REVIEW: POTENTIAL EFFECTS OF KELP SPECIES ON LOCAL FISHERIES

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Summary

1. Kelp species are ecosystem engineers in temperate coasts, where they provide valuable services to humans. Evidence of the declines of kelp forests exists from several regions, but their effects on fisheries still need to be elucidated. More effective management strategies for sustainable fisheries require a synthesis of research findings and an assessment of how research could be improved to fill current gaps.

2. This review aims to: (i) summarize the available evidence on the influence of changes in kelp density and/or area on the abundance and diversity of associated fisheries; and (ii) examine how research on kelp–fisheries interactions could better support effective management.

3. Most studies (67%) reported data ascribable, directly or indirectly, to a positive relationship between kelp and fishery-relevant variables, 11% provided evidence of a negative relationship, 15% indicated species-specific findings and the remaining found unclear or 'neutral' relationships.

4. Important shortcomings were identified, including the paucity of experimental studies suitable to test for unequivocal cause–effect relationships, the disproportion between North America, which is well-studied, and other regions and between the large number of fish-based investigations and the small number of those focusing on other commercially important organisms, and the general lack of studies carried out over spatial and temporal scales comparable to those of global processes driving patterns of distribution of both kelps and fisheries.

5. *Synthesis and applications.* The consistency of most studies in showing a positive kelp–fishery relationship supports the protection of kelp habitats stated by current environmental directives. However, achieving their goals requires that the limitations we detect are addressed through better connections between research, management practice and policy. This would require: (i) researchers to combine multiple approaches (large-scale experimental

studies and modelling) for the analysis of kelp–fisheries relationships; (ii) funding agencies to provide resources needed to fill the existing gaps; and (iii) researchers and institutions from less studied regions to strengthen collaborations with those from regions where there have been more investigations into kelp–fishery systems. This is essential under present and predicted environmental changes, with the ultimate aim of conserving and allowing the sustainable use of critically important habitats and of fishery resources relying on these.

Key-words: ecosystem services, fisheries, habitat-forming species, kelp, plant–animal interactions

Introduction

There is evidence of global and local declines of populations of many marine species due to the direct and indirect effects of human exploitation (Watson & Pauly 2001), including overfishing and the modification and removal of habitats (Jackson *et al.* 2001; Dulvy *et al.* 2003; Worm *et al.* 2006). As a consequence, the implementation of ecosystem-based strategies, such as those examining links between the availability of habitats and fishery yield (Link *et al.* 2011; McClanahan *et al.* 2011), for the sustainable management of fisheries is a major concern for ecologists, policymakers and the general public. Coastal habitats, in particular, are subject to a range of anthropogenic disturbances acting across a range of scales (Kemp *et al.* 2005; Lotze *et al.* 2006; Airoldi & Beck 2007; Wernberg *et al.* 2011a). These can critically alter the ability of habitats to provide ecologically important functions (Worm *et al.* 2006; Seitz *et al.* 2014) and to support goods and services which have an amount per unit of area and estimated economic value larger than those provided by terrestrial systems (Beaumont *et al.* 2008).

Previous studies have examined how coastal habitats can modulate life-traits, such as rates of survival, growth and reproduction of exploited species (Allain *et al.* 2003; Kostecki *et al.* 2011; Vasconcelos *et al.* 2014), while much less knowledge is available on the actual importance of coastal habitats for population-level characteristics of species, with particular focus on their patterns of abundance and, eventually, their fishery yield (but see Seitz *et al.* 2014). Nevertheless, such knowledge is essential for an integrated management of fisheries (Crowder & Norse 2008).

Large brown algae generally indicated as kelps are 'foundation species' (Dayton 1975) found on most shallow rocky coasts from polar to temperate latitudes, supporting diverse associated assemblages and complex food webs (Duggins *et al.* 1989; Reed *et al*. 2008), and providing valuable ecosystem services (Schiel & Foster 1986; Steneck *et al.* 2002; Crain & Bertness 2006; Bolton 2010). They typically include genera of the order Laminariales (e.g. Steneck *et al.* 2002), but the same term has been used to indicate several other groups of seaweeds, all sharing analogous structural and functional traits (reviewed by Fraser 2012). A number of species belonging to all taxonomic groups rely on direct or indirect associations with kelp systems through a variety of interactions (Graham 2004). For example, the net primary productivity of kelp forests can reach values of up to 3000 g C m^{-2} y^{-1}, as described for *Macrocystis* and *Laminaria* (Gao & Mckinley 1994). A great proportion of this production moves into other trophic levels through the activity of grazers, detritivores and the microbial loop (reviewed by Krumhansl & Scheibling 2012). Several species, in particular, depend on kelp forests for finding suitable feeding and nursery areas and protection from predators (e.g. Norderhaug *et al.* 2005; Reisewitz *et al.* 2006; Rosenfeld *et al.* 2014), leading to the hypothesis that their abundances would be drastically affected by changes in patterns of distribution and density of habitat-forming kelps (e.g. O'Connor & Anderson 2010). In fact, alterations of the abundance of kelp forests, in most cases represented by relevant reductions up to local deforestation events, are globally documented (Steneck *et al.* 2002) and predicted to be exacerbated in the near future (Brodie *et al*. 2014). These are attributed to the negative effects of anthropogenic pressures, including over-harvesting, deterioration of water quality through pollution, eutrophication and sedimentation, and, especially in the last decades and in areas where kelp species occur close to the limits of their distribution, climate change (Steneck *et al.* 2002; Smale *et al.* 2013; Brodie *et al*. 2014). On the contrary, the potential impact of changes in the density and overall extent of kelp forests on fishery yields is still poorly known. The available data on the importance of European kelp forests for the functioning of coastal ecosystems are much more fragmented and limited compared to those from other regions, such as North America (Steneck *et al.* 2002; Smale *et al.* 2013).

Nevertheless, assessing and understanding links between patterns of distribution and abundance of kelps and populations of commercially exploited species are needed to support fisheries policies under the framework of several directives taking into account the conservation of marine habitats. This is the case, in particular, for the Marine Strategy Framework Directive (http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2008:164:0019:0040:EN:PDF), which establishes the legal issues for maintaining and restoring the Good Environmental Status (GES) of European's marine waters and the Habitats Directive (http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm), which aims to maintain and restore protected habitats and species. In this context, natural rocky reefs were identified as coastal habitats of community interest whose protection through the application of the Habitats Directive within the Natura 2000 network is at the core of the current EU biodiversity policy. Marine sites included in the Natura 2000 network are intended to provide protection to the relevant habitats and species listed in the Habitats Directive. Unfortunately, the Habitats Directive lists very few marine species and habitats in its annexes and these do not include any of the typical benthic assemblages of reefs, such as kelp species and other important primary producers which can drastically affect other species which are explicitly mentioned in the Directive.

This literature review, based on an adaptation of the protocol developed by Araújo and co-workers (2013), aims to examine links between kelp habitats and exploited species, with the ultimate goal of providing essential information, integrating assessments of fishery production and of the quality of coastal habitats, to management and conservation policies in coastal ecosystems. The specific question examined is about the available evidence for the influence of changes in density and/or area of kelp forests on associated biodiversity and provision of ecosystem services, i.e. the abundance and diversity of fished species.

Materials and methods

LITERATURE SEARCH

The most relevant sources of information suitable to generate a data base of contributions until April 2014 on quantitative relationships between kelp area and density and abundances of exploited species were searched using the following data bases: ISI Web of Knowledge, Electronic Databases available at the Virtual Library of the University of Porto (Springer, Elsevier, Science Direct) and Directory of Open Access Journals. Documents in English, French, Spanish and Portuguese were taken into consideration.

Search terms were organized into two groups, referring, in addition to the general term ‘kelp’, to individual kelp species names (listed in Appendix S1 in Supporting Information) and to relevant key-words (canopy removal, community, ecology, food web, fisheries, fish, functioning, food, habitat engineering, habitat complexity, harvesting, nursery, removal, seafood, shrimps, shellfish).

Although the common name ‘kelp’ has been used to indicate groups of algae from various orders and, in the broadest sense, almost any large brown alga (Fraser 2012), we specifically focused here on the order Laminariales, to which a number of authors referred as ‘kelp’ in the ‘true’ (e.g. Steneck *et al.* 2002, Schiel & Foster 2006), ‘strict’ (e.g. Bolton 2010) or’ ‘technical’ (e.g. Dayton 1985) sense. The only exceptions were represented by ‘pseudokelp' species (e.g. Smale *et al.* 2013) of the order Tilopteridales, recently split from Laminariales, and the fucalean southern bull kelp *Durvillaea antarctica*.

The data base search was conducted by linking all the terms in each group with the Boolean operator 'OR' and linking the two groups with the Boolean operator 'AND'.

Inclusion criteria and evidence assessment

The search produced almost 5000 unique references that were screened for inclusion in the review according to a two-step process. This first focused only on the title of each study, the second on the abstract of those which had passed the first screening. As a control for the quality of the selection, a final step was performed by two independent expert reviewers who examined the full text of a randomly chosen subset of selected papers. The details of the adopted procedure are illustrated in Appendix S2.

The review was aimed at synthesizing references addressing the following questions: (i) what is the available evidence for the influence of changes in kelp forest density and/or area on the abundance and diversity of associated fisheries? (ii) how could research on kelp–fisheries interactions be improved to better support effective management?

Four categories of quality of evidence were taken into account (modified from Pullin & Knight 2003; Pullin & Stewart 2006): (i) evidence from quantitative, replicated studies, including data obtained as estimates of abundance of kelp and exploited species, along randomly chosen and replicated units of space and/or time; (ii) evidence from quantitative, but not properly designed (e.g. lacking replication or appropriate controls, when relevant) studies; (iii) evidence from qualitative field observations or only descriptive studies; (iv) inadequate evidence due to methodological problems. Studies falling into categories i, ii and iii were considered suitable for the review, while studies falling into category iv were excluded.

Results

Our search returned about 5000 studies published between 1983 and April 2014, out of which 62 (Appendix S3) were retained as suitable to link patterns of the presence and abundance of kelp with patterns of presence and abundance of fishery-exploited, or exploitable, species of fish or invertebrates. Most of these studies (59 out of 62) were fully or partially based on a descriptive or manipulative experimental approach involving the collection of field data, while the remaining three involved a manipulative laboratory experiment, the development of habitat/lobster distribution models (based on empirical field data) and a meta-analysis of data from several previous studies, respectively.

Study species and locations

The most commonly examined kelp species were the giant kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh, the leather kelp *Ecklonia radiata* (C. Agardh) J. Agardh and the bull kelp *Nereocystis luetkeana* (K. Mertens) Postels & Ruprecht, collectively appearing in 43 out of 62 studies, while 9 species were the focus of a single study. Five studies reported kelp organisms identified only at the genus level, while one referred just generically to 'kelp' and one defined the examined species as "kelp *Laminaria vesiculosus*", which was impossible to match unequivocally with any taxonomically accepted name. Of the 22 identified species included in this review, 16 were perennial and 6 annual (Table 1).

Patterns of abundance and/or distribution of kelp could be related to fishery-relevant variables of one or more commercially valuable fish species in 77% of studies and invertebrates in 23% of studies, including a single study focusing on both fish and crustacean species (Fig. 1A).

The largest proportion of studies was carried out in North America (50%), followed by Oceania (26%), South America (13%), Europe (8%) and Asia (3%) (Table 1).

Adopted procedures

Only a relatively small proportion (26%, including two laboratory experiments) of studies reported manipulative experiments suitable for examining actual cause–effect relationships between kelp traits and fishery-relevant response variables (Fig. 1B). These included in most cases comparisons between control (unmanipulated) and treated “sites”, where the treatment was represented only by the full removal (5 studies) or by multiple levels of increasing removal of kelp (6 field and 1 laboratory studies). A single study included manipulations aimed at examining the different effects of habitats characterized by the lack of kelp and the presence of natural and artificial kelp. Two studies were based on tethering experiments respectively conducted under the very different purposes of testing whether the kelp bed could provide protection to lobsters against their predators and of examining the export of detached kelp and other macroalgae from rocky reefs to other increasingly distant habitats where they were consumed.

Most studies (39%) were based on sampling *a priori* stratified to compare relevant response variables between habitat types naturally characterized by the presence vs. the absence of kelp (only one case examined periods before and after the establishment of a kelp bed), with only one study including sites differing for levels of kelp density. A considerable proportion (23%) of studies involved sampling at randomly established spatial units of kelp-related and fishery-related variables that were *a posteriori* correlated.

The remaining studies were aimed at addressing more specific issues, such as differences in the effects of the identity of kelp on associated organisms (5 cases), the analysis of stomach content of fishes from sites differing in the abundance of kelp (2 cases) and the collection of acoustic data to identify the preferred spawning grounds of fishes (1 case). Finally, one study reported a meta-analysis of data from previous investigations on possible relationships between habitat types (including different habitat-forming organisms) and fish catches.

As expected, according to the variety of addressed issues, sampling procedures, predictive and response variables, a large range of spatial and temporal scales were represented. In terms of spatial extent, a few studies (5%) were performed over the scale of metres to 10s of metres, while a few more (6%) involved scales of 1000s km. Most papers reported studies performed over the intermediate scales of 100s m to some kilometres and of 10s km to 100s km (39% and 41%, respectively). In the remaining studies, the spatial extent was not clearly indicated or was not relevant for their particular goals (Fig. 1C). In terms of temporal extent, 11% of the studies included just a single collection of data, while all the others were based on samplings replicated at multiple times, although with very different sampling frequency. Most of these (55% of all included in the review) spanned a period of about one year (23 studies) or less (from about 1 month or less, to 3 months, to 5–6 months, with, respectively, four, five and two studies). Within the rest, 16% (of all) covered up to 3 years, 9% between 3 and 5 years, 8% between 5 and 10 years and only three studies (5%) spanned between 18 and 20 years (Fig. 1D). The classification of each reviewed study to the categories illustrated in Fig. 1 is summarized in Appendix S4.

DOCUMENTED KELP–FISHERIES RELATIONSHIPS

Kelp-related variables were examined in 58% of the cases focusing on changes in abundances (e.g. kelp density or area), while the remaining 42% of studies focused more generally on variations of the type of habitat (e.g. kelp presence vs. absence or kelp vs. other habitat-forming organisms). In general, however, most (66%) of the studies reported data that could be directly or indirectly associated to a positive relationship between kelp traits and fishery-relevant variables, while 11% provided evidence of negative relationships and 8% opposite findings depending on the species involved. A small proportion of studies indicated "neutral" (i.e. neither clearly positive nor negative, or impossible to identify univocally) findings or just species-specific differences in the effects of the kelp's identity (6% each) (Fig. 2).

Among the studies indicating positive kelp–fisheries relationships, the majority (31% of the total 62) reported general increases in the abundance or the presence of adults of one or more species of fish associated with kelp. A smaller proportion (11%) documented positive responses of earlier stages, including increases of kelp-associated recruits and juveniles (10%) and kelp beds as preferred spawning areas (1%). An overall increase of the species diversity of fish assemblages in kelp habitats was reported by 6% of the studies. Only two studies showed positive effects of kelp as a source of food for fish, while a single study suggested that the mortality of a fish species typically associated with kelp can be reduced by the structural refuge against its predators provided by the canopy. A positive response of commercially valuable crustaceans to the presence or abundance of kelp was indicated by 6% of the studies, including three cases where the response variable was the abundance of lobsters and one where it was the market landing of decapods. Two studies showed that harvestable quantities of gastropods (i.e. abalone of commercial size) could be obtained only in kelp beds and not in barren habitats, while two other studies documented relatively larger abundances, sizes and gonad weights of sea urchins from kelp forests (Fig. 2).

A negative relationship between kelp and the abundance or the presence of fishes was reported by 11% of studies, including one case where the examined kelp species (*Undaria pinnatifida*) was invasive at that location. The abundance of exploited invertebrates was negatively related to the abundance or presence of kelp in two cases, one involving sea urchins and one abalones (Fig. 2).

In 15% of the studies, species-specific findings were documented (Fig. 2), including five cases where some fish species were less abundant in kelp than in other habitats (i.e. eelgrass beds or barren areas), while other species showed the opposite pattern, and four cases where different species of kelp determined different effects on the density and/or size of lobsters, crabs, both sea urchins and abalones and abalones alone (one study each).

Finally, kelp–fishery issues were explicitly or implicitly addressed by the remaining 5% of studies, but no or not unequivocal relationships could be identified (Fig. 2). These included: one example where the distribution of lobsters was unaffected by the presence of kelp; one where invertebrates (mussels and limpets) were relatively more abundant inside, while others (sea urchins) were more abundant outside kelp beds, but most of the variability occurred in space and time independently of kelp; one where commercially valuable fishes were more abundant at 'no kelp' than at 'kelp' sites, but such sites were themselves spatially segregated over a regional scale.

The classification category of each reviewed study illustrated in Fig. 2 is summarized in Appendix S4.

Discussion

The present review revealed a number of possible generalizations and some limitations or inconsistencies regarding the relationships between kelp beds and fisheries. Two such pieces of knowledge have relevant implications in the policy context of managing natural habitats and the resources they provide and in the scientific context of interpreting previous findings and designing future studies aimed at evaluating fishery-relevant effects of kelp, highlighting ways in which existing and future research can better support currently implemented and future management strategies.

POSITIVE VS. NEGATIVE RELATIONSHIPS BETWEEN KELP AND FISHERIES

The role of kelps as foundation species able to provide space, food and protection to a number of other organisms (e.g. Dayton 1975; Duggins *et al.* 1989; Reisewitz *et al.* 2006; Stephens *et al.* 2006) led to the hypothesis that there is a positive relationship between the amount and structural complexity of these species and the amount of their associated commercially valuable species. Most studies in the present review provided general evidence supporting such expectations, although the ecological mechanisms may differ considerably.

In a number of cases, the abundance of adult fishes was positively related to variations in the total and/or stipe density of kelp. The main mechanisms responsible for these types of response likely involve the provision of a unique habitat to kelp-specialized fishes (Anderson 1994; White & Caselle 2008; O'Connor & Anderson 2010) or of food for fishes typically feeding on epibionts of kelp (Holbrook *et al.* 1990; Norderhaug *et al*. 2005; Davenport & Anderson 2007).

A general finding from this review is that effects of kelp tend to be drastically dependent on the identity of the associated fish species and, in some cases, of their life stage. The abundance of adult fishes, in particular, that feed only opportunistically in kelp beds and that of fishes showing an aggregation behaviour itself suitable to provide protection from predators (Bray & Ebeling 1975; Hobson 1978) could be relatively independent of variations in kelp density. In some systems, instead, species-specific responses of fishes were indicated as being driven by indirect effects of the presence of kelp through its direct negative effect on other understory algae (Holbrook *et al*. 1990). If shading by kelp reduces the cover of understory foliose algae and increases, as a consequence of competitive interactions, that of filamentous turfs (Schiel & Foster 1986; Kennelly 1989), fish species requiring turfs to find prey would benefit from larger cover and density of kelp (Schmitt & Holbrook 1984; DeMartini & Roberts 1990), while species requiring foliose algae as foraging microhabitat (Laur & Ebeling 1983; Schmitt & Coyer 1983) would show the opposite response.

The association of juvenile stages of fish species to kelp beds, however, was generally positive, as observed for gadoids whose abundance was much larger in kelp unharvested areas compared to harvested areas (Lorentsen *et al*. 2010). This response can be primarily driven by the loss of shelter and food following the loss of kelp. Without the protection provided by the kelp canopy, juvenile fish become an easy target for predators (Lorentsen *et al*. 2004).

The positive association between the abundance of lobsters and other decapod crustaceans is particularly important due to the large market value and existing local fisheries of these animals. The importance of *Laminaria* beds as habitat for the American lobster *Homarus americanus* has been explained with the provision of habitable space by the complex architecture of kelp individuals, which can positively affect the recruitment (Herrnkind & Butler 1986) and the population size structure (Howard 1980) of several crustaceans.

For other invertebrates, relationships with kelp were more variable. For example, Claisse and co-workers (2013) have found that a higher mean gonad biomass of exploited sea urchins could be obtained from kelp-dominated than from barren areas, in spite of the opposite pattern in the total density of individuals. This may be due to the fact that urchin gonads are important for energy storage besides reproduction, so that their production could be strongly and positively correlated to the local amount of available macroalgal food (e.g. Rogers-Bennett *et al*. 1995). Contrarily, kelp can inhibit urchins, possibly due to the negative impact of physical abrasion by large macroalgal fronds (e.g. Scheibling *et al*. 1999; Gagnon *et al*. 2005). Similarly, the abundance of commercially valuable abalones was documented as being positively or negatively associated to kelp beds depending, respectively, on the local relative importance of kelp as provider of food and refuge for adult abalones (Won *et al*. 2010) or of habitat for large abundances of competitors for the same resources (Lowry & Pearse 1973).

The identity of kelp itself was indicated as a relevant factor in several studies. A particular case was when the kelp species (i.e. *Undaria pinnatifida*) was invasive at the studied location and it was associated with reduced abundances of reef fishes, likely due to the physical obstruction of rocky shelters by its fronds with consequently lower quality of reefs for fish populations (Irigoyen *et al*. 2011). *Macrocystis pyrifera* and *Nereocystis luetkeana* beds co-occurring in the same area, instead, could support very different patterns of distribution and abundance of associated invertebrates, including sea urchins and abalones, depending on their perennial (more structurally complex) and annual (less structured), respectively, traits (Shaffer 2000).

Detected limitations and knowledge gaps

Although this review indicated that notable research on interactions between kelp beds and fisheries has been performed in the last decades, it also highlighted a number of methodological, geographical and logistical gaps that should be filled in order to get a broader understanding of such interactions and increase the accuracy of their derived predictions.

Perhaps the most important limitation is that only a few studies were based on an experimental approach involving manipulations of kelp-related variables to test explicit hypotheses on actual cause–effect relationships between these and fishery-related response variables. Different degrees of difficulty to unequivocally attribute causal relationships characterized most of the remaining studies.

In a few cases, the adopted design was affected by true biases preventing an unconfounded examination of the intended effects. This happened, in particular, when response variables were compared between two individual units of space, one with kelp naturally present and the other naturally lacking kelp. In such situations, the supposed effect of the presence of kelp could not be separated from that of other uncontrolled factors that could naturally differ over the same scale. This problem is particularly important once relevant patterns of natural variation in the distribution and abundance of populations over a range of scales, depending on different processes, have been documented by several analyses carried out in kelp-dominated systems (Foster 1990; Irving *et al*. 2004; Wernberg *et al*. 2011b).

Most of the remaining studies could only provide correlative evidence of kelp–fishery relationships. This characteristic would, *per se*, prevent the possibility to unequivocally state that the detected responses were actually caused by changes in kelp-related variables.

Nevertheless, when the adopted approach involves tests of explicitly illustrated *a priori* hypotheses and included proper replication, it can still yield useful information, particularly in systems and over spatial scales (such as those of regional and global processes) where experimental manipulations are logistically very difficult or not at all possible (Ford 2000).

Direct comparisons of findings even from similar studies were made difficult by the intrinsic variability of abiotic and biological variables that could be relevant for both the distribution and abundance of kelp beds and the associated fisheries (e.g. Reed *et al.* 2011). For example, the depth range of distribution of the examined kelp beds was reported, unless clearly irrelevant, by all studies, but this is drastically dependent on the almost never reported local turbidity of the water (Lüning 1981), which can also affect the distribution of associated fisheries independently of kelp (e.g. De Robertis *et al*. 2003). Other, not always reported, variables that could be relevant for fisheries independently or in addition to kelp include: the concentration of nutrients, which can alter trophic processes (e.g. Thebault & Loreau 2003); the temperature climate that drastically affects the latitudinal distribution of kelp and, directly and indirectly, that of associated fisheries (e.g. Wernberg *et al*. 2010), although several other environmental factors typically covary across latitude (Wernberg *et al*. 2011b); the wave exposure of the study site (e.g. Ojeda & Dearborn 1990); a range of traits of target species that could affect fishery yield, such as a declining or increasing population status (e.g. Worm *et al.* 2005) and migratory or non-migratory behaviour (e.g. Horwood *et al*. 1998).

Finally, "taxonomic" and "geographic" knowledge gaps were detected. First, kelp–fisheries links were far better investigated for fishes than for other species, in spite of the great ecological and/or socioeconomic importance of many kelp-associated invertebrates such as lobsters and crabs (e.g. Bologna & Steneck 1983; Johnson & Hart 2001). Second, the majority of reviewed studies referred to North America, while much less evidence is available, in particular, for Europe, consistent with the general paucity of data suitable to relate changes in patterns of distribution and abundance of subtidal habitat-forming macroalgae with their provided services in the north-east Atlantic (Smale *et al*. 2013).

RESEARCH AND MANAGEMENT ISSUES

This review, including the summarized evidence and highlighted shortcomings, has important implications for ecological research and management of kelp–fishery associations and for their better integration.

A large proportion of available data are inadequate to inform and support effective management decisions, as they are not from studies based on tests of the effects of specific processes through empirical observations and experiments conducted at the relevant scales. In fact, an experimental approach is currently limited even regarding basic information on distributions of kelp species and associated biodiversity and on species interactions that could shape kelp–fishery relationships. In this context, it is acknowledged that experimental manipulations of relevant variables over the spatial and temporal scales of processes that can drastically affect both kelp beds and associated organisms are difficult to implement (Richardson & Poloczanska 2008). A good alternative could be that of simultaneously performing analogous experiments in regions under different environmental conditions (Wernberg *et al*. 2012) in order to better understand possible causal links between processes affecting the distribution of kelp over large scales (e.g. oceanographic and climate factors) and local interactions between kelp and the associated fauna targeted by fishing. Examples of such 'comparative experimental approach' (Menge *et al*. 2002) were very rare in this review.

This review highlights the need for a spatial and temporal expansion of research in order to increase knowledge in relatively less known regions where kelp species are common and fishing activities intense and to include temporal scales more comparable to those of relevant global processes. This is the case, for example, in Europe, where several kelp species coexist in the north-east Atlantic, some of which are at the limit of their range of distribution (e.g. Smale *et al*. 2013), and climatic factors have critically changed in the last decades (e.g. Lima *et al*. 2007). At the same time, it is estimated that the vast majority of stocks assessed in the European Union are below the maximum sustainable yield (Froese & Proelss 2010). Analogously, kelps are common along the coasts of South Africa, but no case studies suitable to show their possible relationships with local fisheries could be found.

The widely reported positive relationship between the presence and density of kelp forests and fisheries has important management implications. In general, the complex range of involved abiotic and biological interactions calls for an ecosystem-based approach to kelp–fisheries systems not yet implemented as needed (Garcia *et al*. 2003; EC 2008). This would require that effective management actions were based not only on assessments of the target species, but also on other components and functions of the whole ecosystem to which they belong. This approach would facilitate sustainable management not just of the specific resource under examination, but also of the processes responsible for its variations independently, or in addition to, the direct impact of fishing activities. In practice, there is evidence, for example, that the restoration of kelp forests has the potential to drastically increase the production of local fisheries, representing a valuable tool for ecosystem-based management (Claisse *et al*. 2013). In this context, an important development could come from present knowledge on methods of kelp farming available in some regions and from the increasing efforts to develop such methods in others (Sanderson *et al*. 2012; Rebours *et al.* 2014), although usually driven by other primary objectives than supporting associated fisheries, such as using kelp as food (Tseng 1984) and biofuel (Roberts & Upham 2012), and intense kelp farming might exert concomitant detrimental effects (Krumhansl & Scheibling 2012).

Conclusions

This review highlighted important shortcomings and knowledge gaps regarding the actual effect of kelp presence and density on associated fisheries, including the need for an ecosystem-based approach in this field, the current paucity of experimental studies and the need for extending the spatial and temporal scales of investigation. Despite these, the consistency of most studies in terms of directly or indirectly showing a positive kelp–fishery relationship is probably the main evidence for the actual occurrence of the relationship, eventually supporting the protection of kelp habitats stated by current environmental directives. The socioeconomic implications of such protection are clear and huge as kelp forests provide an essential habitat for adults (e.g. the European lobster *Homarus gammarus* in the north-east Atlantic) and juveniles (e.g. the Atlantic cod *Gadus morhua*) of extremely valuable animals. For example, in the UK economy alone, lobster and cod fisheries yielded about £30 million each in 2011 (Elliott *et al.* 2012). The achievement of these goals requires addressing the detected limitations through a better connection between ecological research and conservation and management practice and policy (Hulme 2011). Under the multiple global threats to kelp systems and fisheries, this would imply that: researchers combine experimental studies on large-scale processes affecting kelp distribution with modelling approaches; funding agencies provide resources to support the research needed to fill the existing gaps; researchers and institutions from less studied regions strengthen collaborations and exchange information with those from regions where kelp–fishery systems have been more investigated, in order to develop cross-disciplinary and comparative work. This is likely the only way to effectively improve the understanding and predictions of kelp–fishery interactions in response to environmental changes, with the ultimate aim of conserving and allowing a sustainable use of critically important habitats and associated fishery resources.

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Data accessibility

Data have not been archived because this article does not contain data.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Names of kelp species included as search terms in the literature review.

Appendix S2. Details on procedures adopted for the literature review.

Appendix S3. Studies included in the review.

Appendix S4. Characteristics of studies included in the review.

Table 1. Kelp species (or higher taxonomic groups when not identified) and locations (number of studies in each location in parentheses) that were the focus of the studies included in the present review. Each species listed with its current taxonomically accepted name, even if originally reported with a synonym. Note that several studies included more than one species. Type of life cycle (A: annual; P: perennial) indicated only for identified species

Species	No. of studies	Location	Life cycle
Macrocystis pyrifera	25	Argentina (1), Australia (1), California (15), Chile (5), New Zealand (2), Washington (1)	P
Ecklonia radiata	12	Australia (6), New Zealand (6)	P
Nereocystis luetkeana	7	Alaska (1), California (5), Washington (1)	A
Lessonia trabeculata	5	Chile (5)	P
Laminaria hyperborea	4	Continental Portugal (1), Helgoland (Germany) (1), Norway (2)	P
Saccharina latissima	3[a]	Alaska (2), California (1)	A
Saccharina longicruris	3	Maine (3)	P
Agarum clathratum	2[a]	Alaska (1), California (1)	P
Eisenia arborea	2[a]	California (2)	P

Eisenia bicyclis	2	Japan (2)	P
Laminaria farlowii	2[b]	California (2)	P
Laminaria ochroleuca	2	Continental Portugal (1), NW Spain (1)	P
Pterygophora californica	2	California (2)	P
Saccharina bongardiana	2[a]	Alaska (1), California (1)	P
Undaria pinnatifida	2	Australia (1), Argentina (1[c])	P
Agarum cribrosum	1	Alaska (1)	P
Alaria marginata	1	Alaska (1)	A
Costaria costata	1[a]	California (1)	A
Cymathaere triplicata	1[a]	California (1)	A
Laminaria yezoensis	1[a]	Alaska (1)	P
Lessonia tholiformis	1	New Zealand (1)	P
Saccorhiza polyschides	1	Continental Portugal (1)	A
Durvillaea spp.	1	New Zealand (1)	
Ecklonia sp.	1	Australia (1)	
“Kelp”	1	Alaska (1)	

Laminaria spp.	1	Alaska (1)
"Kelp *Laminaria vesiculosus*"	1	Maine (1)
Phyllariopsis spp.	1	Continental Portugal (1)
Saccharina spp.	1	Alaska (1)

[a] in some cases the species was found in the understory assemblages of canopy-forming kelp; [b] prostrate kelp; [c] non-native species at that location.

FIGURE LEGENDS

Figure 1. (A) Groups of commercially valuable species on which each study (56 in total) included in the review focused. The cumulative percentage exceeds 100% as some studies involved more than one group. (B) Type of studies included in the review. (C) and (D) Spatial and temporal extent of each study included in the review, respectively.

Figure 2. Type of kelp–fishery relationship and response variables included in the review. Some studies included more than one type of relationship and/or variables.

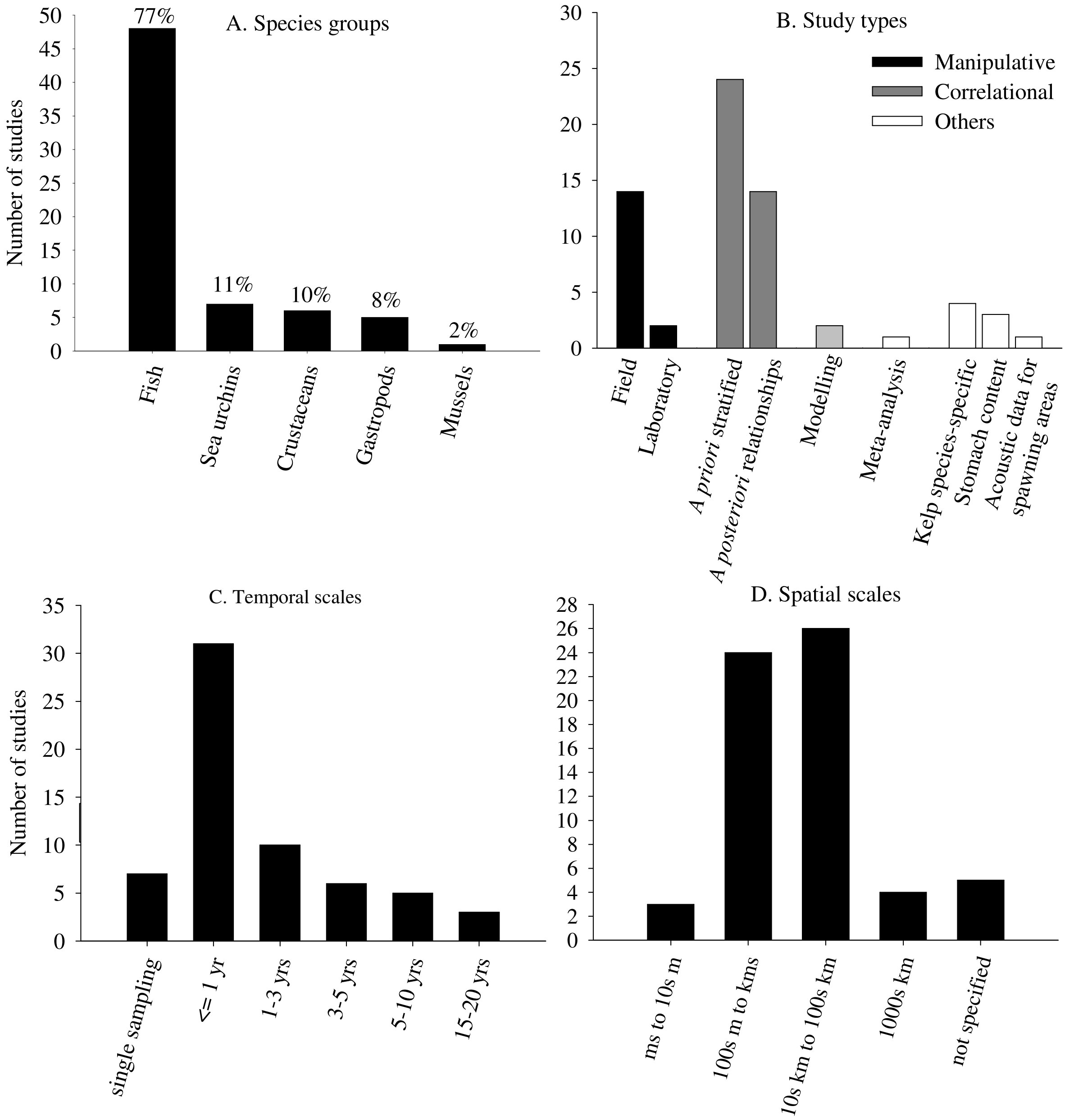
A. Species groups
Number of studies
77%
11%
10%
8%
2%
Fish
Sea urchins
Crustaceans
Gastropods
Mussels
B. Study types
Manipulative
Correlational
Others
Field
Laboratory
A priori stratified
A posteriori relationships
Modelling
Meta-analysis
Kelp species-specific
Stomach content
Acoustic data for spawning areas
C. Temporal scales
Number of studies
single sampling
<= 1 yr
1-3 yrs
3-5 yrs
5-10 yrs
15-20 yrs
D. Spatial scales
ms to 10s m
100s m to kms
10s km to 100s km
1000s km
not specified

Fig. 1

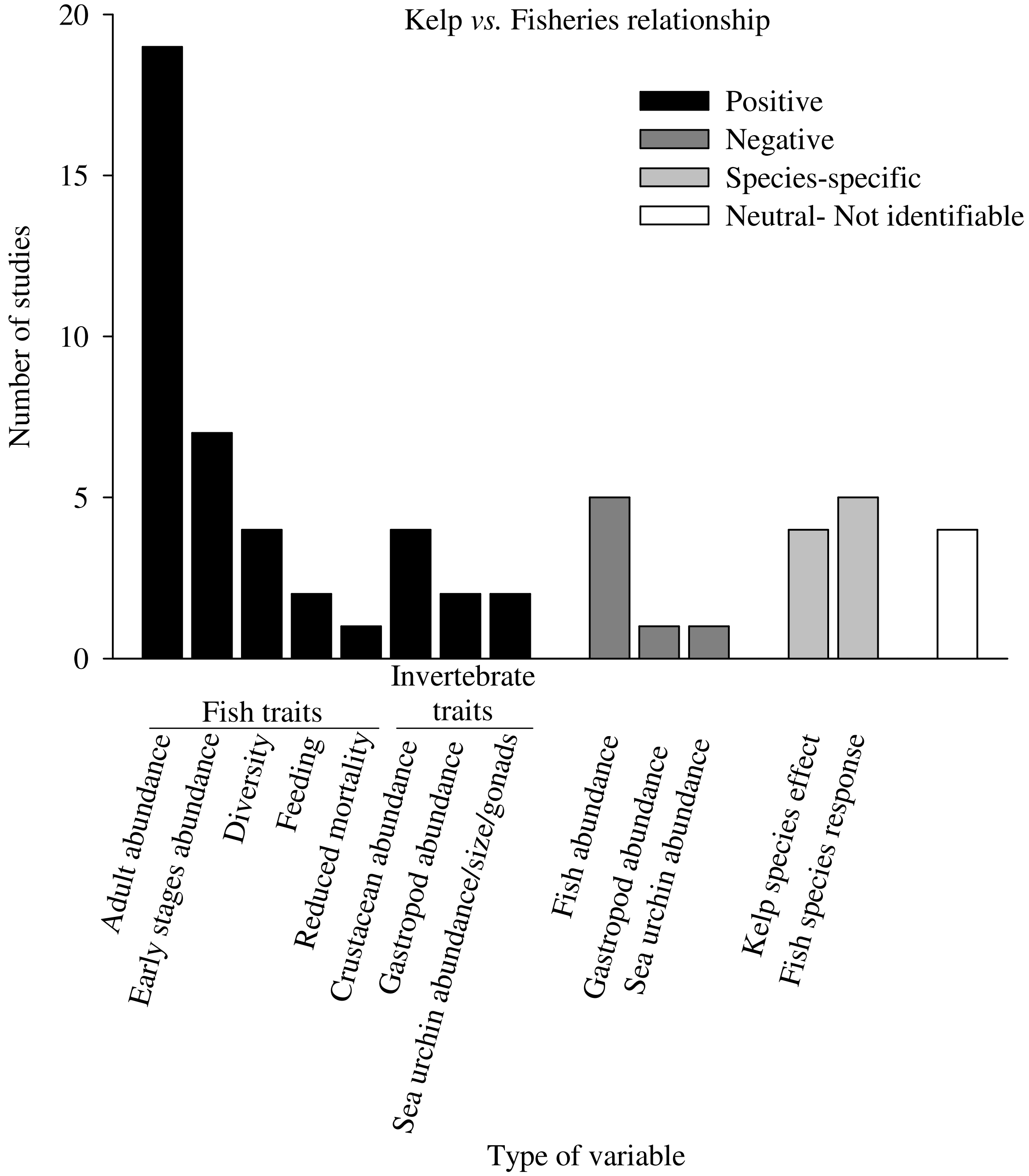
Kelp vs. Fisheries relationship
Positive
Negative
Species-specific
Neutral- Not identifiable
Number of studies
20
15
10
5
0
Fish traits
Invertebrate traits
Adult abundance
Early stages abundance
Diversity
Feeding
Reduced mortality
Crustacean abundance
Gastropod abundance
Sea urchin abundance/size/gonads
Fish abundance
Gastropod abundance
Sea urchin abundance
Kelp species effect
Fish species response
Type of variable

Fig. 2