

Linking marine ecosystems with the services they supply: what are the relevant service providing units?

FIONA E. CULHANE ^{1,5} CHRISTOPHER L. J. FRID,^{1,2} EVA ROYO GELABERT,³ LYDIA WHITE,^{1,4} AND LEONIE A. ROBINSON¹

¹Department of Earth, Ocean and Ecological Sciences, University of Liverpool, Nicholson Building, Liverpool L69 3GP United Kingdom

²Griffith School of Environment, Griffith University, Brisbane, Queensland 4222 Australia

³European Environment Agency, Kongens Nytorv 6, 1050 Copenhagen, Denmark

⁴School of Biological Sciences, Medical Biology Centre, Queen's University Belfast, Belfast BT9 7BL United Kingdom

Abstract. Marine ecosystems support supply of ecosystem services (ESs) through processes and functions carried out by diverse biological elements. Managing sustainability of ES use requires linking services to the parts of ecosystems supplying them. We specified marine service providing units (SPUs) as plausible combinations of a biotic group (e.g., bacteria, seabirds) with an associated major habitat (e.g., sublittoral sediment). We developed a network model for large marine ecosystems, documenting 2,916 links between 153 SPUs with 31 services. Coastal habitats and their taxa accounted for 48% of links, but all habitats with their taxa contribute to at least 20 ESs. Through network analysis, we showed some services link to certain key habitats, while others are less clearly defined in space, being supported by a variety of habitats and their taxa. Analysis highlighted large-scale flows across marine habitats that are essential in underpinning continued supply of certain ESs, for example, seed dispersal. If we only protect habitats where services are used, we will not fully protect the supply of services reliant on mobile taxa moving between habitats. This emerged because we considered habitats and their taxa together. We recommend using combinations of habitats and taxa as SPUs when informing marine ecosystem management and conservation.

Key words: biodiversity; conservation; ecological connectivity; ecosystem service; mobile species; network analysis.

INTRODUCTION

The ecosystem service approach, which recognizes the contribution of the ecosystem to human well-being, has become part of the move toward trying to better document and understand sustainable use (Costanza et al. 1997, Mace 2014). Ecosystem services are the link between underlying ecosystem structures, processes, and functions and derived economic and social values and benefits (Quintessence 2016). The integrity of the ecosystem underpins the generation of services and modifications to ecological structures and systems can thus affect the capacity of the ecosystem to supply ecosystem services (Müller and Burkhard 2007, Quintessence 2016). Accordingly, information on ecosystem state should be able to inform us about potential changes to supply of services (Burkhard et al. 2012). For example, Mace et al. (2015) showed there was a high or moderate risk to the supply of 9 out of 10 services provided by UK ecosystems due to the current impacted status of the habitats supplying them. On a global scale, the capacity of ecosystems to supply services is known to be declining and assessments are required that can more fully capture the state of service supply (MA (Millennium Ecosystem Assessment) 2005).

In marine systems, progress with the ecosystem service concept has been made in: developing typologies of marine ecosystem services (e.g., Beaumont et al. 2007, Böhnke-Henrichs et al. 2013, Liqueste et al. 2013); the identification of indicators of service supply and use (Hattam et al. 2015);

the assessment, quantification, and valuation of services, including from particular habitats (Arkema et al. 2015, Reddy et al. 2016), functions (e.g., carbon storage; Lavery et al. 2013), or taxa (e.g., oyster reefs; Grabowski et al. 2012). At the same time, while the number of studies on marine ecosystem services is increasing, the number of services considered remains limited (Liqueste et al. 2013, Mace et al. 2015, Garcia Rodrigues et al. 2017). Assessments are mostly based around easily valued services, for example, those exploited through commercial fisheries or related to coastal protection, while studies on ecosystem services supplied by open oceans or deep-sea habitats are lacking as most studies consider coastal areas.

We set out to fully document the links between marine ecosystems and the services they supply, to allow for a more comprehensive consideration of the ways in which marine taxa and habitats underpin service supply, in marine conservation and management. In doing so, we considered what should be the relevant ecosystem “service providing units” (SPUs; Kremen 2005, Luck et al. 2009, Kontogianni et al. 2010) that could appropriately define the links between state of the ecosystem and supply of marine services. We considered four key aspects in defining these. First, we accounted for the need to fully capture the biodiversity that provides services through its functioning. Ultimately, it is the individual organisms within habitats that are responsible for the structures, processes, and functions that underpin service supply. For example, sediment stabilization and erosion control can be contributed to by seagrasses, tubes of benthic invertebrates, and films of microphytobenthos (Friedrichs et al. 2000, Aspden et al. 2004). It may be convenient to link erosion control supply to a habitat, for example, saltmarsh,

but this does not recognize the contribution of all the individual groups to its supply (and see the third aspect). Second, we considered the need to reflect the fact that biota can vary in their functioning between habitats and locations. Both anchored and floating clumps of macroalgae can provide habitat for juvenile fish and produce oxygen, but only those forming belts around the coast will also contribute to wave attenuation and flood control (Vandendriessche et al. 2007, Smale et al. 2013). Thus, it is also important to recognize the specific habitat where a service is supplied, as some services, like flood control, are location specific. In addition, while some services are supplied by sessile organisms (e.g., erosion prevention), others are “mobile-agent-based” services (e.g., pollination and seed dispersal), supplied by organisms that rely on resources beyond the local scale where the service is realized (Kremen et al. 2007). Thus, we also need to recognize the reliance on multiple habitats of mobile species in protecting the services they supply. Third, we wanted to be able to account for the fact that there are differences in vulnerability to human pressures between taxa (due to differences in the sensitivity of the biota considered) and between habitats for the same taxa (due to differences in exposure to pressures based on location and the influence of abiotic conditions on resilience). For example, epifauna are more vulnerable to fishing pressure than infauna because they are more exposed to the pressure, while deep-sea biota are less exposed than those in shallow seas but are more sensitive because they are less resilient (Clark et al. 2016). Assessment of the sustainability of service supply in relation to human activities is needed (Hooper et al. 2017). Establishing the links between ecosystem state and service supply, using SPUs that recognize the locational and taxa-specific differences in vulnerability to human pressures, is a first step in doing so. Finally, we set out to make the classification of SPUs relevant to the units used in ecosystem state assessments, such that data collected on marine ecosystem state could be interpreted later to assess state of service supply. We used the large regional seas of Europe as our test cases for this approach, where the state of marine ecosystems is reported on through various policy instruments (such as the EU Marine Strategy Framework Directive (MSFD) (EC 2008), the EU Habitat’s Directive (EC 1992), and regional seas conventions (e.g., OSPAR 2010), in terms of broad habitat types (e.g., the water column, seafloor habitats), functional groups of large taxa (e.g., marine mammals), species, or specific habitats.

The aim of this study was to systematically document the types of taxa and their habitats required to supply a service, that is, the SPUs, for European marine ecosystems, which would fulfill the four criteria set out above. In doing so, we established a typology of marine ecosystem services and a categorization of marine ecosystem components and then identified the links between each pair of these (e.g., “waste treatment” with “infauna in sublittoral sediment habitats”).

Accounting for all linkages between the ecosystem and the services supplied generates a complex set of interactions. In order not to lose sight of the complexity of the system as a whole, we took a network analysis approach, as network science focusses on the connections between parts of a system rather than on individual parts themselves (Mitchell 2009). Network analysis is a mathematical tool used across

disciplines (e.g., criminal intelligence networks [Sparrow 1991]; food webs [Dunne et al. 2002]; human impacts on ecosystems [Knights et al. 2013]) to explore complex sets of connections and can help to interpret properties of the system described (Poisot and Gravel 2014). For example, connectance reflects how many of the possible interactions occur in a system and the number of links can indicate how specialized or generalist an interaction is (Blüthgen et al. 2006, Poisot and Gravel 2014). The potential of using such an approach to fully explore ecosystem-component–ecosystem-service systems has previously been recognized (Harrison et al. 2014, Quintessence 2016) and here we show what this can reveal in terms of how well the ecosystem components as SPUs fulfill key criteria to reflect ecosystem service provision.

MATERIALS AND METHODS

We selected the four marine ecosystems described in the EU MSFD (the Mediterranean Sea, the Baltic Sea, the Black Sea, and the northeast Atlantic Ocean [EC 2008]) to frame the network in terms of the relevant links between marine ecosystem components and services to include. Typologies for ecosystem services and ecosystem components were then developed with relevance to the assessments undertaken in these large regional sea ecosystems.

Typology of ecosystem services

The typology used here is based on the CICES (Common International Classification for Ecosystem Services, version 4.3; Haines-Young and Potschin 2013) typology of ecosystem services, a broad, hierarchical framework that can work across biomes, but can also be applied to specific situations or environments. CICES was developed primarily for the terrestrial system but is widely used, for example, as the EU ecosystem services “reference” typology (Maes et al. 2016). The typology consists of provisioning, regulating and maintenance, and cultural services, and all services are deemed to have at least one direct human benefit. From this, we defined a marine-adapted CICES typology (see further elaboration in Appendix S1: Table S1) that includes, in brief, services fulfilling the criteria: (1) service underpinned by ecological structures, processes, or functions; (2) contribution of marine ecosystem components is not marginal or trivial when compared to terrestrial and/or freshwater ecosystems, or to abiotic elements. These criteria were important in constraining the analysis to focus on services linking closely to the state of marine ecosystem components.

Ecosystem components

Ecosystem components were specified here as combinations of habitat types with specific biotic groups, for example, “fish in oceanic waters.” An association between a biotic group and a habitat reflects the potential for the biotic group to spend some or all its life in that habitat, be it embedded within the habitat, for example, sessile benthic invertebrates, or a highly mobile species, for example, seals feeding temporarily in a habitat. The typology also considers how services are used, for example, “whales on littoral sediment” represents whale carcasses that can be used for

services such as scientific research. Associating biotic groups (including mobile species) with habitats also allows the biotic group to be linked to a spatial unit from where the ecosystem service is derived. Individual, or combinations of, ecosystem components make up the SPUs.

Habitat types were derived from the EU MSFD predominant habitat types (EC 2011) and the MAES (Mapping and Assessment of Ecosystem Services) marine ecosystem types (Maes et al. 2016). Following these, benthic habitats are delineated by substrate and depth, and pelagic habitats by salinity and depth (see Appendix S1: Table S2 for physical properties of habitats). We further assumed that all littoral and shallow sublittoral habitats are photic, while all other benthic habitats are aphotic, but acknowledging that light conditions will actually depend on the turbidity of the water, and this will vary per locality. This division reflects the major ecological distinction between these habitats and the biotic groups that exist within them and thus the services that would be provided.

Biotic groups were based on the functional groups of the MSFD (EC 2011) but modified to account for differences in how groups supply services (Appendix S1: Table S3). For example, seals (which are sometimes hunted [Ministry of Agriculture and Forestry 2007]) may supply services differently from whales (which are not hunted in the seas considered here), thus marine mammals were split into two groups (seals and whales). Bacteria are not monitored but are important contributors to the supply of services, thus are explicitly contained within the typology.

A total of 153 ecosystem components were established given the association of biotic groups with habitat types, with the associations based on ecological knowledge and literature (associations can be seen in the left-hand part of Fig. 3; see Culhane et al. 2014: Section 3 for full details).

Ecosystem component to ecosystem service linkages

A binary, bipartite, and unidirectional network matrix was created linking ecosystem components with the ecosystem services they supply. A bipartite matrix consists of two types of nodes (in this case, components and services), and a node can only link to a node of the other type (Flores et al. 2016). The network links illustrate an interaction, an ecosystem process or function, which can lead to the generation of an ecosystem service. No link indicates the component does not contribute to the supply of a service. The type of interaction (process or function) varies between services or between components within a service and this depends on how the ecosystem components generate the service. For example, the interaction between fish and supply of seafood from wild animals involves the accumulation of biomass, while the interaction between epifauna and waste removal involves filtration.

In some cases, service generation is decoupled from the current state of the ecosystem but is linked to some historical state, for example, for cultural heritage, where an interaction could refer to a historical activity such as whaling. All interactions, regardless of the process or function involved, and regardless of whether current or historical state is relevant, are considered here to be direct links of ecosystem state to ecosystem services. Specific indirect interactions are also included where a habitat supports or is essential to a biotic

group directly contributing to a service in another habitat. Individuals in the biotic groups supplying a service may move in and out of the relevant habitat where the service is supplied. For example, whale-watching from tour boats may occur in coastal areas but the whales found in oceanic waters may be the same individuals (Fig. 1). An interaction is shown for this service both for whales in coastal areas where the service is directly supplied and for whales in oceanic habitats, because the state of whale populations in these habitats is relevant to the supply of the service.

Links included were those known to have at least one current application in the sea areas assessed. The full matrices between marine ecosystem services and marine ecosystem components can be found in Culhane et al. (2018), and details of interactions can be found in Culhane et al. (2014: Annex I). All interactions were identified using a combination of literature, other information sources (e.g., websites), and expert knowledge.

Network properties

Properties of networks calculated were connectance and modularity. Connectance was calculated at the ecosystem component level (habitat-biotic group) as the number of links per node (which could be either an individual ecosystem component or a service) divided by the total number of possible links in the matrix (after Knights et al. 2013, Dorman et al.

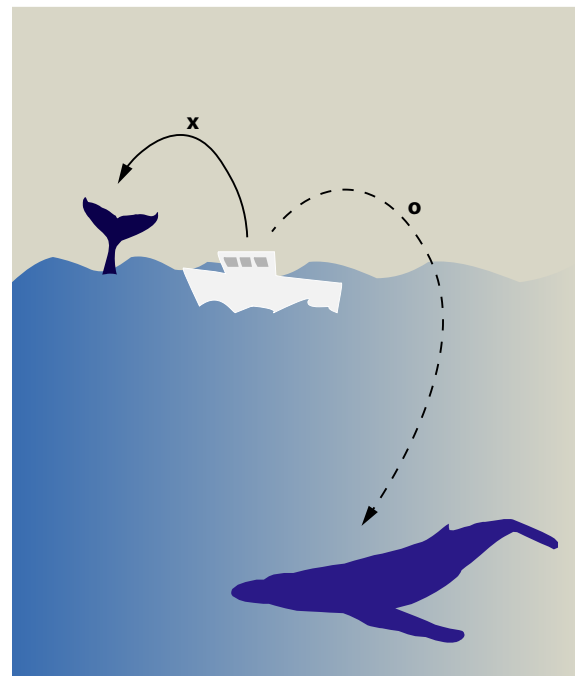


FIG. 1. Illustration representing direct and indirect interactions included in the network. For the service whale-watching, a whale in coastal waters potentially spotted by whale watchers is represented by a direct link (solid line, x). A whale in another habitat, such as deep benthic habitats, is not accessible to whale watchers and therefore does not interact directly. However, this whale may be the same individual or from a connected population to those seen by whale watchers and is represented by an indirect link (dashed line, o). An indirect link is given where a habitat supports or is essential to a biotic group contributing to a service elsewhere (in another habitat).

2017). Connectance is presented for the individual ecosystem components with the greatest connectance, as well as the total connectance summarized per biotic group, per habitat, and per ecosystem service. Greater connectance is found for ecosystem components or services with comparatively more links in the system (Appendix S1: Fig. S1); the connectance to ecosystem service supply of ecosystem components, habitats, and biotic groups was explored on this basis. Modularity identifies subsets of nodes in the network with greater likelihood to interact with each other than with other nodes (Beckett 2016). This was based on Newman's modularity measure and uses simulated annealing to maximize weighted bipartite modularity. It was calculated at the biotic group and the habitat level using the `LDTR_LPA_wb_plus` function (Beckett 2016) in the R package `bipartite` (Dorman et al. 2017). This was used to explore groupings of biotic groups or habitats, underpinned by the individual ecosystem components, in terms of how they supply ecosystem services.

RESULTS

Number of services

Of the 33 generic marine ecosystem services considered (see Appendix S1: Table S1), 31 can be supplied in at least one European regional sea. The services not currently being supported were associated with production of marine biofuels, which is only at the experimental or trial stage, and thus, these services were not considered further. Of the 31 existing services, evidence suggests that there is the potential for supply for these to originate from between 2 and 153 of the 153 broad European marine ecosystem components identified.

At the ecosystem component level, the highest numbers of services that are supported was 27, by epifauna in shallow sublittoral rock and biogenic reef habitats, with the lowest numbers of services being supplied by any one ecosystem component being 11, from (beached) whales on littoral sediment.

All biotic groups and habitats can contribute to more than one-half of the ecosystem services. For the biotic groups, macroalgae and epifauna contribute to the greatest number of services overall, followed by macrophytes and infauna (Fig. 2a); bacteria, followed by whales and microphytobenthos, contribute to the fewest. For habitats, there is a clear decrease in the number of services that habitats can potentially supply moving from the coast (the littoral and shallow sublittoral benthic habitats) to the deep sea, where abyssal habitats contribute to the least (Fig. 2b).

Connectance

Out of a possible 5,049 potential matrix interactions (total number of cells in the matrix), 2,916 links were identified between ecosystem components and services. Connectance of each individual ecosystem component, biotic group or habitat is a proportion of the total potential interactions, thus values of any one of these are low but here we are interested in the relative differences between them. Indirect links made up 3% of all interactions and were formed by whales, seals, reptiles, birds, and in one case, macrophytes.

Ecosystem components with the highest levels of connectance were epifauna, macroalgae, macrophytes, and

infauna, in littoral and shallow sublittoral benthic habitats, and epifauna in shelf sublittoral habitats (Fig. 3). The interactions of the top contributing ecosystem components (16 of 153) make up approximately 14% of the interactions found.

Summarizing the connectance of the underlying ecosystem components by biotic group, fish had the highest connectance, followed by cephalopods, epifauna, whales, and bacteria, respectively (Fig. 2a). All the mobile groups, particularly fish and cephalopods, but also whales, seals, birds, and reptiles, had high to moderate connectance, in part because of indirect links. Microphytobenthos had the lowest connectance, followed by phytoplankton and zooplankton. Macroalgae and macrophytes, which can contribute to high numbers of services, show comparatively low connectance, while bacteria and whales showed the opposite pattern.

Connectance was greatest for shallow sublittoral, followed by littoral habitats. Coastal and variable salinity water habitats followed next, and generally, connectance decreased with distance from the coast and depth (Fig. 2b). While all habitats other than littoral rock and biogenic reef supported some indirect links, for most these made up <3% of interactions. But, for deeper habitats, indirect links were slightly more important, particularly in upper bathyal habitats.

Cultural services showed the greatest degree of connectance to ecosystem components and provisioning the least (inset Fig. 4). Thirteen services have higher connectance because they are contributed to by all, or almost all, ecosystem components: these include a number of cultural (e.g., educational services) and regulating (e.g., global climate regulation) services. Other services have lower connectance because they are supplied by specific ecosystem components: these include a number of provisioning services (e.g., aquaculture from plants and algae, which is only supplied by macroalgae in variable salinity and coastal waters) and regulating services (e.g., flood protection, which is only supplied by macroalgae, macrophytes, epifauna, and infauna in littoral and shallow sublittoral habitats). Some services have a higher proportion of connectance made up of indirect links, in particular, raw materials (32%), seafood from wild animals (24%), and seed and gamete dispersal (39%), where mobile biotic groups that move between habitats, such as fish, whales, reptiles, and birds are important contributors.

Network modularity

Although there was a high degree of overlap, modularity indicated three sets of biotic groups and four sets of habitats that share connections in terms of how biotic groups and habitats supply services (Figs. 5 and 6). Across both sets of modules (related to biotic groups and habitats), two broad groups of services could be identified. The first group was composed mainly of those contributed to by all or almost all components (modules B.A, Fig. 5 and module H.D, Fig. 6) and included a range of diverse services from regulation and maintenance to several cognitive type cultural services. The main contributions from bacteria and more remote habitats—deep-sea benthic habitats, oceanic waters, and ice—are to these services. A second broad group of services was mixed but had in common that they are supplied more in habitats that are accessible to people (H.A–C, Fig. 6). Within this group, mobile biotic groups were associated with services

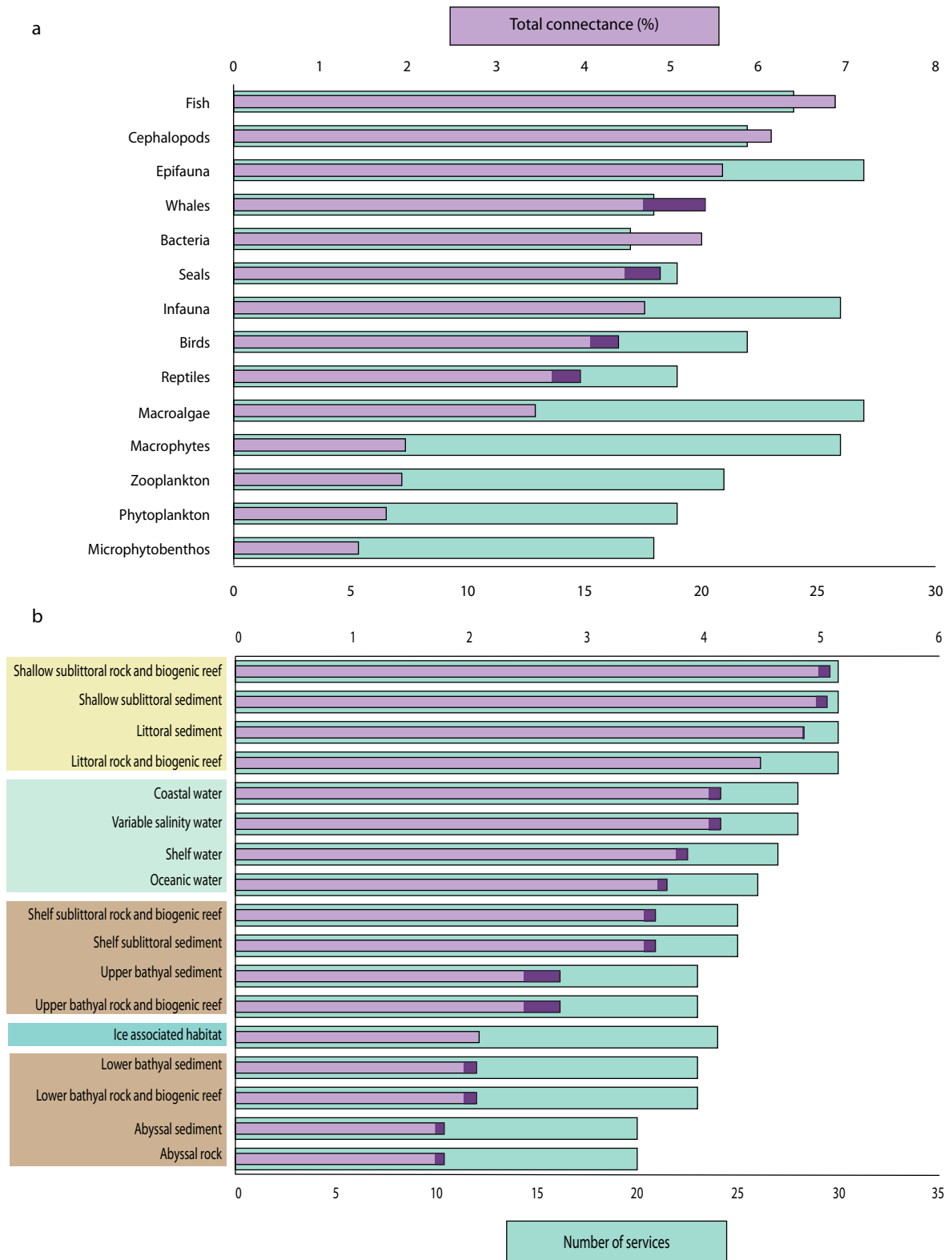


FIG. 2. Total connectance (purple bar) and total number of services contributed (blue bar) to by (a) each biotic group and (b) each habitat. Connectance was calculated as the number of links per ecosystem component divided by the total number of potential interactions and is presented as a proportion of the total (percentage). Darker colored portion of connectance bars represents the proportion of indirect links. Colors in panel b indicate broad habitat types: yellow for photic benthic; brown for aphotic benthic; light blue for pelagic; dark blue for ice.

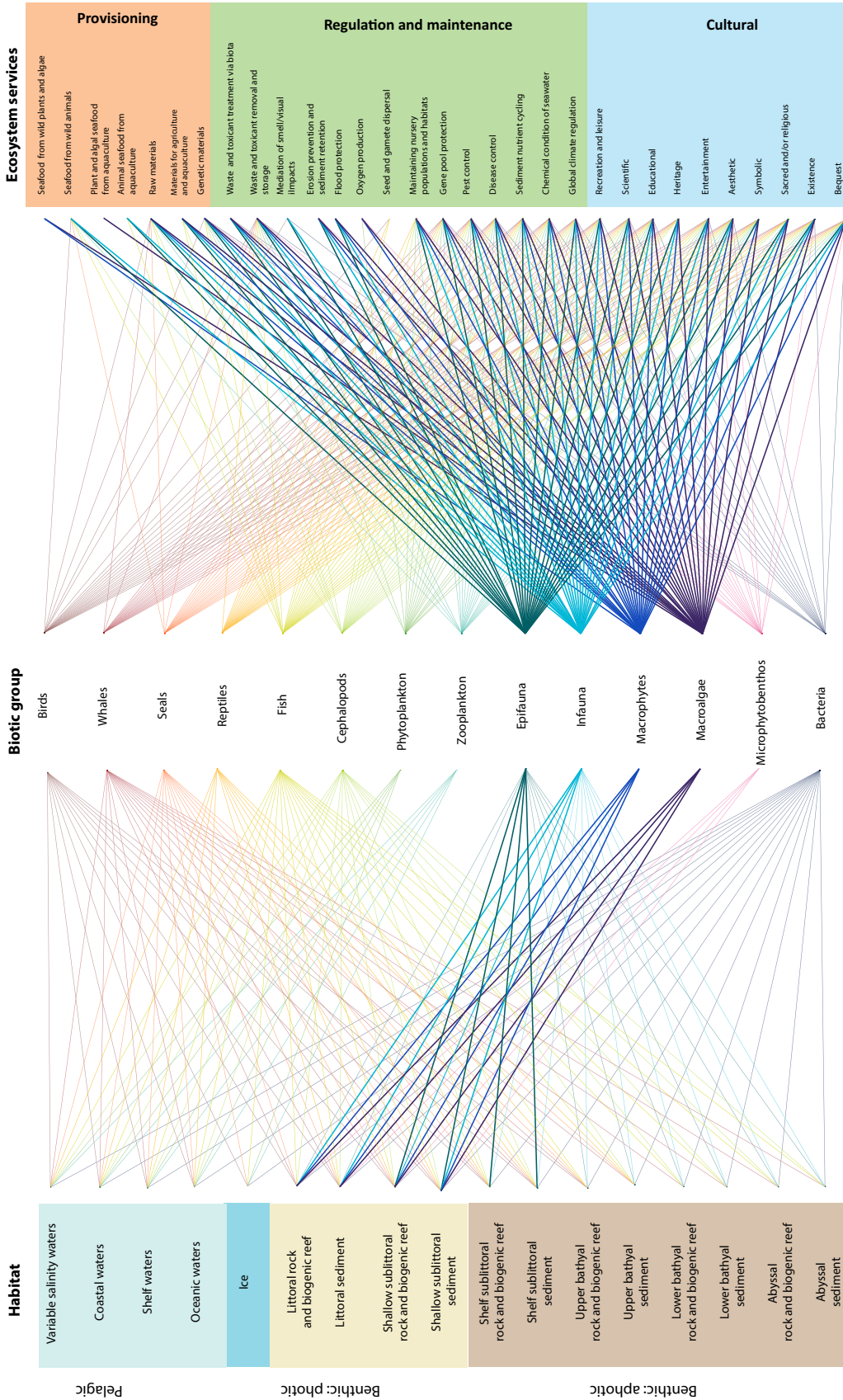


FIG. 3. Full network of ecosystem components (association of biotic groups with habitats) to ecosystem services with highest connectance and the services they can supply in European seas (boldface type). On the left-hand side, each link represents one "ecosystem component," giving a total of 153. On the right-hand side, each line represents a link between a biotic group and an ecosystem service in one or more of the habitats associated with it. Further details of habitat types, biotic groups, and ecosystem services can be found in the supplementary material and in Culhane et al. (2014).

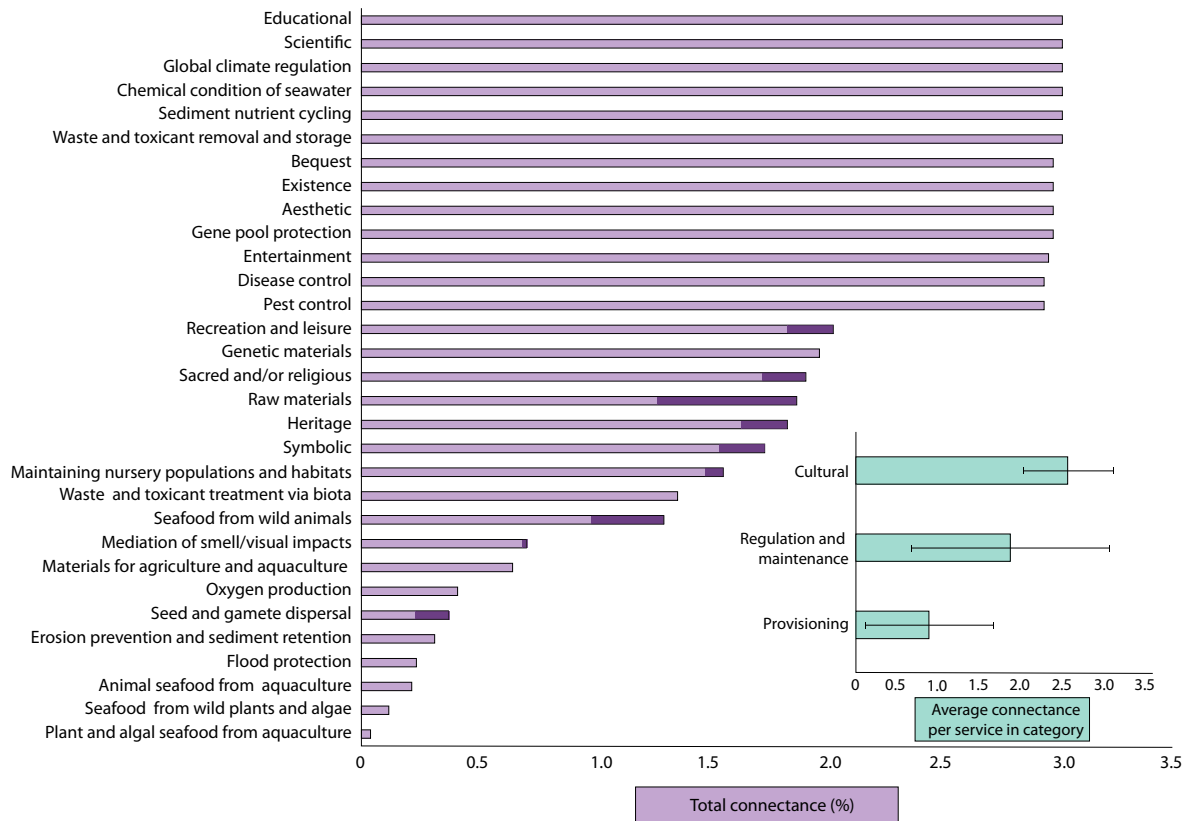


FIG. 4. Connectance per ecosystem service (purple bar). Connectance was calculated as the number of links per ecosystem service divided by the total number of potential interactions and is presented as a proportion of the total. Darker colored portion of connectance bars represents the proportion of indirect links. Inset shows average connectance per ecosystem service broad category (blue bar) with standard deviation.

that are broad but in general have better known and understood links with the ecosystem and benefits for humans, and have tight links to human activities such as harvesting, recreation and leisure, and other cultural services (B.B, Fig. 5). Additionally, five cases were found in which services are uniquely supplied by benthic and planktonic biotic groups (B.C, Fig. 6). These included those that require photosynthetic processes for their supply (oxygen production) and services that require structural support (erosion prevention, maintaining nursery populations and habitats).

DISCUSSION

Ecosystem services support people’s well-being via the actively sought, utilitarian provisions (food, building materials), to passively obtained benefits (clean air, fresh water) that are essential to, or enhance life (Kremen 2005, Mace 2014). It is advocated that a systematic documentation of service providing units (SPUs) is needed to help link the needs and well-being of society to the components of natural ecosystems that must be maintained in order to sustain the benefits for humans from nature (Kremen 2005, Luck et al. 2009, Kontogianni et al. 2010). We considered the following aspects key to representing the SPUs of ecosystem services: (1) fully capturing the biodiversity that provides services through its functioning; (2) reflecting the fact that biota can vary in their functioning between habitats and locations; (3) differences in vulnerability to human pressures; and (4)

relevance of the classification of SPUs to the units used in ecosystem state assessments. We set out to document the SPUs of European marine ecosystem services by considering the associations between habitats and their taxa to fulfill these criteria. The results show that these associations highlight relevant aspects of service provision, including expected outcomes, but also that there are flows across habitats at the marine landscape scale that are essential in underpinning the continued supply of certain ecosystem services.

Specifying both the taxa and the habitats in this study emphasizes the importance of habitats to service supply by giving weight to those habitats that can support more types of biota and their associated functions. Coastal habitats, both pelagic and benthic, emerged as being the most connected to the supply of services accounting for 48% of connectance found and links to all 31 services identified, with four services being exclusively linked to coastal habitats. This is not surprising, given their proximity to the majority of the global population and hence their links with human well-being. However, high connectance of coastal habitats is not just a factor of their proximity to people, but also to the range of biodiversity that they support. These include the photic species, and importantly, three services are only supplied by photic taxa. Benthic coastal habitats alone accounted for 34% of the links and contributed to supporting 30 services. These habitats include seagrass beds, coral and biogenic reefs, salt marshes, stands of macroalgae, and benthic soft sediments, among others, and have been estimated to contribute 44% of

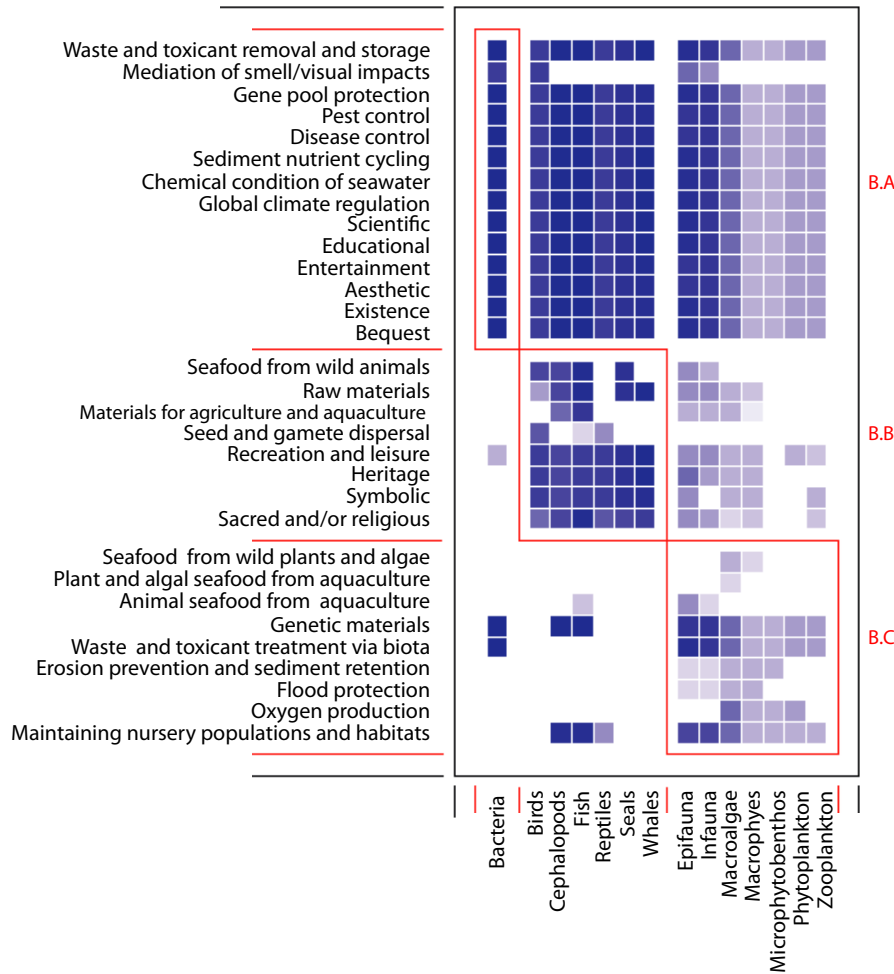


FIG. 5. Visualization of modular subsets of biotic groups and services they supply weighted according to the number of habitats they are associated with as indicated by blue gradation of squares. Modules are identified in red and labeled as B. (biotic) A–C.

the marine contribution to the global economy and 30% of the total global economy (Costanza et al. 2014).

Results here showed that specifying the role of biotic groups in service supply also highlights those that may be less charismatic or less well known to society. Across habitats, the relatively sessile benthic invertebrates (infauna and epifauna) had high connectance to ecosystem services because they are widely distributed and supply many service types. Communities of benthic invertebrates are expensive to study (because of the time spent processing and identifying samples) meaning that the distribution and functioning of their communities are relatively poorly understood (Snelgrove 1999). At the same time, we know they are subject to extensive multiple disturbances, such as those caused by fishing and coastal development (Kaiser et al. 2002, Thrush and Dayton 2002), but the understanding of the full impacts of these on service supply is not well developed. Marine bacteria are even less well studied (ten Hoopen et al. 2015) but we found that, although bacteria contribute to few service types, their ubiquity means they have high connectance with many of the regulation and maintenance services. Less charismatic species may be neglected when prioritization of management is driven by societal values; however, several services, for example, flood protection, are exclusively

supplied by these taxa and focusing protection on only the more charismatic species or habitats will make the future supply of some services vulnerable.

Marine ecosystems are often studied and managed at relatively large scales to account for high levels of connectivity related to the movement of marine taxa and their larvae (Fogarty and Botsford 2007). The findings of this study support the relevance of this approach, because connectivity also affects service supply when services are contributed to by biotic groups that utilize several habitats throughout their lifetime. For example, seafood supply is affected by changes in the condition of nursery habitats, refugia, and feeding areas that exploited species depend on through their lifecycle (Mumby et al. 2004, Barbier et al. 2011). Green turtles that contribute to maintaining fish nursery habitats (seagrass beds) and recreation and leisure (wildlife watching), require nesting sites on land, pelagic habitats for juvenile stages, and seagrass habitats for feeding when adults (Godley et al. 2002). Such biotic groups can be at risk at any of these life stages, if habitats supporting them are being degraded or lost.

In this study, the observed frequency of indirect links from components to services, such as raw material provision, seafood from wild animals, seed and gamete dispersal, and



FIG. 6. Visualization of modular subsets of habitats and services they support weighted according to the number of biotic groups they are associated with as indicated by blue gradation of squares. Modules are identified in red and labeled as H. (habitat) A–D. Colors of habitat names indicate broad habitat types: yellow for photic benthic; brown for aphotic benthic; light blue for pelagic; dark blue for ice.

recreation and leisure, highlights that protecting only the habitats where these services are directly used will not fully protect their supply. We found even where mobile groups do not contribute to many types of service (e.g., whales), they are relying on the support of many habitats (e.g., indirect links showed whales rely on habitats where they do not directly supply services 13% of the time). Some deeper habitats supported more indirect links than shallower habitats, reflecting their importance to mobile biotic groups. However, these habitats may not always be associated to relevant services in the minds of managers. The protection of these habitats needs to be considered to sustain the supply of services from mobile groups that are directly used elsewhere, and this perspective can only be considered if both habitats and their associated taxa are considered together when providing advice for management.

It is important to recognize the links between pressures and ecosystem services we rely on (Cabral et al. 2015, Hooper

et al. 2017). As noted in the criteria used to identify ecosystem components here, specifying habitats and the biota within habitats facilitates consideration of differences in vulnerability to human pressures of species groups within and between habitats, for example, infauna in coastal habitats may be more resilient but also more exposed to pressures than epifauna in the deep sea. While no part of the ocean is untouched by human activity, coastal areas, revealed to support the highest number of ecosystem services here, are subject to the highest cumulative impacts (Halpern et al. 2008). Coastal biodiversity is vulnerable to a range of threats, many originating on land, and including pollution, sedimentation, coastal development, and fishing (Smale et al. 2013). At the same time, an increase in climate-driven events such as flooding relies on the presence of structures provided by coastal biodiversity to provide the services that attenuate flooding or erosion. It is clearly essential that the delicate balance faced in maintaining economic activity while protecting the supply

of numerous ecosystem services is considered in marine conservation and management for the immediate but also long-term well-being of society.

We have revealed that even remote habitats have the capacity to support a substantial number of services. This capacity may not be insignificant: for example, a population of North Atlantic deep-sea fish have been estimated to sequester over 1 million Mg of CO₂ every year (Trueman et al. 2014). The potential for expanding exploitation and diversification of service use into the deep sea through technological advances is recognized, and this will bring new threats, adding to existing and historical pressures in systems that are known for their low ecological resilience (Ramirez-Llodra et al. 2011). Protection of these habitats, for example, recent regulations restricting deep-sea fishing in the European North East Atlantic (Regulation (EU) 2016/2336), will result in lowered opportunities for exploiting some provisioning services, but could protect supply of other less visible yet important services.

This approach enables those informing decision-making to identify all relevant ecosystem components when considering management of an ecosystem service, or all relevant ecosystem services when considering conservation or management of the ecosystem. This comprehensive assessment fills an important gap in the approaches published to date and is essential in being able to truly account for the contributions natural ecosystems make to the well-being of human society. It does not, however, account for the difference in quantitative contribution of ecosystem components to services, actual value of services to humans, or current state of ecosystem components and thus state of supply of services. In order to make management decisions, the equivalence of the different SPUs in terms of their contribution to ecosystem service supply and their conservation status may all need to be considered (see next paragraph on this). However, the identification of the relevant SPUs is a necessary first step, and we ascertain that both numbers of services and connectance are useful measures in helping decision makers to visualize the ways in which the components of the natural ecosystem underpin human well-being.

Because the classifications of ecosystem components and services used in this study are closely linked to those used in policy in Europe, this facilitates the consideration of both relative contributions and status of ecosystem components in a logical next step of the assessment. For example, phytoplankton were found to contribute to relatively few services and to have low connectance, partly because pelagic habitats have lower differentiation than benthic habitats in the classification, but they can still have a large relative contribution to particular services at the scale considered here (large European regional seas) when other factors are taken into account. First, the condition of an ecosystem component may determine its efficiency at carrying out the processes and functions required to supply a service. Second, the location of biotic groups will affect the supply of services. The contribution to services from phytoplankton located in oceanic, nutrient-limited regions is likely to be small compared to those located in nutrient-rich shelf seas. Third, the spatial extent of ecosystem components is important. Shelf habitats are extensive in European regional seas, and therefore, an ecosystem component, such as phytoplankton in shelf waters, has the potential to provide a greater

magnitude of individual services, such as oxygen production, compared to others, such as macroalgae in the littoral habitats, which covers a much smaller spatial extent. In addition, the contribution to services may also depend on the spatial and/or temporal nature of the service itself. For example, the contribution of a component to waste treatment will depend on where the input of the waste is and how it is transported in the system and thus which components can potentially supply this service. In this case, though shelf seas may be more extensive, coastal habitats may contribute more if more waste is deposited in these habitats and the waste is not widely dispersed. Further work can go on to weight this linkage framework by assessing the relative contribution of components to the supply of services, based on, for example, spatial extent (see examples in Culhane et al. 2014: Section 5).

CONCLUSION

We have shown that considering combinations of habitats and taxa as the ecosystem service providing units captures several key aspects of service provision. It is the association between habitats and taxa that generates services, and this approach recognizes the full diversity of taxa, as well as their location, in this supply. This is important because, while it is well known that some parts of the marine ecosystem, like coastal habitats and fish, contribute to multiple ecosystem services and are subject to many pressures, this approach also highlights the role of parts of the ecosystem that are less visible, for example, bacteria, or more vulnerable, for example, the deep sea. Additionally, because mobile biotic groups are widely dispersed and can spend time in many habitats, remote, seemingly unconnected habitats have a role in supporting the services these mobile biota can supply elsewhere. Thus, at the large regional sea scale, there can be a mismatch between, not only where services are supplied versus where they are used (Drakou et al. 2017), but also between where services are supplied and used, and other habitats that support this supply. Not recognizing these distinctions in how services are supplied could lead to a lack of protection of relevant taxa or habitats sustaining service supply, and it is thus important to use the appropriate units, such as the classification of ecosystem components used here, to inform management and conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1779/full>

DATA AVAILABILITY

Data are available from DataCat (The Research Data Catalogue of the University of Liverpool) at: <https://doi.org/10.17638/datacat.liverpool.ac.uk/496>.