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Linking temperate demersal fish species to habitat: scales, patterns and future directions

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Abstract

Adoption of the ecosystem approach to fisheries management relies on recognition of the link between fish and other components of the ecosystem, namely their physical and biological habitat. However, identifying the habitat requirements of marine fishes and hence determining their distribution in space and time is scientifically complex. We analysed the methodologies and findings of research on temperate, demersal fish habitat requirements to highlight the main developments in this field and to identify potential shortfalls. Many studies were undertaken over large spatial scales (≥100s km^2) and these generally correlated abundances of fish to abiotic variables. Biological variables were accounted for less often. Small spatial scale (≤m^2), experimental studies were comparatively sparse and commonly focused on biotic variables. Whilst the number of studies focusing on abiotic variables increased with increasing spatial scale, the proportion of studies finding significant relationships between habitat and fish distribution remained constant. This mismatch indicates there is no justification for the tendency to analyse abiotic habitat variables at large spatial scales. Innovative modelling techniques and habitat mapping technologies are developing rapidly, providing new insights at the larger spatial scales. However, there is a clear need for a reduction in study scale, or increase in resolution additional to the integration of biotic variables. We argue that development of sound predictive science in the field of demersal fish habitat determination is reliant on a change in focus along these lines. This is especially important if spatial management strategies, such as Marine Protected Areas (MPA) or No Take Zones (NTZ), are to be used in future ecosystem-based approaches to fisheries management.

Keywords abiotic and biotic habitat descriptors, conservation, demersal fish, ecosystem approach, essential fish habitat, habitat association.

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Introduction

Resource exploitation, habitat modification, pollution and climatic shifts are having widespread and detrimental consequences for marine ecosystems globally (Vitousek 1997; Jackson *et al.* 2001; Kaiser *et al.* 2002). With more than 20% of the world's human population living in biodiversity hotspots (Cincotta *et al.* 2000) and over 60% living within 60 km of the coast (Alongi 1998), marine ecosystems are now under huge pressure from anthropogenic activities and increasingly demonstrate a reduced capacity to withstand these pressures (Folke *et al.* 2004). Of particular concern to managers and conservationists are the impacts of bottom trawl fisheries on benthic ecosystems. The modification and degradation of habitats associated with bottom fishing can have long-term consequences for benthic biota, reducing productivity, biomass and species richness (Hiddink *et al.* 2006; Queiros *et al.* 2006; Hinz *et al.* 2009). Following growing concerns regarding the long-term sustainability of marine fish exploitation (Pauly *et al.* 2005), fisheries collapse from food web restructuring (Frank *et al.* 2005) and reduced abilities of chronically impacted benthic communities to sustain previous stock levels (Shephard *et al.* 2010; Hiddink *et al.* 2011), traditional and often single-species management practices are being evaluated. The result has been the development of a new ecosystem-based fisheries management paradigm (Pikitch *et al.* 2004; Frid *et al.* 2005) which aims to maintain a sustainable ecosystem state by integrating knowledge of biotic, abiotic and human components of ecosystems and applying them to fisheries within ecologically meaningful boundaries (Link 2002).

Major drivers of this new approach have been the formation of numerous conventions and legislations that have highlighted the importance of defining habitat requirements of key species. Examples include the Conservation of Antarctic Marine Living Resources (1982) and the Sustainable Fisheries Act (SFA) (1996) in the United States. The SFA added Essential Fish Habitat (EFH) provisions to the existing Magnuson–Stevens Fishery Convention (1976) requiring the National Oceanographic and Atmospheric Administration (NOAA) to facilitate the long-term protection of 'those waters and substrates necessary for spawning, breeding, feeding or growth to maturity'. The SFA highlights the importance of defining physical, chemical and biological properties that are used by fish and those that are necessary to support a sustainable fish biomass for each of the fish species listed. Similar initiatives aiming to define the habitat requirements of marine fish species are now being echoed globally [Europe – Directive on the Conservation of Natural Habitats and Wild Fauna and Flora (1992/43/EEC), Australia – Environment Protection and Biodiversity Conservation Act 1999, Canada – Fisheries Act (reforms – sect. 35, 1985) and Species At Risk Act (Bill C-5, 2002)].

Despite the drive towards ecosystem conservation, and long histories of commercial fishing in Europe, Canada and America (Pauly *et al.* 2005), still relatively little is known about the habitat requirements and basic ecology of many temperate demersal fish species (Benaka 1999). With declining marine fish stock levels (Pauly *et al.* 2005) and an increased awareness of the impacts of bottom fisheries (Kaiser 1998), understanding the specific habitat requirements of demersal fishes is more important than ever. Management strategies aiming to attain sustainable exploitation levels of fish stocks can vary widely, from fishing quota implementation (Karagiannakos 1996) or the establishment of no take zones (NTZ) and marine protected areas (MPA) (Gaines *et al.* 2010), to stock restoration projects involving artificial habitat construction (Seaman 2008) and re-stocking (Heenan *et al.* 2009). The latter initiatives are often only feasible over certain habitat types and scales. For example, artificial habitat construction is a relatively straightforward process for tropical reef fish species, which often have small home ranges and require complex three-dimensional habitats (Roberts and Ormond 1987), and has been implemented successfully in numerous locations over generally small spatial scales (Seaman 2008). Temperate systems on the other hand often consist of relatively homogeneous, soft sediment habitat types that may span thousands of square kilometres over which habitat manipulation is not practicable.

Spatial management measures, such as NTZ's and MPA's, can range from access restrictions for certain users at specified times to full protection from all anthropogenic activity within the designated area. These may vary from closing areas greater than 1000 km^2 for the protection of multispecies communities with relatively low habitat specificity and wide distributions as illustrated by ground fish stocks in the Western Gulf of Maine, New England, USA (see Murawski *et al.* 2000) to the closures of smaller areas less than 100 km^2 to deal with single species in areas of high habitat suitability such as the Red mullet (*Mullus barbatus*, Mullidae) in the Gulf of Castellamare, northwestern Sicily, Italy (see Fiorentino *et al.* 2008). Such approaches are now common place; however, their aims with regard to fisheries may vary from the protection of certain life stages of specific species to the overall enhancement of multiple fisheries (Koss *et al.* 2005; Frost and Andersen 2006; Ardron 2008; Gelcich *et al.* 2009). Studies that accurately describe the habitat requirements of target species and the scales over which they operate can facilitate decisions on the type of management strategies that are most viable for the species of concern.

To aid in the sustainable exploitation of demersal fish stocks, researchers must uncover the most important habitat variables determining the distributions of species as well as the range of temporal and spatial scales over which they operate (Hinz *et al.* 2003). Many studies in this field, however, use widely spaced sampling stations (10s–100s km) and combine data collected across temporal scales. Consequently, habitat variables influencing demersal fish habitat distributions that operate over smaller scales may well be overlooked. For example, combinations of monthly to annual data are likely to mask differences in habitat use between seasons. Similarly, collection of data over a scale of hundreds of square kilometres may not allow for inference about differences in distributions at smaller spatial scales. Mismatches between spatial scales examined and the actual scale at which processes occur may at best mean that patterns are missed, and at worst result in drawing erroneous conclusions. Management interventions supported by such outputs may therefore produce questionable management strategies and a lack of sustainable and efficient protection.

The determination of EFH commonly involves relating the abundance of the species under investigation to measured habitat variables thought to be important to the species distribution (Rice 2005). Habitats accommodating the study species are assumed to be of some importance. Stoner (2003), however, points out that seemingly appropriate habitats may never be occupied, with specific locations being more important than particular habitat forms. Ideally, the determination of EFH should be based on more than abundance alone and should also address the growth and survival of individuals, thus considering how their current distribution may affect future generations. This is especially important if predictions derived from research are to be used in management. Such approaches combining measures of growth and fitness are, however, often restricted to small-scale manipulative experiments, as such data collection over large areas is often constrained by methodologies and cost.

Although work in the field of demersal fish habitat determination is becoming an important part of the ecosystem-based approach to fisheries management, we are currently lacking a critical synthesis that assesses the importance of biotic and abiotic habitat variables at different spatial scales. This means that we are currently unaware whether there are particular spatial scales over which different habitat variables affect the distribution of demersal fishes. In this paper, we analyse the number of different habitat variables that have been studied and the spatial scales over which they determine the distribution of temperate, demersal fishes from square metres to more than a hundred thousand square kilometres. We restrict our analysis to temperate, demersal species as the habitat variables determining the distribution of tropical and pelagic species are likely to differ considerably (see Shepherd and Litvak 2004). Over the period 1980–2011, we aim to quantify the following parameters in this field of research: (i) the number of studies in the field of demersal fish habitat identification and the geographic locations in which they were undertaken, (ii) the life stages and fish species analysed, (iii) the types and numbers of habitat variables commonly investigated and the spatial scale of work undertaken, (iv) the proportion of studies reporting significance for each habitat variable over the spatial range studied and (v) the temporal scales considered in the literature. To examine whether trends in research were justified, we compared the relationships between the total number of studies and the proportion of studies reporting significance for each separate habitat variable, as well as for all abiotic and all biotic variables, across the range of spatial scales analysed. Our analyses permit a critical evaluation of current trends and patterns in the field of demersal fish habitat determination. With rising expectations of managers to meet sustainability targets and the growing pressures on marine ecosystems, continued research in the field of demersal fish habitat determination is required if we are to sustainably exploit our bottom fisheries resources. This analysis is therefore both timely and necessary to assess what research has been undertaken in this field to date, in order that we drive future research efforts in the appropriate direction.

Methods

Search criteria

We conducted a literature search for peer-reviewed publications, published in English over the period 1980–2011, describing the habitat requirements of temperate, marine, demersal fish species. Within any particular publication, one or a number of different investigations may be described. We therefore define 'article' as a published journal paper and 'study' refers to the separate investigations of different habitat variables undertaken within an article. The period was chosen due to the accessibility of online articles and because it corresponded approximately with the time over which fisheries science wholly embraced research into the anthropogenic impacts on demersal resources and demersal fish habitat determination [following the annoucement of the Magnuson–Stevens Fishery Convention (1976)]. The literature search was undertaken using the commercial search engine Google Scholar, which indexes the full text of scholarly literature across an array of publishing formats. Combinations of the following search terms were used: 'association', 'choice', 'connectivity', 'demersal', 'determining', 'distribution', 'ecology', 'EFH', 'essential', 'fish', 'habitat', 'requirement', 'scale', 'suitability' and 'use'. Google Scholar was chosen over Web of Science and Scopus as it gives a higher number of results per general search term (on average), covers non-ISI listed journals (wider search base), and gives lower citation noise [lower citation variation (85% unique entries compared with ISI's 60%)] (Belew 2005; Pauly and Stergiou 2005; Meho and Yang 2007; Harzing and Van der Wal 2008).

The first one hundred search results from each keyword combination were examined. From these, only peer-reviewed articles were chosen as they form the main body of literature widely available to researchers. The articles used therefore did not include any university theses, technical governmental reports or conference proceedings. Articles examining larval life stages were excluded from the analysis as they form a significant and separate body of literature. Often these early life stages also show markedly different habitat preferences to post-larval developmental stages (Gibson 1994; Sullivan *et al.* 2006). Articles investigating survivorship, condition or fitness of demersal species under differing habitat conditions were included in the database when they were directly related to habitat preferences of the species. From each article fitting the above search criteria, eight categorical data variables were extracted and entered into a database (see Table 1 for details). The variables were publication year, location and total spatial scale of study, life stages, fish species, habitat variables and time trends analysed, and origin of data utilized. The total spatial scale (total area) of each study was calculated using ARC GIS (version 9.2) if it was not described clearly by the authors within the methods. If replicate sites were tested, the area of each was calculated and the total across all sites used. Data were categorized by their origin into stock assessment, field study and laboratory study to illustrate the origin of data sources within this field of research. Habitat variables investigated by authors were classified into abiotic vs. biotic and further into the sub-categories listed in Table 1.

Table 1 Table summarizing the data extracted from each article fitting the search criteria and entered into the first database.

Parameter	Description of parameter	Database input categories
Year	Year of publication	1980–2010 (1 year intervals)
Location	Geographic location (within temperate zones) of work undertaken	N. America, Europe, Australia, New Zealand, S. America, other
Total study scale	Total area of the study site (both laboratory and field) over which replicates were taken	$\leq 1e^{-5}$km^2 (cm^2), ≤ 1 km^2 (m^2), ≤ 10 km^2, ≤ 100 km^2, ≤ 1000 km^2, $\leq 10\,000$ km^2, $\leq 100\,000$ km^2
Life stages analysed	Ontogenetic stage considered in the analyses	Adult, Juvenile, All
Fish order analysed	Fish species and order under study	Mixed*, Gadiformes, Pleuronectiformes, Perciformes, Scorpaeniformes, Carcharhiniformes
Study type	Origin of data used	Laboratory study, Field study, Stock assessment survey
Habitat variables analysed	Variables analysed/hypothesized to be important to the distribution/habitat requirements	Abiotic: depth, hydrography, other abiotic[a], salinity, substrate, temperature Biotic: competition[b], biogenic complexity[c,†], predation[d,†]
Time trends analysed	Temporal trends formally analysed as part of the hypotheses	Not applicable, day (12 h), day vs. night (24 h), month (30 days), season (90 days), annual (365 days)

*Mixed species are defined as studies looking at four or more different demersal fish species; [a]Includes dissolved oxygen/level of hypoxia and light; [b]Includes intra and interspecific competition; [c]3D habitat structures of biological origin; [d]Predation of the demersal species under investigation. [†]Often exposure to predation is a result of biogenic complexity. The distinction between the two was made by referring to the authors' hypotheses and final conclusions.

Statistical analyses and graphical outputs

Initially, we focused on the distribution of journal articles across the years and spatial scales they addressed. Ordinary least squares (OLS) linear regressions were employed to analyse the relationships between (i) the number of peer-reviewed journal articles published in the field and the year of publication, (ii) the number of studies and total spatial scale of each study.

Next, we examined the relationship between the number of studies conducted at particular scales and the proportion of studies that reported significant results to understand whether the concentration of studies at particular scales was justified. Here, only articles which reported results based on individual species were used because those which only reported relationships for mixed assemblages could potentially mask significant relationships at the species level. Regressions of spatial scale vs. number of studies were undertaken for all of the different habitat variables plus 'Total abiotic' and 'Total biotic' categories. This process excluded geography, hydrography and predation as there were too few studies that investigated these variables. This was then repeated, except the number of studies was replaced with the proportion of these studies which showed a significant relationship.

Data were $\log_{10}$ transformed to ensure normal distributions where required. To test whether there was a significant difference between the spatial scales at which abiotic and biotic habitat variables operate, Wilcoxon rank sum *t*-tests were used.

Results

The literature search identified 109 peer-reviewed journal articles determining the habitat requirements of demersal fish species from the period between 1980 and 2011 (Table 2). The number of articles published increased significantly over time ($R^2 = 0.506$, $F_{1,29} = 29.72$, $P \leq 0.001$); 43% were published since 2005, with the highest number of articles published in 2001 (13), followed by 2009 (12) and 2002/2007 (11 each) (Fig. 1). North America (46%) and Europe (38%) dominated the locations where studies had been undertaken. The remaining 16% of studies were carried out in Australia, New Zealand and South America. No publications came from Africa or Asia.

The majority of studies (67%) made no clear distinction between adult and juvenile life stages

Table 2 Table summarizing separate fish species, life stages and habitat variables analysed.

		Life stage analysed			Habitat variables analysed											
					Abiotic							Biotic				
Fish order	Fish species	Adult	Juvenile	All	Depth	Geography	Hydrography	Salinity	Substrate	Temperature	Other	Competition	Biogenic complexity	Predation	Prey resource	Reference
Carcharhiniformes	*Scyliorhinus canicula*	*								*		*				Sims *et al.* (2001)
Gadiformes	*Gadus morhua*		*			*			*	*		*	*	*	*	Borg *et al.* (1997), Bjornstad *et al.* (1999), Fromentin *et al.* (2001), Lindholm *et al.* (2001), Blanchard *et al.* (2005), Robichaud and Rose (2006)
	Gadus macrocephalus		*	*	*						*		*			Laurel *et al.* (2007, 2009)
	Eleginus gracilis		*	*	*								*			Laurel *et al.* (2007, 2009)
	Merluccius bilinearis	*					*						*	*		Auster *et al.* (2003)
	Merluccius merluccius		*					*		*					*	Cartes *et al.* (2009)
Perciformes	*Cheilodactylus spectabilis*			*											*	McCormick (1998)
	Micropogonius undulatus		*												*	Eby *et al.* (2005)
	Pagrus auratus		*										*			Thrush *et al.* (2002)
	Paralabrax clathratus	*											*			Anderson (2001)
	Sciaenops ocellatus			*				*			*				*	Bacheler *et al.* (2009)
	Tautogolabrus adspersus		*										*			Levin (1994)
Pleuronectiformes	*Buglossidium luteum*			*			*		*	*						Amara *et al.* (2004)
	Hippoglossoides platessoides			*	*							*				Walsh *et al.* (2004)
	Limanda ferruginea			*	*				*	*		*				Simpson and Walsh (2004), Walsh *et al.* (2004)

Table 2 Table summarizing separate fish species, life stages and habitat variables analysed.

		Life stage analysed			Habitat variables analysed											
					Abiotic							Biotic				
Fish order	Fish species	Adult	Juvenile	All	Depth	Geography	Hydrography	Salinity	Substrate	Temperature	Other	Competition	Biogenic complexity	Predation	Prey resource	Reference
	Hippoglossoides stenolepis		*	*					*			*	*	*		Stoner and Abookire (2002), Stoner and Titgen (2003), Ryer *et al.* (2004), 2007)
	Lepidopsetta polyxystra	*	*	*					*				*		*	Stoner and Titgen (2003), Ryer *et al.* (2004), Stoner *et al.* (2007)
	Limanda limanda	*	*		*										*	Gibson and Ezzi (1987), Hinz *et al.* (2005)
	Pleuronectes americanus		*		*			*	*	*			*	*	*	Manderson *et al.* (2000), (2002), (2003), (2006), Phelan *et al.* (2001), Stoner *et al.* (2001)
	Pleuronectes platessa	*	*	*	*		*		*		*				*	Gibson and Robb (1992), Le Pape *et al.* (2003), Hinz *et al.* (2006), Shucksmith *et al.* (2006), Maxwell *et al.* (2009)
	Solea solea	*	*	*	*		*		*		*				*	Eastwood *et al.* (2003), Le Pape *et al.* (2003), Hinz *et al.* (2006), Vinagre *et al.* (2006), Nicolas *et al.* (2007), Maxwell *et al.* (2009)
	Microstomus kitt	*									*					Hinz *et al.* (2006)
	Solea senegalensis			*							*				*	Vinagre *et al.* (2006)
Scorpaenif-ormes	*Sebastes alutus*	*											*			Brodeur (2001)
	Sebastes sp.			*					*							Johnson *et al.* (2003)
Rajiformes	*Raja clavata*			*	*		*		*							Maxwell *et al.* (2009)

Table 2 Table summarizing separate fish species, life stages and habitat variables analysed.

		Life stage analysed			Habitat variables analysed											
					Abiotic						Biotic				
Fish order	Fish species	Adult	Juvenile	All	Depth	Geography	Hydrography	Salinity	Substrate	Temperature	Other	Competition	Biogenic complexity	Predation	Prey resource	Reference
Mixed	*Mixed*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Iglesias (1981), Macpherson (1981), Sedberry and Vandolah (1984), Mahon and Smith (1989), De Ben *et al.* (1990), Ekau (1990), Pihl *et al.* (1991), Gabriel (1992), Gibson (1994), Koslow *et al.* (1994), Edgar and Shaw (1995), Fujita *et al.* (1995), Syms (1995), Gutt and Ekau (1996), Farina *et al.* (1997), McClatchie *et al.* (1997), Moranta *et al.* (1998), Piet *et al.* (1998), Gaertner *et al.* (1999), Hyndes *et al.* (1999), Abookire *et al.* (2000), Dean *et al.* (2000), Demestre *et al.* (2000), Ellis *et al.* (2000), McConnaughey and Smith (2000), Amezcua and Nash (2001), Auster *et al.* (2001), Hindell *et al.* (2001), Methven *et al.* (2001), Williams and Bax (2001), Araujo *et al.* (2002), Biagi *et al.* (2002), Francis *et al.* (2002), Hughes *et al.* (2002), Lazzari and Tupper (2002), Magnussen (2002), Kaiser *et al.* (2004), Pittman *et al.* (2004), Busby *et al.* (2005), Logerwell *et al.* (2005), Massuti and Renones (2005), Perry *et al.* (2005), Leathwick *et al.* (2006), Sullivan *et al.* (2006), Wilhelmsson *et al.* (2006), Anderson and Yoklavich (2007), Medina *et al.* (2007), Stal *et al.* (2007), Bergstad *et al.* (2008), Selleslagh and Amara (2008), Anderson *et al.* (2009), Ehrich *et al.* (2009), Katsanevakis and Maravelias (2009), Katsanevakis *et al.* (2009), Laidig *et al.* (2009), Langhamer and Wilhelmsson (2009), Moore *et al.* (2009), (2011), Ordines and Massuti (2009), Persohn *et al.* (2009), Quiroga *et al.* (2009), Chatfield *et al.* (2010), Colloca *et al.* (2010), Damalas *et al.* (2010), Keller *et al.* (2010), Reiss *et al.* (2010)

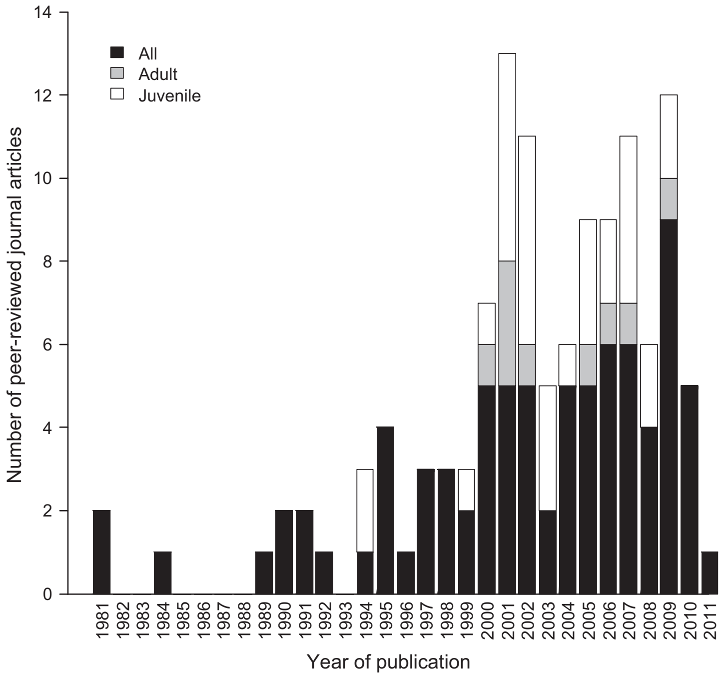

Figure 1 Number of peer-reviewed journal articles that have investigated the habitat requirements of temperate demersal fishes (by year of publication). Studies are separated into the major life stages analysed.

analysed. Juvenile life stages were analysed in 26% of articles whilst 7% studied only the adult life stage (Fig. 1). Mixed-species communities were studied in 57% of the studies analysed. Of the remaining 42%, Pleuronectiformes dominated the literature (52%) followed by Gadiformes (25%) and Perciformes (15%) (Table 2). The most studied single species were the Atlantic cod (*Gadus morhua*, Gadidae), Common sole (*Solea solea*, Soleidae) and Winter flounder (*Pseudopleuronectes americanus*, Pleuronectidae). Ninety per cent of all the non-mixed species studied are currently commercially exploited.

Few studies determining the habitat requirements of temperate demersal fishes came from laboratory studies (8%) with the majority originating from field and stock assessment-derived data (46% each respectively) (Fig. 2). Stock assessment-derived data were predominantly (98%) focussed over medium to large spatial scales of study (100s–100 000s km^2), field study-derived data (85%) over medium scales (10s–100s km^2) and laboratory scale data (100%) over the two smallest scales (cm^2 to m^2).

We found that the majority of studies focussed on the effects of abiotic (72%) rather than biotic (28%) habitat variables (Fig. 3). There was a tendency for abiotic variables to be studied at larger spatial scales ($R^2 = 0.753$, $F_{1,6} = 23.160$, $P = 0.003$). However, no significant relationship between the number of studies analysing biotic habitat variables and the spatial scales of study was demonstrated ($R^2 = 0.046$, $F_{1,6} = 0.305$, $P = 0.6$). Overall, there was a significant difference between the scales at which abiotic and biotic habitat variables were studied ($P < 0.001$, $W_s = 5051$); abiotic variables focussed at larger spatial scales (69% at scales $\geq$100 km^2) and biotic variables at low to medium spatial scales (53% at scales $\leq$ 100 km^2) (Fig. 3).

Assessment of how the proportion of studies showing significant relationships changed with spatial scale was conducted for each habitat variable separately and for the categories 'Total abiotic' and 'Total biotic' (Figs 4 and 5). For the abiotic variables, there was a significant positive relationship between the spatial scale of study and the total number of studies for depth ($R^2 = 0.845$, $F_{1,5} = 35.207$, $P = 0.001$), temperature ($R^2 = 0.767$, $F_{1,4} = 19.766$, $P = 0.004$) and for 'Total abiotic' ($R^2 = 0.846$, $F_{1,7} = 32.990$, $P = 0.001$) (Fig. 4). However when each of these variables and variable combinations was analysed using the

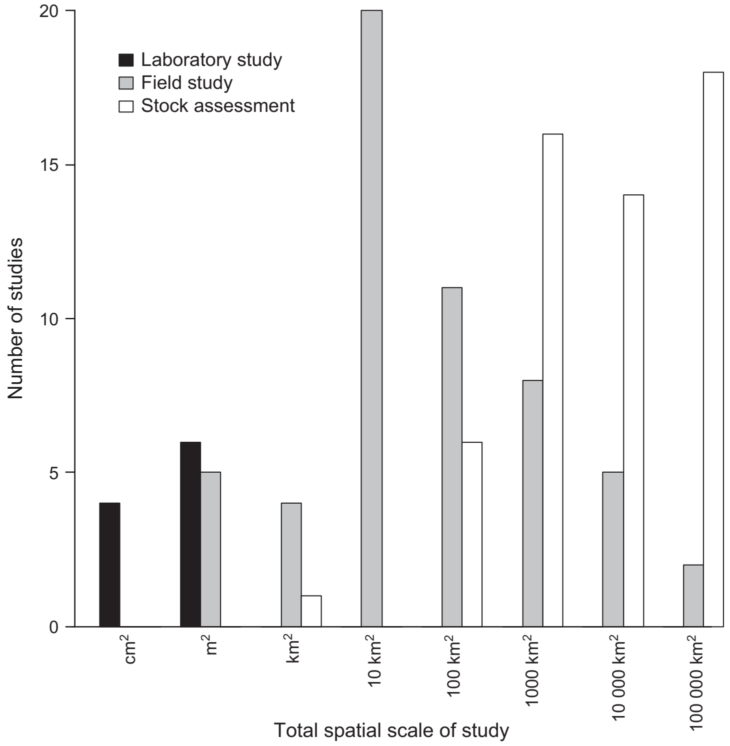

Figure 2 Number of studies originating from laboratory studies, field studies and stock assessments by total spatial scale of study.

proportion of studies which showed a significant relationship, rather than total number of studies, no significant regressions were found. Thus, whilst the total number of studies increased with spatial scale, there was no apparent increase in the proportion of studies showing significant relationships (Fig. 4). For the 'Total biotic' category, there was no clear pattern of change in the number of studies with scale, although one biotic habitat variable (competition) showed an increase in the number of studies with increasing spatial scale ($R^2 = 0.663$, $F_{1,5} = 11.812$, $P = 0.014$) (Fig. 5). There were no significant relationships between the proportion of significant studies and spatial scales of study for any of the individual biotic habitat variables or 'Total biotic' category.

Examination of the distribution of studies among the different habitat variables showed that depth and substrate made up more than half of the abiotic variables analysed (33 and 26%, respectively) (Fig. 4). The most studied biotic habitat variable was biogenic complexity (48%) (Fig. 5). The variables of geography and hydrography, which formed 7 and 0.9% of abiotic habitat variables, respectively, and competition and predation, which made up 7 and 5% of biotic habitat variables, respectively, were seldom analysed.

Temporal trends were formally analysed in 46% of studies (Fig. 6). Annual and monthly differences in habitat requirements were the most common temporal trends analysed in studies (13% each), followed by season (11%) and day (9%).

Discussion

Data limitations and considerations

Our comprehensive literature search has allowed us to highlight some important trends and patterns in the identification of demersal fish habitat. It is, however, important to discuss possible limitations of our approach and the bearing they may have on our conclusions. This quantitative, systematic analysis only included peer-reviewed articles. The inclusion of dissertations, theses, government reports and conference proceedings may have added to the total number of articles reviewed. We do not, however, believe it would have

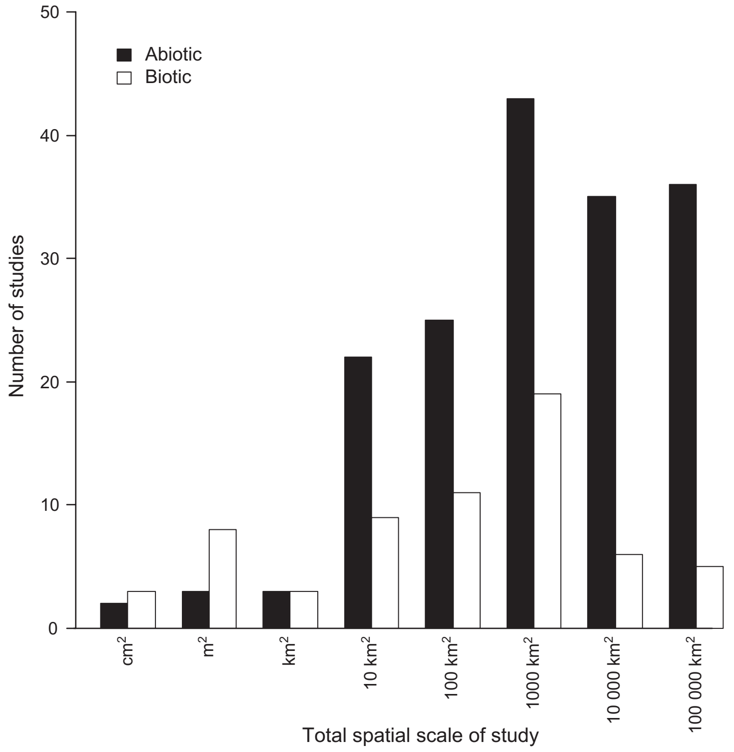

Figure 3 Number of studies analysing abiotic and biotic habitat variables by total spatial scale of study.

broadened the scope of the analyses presented as only five non-peer-reviewed articles appeared within our search criteria, three of which are known to have been published subsequently as peer-reviewed articles which were then included in our analysis. The exclusion of non-English peer-reviewed articles may well explain the low numbers of studies coming from South America and the complete lack of work originating from Africa and Asia. Nonetheless, we have no reason to believe that the patterns identified are likely to be geographically biased other than through the temperate restriction placed on the search criteria. The exclusion of articles prior to 1980 is not likely to have any significant bearing on our findings as we clearly demonstrate that work in this field did not develop substantially until post-1980, with only four articles published between 1980 and 1990. The tendency for authors to more readily report significant than non-significant relationships is likely to have increased the proportion of studies reporting significance. This publication bias is, however, expected to operate equally across all studies and spatial scales (Brett 1997) and therefore have little effect on our findings.

Spatial scale

The significance of scale in ecological investigations is well understood (Wiens 1989), and many studies have demonstrated the variable habitat use of temperate demersal fishes over a range of spatial and temporal scales (Bax *et al.* 1999; Lindholm *et al.* 1999; Walsh *et al.* 2004). Our analysis demonstrates that studies focusing on larger spatial scales primarily analyse abiotic habitat variables, whilst studies addressing biotic variables typically focus at smaller spatial scales. The tendency to study abiotic habitat variables over larger spatial scales may, however, not be wholly justified as our analysis showed no concomitant increase in the proportion of studies reporting significance at these larger spatial scales. As a result, our analyses indicate that there is no reason to limit the study of abiotic variables to large spatial scales. There was, however, no mismatch between the number of studies and the proportion of those studies in which biotic variables had a significant effect; both the total number of studies and the proportion of significant studies showed no pattern with spatial scale, except for the process of competition where

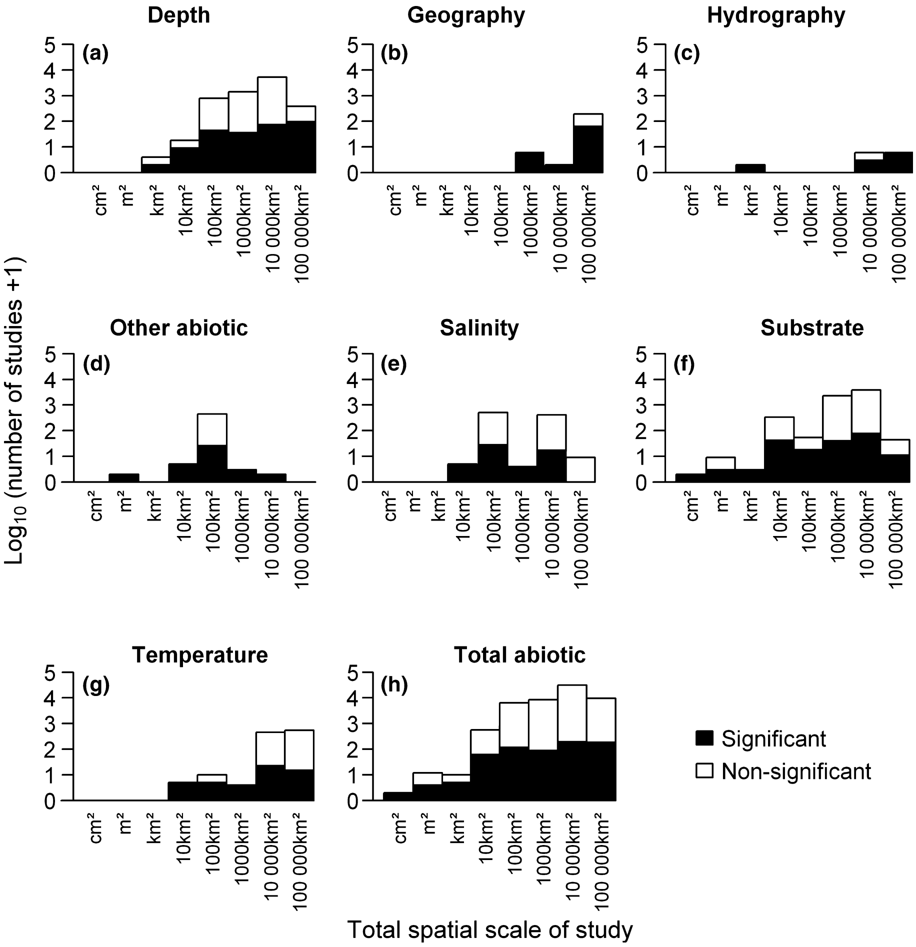

Figure 4 Number of non-mixed species studies (those analysing ≤ 4 species) reporting test statistics for each species and each abiotic habitat variable across the total spatial scales of study. Bars indicate the number of studies reporting significant (black) and non-significant (white) results. 'Other abiotic' includes the habitat variables of dissolved oxygen/level of hypoxia and light. (a) Depth, (b) Geography, (c) Hydrography, (d) Other abiotic, (e) Salinity, (f) Substrate, (g) Temperature, (h) Total abiotic (all abiotic habitat variables combined).

the total number of studies was very low. Thus, although the number of studies of biotic variables is in general low compared with the number of abiotic studies, the spread across all spatial scales for biotic habitat variables is likely justified.

The preponderance of large-scale abiotic studies could be a result of data availability, which will be discussed later. However, we believe that this also highlights the common assumption in this field that abiotic habitat variables are inherently linked to larger spatial scales and are most likely to influence the distribution of demersal fishes over larger spatial scales than do biotic habitat variables. This is, however, unlikely to be wholly the case, and numerous studies demonstrate the importance of abiotic habitat variables over small spatial scales (≤100 km^2) (Stoner *et al.* 2001; Laurel *et al.* 2009; Moore *et al.* 2009) and biotic habitat variables over larger spatial scales (≥100 km^2) (Bjornstad *et al.* 1999; Vinagre *et al.* 2006; Le Pape *et al.* 2007). The lack of a relationship between the total spatial scale of study and the proportion of significant findings for the habitat variables analysed leads to the conclusion that there is no definitive spatial scale at which each of the different habitat variables significantly affect the distribution of temperate adult demersal fishes. It is therefore appropriate to analyse the effects of each habitat variable across all of the spatial scales analysed.

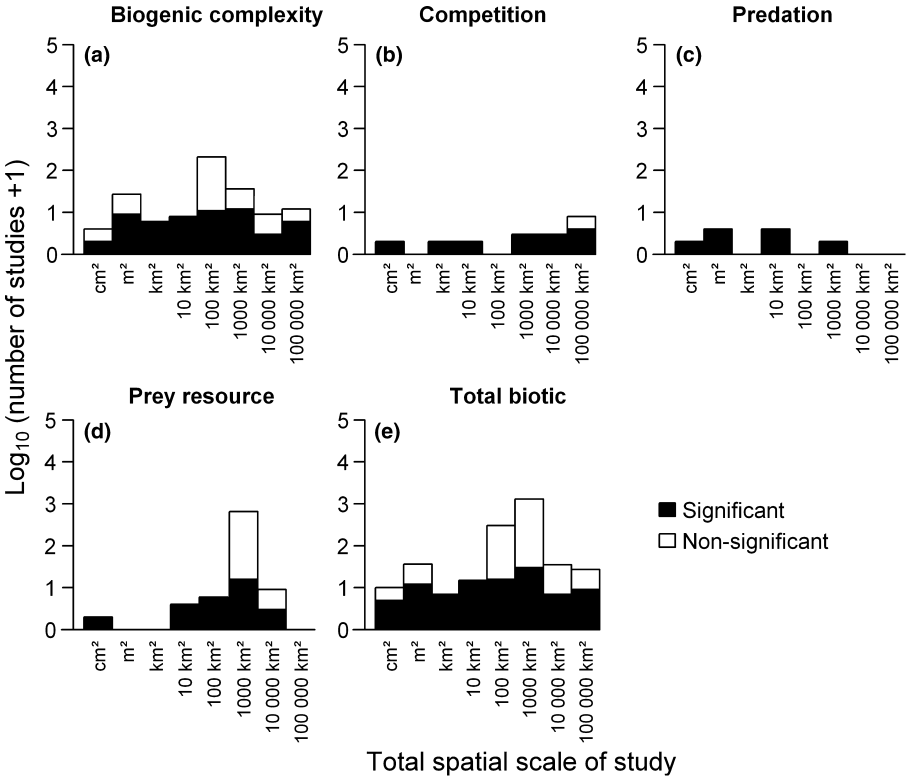

Figure 5 Number of non-mixed species studies (those analysing ≤ 4 species) reporting test statistics for each species and each biotic habitat variable across the total spatial scales of study. Bars indicate the number of studies reporting significant (black) and non-significant (white) results. (a) Biogenic complexity, (b) Competition, (c) Predation, (d) Prey resource, (e) Total biotic (all biotic habitat variables combined).

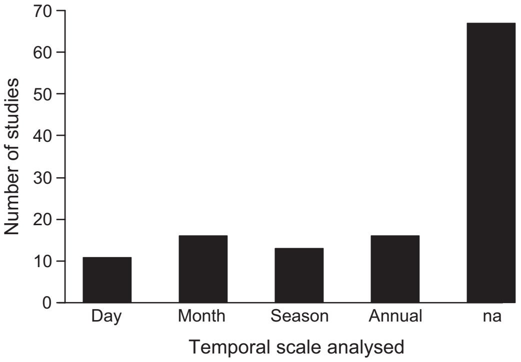

Figure 6 Number of studies carried out over different temporal scales: day = 0–24 h, month = 30 days, season = 90 days, annual = 365 days, na represents the studies that did not analyse any temporal pattern in fish abundance and/or distribution.

The high number of studies focussing on large spatial scales may also be explained by the origin of abiotic data. Almost half of the data used in studies have originated from government-funded stock assessments and long-term, large spatial scale, scientific fish surveys. These data sources provide regular and large spatial scale information on fish abundance and local environmental variables that are directly comparable to the spatial scales of commercial fisheries. It is, however, important to consider that the large distances between sampling stations inherent with fishery-scale data sets mean that researchers are often unable to address the processes determining fish distribution that operate at smaller spatial scales (Hinz *et al.* 2006; Sullivan *et al.* 2006). An alternative but more costly approach, the use of multiscale, hierarchical surveys is likely to prove successful in elucidating the role of spatial scale in fish distribution (Pittman *et al.* 2004; Anderson and Yoklavich 2007; Anderson *et al.* 2009; Monk *et al.* 2011). These approaches warrant further investigation and development as there is still a paucity of studies using hierarchical designs in the field of demersal fish habitat determination.

Many studies utilizing large spatial scale data sets often take a 'data-mining' approach, searching for significant relationships between demersal fish abundances and measured habitat variables. This approach has been criticized for shifting our focus away from hypothesis-driven science, and potentially ascribing coincidental correlations or indirect relationships as direct causal links (Guisan *et al.* 2002). Insufficient knowledge of the multiple factors influencing the population dynamics of marine species makes it difficult to form prior assumptions about causal relationships. Consequently, correlative approaches that make few or even no prior assumptions about underlying causal relationships are considered a legitimate approach when attempting to understand the complex interactions between fish populations and their environment (see Valavanis *et al.* 2008). Correlations revealed from these approaches can in turn be used as the basis for subsequent hypothesis-driven studies aiming to determine demersal fish habitat requirements. New statistical approaches such as Quantile Regression (QR) and Structural Equation Modelling (SEM) allow better integration of sound ecological and statistical theory as well as the possibility of testing whether data are consistent with hypothesized causal pathways. Development of these approaches provides promising areas for future development (see Pittman *et al.* 2004; Vaz *et al.* 2008; Hermoso *et al.* 2011; Johnson *et al.* 2012).

Abiotic habitat variables

The bias towards focusing on abiotic variables may be related to the ease with which abiotic data are collected. With the exception of grain size analysis to determine sediment composition, all of the abiotic variables examined require relatively low sampling effort in comparison with that needed to investigate biotic variables (see Levin 1992). Abiotic habitat variables therefore provide a quick and often resource-effective means of collecting information on some of the habitat requirements that may determine the distribution and abundance of demersal fish species. Whether these variables and the relationships demonstrated are relevant to management strategies will likely be case dependent, determined by the species of interest, the habitat types covered and the spatial scales over which they occur.

Of the habitat variables studied, depth and substrate have received the most attention. Both may be considered as useful proxies of other variables affecting the habitat choice of demersal fishes. Many previous studies note significant changes in community composition with depth and sediment type in benthic marine assemblages (Moranta *et al.* 1998; Kostylev *et al.* 2001; Hagberg *et al.* 2003). These relationships may indicate more complex associations with available prey communities and/or changes in habitat structure and complexity (Williams and Bax 2001; Anderson and Yoklavich 2007; Anderson *et al.* 2009). Although studies have successfully used depth, substrate and additional abiotic habitat variables to fill gaps in habitat knowledge (Last *et al.* 2010) and as surrogates for habitat suitability (Blanchard *et al.* 2005), this approach may be misleading depending on the scale of observation and the system under analysis (Chapman *et al.* 2010). Stevens and Connolly (2004) discuss the inadequacies of using surrogate abiotic measures to describe biotic communities at a range of spatial scales, concluding that less than 30% of the biological similarity between areas at scales covering tens of square kilometres could be explained using their abiotic proxies. Williams *et al.* (2009) similarly demonstrated that using a habitat characteristic describing geomorphic features over thousands of square kilometres to describe megafaunal communities led to a misrepresentation of species' rarities. It is therefore necessary that to describe and classify benthic communities and habitats with accuracy using only abiotic variables, they must first be calibrated against correlated biotic variables. This has been reflected in some habitat suitability studies that find that the best predictors of habitat suitability are models combining abiotic variables with biotic ones, such as prey density (Vinagre *et al.* 2006) and individual organismal traits (Le Pape *et al.* 2007). Planque *et al.* (2011) also discuss the inadequacy of expecting environmental (abiotic) habitat variables to fully explain the spatial distributions of fish populations unless their forcing effects are so strong as to override all other factors driving the distribution.

Biotic habitat variables

There is a general paucity of studies addressing the importance of biotic habitat variables in determining the distribution of demersal fish populations. Authors investigating the importance of different abiotic habitat variables often explained their results with reference to biotic habitat variables. Few studies, however, formally analysed the influence of biotic habitat variables, particularly predation and competition, despite their known importance in determining the abundance and distribution of marine fishes (see Ward *et al.* 2006; Engelhard *et al.* 2008; Laurel *et al.* 2009). Studies addressing the importance of biotic habitat variables tended to focus at smaller total spatial scales of study compared with abiotic variables. Apart from substrate choice experiments, the two smallest spatial scale classes analysed (cm^2 and m^2) were dominated by biotic habitat variables. These spatial scales represent studies simulating environmental conditions using artificial laboratory habitat constructions. This approach provides the advantage of direct and continuous observation whilst controlling for additional habitat variables. The disadvantages, however, are well documented and highlighted by many authors working at this spatial scale. In an experiment aiming to investigate the role of variability in seafloor habitat structure on the survivorship of post-settlement juvenile Atlantic cod, Lindholm *et al.* (1999) acknowledged that limited space in such experiments does not allow for realistic foraging of predators or escape responses of prey. Manderson *et al.* (2000) also note that long experimental durations and small arena sizes provide increased predator-prey encounter rates in the laboratory, which are not wholly realistic for scaling up to conditions in the field.

Field validation of results from laboratory studies can help substantiate laboratory findings and may also elucidate previously overlooked variables important in determining habitat choice. Such validation may be undertaken directly by designing comparable experiments in the field or alternatively using pre-existing data to test relationships found within the laboratory. Stoner and Abookire (2002) provide an excellent example of the combination of laboratory and field experiments in their study of sediment preferences in Pacific halibut (*Hippoglossus stenolepis*, Pleuronectidae). Laboratory experiments showed detailed sediment preferences associated with fish size and burial capability. Subsequent field results overestimated the preferred sediment grain size of fish but still supported the hypothesis that sediment suitability was based on settlement capability. The authors also go on to discuss dissimilarities between laboratory and field results, highlighting discrepancies that may exist when extrapolating from small-scale manipulative studies to larger spatial scales.

Temporal aspects of habitat

Although the dynamic nature of fish habitat is widely acknowledged (Rice 2005), less than half of the studies reviewed looked at temporal patterns in habitat usage. Many studies utilizing data from long-term, large-scale stock assessment surveys grouped annual data, meaning that between-year differences in abundance and distribution were not considered. Pooling data may give wider applicability to findings but it also reduces the accuracy and hence predictive power of the results for the specific scenario that has been analysed (Valavanis *et al.* 2008). Differences in habitat suitability within and between habitats as well as important additional information such as fish year-class strength, variations in abundance and shifts in habitat use may be missed when temporal data are pooled. For example, studies by Manderson *et al.* (2002, 2003) on the growth, habitat variation and dynamic settlement in Winter flounder demonstrated that the influence of temperature and salinity on growth varied considerably from late spring into summer. Such studies also highlight the importance of considering location when analysing temporal differences in habitat suitability. In the previous example, freshwater inputs associated with estuaries caused complex changes in temperature and salinity. This is likely to cause large variations in predator-prey dynamics and the overall suitability of habitat important to the juvenile life stage of the study species (Gibson 1994; Manderson *et al.* 2006; Bacheler *et al.* 2009).

If researchers are to provide sound advice to managers on temporal distributions and predictions of future abundances, spatio-temporal approaches must be taken, in which temporal and spatial scales are matched *a priori*. For example, it would be impractical for a study covering thousands of square kilometres to attempt to analyse changes in habitat use over daily time scales. Similarly, over very small spatial scales, it would be inefficient to look at seasonal patterns in habitat use in demersal fish species, some of which are known to migrate large distances during annual spawning events (Armstrong *et al.* 1992; Hunter *et al.* 2003a). Such obvious examples highlight the clear need to plan sampling campaigns which incorporate appropriately matched temporal and spatial scales.

Ontogenetic changes in habitat use

Consideration of temporal patterns in habitat suitability is also important with respect to the ontogenetic changes which demersal fish species undergo during their development. Bacheler *et al.* (2009) showed how habitat use patterns of sub-adult red drum (*Sciaenops ocellatus,* Scianidae) in estuarine environments were age-dependent as well as region-dependent at large spatial scales, whilst Laurel *et al.* (2007) demonstrated habitat selection in Pacific halibut and rock sole (*Lepidopsetta polyxystra,* Pleuronectidae) was mediated by the interaction between temperature, ontogeny and density under laboratory conditions. Our analysis showed that fewer than half of studies clearly defined the life stages of the fish species analysed. Although combining juvenile and adult life stages may simplify sampling strategies and increase statistical power, it prevents ontogenetic changes in sensitivity and habitat requirements from being exposed. Those studies that did define life stage were often those focussed on post-larval settlement and habitat choices of juvenile fishes. Such investigations typically operate at small spatial scales, ranging from square centimetres to tens of square kilometres, often in laboratory or estuarine and shallow coastal environments (Stoner and Titgen 2003; Manderson *et al.* 2006; Laurel *et al.* 2007, 2009). To facilitate comparisons among studies and reduce ambiguity, there is a clear need for the specific life stages examined to be clarified. If neglected, conclusions may apply only to the dominant life stages within original samples and direct comparisons among studies may prove difficult.

Non-commercial and rare species

As well as a clear focus on mixed life stages and mixed species, studies have generally concentrated on commercially targeted demersal fish species. Few studies, however, have attempted to define the habitat variables determining the distribution and abundance of rare species, even where these are commercially valuable. For example, skate and ray species (Batoidea), which are known to be threatened by overfishing and habitat degradation (Hilton-Taylor 2010), have been seldom studied, even though such species often require species-specific studies to detect declines in population numbers (Dulvy *et al.* 2000). Such deficiencies in data and studies of rare species distributions may hamper advice for conservation management strategies aiming to protect these or similar species.

Habitat suitability modelling

The number of studies in the field of demersal fish habitat associations has increased significantly over the past 20 years. This increased research effort has led to many advances in the methods and techniques used to address demersal fish habitat associations. Habitat suitability modelling has provided one attractive approach, as theoretically, results for a particular species should be applicable across systems (Rubec *et al.* 1999). Traditionally, many of these models assumed smooth, continuous and linear or simple polynomial relationships between habitat variables and fish populations. It is, however, often apparent that such functions cannot wholly predict the main processes modulating fish occurrence (see Caddy 2007). There now exist a suite of modelling approaches that are able to deal with more complex and biologically realistic relationships; GAMs combined with GIS platforms are generally considered the most well-developed method for modelling fish habitat use (Stoner *et al.* 2001, 2007; Valavanis *et al.* 2008; Bacheler *et al.* 2009; Katsanevakis and Maravelias 2009).

Progress may also be made through combinations of different models that account for weaknesses of each of the constituent models used. For example, machine-learning techniques are accurate predictors of complex nonlinear relationships with the additional ability to learn using training algorithms applied to random data subsets. They are, however, not good predictors of habitat suitability for new or unsampled sites (Maravelias *et al.* 2003; Pittman *et al.* 2009; Knudby *et al.* 2010). Presence-only algorithms on the other hand are able to assess new site suitabilities defined in terms of their environmental similarity (see Monk *et al.* 2010). Such algorithms could therefore potentially be integrated with machine-learning techniques to improve shortfalls in assessments of new site suitabilities whilst accurately predicting complex nonlinear relationships. Planque *et al.* (2011) also recommend a combinatory, multimodel approach to increase the accuracy of predictions and our overall understanding of factors controlling the spatial distribution of fish populations. Although an area showing promise, complex modelling approaches still need to address the numerous issues related to assumption violation, particularly with respect to spatial auto-correlation and data independence as well as model validation, evaluation and the integration of sound ecological theory (Knudby *et al.* 2010).

Technological advancements

Technological developments have also played an important role in allowing researchers to answer increasingly complex and logistically challenging questions. Direct, *in situ* observations using underwater camera apparatus can inform us about patterns of distribution on small scales (Holmes *et al.* 2008), certain fish–habitat associations (Busby *et al.* 2005; Anderson and Yoklavich 2007) as well as detailed behavioural information (Stoner *et al.* 2008), all of which are unattainable using trawl methodologies alone. Similarly, advances in tagging technologies and in particular acoustic telemetry tags can give us information on locations and times of residency of individual fish (Lindholm *et al.* 2007; Alos *et al.* 2011; Andrews *et al.* 2011) as well as additional data such as depth, temperature and information on swimming behaviours (Hunter *et al.* 2003a,b). Such precise observations can give in-depth, real-time insights into the movement and behaviour of demersal fish and differential habitat uses when analysed in conjunction with corresponding habitat maps or benthic images (Sims *et al.* 2001).

Only 5-10% of the world's seafloor is currently mapped at resolutions similar to terrestrial studies (see Wright and Heyman 2008). This lack of benthic habitat maps over large scales has somewhat limited our ability to study the importance of landscape configuration and composition as well as benthic community structure on demersal fish distributions (Wright and Heyman 2008; Moore *et al.* 2011). Acoustic sensing devices are now widely recommended as a method to sample large areas of the benthic marine environment (Williams and Bax 2001). Sidescan sonars and multibeam swath bathymetry systems may now be used to produce accurate maps of seafloor substrates and bottom topography, allowing characterization of benthic habitats across large areas with potentially increased accuracy and decreased sampling times compared with sediment surveys and fishers' interpretations (Kloser *et al.* 2001; Kostylev *et al.* 2001; Freitas *et al.* 2006; Van der Kooij *et al.* 2011). However, the accuracy of a ground-truthed acoustic map, when extrapolated to larger scales, has often been debated (Bax *et al.* 1999; Diaz *et al.* 2004; Brown *et al.* 2011). Such an approach for large-scale habitat classification has potential but will often require costly ground-truthing during field surveys (Freeman and Rogers 2003; Roberts *et al.* 2005; Holmes *et al.* 2008). The data density mismatches between physical and biological methods will, however, remain unsolved unless acoustic methods can routinely resolve the elusive biological components that make a physical substrate a habitat (Diaz *et al.* 2004). Until then, acoustic methods may still be used to better target benthic sampling, aid decisions regarding study scale or resolution, and provide good baselines from which more detailed habitat information can be determined (Freeman and Rogers 2003; Roberts *et al.* 2005).

A lot of work has been undertaken to relate acoustic maps with benthic communities, using a variety of ground-truthing methods in combination with multivariate analysis techniques (Walsh *et al.* 2004; Anderson and Yoklavich 2007; Holmes *et al.* 2008). Moore *et al.* (2010, 2011) provide a good example of the 'landscape' approach, relating benthic habitat to demersal fish distribution using a distance-based multivariate linear model (DISTLM). The authors found that a combination of depth and six of the 23 abiotic landscape indices explained 34.8% of the variation in the fish assemblage, demonstrating the validity of using broad-scale landscape analysis along with indices of landscape configuration and composition to explain distribution patterns in temperate demersal fish assemblages. Such approaches are now considered a vital first step in unravelling ecological complexities providing improved spatial information for management of marine systems (Brown *et al.* 2011).

Conclusion

Determining the habitat requirements of demersal fish species is inherently difficult because of the complex nature of marine ecosystems, the multiple factors affecting fish–habitat associations, the range of scales over which they act and the general difficulties of sampling marine habitats. Defining fish–habitat relationships will, however, be one of the necessary steps towards the advocated ecosystem-based approach to fisheries management and the sustainable exploitation of demersal fish stocks. Many developments in techniques and technologies show promise in elucidating the complex interactions between demersal fishes and their habitat. The successful application of such developments will, however, strongly rely on the quality of the data used combined with understanding of the fundamental ecology of the systems and species under study (Austin 2007). Where possible, it will therefore be advantageous to test habitat variables under controlled experimental conditions (i.e. small-medium spatial scales), building results from such studies into larger scale models.

Our analysis highlights some important trends in the field of demersal fish habitat determination. The reasons behind the focus on larger scales are no doubt a result of a combination of factors. It is, however, clear that to advance the field, there should be a move towards the investigation of abiotic variables at smaller spatial scales as well as increased attention to the analysis of biotic habitat variables over all spatial scales of study. This will help describe distributions determined by abiotic habitat variables that may act over small spatial scales not previously considered and allow biotic-based causal relationships to be better explained. It will therefore be necessary to invest in the implementation of more, smaller spatial scale data collections or alternatively increase the resolution of larger spatial scale data sets. Work investigating the power of monitoring surveys to detect trends in abundance (e.g. Blanchard *et al.* 2008) will therefore prove invaluable in the design of future studies and surveys.

Defining temporal aspects of habitat will also prove valuable in advancing ecological understanding of the species under study. The inclusion of longer time scales and the consideration of temporal differences in habitat use may also provide important information on the cumulative effects of human-induced impacts, the overall status and recovery of impacted systems and increase capabilities to predict future change of the species or system under study (Hewitt *et al.* 2001). We argue that through attention to the areas highlighted herein, along with more holistic definitions of habitat, researchers are likely to be better equipped to inform management at a range of spatial and temporal scales.

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