Short communication

Food web indicators under the Marine Strategy Framework Directive: From complexity to simplicity?

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ABSTRACT

The Marine Strategy Framework Directive (MSFD) requires that European Union Member States achieve "Good Environmental Status" (GES) in respect of 11 Descriptors of the marine environment by 2020. Of those, Descriptor 4, which focuses on marine food webs, is perhaps the most challenging to implement since the identification of simple indicators able to assess the health of highly dynamic and complex interactions is difficult. Here, we present the proposed food web criteria/indicators and analyse their theoretical background and applicability in order to highlight both the current knowledge gaps and the difficulties associated with the assessment of GES. We conclude that the existing suite of indicators gives variable focus to the three important food web properties: structure, functioning and dynamics, and more emphasis should be given to the latter two and the general principles that relate these three properties. The development of food web indicators should be directed towards more integrative and process-based indicators with an emphasis on their responsiveness to multiple anthropogenic pressures.

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1. Introduction

Food webs describe biological communities in terms of their consumer–resource relationships, and are often referred to in terms of their structure (e.g. diversity, trophic levels) and dynamics (e.g. robustness, resilience). These two types of characteristics are often interrelated (Rooney and McCann, 2012; Thébault and Loreau, 2005), and both influence ecosystem functioning (e.g. Cardinale et al., 2006; Pfisterer and Schmid, 2002). Marine food webs are becoming increasingly important as a factor in conservation management, with particular focus on assessing and minimising ecological risk from human activities (de Ruiter et al., 2005; Sala and Sugihara, 2005). In contrast to single-species approaches, a system-level approach is attractive because both the direct and indirect effects of disturbance can be considered in a single interaction network (Raffaelli, 2005). However, considering the high functional diversity in marine ecosystems and, consequently, of the high food-web complexity, practical application remains a challenge.

Human activities cause direct, indirect, diffuse and emergent changes in food webs (Layman et al., 2005; Raffaelli, 2005). In fact,

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Table 1
Criteria and associated indicators for the MSFD Descriptor 4 (food webs).

Attribute	Criterion	Indicator	Operational indicators
Energy flow in the food web	Productivity of key species or trophic groups (4.1)	Performance of key predator species using their production per unit biomass (4.1.1)	E.g. Pup recruitment of grey seals (OSPAR, 2005)
Structure of the food web (size)	Proportion of selected species at the top of food webs (4.2)	Large fish (by weight) (4.2.1)	Large Fish Indicator (OSPAR, 2008; Greenstreet et al., 2011)
Structure of the food web (abundance)	Abundance/distribution of key trophic groups/species (4.3)	Abundance trends of functionally important selected groups/species (4.3.1)	None

events such as overexploitation (Pauly et al., 1998), pollution (Boon et al., 2002), eutrophication (Cloern, 2001), habitat fragmentation and destruction (Layman et al., 2007; Melian and Bascompte, 2002), invasions of species (Vander Zanden et al., 1999) and anthropogenic climate change (Kirby and Beaugrand, 2009; Muren et al., 2005) all pose potential threats to the structure and dynamics of food webs, acting at variable spatial scales and affecting food webs in different ways (Moloney et al., 2010). Nutrient enrichment, for example, can drive bottom-up effects, propagated up food webs from lower trophic levels (Davis et al., 2010; Rosenzweig, 1971), whereas the removal of top-predators can initiate top-down cascade effects through to basal trophic levels (e.g. Cury et al., 2003). Successfully identifying and then monitoring all these processes presents major obstacles, making the setting of management objectives and the provision of scientific advice as to how these objectives might be achieved, difficult prospects.

The use of appropriate ecological indicators is an effective method of conveying complex information to a range of different stakeholders (Jørgensen et al., 2010; Rice, 2003). In Europe, the immediate need for such indicators, particularly in the marine environment, has emerged as a consequence of recent legislative commitments, such as the Water Framework Directive (2000/60/EC), Habitat Directive (92/43/EC), and Marine Strategy Framework Directive (MSFD; 2008/56/EC). The MSFD, for example, requires that European Union Member States achieve "Good Environmental Status" (GES) in respect of 11 Descriptors of the marine environment by 2020. Descriptor 4 (D4) addresses the marine food webs: "*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*". The D4 indicators stipulated in the Commission Decision (European Commission, 2010; 2010/477/EU), following extensive review by the JRC/ICES Task Group (TG4) on food webs (Rogers et al., 2010), address three criteria related to food web structure and energy transfer between different components (Table 1). The TG4 report and the Commission Decision (European Commission, 2010; 2010/477/EU) both acknowledge that "*Additional scientific and technical support is required, at this stage, for the further development of criteria and potentially useful indicators to address the relationships within the food web*". Nevertheless, each Member State is supposed to implement the indicators currently proposed and set environmental targets for these by 2012. Here, we undertake a conceptual assessment of the food web indicators stipulated in the Commission Decision: firstly to evaluate their usefulness in determining GES in respect of marine food webs; and secondly to identify current gaps in our knowledge in order to highlight the sort of research needed to underpin future development of both the criteria and indicators used in support of the MSFD food webs Descriptor.

Even though progress in scientific understanding of food webs is expanding, few tools and methods are currently in use to derive food web indicators (Rogers et al., 2010). Since different schools of thought in food web ecology have led to a variable focus on the structure, functioning and dynamics of food webs, different approaches are currently being used to investigate food web

properties. For example, whilst data-based approaches can be applied to reveal natural processes, modelling techniques can advance our knowledge of food web theory to provide a more integrative image of the structure, functioning and dynamics of systems. Whilst an ecosystem perspective is increasingly used in fisheries management to study ecosystem responses to different stressors and to assure sustainable use of resources (Coll et al., 2008), similar holistic approaches to evaluate the combined influences of other anthropogenic stressors on food webs has received less attention to date. Unfortunately, the application of food web models to derive indicators, in general, is often constrained by the extensive data requirements for specifying parameters (Latour et al., 2003).

2. Analysis of food web indicators under the MSFD

Descriptor 4 (D4) "*concerns important functional aspects such as energy flows and the structure of food webs (size and abundance)*" (European Commission, 2010; 2010/477/EU). Whereas criterion 4.1 and its associated indicator 4.1.1 is proposed mainly as a proxy measure of energy flow within marine food webs, structural properties of food webs are covered by criteria 4.2 and 4.3 (Table 1). Since many food webs components are also relevant to other MSFD descriptors, notably Descriptor 1 (D1; biodiversity), Descriptor 3 (D3; commercial fish species) and Descriptor 6 (D6; seafloor integrity), it is likely that indicators used for D4 may also overlap those used for the other Descriptors.

In the following sections, each D4 indicator is scrutinised in terms of its theoretical background, its practicality in terms of the food web attributes the indicator purports to measure, the biological groups for which the indicator can be derived, and its specificity to a manageable anthropogenic pressure, as required by the MSFD. The setting of reference levels and quantitative target values for evaluating GES will not be discussed here, since to do so would be premature as most indicators are still under development and thus not yet operational.

2.1. Performance of key predator species determined from their production per unit biomass (productivity) (indicator 4.1.1)

2.1.1. Theoretical background

Performance can be expressed by several metrics including productivity (production per unit biomass, as suggested in the Directive), reproductive success (e.g. number of chicks fledged per pair, pup recruitment) and mortality rates. Simple theoretical pictures suggest that predator productivity reflects the assimilated energy from prey intake, and so, assuming conversion efficiency to be fixed, might be used as an indirect measure of energy flux between trophic levels. However, conversion efficiencies vary naturally depending on the quantity and quality of prey resources available to predators (Cury et al., 2011) but also their daily food ingestion rates, energy requirements and dietary plasticity (Charmantier et al., 2008; Rosen et al., 2012). Furthermore, predator productivity can vary naturally over time, displaying annual and seasonal cycles, as well as being subject to environmental influence

(Cury et al., 2008; Frederiksen et al., 2007). A key point that under-lines the limits of this indicator is that unless predators are actually food limited, then variation in predator performance will infer lit-tle about food web processes in lower trophic levels, and as such would not be appropriate for use as indicators of food web function-ing. In relation to other descriptors of the MSFD, a similar metric of reproductive success, namely fecundity rate, is proposed in the D1 indicator 1.3.1. "*population demographic characteristics*".

Top predators, such as seabirds and mammals, can be highly sen-sitive to changes in the abundance and diversity of their primary prey, whether driven by climate, exploitation, or both (Cury et al., 2011; Montevecchi, 2007; Frederiksen et al., 2007). Abrupt declines in prey abundance may result in reduced seabird breeding perfor-mance, potentially leading to declines in population size. However, such responses may be slow and non-linear (Croxall et al., 1999; Furness and Tasker, 2000; Piatt et al., 2007). Many seabird species are able to switch to alternative prey, and breeding success can recover after a few years (Asseburg et al., 2006; Chiaradia et al., 2010). So, ideally, if an indicator species was to be used, it should be a specialist, central place forager and with little alternative prey available in the environment (Danhärdt et al., 2011; Furness and Tasker, 2000).

In fisheries science, productivity can be assessed in terms of fish growth and reproductive potential (Dutil and Brander, 2003; Morgan, 2008). The practical applicability of these two variables for fisheries management has however, been questioned since both fish growth and reproductive potential can show large vari-ability and can be influenced by several factors that are often difficult to determine; these factors include temperature, growth period, food availability, and greater metabolic scope for growth and activity, etc. (Dutil and Brander, 2003). Fish are characterised by non-deterministic reproduction and the fate of their eggs largely dependent on environmental conditions (Laprise and Pepin, 1995), hence fish reproductive success is a less useful measure of top-predator performance. Alternatively, indices based on growth rate for fish communities, which utilise survey-derived species abundance-at-length data, could be more promising (Greenstreet et al., 2012).

2.1.2. Applications

In its aim to protect and conserve marine ecosystems, the OSPAR Commission has coordinated the development of Ecological Quality Objectives (EcoQO; OSPAR, 2005; Heslenfeld and Enserink, 2008). Two North Sea EcoQOs are related to the concept of indicator 4.1 (predator performance), namely "Seal population size and pup pro-duction" (OSPAR, 2005) and "Seabird survival/breeding success and the availability of key prey species" (ICES, 2008). The initial objec-tive of these indicators was to monitor the impact of anthropogenic activity on the health of the ecosystem rather than to portray varia-tion in the functioning of the food web. Consequently, the existing EcoQO's may need to be redefined if they are to be used as food web indicators. Reassessment of the targets may also be necessary to ensure that these reflect the MSFD context of sustainable use, rather than the aims of the EcoQO pilot project. Moreover, to region-alise these EcoQOs, they will need to be further tested and validated across each sub-region in order to become fully operational.

So as to evaluate fish predator performance, Borja et al. (2011) recently assessed hake productivity in the Bay of Biscay (recruits/standing stock biomass) as a potential indicator to sup-port D4 of the MSFD. Over a 30 year period, 1970–2008, increased productivity was suggested, but this result is difficult to interpret in a food web context since it could be related to variation in com-petitor pressure and/or change in the physical environment (Borja et al., 2011). Other large predators in the region are often long dis-tance migratory species and therefore even more difficult to relate to local resource availability.

2.1.3. Future directions

In order to certify that variation in predator performance provides a measure of food web functioning, the predator–prey relationships involved need to be adequately understood. The potential influences of external factors on predator performance in particular need to be identified. Species differ in their sensitiv-ity, robustness or resilience to particular changes in circumstances, their ability to resist to, respond to, or cope with changing envi-ronmental conditions varies as a consequence of their time/energy budget, dietary preferences and plasticity, and specific life-history traits, so these factors need to be taken into account when identi-fying the most suitable indicator species or set of species (Einoder, 2009). To calibrate the predator performance–prey intake rela-tionship, for example, it is important to understand the way that prey consumption is affected by changes in the abundances of all potential prey species and therefore, some information on prey abundance will be required (Asseburg et al., 2006). In turn, the vari-ability in prey consumption can be assessed from stomach flushing and stable isotope analyses to provide indirect information on the trophic structure of the food web (Chiaradia et al., 2010).

The use of additional measures associated with the predator's physiology, such as body condition and growth, could indicate if changes in performance are either food-related or the result of other confounding factors. For example, increased predation of chicks by predators would certainly reduce the reproductive success of any selected indicator species (Bonnaud et al., 2012). Reproductive success could even be directly influenced by the management of human activity, such as measures taken to reduce discarding (Garthe et al., 1996; Votier et al., 2008). In these circum-stances, changes in predator reproductive success would infer little regarding any changes occurring in lower trophic level processes.

Since climate can modify predator–prey interactions (e.g. Kirby and Beaugrand, 2009; Winder and Schindler, 2004), it is impor-tant to consider the relationship between predator performance and their prey in a changing environment to appreciate effects within the food web (Aebischer et al., 1990; Beaugrand et al., 2003). Scott et al. (2006) have suggested that linking seabird breeding success to the availability of sandeels, via the timing of stratifi-cation and the spring bloom, can provide insights into some of the mechanisms responsible for the variability in seabird perfor-mance, for example. However, the way in which oceanographic features will affect seabird breeding success does not seem generic but is likely to be geographically and species' specific. To separate the internal food web variability from influences of environmen-tal changes, variations in the indicator signals can be related to the dynamics of hydrological factors and/or other non-food related pressures, such as pollution and eutrophication. For this purpose, concurrent assessment using MSFD Descriptor 5 (eutrophication) and Descriptor 8 (concentrations of contaminants) indicators will provide complementary information on potential sources of pres-sure.

The most efficient approach to reining the complexity of factors that can influence productivity at higher trophic levels might be statistical methods that average over many species located high in the food web, rather than attempting to identify the ideal "indica-tor species". Theory for such averaged descriptions is much better developed (Rossberg, 2012), providing guidance towards disentan-gling those aspects of the population responses of top predators that do reflect the energy flux to higher trophic levels from those that do not.

2.2. Large fish (by weight; indicator 4.2.1)

2.2.1. Theoretical background

In a size-based food web, predators are larger than the prey they consume (e.g. Barnes, 2008; Brose et al., 2006) and thus larger

individuals tend to occupy higher trophic levels. However, the body size-trophic level relationships in marine systems are often transient, resulting from the exceptional scope for growth within most marine species and the variability in growth within and amongst species (Brey, 1999; Jennings et al., 2002a,b). Fish species, for example, are characterised by non-deterministic growth and often exhibit life-history omnivory, i.e. they prey on different trophic levels as they grow (Pimm and Rice, 1987). In other words, similar-sized individuals of different species may have similar trophic levels during their lifecycle. Hence, for fish communities, body size has often been suggested to describe trophic position in addition to species identity (Jennings, 2010).

Considering the size-based structure of aquatic food webs, an understanding of the interactions between body size and exploitation provides the basis for managing the effects of fishing (Jennings and Reynolds, 2007). Fishing leads to selective removal of large, high-trophic levels fish species thereby decreasing the average size of fish (Greenstreet et al., 2011; Shin et al., 2005; Shephard et al., 2012), reducing the proportional contribution of piscivorous predatory fish (e.g. Myers and Worm, 2003; Frank et al., 2011) and increasing the relative abundance of smaller species in the community, following a release from predation pressure (Shin et al., 2005; Blanchard et al., 2009). These direct and indirect effects of fishing thus alter the population and community size structure, predator–prey relationships and consequently, affect the flow of energy and dynamics within the system (Dickie et al., 1987; Barnes, 2008).

2.2.2. Applications

Size-based indicators have been widely used to demonstrate the effects of fishing on fish community structure, and the Large Fish Indicator (LFI) has been specifically developed to support the OSPAR EcoQO ecosystem approach to marine management (Greenstreet et al., 2011; Shephard et al., 2012). The LFI describes the proportion of fish biomass contributed by large individuals in the demersal fish community and is defined as the ratio between the biomass of demersal fish above a length threshold over the total fish biomass. As the name implies, the LFI is an indicator of fish community size composition and was not intended to be an indicator of fish community trophic structure. In proposing the LFI as an indicator of the proportion of high trophic level fish in the community, one suspects that some form of linear, or at least monotonic, relationship was assumed.

The threshold lengths used to define "large fish", 40 cm in the North Sea (Greenstreet et al., 2011), where the development of the index is most advanced, and 50 cm in the Celtic Sea (Shephard et al., 2012) were set with the single intent of deriving an indicator that was as sensitive to fishing pressure, and as insensitive to other drivers, as possible (Greenstreet et al., 2011; Shephard et al., 2012; Houle et al., 2012). For the characterisation of trophic structure, other length thresholds or even entirely different characterisations of population size structure may be more appropriate. Besides, the LFIs in both the North Sea and the Celtic Sea currently only consider the suite of primarily demersal fish species likely to be relatively well sampled by the survey trawl gear (Greenstreet et al., 2011; Shephard et al., 2012). Many demersal piscivorous fish consume large quantities of pelagic fish species, such as juvenile herring, sprats and sandeels (Greenstreet et al., 1997). As the LFI is currently defined, these pelagic fish prey are not included in the denominator part of the LFI calculation. Consequently, any variation in the LFI would not reflect real variation in the relative abundance of demersal fish top predators and all of their fish prey.

2.2.3. Future directions

Fishing alters community size structure resulting from potential changes in species diversity and/or trophic structure of food webs (Hiddink and ter Hofstede, 2008). Currently, the LFI does not distinguish between the relative importance of demographic changes, i.e. large, mature individuals, or changes in species composition, i.e. relative abundance of different-sized species. Whilst initially it was thought that the LFI reflects changes in the size distribution of individuals within populations (Greenstreet et al., 2011), it later became clear that this metric largely reflects changes in the relative biomasses of small and large fish species (Shephard et al., 2012). Because population-dynamical relaxation times can be considerably larger than generation times (Rossberg, 2012), this explains the absence of notable recovery of the LFI in both North Sea (Fung et al., 2012) and Celtic Sea (Shephard et al., 2012).

As currently defined, the LFI acts as an indicator of the "health" of the demersal fish community in response to variation in fishing pressure and might therefore not appear to be particularly suited as a food web indicator. To better fulfil its food web role, the LFI clearly needs critical examination and validation. Firstly, the suite of species to which it is applied could be expanded to include some of the pelagic fish species which constitute such a high proportion of the diet of demersal piscivores. Secondly, the length threshold might need adjustment to better reflect trophic structure. In its current form, the LFI is nevertheless suited to fulfil the indicator role 1.7.1 "*Composition and relative proportions of ecosystem components (habitats and species)*" of Descriptor 1 "*Biological diversity is maintained*" since it portrays variation in the relative proportions of "large" and "small" fish in the community.

Even though the development of the LFI is well advanced, its interpretation can nevertheless be difficult since the relationship between fishing pressure and community response is currently not sufficiently known (Greenstreet et al., 2011). In this respect, the development of theoretical size-structured and species-resolved fish community models can help our understanding of the pressure-state dynamics and our ability to assess the relationship between specific structural, functional and dynamical food web indicators (ICES, 2012; Houle et al., 2012; Rossberg, 2012). Moreover, the evolution of community size structure should be evaluated in relation to environmental factors since climate-induced temperature warming has already led to smaller-sized community assemblages across several pelagic trophic levels, for example in plankton (Beaugrand et al., 2010) and fish (Daufresne et al., 2009).

2.3. Abundance trends of functionally important selected groups/species (indicator 4.3.1)

2.3.1. Theoretical background

Indicator 4.3.1 is based on the rationale that changes in population status of functionally important species or groups will affect food web structure and functioning. Total biomass within one or more trophic levels, for example, is often correlated with the rate or level of ecosystem function, such as primary and secondary productivity (Naeem et al., 1994; Fox, 2005). Similar structural metrics are considered under the MSFD D1 criteria 1.1 "*Species distribution*" and 1.2 "*Population size*", but in the case of the food web indicators, attention should focus on the functional importance of abundance. In order to capture aspects of food web dynamics from these purely structural indicators, integrative approaches taking account multiple trophic levels, such as trophic biomass spectra, production:biomass ratios and predator/prey abundance ratios, could all be considered (see Rogers et al., 2010).

In practice, the use of functional groups is often favoured over indicator species since indices of species abundance are frequently subject to large inter-annual variation, often due to natural physical dynamics rather than anthropogenic stressors (de Jonge, 2007). Functional group abundance is often less variable because variability in the abundances of the group's constituent species averages

Table 2
List of criteria for selecting key species/groups for indicator 4.3.1 "*Abundance/distribution of key trophic groups/species*" as proposed by the Commission Decision (2010/477/EU).

Criterion	Indicator	Selection criteria for key trophic groups/species
Abundance/distribution of key trophic groups/species (4.3)	Abundance trends of functionally important selected groups/species (4.3.1)	(i) Groups with fast turnover rates (ii) Groups/species that are targeted by human activities or that are indirectly affected by them (iii) Habitat-defining groups/species (iv) Groups/species at the top of the food web (v) Long-distance anadromous and catadromous migrating species (vi) Groups/species that are tightly linked to specific groups/species at another trophic level

out. In this respect, indicators based on functional traits of key groups combined with information of species distributions in communities are increasingly common (Bremner, 2008; Vandewalle et al., 2010; de Bello et al., 2010), for example in assessing community response to sewage pollution (Charvet et al., 1998; Tett et al., 2008), anoxia (Rakocinski, 2012), fishing (Bremner et al., 2004) and climate change (Beaugrand, 2005). In contrast to taxonomical indicators, trait-based indicators can be easily extrapolated and therefore applied across regions (e.g. Vandewalle et al., 2010).

Whereas the indicators 4.1.1 and 4.2.1 are mainly concerned with the top of food webs, the criteria for selecting key species/groups to calculate indicator 4.3.1 stated in the Commission Decision relate to many possible food web components (Table 2). In deriving metrics to support indicator 4.3.1, greater emphasis might be directed towards the lower trophic levels of pelagic and benthic components of marine food webs so that, in combination with indicators 4.1.1 and 4.2.1, a better whole-system view might be obtained. Due to the influence of benthic processes on energy flows and nutrient cycling within food webs (Covich et al., 1999), indicators based on the structure (abundance and diversity) and processes (production and metabolism) of benthic groups can help to describe trophic functioning (Borja et al., 2008; Frid et al., 2008; Rombouts et al., 2013). Organisms located at the lower levels play an important role in the production of organic matter (primary producers) and the transfer of this energy by primary consumers through to organisms in higher trophic levels. In many coastal systems, such as in the Bay of Biscay for example, phytoplankton and zooplankton are responsible for strong bottom-up processes that control the structure and dynamics of upper trophic levels (Lassalle et al., 2011). Moreover, since these low-trophic groups have high turn-over rates, they respond rapidly to changes in environmental conditions (Beaugrand et al., 2008; Hatun et al., 2009) and the availability of organic matter (Livingston et al., 1997).

2.3.2. Applications

Despite the utility of functional traits as reliable indicator tools, they are not yet widely applied in current monitoring schemes of biodiversity, especially with respect to animal groups (Vandewalle et al., 2010). An exception are phytoplankton traits that have been proposed for defining water quality in coastal and marine systems as referred to in the European Union Water Framework Directive (WFD, 2000/60/EC) and in the MSFD (Ferreira et al., 2011). The Phytoplankton Community Index (PCI) is an example of an operational indicator based on the abundance of "life-forms" such as "pelagic diatoms" or "medium-sized autotrophic dinoflagellates" using a state-space approach (Tett et al., 2008). Using the same concept but now from a food web perspective, life-form pairs can be selected to provide an indication of changes in: (1) the transfer of energy from primary to secondary producers, e.g. phytoplankton and copepods ratio; (2) the pathway of energy flow and top predators, e.g. gelatinous zooplankton and fish larvae ratio; and (3) benthic/pelagic coupling, e.g. holoplankton and meroplankton ratio (Gowen et al., 2011).

In the context of the Helsinki Commission, similar plankton indicators have recently been proposed, also in relation to higher trophic levels. In the Baltic Sea, for example, fish body condition and weight-at-age of sprat and young herring correlate positively with copepod abundance/biomass (Cardinale et al., 2002; Ronkkonen et al., 2004). Consequently, indicators based on biomass of zooplankton and zooplankton/phytoplankton ratios are being used to assess environmentally driven changes in the food web, and the possible impact of eutrophication (HELCOM, 2012). The underlying principle of the zooplankton/phytoplankton ratio is that higher grazing efficiency implies fewer losses in the food web, less energy and nutrients passing through the microbial loop, and, consequently, more energy transferred to the higher trophic levels such as fish. An important advantage of these plankton indicators is that the proposed concepts are relatively easy transferable to other European waters. Before these indicators can be used across ecosystems, however, the fish species or feeding groups for which the zooplankton-as-food indicator is relevant will need to be identified and further research will be necessary to understand the responses of zooplankton to water quality (HELCOM, 2012).

Size-based approaches, however, may be inappropriate for assessing processes in benthic communities, since both size-dependent (e.g. predation) and size independent interactions (e.g. consumption of amorphous detritus) can co-occur, suggesting that the energy available to species of a particular size is not solely derived from smaller species in the food web (Dossena et al., 2012 and references therein). The theoretically expected even distributions of biomass over logarithmic body size can therefore arise only when top-down control of size structure dominates over bottom-up control (Rossberg et al., 2008). Rakocinski (2012) recently proposed macrofaunal process indicators for estuarine ecosystem functioning that are based on the hypothesis that body size is linked to trophic transfer (Díaz and Rosenberg, 2008) and biogeochemical processes (Lohrer et al., 2004). Before these indicators can be used for management purposes however, several practical challenges, such as the determination of operational thresholds, must be resolved (Rakocinski, 2012).

2.3.3. Future directions

Whereas the currently proposed indicator 4.3.1 is suggested to relate to a single group/species, biomass can be considered over several trophic levels simultaneously, and can therefore become an ecosystem-based indicator; for example, biomass trophic spectra, defined as the biomass distribution by trophic class (from herbivores and detritivores to top predators), have been used to assess trophic structure and functioning in relation to fishing pressure (Gascuel et al., 2005, 2011). The biomass trophic spectrum of total consumers by trophic class can be considered as the result of three processes: (i) input of biomass at lower trophic levels, i.e. production of primary consumers through grazing and recruitment of early-stage larvae feeding on phytoplankton; (ii) transfer of biomass from one trophic level (TL) to the next, i.e. predation and ontogenetic changes in TL during the life history of organisms; (iii) loss of biomass at all TLs as a consequence of fishing mortality, all natural mortality other than predation, and respiration and digestive inefficiencies (Gascuel et al., 2005). Model simulations based on this concept illustrate that exploitation can affect biomass flow

and flow kinetics in different ways according to the ecosystem control (Gascuel et al., 2011). In an ecosystem under bottom-up control (i.e. by the lowest trophic levels), for example, exploitation has a large impact on total ecosystem biomass, and may lead to strong biomass depletion, especially when the mean trophic level at first capture is low. Since community body size and trophic level are correlated in the pelagic environment (Jennings et al., 2001), size-based analysis could complement the outcomes of trophic biomass spectra analyses.

3. Discussion

A major challenge in the implementation of the MSFD is to acquire the necessary scientific knowledge of the various elements that define the state of the marine environment. In the case of food webs, where predator–prey interactions are transient in space and time (Kingsford, 1992; Kirby and Beaugrand, 2009), the study of trophic relationships requires extensive datasets (Jennings et al., 2002a,b). Currently, comprehensive datasets on the feeding ecology of many of the key species in marine food webs are insufficient, and this is especially true for species at lower trophic levels. The first requirement therefore is further extensive data collection to fill these gaps in our knowledge of food web structure and connectivity (Carafa et al., 2007, Moloney et al., 2010; Rossberg et al., 2011). The same condition holds for current indicators that are locally operational, for example the North Sea OSPAR EcoQO's, but where the trans-regional applicability still needs to be demonstrated. In any case, the practical utility of information derived from certain biological components should not be ignored because of low data availability and/or insufficient knowledge; so ideally, management bodies should adjust monitoring programmes to fill in data gaps based on scientific advice concerning the theoretical advances in food web ecology (de Jonge, 2007).

Whilst the current criteria and indicators of Descriptor 4 (D4) under the MSFD can be informative on trophic functioning, they are, at their current state of development, possibly insufficient to assess whether marine food webs in European waters really are at, what the MSFD defines as, "Good Environmental Status" (GES). The proposed indicators, in particular those based on abundance and biomass, can inform on the structural properties of food webs but they may provide only partial information about its functioning. Current trophic criteria/indicators mostly focus on a single trophic level (i.e. a key component of the food web), thereby failing to consider complex trophic interactions and whole-system energy flow; indicator 4.1.1 for example, assumes that attributes of key predators integrate transfer efficiencies of underlying trophic levels and thus are used to infer the functioning of the whole system. In reality, dynamics of key predators are often influenced by other intrinsic and extrinsic factors than food availability alone, the main assumption underlying this indicator.

The assessment of food webs, therefore, should move beyond the use of species and population indicators since they are unlikely to reflect the inherent complex dynamics of the system. Moreover, by focusing on only one or a subset of food web properties, key information on the human impacts may be missed (O'Gorman et al., 2012) and the interpretation of GES for food webs may be misleading. An awareness of principles relating dynamics to the structure of food webs is necessary to inform conservation and management, emphasising the need for an ecosystem perspective (Sala and Sugihara, 2005). Hence, the development of criteria for D4 should be directed towards more integrative and functional indicators that consider (1) multiple trophic levels or whole-system approach (i.e. ecosystem-based indicators), (2) processes and linkages, e.g. trophic transfer efficiencies, connectance and material

cycling, and (3) the dynamics of food webs in relation to specific anthropogenic pressures.

In relation to food web dynamics, the resistance and resilience of a system to external pressures can suitably assess the state and/or health of an ecosystem (Costanza, 1992), as was also suggested in criterion 1.7 "Ecosystem structure" of the Commission Decision (European Commission, 2010; 2010/477/EU). In this context, theoretical models can be used to measure the resistance and resilience of food webs to multiple pressures whilst maintaining its 'normal' functioning, cfr. GES (Fig. 1). Sala and Sugihara (2005) further suggest integrating ecological succession in marine conservation but this approach can be complex since there is currently little known about the rates of recovery after disturbances. Other useful suggestions for criteria/indicators related to the functioning of food webs were evoked by the TG4 (Rogers et al., 2010), but, probably because of their currently low state of development, not retained in the Commission Decision (European Commission, 2010; 2010/477/EU).

Sustainable ecosystem-based management calls for a thorough understanding of cause and effect relationships between human pressures and ecosystem states (Jennings, 2005; Probst et al., 2012). Ultimately, the choice of the "best" indicator to support the achievement of GES will depend on several selection criteria and evaluation processes, and conceptual frameworks to facilitate decision making have been discussed in the literature (e.g. Borja and Dauer, 2008; Kershner et al., 2011; ICES, 2012 and references therein). Key amongst these selection criteria is the responsiveness of the indicator to a particular disturbance so that appropriate and effective management action can be taken. Since overexploitation of large fish is a top-down pressure, the direct impacts will be most efficiently assessed by indicators 4.1.1 (predator performance) and 4.2.1 (proportion of large fish), which are calculated using high trophic level groups. In addition, indirect effects of fishing on lower trophic levels, e.g. trophic cascades, could be evaluated by indicator 4.3.1. In contrast to top-down pressures, direct impacts from bottom-up, caused by pollution and eutrophication, will be expressed by rapid changes of abundances and distribution of lower trophic levels (indicator 4.3.1). However, the impacts of species invasions, another important pressure on food webs, will be more difficult to predict, detect or measure (Vander Zanden et al., 1999) since they can affect all trophic levels. Moreover, when multiple pressures act simultaneously, as is often the case in natural systems, the direct and indirect effects on food webs can be even more difficult to identify (Moloney et al., 2010).

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 through non-linearities in the system may even lead to counterintuitive outcomes (Fulton et al., 2003; Rogers et al., 2010). For example, nutrient enrichment can lead to non-linear responses in macro-invertebrate production and diversity, where production peaks at moderate levels of enrichment but will subsequently decrease with further enrichment, a phenomenon termed the enrichment paradox (Rosenzweig, 1971). Moreover, climate and hydrodynamics can further influence food web components, often with divergent responses (e.g. Link et al., 2010; Woodward et al., 2010). Climate warming, for example, has already altered trophic structures and dynamics and consequently, the rates of key ecosystem processes, such as nutrient and carbon cycling (e.g. Dossena et al., 2012 and references therein).

As the rates of anthropogenic climate change and exploitation accelerate, additive and synergistic interactions between them are becoming increasingly important to the dynamics of marine ecosystems and the sustainability of marine fisheries (Harley and Rogers-Bennett, 2005; Kirby et al., 2009). As an example, fish exploitation can trigger a switch from internally generated to externally forced population fluctuations, and so, the population dynamics will become more responsive to environmental variability
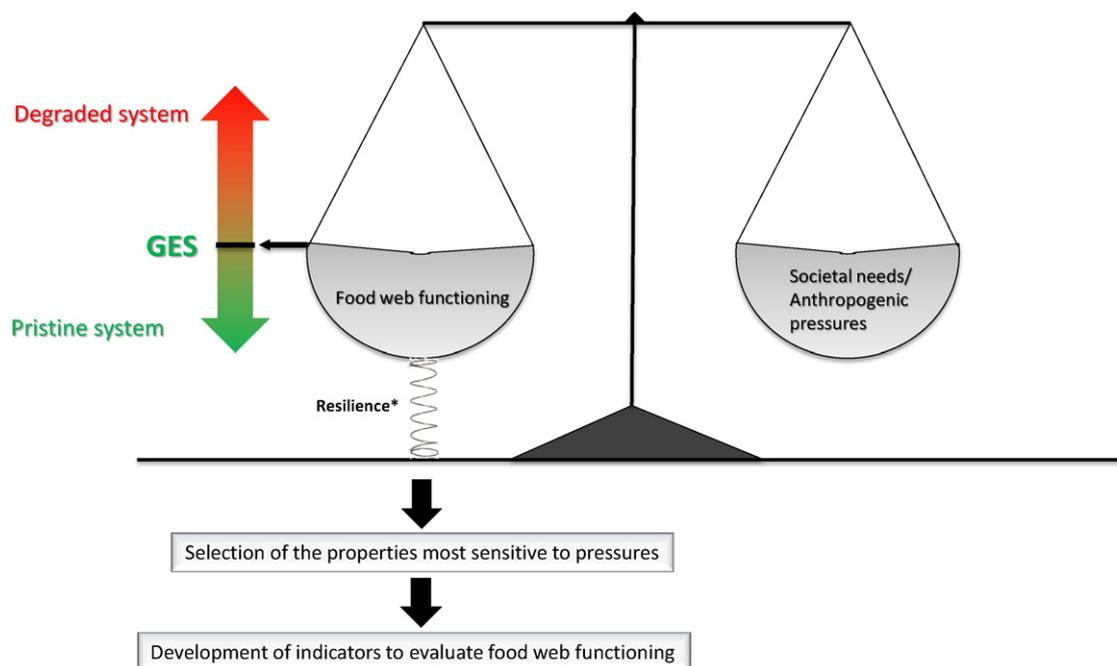
Fig. 1. Conceptual diagram to illustrate the relationship between food web functioning and anthropogenic stressors as a framework for developing food web indicators. *Resilience is defined here as the capacity of an ecosystem to return to the pre-condition state following a perturbation, including maintaining its essential characteristics taxonomic composition, structures, ecosystem functions, and process rates (*sensu* Holling).

(Hidalgo et al., 2011). Other synergistic consequences of climate change and overfishing, such as changes in the productivity and structure of marine ecosystems, have already taken place. In the North Sea, for example, it may be that marine ecosystem resources cannot be managed to reverse current climate and human-induced changes and it has been suggested that rather than attempting recovery, management goals reflecting current ecological regimes should instead be set (Kirby et al., 2009).

Before responses of food webs to change can be anticipated, they need to be both unravelled, i.e. to identify appropriate levels of detail, and rewoven, i.e. to capture the essential elements for simplification and generalisation (Moloney et al., 2010). Theoretical and empirical models may then help to identify potential impacts and elucidate key properties that should be monitored, thereby promoting the development of more effective and comprehensive operational food web indicators (Fig. 1). The combination of theoretical modelling with empirical analysis offers the potential for testing theoretical considerations whose findings may then be used for practical ecological and management applications, and policy strategies (de Jonge, 2007). The complementary use of empirical and modelling approaches to derive population, community and ecosystem indicators is key to the development operational food web indicators for ecosystem-based management in the marine environment (Rombouts et al., 2013). To accommodate the difficulty of integrating across so many levels of organisation, however, requires new information as well as new methods (Moloney et al., 2010).

4. Conclusion

By considering the theoretical background and applicability of the proposed criteria/indicators of D4 under the MSFD, we tried to highlight the current knowledge gaps and difficulties in defining GES for food webs. The existing suite of indicators in the Commission Decision gives variable focus to the three important properties of food webs: structure, functioning and dynamics, and we suggest that more emphasis should be given to the latter two. In any case,

the sheer complexity of marine food webs makes them difficult to predict and this creates a key challenge for conservation management (Link et al., 2010). Hopefully, this paper will stimulate the further development of existing food web indicators and advances in food web theory for its application in a management context.

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