensen *et al.*, 2000) and the European Regional Seas Ecosystem Model (ERSEM) (Baretta *et al.*, 1995) has been applied in 18 locations. This rise in popularity is driven by at least three things: (1) an international push for the management of ecosystems rather

than individual resources, (2) it is hard to compare results across systems if they are built on differing premises and assumptions, and (3) little has been published on the effects of complexity on ecosystem model performance. Given the increasingly widespread use of marine ecosystem models, it is clear that the effect of model complexity on model performance is an important issue.

ECOSYSTEM MODELS

Terminology associated with ecosystem models is confusing, in that ecosystem models can refer to everything from total system models (dealing with biotic components from multiple trophic levels as well as abiotic components and forcing) to models that focus solely on fisheries (the ‘top end’ of the web) or water quality (the ‘bottom end’ of the web). Here we use the term ecosystem model to refer to total system models rather than those multispecies models tied to one end of the food web or the other. Within the last few decades, increasing computer power and a shift in the focus of scientific and political thought has led to a rapid growth in the number of multispecies and ecosystem models in existence (Silvert 1981, Breckling & Müller 1994). The majority of published and applied multispecies models tend to concentrate around fishes or nutrients and in both cases, the history of model development can be ‘characterised by the growing intricacy of their internal structure’ (Fransz *et al.*, 1991). There have been a number of attempts at producing trophic ‘whole ecosystem’ models for the marine environment, including the cove model of Patten *et al.* (1975), the multispecies model of Andersen and Ursin (1977), the fjord model of Bax & Eliassen (1990), the ECOPATH with ECOSIM model (Christensen *et al.*, 2000); the European regional seas ecosystem (ERSEM I [Baretta *et al.*, 1995] and II [Baretta-Bekker and Baretta 1997] models; the integrated generic bay ecosystem [IGBEM]) model and Bay Model 2 (BM2) (Fulton 2001). Nevertheless, compared with the widespread use of water quality and fisheries multispecies models, the use of ecosystem models remains limited. As a result, there is still a lot of scope for the development of a thorough understanding of the implications of model structure on performance for these kinds of models.

The various types of multispecies and ecosystem models each have associated advantages and problems, but there is a list of features and potential drawbacks common to them all. In general, such models improve our understanding of systems by reflecting the 2-way nature of system dynamics. Human impact on one part of a system can spread to other parts of the system, but system feedbacks and interrelations can also mean that an impact can have unexpected consequences even for those groups directly affected by anthropogenic activities (Hollowed *et al.*, 2000, Fulton 2001, Mace 2001). There are also a number of potential problems common to multispecies and ecosystem models: (1) they inevitably require more information than single-species models (which incur associated costs); (2) they are more likely to suffer from issues about optimal complexity (i.e. what groups and processes should be included); (3) operational objectives and monitoring indices can be hard to define for the real systems to be modelled; (4) it can be difficult to define appropriate indices to summarise model output; (5) there are often alternative hypotheses about system structure and function (Silvert 1981, Jørgensen 1994, Mace 2001). These features are particularly important when dealing with ecosystem models. However, as multispecies and ecosystem models are the only models with the potential to answer the environmental questions that single-species and pure hydrodynamic models cannot (Hollowed *et al.*, 2000, Mace 2001), the advantages of intelligent and attentive application of such models can outweigh their potential pitfalls.

One of the main criticisms aimed at ecosystem models is that their potentially immense complexity can make predictions highly uncertain (Duplisea 2000). If the model output is to be used directly to determine management actions (as in a fisheries stock assessment model), such a characteristic is clearly undesirable (Butterworth 1989). In contrast, when such models are used as a guide to possible impacts and to explore implications of alterna-

tive broad policies, this property is no longer such a problem. This is particularly true if the robustness of the conclusions is tested against a range of models incorporating different structural and parametric assumptions, representing a range of plausible alternatives about how the particular system may work. This approach permits identification of effects and policies that are robust across levels of complexity, uncertainty and underlying system and model assumptions (Reichert and Omlin 1997, Duplisea 2000, Fulton 2001). A related use for more complex ecosystem models is as a test bed for simpler models that may be used in assessment of the system, or part of it. Applying simpler assessment models to 'data' generated from complex ecosystem models is a useful way of checking the robustness of the assessment models, and of identifying the circumstances in which it may be appropriate to use them for more 'tactical' management advice. Using these approaches, ecosystem models have the potential to identify issues and causes beyond the bounds possible in single-species models, or even multi-species models in some cases. Management strategies implemented to achieve a certain goal may have the opposite effect if multispecies or ecosystem considerations are not included. For example, a simple predator-prey model, where seals are the predators and fishes the only type of prey, might suggest that culling seals will increase fish abundance for a given prey species. However, a more complex multispecies model might show the opposite effect if seals suppress other predators (or competitors) of that fish species (Punt and Leslie 1995, Yodzis 2001a). Beyond even these multispecies considerations, without the inclusion of the links between the upper and lower ends of the food web and the forces driving them, erroneous conclusions may be drawn about environmental and anthropogenic impacts, as alternative explanations and scenarios are overlooked (Steele 1998, Fulton 2001, Yodzis 2001b). For example, a decline in the biomass of a herbivorous fish may indicate overfishing, but it may equally indicate degradation of their main food reserves as a result of eutrophication (Fulton 2001).

Nutrients included explicitly in models

Tett & Wilson (2000) advised that ecosystem models should be biogeochemical, as they must conserve 1 or more elements so that the potential growth of groups can be capped. The success of ECOSIM models (Walters 1998) suggests that conservation of biomass may also be sufficient. In biogeochemical models, it is common to use the most limiting macronutrient (carbon, nitrogen or phosphorus) as the model currency and assume that the conversion of the other nutrients conforms to the Redfield ratio. However, this approach does not allow the model to adjust to spatial and temporal differences in nutrient availability (Baretta *et al.*, 1995). This inability should not present a significant problem and will not (in general) lead to large model divergences if the system state is mesotrophic to eutrophic. This is because the other nutrients should remain in excess, even if not exactly in Redfield ratios. However, when a system is in an oligotrophic state, the dependence of the model on a single macronutrient currency can be a problem (Fulton 2001). Under these conditions the identity of the limiting nutrient may well change and the preferential remineralisation of nitrogen and phosphorus will cause significant departures from the Redfield ratio, with potentially catastrophic implications for production estimates and the dynamics of transmission up the food web. The successful application of models such as ECOPATH with ECOSIM to the open oceans (Christensen *et al.*, 2000) suggests that models employing the conservation of biomass may not suffer as much from this problem. However, environmental influences are not usually present in such models, and if they are they are usually in the form of prescribed forcing functions (Hollowed *et al.*, 2000). If environmental conditions became a more integrated part of these models, then the problems observed in biogeochemical models may also appear in models like ECOSIM.

Physical scope

Another important aspect of model scope that can affect model behaviour is the physical scope of the model, and in particular its spatial resolution. Many multispecies and ecosystem models (e.g. mass balance aggregate-system models such as ECOSIM) do not include any explicit spatial representation. However, space is a vital system resource in its own right in many marine systems and, as such, the way in which it is represented can have a significant impact on model dynamics and predictions (Murray 2001, Fulton 2001). Many of the model stability issues identified in ecological and ecosystem models in the past (May 1974, Cohen and Newman 1988, Christensen *et al.*, 2000) disappear with the introduction of explicit spatial (and thus environmental and/or ecological) heterogeneity (Johnson 1997, Fulton 2001). This assertion does not apply only to biogeochemical ecosystem models (such as those employed by Fulton 2001), but extends to other types of multispecies and aggregate system models (like ECOSIM). There are many examples of these models being explicitly (through the development of ECOSPACE, Walters *et al.*, 1999) or implicitly (by separating individual model groups into inshore and offshore components; V. Christensen pers. com.) expanded to incorporate spatial partitioning. This is not to say that ecosystem models must be tied to general circulation models. Such a move would be computationally prohibitive and probably of little assistance. The box-model approach to transport processes is useful as it neglects small-scale gradients but still allows for regional differences and spatial self-structuring which, in turn, lead to the formation of distinct communities and ecological zones (Baretta *et al.*, 1995, Fulton 2001). Even when using box-models, large numbers of cells may not be necessary if they are defined such that they resolve hydrographic discontinuities, which have important ecological implications (Nihoul and Djenidi 1998). For example, Fulton *et al.*, (2001) found that an 8-box model was a good compromise between the computational intensity associated with a 59-box version and the trophic self-simplification and degradation in performance associated with 3- and 1-box versions of the same model. This is another facet of model structure in which intermediate complexity is optimal.

The work of Tett and Wilson (2000) on multispecies models helps to define limits to simplifying key underlying processes. They found that models which sacrifice large amounts of either biogeochemical or of ecological detail in favour of the other cannot adequately describe the dynamics of the plankton. Tett and Wilson (2000) concluded that to realistically capture the dynamics of marine plankton the models must be biogeochemical and include trophic webs, not simple trophic chains. These minimum requirements provide realistic restrictions and alternative pathways which stabilise the models and lead to realistic simulations of seasonal changes and other observed phenomena. The research of Murray and Parslow (1999a) and Murray (2001) arrived at a similar conclusion. They advocated the use of simpler models as aids in the development of more sophisticated models. For example, the analysis of the simpler model indicated that explicit representation of zooplankton was necessary in multispecies plankton models and that model closure had to be carefully considered (see later subsection 'Model closure'). Ultimately however, Murray (2001) stated that the extra spatial and formulation detail included in the larger model was required for fully informed system management and to allow scientists and managers to understand and consider a number of alternative scenarios. Studies comparing the performance or predictions of different types of model are useful for judging how robust general findings are to the underlying assumptions of the models (Fulton 2001). However, they are also an excellent source of information on the effects of process detail on model dynamics. Duplisea and Bravington (1999) found that the results from a length cohort model (a multispecies forecast [MSFOR] model) and a size-spectrum mass-transfer model both led to the same conclusions regarding fisheries management strategies. Thus, for the particular question of interest, the explicit process detail of the MSFOR did not

confer any advantage over the far simpler size-spectrum model. In general, size-spectrum models are a successful methodology, at least for pelagic aquatic ecosystems (Silvert 1996). However, in the context of the evaluation of management strategies, Duplisea and Bravington (1999) recommend a few modifications, such as allowing some disaggregation into functional trophic groups and including more realistic grazing terms. The popularity of ECOSIM suggests that it may also be a successful methodology. This is supported by the finding of Fulton (2001) that, with a few exceptions, ECOSIM gave the same qualitative predictions as the biogeochemical ecosystem models IGBEM and BM2. The differences observed stem mostly from the lack of spatial detail in ECOSIM, or parts of the trophic web that are poorly known. The main differences between the biogeochemical models and ECOSIM that are a direct result of model formulation are that the biogeochemical models are not as buffered against changes in fisheries as ECOSIM, but are more buffered against changes in nutrient loading. This is a reflection of the more realistic behaviour of the low to middle trophic groups in the biogeochemical models, whereas the higher trophic groups react more sensibly in ECOSIM (Fulton 2001). This is not surprising given their respective development histories and structure, but does caution against the assumption that a formulation that works at 1 level will work at every level.

Forcing functions and empirical submodels

The last facet of model formulation to have received some attention is the value and usage of empirical formulations. Empirical formulations (or empirical models as they are sometimes known) are functions that describe observed patterns or relationships in data, but without capturing real-process dynamics. These formulations have both advantages and disadvantages. They can be developed without much understanding of the phenomenon of interest, they are simple because they do not include complex causality, and they can be developed rapidly (DeCoursey 1992). All these features make empirical models attractive, and within their range of applicability they can often provide better predictive power than dynamic models (Håkanson 1997). Their limiting feature is that many domains of interest can be outside the range of applicability. This, along with the arbitrary nature of these models and the associated risk of adopting a misleading approach or false assumptions, can mean they are less than ideal (DeCoursey 1992). Within the realm of marine ecosystem models, the model development choices are more complex than empirical versus purely process models because empirical models can play a role within dynamic process models. Given that the understanding of some components of marine ecosystems are poor (e.g. the processes and forces shaping the behaviour of the benthic infauna), the use of empirical submodels for the least known parts of the system is an attractive alternative. The inappropriate use of simple forcing functions can lead to very poor model performance, while the use of a structured empirical submodel can work very well (Fulton 2001). Alternatively, the use of an empirical representation of an important process can prevent degradation of model performance. This is especially true if the causal mechanisms for the process are poorly known, or if explicit inclusion of the details of the mechanism is beyond the scope of the model or the capability of the available data or computational resources. For example, the empirically based bacteria-denitrification submodel employed in BM2 is a vast improvement over another process-based attempt at modelling bacteria and denitrification (Fulton 2001), both of which components are still poorly known in many respects.

DISCUSSION AND CONCLUSIONS

The multitude of links and processes that make up a real ecosystem mean that the ultimate effects of anthropogenic actions will probably be much wider than expected and, because of inevitable non-linearities, may even lead to counterintuitive outcomes. Ecosystem models are a prime candidate as a tool to aid in the understanding of these potential outcomes.

This does not mean that they do not have potential drawbacks associated with their own size and complexity, but careful consideration of these problems and the intelligent application of the models can avoid or minimise many of these problems. However, greater understanding of the effects of model structure and scope on model performance is necessary. This is particularly the case if we are to avoid the situation where frustration resulting from poorly structured ecosystem models, or the inappropriate use of existing ecosystem models, leads us to reject the modeling approach altogether.

Studies of the effect of model structure that have already taken place indicate that there is a humped form to the relationship between model detail and performance (Costanza and Sklar 1985, Håkanson 1997, Fulton 2001). Too much complexity leads to too much uncertainty and problems with interpretation of the model's dynamics and predictions, while too little detail results in models that cannot produce realistic behaviours. These studies have also identified some important guidelines which can usefully extend or augment those proposed in earlier works on ecological models (Wiegert 1977, O'Neill and Rust 1979, Cale & Odell 1980, Gardner *et al.*, 1982, Halfon 1983a,b, Innis and Rexstad 1983, Iwasa *et al.*, 1987): (1) Explicit physiological detail of every trophic group is not always necessary. However, the use of explicit physiological detail can be important in certain circumstances (such as oligotrophic conditions when simple assumptions about nutrient uptake and the ratio of limiting nutrients are violated). (2) If an important process or linkage (e.g. to an external web) is poorly known, or is not explicitly represented in the model, then an empirical representation should be included in its place. This can avoid introducing uncertainty without risking the degradation of performance associated with neglecting a crucial aspect of a system. (3) Some level of spatial resolution is likely to be necessary for adequate performance of the model. A 1-box model is unlikely to be sufficient, as space is itself an important and self-organising system resource. This is particularly true in systems where benthic groups are important. Moreover, there must be enough spatial resolution in the model to capture the major physical characteristics of the system. Trophic self-simplification of the trophic web (the loss of 1 or more components from the web) is often a good indicator that spatial representation is overly restricted. (4) The inclusion of a complete trophic web at the level of species is neither necessary nor desirable, but the way in which the web is handled is critical. The use of functional groups (defined based on size and shared predators and prey) is a successful means of representing the system web realistically (particularly if some age or size structure is included for the highest groups). Aggregation beyond the level of functional groups is ill-advised, and omission of the least important groups is a better strategy if further simplification is necessary. Moreover, simplifying a model web (which represents the food web of an entire system aggregated to the level of functional groups) to less than 20 to 25% of its original size is rarely beneficial, as representing the distinctions between large and small or mobile and sedentary groups may be crucial. (5) Quadratic closure of the topmost parts of the trophic web is a successful method of closing the web, regardless of its size, but there is some debate about whether this solution is ecologically justified. The explicit inclusion of the highest predators may only be necessary when they are of direct interest. (6) The form of the grazing functions used must be given careful consideration so that they contain enough flexibility without introducing extraneous detail. Holling Type I responses are unlikely to be sufficient (especially under changing conditions), but the more complex Holling type functions (e.g. Type II) may be acceptable. More sophisticated responses, incorporating more behavioural dynamics (e.g. balancing predator avoidance with the need to forage) may be required in some circumstances, but the value of their inclusion should be checked.

ANNEX 2. SHELLFISH PRODUCTION REQUIREMENT RATIO TO SUPPORT EIDER DUCKS (*SOMATERIA MOLLISSIMA*) IN THE WASH, UK

For several decades, marine biologists have attempted to estimate the prey consumption of seabird communities and to understand the role of food in determining population size and community structure (e.g. Furness 1978). Quantifying the prey harvest of bird populations requires a bioenergetics modelling approach, incorporating a consideration of the energy or food consumption of an individual bird and scaling up to the consumption of the whole population within the area under consideration. In order to generate realistic estimates of food consumption under a range of scenarios, models need to adequately represent the key relationships and simple models are unlikely to perform well under a range of diverse situations. The Centre for Ecology and Hydrology (UK) in 2003 used an energetic model to determine the capacity of The Wash shellfish stocks to support eider ducks (Caldow *et al.*, 2007). An existing behaviour-based model developed previously by CEH was parameterised to create a model of the populations of eider ducks and oystercatchers *Haematopus ostralegus* within The Wash and of the principle populations of shellfish that they exploit within it; cockles *Cerastoderma edule* and American jack-knife clam *Ensis directus*. Parameterisation was based on information gleaned from the literature and on the results of surveys of the shellfish stocks of The Wash. The output generated by the model was validated against independent data concerning: the proportion of time that birds spend feeding, their daily consumption of food, daily energy expenditure, body mass, distribution and over-winter mortality.

One series of model simulations was conducted to explore the consequences for the existing over-wintering populations of eiders and oystercatchers of changes to the total quantity of mussels available to them on commercially cultivated lays against a number of alternative backgrounds in which the other shellfish stocks were varied in the light of the historical variation that they have shown. These simulations served to explore the impact on the existing eider and oystercatcher populations of a reduction in the stock of lay mussels and whether this impact varied in relation to the abundance of other shellfish stocks available to the birds. The model predicted that the eiders consume c 600 tonnes of mussels from two cultivated lays. It also predicts that, as observed, the eiders switch in late winter to feed on *Ensis directus*. The model predictions indicated that by exploiting these two resources alone, the current peak population of c 3,000 eider ducks can be supported, with only around 4 per cent being at risk of not being supported.

ANNEX 3. CHANGES IN THE FOOD WEB OF NORTHWESTERN ATLANTIC SHELF SEAS AS A RESULT OF COLLAPSE IN COD STOCKS

In the early 1990s, Atlantic cod (*Gadus morhua*) stocks on the Grand Banks, the eastern Scotian Shelf and in the northern and southern Gulf of St. Lawrence collapsed after centuries of exploitation. Despite substantial reductions in harvesting rates of cod, there has been little recovery of stocks in any of these areas (Fanning et al., 2003).

Bundy et al. (2009) derived various ratio indicators from Ecopath analyses to investigate how the ecosystems of four northwestern Atlantic shelf areas (eastern Scotian Shelf (ESS), Newfoundland-Labrador Shelf (NFLD), northern Gulf of St Lawrence (NGSL) and southern Gulf of St Lawrence (SGSL)), had changed as a result of the cod collapses. Along with cod, many other groundfish species, such as white hake (*Urophycis tenuis*), redfish (*Sebastes* spp.), and flatfish such as American plaice (*Hippoglossoides platessoides*) suffered serious declines, as reflected by steep decreases in total landings. Meanwhile, other changes in these ecosystems were also occurring, such as large increases in seals, due to population recovery from hunting (Mohn and Bowen, 1996; Hammill and Stenson, 2005) and, at least in some areas, of forage fish, which may be due to predation release (Lilly, 1991; Bundy, 2005).

Biomass and production ratios (Table 3-1) showed that the systems shifted to different food web structure after the cod collapse, with changes in the main predators and the flows through the system. Following the decline of cod, marine mammals such as seals became the main top predators of many species during the mid- 1990s, and had profound effects over all trophic levels (top-down effects) in Newfoundland–Labrador, the northern Gulf and the southern Gulf. This, coupled with the partial re-opening of fisheries before cod stocks had recovered, may explain why cod biomass is still at extremely low levels in these ecosystems.

On the eastern Scotian Shelf, top-down predation by seals does not appear to be a significant energy flow or cause of mortality of cod, nor has there been a fishery since 1993. However, the high ratio of pelagic forage fish to total fish biomass may indicate that pelagic fish are out-competing small cod for food (small zooplankton), and larval cod may be consumed by forage fish. All systems show evidence of a potential trophic cascade following the result of the removal of the top fish predators by fishing. Thus, the changes in top-predator abundance driven by human exploitation of selected species resulted in a major perturbation of the structure and functioning of the four Northwest Atlantic ecosystems. Each represents a case of fishery-induced regime shift, to alternate states that may not be reversible in the short term.

Table 3-1 Reproduced from Bundy et al. (2009); Time trends (before and after cod stock collapse) in various ecosystem ratios and indicators from Ecopath analyses of the eastern Scotian Shelf (ESS), Newfoundland-Labrador Shelf (NFLD), northern Gulf of St Lawrence (NGSL) and southern Gulf of St Lawrence (SGSL).

Summary of changes in ecological indicators from the 1980s to 1990s for the four NW Atlantic ecosystems (+ = increase, – = decrease and ~ = no significant change). All values are t km^{-2} , with the exception of the ratios which are dimensionless. Values are the average of the 31 estimated models, with the exception of the biomass estimates for the two Gulf models. See text for further details.

	ESS			NFLD			NGSL			SGSL		
	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change	80s	90s	Direction of change
Total landings	1.73	0.49	–	1.31	0.28	–	1.89	0.48	–	2.81	1.99	–
Mean trophic level of landings	3.54	3.29	–	3.81	3.16	–	3.83	3.1	–	3.33	3.17	–
Finfish biomass	16.46	30.07	+ ^a	34.57	20.65	–	46.41	22.41	– ^b	29.95	22.55	– ^b
Planktivorous biomass + capelin	2.43	22.13	+ ^a	17.45	9.97	– ^a	22.12	17.96	~	10.24	13.02	~
Demersal biomass	12.83	7.25	– ^a	12.42	8.10	– ^a	21.78	3.85	– ^b	14.74	8.24	– ^b
Flatfish biomass	1.81	1.41	– ^a	3.28	2.79	– ^a	1.58	1.46	~	6.92	5.74	– ^b
Pelagic:demersal biomass ratio	0.19	3.13	+ ^a	1.44	1.22	– ^a	1.02	4.67	+ ^b	0.69	1.58	+ ^b
Invertebrate biomass	3.90	19.24	+ ^a	4.70	4.04	– ^a	1.69	1.48	~	3.35	3.61	~
Commercial invertebrate:demersal fish biomass ratio	0.42	3.80	+ ^a	0.53	0.69	+ ^a	0.08	0.38	+ ^b	0.23	0.44	+ ^b

^a Significant change (Mann-Whitney *U* test).

^b Significant change (Student's *t*-test).

ANNEX 4. RATIOS OF FISHERY LANDINGS (OR DERIVATIVES OF LANDINGS) TO PRODUCTION OF LOWER TROPHIC LEVELS

Heath (2005) estimated the annual requirements, or demand, of fishery landings during 1973-2000 from the North Sea, West of Scotland, and the Celtic Sea for a) omnivorous zooplankton production, b) carnivorous zooplankton production, and c) macrobenthos carnivore production. These requirements were then compared with independent estimates of the total annual production of these prey categories derived from Continuous Plankton recorder and temperature data. Production requirements of the landings were estimated by applying consumption to production ratios and diet composition data to the landed species to estimate ingestion, and cascading these calculations down through the food web to the desired level of plankton or benthos component. In the case of macrobenthos carnivores there was a direct fishery catch of these taxa, which was added to the indirect requirement due to predation by fish on benthos. The results (Figure 4-1) show systematic differences in the ratio of demand to production between the three regions, and also time trends within some regions. In principle, high ratios indicate more intense pressure on the food web from fisheries.

The zooplankton production requirement ratio indicates rising and more extreme fishing pressure in the North Sea and west of Scotland areas compared to the Celtic Sea. Pressure in the Celtic Sea appears lower than the other area due to the lack of large scale industrial fisheries for small pelagic species. The benthos production requirement ratio also indicates more extreme fishing pressure in the west of Scotland area compared to the others. Pressure in the Celtic Sea appears to be increasing due to escalating removals of high trophic level species, and Horse Mackerel. The latter has a benthic component of diet and has increased in abundance in the region due to poleward changes in geographic range.

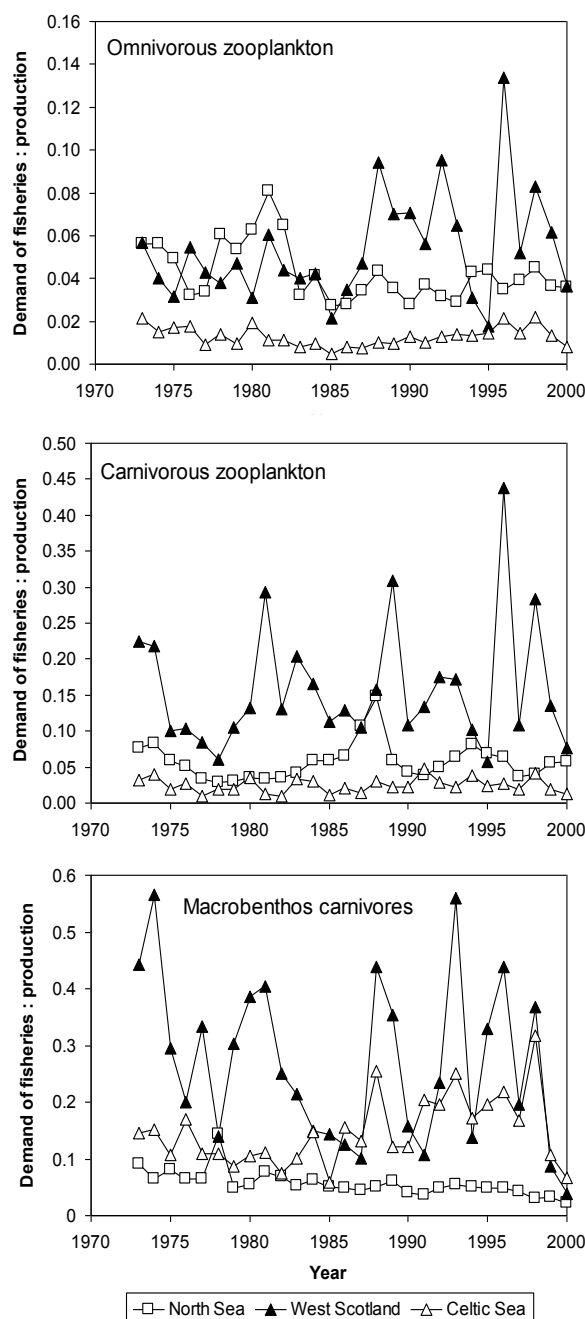


Figure 4-1 Ratios of (upper panel) the annual demand of landed fish for omnivorous zooplankton production compared to total annual omnivorous zooplankton production; (middle panel) the annual demand of landed fish for carnivorous zooplankton production compared to total annual carnivorous zooplankton production; (lower panel) the annual demand of landed fish for carnivorous benthos production compared to total annual carnivorous benthos production. In each case, demand was calculated from landings data, diet composition and consumption to production estimates, and total annual production from Continuous Plankton recorder and temperature data. Methods described by Heath 2005.

ANNEX 5. BACKGROUND INFORMATION ON THE MARINE TROPHIC INDEX (MTI)

The calculation of MTI (for a given region, nation or ecosystem) requires two types of data: the Trophic Level (TL) value of all species comprising the landings, and long time series of landings per species for which TL is available. Area or ecosystem-specific TL values can be

obtained from databases available online (e.g. FishBase, www.fishbase.org, for fishes, Sea-LifeBase, www.sealifebase.org, for other exploited marine organisms) or from local studies (i.e., stomach contents, isotope data). Time series of landings data are also largely available at various spatial levels (regional; national statistics; national statistics as reported by the Food and Agriculture Organisation, FAO; reconstructed national landings: Sea Around Us, www.seaaroundus.org). Based on the above, the mean weighted TL value of landings is calculated annually to provide an MTI time series for a given region, nation or ecosystem.

The MTI has been estimated as the mean weighted TL of fisheries landings for a cut-off TL (i.e., $TL > \text{value } 3.25$) (Pauly and Watson 2005), depending on the specific area/region/ecosystem and fishery (Pilling *et al.*, 2007). The use of a cut-off TL value for the estimation of MTI allows this index to put emphasis on the effects of fishing on the relative abundances of the high-TL organisms (mainly fish), which are generally more threatened than low TL species, the abundance of which is also more affected by other factors such as climate variability (Pauly and Watson 2005).

The original methodology has been developed further and MTIs at different scales are available from the Sea Around Us website, hosted by the Fisheries Centre of the University of British Columbia (<http://www.seaaroundus.org/>). The MTIs are calculated from data in the Food and Agriculture Organisation (FAO) database on commercial fisheries landings (which for some countries have been reconstructed to account for various aspects, notably for small-scale landings).

Interpreting the MTI

MTI addresses issues related to food web integrity, ecosystem functioning, and biodiversity loss. Although year to year variability in MTI can be related to natural change in populations and is not a key issue in MTI analysis, the existence of a significant downward trend (i.e., decline over time) in MTI signifies a reduction in the complexity of the food web, with an increasing proportion of the landings consisting of invertebrates and small, short-lived fish. The consequences of a reduction in food web complexity are twofold. Firstly, if marine food webs have evolved over time to acquire a certain distribution of biomass at different trophic levels, then human-induced changes in these relative proportions could have unexpected and potentially irreversible consequences for food web integrity. Secondly, any decline in mean trophic levels of fisheries landings cannot continue indefinitely and ultimately the overall supply of fish for human consumption will also decline.

The estimation of MTI is based on a few assumptions and has drawbacks. Firstly, when using commercial landings data it is calculated for the exploitable fraction of the ecosystem (i.e., algae, invertebrates, fish, marine mammals) and does not take into account other important biotic components of the marine ecosystems (i.e., bacteria, viruses, phytoplankton, micro-zooplankton, various marine mammals and turtles). Thus, its use assumes that the exploitable fraction is representative of the wider marine bio-diversity. This is not unreasonable since this fraction comprises a main part of the ecosystem biomass and is subject to the major drivers of change, particularly fisheries exploitation. Secondly, the TL of fish can change as fish grow and some species change trophic levels as they get older. TL can also change from year to year. Thus the use of a generic TL value might affect the MTI value and the significance and sign of the trend. This can be overcome by either using size-based TL when available (Stergiou and Karpouzi, 2002) or other trophic metrics (Jennings *et al.*, 2002). In any case, any trophic measure is still insensitive to threatened and declining species such as the basking shark and some species of skates, which often occupy low trophic levels. Finally, the MTI is sensitive to the TL values used for different species (e.g. Cury *et al.*, 2005), it might partially reflect changes in the way fishers target different species, and does not include discards or illegal landings (which however can be included should data or estimates become available). All of the above might account for the fact that the mean trophic level has been found to be

rather insensitive to fishing impacts in certain fish communities (e.g. North Sea: Jennings *et al.*, 2002).

Despite the above mentioned assumptions and drawbacks, the MTI is easy-to-estimate and apply as a ‘large-scale’ indicator of the health of both fisheries and marine ecosystems, using the full range of ecosystem trophic levels, and has been widely used for areas of different spatial scales in both data-rich (e.g., Canada, Iceland, North-Sea) and data-poor areas (e.g., Greece, Cuba, Portugal, India, Brazil, Uruguay) (Stergiou in press).

The Fishing in Balance (FiB) index

The Fishing in Balance (FiB) index is usually used in conjunction with the MTI and expresses the fishery condition in relation to a reference year. It is estimated as follows:

$$FiB = \log \left(\frac{Catch_y \times TE_y^{TL-1}}{Catch_1 \times TE_1^{TL-1}} \right),$$

where y is the year of the time-series, TL is the mean trophic level of the catch, TE is the mean energy-transfer efficiency between trophic levels (assumed to be 10%), and 1 refers to the first year in a time-series that is used as a baseline. FiB attains a value of 0 for the first year of the series and does not vary in periods in which TL and catches change in opposite directions. An increase in FiB indicates a geographic expansion of fisheries, and/or exploitation of new species, and/or eutrophication effects. A decline in FiB indicates geographic shrinkage in fisheries and/or stock collapses. FiB addresses the same questions and spatial and temporal scales are as for MTI.

ANNEX 6. ABUNDANCE OF SPECIES

Below is additional text validation the indicators of the criterion abundance of species.

Some examples of food web indicator species

Phytoplankton:

It is well established that phytoplankton chlorophyll-a increases following elevated nutrient input. For example, higher mean concentration of total nitrogen and phosphorus in the water column correlated positively with chlorophyll-a, based on a compilation from 92 countries world-wide (Smith 2006). Also *in situ* enrichment experiments (i.e. Fe) at several ocean sites consistently results in markedly elevated phytoplankton biomass (Boyd *et al.*, 2007). At the same time caution is advocated in interpreting phytoplankton abundance at larger scales as a precise measure of trophic status only. This is due to several factors such as, nutrient limitation, predation, nutrient recycling and physical mixing processes which all influence phytoplankton growth and their abundance (Thingstad and Sakshaug 1990).

Interpretation of phytoplankton indicators at higher taxonomic resolution may be strongly dependent on specific characteristics of regional seas, and no single indicator can currently be employed to adequately compare e.g. the eutrophication state between European seas (McQuatters-Gollop *et al.*, 2009). However, some recent reports from different regions can provide good examples to be further developed.

Seven phytoplankton indices have been proposed for the southern Baltic Sea (Sagert *et al.*, 2008). Among these were total phytoplankton biovolume, the percentage of diatoms and the biovolume of different size ranges of diatoms and one indicative species (*Woronichinia compacta*). This analysis was based on 1163 data sets from 15 sites covering salinities between 5-10 psu and 13 years of data. The proposed indices were shown to properly classify 3 environments with different trophic status. Especially a decrease in Diatoms, accompanied by an increase in Dinophytes and Cryptophytes, was also in accordance with observations from other marine areas. Hydrographical drivers were not important for the observed phytoplankton response in this study.

Other investigators, however, suggest phytoplankton metrics as promising, but advocate further development (Tett *et al.*, 2008, Devlin *et al.*, 2009, Tsirtsis *et al.*, 2008).

Bacterioplankton:

Bacterioplankton constitute one of the largest heterotrophic biomasses in the Sea and may be used as a proxy for the flux of matter through the microbial compartments in the food web (Azam and Malfatti 2007). Billen *et al.*, (1990) showed that bacterioplankton growth and biomass are positively related to environment trophic status, also suggesting a general resource control of the bacterioplankton community. The relationship to trophic status has also been found in other compilations over different environments (Cole *et al.*, 1988), and is also established on other scales e.g. as a co-variation with seasons and depths associated with high organic productivity (Wikner and Hagström 1999). Modelling studies also support a positive response of bacterioplankton to nutrient enrichment (Thingstad 2000).

Micro-zooplankton and meso-zooplankton:

Micro- and meso-zooplankton play a key pivotal role in marine food webs. The zooplankton community responds to human activities through bottom-up (eutrophication) and top-down (fishing) forcing (e.g. Frank *et al.*, 2005). The speed at which the micro- and zooplankton population increase responds to phytoplankton growth determines either the amount of energy

directed towards higher trophic levels in the pelagic environment or sinking to the sea floor (benthos). The speed of that response may even determine whether phytoplankton blooms occur (Irigoien *et al.*, 2005; Rose and Caron 2007).

Macrobenthos:

Macrobenthos is mainly exploited in coastal areas rather than deeper waters, however macrobenthos is a good indicator of the disturbances induced by human pressures in the benthic food web such as, deep trawling, oil exploitation, eutrophication, acidification etc (Jones 1992; Queiros *et al.*, 2006; Rosenberg *et al.*, 2004, Turley *et al.*, 2007). Macrobenthos sampling procedures and analysis protocols are well established for the shelf communities, however shelf break and in particular deep oceanic areas may require some effort to standardize the sampling procedures (Gage 2001).

Jellyfish:

Jellyfish are not directly exploited in European waters and therefore not directly manageable. However they are sensitive to human pressure through modifications of the benthic habitat where the sessile stages develop, and respond to eutrophication, changes in turbidity, over-fishing of competitors and predators (Purcell *et al.*, 2007; Daskalov 2002). Jellyfish are involved in some spectacular modifications of the food web structure and ecosystem functioning such as in the Black Sea (Daskalov 2002) and there are indications of increased abundance (Gibbons and Richardson, 2009). Most sampling methods based on nets tend to seriously underestimate their abundance (Remsem *et al.*, 2004), although abundance indexes have been extracted from routine sampling programs such as the continuous plankton recorder (CPR, Gibbons and Richardson, 2009). Furthermore, new methods based on acoustics are promising for routine assessment of jellyfish abundance (Brierley *et al.*, 2001; Han and Uye, 2009; Klevjer *et al.*, 2009).

Fish (small pelagics and demersal):

Some small pelagic (e.g. herring, sprat, anchovies) fish and demersal fish (e.g. cod, haddock) are directly exploited by human pressure and respond to management. Moreover, both exploited and non-exploited species can indirectly respond to human perturbation through by-catch or food web interactions, e.g. trophic cascades (Frank *et al.* 2005; Casini *et al.* 2008). For example, in the Black Sea the fishery-related decrease in mammals and large pelagic predators (e.g. tuna, swordfish, Black Sea mackerel) produced an increase in small planktivorous fish (sprat, anchovy) with further top-down effects on plankton. A similar process was observed in the Baltic Sea, which after the collapse of cod shifted to a sprat-dominated system with implication for the lower trophic levels (Casini *et al.* 2008). Routine sampling programs of fish are ongoing in most of the exploited ecosystems.

Top predators (tuna, sharks, marine mammals and turtles):

The abundance of top predators is a measure of the health of the food web. Some of the top predators are directly exploited and respond to management (tuna, sharks, seals and birds) whereas others are indirectly affected through bycatch (sharks, turtles and porpoises), pollution and lack of food. Furthermore the selective exploitation of top predators influences the food web structure (Bascompte *et al.*, 2005; Frank *et al.*, 2005; Rooney *et al.*, 2006). The discussion around the role of the decline of tuna and turtles in the increase of jellyfish populations (Gibbons and Richardson, 2009) indicates that their role in the food web functioning is not anecdotal. Monitoring for some species of tuna and marine mammals is relatively well developed. Some other species of tuna, sharks and turtles will need to improve the existing monitoring systems.

European Commission

EUR 24343 EN – Joint Research Centre

Title: Marine Strategy Framework Directive – Task Group 4 Report Food webs.

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Luxembourg: Office for Official Publications of the European Communities
2010 – 55 pp. – 21 x 29.7 cm
EUR – Scientific and Technical Research series – ISSN 1018-5593
ISBN 978-92-79-15656-4
DOI 10.2788/87659

Abstract

The Marine Strategy Framework Directive (2008/56/EC) (MSFD) requires that the European Commission (by 15 July 2010) should lay down criteria and methodological standards to allow consistency in approach in evaluating the extent to which Good Environmental Status (GES) is being achieved. ICES and JRC were contracted to provide scientific support for the Commission in meeting this obligation.

A total of 10 reports have been prepared relating to the descriptors of GES listed in Annex I of the Directive. Eight reports have been prepared by groups of independent experts coordinated by JRC and ICES in response to this contract. In addition, reports for two descriptors (Contaminants in fish and other seafood and Marine Litter) were written by expert groups coordinated by DG SANCO and IFREMER respectively.

A Task Group was established for each of the qualitative Descriptors. Each Task Group consisted of selected experts providing experience related to the four marine regions (the Baltic Sea, the North-east Atlantic, the Mediterranean Sea and the Black Sea) and an appropriate scope of relevant scientific expertise. Observers from the Regional Seas Conventions were also invited to each Task Group to help ensure the inclusion of relevant work by those Conventions. This is the report of Task Group 4 Food webs.

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The Mission of ICES is to advance the scientific capacity to give advice on human activities affecting, and affected by, marine ecosystems.



ISBN 978-92-79-15656-4

