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Integrating ecosystem services into conservation strategies for freshwater and marine habitats: a review

ANDREW J. BOULTON[a,*], JAN EKEBOM[b] and GÍSLI MÁR GÍSLASON[c]

[a]*School of Environmental and Rural Science, University of New England, Armidale, Australia*

[b]*Metsähallitus Parks and Wildlife Finland, Steering Unit, Vantaa, Finland*

[c]*Institute of Life and Environmental Sciences, University of Iceland, Reykjavík, Iceland*

ABSTRACT

1. Over the last two decades, there has been increasing public and political recognition of society's dependency upon natural habitat complexity and ecological processes to sustain provision of crucial ecosystem services, ranging from supplying potable water through to climate regulation. How has the ecosystem-services perspective been integrated into strategies for aquatic habitat conservation?

2. Literature on conservation of diverse freshwater and marine habitats was reviewed to assess the extent to which past and current strategies specifically targeted ecosystem services, and considered ecosystem functions, potential trade-offs and social issues when formulating protection measures for conserving aquatic habitats.

3. Surprisingly few published examples exist where comprehensive assessment of ecosystem services supported development of conservation plans. Seldom were aquatic habitat conservation objectives framed in terms of balancing trade-offs, assessing social values and evaluating suites of ecosystem services under different strategies. Time frames for achieving these objectives were also rarely specified. There was no evidence for fundamental differences between marine and freshwater habitats with respect to their ecosystem services that should be considered when setting targets for their conservation.

4. When an ecosystem-service perspective is used for setting objectives in aquatic habitat conservation, the following actions are recommended: (1) explicitly listing and evaluating full suites of ecosystem services to be conserved; (2) identifying current and future potential trade-offs arising from conservation; (3) specifying time frames within which particular strategies might protect or enhance desired services; and (4) predicting how different proposed strategies might affect each ecosystem function, service flow and public benefit.

5. This approach will help ensure that less-apparent ecosystem services (e.g. regulating, supporting) and their associated ecosystem functions receive adequate recognition and protection in aquatic conservation of freshwater and marine habitats. However, conservation objectives should not focus solely on protecting or enhancing ecosystem services but complement current strategies targeting biodiversity and other conservation goals.

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*Correspondence to: Andrew Boulton, Ecosystem Management, School of Environmental and Rural Science, University of New England, Armidale, 2351, New South Wales, Australia. Email: aboulton@une.edu.au

INTRODUCTION

In the last few decades, there has been an increasingly utilitarian attitude to habitat conservation that emphasizes improved economic gains and benefits for human society over the perspective that nature and biodiversity should be conserved 'for its own sake'. Underpinning this utilitarian attitude is the assumption that ecosystem goods and services, defined as the benefits for humans that are directly attributable to the ecological functioning of ecosystems (De Groot *et al.,* 2002), have a quantifiable value that can be optimized by strategic ecosystem-based management, including conservation and restoration (Daily *et al.*, 2009; Palmer *et al.,* 2014). Although this perspective has its critics (Boon, 2012; Dudgeon, 2014; Silvertown, 2015), others argue that the utilitarian approach is more effective when garnering support for conservation programmes (Naidoo and Ricketts, 2006; Turner and Daily, 2008; Miteva *et al.,* 2015). Either way, the term 'ecosystem services' now appears in conservation plans at global (e.g. Aichi Biodiversity Targets in the Strategic Plan for Biodiversity 2011–2020, Convention on Biological Diversity, 2010), continental (e.g. European Biodiversity 2020 targets, European Commission, 2011) and local (Wen *et al.,* 2011) scales. Even the current more-nuanced perspective that emphasizes the two-way relationship between people and nature (Mace, 2014) still advocates conserving ecosystem services.

Conceptually, the ecosystem services perspective is a complex one (Nahlik *et al.,* 2012) that views ecosystems as socio-ecological entities where natural ecosystems and their biodiversity are linked with socio-economic systems (Figure 1). Often, this link is portrayed as a 'cascade' (Haines-Young and Potschin, 2010) where biophysical structure (e.g. physical habitat complexity) and ecological processes (e.g. organic matter decomposition) support various ecosystem functions, some of whose services flow to socio-economic systems, providing goods and services that are valued by humans (Figure 1). Although the cascade model is shown as unidirectional, feedbacks to ecosystems and service flows occur via institutional governance, management and restoration (TEEB, 2010).

This model highlights a key point often missed in discussion about ecosystem services: benefits must be known to flow from ecosystems to end-users before an ecosystem function is considered to provide an ecosystem service (Fisher *et al.,* 2009; Schwerdtner Máñez *et al.,* 2014). Thus, adoption of this perspective in aquatic conservation requires a full understanding not only of the complexity of the ecosystem and its biodiversity, ecological processes and ecosystem functions, but also the pathways and scales of service flow, the diverse benefits (usually perceived differently by different end-users), and the importance of using appropriate evaluation procedures and associated risks (Sukhdev *et al.,* 2014; Olander *et al.,* 2015;

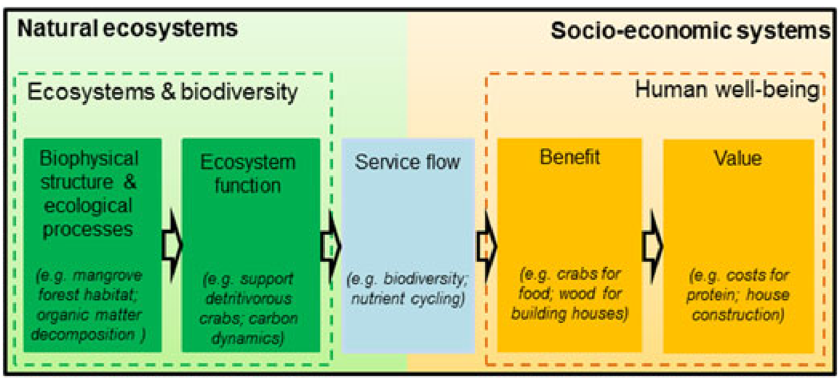

Figure 1. The 'cascade model' of ecosystem services (modified from Haines-Young and Potschin, 2010; Liquete *et al.,* 2013), portrayed from a socio-ecological perspective. The sequence of panels from left to right represents how the biophysical structure and ecological processes in a given ecosystem (together with its biodiversity) govern ecosystem functions that flow on as services to provide benefits whose values are defined socio-economically. All of the steps must be assessed when targeting protection of ecosystem services in aquatic habitat conservation.

Terrado *et al.,* 2016). We suspect that although many current conservation plans claim to target protection of ecosystem services, the requirements for fully demonstrating achievement of these targets are often under-estimated. This review focuses on how the concept of ecosystem services is currently integrated in marine and freshwater habitat conservation, and complements the broader empirical analysis by Fisher and Brown (2014). It also explores whether there are any fundamental differences between marine and freshwater habitats with respect to their ecosystem services that should be considered when setting targets for their conservation.

Scope and goals of this review

This review is confined to assessing strategies to conserve ecosystem services of aquatic *habitats* (and by extension, their biophysical structure, biodiversity, ecological processes and ecosystem functions, Figure 1). Therefore, it includes studies in which habitat conservation is only part of a broader management plan, such as for many marine and freshwater protected areas, that encompasses other goals and uses (Great Barrier Reef Marine Park Authority, 2014; Arkema *et al.,* 2015). Traditional management efforts may lack the holistic focus that encompasses a range of ecosystem services, and therefore fail to integrate conservation in a broader ecosystem-based management framework (Leslie and McLeod, 2007; Halpern *et al.,* 2010). Fundamentally, ecosystem-based management is a place-based approach that seeks to maintain the long-term health, resilience and potential of ecosystems so that they can deliver a broad suite of ecosystem services (Barbier, 2009; McLeod and Leslie, 2009).

Habitat conservation was chosen because it is a common focus in many programmes. Habitats are often used as management units (e.g. when mapping ecosystem services, Galparsoro *et al.,* 2014) and specific targets for conservation (Rees *et al.,* 2012; Eastwood *et al.,* 2016). Furthermore, many regional or global environmental policies are aimed at conserving marine or freshwater habitats (Secretariat of the Convention on Biological Diversity, 2005; EU, 2008; NOAA, 2015), providing the legislative basis for preserving habitat-related ecosystem services.

Our first goal was to review the extent to which current aquatic habitat conservation strategies target ecosystem services as one of their objectives, and how adoption of this perspective has changed over time. When did it start to be widely adopted? Is it more prevalent in marine than freshwater habitat conservation, or vice versa? Is it more prevalent in certain aquatic habitats? Our second goal was to assess which groups of ecosystem services have been evaluated and incorporated when developing aquatic habitat conservation strategies. Although there are numerous classifications of ecosystem services (discussed in the next section), the most commonly used one is that proposed by the Millennium Ecosystem Assessment (MEA, 2005). This recognizes four broad groups: provisioning services such as supply of water and food, regulating services such as water purification and erosion control, supporting services such as nutrient cycling, and cultural services including spiritual, educational and aesthetic benefits. Do most aquatic conservation strategies target representatives of all four groups? Has recognition of the more subtle supporting and regulating services increased over time?

The third goal was to explore issues of scale, trade-offs and social factors, and the extent to which these are explicitly considered in aquatic conservation strategies. The relevant ecosystem functions and service flows underpinning the provision of ecosystem services (Figure 1) occur at multiple spatial and temporal scales, and we sought to determine whether these scales are specified in aquatic habitat conservation plans. Understanding the scales of relevant ecosystem functions and service flows helps reveal how anthropogenic changes to ecosystems affect the delivery of ecosystem services, allowing conservation managers to identify which human impacts are likely to be especially severe in a given region and therefore what mitigation strategies might be most effective. To what extent do aquatic conservation programmes specify ecosystem functions and their inferred ecosystem services? If so, are scales of spatial and temporal responses explicitly considered?

Ecosystem services do not act in isolation. Instead, 'bundles' of ecosystem services co-occur (Raudsepp-Hearne *et al.,* 2010), usually necessitating trade-offs when seeking conservation strategies to optimize their collective benefit. Have aquatic conservation strategies acknowledged these trade-offs when evaluating multiple ecosystem services and proposing approaches to protect or enhance particular ones? Many trade-offs also involve social factors because these govern valuation and prioritization of different ecosystem services by different people and at different times (Turner and Daily, 2008; Huxham *et al.,* 2015) and underpin the likelihood of stakeholder support for proposed conservation strategies. To what extent have social factors such as income, geographic location, gender and health been considered when weighing up trade-offs in ecosystem services in aquatic habitat conservation plans? Do the plans also attempt valuation of ecosystem services, and is this aspect becoming increasingly common in marine and freshwater conservation?

Our final goal was to assess whether there are any fundamental differences between marine and freshwater habitats with respect to their ecosystem services that should be considered when setting targets for their conservation. If these differences existed, recommendations for integrating an ecosystem-service perspective into conservation of marine and freshwater habitats could need to be tailored according to specific differences in habitats between the two realms. Alternatively, if there are no major differences at a general level, then the challenges facing conservation managers may be consistent across both realms. This implies insights gained from research in either marine or freshwater habitats are equally relevant when assessing literature for setting targets for ecosystem services in aquatic conservation.

The paper begins with a brief review of relevant literature on aquatic ecosystem services and habitat conservation, focusing on service classifications, scale and connectivity, trade-offs, valuation methods and relevant social factors. This sets the stage for interpreting the results of a bibliometric analysis exploring how aquatic habitat conservation plans currently integrate ecosystem services, addressing the questions posed above. The paper concludes with some recommendations on setting objectives for conservation plans that seek to target ecosystem services as an adjunct to other goals such as biodiversity protection.

CLASSIFYING AQUATIC ECOSYSTEM SERVICES FOR HABITAT CONSERVATION

Although the MEA (2005) classification of ecosystem services into four groups is widely used, it has been criticized for its ambiguity, double-counting of some services (discussed later) and inability to explicitly match services with people (Fisher *et al.,* 2009; Landers and Nahlik, 2013). This has led to a plethora of different classifications, including those by Beaumont *et al.* (2007); Brauman *et al.* (2007); TEEB (2010); Haines-Young and Potschin (2010); Landers and Nahlik (2013) and Liquete *et al.* (2013). The classification by Liquete *et al.* (2013) is especially relevant because it focuses on marine and coastal ecosystem services, proposing three broad groups of services: provisioning, regulating and maintenance, and cultural (Table 1). The second of their groups pools the services classified separately as regulating and supporting services by the MEA (2005) and replaces MEA's largely terrestrial 'pollination' service with the functionally equivalent 'life cycle maintenance' (Table 1), defined as 'biological and physical support to facilitate the healthy and diverse reproduction of species' (Liquete *et al.,* 2013: 6). The conservation significance of this service is obvious because it includes the maintenance of habitats (e.g. seagrasses, coastal wetlands, coral reefs, mangroves) that act as nurseries, spawning areas or migratory routes and the connectivity among them that ensures successful completion of the life cycle of many species, thus protecting genetic diversity.

Another relevant classification is that of Brauman *et al.* (2007) that focuses on terrestrial freshwater ecosystem services, grouping them into five 'hydrologic services': improvement of extractive water supply, improvement of in-stream water supply, water damage mitigation, provision

Table 1. Comparison of the categories (coloured boxes) and ecosystem services proposed by MEA (2005) and, for marine and coastal ecosystems, Liquete *et al.* (2013). Nutrient cycling is duplicated in the second column because it is matched with both services in the fourth column. Three services defined by MEA (2005) lack equivalents in the classification by Liquete *et al.* (2013): photosynthesis, primary production and water cycling. Modified from Liquete *et al.* (2013)

<table>
<tr><th colspan="2">MEA (2005)</th><th colspan="2">Liquete et al. (2013)</th></tr>
<tr><td rowspan="6">Provisioning</td><td>Food</td><td rowspan="6">Provisioning</td><td>Food provision</td></tr>
<tr><td>Fresh water</td><td>Water storage and provision</td></tr>
<tr><td>Ornamental resources</td><td rowspan="4">Biotic materials and biofuels</td></tr>
<tr><td>Genetic resources</td></tr>
<tr><td>Biochemicals</td></tr>
<tr><td>Fibre</td></tr>
<tr><td rowspan="9">Regulating</td><td>Air quality regulation</td><td rowspan="12">Regulating and maintenance</td><td>Air quality regulation</td></tr>
<tr><td>Natural hazard regulation</td><td rowspan="3">Coastal protection</td></tr>
<tr><td>Water regulation</td></tr>
<tr><td>Erosion regulation</td></tr>
<tr><td>Climate regulation</td><td>Climate regulation
Weather regulation</td></tr>
<tr><td>Pollination</td><td>Life cycle maintenance</td></tr>
<tr><td>Pest regulation</td><td rowspan="2">Biological regulation</td></tr>
<tr><td>Disease regulation</td></tr>
<tr><td>Water purification and waste treatment</td><td rowspan="2">Water purification</td></tr>
<tr><td rowspan="3">Supporting</td><td>Nutrient cycling</td></tr>
<tr><td>Nutrient cycling</td><td rowspan="2">Ocean nourishment</td></tr>
<tr><td>Soil formation</td></tr>
<tr><td rowspan="10">Cultural</td><td>Spiritual and religious values</td><td rowspan="10">Cultural</td><td rowspan="5">Symbolic and aesthetic values</td></tr>
<tr><td>Cultural heritage values</td></tr>
<tr><td>Cultural diversity</td></tr>
<tr><td>Sense of place</td></tr>
<tr><td>Aesthetic values</td></tr>
<tr><td>Recreation and ecotourism</td><td rowspan="2">Recreation and tourism</td></tr>
<tr><td>Social relations</td></tr>
<tr><td>Inspiration</td><td rowspan="3">Cognitive effects</td></tr>
<tr><td>Knowledge systems</td></tr>
<tr><td>Educational values</td></tr>
</table>

of water-related cultural services, and water-associated supporting services. The parallels with the MEA (2005) classification are clear, and Brauman *et al.* (2007) list the various users and uses of these services, emphasizing that trade-offs arise when one service is exploited at the expense of one or more others. This paper was one of the earliest to propose that the ecosystem service concept had 'tremendous potential' for conservation programmes but highlighted major knowledge gaps in methods for mapping and quantifying different services and identifying social factors relevant for identifying, prioritizing and targeting ecosystems for protection.

Finally, there is the comprehensive classification developed for the US Environmental Protection Agency by Landers and Nahlik (2013) that identifies 352 'Final Ecosystem Goods and Services' (FEGS) provided by 15 environmental subclasses (broad habitats) and used by 38 beneficiary subcategories (e.g. irrigators, aquaculturalists, researchers). This classification was developed to underpin consistent measurement, quantification, mapping, modelling and valuation of ecosystem services for policy development and decision making at multiple scales, and focuses on the service flows from natural systems to socio-economic ones (Figure 1) by matching users with FEGS in each environmental subclass in a matrix. Six of the 15 environmental subclasses are aquatic: rivers and streams, wetlands, lakes and ponds, estuaries and near-coastal marine, open oceans and seas, and groundwater.

No published applications of this classification in conservation strategies of specific aquatic habitats were found, but its potential value is substantial because it (1) defines rigorous boundaries around services and environmental subclasses, (2) specifies the user of a given service, acknowledging that different users typically value the same service differently, and (3) avoids double-counting ecosystem services. This last problem occurs with the MEA (2005) classification and others where 'intermediate services' are mixed with 'final services' (Landers and Nahlik, 2013). For example, consider a mangrove forest where the trees photosynthesize as they produce wood. According to the MEA (2005) classification, the tree is providing both a supporting service (primary production) and a provisioning service (wood) even though the supply of wood results from primary production. In contrast, the FEGS classification excludes the 'intermediate service' of primary production and wood is identified as the only FEGS for which there may be multiple users and associated values. A final benefit of the FEGS classification for aquatic conservation is the extension that maps service flows to end-users (http://www.epa.gov/research/ecoscience/eco-negscs.htm), providing policy-makers with a tool to gauge different impacts to human well-being resulting from different environmental management options (Yoskowitz and Russell, 2015).

If a classification approach (in contrast to, for example, causal chains and conceptual maps, Olander *et al.,* 2015) is to be adopted for integrating ecosystem services into aquatic conservation plans, it seems wise to adopt two, related perspectives and use them for different but complementary purposes. The first is the heuristic perspective that groups services into three or four broad categories (Table 1) and is familiar and relatively simple. This aids communication and helps ensure conservation of 'intermediate' services and ecosystem functions (Figure 1) as well as the more obvious provisioning and cultural services. The second entails use of a more detailed and rigorous classification such as the FEGS one so that conservation plans can specify approaches for measuring, quantifying and mapping ecosystem services in an area to provide a baseline against which to assess the success of various conservation strategies. Tools to do this are being developed (e.g. Drakou *et al.,* 2015) along with protocols for prioritizing ecosystem services (e.g. Werner *et al.,* 2014). As needed, these tools and the classification can be used to weigh up different conservation options, especially when trade-offs are necessary. Such trade-offs are governed by spatial scales and connectivity of ecosystem function and service flow within and among habitats.

SPATIAL SCALE AND CONNECTIVITY OF ECOSYSTEM SERVICES IN AQUATIC HABITAT CONSERVATION

Strategic objectives for habitat conservation often specify spatial criteria and the importance of connectivity. For example, part of Aichi Target 11 is to protect at least 17% of inland waters and 10% of coastal and marine areas that are important for biodiversity and ecosystem services (Convention on Biological Diversity, 2010), and recommends that these protected areas should be well-connected. Consequently, coverage exceeding 10% and with good connectivity among sites is considered beneficial for the protection of marine ecosystem services. One of the few marine regions where this objective has been reached is the marine protected areas (MPAs) of the Baltic Sea (Reker *et al.,* 2015). However, despite a desire for consistency in criteria for site designation (Kelleher, 1999), many of the MPAs were proposed to protect local biological values. Further, there is a need for improved connectivity across several landscape types and for some species with limited dispersal abilities (HELCOM, 2010). These MPAs, spanning nine countries, were designated over a period of several decades before broad-scale ecological issues such as habitat connectivity or ecosystem services became primary criteria.

Ecosystem service provision and flows in aquatic habitats often require large areas and extensive connectivity, posing significant conservation challenges. One solution is to create protected-area networks to meet objectives that individual marine or freshwater protected areas cannot achieve; i.e. that sites operate synergistically, at large spatial scales and across a range of protection levels (Reker *et al.,* 2015). However, protected-area networks, based on diverse policies and legislation, may not suffice to protect widely distributed ecosystem components. Similarly, management plans aiming to guide sustainable long-term use of ecosystem services may not provide the desired degree of protection. The problem is that protected areas do not exist in splendid isolation but connect and interact with their surrounding waters and land areas, resulting in pressures that weaken the capacity of the aquatic habitats to provide the necessary ecosystem services (Ehler and Douvere, 2009). In marine habitats, this problem has been tackled using a holistic planning process called marine spatial planning (also called coastal and marine spatial planning (The White House Council on Environmental Quality, 2010) or maritime spatial planning (EU, 2014)). It is defined as 'the public process of analysing and allocating the spatial and temporal distribution of human activities in marine areas to achieve ecological, economic and social objectives that are usually specified through a political process' (Ehler and Douvere, 2009), and seeks to protect ecosystem services and their flows to diverse stakeholders.

One outstanding example is the process that resulted in a plan for the Australian Great Barrier Reef (GBR), an immense area (345 000 km^2) comprising almost 3000 individual reefs and almost 1000 islands and coral cays (Day, 2002). Since the plan's adoption in 2004, regular assessments have been made (Great Barrier Reef Marine Park Authority, 2014) revealing that several key habitats show poor and declining conditions in parts of the region. This environmental decline has jeopardized the World Heritage Sites status of the GBR, with major consequences for the tourism industry and other revenue from the region's lucrative cultural and provisioning ecosystem services. For example, ecosystem services from the GBR are estimated to be at least AUD454 million per year for reef-based tourism, AUD108 million per year for recreational fishing and boating, and AUD136 million per year for commercial fishing (Stoeckl *et al.,* 2011).

Understanding how connectivity affects ecosystem-service provision in the GBR is also crucial. The GBR's future not only depends on how well the coral reefs and their surrounding seas are protected but also on the quality of freshwater runoff from the terrestrial habitats bordering the GBR (Great Barrier Reef Marine Park Authority, 2014). Much has been done to reduce poor-quality run-off by improving land-use practices (e.g. erosion and nutrient control) but this still continues to be one of the main threats. The GBR still maintains its World Heritage Site status and continues to serve as an example of how marine spatial planning and conservation can be applied for the benefit of ecosystem services.

Where conservation strategies focus on protecting 'ecosystem service hotspots' (areas that offer disproportionately high ecosystem services, (Crossman and Bryan, 2009)), spatial scales are particularly relevant when mapping their vulnerability to human impacts. For example, an ecosystem-service mapping study in Massachusetts indicated that freshwater provisioning and flood regulation experienced local declines in response to shifting land-uses but changed little when measured at the state level (Blumstein and Thompson, 2015). The same scale-dependency applies to mapping longitudinal changes in ecosystem services along rivers (Large and Gilvear, 2015), and different services are likely to show widely variable responses to the scale of mapping in different regions. Finally, from an ecosystem-services perspective spatial and temporal scales must encompass both 'point-of-service' and 'point-of-use', exemplified by the upstream provision of services for downstream users in river ecosystems (Green *et al.,* 2015; Liu *et al.,* 2016), and this adds further challenges to developing effective conservation strategies.

Assessments of ecosystem services typically focus on quantifying and mapping their delivery at a single point in time (Nicholson *et al.,* 2009; Felipe-Lucia *et al.,* 2015). However, provision of most ecosystem services changes over time in response to biophysical and socio-economic drivers (Renard *et al.,* 2015). This is especially relevant as demand is increasing for most ecosystem services provided by marine and freshwater habitats (Luisetti *et al.,* 2014; Rogers *et al.,* 2015) and there will also be temporal changes in synergies and trade-offs among different ecosystem services (see next section). Therefore, applications of the ecosystem-services perspective in conservation strategies must include a temporal component, preferably integrated with spatial analysis.

Most habitat conservation plans encompass only a single environmental realm (terrestrial, fresh water or marine), usually because of logistical, institutional and political constraints (Stoms *et al.,* 2005). This is seldom adequate because all three realms interact through processes that involve physical, chemical, and ecological connections essential for the persistence of many species and ecosystem functions (Beger *et al.,* 2010) and, by extension, ecosystem services. Temporal changes in the physical and hydrological connectivity and spatial arrangement of aquatic habitats within and among these realms underpins the provision and flow of most ecosystem services (Syrbe and Walz, 2012). Tools for detecting the effects on ecosystem services of impaired connectivity as well as reduced habitat area (Ng *et al.,* 2013) currently seem under-utilized for aquatic habitat conservation.

Ecological connectivity among aquatic habitats is largely mediated by mobile organisms such as invertebrates (larval, adult or both), fish, some reptiles and birds, and in marine environments, mammals such as seals and cetaceans. This ecological connectivity sustains biodiversity and production of many ecosystem services (Staddon *et al.,* 2010) as well as conferring resilience and other desirable features that deserve conservation (Olds *et al.,* 2012). Ecological connectivity mediated by mobile organisms occurs to varying degrees in different habitats. For example, in tropical reef fisheries where fish stocks are typically restricted to specific habitats, 'spill-over' from marine protected areas often increases the catches per unit effort outside the protected area and connect the habitats important for these fishes (Leenhardt *et al.,* 2015), although this is not the case for temperate fish stocks such as cod and haddock where the fish are very mobile and are not so tightly constrained by habitat.

Understanding the mechanisms of such connectivity is crucial when designing networks of multiple conserved habitats to promote provision of ecosystem services (Rees *et al.,* 2012). Many sets of protected areas in the marine environment claim to be networks but their design has seldom taken into account any sort of critical connectivity because the focus has been on criteria such as representativeness and geographic coverage. In rare cases, these criteria may provide a degree of connectivity by default but whether this translates into flows of ecosystem services is poorly understood. Where ecological connectivity does occur, it potentially helps reduce the effects of trade-offs between fisheries and conservation reserves (Gaines *et al.,* 2010). When applying an ecosystem-services perspective to aquatic habitat conservation, spatio-temporal scales and connectivity among habitats within and among conserved areas strongly govern the types, provision and flows of ecosystem services, and must be explicitly considered in conservation strategies.

Many aquatic habitats are transitional ecotones (e.g. marine intertidal zones, mangrove belts, riparian zones, hyporheic zones) across which services flow and where gradients in ecosystem functions provide numerous ecosystem services (Sanon *et al.,* 2012; Clerici *et al.,* 2013; Mugnai *et al.,* 2015). Conservation of ecosystem services in these transitional habitats, especially at the land–water interface, is particularly challenging because of jurisdictional ambiguities between administrations, competing demands for ecosystem services and inherent vulnerability to terrestrial and aquatic pressures (Walters *et al.,* 2008; Maltby *et al.,* 2013). Resolving these challenges when conserving transitional and other aquatic habitats requires a good understanding of trade-offs among different ecosystem services, appropriate valuation approaches to compare options (including in non-economic terms, TEEB, 2010), and social factors at multiple scales that influence access to ecosystem services and that motivate conservation concerns (Luisetti *et al.,* 2014).

TRADE-OFFS, VALUATIONS AND SOCIAL FACTORS

Ecosystem service trade-offs occur when enhanced provision of one service causes declines in one or more different services (Rodríguez *et al.,* 2006). For example, management strategies that raise water levels in the Somerset Levels and Moors wetland system in south-west England to increase habitat for wetland birdlife may reduce potential flood water storage and increase methane emissions (Acreman *et al.,* 2011). Trade-offs occur in both space and time (Rodríguez *et al.,* 2006). Spatial trade-offs frequently entail use of a provisioning service which is traded off against one or more services elsewhere. For example, enhancing agricultural production in farms along a river by increasing fertilizer use has broad-scale effects on water quality downstream. Temporal trade-offs commonly focus on immediate provision of an ecosystem service at the expense of the same or other services in the future (e.g. overfishing). Often, spatial and temporal trade-offs in ecosystem services co-occur (Turkelboom *et al.,* 2015). Partial logging of a mangrove forest reduces its services of soil stabilization and flood control at various spatial scales, often with some time-lag (Schwerdtner Máñez *et al.,* 2014).

Therefore, when planning conservation (or restoration) strategies, it is essential to understand interactions and feedback between conflicting ecosystem services so that priorities can be set (Sanon *et al.,* 2012; Schirmer *et al.,* 2014). Any change in the management of one ecosystem service will affect the 'bundle' of services provided by that system (De Groot *et al.,* 2010). Further, this effect varies over time and space, governed by the spatial and temporal dynamics of the underlying ecosystem functions (Hein *et al.,* 2006). Conservation strategies must consider the spatio-temporal variance of these bundles, particularly because this variance underpins the resilience of the ecosystem that, if weakened, may affect its capacity to deliver ecosystem services (Schwerdtner Máñez *et al.,* 2014). Tools such as multi-criteria decision analysis have proved useful to quantify trade-offs when developing conservation strategies. For example, multi-criteria decision analysis was used to evaluate several management options for the Lobau floodplain, an urban floodplain along the Danube River, to determine which set of trade-offs theoretically offered the best compromise among diverse stakeholders (Sanon *et al.,* 2012).

Another important aspect of trade-offs within bundles of ecosystem services provided by aquatic habitats is their interdependence with adjacent aquatic habitats (Luisetti *et al.,* 2014) and hydrologically linked terrestrial ones. Although conservation strategies may entail inventories of ecosystem services for specific habitats, provision of these services are often governed by processes occurring outside the inventoried habitat. For example, the 2011 Las Conchas wildfires in northern New Mexico severely compromised water-quality regulation and erosion control services; such large amounts of ash and sediment washed into the Rio Grande, which supplies 50% of the drinking water for Albuquerque, that water withdrawals by the city were stopped for a week and reduced for several months afterwards because of the expense of treating water with high sediment content (Grimm *et al.,* 2013).

The most common landscape-level trade-offs occur between the provisioning services and nearly all the regulating, supporting and cultural sevices (Rodríguez *et al.,* 2006). Frequently, conservation strategies seek to restrict exploitation of provisioning services as a means of promoting the other three broad types of ecosystem services. Extreme examples in aquatic habitat conservation include ‘sanctuary’ or ‘no-take zones’ in freshwater and marine protected areas where access to fish and other goods are prohibited or strictly limited (Lester and Halpern, 2008; Leenhardt *et al.,* 2015). A major challenge for managers is demonstrating the success of this type of management in protecting regulating, supporting and cultural ecosystem services (Gaines *et al.,* 2010; Rees *et al.,* 2012; Castro *et al.,* 2015), especially when criteria for success rely on some form of valuation of the different services. For example, when valuing the ecosystem services provided by marine protected areas, the limited availability of economic data at a relevant scale usually hinders full assessment of the influence of protected areas on the economy of the neighbouring zones (Laurans *et al.,* 2013) while measurement of non-market values (e.g. non-use value of marine biodiversity) is extremely difficult (Leenhardt *et al.,* 2015; Leimona *et al.,* 2015).

Even when aquatic habitats are exploited for provisioning services, there may be scope to also conserve regulating, supporting and cultural ecosystem services by targeted management (Fisher *et al.,* 2011). For example, dual-purpose aquaculture ponds can be designed to produce economically viable quantities of fish and shrimp yet also perform regulating and supporting services such as nutrient absorption and bird habitat, respectively (Walton *et al.,* 2015). However, it is important to remember that provision of many ecosystem services changes non-linearly with habitat area (Barbier *et al.,* 2008). When designing dual-purpose production systems, the spatial (and, if possible, temporal) relationships of ecosystem-service provision and the areas of different habitats should be known, as well as the effects of adjacent habitats that might modify these relationships.

One common situation when aquatic habitats are exploited is for plans to be drafted that focus on only a few services, potentially introducing major bias in their valuation. In the early 1980s, the Norwegian government decided to evaluate hydroelectric development in different catchment areas and compare this with other ecosystem services. The first stage involved 310 watercourses with 542 alternatives for development (Miljøverndepartementet, 1984). Representation came from diverse user groups with interests in energy generation, outdoor recreation, agriculture and forestry, reindeer herding, nature conservation, wildlife and fisheries management, preservation of cultural monuments, and prevention of flooding and erosion. The final plan was legislated by the Norwegian Parliament, resulting in, among other things, protection of the most valuable undisturbed catchments (39.1% of project proposals) (Miljøverndepartementet, 1984). Despite the representation by diverse user groups, Carlsen *et al.* (1993) concluded that they had little systematic effect on the final outcome of the plan, which has been re-evaluated twice (1987 and 1992) (Thórhallsdóttir, 2007a).

Influenced by the Norwegian plan, a programme to evaluate and rank energy projects by environmental impact and user interests was done in Iceland. It covered 19 hydroelectric and 22 geothermal developments, and was developed by four specialist groups focusing on different ecosystem services and perspectives (Thórhallsdóttir, 2007b). The outcome led to a resolution by the Icelandic Parliament in 2013 to protect the most valuable catchment and geothermal areas, and prompted the current assessment of a further nine river catchments with 16 alternatives for development and four geothermal areas with seven development alternatives. Although ecosystem services of river catchments and geothermal areas have been explicitly evaluated in these examples from Norway and Iceland, functional ecosystem components such as organic carbon dynamics and primary production were not considered (Thórhallsdóttir, 2007a), potentially providing an incomplete perspective of the situation.

Presently, the Icelandic Master Plan for Nature Protection and Energy Utilization is under re-evaluation, with 17 hydropower projects, seven geothermal projects and two wind-farm projects. Most were new projects, but some were from the group put on hold during the earlier phase until more information had been gathered. Evaluation was completed in February 2016 (Gíslason, 2016). Final results will be sent to the Ministry for Natural Resources and the Environment in September 2016, followed by discussion and a resolution on protected areas, areas for further consideration and areas for utilization for energy production.

Although fundamental to the ecosystem-services concept, the idea of valuation of services relies on the dangerous premise that 'nature' can be reduced to a single (usually monetary) metric and therefore is commensurable (Sukhdev *et al.,* 2014). In reality, valuation of ecosystem services is subjective (Balmford *et al.,* 2011; Leimona *et al.,* 2015), embedded in how certain people view and value their natural environment at a certain point in time. The various valuation methods for ecosystem services (reviews in TEEB, 2010; Chan *et al.,* 2012) give very different perspectives (de Groot *et al.,* 2012; Felipe-Lucia *et al.,* 2015), and different valuation methods result in different rankings of conservation values (Rouquette *et al.,* 2009). Valuing cultural services for aquatic habitat conservation is especially challenging (Ruiz-Frau *et al.,* 2013).

One of the most commonly used approaches involves payments for ecosystem services (PES), defined as 'a transfer of resources between social actors, which aims to create incentives to align individual and/or collective land-use decisions with the social interest in management of natural resources' (Muradian *et al.,* 2010: p. 1205). Although often framed as 'willingness to pay' (WTP), the resource transfer can be either monetary or in-kind, such as capacity building or the provision of alternative livelihoods (Lau, 2013). For example, exploiting recreational angling markets for mahseer fishes, a prized freshwater Indian sports-fish, to advance habitat conservation in the Western Ramganga River is an ideal basis for a PES market to benefit river ecosystems, local people, tour operators and visiting anglers (Everard and Kataria, 2011). A study by Jobstvogt *et al.* (2014) assessed WTP by divers and anglers for potential marine protected areas in the UK, highlighting the importance of cultural ecosystem services to different stakeholders in marine habitat conservation. User-WTP was influenced by a wide variety of marine spaces whereas stewardship-WTP was most influenced by management restrictions, species protection and attitudes towards marine conservation.

However, PES is not universally popular (Silvertown, 2015), and these schemes have been criticized as a 'commodity fetishism' that reduces ecosystem values to a single exchange-value measure, obscuring the social relations embodied in 'producing' and 'selling' ecosystem services (Kosoy and Corbera, 2010). In particular, over-reliance on PES as a win-win solution to the conservation-development dilemma risks ineffective or even counter-productive outcomes if social context is poorly understood (Warren-Rhodes *et al.,* 2011; Luck *et al.,* 2012; Muradian *et al.,* 2013). Our point here is that although ecosystem service-based strategies for aquatic habitat conservation typically require some form of valuation approach, policy-makers and conservation managers must recognize the biases and constraints in such exercises and adopt options that combine efficiency and fairness (Leimona *et al.,* 2015).

Furthermore, regardless of which valuation method is used, 'functional mismatches' (Folke *et al.,* 2007) arise when management, including conservation, is driven by a strong interest by resource users in selected ecosystem benefits only. Thus, social analysis of the interests and perceptions of stakeholder groups at different governance levels reveals functional mismatches (Jobstvogt *et al.,* 2014; Luisetti *et al.,* 2014) and indicates which institutions are needed for effective management (Hein *et al.,* 2006). Most of the ecosystem services that are being degraded are categorized as public goods and services for which 'market solutions' involving buyers and sellers are far from ideal (de Groot *et al.,* 2012; Sukhdev *et al.,* 2014). Seldom is any uncertainty analysis performed (Boithias *et al.,* 2016), adding further to the challenge of interpreting outputs from valuations of different conservation strategies. Some authors argue that multiple valuation methods spanning diverse stakeholders are needed (Felipe-Lucia *et al.,* 2015) and this may partly resolve some of the uncertainty associated with functional mismatches.

Who should actually be setting the values, especially when conservation efforts will deprive some users of immediate access to provisioning services? Brondizio *et al.* (2009) argue that choosing the institution to articulate the values is more important than the actual identification of a value; a more socially embedded valuation is needed in the context of local and regional decision making and resource management. The values and needs of different users should guide the application of the ecosystem service concept in conservation (Menzel and Teng, 2010), following an operational model like that proposed by Cowling *et al.* (2008) where the three consecutive steps of assessment, planning and management are guided by social values and stakeholders rather than being a predominantly scientific, expert-driven exercise. It is beyond the scope of this review to stray far into institutional governance issues; we simply want to emphasize the point that valuation and social issues are inextricably linked in aquatic habitat conservation, and must be considered when setting targets.

Of course, all valuation methods are social constructs and their 'currency' is entirely dictated by human value systems and social attitudes (Larson *et al.,* 2013; Sukhdev *et al.,* 2014). The social dimension complements the ecological one in defining any ecosystem service (Figure 1), and therefore social factors must be explicitly considered when using an ecosystem-services perspective to set conservation targets in a given area (Warren-Rhodes *et al.,* 2011; Luisetti *et al.,* 2014). A striking example is conservation of Cantareira State Park, an urban park in São Paulo, Brazil, where the close proximity of a very large population of socio-economically vulnerable people puts intense pressure (water theft, illegal fishing and bathing, religious practices) on the park's aquatic habitats, acknowledged in its conservation plan (de Souza Rares and Brandimarte, 2014).

In many cultures, social factors such as gender, local religious beliefs and village customs influence the recognition (and thus, perceived value) of different ecosystem services. Perceptions of ecosystem services provided by mangroves differed between resource users in three Solomon Island villages, associated with gender and religious denomination, influencing the likely success of PES schemes for Pacific carbon credit programmes (Warren-Rhodes *et al.,* 2011). Gender issues are especially relevant because in many cultures, men and women access and value aquatic ecosystem services very differently (Kelemen *et al.,* 2015), governing their responses to different conservation strategies. Similar principles apply to ethical and social-justice factors (Luck *et al.,* 2012; Kretsch and Kelemen, 2015). Despite the significance of these diverse social factors on perceptions of ecosystem services in marine and freshwater habitats, there seems little evidence that they are explicitly considered in current conservation strategies.

INTEGRATING ECOSYSTEM SERVICES INTO AQUATIC HABITAT CONSERVATION: A BIBLIOMETRIC ANALYSIS

Habitat differences and temporal trends

To address the questions posed in the Introduction, standard bibliometric analysis (Egoh *et al.,* 2007; Trabucchi *et al.,* 2012) was done on English-language peer-reviewed papers published before 2016 covered by the Thomson Reuters database Web of Science (http://wokinfo.com/). All searches were made on 8–12 January, 2016. Searching 'ecosystem service*' (where * represents a wildcard suffix) yielded 15 777 titles, adding 'habitat*' reduced this to 2200 titles, and adding 'conserv*' further trimmed the list to 1057 titles. Finally, a list of adjectives for various aquatic habitats ('aquatic OR freshwat* OR marine OR river* OR stream* OR mangrov* OR seagrass* OR reef* OR coral* OR ocean* OR intertidal OR groundwater OR estuar* OR wetland* OR lake* OR riparia* OR beach* OR saltmarsh*') was added to refine the sample to 473 titles.

Papers considering ecosystem services always comprised only a small proportion (< 20%) of the total numbers of papers on aquatic habitat conservation, collectively and within individual habitats (Figure 2). Within specific aquatic habitat types, papers on conservation were most common for 'ocean*', 'river*' and 'wetland*' followed by 'stream*', 'riparia*' and 'lake*' (Figure 2). In

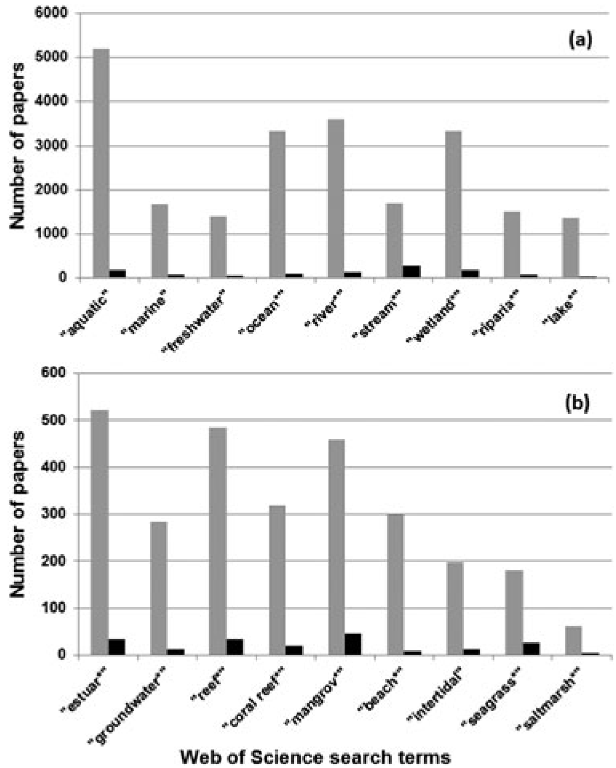

Figure 2. Number of papers that use these words in conjunction with "habitat* conservation" (grey shading) and "habitat* conservation AND ecosystem service*" (black shading). Note different vertical scales between panels (a) and (b). See text for more details

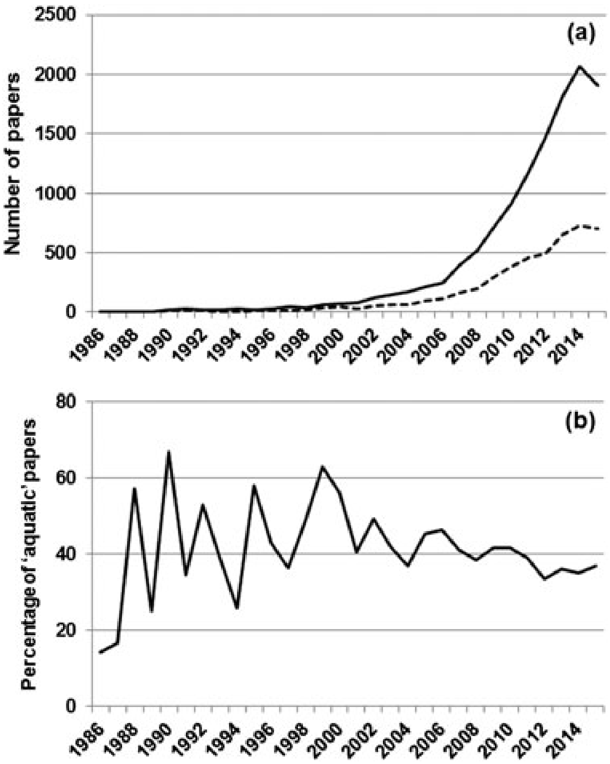

Figure 3. (a) Number of papers published each year from 1986–2015 that use the words "ecosystem service*" (solid line) and "ecosystem service*" with one or more adjectives listed in Figure 2 (broken line); (b) annual changes (1986–2015) in the percentage of 'aquatic' papers (lower line in (a)) mentioning "ecosystem service*" (upper line in (a)).

contrast, the total number and proportion of habitat-specific papers that also mentioned 'ecosystem service*' were greatest in 'stream*'. Surprisingly few papers covered habitat conservation of groundwater, intertidal zones, seagrasses and saltmarshes (Figure 2(b)).

Since 1986, there has been an exponential increase in the numbers of papers published per year that contain the term 'ecosystem service*' and a more gradual rise in those that include one of the aquatic adjectives listed above (Figure 3(a)). The slight dips in both lines in 2015 is probably an artefact through incomplete records for this year at the time of the search (January 2016). Disregarding the erratic fluctuations caused by small sample sizes before 2000, approximately 40% of aquatic-habitat papers also mentioned ecosystem services, a proportion that appears to be gradually falling (Figure 3(b)). Similar temporal trends are evident for papers containing the term 'ecosystem service* AND habitat*' (Figure 4) although the proportion of aquatic-habitat papers is higher (approximately 45% over the last 10 years) and not declining (Figure 4(b)).

The increasing numbers of papers published annually on aquatic habitat conservation that mention ecosystem services match temporal trends identified in a similar analysis of restoration literature by Trabucchi *et al.* (2012) and of literature on marine and coastal ecosystem services by Liquete *et al.* (2013) who also found a sharp rise in the numbers of papers on this topic published after 2006. This sharp rise is probably a response to publication of the influential MEA (2005) report that included lists of ecosystem services provided by various marine and freshwater habitats. Given the exponential increase in literature on ecosystem services in general (Figure 3(a)), the trends in proportions of aquatic habitats and conservation in this literature are more revealing. The striking observation that in the last decade, almost half the literature on

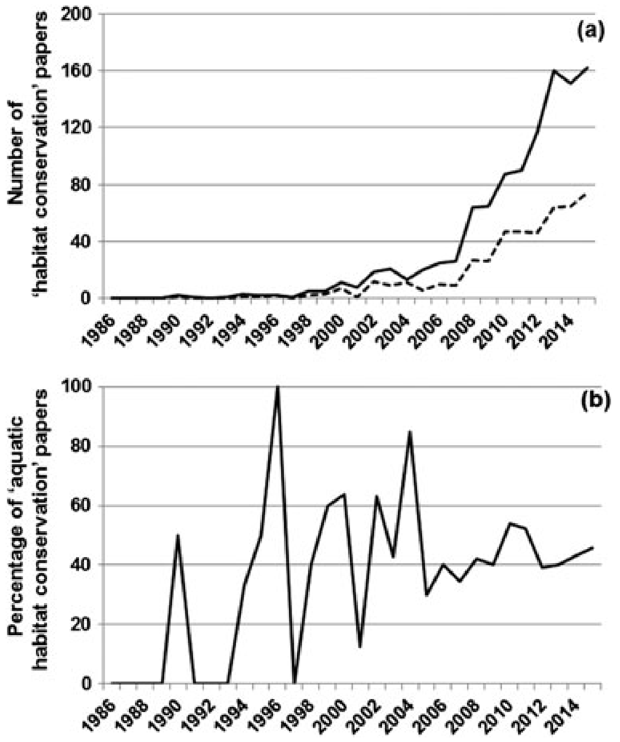

Figure 4. (a) Number of papers published each year from 1986–2015 that use the words "ecosystem service* AND habitat* conservation" (solid line) and "ecosystem service* AND habitat* conservation" with one or more adjectives listed in Figure 2 (broken line); (b) annual changes (1986–2015) in percentage of 'aquatic' papers (lower line in (a)) mentioning "ecosystem service* AND habitat*" (upper line in (a)).

ecosystem services in habitat conservation was from aquatic habitats led us to analyse the 473 papers (the data set of the broken line in Figure 4(a)) in more detail.

Spatio-temporal scales, ecosystem functions, trade-offs and social factors: 30 case studies

The titles and abstracts of each of these 473 papers were assessed for their match to four criteria: the work dealt with conservation rather than restoration, at least two of the four MEA (2005) groups of ecosystem services (Table 1) were considered, the work described one or more habitat-level case studies (to exclude general commentaries and reviews), and the work was not primarily a regional valuation exercise or mapping study (Blumstein and Thompson, 2015). This cull resulted in a final data set (Table S1) of 30 case studies, comprising 13 marine or estuarine habitats and 17 inland, mainly freshwater habitats. Generally, each case study was described fully in a single paper but occasionally additional papers and information sources were pursued to complement information from the primary reference. Only three marine and five freshwater case studies could be considered as field applications of aquatic conservation plans whereas the remaining studies were research-based (Table S1). As there did not appear to be gross differences in perspective between the two approaches, they were pooled for the analysis.

Of the 13 marine studies, five included mangrove habitats, three were coral reefs and two were coastal wetlands; the rest were single habitats including offshore banks, rocky sublittoral zones and estuarine saltmarshes. Of the 17 freshwater studies, five were various types of wetlands, three were

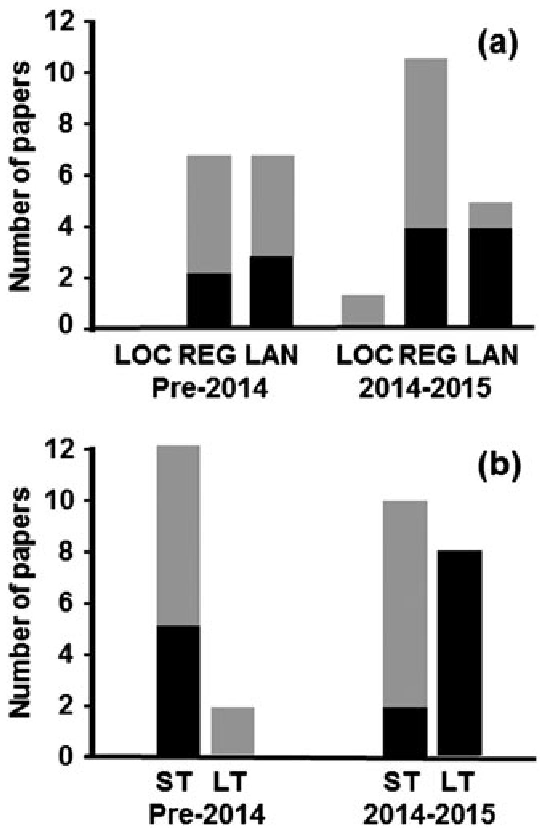

Figure 5. The spatial (a) and temporal (b) scales of 30 case studies of marine (black) and freshwater (grey) habitats, expressed as numbers of early (published pre-2014) and recent (2014–2015) papers to estimate temporal changes. Spatial scale was classified as 'local' (LOC, < 10 km^2), regional (REG, 10–1000 km^2) and landscape (LAN, > 1000 km^2). Temporal scale was classified as short-term (ST, < 10 y) or long-term (LT, ≥ 10 y).

floodplains, two were rivers and the rest were single habitats such as brackish lagoons and urban streams (Table S1). Only two of the habitats were primarily temporary, reflecting the tendency for freshwater conservation efforts to focus on perennially aquatic habitats (Boulton, 2014; Van den Broeck *et al.,* 2015; Leigh *et al.,* 2016).

Most of the 30 studies were published in 2015 (five marine, four freshwater) and 2014 (three, four). Therefore, to crudely assess temporal changes, studies were divided into ‘recent’ ones (published in 2014 or 2015) and ‘early’ ones (pre-2014 publication date). Of course, a paper’s publication date does not equate to when a conservation plan was developed; our intention was simply to estimate whether, for example, supporting and regulating services were more often considered in recent than early papers. We acknowledge the limitations of this simple binary approach but there were not enough papers to ascertain yearly trends.

The spatial scale of each case study was classified as ‘local’ (study region <10 km^2), ‘regional’ (10–1000 km^2) and ‘landscape’ (>1000 km^2). Only one study (Fleming *et al.,* 2014) was local in scale (Figure 5(a)), contrasting with the prevalence of local-scale studies (48%) reported for marine and coastal ecosystem services by Liquete *et al.* (2013). The other 29 studies were regional- and landscape-scale studies, with no marked differences between marine and freshwater except for proportionally fewer freshwater landscape-scale studies in 2014–2015 (Figure 5(a)). Before 2014, most of the studies were short-term whereas eight long-term (≥10 y) studies were published in 2014–2015, all of them marine (Figure 5(b)). This increase reflected greater use of temporal modelling, especially of climate change predictions (e.g. effects on coral reef ecosystem services, Rogers *et al.,* 2015). However, the absence of long-term studies in the 2014–2015 data set for freshwater habitats was unexpected.

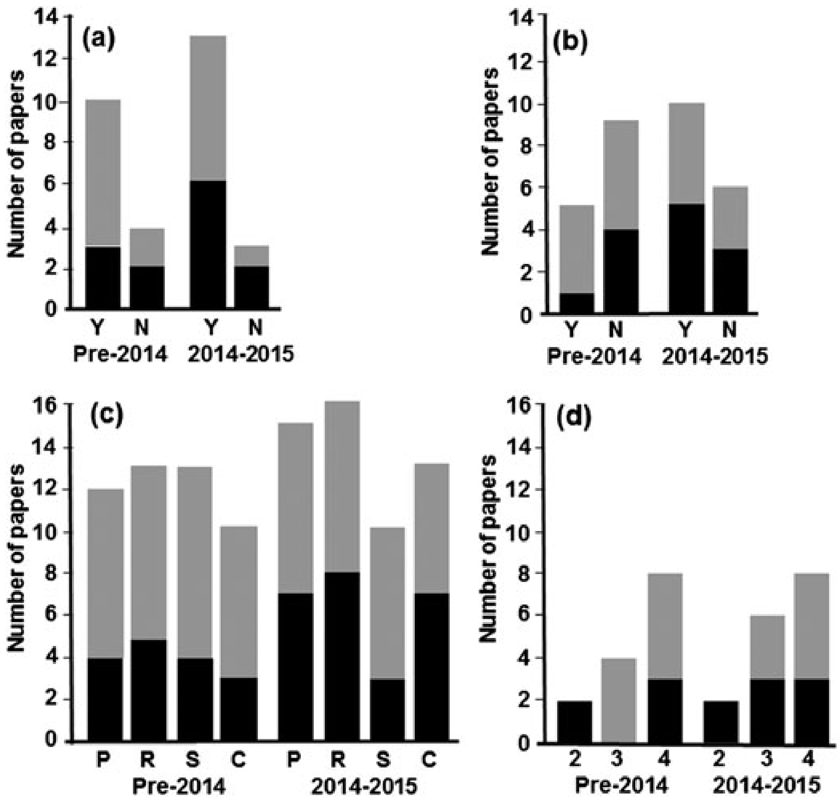

Figure 6. The numbers of early (published pre-2014) and recent (2014–2015) papers, describing 30 case studies of marine (black) and freshwater (grey) habitats, that (a) specified ecosystem services as conservation targets, (b) actually measured these ecosystem services, (c) included provisioning (P), regulating (R), supporting (S) and cultural (C) services, and (d) included 2, 3 or 4 services in total. See text for more details.

Only seven of the 30 studies did not specify ecosystem services as conservation targets; four published before 2014 and three in 2014 and 2015 (Figure 6(a)). Conserving ecosystem services as a specific target appears to be gaining increasing acceptance, indicated by the greater number of studies in 2014–2015, especially in marine habitats (Figure 6(a)). This also matches a rise over time of actually measuring ecosystem services (Figure 6 (b)), correlated with the increasing numbers of papers suggesting and validating measures for different services in aquatic habitats. From analysis of 25 years of conservation management plans in southern France, Ernoul *et al.* (2015) found that ecosystem services started being incorporated only after 2010, broadly corroborating our findings.

We expected earlier papers to assess provisioning ecosystem services in preference to the other three proposed by the MEA (2005) because of their more obvious material benefits and the greater ease of measurement (e.g. economic value). However, all four services received approximately equal attention, particularly in freshwater habitats (Figure 6(c)), probably because the main goal was conservation rather than, for example, exploitation for a fishery or potable water. The slight dip in the number of papers assessing supporting services in 2014 and 2015 coupled with increases for the other three services (Figure 6(c)) may reflect growing recognition that many supporting services are 'intermediate' rather than final services (Landers and Nahlik, 2013). Finally, we also expected that each of the papers published in 2014 and 2015 would assess more types of services than in earlier papers; another prediction not supported by the data (Figure 6(d)).

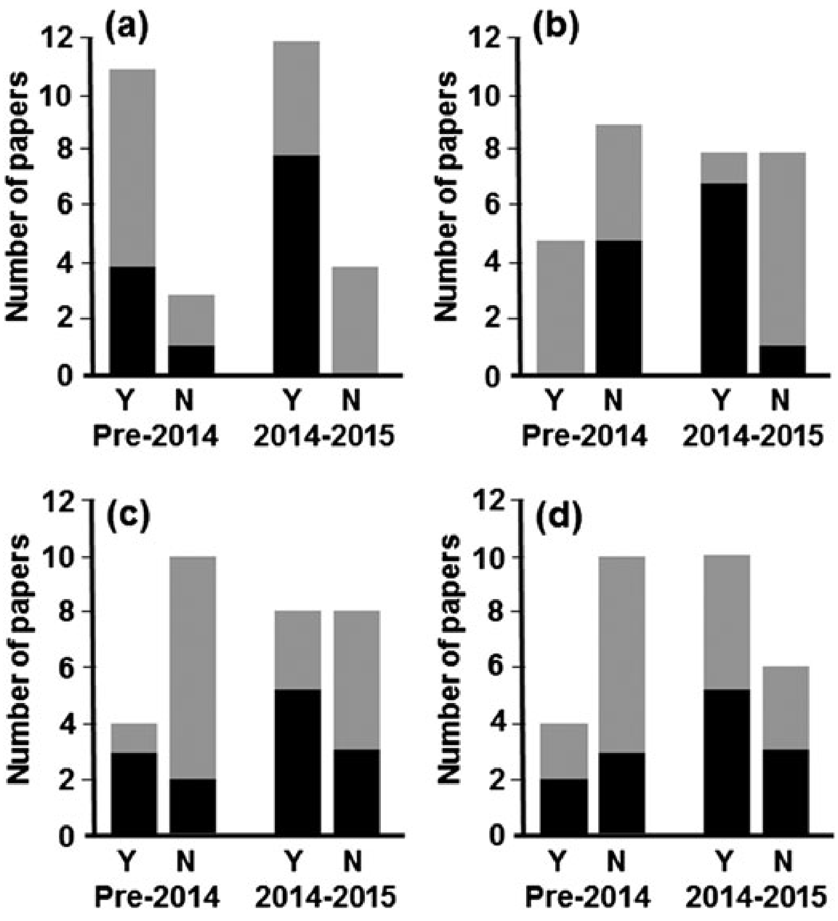

Figure 7. The numbers of early (published pre-2014) and recent (2014–2015) papers, describing 30 case studies of marine (black) and freshwater (grey) habitats, that (a) specified ecosystem functions or ecological processes underpinning targeted ecosystem services, (b) assessed trade-offs, (c) directly measured social factors, and (d) included valuation of ecosystem services.

Instead, most papers from both time periods assessed all four types (Figure 6(d)).

Most papers, especially those on marine habitats, specified the ecosystem functions or ecological processes underpinning targeted ecosystem services (Figure 7(a)). This is a reassuring finding, especially as conserving ecosystem functions and ecological processes usefully complements other conservation goals such as biodiversity (Kettunen and ten Brink, 2013). Fewer than half the papers assessed trade-offs (Figure 7(b)), even though this issue is likely to be common to all conservation strategies, as discussed earlier. Oddly, most of the recent papers on marine habitats tackled trade-offs whereas freshwater papers did not (Figure 7(b)), a pattern whose cause remains unclear. Few of the early papers, particularly those on freshwater habitats, directly measured social factors (Figure 7(c)). However, there seemed an increasing awareness of the importance of social factors, especially in marine habitat conservation (Figure 7(c)), perhaps aided by the greater availability of non-monetary assessment tools. Most of the recent papers included valuation of ecosystem services (Figure 7(d)) and again, this likely reflects the wider array of valuation techniques (Leimona *et al.,* 2015). It may also be a symptom of an increasingly utilitarian attitude to aquatic conservation as natural resources dwindle in the face of population growth.

None of the 30 case studies specified the spatial scale of expected responses to conservation strategies targeting ecosystem services in the various marine and freshwater habitats (Table S1), leaving the reader to infer that the response encompassed at least the conserved area. Only one study estimated temporal scales of response. Luisetti *et al.* (2014) compared provision of three ecosystem services (food, healthy climate and nature recreation) in two UK estuaries over three modelled scenarios, one of which involved extended conservation of coastal ecosystems, spanning the temporal scale of 2010–2110. The remaining 29 studies either did not consider temporal scales of response at all or used non-specific language, typically to infer that responses would be gradual and 'long-term' (Table S1).

CONCLUSIONS AND RECOMMENDATIONS

Our first goal was to review the extent to which current aquatic habitat conservation strategies target ecosystem services as one of their objectives, and how adoption of this perspective has changed over time. Most current descriptions of aquatic habitat conservation strategies acknowledge the importance of ecosystem services, and this appears to date back to about 2006, following publication of the influential MEA (2005) report. Since about 2010, specifically targeting ecosystem services as a conservation target has become more common, especially in marine habitats. Our second goal was to assess which groups of ecosystem services have been evaluated and incorporated when developing aquatic habitat conservation strategies. Contrary to expectation that provisioning services would feature most prominently, we found that all four groups of services were targeted by aquatic conservation strategies and there was no trend of increasing recognition of the more subtle supporting and regulating services over time.

Our third goal was to explore issues of scale, trade-offs and social factors, and the extent to which these are explicitly considered in aquatic conservation strategies. Although spatial scale was often considered explicitly, seldom did strategies predict temporal scales of response to conservation measures. Fewer than half the papers in the literature review of 30 case studies assessed trade-offs or considered social factors, despite the central importance of both these aspects when weighing up conservation options. Both factors attracted more consideration in marine habitats than freshwater ones. Valuation of ecosystem services in both habitats is becoming more prevalent in aquatic conservation. Our final goal was to assess whether there are any fundamental differences between marine and freshwater habitats with respect to their ecosystem services that should be considered when setting targets for their conservation. We found no evidence for any such differences, implying that experiences from both habitats are equally relevant for informing strategies for conservation of ecosystem services in either marine or freshwater habitats. More important considerations appeared to be the spatial and temporal extent of ecological connectivity within and among different habitats as well as stakeholders' perceptions of threats to and values of ecosystem services provided by a given habitat.

Protection of biodiversity, biophysical complexity and ecological processes has always been core to conservation strategies of marine and freshwater habitats; the perspective of conserving ecosystem services should be seen as complementary rather than a replacement (Ormerod, 2014). Increasing recognition of links between these features and societal benefits (Figure 1) has led to greater efforts to assign economic values to ecosystem services from different habitats (de Groot *et al.,* 2012), potentially favouring a socio-economic 'utilitarian' attitude to conservation at the expense of conservation of nature for its own sake (Silvertown, 2015). Debate about this dichotomy is growing more acrimonious, especially as members of many conservation organizations hold widely varying views (Fisher and Brown, 2014). Tallis *et al.* (2014) suggest the issue is best resolved by a more inclusive perspective that unifies both ethical stances. We agree, and recommend integrating protection of ecosystem services with other conservation goals in a way that acknowledges diverse cultures and value systems – the 'people and nature' perspective (Mace, 2014).

Our review of the literature revealed that most studies of ecosystem services in aquatic habitat conservation either focus on quite specific aspects (e.g. mapping services, Clerici *et al.,* 2013; Galparsoro *et al.,* 2014) or assessed only one or two habitats (Table S1). Some habitats (e.g. mangroves, coral reefs, floodplains) attracted much more attention than others such as groundwater, rocky sublittoral zones and off-shore banks. Few studies address all the aspects and links portrayed in Figure 1 for complete suites of ecosystem services, and none of the 30 case studies examined in detail was based on conservation strategies that included a complete inventory of ecosystem services, the ecological processes and ecosystem functions underpinning them, and assessment of spatial and temporal scales of service flow, potential trade-offs, social factors, and values for each service.

Therefore, we offer several recommendations when an ecosystem-service perspective is proposed for setting targets for conservation of marine and freshwater habitats:

1. Integrate the ecosystem-service approach with current conservation goals (e.g. biodiversity protection) rather than adopt this approach as an alternative.
2. Specify each ecosystem service and its beneficiaries as precisely as possible. Although heuristic classifications such as the one by MEA (2005) are valuable communication tools, they must be supplemented with operational classifications that explicitly combine ecological and environmental components with social values (e.g. the 'Final Ecosystem Goods and Services' classification system described by Landers and Nahlik (2013)). This helps ensure a comprehensive inventory of ecosystem services specifically associated with each habitat and potential beneficiary, acknowledging the diverse array of stakeholders deriving different values from conservation of a particular habitat.
3. Specify spatial and temporal scales for the provision and flow of each ecosystem service. This clarifies which aspects of biophysical complexity and ecosystem function are likely to be adequately protected by a given conservation strategy, especially where connectivity between habitats is relevant. These temporal scales should also include 'anticipatory management' (Rogers *et al.,* 2015) that incorporates projected future changes in, for example, climate and social pressures, so that conservation strategies can be tailored accordingly.
4. Specify the aspects of biophysical complexity and ecosystem function required for each ecosystem service, providing evidence to describe the ecological mechanism(s) underpinning the derivative services. Poorly known mechanisms may be supplemented by conceptual models (Wen *et al.,* 2011; Harrison, 2013) to generate testable hypotheses for future work and to support scenario-modelling of different conservation strategies.
5. Specify current and future trade-offs among ecosystem services, especially where these potentially affect the outcomes of different conservation strategies. Identifying trade-offs

enables policy-makers and conservation managers to understand the long-term effects of protecting one service over one or more others, and the consequences of focusing only on the present provision of a service rather than its future (Rodríguez *et al.,* 2006).

6. Identify social factors that might influence the flow of services, changes in values over time, and different expectations of stakeholders and beneficiaries. Social factors also influence prioritization of conservation actions, especially the perception by stakeholders of the success of particular strategies (Geist, 2015) and their cost-effectiveness (Terrado *et al.,* 2016). Choose valuation methods carefully, acknowledging their context-dependency, constraints and limitations (Sukhdev *et al.,* 2014).
7. Couch conservation goals for protecting ecosystem services in terms of reliable and measurable indicators that can support consistent decision making (Olander *et al.,* 2015), and develop a monitoring programme sufficiently powerful to assess progress towards these goals. This programme should complement current monitoring and include ecological and sociological variables to assess successful provision of desired ecosystem services. Rapid prioritization methods (Werner *et al.,* 2014) may be useful to identify indicators and guide their monitoring and analysis.

These recommendations should be supplemented with appropriate tools and frameworks for ecosystem-service assessment (Felipe-Lucia *et al.,* 2015; Mongruel *et al.,* 2015; Boithias *et al.,* 2016). We reiterate that aquatic habitat conservation objectives should not focus solely on protecting or enhancing ecosystem services but should complement current strategies targeting biodiversity and other conservation goals. The ecosystem-services perspective helps communicate to society some of the values of the less-tangible benefits of natural ecosystems (e.g. justification for conserving maerl beds for their carbon storage potential (Burrows *et al.,* 2014) as well as their provision of nursery habitat for larvae of many commercial fish species), but there are many other reasons for conserving marine and freshwater habitats and their connectivity. As with so many conservation issues, a holistic perspective is the most effective and so there is value in integrating ecosystem services into conservation strategies for freshwater and marine habitats.

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REFERENCES

Acreman MC, Harding RJ, Lloyd C, McNamara NP, Mountford JO, Mould DJ, Purse BV, Heard MS, Stratford CJ, Dury SJ. 2011. Trade-off in ecosystem services of the Somerset Levels and Moors wetlands. *Hydrological Sciences Journal* **56**: 1543–1565.

Arkema KK, Verutes GM, Wood SA, Clarke-Samuels C, Rosado S, Canto M, Rosenthal A, Ruckelshaus M, Guannel G, Toft J, *et al.* 2015. Embedding ecosystem services in coastal planning leads to better outcomes for people and nature. *Proceedings of the National Academy of Sciences of the United States of America* **112**: 7390–7395.

Balmford AB, Fisher R, Green R, Naidoo B, Strassburg R, Turner K, Rodrigues AL. 2011. Bringing ecosystem services into the real world: an operational framework for assessing the economic consequences of losing wild nature. *Environmental and Resource Economics* **48**: 161–175.

Barbier EB. 2009. Ecosystem services trade-offs. In *Ecosystem-Based Management for the Oceans*, McLeod K, Leslie H. (eds). Island Press: Washington; 129–144.

Barbier EB, Koch, EW, Silliman BR, Hacker SD, Wolanski E, Primavera J, Granek EF, Polasky S, Aswani S, Cramer LA, *et al.* 2008. Coastal ecosystem-based management with nonlinear ecological functions and values. *Science* **319**: 321–323.

Beaumont N, Austen MC, Atkins J, Burdon D, Degraer S, Dentinho TP, Derous S, Holm P, Horton T, van Ierland E, *et al.* 2007. Identification, definition and quantification of goods and services provided by marine biodiversity: Implications for the ecosystem approach. *Marine Pollution Bulletin* **54**: 253–265.

Beger M, Grantham HS, Pressey RL, Wilson KA, Peterson EL, Dorfman D, Mumby PJ, Lourival R, Brumbaugh DR, Possingham HP. 2010. Conservation planning for connectivity across marine, freshwater, and terrestrial realms. *Biological Conservation* **143**: 565–575.

Blumstein M, Thompson JR. 2015. Land-use impacts on the quantity and configuration of ecosystem service provisioning in Massachusetts, USA. *Journal of Applied Ecology* **52**: 1009–1019.

Boithias L, Terrado M, Corominas L, Ziv G, Kumar V, Marqués M, Schuhmacher M, Acuña V. 2016. Analysis of the uncertainty in the monetary valuation of ecosystem services - A case study at the river basin scale. *The Science of the Total Environment* **543**: 683–690.

Boon PJ. 2012. Revisiting the case for river conservation. In *River Conservation and Management*, Boon PJ, Raven PJ (eds). John Wiley: Chichester; pp. 3–14.
Boulton AJ. 2014. Conservation of ephemeral streams and their ecosystem services: what are we missing? *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**: 733–738.
Brauman KA, Daily GC, Duarte TK, Mooney HA. 2007. The nature and value of ecosystem services: an overview highlighting hydrologic services. *Annual Review of Environment and Resources* **32**: 67–98.
Brondizio ES, Ostrom E, Young O. 2009. Connectivity and the governance of multilevel socio-ecological systems: the role of social capital. *Annual Review of Environment and Resources* **34**: 253–278.
Burrows MT, Kamenos NA, Hughes DJ, Stahl H, Howe JA, Tett P. 2014. Assessment of carbon budgets and potential blue carbon stores in Scotland's coastal and marine environment. Scottish Natural Heritage Commissioned Report No. 761, Edinburgh.
Carlsen AJ, Strand J, Wenstöp F. 1993. Implicit environmental costs in hydroelectric development: an analysis of the Norwegian master plan for water resources. *Journal of Environmental Economics and Management* **25**: 201–211.
Castro AJ, Martín-López B, López E, Plieninger T, Alcaraz-Segura D, Vaughn CC, Cabello J. 2015. Do protected areas networks ensure the supply of ecosystem services? Spatial patterns of two nature reserve systems in semi-arid Spain. *Applied Geography* **60**: 1–9.
Chan KM, Guerry AD, Balvanera P, Klain S, Satterfield T, Basurto X, Bostrom A, Chuenpagdee R, Gould R, Halpern BS, *et al.* 2012. Where are *cultural* and *social* in ecosystem services? A framework for constructive engagement. *BioScience* **62**: 744–756.
Clerici N, Weissteiner CJ, Paracchini ML, Boschetti L, Baraldi A, Strobl P. 2013. Pan-European distribution modelling of stream riparian zones based on multi-source Earth Observation data. *Ecological Indicators* **24**: 211–223.
Convention on Biological Diversity. 2010. Strategic plan for biodiversity 2011-2020 and the Aichi targets. https://www.cbd.int/doc/strategic-plan/2011-2020/Aichi-Targets-EN.pdf [14 February 2016]
Cowling RM, Egoh B, Knight AT, O'Farrell PJ, Reyers B, Rouget M, Roux DJ, Welz A, Wilhelm-Rechman A. 2008. An operational model for mainstreaming ecosystem services for implementation. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 9483–9488.
Crossman ND, Bryan BA. 2009. Identifying cost-effective hotspots for restoring natural capital and enhancing landscape multifunctionality. *Ecological Economics* **68**: 654–656.
Daily GC, Polasky S, Goldstein J, Kareiva PM, Mooney HA, Pejchar L, Ricketts TH, Salzman J, Shallenberger R. 2009. Ecosystem services in decision making: time to deliver. *Frontiers in Ecology and the Environment* **7**: 21–28.
Day JC. 2002. Zoning — lessons from the Great Barrier Reef Marine Park. *Ocean and Coastal Management* **45**: 139–156.
De Groot RS, Wilson MA, Boumans RMJ. 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics* **41**: 393–408.
De Groot RS, Alkemade R, Braat L, Hein L, Willemen L. 2010. Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecological Complexity* **7**: 260–272.
De Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M, Crossman N, Ghermandi A, Hein L, *et al.* 2012. Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services* **1**: 50–61.
Drakou EG, Crossman ND, Willemen L, Burkhard B, Palomog I, Maes J, Peedell S. 2015. A visualization and data-sharing tool for ecosystem service maps: Lessons learnt, challenges and the way forward. *Ecosystem Services* **13**: 134–140.
Dudgeon D. 2014. Accept no substitute: biodiversity matters. *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**: 435–440.
Eastwood A, Brooker R, Irvine RJ, Artz RRE, Norton LR, Bullock JM, Ross L, Fielding D, Ramsay S, Roberts J, *et al.* 2016. Does nature conservation enhance ecosystem services delivery? *Ecosystem Services* **17**: 152–162.
Egoh B, Rouget M, Reyers B, Knight AT, Cowling RM, van Jaarsveld AS, Welz A. 2007. Integrating ecosystem services into conservation assessments: a review. *Ecological Economics* **63**: 714–721.
Ehler C, Douvere F. 2009. Marine Spatial Planning: a step-by-step approach toward ecosystem-based management. Intergovernmental Oceanographic Commission and Man and the Biosphere Programme, IOC Manual and Guides No. 53, ICAM Dossier No. 6. UNESCO, Paris.
Ernoul L, Beck N, Cohez D, Perennou C, Thibault M, Willm L, Poulin B. 2015. Trends in management plans and guides: 25 years of experience from Southern France. *Journal of Environmental Planning and Management* **58**: 1096–1112.
EU 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive*). Official Journal of the European Union* **L 164**: 1–22.
EU 2014. Directive 2014/89/EU of the European Parliament and of the Council of 23 July 2014 establishing a framework for maritime spatial planning. *Official Journal of the European Union L* **257**: 135–145.
European Commission. 2011. Our life insurance, our natural capital: An EU biodiversity strategy to 2020. http://ec.europa.eu/environment/nature/biodiversity/comm2006/pdf/EP_resolution_april2012.pdf. [14 February 2015]
Everard M, Kataria G. 2011. Recreational angling markets to advance the conservation of a reach of the Western Ramganga River, India. *Aquatic Conservation: Marine and Freshwater Ecosystems* **21**: 101–108.
Felipe-Lucia MR, Comín FA, Escalera-Reyes J. 2015. A framework for the social valuation of ecosystem services. *Ambio* **44**: 308–318.
Fisher B, Turner RK, Morling P. 2009. Defining and classifying ecosystem services for decision making. *Ecological Economics* **68**: 643–653.
Fisher B, Bradbury RB, Andrews JE, Ausden M, Bentham-Green S, White SM, Gill JA. 2011. Impacts of species-led conservation on ecosystem services of wetlands: understanding co-benefits and tradeoffs. *Biodiversity and Conservation* **20**: 2461–2481.
Fisher JA, Brown K. 2014. Ecosystem services concepts and approaches in conservation: Just a rhetorical tool? *Ecological Economics* **108**: 257–265.

Fleming WM, Rivera JA, Miller A, Piccarello M. 2014. Ecosystem services of traditional irrigation systems in northern New Mexico, USA. *International Journal of Biodiversity Science, Ecosystem Services and Management* **10**: 343–350.

Folke C, Pritchard L, Berkes F, Colding J, Svedin U. 2007. The problem of fit between ecosystems and institutions: ten years later. *Ecology and Society* **12**(1): Article 30.

Gaines SD, White C, Carr MH, Palumbi SR. 2010. Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Sciences of the United States of America* **107**: 18286–18293.

Galparsoro I, Borja A, Uyarra MC. 2014. Mapping ecosystem services provided by benthic habitats in the European North Atlantic Ocean. *Frontiers in Marine Science* **1**: Article 23. doi 10.3389/fmars.2014.00023.

Geist J. 2015. Seven steps towards improving freshwater conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **25**: 447–453.

Gíslason S. 2016. Verkefnisstjórn 3. áfanga verndar- og orkunýtingaráætlunar. Drög að lokaskýrslu (Steering Committee of Strategic Planning 3rd milestone of conservation and energy utilization. Draft of final report. Results of the 2nd results of the framework plan for the use of hydropower and geothermal energy). Icelandic Ministry for the Environment and Natural Resources, Reykjavik [In Icelandic].

Great Barrier Reef Marine Park Authority. 2014. *Great Barrier Reef Region Strategic Assessment: Strategic Assessment Report*, GBRMPA, Townsville, Queensland.

Green PA, Vörösmarty CJ, Harrison I, Farrell T, Sáenzc L, Fekete BM. 2015. Freshwater ecosystem services supporting humans: Pivoting from water crisis to water solutions. *Global Environmental Change* **34**: 108–118.

Grimm NB, Staudinger MD, Staudt A, Carter SL, Chapin FS, Kareiva P, Ruckelshaus M, Stein BA. 2013. Climate-change impacts on ecological systems: introduction to a US assessment. *Frontiers in Ecology and the Environment* **11**: 456–464.

Haines-Young R, Potschin M. 2010. The links between biodiversity, ecosystem services and human well-being. In *Ecosystem Ecology: A New Synthesis*, Raffaelli DG, Frid CLJ (eds). Cambridge University Press: Cambridge; pp. 110–139.

Halpern BS, Lester SE, McLeod KL. 2010. Placing marine protected areas onto the ecosystem-based management seascape. *Proceedings of the National Academy of Sciences of the United States of America* **107**: 18312–18317.

Harrison ME. 2013. Using conceptual models to understand ecosystem function and impacts of human activities in tropical peat-swamp forests. *Wetlands* **33**: 257–267.

Hein L, van Koppen K, de Groot RS, van Ierland EC. 2006. Spatial scales, stakeholders and the valuation of ecosystem services. *Ecological Economics* **57**: 209–228.

HELCOM. 2010. Towards an ecologically coherent network of well-managed Marine Protected Areas – Implementation report on the status and ecological coherence of the HELCOM BSPA network. Baltic Sea Environment Proceedings No. 124 A. Baltic Marine Environment Protection Commission, Helsinki, Finland.

Huxham M, Emerton L, Kairo J, Munyi F, Abdirizak H, Muriuki T, Nunan F, Briers RA. 2015. Applying climate compatible development and economic valuation to coastal management: A case study of Kenya's mangrove forests. *Journal of Environmental Management* **157**: 168–181.

Jobstvogt N, Watson V, Kenter JO. 2014. Looking below the surface: the cultural ecosystem service values of UK marine protected areas (MPAs). *Ecosystem Services* **10**: 97–110.

Kelleher G. 1999. *Guidelines for Marine Protected Areas*. IUCN: Gland, Switzerland and Cambridge, UK.

Kelemen E, Potschin M, Martín-López B, Pataki G. 2015. Ecosystem services: A gender perspective. In *OpenNESS Reference Book*, Potschin M, Jax K (eds), Synthesis Paper #23. www.openness-project.eu/library/reference-book [10 February 2015]

Kettunen, M, ten Brink P. 2013. *Social and Economic Benefits of Protected Areas: An Assessment Guide*. Taylor and Francis: London.

Kosoy N, Corbera E. 2010. Payments for ecosystem services as commodity fetishism. *Ecological Economics* **69**: 1228–1236.

Kretsch C, Kelemen E. 2015. Ecosystem services and social justice. In *OpenNESS Reference Book*, Potschin M, Jax K (eds), Synthesis Paper #24. www.openness-project.eu/library/reference-book [8 February 2015]

Landers DH, Nahlik AM. 2013. Final Ecosystem Goods and Services Classification System (FEGS-CS). EPA/600/R-13/ORD-004914. US Environmental Protection Agency, Office of Research and Development, Washington DC.

Large ARG, Gilvear DJ. 2015. Using *Google Earth*, a virtual-globe imaging platform, for ecosystem services-based river assessment. *River Research and Applications* **31**: 406–421.

Larson S, Stoeckl N, Neil B, Welters R. 2013. Using resident perceptions of values associated with the Australian Tropical Rivers to identify policy and management priorities. *Ecological Economics* **94**: 9–18.

Lau WWY. 2013. Beyond carbon: Conceptualizing payments for ecosystem services in blue forests on carbon and other marine and coastal ecosystem services. *Ocean and Coastal Management* **83**: 5–14.

Laurans Y, Pascal N, Binet T, Brander L. 2013. Economic valuation of ecosystem services from coral reefs in the South Pacific: taking stock of recent experience. *Journal of Environmental Management* **116**: 135–144.

Leenhardt P, Low N, Pascal N, Micheli F, Claudet J. 2015. The role of marine protected areas in providing ecosystem services. In *Aquatic Functional Biodiversity: An Ecological and Evolutionary Perspective*, Belgrano A, Woodward G, Jacob U. (eds). Elsevier: London; pp. 211–239.

Leigh C, Boulton AJ, Courtwright JL, Fritz K, May CL, Walker RH, Datry T. 2016. Ecological research and management of intermittent rivers: an historical review and future directions. *Freshwater Biology* **61**: 1181–1199. doi:10.1111/fwb.12646

Leimona B, Noordwijk M, deGroot R, Leemans R. 2015. Fairly efficient, efficiently fair: Lessons from designing and testing payment schemes for ecosystem services in Asia. *Ecosystem Services* **12**: 16–28.

Leslie HM, McLeod KL. 2007. Confronting the challenges of implementing marine ecosystem-based management. *Frontiers in Ecology and the Environment* **5**: 540–548.

Lester SE, Halpern BS. 2008. Biological responses in marine no-take reserves versus partially protected areas. *Marine Ecology Progress Series* **367**: 49–56.

Liquete C, Piroddi C, Drakou EG, Gurney L, Katsanevakis S, Charef A, Egoh B. 2013. Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. *PLoS ONE* **8**: e67737.

Liu J, Yang W, Li S. 2016. Framing ecosystem services in the telecoupled Anthropocene. *Frontiers in Ecology and the Environment* **14**: 27–36.

Luck GW, Chan KMA, Eser U, Gomez-Baggethun E, Matzdorf B, Norton B, Potschin MB. 2012. Ethical considerations in on-ground applications of the ecosystem services concept. *BioScience* **62**: 1020–1029.

Luisetti T, Turner RK, Jickells T, Andrews J, Elliott M, Schaafsma M, Beaumont N, Malcolm S, Burdon D, Adams C, *et al.* 2014. Coastal zone ecosystem services: From science to values and decision making; a case study. *Science of the Total Environment* **493**: 682–693.

Mace GM. 2014. Whose conservation? *Science* **345**: 1558–1560.

Maltby E, Acreman M, Blackwell MSA, Everard M, Morris J. 2013. The challenges and implications of linking wetland science to policy in agricultural landscapes - experience from the UK National Ecosystem Assessment. *Ecological Engineering* **56**: 121–133.

McLeod KL, Leslie HM. 2009. Why ecosystem-based management? In *Ecosystem-Based Management for the Oceans*, McLeod K, Leslie H. (eds). Island Press, Washington; pp. 3–12.

Menzel S, Teng J. 2010. Ecosystem services as a stakeholder-driven concept for conservation science. *Conservation Biology* **24**: 907–909.

MEA. 2005. *Ecosystems and Human Well-Being: Synthesis*. Millennium Ecosystem Assessment, Island Press: Washington.

Miljøverndepartementet. 1984. Samlet Plan for Vassdrag Hovedrapport. 1984. Master plan for catchments: main report. Miljøverndepartementet, Oslo. [In Norwegian].

Miteva DA, Murray BC, Pattanayak SK. 2015. Do protected areas reduce blue carbon emissions? A quasi-experimental evaluation of mangroves in Indonesia. *Ecological Economics* **119**: 127–135.

Mongruel R, Beaumont N, Hooper T, Levrel H, Somerfield P, Thiébaut E, Langmead O, Charles M. 2015. A framework for the operational assessment of marine ecosystem services. VALMER WP1 Guidelines Document, INTERREG IV A France (Channel) – England, ERDF. http://www.valmer.eu/wp-content/uploads/2015/03/A-framework-for-the-operational-assessment-of-marine-ecosystem-services.pdf. [14 February 2016]

Mugnai R, Messana G, Di Lorenzo T. 2015. The hyporheic zone and its functions: revision and research status in Neotropical regions. *Brazilian Journal of Biology* **75**: 524–534.

Muradian R, Corbera E, Pascual U, Kosoy N, May P. 2010. Reconciling theory and practice: an alternative conceptual framework for understanding payments for ecosystem services. *Ecological Economics* **69**: 1202–1208.

Muradian R, Arsel M, Pellegrini L, Adaman F, Aguilar B, Agarwal B, Corbera E, Ezzine de Blas D, Farley J, Froger G, *et al.* 2013. Payments for ecosystem services and the fatal attraction of win-win solutions. *Conservation Letters* **6**: 274–279.

Nahlik AM, Kentula ME, Fennessy MS, Landers DH. 2012. Where is the consensus? A proposed foundation for moving ecosystem service concepts into practice. *Ecological Economics* **77**: 27–35.

Naidoo R, Ricketts TH. 2006. Mapping the economic costs and benefits of conservation. *PLoS Biology* **4**: 2153–2164.

Ng CN, Xie YJ, Yu XJ. 2013. Integrating landscape connectivity into the evaluation of ecosystem services for biodiversity conservation and its implications for landscape planning. *Applied Geography* **42**: 1–12.

Nicholson E, Mace GM, Armsworth PR, Atkinson G, Buckle S, Clements T, Ewers RM, Fa JE, Gardner TA, Gibbons J, *et al.* 2009. Priority research areas for ecosystem services in a changing world. *Journal of Applied Ecology* **46**: 1139–1144.

NOAA. 2015. National Habitat Policy. National Oceanic and Atmospheric Administration (NOAA). Administrative order 216–117, NOAA Administrative Order Series.

Olander L, Johnston RJ, Tallis H, Kagan J, Maguire L, Polasky S, Urban D, Boyd J, Wainger L, Palmer M. 2015. Best practices for integrating ecosystem services into federal decision making. National Ecosystem Services Partnership, Duke University, Durham.

Olds AD, Pitt KA, Maxwell PS, Connolly RM. 2012. Synergistic effects of reserves and connectivity on ecological resilience. *Journal of Applied Ecology* **49**: 1195–1203.

Ormerod SJ. 2014. Rebalancing the philosophy of river conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**: 147–152.

Palmer MY, Filoso S, Fanelli RM. 2014. From ecosystems to ecosystem services: stream restoration as ecological engineering. *Ecological Engineering* **65**: 62–70.

de Souza Rares C, Brandimarte AL. 2014. The challenge of aquatic environments conservation and continuity of environmental services in urban green areas: the case of Cantareira State Park. *Ambiente y Sociedade* **17**: 111–128.

Raudsepp-Hearne C, Peterson GD, Bennett EM. 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proceedings of the National Academy of Sciences of the United States of America* **107**: 5242–5247.

Reker J, Annunziatellis A, Mo G, Tunesi L, Globevnik L, Snoj L, Agnesi S, Korpinen S. 2015. Marine protected areas in Europe's seas - An overview and perspectives for the future. EEA Report 3, European Environment Agency, Luxembourg.

Rees SE, Austen MC, Attrill MJ, Rodwell LD. 2012. Incorporating indirect ecosystem services into marine protected area planning and management. *International Journal of Biodiversity Science, Ecosystem Services and Management* **8**: 273–285.

Renard D, Rhemtulla JM, Bennett EM. 2015. Historical dynamics in ecosystem service bundles. *Proceedings of the National Academy of Sciences of the United States of America* **112**: 13411–13416.

Rodríguez JP, Beard TD, Bennett EM, Cumming GS, Cork SJ, Agard J, Dobson AP, Peterson GD. 2006. Trade-offs across space, time, and ecosystem services. *Ecology and Society* **11**(1): Article 28.

Rogers A, Harborne AR, Brown C, Bozec Y-M, Castro C, Chollett I, Hock K, Knowland CA, Marshell A, Ortiz JC, *et al.* 2015. Anticipative management for coral reef ecosystem services in the 21st century. *Global Change Biology* **21**: 504–514.

Rouquette JR, Posthumus H, Gowing DJG, Tucker G, Dawson QL, Hess TM, Morris J. 2009. Valuing nature-conservation interests on agricultural floodplains. *Journal of Applied Ecology* **46**: 289–296.

Ruiz-Frau A, Hinz H, Edwards-Jones G, Kaiser MJ. 2013. Spatially explicit economic assessment of cultural ecosystem services: Non-extractive recreational uses of the coastal environment related to marine biodiversity. *Marine Policy* **38**: 90–98.

Sanon S, Hein T, Douven W, Winkler P. 2012. Quantifying ecosystem service trade-offs: The case of an urban floodplain in Vienna, Austria. *Journal of Environmental Management* **111**: 159–172.

Schirmer M, Luster J, Linde N, Perona P, Mitchell EAD, Barry DA, Hollender J, Cirpka OA, Schneider P, Vogt T, *et al.* 2014. Morphological, hydrological, biogeochemical and ecological changes and challenges in river restoration - the Thur River case study. *Hydrology and Earth System Sciences* **18**: 2449–2462.

Schwerdtner Máñez K, Krause G, Ring I, Glaser M. 2014. The Gordian knot of mangrove conservation: Disentangling the role of scale, services and benefits. *Global Environmental Change* **28**: 120–128.

Secretariat of the Convention on Biological Diversity. 2005. *Handbook of the Convention on Biological Diversity Including its Cartagena Protocol on Biosafety*, 3rd ed. Convention on Biological Diversity: Montreal.

Silvertown J. 2015. Have ecosystem services been oversold? *Trends in Ecology & Evolution* **30**: 641–648.

Staddon P, Lindo Z, Crittenden PD, Gilbert F, Gonzalez A. 2010. Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecology Letters* **13**: 543–552.

Stoeckl N, Hicks CC, Mills M, Fabricius K, Esparon M, Kroon F, Kaur K, Constanza R. 2011. The economic value of ecosystem services in the Great Barrier Reef: our state of knowledge. *Annals of the New York Academy of Sciences* **1219**: 113–133.

Stoms DM, Davis FW, Andelman SJ, Carr MH, Gaines SD, Halpern BS, Hoenicke R, Leibowitz SG, Leydecker A, Madin EMP, *et al.* 2005. Integrated coastal reserve planning: making the land–sea connection. *Frontiers in Ecology and the Environment* **3**: 429–436.

Sukhdev P, Wittmer H, Miller D. 2014. The Economics of Ecosystems and Biodiversity (TEEB): Challenges and responses. In *Nature in the Balance: The Economics of Biodiversity*, Helm D, Hepburn C. (eds). Oxford University Press: Oxford; pp. 135–150.

Syrbe RU, Walz U. 2012. Spatial indicators for the assessment of ecosystem services: providing, benefiting and connecting areas and landscape metrics. *Ecological Indicators* **21**: 80–88.

Tallis H, Lubchenko J, 238 cosignatories. 2014. A call for inclusive conservation. *Nature* **515**: 27–28.

TEEB. 2010. *The Economics of Ecosystems and Biodiversity: Ecological and Economic Foundation*. Earthscan: London and Washington.

Terrado M, Momblanch A, Bardina M, Boithias L, Munné A, Sabater S, Solera A, Acuña V. 2016. Integrating ecosystem services in river basin management plans. *Journal of Applied Ecology* 53: doi: 10.1111/1365-2664.12613.

The White House Council on Environmental Quality. 2010. *Final recommendations of the Interagency Ocean Policy Task Force July 19, 2010. Executive Office of the President of the United States*, Washington, DC.

Thórhallsdóttir TEl. 2007a. Strategic planning at the national level: Evaluating and ranking energy projects by environmental impact. *Environmental Impact Assessment Review* **27**: 545–568.

Thórhallsdóttir TEl. 2007b. Environment and energy in Iceland: A comparative analysis of values and impacts. *Environmental Impact Assessment Review* **27**: 522–544.

Trabucchi M, Ntshotsho P, O'Farrell P, Comín FA. 2012. Ecosystem service trends in basin-scale restoration initiatives: A review. *Journal of Environmental Management* **111**: 18–23.

Turkelboom F, Thoonen M, Jacobs S, García-Llorente M, Martín-López B, Berry P. 2015. Ecosystem services trade-offs and synergies (draft). In *OpenNESS Reference Book*, Potschin M, Jax K (eds), Synthesis Paper #27. www.openness-project.eu/library/reference-book [8 February 2015]

Turner RK, Daily GC. 2008. The ecosystem services framework and natural capital conservation. *Environmental and Resource Economics* **39**: 25–35.

Van den Broeck M, Waterkeyn A, Rhazic L, Grillas P, Brendonck L. 2015. Assessing the ecological integrity of endorheic wetlands, with focus on Mediterranean temporary ponds. *Ecological Indicators* **54**: 1–11.

Walters BB, Rönnbäck P, Kovacsc JM, Crona B, Hussain SA, Badolad R, Primavera JH, Barbier E, Dahdouh-Guebas F. 2008. Ethnobiology, socio-economics and management of mangrove forests: a review. *Aquatic Botany* **89**: 220–236.

Walton MEM, Vilas C, Canavate JP, Gonzalez-Ortegon E, Prieto A, van Bergeijk SA, Green AJ, Librero M, Mazuelos N, le Vay L. 2015. A model for the future: Ecosystem services provided by the aquaculture activities of Veta la Palma, Southern Spain. *Aquaculture* **448**: 382–390.

Warren-Rhodes K, Schwarz AM, Boyle LN, Albert J, Agalo SS, Warren R, Bana A, Paul C, Kodosiku R, Bosma W, *et al.* 2011. Mangrove ecosystem services and the potential for carbon revenue programmes in Solomon Islands. *Environmental Conservation* **38**: 485–496.

Wen L, Saintilan N, Ling J. 2011. Description of wetland ecological character: Yanga National Park. Office of Environment and Heritage, Department of Premier and Cabinet, Sydney, Australia.

Werner SR, Spurgeon JPG, Isaksen GH, Smith JP, Springer NK, Gettleson DA, N'Guessan L, Dupont JM. 2014. Rapid prioritization of marine ecosystem services and ecosystem indicators. *Marine Policy* **50**: 178–189.

Yoskowitz D, Russell M. 2015. Human dimensions of our estuaries and coasts. *Estuaries and Coasts* **38**(Supplement 1): S1–S8.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site.

Table S1. Summary table of 13 aspects of 30 case studies of aquatic habitat conservation involving ecosystem services, with information derived from the references listed in the right-hand columns, and given in full below. Abbreviations are: Y = yes, N = No, Inf = Inferred, N/A = not applicable. Data from this table are plotted in Figures 3–7.

