Characterising the marine Natura 2000 network for the Atlantic region

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ABSTRACT

1. One of the goals for Natura 2000, a key European Community programme of nature conservation, is to produce a network of protected areas. An analysis of the Natura 2000 marine sites proposed in the most recently agreed list for the Atlantic region (Northern Portugal to Denmark, n = 298) was used to characterize the network in terms of site areas and inter site distances. Sites were considered as part of the network when they included any of the marine Natura 2000 Annex I habitat types found in the Atlantic region (excluding lagoons).

2. The median size of individual sites was 7.6 km² with a median separation among neighbouring sites of 21 km (range 2–138 km).

3. A connectivity analysis was used to identify the potential reliance of species on areas of habitat outside the proposed network. This analysis was based on the assumptions that: a) species with low dispersal capacity will persist in sites when local reproductive effort sustains the resident population and b) greater dispersal scale will link sites in the network, but implies a greater loss of recruits from the local population. For intermediate dispersal scales (2 - 20 km), at least half of the proposed sites are likely to be both too small and too isolated to support populations in the network. The conservation of intermediate dispersers in such sites may therefore be more dependent on habitat outside the network than is the case for other dispersal capabilities. Species with both dispersal scales above 20 km and low habitat specificity may have a metapopulation structure with exchange of dispersing individuals occurring among protected sites. Species with increasing degrees of habitat specificity will need dispersal scales greater than 20 km to avoid dependence on areas outside the proposed network.
4. Most sections of the Atlantic region coastline contain proposed Nature 2000 sites. An analysis of site area and average isolation at the 1° latitude by 1° longitude scale indicated that relatively well designated sections (in terms of area and site spacing) of the coast were interspersed with less designated sections. Analyses of overall habitat availability and population genetic studies are required to assess the significance of varying levels of protection at this scale.
INTRODUCTION

An increasing number of marine habitats are being protected as part of the global commitments to conserve natural resources. A significant part of this effort in Europe is associated with the European Community’s Habitats Directive (European Council, 1992). This directive includes a framework for conserving particular habitats and species within Special Areas of Conservation (SACs). These protected areas are intended to function as a network of sites (‘Natura 2000’). A key feature of this network function is the concept of ‘ecological coherence’. This term can be interpreted in a number of ways, but the directive invokes the perceived benefits of dispersal between sites (article 10 of Habitats Directive). The UK Review of Marine Nature Conservation (Anon, 2004) is more explicit in interpreting the definition of ecological coherence in Natura 2000: Coherence is seen in terms of the capacity for individual protected areas to support each other and in the interactions with habitat surrounding protected areas.

When dealing with the population dynamics of species, the supportive interactions among areas will occur through dispersal. Dispersal between sites is thought to be beneficial as it buffers population fluctuations (Eckert, 2003), allows recolonization after isolated impacts (such as oil spills) and allows species ranges to shift in the face of climate change. With the publication of agreed site lists by the European Community (European Council, 2004) it is now possible to assess the characteristics of the marine sites within Natura 2000. This paper will address whether multinational agreements can produce coherent networks of sites and how species conservation objectives are influenced by the properties of such networks.
Although theory exists for designing networks of reserves (Gerber et al., 2003; Hastings and Botsford, 2003), many of the population dynamic processes and hydrographic features are poorly understood at population level scales. In practice, site selection has generally been based on expert opinion, guided by criteria for identifying sites (Lieberknecht et al., 2004). The Habitats Directive functions by identifying particular species and habitats to be considered for protection with a set of criteria for identifying sites (Annex III). Similarly, the OSPAR Convention has developed criteria (with a remit wider than the Habitats Directive) for identifying and prioritising areas for conservation (the Texel-Faial Criteria: OSPAR Commission, 2003). Such selection criteria can produce networks with consistent habitat representation and spatial coverage. More recently, computer programs have been used to search for optimum selections of sites within networks based on different management objectives (Sala et al., 2002; Lieberknecht et al., 2004). Inevitably site choices will involve compromises and connectivity among sites is only one of the issues at stake. Due to the trade-offs made during design, many of the characteristics of networks will be emergent. In other words it is difficult to specify exact site spacings and areas before designing a network, these features only become clear after the configuration of sites is specified during the design stage.

In a network of protected areas it is easier, given the availability of data, to assess the connectivity among sites than it is to consider interactions with habitat outside the network. We therefore analyse the properties of the marine Natura 2000 sites proposed for the Atlantic region as though the network was an entirely independent entity with no larval supply from non-designated habitat. This depiction of an independent network
may be unrealistic for many species, but it reflects one of the aspects of coherence as defined above: the capacity for protected areas to support each other. The potential dependence of species on non-designated habitat can be inferred by analysing the deficiencies of an independent network. This is relevant to conservation planning, as it is useful to identify the range of dispersal scales where reliance on habitat outside the network is likely to be greatest. Proposed sites often contain a subset of the possible habitat types specified under Natura 2000. To illustrate the range of habitat specialization, we contrast a ‘best case’ scenario of a hypothetical species that can reproduce in all relevant Natura 2000 habitat types with the situation for habitat specialist.

When considering the capacity for a species to persist solely within a network, the key characteristics of individual sites are area and distance to the nearest suitable site. These variables determine the fraction of a population staying within the site each generation and the supply of potential recruits from neighbouring sites. At a larger spatial scale (e.g., multinational), a simple recommendation is that the spacing and sizes of sites should be reasonably consistent given local constraints on site selection: ‘connectivity may be approximated by ensuring the MPA network is well distributed in space’, (OSPAR Commission, 2006). This recommendation is essentially a response to a general lack of detailed dispersal data. In these circumstances an even coverage of sites is a precautionary approach to avoid designating isolated sites or groups of sites. Isolation of sites is thought to be an issue as it reduces the probability of larval connectivity and hence coherence with other protected areas. Furthermore, if species ranges are to shift with climate change, a consistency in site spacing acts as insurance
against a formally well-protected species moving into an area with lower levels of protection. The analyses in this paper therefore consider the areas and nearest neighbour distances of individual proposed sites and collate information on the numbers, areas and average separation of sites in 1° latitude by 1° longitude boxes ('1° boxes', approximately 8500 km², depending on latitude).

**METHODS**

**Network summaries**

The European Community publishes lists of areas adopted as Sites of Community Importance following submissions from individual member states (http://europa.eu.int/comm/environment/nature/home.htm). These sites may or may not be designated at the time of publication, but states are committed to legal protection of the sites as Special Areas of Conservation within six years. We used the list of adopted sites for the Atlantic biogeographical region as the basis for this study (European Council, 2004). The region’s southern limit is in Portugal and it stretches as far north as the Shetland Islands and as far east as the North Sea coastline of Denmark.

As site identification and designation is an ongoing process, the Atlantic list is incomplete (in particular, there is a great deal of activity in the identification and designation of offshore sites (e.g., http://www.bfn.de/marinehabitate/)). The Atlantic list should therefore be thought of as the intended network for inshore sites at a fairly advanced stage of planning.
The Habitats Directive lists eight ‘open sea and tidal’ habitat types as part of the rationale for designating sites of community importance (Annex I habitats ‘of community interest whose conservation requires the designation of special areas of conservation’). An additional marine habitat (sea caves) is in the Natura 2000 Annex I under ‘other rocky habitats’. Two of the Annex I open sea and tidal habitats do not appear in sites of the Atlantic region list: *Posidonia* beds and ‘Submarine structures made by leaking gases’, and the habitat type of ‘lagoons’ was excluded from the connectivity analysis as these habitats are wholly or partially separated from the open sea. This separation will reduce larval exchange and excludes lagoons from playing a part in a network linked by dispersal. Thus the connectivity analysis of the Atlantic region sites considered six marine habitat types:

a) Sandbanks which are slightly covered by sea water all the time (Natura 2000 code 1110)

b) Estuaries (code 1130)

c) Mudflats and sandflats not covered by seawater at low tide (code 1140)

d) Large shallow inlets and bays (code 1160)

e) Reefs (code 1170)

f) Submerged or partly submerged sea caves (code 8330)

Location (usually the centre) and the total area for each site in the Atlantic region are collated in the published list of adopted sites (European Council, 2004). Details on the area of specific habitat types in each site were taken from EUNIS, the European Nature Information System (http://eunis.eea.eu.int/index.jsp). The isolation of each site was
estimated on 1:1000000 maps as the shortest open water distance from the centre of a site to the centre of the nearest neighbouring site.

**Connectivity analysis**

Species may persist in a network of protected areas by three, non-exclusive, means:

1) Protected areas may be large enough to contain self-supporting populations. In this case, populations are close to being ‘genetically closed’ (Johnson, 2005) as recruitment of a species is dependent on the local population of adults. This situation could be characterized as a network of high value refuges. In such a network, recovery from local extinction may be slow or nonexistent due to the limited external supply of new recruits (c.f. Reed *et al.*, 2000). If a species is to persist across a network of high value refuges, the refuges need to be replicated and widespread, so that the risk of synchronous extinction of separate populations is minimal.

2) The distances among protected areas may be less than the dispersal capability of a species. In this situation, recruits from elsewhere can supply populations in any individual protected area. Local populations are genetically open and a species can persist as a metapopulation across the sites of the network. In such a metapopulation, the extinction of a population at the site scale is reversible as colonists can arrive from elsewhere in the network.

3) Species in protected areas can be also sustained by recruits from outside the protected areas network. This final means of supporting species in a network emphasizes the dependence of protected areas on the surrounding habitat. An extreme case would be a
single isolated site, where the long-term persistence of most species will be dependent on recruitment from outside the protected area. The logical opposite of this is when all examples of a particular habitat are within protected areas. In this case the recruitment of habitat-dependent species can only be from protected sites. Clearly real protected area networks are likely to lie somewhere between these extremes. Extensive habitat modification may increase the relative importance of protected areas if this reduces suitable habitat outside a network (it is possible that trawling may produce such widespread modification, Collie et al., 2000). Interspecific variation in the relative importance of protected and non-protected areas as sources of recruits has conservation planning implications as it affects the degree of consideration that should be given to unmanaged (or less intensively managed) areas of habitat.

Ideally species-specific conservation management would reflect the overall balance among self-recruitment, inter site metapopulation dynamics and recruitment from non-protected areas. It would therefore be useful to define the importance of these different mechanisms for individual species. Dispersal scale can be used for this purpose. If dispersal scales exceed the spacing between protected areas containing suitable habitat, then a metapopulation structure can exist (mechanism 2). Species that do not disperse far are unlikely to form a metapopulation. Short dispersal scales may, however, make self-supporting local populations more likely. The size of a protected area places a theoretical restriction on the retention of dispersing propagules. If a protected area is too small, propagules may leave the site before they have a chance to settle. Hence a limited dispersal may allow a species to persist in a small, isolated fragment of suitable habitat (and by implication a small protected area). This mechanism is thought to explain how
species with very limited dispersal persist on the island shores of Rockall while species with planktonic larvae do not (Johannesson, 1988). A reserve diameter of twice a species’ dispersal scale has been suggested as a threshold size for retaining sufficient numbers of propagules to permit independent self sustaining populations (mechanism 1, Shanks et al., 2003).

Estimates of dispersal scale can therefore be used to estimate whether a species can persist in a network as a metapopulation or as self-supporting local populations. Without detailed information on the availability and configuration of suitable habitat (and probably some population genetic work), it is not possible to evaluate the additional contribution from areas outside the network. If, however, mechanisms 1 and 2 are insufficient to support a species within a network, this identifies recruitment from outside the existing protected areas as a key process in maintaining that species within network sites.

Applying a filter to individual sites identified the degree of support that the proposed Atlantic network offers to different dispersal scales. Sites in the network were considered unable to support species as a metapopulation or a self-supporting population if: 1) the nearest neighbour protected area was too far away to provide a source of potential recruits; and 2) the site itself was too small for dispersing propagules to recruit in the same population as their parents. This analysis relies on the following assumptions. While dispersal depends on a number of factors including the presence and variability of coastal currents (e.g. Alexander and Roughgarden, 1996; Hohenlohe, 2004), it was assumed that enhanced and reduced transport effects due to advection in
coastal currents average out over the network as a whole. Given the lack of information on local hydrodynamics and relative positioning of populations within sites, it was assumed that a proposed site was too small to retain propagules if its diameter (based on a representation of each protected area as circular) is less than two times the dispersal distance (Lockwood et al., 2002; Shanks et al., 2003). Most proposed sites are not circular, but more accurate estimates of species-specific larval retention are unlikely on the basis of shape analysis alone.

The connectivity analysis is further complicated by the varied habitat associations of different species. As a first step, a ‘best-case’ scenario was considered: where habitat in the SACs is ignored. This allows us an assessment of the suitability of the network for hypothetical cosmopolitan species found in each of the six Natura habitat types considered. As the different habitat types are not found in every protected area, any habitat specialization will reduce the capacity of the network to support species. To demonstrate this, we present an example based on the distribution of sandbanks slightly covered by seawater all the time (code 1110). This habitat type is likely to have a relatively low degree of species overlap with other Atlantic marine habitats in Natura 2000 (in comparison, mud and sandflats (code 1140) often form a major component of estuaries (1130) and large shallow inlets and bays (1160)).

RESULTS

Network summaries

The Atlantic list has 298 sites that contain at least one of the six Natura 2000 marine habitats given in the methods (Figure 1). The total area of marine habitat in individual
sites had a skewed distribution, with a median of 7.6 km$^2$, and a maximum of 2763 km$^2$. When approximated as circular, site areas represent diameters ranging from 0 (habitat present, but rounded to 0% of total area in the original data set) to 59 km, with a median of 3.1 km (Figure 2). The distribution of nearest neighbour distances was also skewed, with a median of 21 km, minimum 2 km and maximum 138 km. There was a weak, but significant tendency for more remote sites (greater nearest neighbour distances) to be larger (correlation coefficient = 0.223, p < 0.05). The different habitat codes were found in between 15 % (code 8330) and 64 % (code 1140) of sites. The network is therefore sparser when considering nearest neighbours containing the same habitat. In the case of sandbanks slightly covered all the time (code 1110), the median separation among sites with this habitat is 49 km, minimum 2 km, maximum 491 km.

There are 1º boxes containing sites along most of the region’s coastline (Figure 3a). The only gaps occur along the east coasts of Scotland and England. The total proposed protected area in each box was relatively more variable (coefficient of variation 202%) than the average nearest neighbour distance within boxes (cv 74%, Figure 3b). This conclusion is not affected by a shift in the origin used to calculate boxes or by using equal area boxes based on a Universal Transverse Mercator projection (to correct for the reduction in area of 1º boxes with increasing latitude). For example, in 100 by 100 km boxes the coefficient of variation for mean nearest neighbour distance is 65 % compared to 168 % for total area. A ranking procedure was used to compare the 1º boxes in terms of both total area and average separation of sites. Equal weight was given to area and distance, with those boxes containing the largest areas with the smallest mean separation among sites being considered the most designated sections of the coast.
The ten boxes with the lowest extent of designation are therefore those with a small total area of sites with relatively large distances to nearest neighbours. No part of the Atlantic biogeographic region coast appears to contain a high concentration of boxes with low levels of designation. One-degree boxes with relatively high levels of site designation occur throughout the Atlantic region. In some sections of the region, relatively poorly designated boxes are adjacent to boxes with high levels of site designation.

**Connectivity analyses**

Applying the size and separation criteria to the proposed Atlantic network suggests that, even in the best-case situation that species are cosmopolitan, as many as 80% of protected areas may be too isolated and too small to support species persisting as inter site metapopulations or self sustaining local populations (Figure 5). At least half the proposed sites could be unsuitable for species with what might be considered intermediate dispersal scales (2 – 20 km). Persistence in the Natura 2000 network for such species is therefore more likely to be dependent on recruitment from habitat outside protected sites.

Increasing the degree of habitat specialization inevitably increases the fraction of sites dependent on areas outside the network. Sandbanks slightly covered at all times are present in 34% of the proposed sites. This reduction in occurrence tends to increase nearest neighbour distances (Figure 2), with the result that a larger dispersal scale is required to disperse between protected areas. Hence, the range of dispersal scales where over half of proposed sites are unsuitable is between 2 and 49 km.
DISCUSSION

The network of proposed marine sites for the Atlantic region represents an enormous amount of work by national and European Community conservation bodies. The application of an agreed set of site selection criteria is probably reflected in the relatively uniform spatial coverage of proposed sites across the Atlantic region.

Many analyses of protected area networks are presented at the national level. For example, the European Environment Agency presents a state-by-state analysis of Natura 2000 in terms of the total and proportional areas declared as Sites of Community Importance (http://themes.eea.europa.eu/). National comparisons contrast states with very different coastline extents. Analysis at a particular spatial resolution avoids this issue, but still imposes a particular scale. Just as there is no ‘correct’ scale in ecology (Levin, 1992), there is likely to be no correct scale at which networks can be analysed. If species were dependent on protected sites, approximately 70 % of marine species (Kinlan and Gaines, 2003) would not be able to disperse through an average sized 1º box lacking designated sites. A more detailed treatment of scale is given by considering a range of dispersal scales (Figure 5). Subdivision of the network at the 1º scale can, however, indicate bottlenecks or uneven distributions of designated sites in the network for the majority of marine species. Whether 1º boxes with relatively low levels of protection are likely to have an impact on the local persistence of species should be a focus for further research. This research could involve comparisons of habitat availability and biodiversity (including population genetic structure) among boxes with different levels of site designation.
The connectivity analysis suggests that, when considering the network in isolation, species with dispersal scales between 2 and 20 km are not likely to persist as self-sustaining populations or subpopulations of a metapopulation in the majority of proposed sites. The coherence of the network for such species is therefore dependent on interactions with populations outside protected areas. These dispersal scales may represent between 5 and 23% of marine species (Kinlan and Gaines, 2003; Shanks et al., 2003). Although the Kinlan and Gaines (2003) dispersal data are not completely representative (in terms of a random selection of taxa), there may be a taxonomic bias in the species most likely to belong to the ‘intermediate disperser’ category (2-20 km dispersal scale). A greater proportion of invertebrates and attached macrophytes appear to have intermediate dispersal scales when compared to fish. Kinlan and Gaines (2003) report on three species of seagrasses, two of which have dispersal scales in the intermediate range, 48 invertebrates (13 of which are intermediate dispersers), 13 macrophytes (2 of which are intermediate dispersers) and 25 species of fish (3 of which are intermediate dispersers).

Given the existing national commitments to designate the published Sites of Community Importance as part of Natura 2000, it seems unlikely that the overall properties of the network will change much beyond the scope for local ‘fine tuning’. Species of intermediate dispersal capability are likely to remain more dependent on connectivity with populations outside the proposed network. It is difficult to assess whether any particular habitat code comprises such species. Some species will occur in different habitat codes, making the best-case scenario more applicable (for example, the
overlap between intertidal mudflats and sandflats and large shallow inlets and bays). Other species only occur in a subset of a single habitat code, increasing the effective separation between sites and the potential reliance on unprotected areas.

As the Annex I habitats are generally identified on the basis of a few key or typical species, the dispersal capabilities of these species could be an appropriate basis for comparing different the potential reliance of different habitats on non-network areas. Of particular importance are cases of keystone or habitat forming species. Examples of this are Natura 2000 Annex I habitat types formed by species such as *Modiolus, Mytilus, Sabellaria* and seagrasses. Included in the Kinlan and Gaines (2003) summary is *Zostera marina* (eelgrass), a habitat forming species defining a subtype of code 1110 habitats. *Z. marina* has an estimated dispersal scale of 5.3 km (Kinlan and Gaines, 2003), which would indicate that long-term persistence is dependent on interactions with areas outside the network. As it happens, this is not the case as vegetative reproduction means that the minimum area criterion is less applicable. Small *Zostera* beds can be supported by local recruitment of clones. *Zostera*, however, provides an indication of the importance of dispersal scale when species ranges are changing. Recovery of *Zostera* beds in Denmark following the wasting disease of the 1930s took over a decade to occur, with distance to the nearest viable eelgrass bed considered to be a limiting factor in this recovery (Frederiksen et al., 2004).

While there may, on the basis of Kinlan and Gaines (2003) summary, be little inter site connectivity of eelgrass and macroalgae across the Atlantic region network, many of the reef forming animals relevant to Natura 2000 habitats have a relatively long planktonic
larval duration. Estimates of *Mytilus edulis* dispersal are of the order of 30 km (Gilg and Hilbish, 2003) and *Ostrea edulis* has a dispersal scale of 88 km (Kinlan and Gaines, 2003). Hence habitat-forming bivalve populations in the majority of SACs may potentially receive recruits from neighbouring protected sites. The extent to which this inter site connectivity is the case is also a function of the amount of suitable habitat present within potential source sites. For example the fairly narrow range of habitats suitable for *Modiolus modiolus* may make connectivity unlikely even with a dispersal potential exceeding 10 km (www.marlin.ac.uk). In contrast, *Mytilus* may approach the best-case scenario of a cosmopolitan species found in most of the Annex I marine habitats as it is found in a variety of salinities, in sheltered and exposed areas and on both hard and soft substrata (www.marlin.ac.uk). Such general habitat preferences, in tandem with a dispersal scale exceeding the median site separation, probably result in *Mytilus* population connectivity among most Natura 2000 network sites.

Although the coherence of Natura 2000 habitat types can be compared on the basis of their listed key or typical species (see above), this is an incomplete picture of the entire assemblage associated with each habitat code. Other, potentially inconspicuous, species may contribute to the stability of the habitats where they are found. The Habitats Directive provides for measures to ensure that the ‘structure and function’ of the Annex I habitats are maintained. Current knowledge is probably insufficient to determine exactly which species are key to maintaining the structure and function of different habitat types. Investigations of the importance of species to marine ecosystem structure and function are relatively uncommon and hampered by issues of scale (Solan *et al.*, 2006). It is not easy to judge *a priori* which species are most important to the
assemblage associated with a particular habitat. The available evidence suggests that many species may perform important functional roles in Natura 2000 habitat types (e.g. Birkett et al., 1998). The knowledge gaps concerning the importance of different species to community stability imply that a habitat should not be considered to be in a coherent network solely on the basis of its key species fitting this description.

There has been little consideration in the literature of how the aspirations for ecological coherence within Natura 2000 are likely to be achieved. We suggest that coherence may be achieved by the three mechanisms of self-supporting local populations, inter site metapopulation structure or reliance on habitat outside the network. The relative importance of these mechanisms to individual species will often reflect dispersal scales. Conservation planning for intermediate dispersers therefore needs to be more strongly focused on habitat protection in areas outside the network than is the case for short distance dispersers (where local site protection is most important). Only good dispersers (> 20 km dispersal scale) with broad habitat preferences are likely to be ecologically coherent in terms of the majority of individual protected areas supporting each other. Habitat types with large spatial coverage, such as mud and sandflats (code 1140), are likely to be ecologically coherent in terms of the supply of recruits to protected areas from unprotected habitat. Sparsely distributed habitat (e.g. sandbanks (1110): see example habitat map at http://www.jncc.gov.uk/publications/JNCC312/habitat.asp?FeatureIntCode=H1110) is likely to require more detailed and spatially explicit assessment of the potential links between protected areas and between protected and unprotected habitat. Species present in a naturally sparsely distributed habitat are clearly able to overcome any dispersal
limitations in reaching suitable habitat. The relative contribution of individual areas of sparse habitat as propagule sources is, however, likely to be greater than the relative importance (as larval sources to other habitat patches) of equivalent areas of a widely distributed habitat. It may therefore be necessary to protect all examples of a sparsely distributed habitat as any alteration of the status of such locations is of more significance than alterations to a widely distributed habitat. Given the roles of dispersal and habitat frequency, we predict that the species for which ecological coherence is most difficult to achieve are obligate intermediate dispersers in a sparsely distributed habitat type. By analysing the separation between sites it is possible to define the dispersal scales that fall into the category of ‘intermediate’ for any particular network. Identifying the species in this category, their habitat specificity and ecological importance is therefore an important area for future assessments of Natura 2000 and other protected area networks.

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References


Figure legends

Figure 1. Locations of sites of community importance for the Atlantic biogeographical region that contain marine habitats (excluding lagoons). Apparently inland sites are predominantly estuarine.

Fig 2. Characteristics of marine sites of community importance in comparison to the estimated dispersal scales for marine organisms summarised by Kinlan and Gaines (2003). Diameter of proposed sites is estimated using an approximation based on a circular area. Box plots show the range of 95% of data, points lying outside this range, and a box divided into the median and upper and lower quartiles.

Fig 3. 1º box summary of (a) total area and (b) mean separation of proposed sites in the Atlantic region. The scale overemphasizes area. The mean total protected area in approximately 1% of each 1º box and hence would not generally be visible if plotted to scale.

Figure 4. Distribution of boxes ranked as most (grey fill) and least (unfilled) designated across the Atlantic region. Designation levels are summarised using the total area proposed for Natura 2000 and the average separation among sites in each box, with equal ranking to both variables.

Fig 5. Relationship between a species’ dispersal capability and the fraction of unsuitable sites (where local persistence is dependent on self sustaining populations or immigration from neighbouring protected sites). Dispersal scales are compared from 0 to 200 km in
0.5 km steps. An individual site is considered unsuitable if it is both small (diameter less than two times the dispersal scale) and isolated (distance to nearest site exceeds the dispersal scale). The solid line summarizes the results for species capable of reproducing in all habitats (298 sites). The dashed line indicates how habitat specialization (here to sandbanks slightly coved at all times, 100 sites) affects the capacity the network to support species of differing dispersal scales.
Figure 1. Johnson et al.
Figure 2. Johnson et al.

- Habitat 1110 nearest neighbour distance
- Nearest neighbour distance
- Estimated diameter
- Estimated dispersal scale

Km

Estimated dispersal scale

Habitat 1110 nearest neighbour distance

Nearest neighbour distance

Estimated diameter
Figure 3. Johnson et al.
Fig 4. Johnson et al.
Fig 5. Johnson et al.