Oceanography and Marine Biology: An Annual Review, 2016, **54**, 173-191

Taylor & Francis

DISENTANGLING HABITAT CONCEPTS FOR DEMERSAL MARINE FISH MANAGEMENT

SOPHIE A.M. ELLIOTT[1,*], ROSANNA J. MILLIGAN[1], MICHAEL R. HEATH[2], WILLIAM R. TURRELL[3] & DAVID M. BAILEY[1]

[1]*Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, G12 8QQ, United Kingdom*
*E-mail: sophie_elliott@yahoo.com (corresponding author)
[2]*Department of Mathematics and Statistics, University of Strathclyde, 16 Richmond Street, Glasgow, G1 1XQ, United Kingdom*
[3]*Marine Scotland Science, Marine Laboratory, P.O. Box 101, 375 Victoria Road, Aberdeen, AB11 9DB, United Kingdom*

Fishing and other anthropogenic impacts have led to declines in many fish stocks and modification of the seabed. As a result, efforts to restore marine ecosystems have become increasingly focused on spatially explicit management methods to protect fish and the habitats they require for survival. This has led to a proliferation of investigations trying to map 'habitats' vulnerable to anthropogenic impacts and identify fish resource requirements to meet conservation and management needs. A wide range of habitat-related concepts, with different uses and understandings of the word 'habitat' itself has arisen as a consequence. Inconsistencies in terminology can cause confusion between studies, making it difficult to investigate and understand the ecology of fish and the factors that affect their survival. Ultimately, the inability to discern the relationships between fish and their environment clearly can hinder conservation and management measures for fish populations. This review identifies and addresses the present ambiguity surrounding definitions of habitat and habitat-related concepts currently used in spatial management of demersal marine fish populations. The role of spatial and temporal scales is considered, in addition to examples of how to assess fish habitat for conservation and management purposes.

Introduction

Fish represent a highly diverse group of animals (Eschmeyer et al. 2010). They are known to play important roles in ecosystem structuring and provide essential resources for humans through the provision of food, regulation of food web dynamics, and carbon cycling (Holmlund & Hammer 1999, Baum & Worm 2009). However, fishing and other anthropogenic pressures have led to declines in many fish species and modification of the seafloor (Jennings & Kaiser 1998, Crain et al. 2009). As a result, much effort has been expended on identifying management mechanisms to protect, sustain, and restore depleted fish stocks. There has also been an increasing emphasis on the application of ecosystem-based fisheries management (EBFM) (Box 1), in addition to species-by-species assessment and fisheries management (Schmitten 1999, Sinclair et al. 2002, Gavaris 2009).

The transition to EBFM has led to a proliferation of investigations to identify fish habitats for fisheries management purposes, habitat mapping for seabed conservation purposes, and habitat characterization to explain ecosystem (Box 1) functioning (Christensen et al. 1996, Diaz et al. 2004, Francis et al. 2007). In many cases, the term 'habitat' is not well defined and can have different meanings or implications, which may lead to confusion when interpreting the results of different studies, as reviewed by Block & Brennan (1993) and Hall et al. (1997). The use of 'habitat' to refer to seabed characteristics for mapping purposes and ecosystem functioning has been formalized through legislation that requires habitats to be classified and protected, such as the European Union Habitats Directive (92/43/EEC; Council of the European Communities [CEC] 1992) and the Marine Strategy Framework Directive (2008/56/EC; European Union 2008). These uses of the term 'habitat' have become synonymous with descriptions of physical characteristics of the seabed, such as substratum type (e.g., seagrass, coral reefs, or maerl beds) (Box 1) or marine biotopes (Box 1) (Olenin & Ducrotoy 2006, Dauvin et al. 2008a). These definitions of habitat are fundamentally different from Darwin's definition, which relates to the place in which a species lives (Dauvin et al. 2008b).

Because the definition of habitat is not standardized, further confusion has been caused by terms for certain characteristics of habitat (e.g., habitat complexity, heterogeneity or quality) (Box 1), which also have often lacked clear explanation (Block & Brennan 1993, McCormick 1994, Hall et al. 1997). Part of the difficulty is that much of the terminology is entirely dependent on spatial and temporal scales (Levin 1992, Chave 2013). For example, a demersal fish might utilize distinct substrata for feeding or protection at different times or during a particular stage in its ontogeny (e.g., Laurel et al. 2009, Grol et al. 2014). Equally, the type of substratum required to provide physical protection will depend on the size of the demersal fish (Chave 2013; Figure 2). A substratum's 'complexity' is therefore entirely dependent on the size and morphology of the species.

Misused or undefined terminology could lead to misinterpretation of the role of a particular substratum type for individual species or to the use of inappropriate methodologies when analysing the role of a habitat or substratum type to a fish. For instance, if species' abundance is greater around one substratum type than another, is that species displaying 'habitat selection' based on a particular 'preference' (Box 1), or is that observation related to other environmental or life-history parameters that were not measured? Could the substratum type be considered 'essential' to the fish if other habitat components (e.g., appropriate depth range or other substrata) were not present? If definitions of habitat are unclear, variables that could affect fish distribution or abundance may not be recorded. Ultimately, the inappropriate use of the term 'habitat' and related terminology could have implications for the effectiveness of EBFM, especially where different fields of marine science use the same term with different connotations.

The present review, while not exhaustive, addresses the ambiguity surrounding habitat and habitat-related concepts currently used in the spatial management of demersal marine fish. Particular attention is therefore paid to the role of the seabed. For each concept discussed, a conceptual definition is provided, followed by examples of how to assess fish habitat for conservation and management purposes. These definitions provide a possible conceptual framework for consideration of demersal fish-environment relationships, which could equally be applied to other areas of ecology.

Concepts and definitions

Habitat

The first use of the term 'habitat' discussed here, referred to hereinafter as interpretation I, is derived from Darwin's (1872) definition, describing the place in which a plant or animal lives (Box 1). This encompasses the resources and environmental conditions that determine the presence, survival, and reproduction of a species (Hall et al. 1997, Gaillard et al. 2010). Interpretation I therefore encompasses the physical (e.g., depth, substratum type, wave exposure); chemical (e.g., oxygen concentration, pH, salinity); and biological characteristics (e.g., predator-prey dynamics, competition, and fauna providing structure to the seabed) of the environment (Hall et al. 1997, Kaiser et al. 1999, Diaz et al. 2004). Figure 1 illustrates schematically how the habitat of a demersal fish can be considered as the intersection of appropriate substratum type, physico-chemical parameters, and biological characteristics.

For quantitative purposes, this interpretation of habitat (interpretation I) has been explained as the 'environmental space' that a species is found within (e.g., Aarts et al. 2008, Matthiopoulos et al. 2015). However, many studies of fish habitat have often only described one or two habitat components, which may concern the seabed type (Figure 1A), the physico-chemical properties of the water column (Figure 1B), or both, with no mention of biological characteristics (Figure 1C) (Kaiser et al. 1999). Examples include seagrass or coral-reef substratum types that a particular fish is found over, around, or among (Costello et al. 2005, Seitz et al. 2014) or the depth and temperature ranges (e.g., Smale et al. 1993, Perry & Smith 1994). As stated by Lima & Dill (1990) and Able (1999), the lack of studies incorporating biological characteristics and interactions in the identification of fish habitat is most likely due to the difficulties of quantifying these aspects and collecting the required data *in situ*.

The second use of habitat (interpretation II), follows arbitrary classifications of the seabed or features based on differences obvious to human observers (e.g., different types of sediment, macroalgal beds, or biogenic reefs; Figure 1A) (Fraschetti et al. 2008). Interpretation II does not explicitly consider the ecological requirements of a particular species; however, it has been used to identify associations of some species with particular substrata (e.g., Seitz et al. 2014). Kenny et al. (2003) provided an overview of seabed mapping technologies available for classification purposes.

The third use of habitat (interpretation III) encompasses an ecosystem- or a marine biotope–based view of habitat (Olenin & Ducrotoy 2006, Airoldi & Beck 2007, Dauvin et al. 2008a). Descriptions under interpretation III typically include seabed properties (Figure 1A), physico-chemical properties of the water column (Figure 1B), and the fauna found in that specific area, although interactions between those fauna are not considered. Interpretation III is typically characterized in terms of the community of flora and fauna present, rather than a particular focal species (Olenin & Ducrotoy 2006, Dauvin et al. 2008a).

Interpretations II and III derive from conservation and planning requirements to classify and map habitats in measurable geographical units for national and international management and monitoring purposes (Airoldi & Beck 2007, Fraschetti et al. 2008, Galparsoro et al. 2012). Classification of seabed types and their associated communities facilitates the implementation of policies to assess, maintain, or restore marine environments subject to anthropogenic impacts (Airoldi & Beck 2007, Fraschetti et al. 2008, Galparsoro et al. 2012), but legal definitions of habitat can be inconsistent. For instance, the EU Habitats Directive (92/43/EEC) defines "natural habitats" as "terrestrial or aquatic areas distinguished by geographic, abiotic and biotic features" (CEC 1992, p. 8), but confusingly also defines the "habitat of a species" as "an environment defined by abiotic and biotic factors in which a species lives at any stage of its biological cycle" (CEC 1992, p. 9, Dauvin et al. 2008b). Examples of natural habitats defined under the Habitats Directive include reefs, *Posidonia* beds, and estuaries (CEC 1992). The same word is therefore used to describe geological, biological, and geographical entities at spatial scales varying from metres to many kilometres (Dauvin et al. 2008b). Similarly, the vulnerable marine ecosystem (VME) concept (Food and Agriculture Organization [FAO] 2009) refers to classifications of the seabed and includes associated species, but has no clear description of what an ecosystem or habitat is (FAO 2009, Auster et al. 2010). Such classification systems move away from the traditional definitions of habitat by focusing only on certain habitat components without considering biological or physico-chemical linkages. Interpretations II and III also instigate and perpetuate confusion in terminology across different fields of marine science and policy (Dauvin et al. 2008a,b, Galparsoro et al. 2012). Further, if the classified seabed types or identified fish habitats are used for conservation and management purposes without taking due account of varying temporal and spatial scales, efforts to protect and restore fish stocks and their habitats may be ineffective (Hilborn et al. 2004b, Guarinello et al. 2010). For example, a poorly planned Atlantic cod, *Gadus morhua*, fisheries closure established in the North Sea in 2001 not only had negligible effects on cod stocks, but also displaced fishing activity, increased discarding, and had a negative impact on vulnerable populations of common skate, *Dipturus batis* (Rijnsdorp et al. 2001, Hilborn et al. 2004b).

Identifying and collecting data on fish habitat are by no means straightforward because habitats vary not only among species, but also between sexes of the same species, life-history stages, and among different stocks. Investigations conducted over different temporal and spatial scales will also produce different outcomes when identifying a particular species' habitat. Managers are therefore faced with daunting tasks of managing and monitoring stocks, often with little prior information on fish distribution and abundance and insufficient funds (Bailey 1982, Langton et al. 1996). Loose definitions can therefore be beneficial for managers trying to implement measures to conserve and restore stocks with little baseline information (Fletcher & O'Shea 2000, Elliott & McLusky 2002). However, if simplified managerial definitions are adopted in the scientific literature, ecological meanings can become lost or confused, partly due to a lack of consensus within the scientific community itself (Dauvin et al. 2008a). As a result, habitats frequently lack metrics, threshold values, or analytical approaches for their identification, monitoring, and management (Murphy & Noon 1991, Auster et al. 2010) and end up becoming separated from their theoretical roots (Dauvin et al. 2008b).

In an attempt to reduce the confusion surrounding the term 'habitat', the present review uses interpretation I, which refers to the combination of the types of substrata, biological characteristics, and physico-chemical properties required by a species during a particular stage in its ontogeny (Figure 1D) (Hall et al. 1997, Kaiser et al. 1999). A species' habitat can therefore be applied both to individuals and to populations or stocks. Appropriate scales of time and space will vary according to the hierarchical level in question. 'Substratum type' (Box 1) is used to define seabed characteristics (Figure 1A). If only physico-chemical properties of water and substrata are taken into account when identifying a species' habitat, this is referred to as 'physico-chemical space' (Box 1; Figure 1E), a term modified from the 'environmental space' of Aarts et al. (2008). The incorporation of biotic communities into the classification of substratum types (interpretation III) is referred to as a species' 'biotope' (Olenin & Ducrotoy 2006, Dauvin et al. 2008a).

The use of interpretation II or III rather than interpretation I is thought to have contributed to underperformance of fisheries management through lack of consideration of variables that might have an effect on fish abundance and spatial distribution (Degnbol et al. 2006). When trying to protect a certain species' habitat, understanding the variables affecting its distribution and abundance is more likely to provide benefits to that focal species than using artificial constructs of substratum categories. Marine protected areas (MPAs), for example, are commonly designed to limit or exclude fishing and other damaging activities within a defined area (Halpern et al. 2010). Nonetheless, there is often a mismatch between the objectives of MPAs and ecosystem-based goals arising from different biological disciplines and specialisms (Degnbol et al. 2006, Halpern et al. 2010). In the United Kingdom, for example, the majority of MPAs have been designated for the protection of benthic features, with little understanding of whether these features are of value to commercial fish species, and may therefore miss potential EBFM benefits (Hilborn et al. 2004b, Hilborn 2011). It should be noted that clarification of terminology and more widespread adoption of EBFM will not solve all fisheries management problems (Degnbol et al. 2006, Marasco et al. 2007). There are no blanket solutions to all fisheries management problems (Degnbol et al. 2006, Beddington et al. 2007, Hilborn 2007). Nonetheless, addressing discrepancies in language to facilitate cross-sector collaboration can only be beneficial.

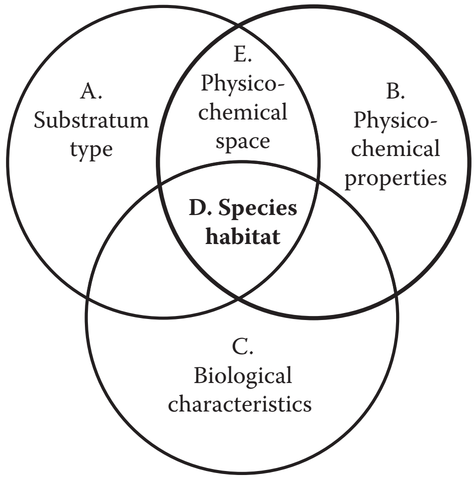

Figure 1 The three major components making up a species' habitat. These include the substratum type (A), physico-chemical properties of the water column (B), and biological characteristics (C), which together comprise a species' habitat (D; interpretation I). Circle A on its own encompasses interpretation II; the intersection of circles A and B (area E) is referred to as physico-chemical space. Interpretation III of habitat would also be represented by area D, but considers communities rather than individual species (a biotope).

Habitat complexity

McCoy & Bell (1991) highlighted three structural variables in relation to the ecological significance of habitats (defined here as 'substrata'): complexity, heterogeneity, and scale. 'Habitat complexity' has been used to refer to the rugosity (Box 1) of the seafloor (e.g., Friedlander & Parrish 1998a, Wilding & Sayer 2002); the type and density of vegetation (e.g., McCoy & Bell 1991, Jackson et al. 2001); the presence and diversity of biota on the seabed (e.g., Kovalenko et al. 2012); as well as substrata that provide vertical relief (e.g., Bohnsack 1991, Santos et al. 2012). At larger spatial scales, 'complexity' has been used in relation to the diversity or 'heterogeneity' of substratum types available within a benthic 'landscape' (Box 1) (e.g., Dutilleul 1993, Kovalenko et al. 2012). The catch-all term 'complexity' has become a convenient shorthand despite the diverse measures used and the variety of scales at which it is quantified (McCormick 1994, Bartholomew et al. 2000). Although habitat complexity and heterogeneity are well-established concepts, few policy documents address or define them. Within the international guidelines for deep-sea fisheries management (FAO 2009), structural complexity is characterized "by complex physical structures created by significant concentrations of biotic and abiotic features" (FAO 2009, p. 10). Although the FAO (2009) separated vulnerability and species diversity, their definition of complexity is circular and based on anthropocentric perceptions rather than being framed in terms of the resource requirements of particular focal species and has no reference to scale or how complexity should be measured.

Complex habitats are considered important to the survival of many fishes because the interstices that characterize them may provide refugia from predators, currents, and strong wave surges and could potentially lead to reduced mortality (Sebens 1991). Some substrata, such as rock, calcareous shells of sessile invertebrates, macroalgae, and seagrass, can also provide areas of attachment for other biota (e.g., algae, hydroids, and bryozoans), which may in turn form new substrata (Sebens 1991, Gratwicke & Speight 2005). Such biotic substrata can lead to increased rugosity and heterogeneity, which may provide a wider range of refugia, biological diversity, and food resources than an area of seabed with fewer types of substrata (Auster et al. 1996, Kaiser et al. 1999, Kovalenko et al.

2012). Rugosity may also cause heterogeneity in aspect and flow regime, leading to a wider range of conditions suitable to more species (Sebens 1991, Kovalenko et al. 2012). Numerous studies that have investigated the roles of different marine substrata for fish species highlighted the importance of structurally 'complex' substratum types (e.g., maerl or coral reefs), raising their profile in terms of management priorities (e.g., Almany 2004, Kamenos 2004, Kutti et al. 2015). Yet a combination of sediment grain sizes such as boulders with sparse coral may provide functionally equivalent rugosity for a particular species as a dense coral reef (Auster 2005). The use of the term 'complexity' to refer to 'important' biotic substrata has been reinforced because many are themselves vulnerable to anthropogenic impacts, such as trawling and dredging (Jennings & Kaiser 1998, Halpern et al. 2008).

The diverse ways in which substratum complexity can be measured has made the term difficult to apply in practice and compare between studies. To be able to measure and define the role of substrata, the present review adopts the substratum terms 'rugosity' and 'heterogeneity' (Box 1), which can be applied regardless of the scale at which they are measured, but the appropriate scale of measurement will depend on the size, behaviour and mobility of the species in question (McCoy & Bell 1991, Levin 1992). Rugosity is the measure of corrugation of a substratum and the degree of angulation that together provide a 3-dimensional space (McCormick 1994) that a fish may occupy during a particular stage in its ontogeny. This can therefore include interstices and interstructural spaces of relevance to the species in question (Bartholomew et al. 2000). The rugosity of a substratum may therefore affect the availability (Box 1) of refugia and possible food resources (Figure 2) (Bartholomew et al. 2000). On a larger scale, substratum heterogeneity refers to the frequency, composition, and pattern of substratum types and patches (Box 1; Figure 2) within a benthic landscape (Sebens 1991, Dutilleul 1993, Tews et al. 2004). The different types of substrata that occur within a particular species' habitat will depend on the size, longevity, behaviour and mobility of the respective fish.

Usually a variety of different factors or gradients generating substratum rugosity or heterogeneity exist from a fish's perspective (Sebens 1991, Gratwicke & Speight 2005, Du Preez 2015). For example,

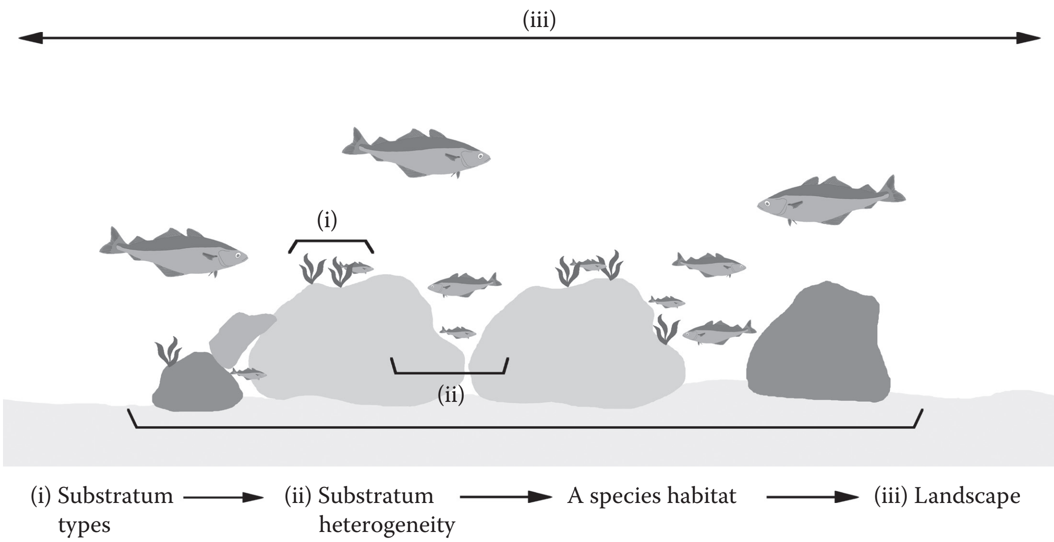

Figure 2 Substratum rugosity and heterogeneity relative to the size of fish. A species' habitat during a particular stage in its ontogeny may encompass rugose or heterogeneous substrata. Over the course of its life cycle, an individual may occupy different parts of the submarine 'landscape'.

substratum height, height variation, and interstitial space will affect the rugosity, while diversity of substratum composition, areal extent, and spatial distribution will affect the heterogeneity (Gratwicke & Speight 2005, Wilson et al. 2006). It is also important to be aware that substrata and community composition of the habitat may vary over time following successional processes or anthropogenic impacts (Sale 1991, Friedlander & Parrish 1998b, Kamenos et al. 2003). Table 1 gives some examples of methodological studies in which substratum rugosity and heterogeneity have been measured.

Habitat association, selection, and preference

To relate species to habitat components, terms such as 'habitat association', 'selection', and 'preference' are frequently used to identify environmental variables of relevance to the individual organism, population, or stock. Theoretical and modelled applications in this field seem to be well established (e.g., Johnson 1980, Aarts et al. 2008, 2013), but both field and laboratory studies have frequently lacked clarity, and the terms 'association', 'selection', and 'preference' have been used interchangeably (e.g., Atkinson et al. 2004, Laurel et al. 2007, Misa et al. 2013). This interchangeable use of terms may arise from the overlapping definitions of association, selection, and preference (e.g., Krausman 1999, Morris 2003). To support implementation of the essential fish habitat (EFH) concept under the US Sustainable Fisheries Act (SFA) (US Department of Commerce [USDOC] 1996), the National Marine Fisheries Service considered four levels of information on fish populations in different substrata that could be used (following Able 1999). These levels are 1) species presence-absence data; 2) population densities; 3) information derived from estimated growth, reproduction or survival rates; and (4) estimates of fish production (Able 1999). The different options for the identification of an EFH is beneficial to managers when considering data-poor ecosystems but can lead to further lack of clarity in the terminology used to describe the role of a particular substratum for an individual fish.

The present review focuses primarily on interactions with substrata, so for clarity the term 'substratum' rather than another habitat component is considered in relation to association, selection, and preference. This terminology could, however, be applied to other habitat components (e.g., depth or temperature ranges) in a similar way. Specifically, substratum association has been defined as the substratum type(s) that a fish is observed to occupy during a particular time and place (Box 1) (Hall et al. 1997). This has typically been measured by comparing relative abundances or densities of individuals in, on, or over different substratum types (e.g., Nickell & Sayer 1998, Misa et al. 2013). Here, substratum association refers to all the substrata that the fish occupies during a particular stage in its life cycle without any consideration about whether an active choice was made to reside in the given substrata.

Substratum selection refers to the process by which fish actively choose to occupy a particular substratum type at a given time and therefore results from voluntary movements that cannot be attributed to passive transport (Box 1) (Johnson 1980, Kramer et al. 1997). Factors affecting substratum selection may include individual preference, the availability or condition of substrata in the landscape, or predation risk (Johnson 1980, Kramer et al. 1997, Gaillard et al. 2010). Selection has been measured as the disproportionate use of one substratum type with respect to its availability (Aarts et al. 2013).

Substratum preference (Box 1) is defined as a substratum type that an individual would associate with given a free choice (i.e., in the absence of predators or competitors) at a given time (Gaillard et al. 2010). Confusingly, preference has also been measured as the relative abundances of the focal species in the areas of different substrata in relation to their relative availability (Johnson 1980, Aarts et al. 2008). The latter would only measure a species' innate preference after it has been modified by other, presumably unmeasured effects, such as predator-prey or competitive dynamics.

Arguably, this usage concerns the realized substratum selection. Laboratory experiments or field enclosures may be a more appropriate test for preference (Kramer et al. 1997).

A practical problem when measuring substratum association, preference, or selection by only comparing one or a few substratum types is that patches are rarely a uniform shape, size, and condition. These aspects may have a strong influence on the extent, spatial distribution, and refuge value of habitat for a particular species (Morrison et al. 1992, Block & Brennan 1993). For example, in a field experiment to investigate the significance of eelgrass patches for survival of juvenile Atlantic cod, *Gadus morhua*, Laurel et al. (2003) found that predation rates were negatively correlated with patch size. Methods to measure substratum preference are not always straightforward. Laboratory techniques usually simplify the environment to one or a few variables from complex natural marine systems (Kramer et al. 1997). Studies using a combination of field and laboratory methods may lead to more reliable conclusions (e.g., Stoner et al. 2008, Laurel et al. 2009). Table 1 provides examples of studies that used quantitative methods to study preference and selection for habitat components by demersal fish.

Important habitats

The ultimate aim of spatial management for the protection of fish species is often to protect 'important', 'critical', or 'essential' habitats. An EFH is defined under the US SFA as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity" (USDOC 1996, p. 6). A key element of the EFH concept is the identification of existing and potential threats to habitat components and conservation measures that may improve the quality of the habitat and eliminate or minimize anthropogenic threats (Schmitten 1999). The provision of EFHs through the SFA enabled a significant step towards EBFM (Fletcher & O'Shea 2000, Marasco et al. 2007). Unfortunately, although the SFA provided a platform to better understand the EFH and a capacity to protect fish habitat through spatial management measures, the SFA's definition of what an EFH actually meant is limited in scope (Sarthou 1999, Fletcher & O'Shea 2000), as reviewed and applied by Able (1999).

Similar terms to EFH include 'important' and 'critical habitats' (Box 1), which are typically defined as areas required by fish to carry out key life-history processes, such as reproduction, foraging, and migration (Langton et al. 1996, Able 1999, Bradbury et al. 2008). These habitats may include nursery areas, defined by Beck et al. (2001, p. 635) as areas whose "contribution per unit area to the production of individuals that recruit to the adult population is greater, on average, than production from other habitats in which juveniles occur". Jackson et al. (2001) pointed out that assessing the importance of a substratum type to a fish species should include consideration of whether the substratum type is needed to sustain their populations. In the present review, an important or critical habitat component is considered to be a property of the environment (e.g., a type of substratum or temperature range) that, if altered or reduced in availability, could adversely affect the probability of survival of an individual, or the survival rate of a population, or stock. This definition is linked to habitat quality (Box 1) but focuses on certain components of the habitat rather than its entirety (Krausman 1999). At a population level, an important habitat component would therefore affect the long-term viability of a population (Murphy & Noon 1991). It should be noted that different population subunits (e.g., stocks) may utilize different but functionally equivalent habitat components. Isolating important habitat components rather than important habitats (which include substratum, physico-chemical, and biological characteristics) allows usable definitions to be developed for decision-making and policy implementation (Langton et al. 1996). Attempts to achieve this in a cost-effective and practicable manner are likely why management strategies often rely on identifying apparent associations between species and particular substrata.

The identification of EFH or important habitat components for spatial management measures have similar issues as described previously for habitats, in that managers are tasked with identifying areas for protection with little baseline information and minimal resources (Langton et al. 1996, Rubec et al. 1999). The lack of detail in the SFA about how to identify EFHs can therefore be beneficial in enabling management authorities to identify EFH with little baseline information or by using the best-available evidence. However, in some cases, using the best-available evidence may amount to basing decisions on apparent selection for, or even just simple association with, certain habitat components rather than identifying genuine EFHs, and in the worst cases this could lead to ineffective or counterproductive management measures (Able 1999, Fletcher & O'Shea 2000). Gaillard et al. (2010, p. 2260) proposed that for conservation and management purposes, attention should be focused on habitats that "increase average individual fitness". This approach would require measurement of parameters such as survival, future reproductive potential, and growth rate, which can be difficult to quantify. Langton et al. (1996) and Able (1999) recommended focusing on critical life phases that determine cohort size. We recommend that when examining important fish habitat components, habitat quality should be assessed and linked to population demographics over different temporal and spatial scales (Gibson 1994, Able 1999, Gaillard et al. 2010). These sorts of studies require an understanding of the type, quantity, and range of conditions required for the fish's survival at each major life-history stage (Gibson 1994, Langton et al. 1996, Able 1999). Most demersal marine fishes, including most commercially exploited species, are highly mobile and occupy different substrata and depth ranges during different life-history phases and according to varying environmental conditions. Spatial and temporal processes, such as diel, seasonal, and ontogenetic movements between habitats must therefore be taken into consideration when identifying important fish habitat components and applying EBFM (Hilborn et al. 2004b). Table 1 highlights works that provide quantitative methods for identifying important habitat components for species and management applications of this information.

Table 1 Examples of methodological papers relevant to habitat-related terminology

Habitat-related terminology	Summary description	Species/life stage	Habitat component	Geographic zone/location	Reference
Substratum rugosity and heterogeneity	A method to assess substratum complexity using habitat assessment scores to take into account different aspects of substratum structure and composition.	Species richness and general fish abundance	Sandy, algal, seagrass and reef substrata	Tropical: British Virgin Islands	Gratwicke & Speight 2005
	A comparison of methods to measure and quantify substratum topography for reef fish.	Tropical reef fish	Coral and rocky reefs	Tropical: Australia	McCormick 1994
	A review of the relationship between species diversity and heterogeneity, looking at different spatial scales. Includes measurements of heterogeneity.	Generic, terrestrial	Generic	Generic	Tews et al. 2004

Continued

Table 1 (Continued) Examples of methodological papers relevant to habitat-related terminology

Habitat-related terminology	Summary description	Species/life stage	Habitat component	Geographic zone/location	Reference
Habitat component preference and selection	A review of regression models for analysis of space use and habitat preference using telemetry data and applied to tagged grey seals, *Halichoerus grypus*.	Generic, but applied to grey seals	Generic, applied to sediment type, depth and distance from haul out	Generic, temperate, Scotland	Aarts et al. 2008
	Methods to quantify the effects of habitat availability on species distribution to measure and apply habitat selection functions.	Generic, applied to model simulations	Generic, using continuous and discrete covariates	Generic	Aarts et al. 2013
	Methods and application of habitat component usage and availability to understand selection and preference.	Generic, but applied to mallards, *Anas platyrhynchos*	Terrestrial, wetland, and open-water areas	Generic, temperate, USA	Johnson 1980
Habitat component importance	A review and application for the identification of essential fish habitats (EFHs).	Juvenile estuarine fish	Estuaries; oxygen, pH, salinity, and temperature	Temperate, USA	Able 1999
	A conceptual framework for understanding habitat performance relationships using long-term telemetry information from animals and indices of habitat quality at different spatial scales.	Generic	Generic	Generic	Gaillard et al. 2010
	Advice to managers on prioritizing information for the identification of EFHs, taking into account fisheries impacts.	Generic	Generic	Generic, temperate, USA	Langton et al. 1996
	Modelling fitness to link habitat availability to density-dependent population growth rates of mobile species.	Generic, mobile species	Generic	Generic	Matthiopoulos et al. 2015

Note: Examples include peer-reviewed papers that encompass a range of different methodological and quantitative applications to concepts outlined within the present review. NB: Terminology in the selected papers may not be consistent with definitions used within this review.

BOX 1: GLOSSARY OF TERMS RELATING TO HABITAT CONSERVATION FOR DEMERSAL MARINE FISH

Biotope: The definition of what a biotope consists of has evolved through time, as reviewed by Olenin & Ducrotoy (2006). The present review adopts the modern definition, which describes the "physical environment and the community" (Olenin & Ducrotoy 2006) and therefore encompasses a biocoenosis (group of organisms found living together) rather than focusing on the habitat requirements of an individual species or "the ecosystem linkages between abiotic and biotic components" (Olenin & Ducrotoy 2006).

Ecosystem: An ecosystem consists of biotic (community of organisms) and abiotic (physical, chemical, and biogeochemical) features, processes, and interactions in a defined space at a given time (Dauvin et al. 2008a, Curtin & Prellezo 2010) and may encompass many (potentially overlapping) biotopes. Dauvin et al. (2008a) provided an overview of the development of the term 'ecosystem'.

Ecosystem-based fishery management (EBFM): A variety of definitions and interpretations of EBFM exists (Hilborn et al. 2004a, Marasco et al. 2007). The present review adopts the definition of Marasco et al. (2007, p. 930): "Ecosystem-based fishery management recognizes the physical, biological, economic, and social interactions among the affected components of the ecosystem and attempts to manage fisheries to achieve a stipulated spectrum of societal goals, some of which may be in competition." Not all aspects of EBFM are touched on in this review.

Habitat: The required types of substrata, physico-chemical parameters, and biological characteristics of an area occupied by a species during a particular stage of its ontogeny. A species' habitat can therefore be applied to individuals and populations or stocks. Variables making up a species' habitat can be dynamic or static (e.g., predator or prey density, or depth; Beyer et al. 2010). A habitat will have spatial and temporal scales relevant to the body size and mobility of the study organism (Hall et al. 1997, Diaz et al. 2004).

Habitat component availability: The availability of a habitat component is the proportion of its total areal extent that could be occupied by an additional individual fish, taking account of prior occupation. For example, a fish's choice of substratum will depend on both its preferences and the availability of preferred substrata (Johnson 1980, Laurel et al. 2004).

Habitat components: The components of a habitat are the individual features and their properties that constitute a habitat, that is, types of substratum and physico-chemical and biotic conditions (Figure 1) (Langton et al. 1996, Kaiser et al. 1999).

Habitat quality: The quality of a habitat is the degree to which a habitat directly influences the growth, survival, and future reproductive potential of an individual fish depending on the condition and range of the individual habitat components (Gibson 1994, Hall et al. 1997). Factors affecting a habitat's quality include the quantity and nutritional value of food available for the organism in question, the optimality of the ranges of physico-chemical parameters, and the degree of protection afforded (Gibson 1994). Nonetheless, habitat quality should be measured by the habitat's ability to promote growth, survival and reproduction (Gibson 1994, Able 1999).

Important or critical habitat component: An important or critical habitat component is one for which a change in its condition or availability has the ability to directly affect the success (survival, growth, and reproduction) of an individual or metapopulation. At a population level, a critical habitat component is essential for the long-term viability of the population (Murphy & Noon 1991).

Landscape: The composition, distribution, and topography of (abiotic and biotic) substratum types within a given area or volume of water is its landscape (Saab 1999). A landscape typically encompasses several species' habitats, and one habitat will occupy only part of the landscape (Figure 2). The spatial characteristics (size, shape, orientation, arrangement of components) of a landscape may influence the ecological function of the area, such as acting as a corridor for migration (Zajac 1999).

Physico-chemical space: A physico-chemical space is bounded by the limits of the tolerable ranges of the abiotic variables that influence where an individual can live. These may include variables such as current velocity, depth, temperature, salinity, oxygen concentration, pH, and so on. The physico-chemical space may vary over an individual's lifespan and between sexes.

Substratum association: The substratum type that is occupied by a fish during a particular stage in its life cycle is its substratum association.

Substratum heterogeneity: The diversity and pattern of substratum types and patches within a habitat or a landscape and the level of substratum rugosity comprise its heterogeneity (Dutilleul 1993, Tews et al. 2004). Substratum heterogeneity should be measured on the same spatial scale as the home range of the life stage in question.

Substratum patch: A continuous or homogeneous area of unbroken substratum type is its patch (Morrison et al. 1992) (e.g., an extent of seagrass or sand). The patch size should be measured at a scale appropriate to the life stage of interest.

Substratum preference: The preference is the type of substratum that an individual would associate with given an unconstrained choice at a given time, for example, in the absence of predators and competitors (Johnson 1980, Hall et al. 1997).

Substratum rugosity: The rugosity is the degree of corrugation and angulation of a substratum, which together provide a 3-dimensional space (McCormick 1994) that a fish may occupy during a particular stage in its ontogeny. This includes interstitial and interstructural spaces of appropriate size and shape for the life stage in question (Bartholomew et al. 2000). Substratum rugosity should be measured at the scale appropriate to the focal species.

Substratum selection: The substratum selection is the active choice made by a fish to associate with a particular substratum type. This may be affected by behavioural responses such as preference, inter- or intraspecific competition, the availability or quality of other substrata or resources in the immediate surroundings, or predator presence. Selection is therefore indicated by the substratum type a species resides in at a particular time, taking into account the aforementioned behavioural responses (Johnson 1980, Hall et al. 1997, Kramer et al. 1997, Gaillard et al. 2010).

Substratum type: A substratum type is a class of seabed of distinctive character composed of abiotic or biogenic material, or a combination, used to characterize sediment, algae, flora, or biogenic reef, for conservation and explanatory purposes. Examples include seagrass, mud, or maerl that may be found in an area. The appropriate degree of specificity will depend on the requirements of the study.

Discussion and recommendations

With the continued decline in many fish stocks and anthropogenic pressure on marine ecosystems, there is a clear need to identify habitat components of importance to marine fishes and to introduce effective management mechanisms (Parma et al. 2006). Considerable effort has been spent on substratum mapping, ecosystem conservation, and identification of fish habitat components (Diaz et al. 2004, Francis et al. 2007), yet an integrated approach to EBFM is required for its successful implementation (Francis et al. 2007, Curtin & Prellezo 2010, Guarinello et al. 2010). The impacts of fishing gear on substrata and on fish have been described, but the effects of substrata and loss of benthic fauna on fish stocks are rarely included in demersal stock assessments (Auster & Langton 1999, Armstrong & Falk-Petersen 2008). For spatial management to be effective for fish, protection of important components of their habitat is clearly essential (Schmitten 1999, Francis et al. 2007). Throughout the world, there has been increased use of spatial management measures to manage fish populations, promote biodiversity, and improve ecosystems as a whole. However, benefits from such spatial management measures have not always been evident (Hsu & Wilen 1997, Hilborn et al. 2004a,b), and spatial management measures should not be seen as the only option to restore depleted stocks (Hilborn 2011). In endeavouring to protect important habitat components, careful planning and consideration of spatial and temporal scales are essential, in addition to adaptive management and monitoring (Hilborn 2011). Temporal and spatial scales are particularly important when managing fishing activities to help reduce and resolve conflicts between different sea user groups through zoning (Marasco et al. 2007). Such consideration may also avoid unintended consequences of increased fishing prior to the implementation of spatial management (Hsu & Wilen 1997) and displacement of fishing effort to other areas with potentially harmful effects (Murawski et al. 2000, Hilborn et al. 2004b).

Language in science has changed over time and differs between disciplines; however, at a minimum, clarity in the use of language is necessary (Murphy & Noon 1991, Olenin & Ducrotoy 2006). The term ‘habitat’ has been used in different ways and has become synonymous with ‘substratum type’, and in some cases with ‘biotope’ or even ‘ecosystem’, through its adoption into policy and legislation (Hall et al. 1997, Olenin & Ducrotoy 2006). Habitat-related terminology has become confused through widespread use for different purposes without clear definitions, and through inconsistent usage in scientific research (Murphy & Noon 1991, Hall et al. 1997). To be able to manage marine resources, terminology must be ‘operational’, so that concepts can be realized and accurately measured (Murphy & Noon 1991, Hall et al. 1997). Papers focusing on reasons for the failure to properly manage marine resources consistently point to the need for improved clarity, transparency, and clearly defined management objectives (Hsu & Wilen 1997, Fletcher & O’Shea 2000, Parma et al. 2006).

Many of the terms relating to a species’ habitat are inherently scale dependent (Levin 1992, Hall et al. 1997, Chave 2013). The terms proposed in this review are scale independent insofar as they can be applied to any spatial or temporal scale deemed relevant to a particular study species. This avoids the need for additional, unnecessary terms (e.g., ‘microhabitats’). Nonetheless, scale must be carefully considered in the design and interpretation of any investigation of habitat and should be explicitly stated to allow meaningful comparison between studies. When using the term ‘habitat’ from the point of view of the individual, population, or species, it is essential to consider the temporal and spatial scales relevant to the needs of the organism(s) in question and for the concept to be biologically meaningful (Hall et al. 1997, Diaz et al. 2004, Guarinello et al. 2010).

The present review has identified some of the causes of confusion in use of the term ‘habitat’ and habitat-related terminology and provides a conceptual framework for managers to work with and apply to spatial management programmes. It is widely agreed that the different specialisms within marine or even terrestrial science and policy have not been well integrated, and better integration is required, particularly to achieve EBFM (Degnbol et al. 2006, Marasco et al. 2007). With the increasing number of studies relating to fish habitat, standardized and consistent terminology is a prerequisite for developing clear hypotheses and carrying out comparable research (Murphy & Noon 1991, Levin 1992, Hall et al. 1997). By reviewing habitat-related concepts and reemphasizing existing definitions for researchers and managers to work with, some standardization may be possible. This could help align language used in different fields of marine science and management, and help improve interdisciplinary collaboration, enabling a more coherent and effective implementation of EBFM.

Acknowledgements

We would like to thank the editor, I.P. Smith, who supported the development of this manuscript, and P. Auster, who independently reviewed this paper and provided useful feedback and comments. We would also like to thank D. Haydon, J. Clarke, and S. Auer, who also provided helpful feedback on earlier drafts. This study was conducted while the first author was in receipt of the ClimateXChange centre scholarship and Marine Scotland (Clyde 2020) student support, for which we are very grateful.

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