Natural England Commissioned Report NECR037

Guidance on the size and spacing of Marine Protected Areas in England

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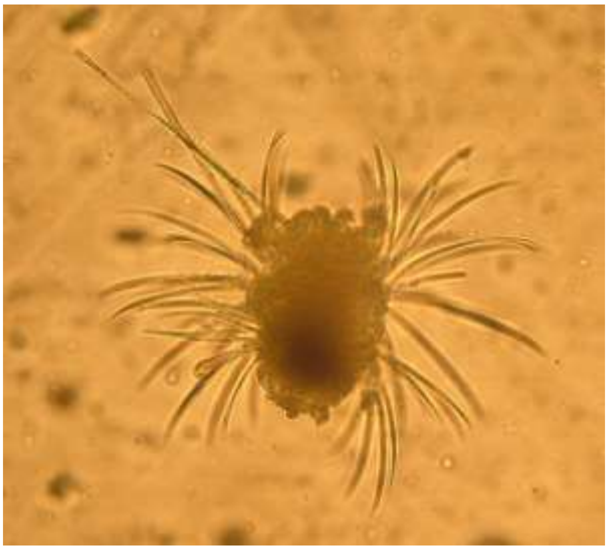
Foreword

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.



© **www.seasurvey.co.uk** (Pearce, B. Grubb, L. & Roberts, P. (2008-2011)

Sabellaria spinulosa larva

Background

This report was commissioned by Natural England to review existing evidence on adult movements and larval dispersal distances of species found in our waters and provide suggestions on how to maximise connectivity between areas and ensure viability of individual sites within the Marine Protected Area (MPA) network. Connectivity and viability are two of the seven network design principles we are using to identify sites to contribute to an ecologically coherent MPA network through the Marine and Coastal Access Act.

The findings are being used by Natural England and the JNCC to produce Ecological Network Guidance for the regional Marine Conservation Zone Project. The Ecological Network Guidance will guide stakeholders in identifying Marine Conservation Zones to contribute to the ecologically coherent MPA network.

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Keywords - Marine Protected Areas, Marine Conservation Zone Project, network design, connectivity, viability, larval dispersal, marine species

Further information

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Guidance on the size and spacing of Marine Protected Areas in England

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1. Summary Terms of Reference

International best practice recognises that there are several Marine Protected Area (MPA) network design criteria necessary to achieve ecological coherence. They include, among others: (1) Adequacy/viability – MPAs should be ecologically viable. They should be large enough that most ecological processes will be able to operate within the area. Sites should be self-sustaining as far as possible and encompass home ranges of species. (2) Connectivity – The design of the MPA network should maximise connectivity through enhancing the linkages amongst MPAs within the network. This can be achieved through propagule dispersal and movement of adults. The research will address these two criteria of adequacy and connectivity.

In order to incorporate adequacy into MPA design, this research should examine evidence of the home ranges of key English marine species from a variety of habitats, taking examples from a wide range of taxa. From the best available literature on home ranges of these species, and possibly modelling, contractors should draw up guidance on the size MPAs should be in order to be ecologically viable.

Connectivity between MPAs can occur through either movement of adults or propagule[1] dispersal. In order to investigate connectivity between MPAs within a network, the dispersal rates of propagules from selected species should be combined with information on currents, nursery areas and species mobility. From the best available literature, and possibly modelling, contractors should draw up guidance on the average spacing needed between MPAs within the network to aid connectivity.

2. Executive Summary

This report aims to answer two key questions about the design of Marine Protected Area (MPA) networks: (1) how large should individual MPAs be in order to support habitats and populations of species that will be viable over the long term, and (2) how closely spaced do MPAs have to be in networks in order to exchange sufficient organisms via dispersal and movement to sustain populations?

The report addresses these questions based on the underlying ecology of marine organisms. It attempts to derive general management principles on size and spacing of MPAs that will be applicable across a broad spectrum of marine life and across the full geographic span within which MPAs will be established in England. The aim is to assist managers in practical ways in the development of a national MPA network. However, it must be recognised that general principles will not always capture the needs of all of the species that are subjects of conservation action. Hence, these principles may need to be supplemented with more detailed knowledge of the needs of particular species to ensure they receive adequate protection. In addition, the principles will need to be applied with common sense and flexibility to take into account other factors that affect the success of MPA management, such as public support and practicality of enforcement.

The size of an MPA necessary to afford adequate protection over the long term is influenced by a variety of factors, both ecological and human. To gain protection from an MPA, organisms must spend at least part of their time within its boundaries. Species whose ranges of movement can be entirely enclosed by an MPA will gain full time protection from effectively managed sites, while those that move beyond MPA boundaries will gain partial protection. Other things being equal, the less species move around, the greater the protection they will gain from an MPA. Larger MPAs will afford protection to a wider range of organisms because they will accommodate the range of movements of more species.

Movement distances of mature adults of 72 species from a wide range of invertebrate, fish and seaweed taxa were examined. The sample is not a random sample of the species found in UK waters but instead was intended to include representatives of many taxa with different evolutionary origins, physiology and life histories. Thirty-one species (43% of the sample) did not move at all after settlement from the plankton. Twenty-seven species (38% of the sample) typically moved less than 10 km after reaching maturity. This means that four out of five of the species sampled should gain good protection from MPAs that have a minimum dimension of 10 km. For more mobile species, lower levels of protection will be afforded by MPAs of this size. However, strategic placement of MPAs in places important to such species, such as spawning sites, nursery grounds and migration bottlenecks could provide valuable protection to highly mobile and migratory species. Research reviewed here on the effectiveness of existing MPAs show that highly mobile species

[1] Propagules include eggs, larvae, seeds, spores or other reproductive structures (such as fragments).

do respond positively to protection. Nonetheless, such species will usually require complementary management measures outside MPAs.

Research throughout the world reviewed in this report indicates that well managed MPAs smaller than 10 km in their minimum dimension have provided good protection to many species. Hence, smaller sites can be included within the MPA network, especially where human pressures make large MPAs impractical. However, large MPAs will give better protection than small. **It is recommended that, for English territorial seas, the median size of MPAs in the network should be no less than 5 km in their minimum dimension, and that the average size of MPAs in the network should lie between 10 and 20 km in their minimum dimension.**

Many species of commercial importance to fisheries that inhabit offshore areas move longer distances than nearshore species, sometimes tens to hundreds of kilometres seasonally. In light of this and experience with successful fisheries closures to mobile fishing gears in the USA and Iceland, **it is recommended that MPAs in the region 12-200 nautical miles offshore that are intended to protect commercial species should be at least 30 to 60 km in their minimum dimension. Both average and median sizes of MPAs in the offshore network should lie between 30 and 60km in their minimum dimension.**

The second question addressed referred to the spacing of MPAs in the network. Spacing is particularly important to assuring long-term viability of populations because of the nature of dispersal of propagules of marine organisms. Most marine species have a planktonic dispersal phase during which propagules spend time in the water column and can be transported to other sites. MPAs of the sizes recommended above should be able to support self-sustaining populations of species that disperse only short distances, but may be unable to sustain populations of long-distance dispersers. For the latter species, it is necessary that MPAs are established in networks of sites that are sufficiently close that they can exchange enough offspring of these organisms to affect growth rate of populations within MPAs.

There is no detailed, reliable evidence of planktonic dispersal characteristics for any marine organism in England. Therefore, this question was examined from a number of perspectives and inferences were made about likely dispersal distances. Sources of evidence examined included oceanography, modelling, chemistry, population genetics, the rate of spread of invasive species, and the separation of known spawning and nursery grounds. Evidence from this wide range of sources indicates that typical dispersal distances are of a few tens to 100+ kilometres per year.

There is another dimension to population connectivity, which is the distribution of suitable habitat. Propagules will only be able to survive when they reach sites that have appropriate habitats. MPAs receiving propagules from others in a network will only connect populations of species whose habitats are present within them. **Therefore it is recommended that sites in the network supporting similar habitats should be no more than 40 to 80 km apart in order to assure sufficient ecological connectivity. This spacing recommendation applies to waters from the coast to 200 nautical miles offshore, both alongshore and across the continental shelf.** The protection needs of short-distance dispersers will be met within individual MPAs, provided these are in the range 10 to 20 km in their minimum dimension. However, one implication of very limited dispersal is that vulnerable species will need high levels of protection to be given where they currently occur, as there is little prospect of MPAs being colonised from long-distances away.

The required spacing of MPAs also depends on the level of protection afforded to them. In making the recommendations above, no particular level of protection has been assumed for MPAs in the network. However, high levels of protection from exploitation and harm will foster greater build up of abundance, biomass and egg producing capacity in protected populations. Highly protected sites will therefore support more viable populations and export more offspring than less protected places. They will therefore foster greater ecological resilience and have lower extinction risks than more lightly protected sites. Higher reproductive outputs mean that highly protected marine reserves will potentially remain connected by exchange of offspring over greater distances than MPAs that offer only limited protection. **The trade off between level of protection, connectivity and size of MPAs is clear. A lightly protected network will need to have more closely spaced and larger MPAs than a highly protected network to deliver the same benefits. Furthermore, networks that contain a greater coverage of highly protected sites can be expected to perform better under changing environmental conditions (i.e. climate change) than networks that have few such sites.**

As noted above, this report considers only ecological aspects of the size and spacing of MPAs. Human factors also play a role in determining the most effective size and configuration of MPAs in a network. A greater density of human pressures will necessitate a correspondingly greater density of MPAs. Species and habitats will benefit little if an MPA cannot be effectively enforced. MPA size, for example, has an important bearing on enforcement and compliance, as does location. The recommendations on size and spacing of MPAs made in this report represent managerial rules of thumb distilled from present ecological understanding, which is limited in several respects. They provide a strategic framework against which candidate sites can be screened and with which the adequacy of MPA network designs can be evaluated. The recommendations are not intended to be applied so rigidly that they would override important practical considerations at a local level, such as the ability to enforce a site, or degree of local acceptance.

3. Introduction and Aims

Marine protected areas (MPAs) are areas of the sea and/or intertidal habitat that are protected by legal or other means from one or more harmful human activities. This report examines the question of how to design MPAs so that they will support areas of habitat and populations that are large enough to remain viable over the long term, and will be sufficiently connected with others in the network via movement of animals, plants and their offspring/propagules (e.g. seeds, spores, eggs and larvae)(Cowen *et al.* 2007).

To sustain populations over the long term, MPAs must incorporate sufficiently large areas of habitat and associated populations that species will persist at the scale of individual MPAs or across the network. Many species in the sea have relatively short dispersal distances as propagules, juveniles and adults, particularly many species of plants and sessile invertebrate (i.e. those attached to the seabed). For such species, even relatively small MPAs may be able to support self-sustaining populations that are replenished from local reproduction. However, for a wide range of other species, such as many fish, echinoderms and crustaceans, dispersal distances or movements could be much larger, particularly of young life stages. For long-distance dispersers, it may not be possible to assure that an individual MPA will support self-sustaining populations. Offspring and/or adults may disperse far beyond the boundaries of the MPA with few left to replenish the local population. Under these circumstances, population persistence has to be considered at the scale of multiple MPAs or networks. MPAs must therefore be located sufficiently close to one another that they can exchange offspring of these species, assuring regular replenishment of protected populations. Many species will be able to sustain populations outside MPAs, albeit at reduced levels. Reproduction by these populations may also contribute to replenishment of their populations within MPAs via dispersal of offspring and movement of juveniles and adults. For species that cannot persist outside MPAs – i.e. that are highly affected by exploitation or other sources of impact – MPAs must be spaced closely enough that their offspring can disperse among protected areas. For example, species such as common skate (*Dipturus batis*[2]) and angel sharks (*Squatina squatina*) have been extirpated from large areas of European seas (Dulvy et al., 2003), persisting in places that have provided de facto protection, and that are now good candidates for designation as MPAs. How close MPAs should be depends on the distances that organisms disperse and on the spatial distribution of their habitats.

Individual MPAs will be best able to protect species that have limited movements. For those species whose movements regularly take them beyond the boundaries of MPAs, protection will be less complete. All else being equal, large MPAs will afford protection to a broader range of species than small ones, because they will accommodate the scales of habitual movements by greater numbers of species. How large MPAs must be to protect viable populations depends on the range of movements undertaken by species. Here scientific evidence pertaining to two questions is reviewed: (1) how large should individual MPAs be, and (2) how closely spaced should they be within a network? New analyses of potential propagule dispersal and adult movements of organisms found around the coasts of England and the UK were undertaken to help answer these questions. Based on the evidence assembled, recommendations are made on ways to design a network of MPAs around England to assure that they are adequate in size and sufficiently connected to one another in ecological terms to sustain populations over the long term.

This report attempts to derive general design principles on size and spacing of MPAs that will be applicable across a broad spectrum of marine life and across the full geographic span within which MPAs will be established in England. The aim is to provide practical advice to managers developing the national MPA network. It is recognised that the science upon which these principles are based is incomplete and developing rapidly. The recommendations made must be viewed in this context. However, such management guidance has proven valuable in many parts of the world where MPA networks are under development (e.g. Airame et al. 2003, Anon. 2003, Day et al. 2002).

There are, of course, many other criteria upon which candidate sites for MPAs can be judged (e.g. Roberts et al., 2003). They include criteria for which there may be greater certainty in their application for particular sites, like habitat representation or inclusion of species of concern, for example. In such cases, it may be sensible to prioritise these criteria over connectivity guidance developed in this report.

General principles will not always capture the needs of all of the species that are subjects of conservation action. Hence, these principles may need to be supplemented with more detailed knowledge of the needs of particular species to ensure they receive adequate protection. In addition, the principles should be applied with common sense and flexibility to take into account other factors that affect the success of MPA management, such as public support and practicality of enforcement.

[2] The common skate has recently been recognised to consist of two species, which are in the process of being formally named (Iglesias et al., 2009).

4. Estimating dispersal using currents and propagule dispersal durations

Many species that live in the sea, and the majority of those we exploit, have a planktonic dispersal phase. During this phase, the eggs, larvae, seeds, spores or other propagules (e.g. plant fragments) drift or swim in open water and have the opportunity to disperse from the natal site. The duration of the planktonic dispersal phase can be expected to influence potential dispersal distances; the more time an organism spends in the plankton, the further it can potentially disperse. Dispersal is also affected by local hydrodynamics and larval swimming behaviour (Montgomery et al., 2006).

Shanks et al. (2003) assembled evidence of dispersal distances and planktonic duration for 25 different species of animal and plant from a wide range of taxa from different parts of the world (including fish and invertebrates). Planktonic duration for this sample was bimodal. Many species spent less than a few days in the plankton, while many spent more than 10-12 days. There was a strong positive correlation between the log-transformed dispersal distances and log-transformed time spent in the plankton (Figure 1; $r^2 = 0.60$, $p < 0.001$). When several species known to spend much of their planktonic life in near-bottom water layers (which have slower current speeds) were removed from the analysis, the correlation strengthened ($r^2 = 0.90$, $P < 0.001$). Time spent in the plankton clearly had an important influence on a species' ability to disperse to other sites.

Currents are the main vectors of dispersal for the propagules of organisms during their pelagic dispersal phase. Particles like eggs, spores and seeds probably disperse passively with currents, while larvae have a greater ability to control their dispersal by active swimming (Shanks et al. 2003). It is possible to use data on the strength and direction of ocean currents to estimate how far passively dispersed propagules might travel and where they could disperse to (e.g. Roberts 1997). This approach was used to estimate potential dispersal trajectories for a range of marine species common around Great Britain. Consideration was given to limiting this work to English waters only, but it quickly became clear that there is likely to be so much cross-border movement of propagules that such an approach would give limited insights into dispersal.

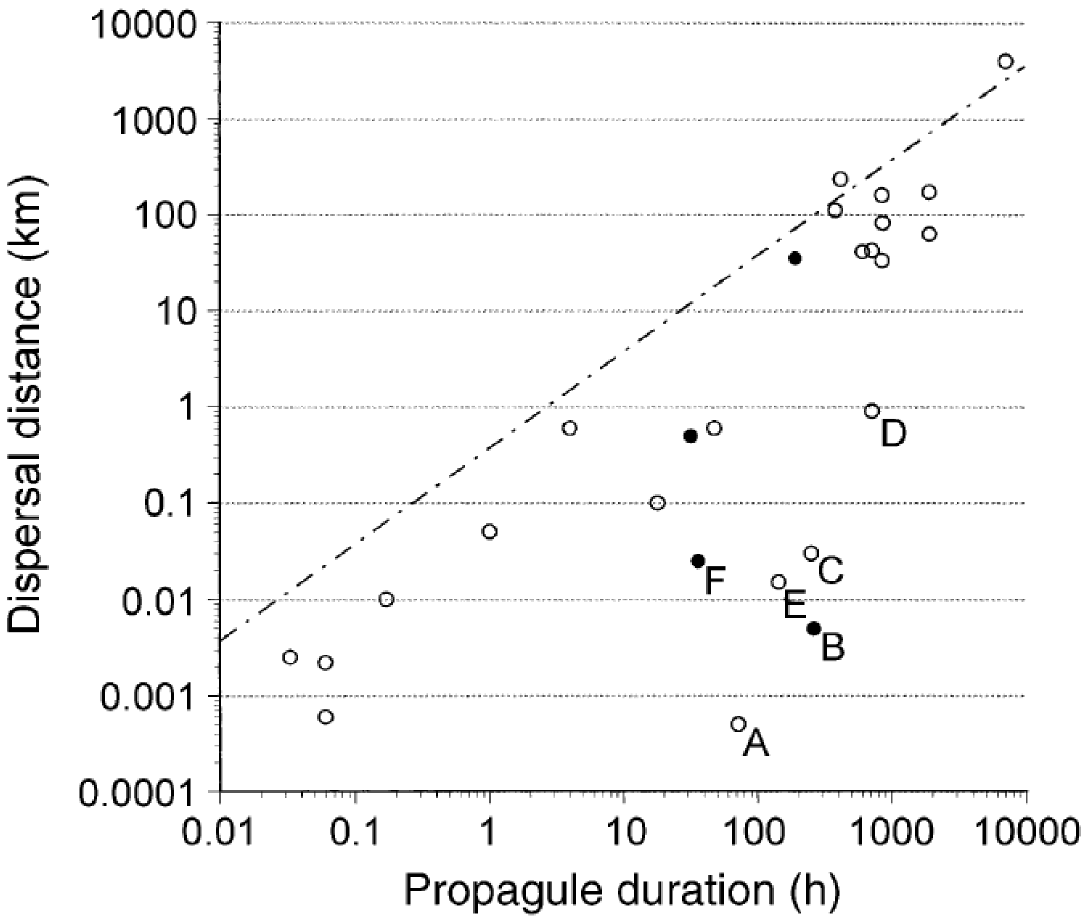


Figure 1: The relationship between estimated dispersal distance for different species of animals (open circles) and plants (filled circles), based on evidence from experiments, the spread of invasive species, behavioural observations, and measurements of larval distribution. The points labelled A to F represent species whose propagules sink to or seek out bottom water layers where currents are slower and dispersion therefore less than expected on the basis of planktonic duration. Figure reproduced from Shanks et al. (2003).

4.1 Species data

To gain a broad understanding of the connectivity among possible MPAs established in British waters, a number of species from a range of different phyla were considered. Data were compiled for 84 species of marine invertebrates and vertebrates belonging to 13 phyla: Bryozoa, Porifera, Cnidaria, Echinodermata, Mollusca, Chlorophyta, Ochrophyta, Chromophycota, Rhodophycota, Anthophyta, Annelida, Arthropoda and Chordata. They comprised eight phyla from the animal kingdom, four phyla from the protoctist kingdom, and two species from the plant kingdom. For each species, information was assembled on classification, adult distribution (only species that occur within English waters were included), planktonic duration, and range of movements after settlement from the plankton. Species, data and sources are listed in Appendix 1. The inclusion of examples from such a wide range of taxa is intended to increase the generality of the results produced. Not all of the taxa included yielded data to answer all of the questions addressed. In each case that data are presented, the number of species they are based on is given.

Information was sourced from online databases, primarily MarLIN, CEFAS and SeaLifeBase, and also directly from primary literature. Our search included several types of data that quantify propagule duration. These include direct observations of propagules as they disperse, spatial observations of larval distributions, and experimental estimates of planktonic duration obtained by growing larvae in captivity.

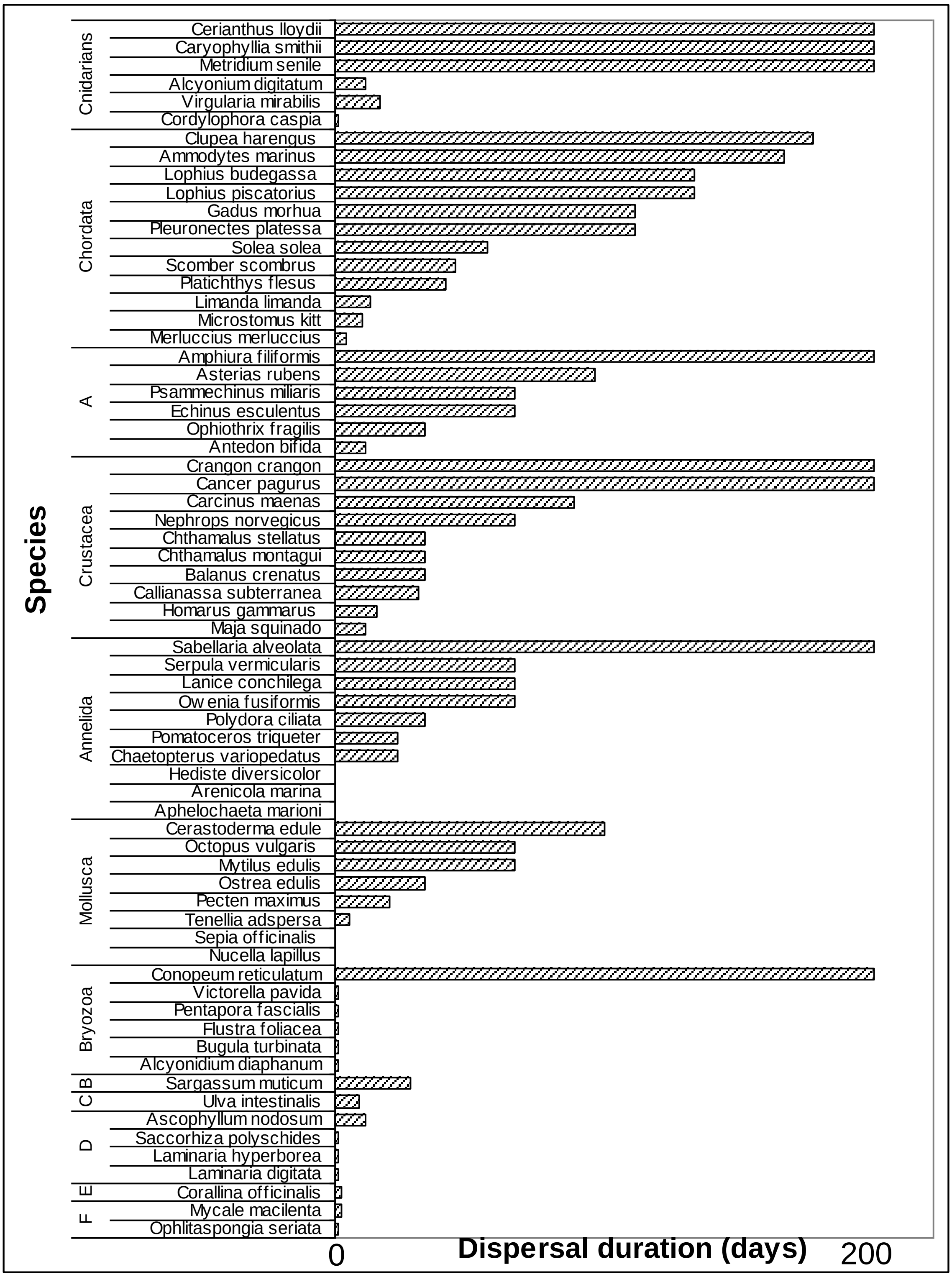


Figure 2: Species planktonic dispersal duration sorted by phyla. Key to phyla marked as letters are: A - Echinodermata, B - Ochrophyta, C - Chlorophyta, D - Chromophyta, E - Rhodophycota and F - Porifera. Data and sources are listed in Appendix 1.

The literature search produced estimates of propagule dispersal duration for 74 of the 84 taxa (Figure 1; Appendix 1). For some organisms there were multiple estimates of propagule duration and for many species the estimates given were as a range of values. The duration ranged from as little as a few minutes to greater than six months. The online source MarLIN sometimes contained values that were broadly classified and resulted in 'blocks' of organisms with identical propagule durations (Figure 1). Using the maximum known planktonic durations, the mean duration was 52 days and the median duration was 30 days. Like Shanks et al. (2003), we found evidence of modality in dispersal duration, with a number of species (28 of 74; 38%) having dispersal durations of 10 days or less, with others having longer planktonic durations.

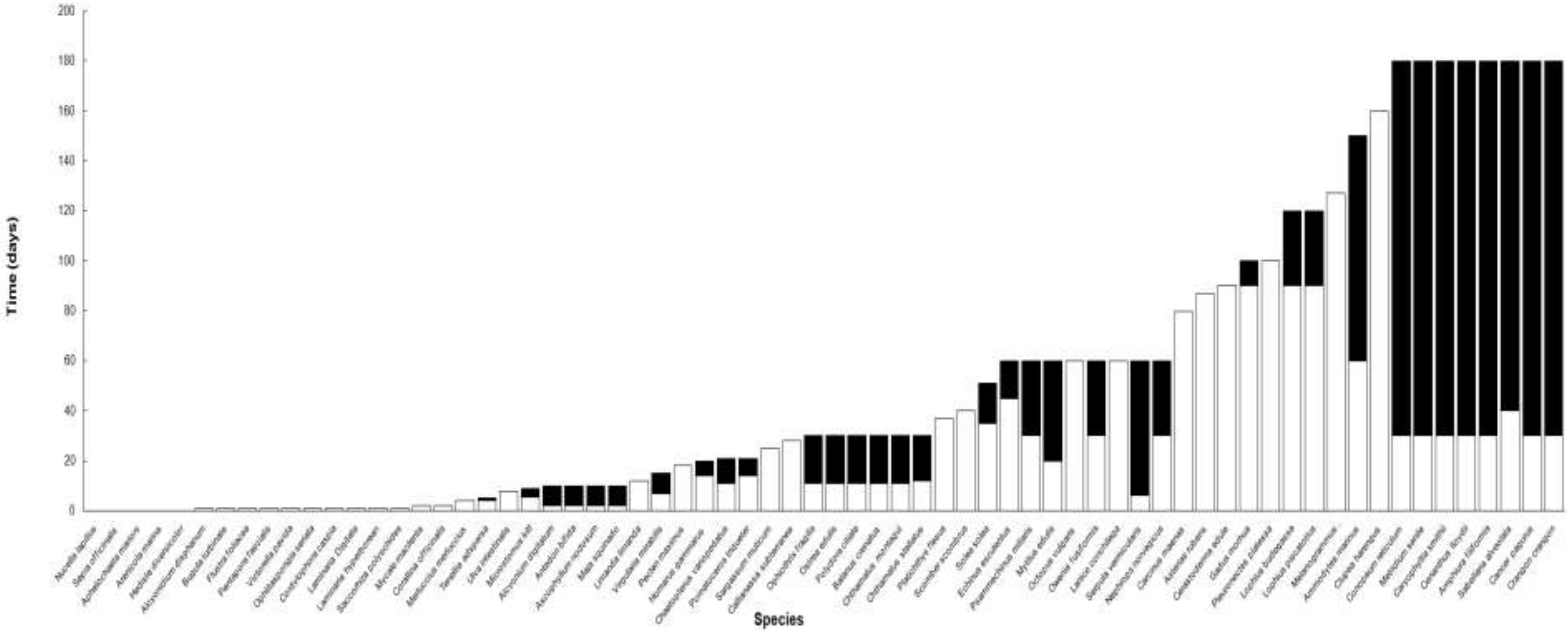


Figure 3: Species distributed in relation to maximum length of propagule duration. Data are given in Appendix 1. The dark sections of the bars represent the range of dispersal durations for a given species.

4.2 Planktonic dispersal kernels

To understand the distances larvae, spores or other propagules may travel it is first important to understand the direction and strength of currents around the United Kingdom. Figure 4 shows a map of prevailing currents around the UK in the form of a map of average annual residual currents based on data from 1955 to 1993 (DTI 2004, IACMST 2005). Current vectors on the map give an indication of the prevailing directions of drift that might be followed by propagules released at various points around the Great Britain.

Figure 4: Current Vector Map for Great Britain showing typical average annual directions of residual currents. The length of the arrows is proportional to current speed. Data from IACMST (2005) and DTI (2004).

To estimate potential dispersal distances for propagules released from various points around the UK, the tidal prediction software POLPRED 2.0 (Proudman Oceaographic Laboratory) was used. Vectors for 1, 10, 30 and 50 day durations were mapped. The 1-day to 10-day durations represent typical limits for short distance dispersers (eighteen species in our sample of 74 species dispersed for less than one day and 38%, twenty-eight species, for less than 10 days). Thirty days was the median planktonic duration and 50 days approximates the average planktonic duration in our sample of species.

Dispersal in this model is driven only by tidal currents and is assumed to be by passive drift. Wind stress is very important in generating currents around the UK and interacts with tides to determine the destinations of dispersing propagules, a point discussed further below. The assumption of passive dispersal means that distances travelled are likely to represent the upper limits to dispersal for the respective time periods. Organisms that control dispersal in the plankton are likely to act in ways that increase local retention (because the natal site is evidently suitable for survival of the species) rather than which maximise dispersal distance (Roberts 1997). However, it should be noted that this generalisation may not always hold. For example, Knights et al. (2006) found that *Mytilus edulis* mussel larvae in the Irish Sea were distributed throughout the water column during flood tides but remained close to the bottom on the ebb. This behavioural mechanism could increase net dispersal away from the natal site.

Dispersal distances were charted from 48 drift start points distributed around the United Kingdom, most of them within the 12 nautical mile territorial seas (Figure 5). The tidal prediction software is unreliable in areas closer than approximately 5km from the shore, so start points were placed greater than this distance away from land[3]. Dispersal occurs as a combination of advection (movement of a group of propagules away from a given start point by currents) and diffusion. The diffusion coefficient was set to $1m^2\ s^{-1}$. POLPRED 2.0 was used to calculate dispersal tracks for 300 propagules released from each start point for each of the dispersal durations. Figure 6 shows an example output from the program. The minimum, median and maximum distances dispersed were measured in kilometres from the resulting maps.

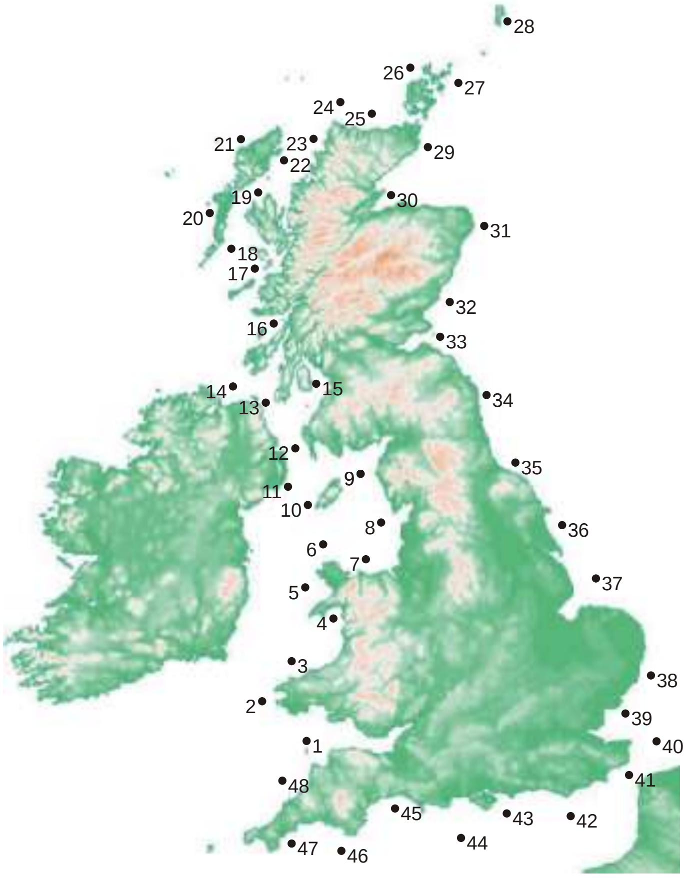


Figure 5: The starting locations around the United Kingdom from which estimates were made of propagule dispersal on tidal currents. Most points are within 12 nautical miles of the coastline in territorial waters, the region of primary interest for Natural England.

[3] Modelling of dispersal therefore does not produce estimates of dispersal distances for species that spawn or recruit to nearshore coastal waters, which comprise a significant component of overall marine biodiversity.

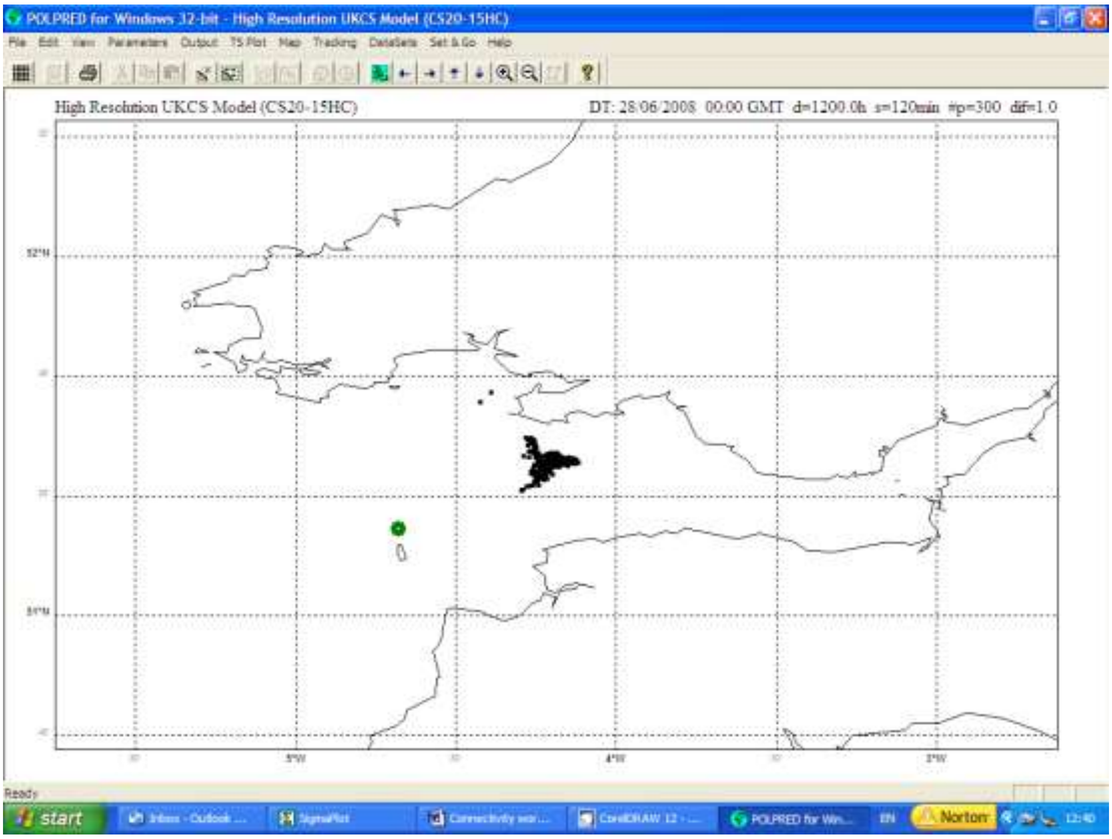


Figure 6: Typical model output for a run using POLPRED 2.0 tidal prediction software. The circle shows the point of release for 300 particles (= eggs) which were tracked dispersing on tidal currents for a period of 50 days. Squares show the points reached by each particle by the end of this dispersal period.

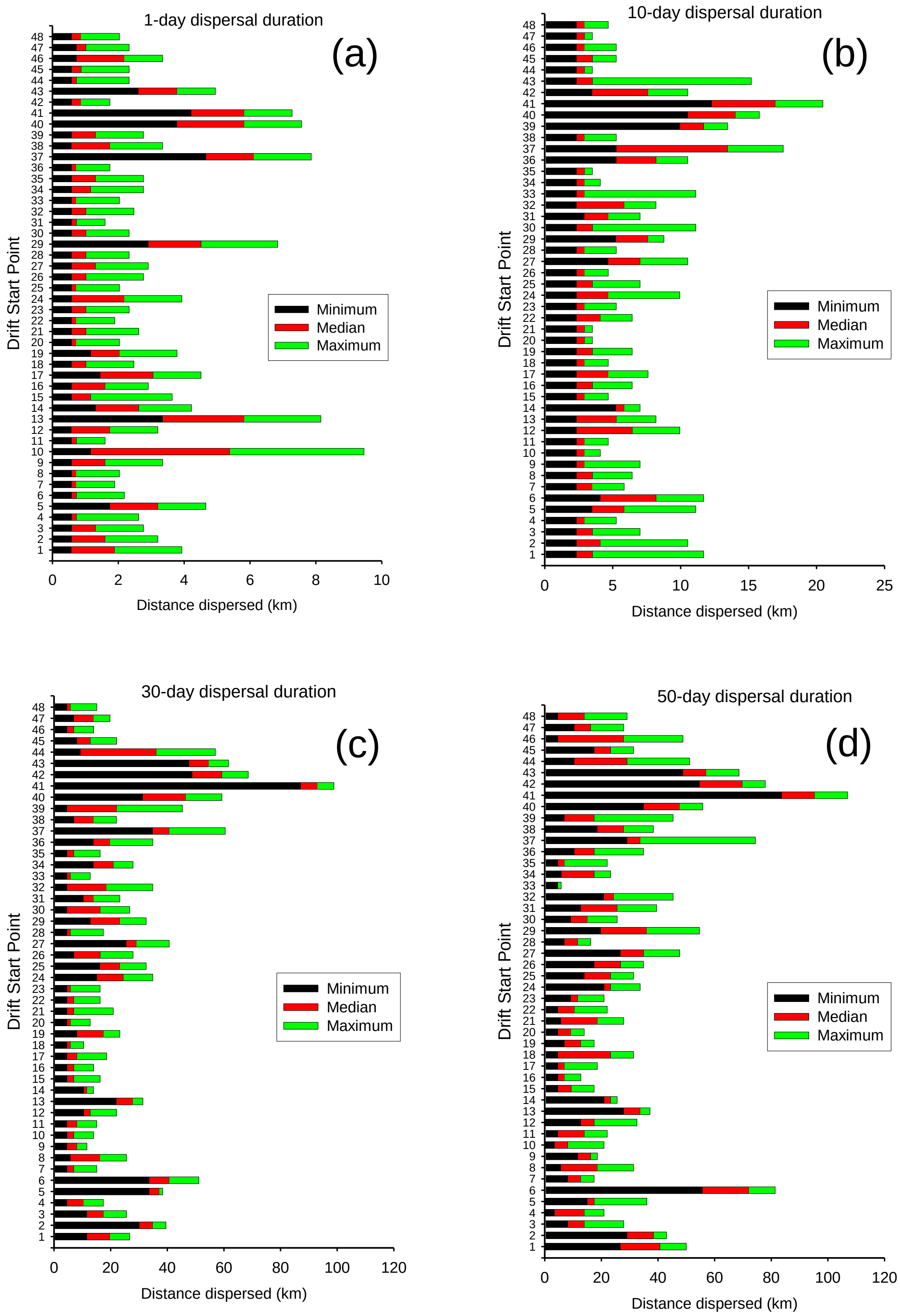


Figure 7: Minimum, median and maximum distances dispersed by 300 particles on tidal currents 'released' from each of the Drift Start Points (numbers correspond to the locations given in Figure 5) for four different planktonic dispersal durations. One run was made for each dispersal duration.

Table 1 and Figure 7 summarise the distances dispersed on tidal currents. Median values best represent typical dispersal. For short duration dispersers (i.e. 1 day), the great majority of individuals end up less than 5 km from their point of release. For 10-day dispersers, most remain within 5 km of the release site and the majority disperse less than 10 km. For 30-day and 50-day planktonic periods, most individuals disperse 20 to 25 km from the point of release. It should be noted that real dispersal distances for species that live near to coasts are probably much less. We simulated dispersal from starting points well offshore due to limitations of the oceanography software. Animals or plants dispersing from close inshore would experience coastal boundary layer effects that would likely reduce these estimated dispersal distances.

As mentioned above, tidal currents only represent part of the oceanographic circulation picture. The other major force generating currents is wind blowing across the sea surface. Wind generated currents tend to flow fastest at the surface, reducing in velocity with increasing depth. Many dispersing eggs float near the surface increasing potential for wind-drift, while larvae can be more active swimmers and can modulate the current field to which they are exposed by migrating vertically in the water column. According to the oceanographer Johan Van Der Molen, from CEFAS (personal communication to Callum Roberts), "Annually averaged wind-driven residual current flows around the UK are typically less than 10 cm/s. Typical directions are northeastward in the English Channel and the southern bight of the North Sea, counterclockwise in the larger North Sea, northward in the Celtic and western Irish Sea, and undetermined in the eastern Irish Sea. This is in response to the prevailing southwesterly winds. In deeper areas (over ~ 50 m deep) these residuals tend to be larger than tidal residuals. In more shallow areas, the two can be of similar magnitude. This has to do with the physical mechanisms that generate tidal residual velocities, making them stronger in shallower water. On shorter time scales, wind-driven flows react to the weather, which varies in time and space. Displacements of water bodies can be as large as several tens of kilometres in response to a single storm (a few days). The magnitude of the response to an individual storm depends on the local topography and the storm characteristics. And then of course a subsequent storm may push things back, or even further."

Van Der Molen reckons that tidal currents make up only about half or less of typical residual flows around the UK. Hence the figures for dispersal distances from POLPRED 2.0 are significant underestimates of dispersal potential. To make a rough accounting for the degree of underestimation, Table 1 also shows the estimated tidal dispersal distances multiplied by two. 1-day dispersers still typically go less than 5 km from the point of release and 10-day dispersers less than 10 km. For long-distance dispersers with 30- to 50-day dispersal periods, typical distances dispersed fell in the range of 40 to 50 km, with some individuals travelling farther.

Table 1: Distances dispersed on currents averaged across all 48 Drift Start Points. The values for hypothetical distances dispersed with added wind-generated currents were obtained by doubling estimates for tidal dispersal alone (see text for explanation).

	1-day dispersal	**10-days dispersal**	**30-days dispersal**	**50-days dispersal**
Distances dispersed by tidal currents				
Average minimum (± SD)	1.0 ± 1.1 km	3.3 ± 2.2 km	14.0 ± 15.9 km	16.3 ± 16.3 km
Average median (± SD)	1.9 ± 1.6 km	4.9 ± 3.2 km	20.0 ± 17.3 km	24.5 ± 18.3 km
Average maximum (± SD)	3.4 ± 1.9 km	7.9 ± 3.9 km	29.2 ± 18.2 km	35.8 ± 20.1 km
Hypothetical distances dispersed with added wind-generated currents				
Average minimum	2.0 km	6.6 km	28.0 km	32.6 km
Average median	3.8 km	9.8 km	40.0 km	49.0 km
Average maximum	6.8 km	15.8 km	58.4 km	71.6 km

Can anything meaningful be said about connectivity from these tidal current predictions about regional variation in potential dispersal distances? There was substantial variation in dispersal distances between different Drift Start Points, as Figure 7 shows. Some areas clearly have more dynamic tidal current fields than others. For example, points in the eastern English Channel had much longer potential dispersal distances than many others. However, without knowing more about how the strength of winds varies from place to place around the UK, it is not possible to say whether these patterns of difference in dispersal potential would remain the same once wind stress is also taken into account. However, some studies have explored the effects of wind stress directly. For example, Mitarai et al. (2008) estimated dispersal distances of 'model' larvae in the California current system subject to alongshore currents and wind stress. Larvae with a pelagic duration of 20-40 days had a mean travel distance of 135 km, compared with 66 km for a 10-20 day larval duration, and 34km for a 5-10 day duration.

There are some places where biogeographic differences between areas suggests low connectivity. For example, the well-known biogeographic break around Portland Bill in the English Channel (Herbert et al. 2007), separates east from west faunas, and corresponds to a discontinuity in current flows (Figure 4). To the west of Portland Bill, currents circulate in a clockwise loop, while to the east they flow from west to east. This separation of circulation patterns may limit propagule transport across the divide, although the biogeographic separation is also believed to reflect the warmer water found to the west and cooler water to the east. There is likely to be low connectivity among MPAs established to the east and west of this boundary.

Carpenter (2007, Jones and Carpenter, in press) examined dispersal potential of 31 species of rare marine invertebrate species around the UK. Based on dispersal duration and developmental type of larvae, she estimated that 10 (32%) had high dispersal potential (> 100 km per generation), 4 (13%) had medium dispersal potential (1-100 km), and 17 (55%) had low dispersal potential (< 1 km). These figures suggest that threatened species have similar dispersal potential as others examined in the present study. Species in the long-distance dispersal categories emphasise the need for a well-connected MPA network.

There are other limitations to the particle tracking work described above. For example, we took no account of possible seasonal differences in dispersal potential (e.g. if there are stronger winds at certain times of year dispersal may be greater).

Many species reproduce during particular seasons and may time spawning to coincide with oceanographic conditions that influence dispersal in particular ways. Another limitation is that potential distances travelled by propagules only provide a part of the connectivity picture. Larvae/propagules that are unable to find suitable habitat once they have completed their planktonic dispersal phase will die. Therefore realised connectivity distances will be a product of distances dispersed by planktonic propagules and the distribution of their habitats. MPAs will only connect populations of species for which they contain suitable habitats. Information on the distribution of different habitats is therefore important to assess how well connected networks of MPAs or sets of candidate sites will be for each habitat type.

A corollary of this point is that MPA networks will provide better connectivity among populations for habitat generalists than they will for specialists, since suitable habitats will be present in a higher proportion of MPAs. Furthermore, if a habitat is patchy and/or rare, special consideration will need to be given to incorporating these habitats into MPAs to promote connectivity. If species of special concern are to be adequately protected, MPA sites and network designs will need to be evaluated for suitability based on a thorough knowledge of habitat needs and, if possible, dispersal characteristics of these species.

5. Other particle tracking models

Van der Molen *et al.* (2007) used a regional scale, coupled physical-biological model for the relatively enclosed Irish Sea to simulate the dispersal of eggs and larvae for five commercially important fish species. They did this to examine connectivity between spawning grounds and juvenile nursery areas for pelagic dispersal durations of up to 115 days. Their study used a weather-forced computational particle-tracking model along with field observations to predict dispersal of the following species: cod *Gadus morhua*, plaice *Pleuronectes platessa*, witch *Glyptocephalus cynoglossus*, sprat *Sprattus sprattus* and pogge *Agonus cataphractus* (Van der Molen *et al.* 2007).

Van der Molen *et al.*'s study (2007) was more sophisticated than this one, taking into account factors such as the time of spawning and larval behaviour, especially vertical diurnal migration of larvae, and oceanographic forcing functions such as wind drift, temperature and salinity. However, in order to do this they were forced to make a number of assumptions, some of which they openly admit were contradicted by published data. According to the authors, the modelled larval distributions and settlement areas were similar to field observations of the distribution of larvae and juvenile fish. Places where species settled from the plankton (or the onset of shoaling behaviour for sprat) were affected by spawning location and by the species-specific development rates and behaviours coded into the model. Eggs and larvae typically remained within 160 km of their spawning origin, although they travelled up to 300km from some release points modelled. However, modal distances travelled were less from some release sites, with larvae typically dispersing 30 to 100 km depending on the release point.

How do these findings compare with the simpler tide-driven model used in the present study? The distances dispersed by eggs and larvae in Van der Molen *et al.*'s (2007) model were longer than those generated by tides alone in simulations described here. The lower range of dispersal distances they estimated accord more closely with our doubled distances to approximate the effects of wind on dispersal. However, some of the species simulated by Van Der Molen *et al.* had significantly longer dispersal durations than the ones modelled here, spending up to 115-days in the plankton. It is not surprising therefore that dispersal potential was somewhat greater than reported here.

Roberts (1997) created a model of dispersal by coral reef organisms in the Caribbean. Based on current patterns and speeds, he looked at potential dispersal of propagules produced at 18 different sites throughout the region, as well as at potential sources of replenishment to these sites, for species with pelagic larval durations of one and two months. The model assumed that species were passively dispersed with currents, as in the present study. His findings suggested that species might disperse an average of 145 km with a one-month pelagic larval duration, and 215 km with a two-month duration. Potential inputs of larvae to sites varied by over an order of magnitude based on differences in the upstream area of coral reef habitat. Some sites with large quantities of upstream reef habitat were probably well supplied by larvae, whereas populations in other sites had to be much more self-reliant for replenishment because there was little upstream habitat. The effects of habitat on connectivity are important and were not considered in the tidal current particle-tracking model used to estimate potential dispersal distances around the UK and England. As noted above, populations will only be able to connect among places with suitable habitat. If an MPA does not have suitable habitat for a particular species, it will not be able to support a population of the species regardless of whether or not larvae could potentially reach the site. Where habitat patches are widely separated, there may be little real connectivity of populations that are specialists on that type of habitat.

Cowen et al. (2006) developed a more sophisticated model based on larval dispersal for Caribbean coral reef fish. Their model incorporated biogeographic and high-resolution biophysical data. These included information on pelagic larval duration and swimming ability, spawning frequency and seasonality, adult mortality, habitat availability and oceanography. Adding larval behaviour to the models suggested that there was significant larval retention within sites, defined as settlement within 50km of the point of release, estimated at ~ 21% of recruits region wide. While rates of local larval retention tended to be high the importance of this varied across the region, with some sites having a low capacity for self-recruitment. The self-recruitment figure varied across the Caribbean from a low of 9% in a site off Mexico which was affected by a strong western boundary current, to a maximum of 57% in a site off Columbia near to the Panama-Columbia Gyre. Some areas experienced recruitment limitation (e.g. the Windward Isles and Yucatan) due to having little upstream reef area. Others were isolated by lack of stepping stone reef habitats.

Cowen et al.'s (2006) model also included a critically important element, which is the mortality of larvae in the plankton as they disperse. Typically, between 10 and 50% of fish eggs and larvae die per day during dispersal, mainly from predation. Taking this into account means that ecologically meaningful numbers of larvae may disperse much less far than the upper limits of possible dispersal. Cowen *et al.* estimated that ecologically significant larval dispersal distances ranged from about 10 to 100 km, less than the distances calculated based on passive dispersal by Roberts (1997), with most species falling in the range of 50 to 100 km. The authors' concluded that populations throughout the region could not be maintained by passive larval dispersal alone. Instead, biological factors (behaviour etc.) were as important as physical ones (currents etc.) in determining connectivity among fish populations, because fish tended to act in ways that increased their probability of remaining close to the natal site. The authors also noted that where fishing pressure is high, inputs of larvae from outside areas may be particularly important in maintaining populations because of low local production of offspring. This point and the effects of larval mortality on connectivity are highly relevant in a UK context and are revisited in Section 12.

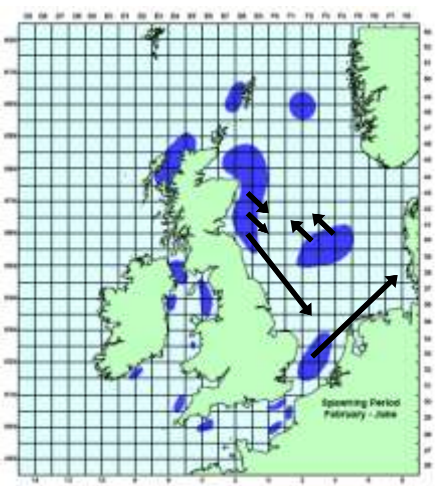
6. Evidence from linkages between spawning and nursery areas

Another technique that can be used to estimate propagule dispersal is to examine the linkage of known spawning and nursery grounds of species. Many marine organisms have life histories in which there are geographically distinct spawning sites and juveniles occupy distinct nursery areas (Roberts *et al.* 2003). Taking life histories of species such as spawning areas and larval durations, and assuming dispersal by currents, it is possible to predict likely directions of larval drift between specific spawning and nursery grounds using vector mapping. Coull *et al.* (1998) produced maps of known spawning and nursery grounds for major fishery species around the UK. For example, many of the whiting spawning areas shown in Figure 8, although not all, appear to be connected to particular nursery grounds that concord well with current speed and direction data shown in Figure 4. In other locations, spawning and nursery grounds appear to be nearly coincident, such as off the northwest coast of Scotland and in the Bristol Channel and English Channel. Nursery grounds in these locations appear only slightly more extensive than spawning areas, and overlap them, suggesting limited dispersion of propagules (i.e. retention of larvae and self-recruitment).

Looking at all of the maps of spawning and nursery grounds included in Coull *et al.* (1998), typical distances over which these areas appear to be connected are of the order of 10 to more than 100km, in keeping with distances found from in the present study and the particle tracking method used by Van Der Molen *et al.* (2007).

A study by Symonds and Rogers (1995) examined connectivity between known spawning and nursery grounds of Sole (*Solea solea*) using various techniques such as trawling and tagging of different aged fish. Although some tagged juveniles were found in nursery grounds it was clear that there was great variation in distributions for the Irish Sea and the Bristol Channel. The authors concluded that hydrographic features such as current speed were important to dispersal and that planktonic transport processes were more influential than behavioural selection of settlement sites by larvae (Symonds and Rogers 1995).

(a)



(b)

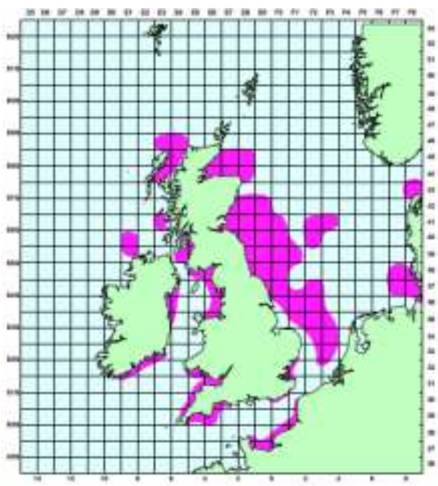


Figure 8: The spawning (a) and nursery (b) grounds of *Merlangius merlangus* (Whiting), both images are taken from Coull *et al.* (1998).

7. Evidence from genetics

Genetic data can be used to estimate average dispersal distances of organisms based on the gradient of genetic change from place to place. Palumbi (2003), Kinlan and Gaines (2003), and Kinlan et al. (2005) plotted the slopes of gradients of genetic isolation over distance for more than 100 species of seaweeds, invertebrates and fish (Figure 9). Seaweeds had the shortest average dispersal distances, spanning metres to a few kilometres per generation. Invertebrates spanned a broad range of dispersal distances, from less than 10 metres to hundreds of kilometres. The majority of species sampled typically dispersed hundreds of metres to several tens of kilometres per generation. Fish generally had relatively long dispersal distances, spanning a few to many hundreds of kilometres. Taken together, the majority of species dispersed less than 100 km per generation. Longer distances were infrequent in the sample of species studied.

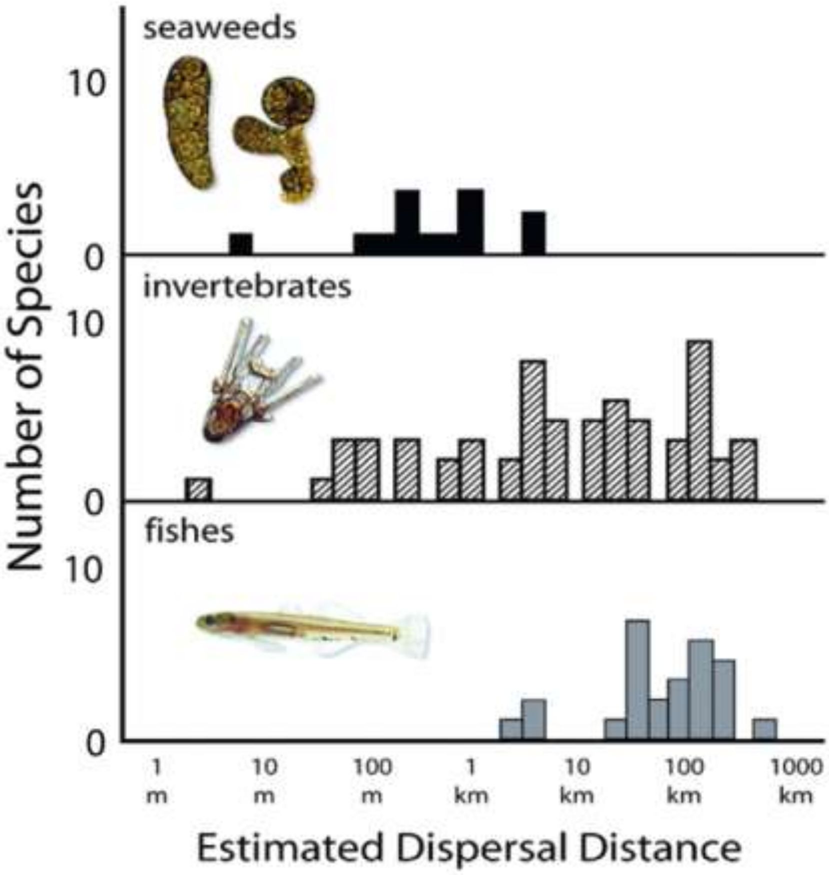


Figure 9: Estimates of the average distances dispersed by propagules (spores and eggs/larvae) of more than 100 species of fish, invertebrate and seaweed. Average dispersal distances were estimated from data on genetic variation among populations by plotting the slopes of plots of genetic isolation by distance (data from Palumbi 2003; Kinlan and Gaines 2003, and Kinlan et al. 2005).

Gilg and Hilbish (2003) estimated dispersal and population connectivity of two species of mussels in southwest England using genetic distances and an oceanographic model of circulation in the region. They found that dispersal distances were typically of the order of 30 km per generation, although could reach over 60 km. The oceanographic model predicted quite accurately the scale and general patterns of larval dispersal, suggesting oceanographic processes were important determinants of connectivity for these species. In another study of an English marine species, the netted dog whelk (*Nassarius reticulatus*), Couceiro *et al.* (2007) estimated that average dispersal distance for propagules was 70 km per generation.

8. Evidence from the micro-chemistry of calcified structures

Elemental signatures in calcified structures like shells, otoliths (ear bones) or statoliths (like otoliths, but in invertebrates) of organisms can help reveal their origins (Thorrold *et al.* 2007). Water chemistry varies from place to place in coastal regions over quite short spatial scales reflecting differences in local geology, temperature and salinity. By analysing the elemental composition of calcified structures of animals that have newly settled from the plankton, it may be possible to determine their origins based on regional maps of variation in elemental signatures from place to place. As markers are laid down periodically as growth layers, it may be possible to reconstruct the history of dispersal by investigating the chemistry of elemental markers layer by layer.

Becker et al. (2007) raised larvae of two species of closely related mussel (*Mytilus galloprovincialis* and *M. californianus*) *in situ* at a number of locations along a 75km stretch of the California coast to generate a regional map of variation in elemental composition of larvae. They found that elemental composition could distinguish larval origins down to scales of around 20 km along the coast. They then examined animals settling along the coast and used this regional map to determine where they had come from. The species differed in both connectivity patterns and rates of self-recruitment. For *M. californianus*, 88% of individuals settling at all sites came from northern regions, with a high degree of self-recruitment to northern sites (87%). By contrast, in the south, 91% of settling animals originated from outside the region. Most larval transport was therefore from north to south. *M. galloprovincialis* came from a more diverse set of origins with low levels of self-recruitment. The findings are intriguing as they indicate different outcomes of dispersal in the same region. Since larvae of these two species have poor swimming ability, they might be expected to have limited control over dispersal on currents. The result suggests that inferences about dispersal from particle tracking models must be treated with caution.

Swearer et al (1999) examined elemental signatures in otoliths of bluehead wrasse (*Thalassoma bifasciatum*) at St Croix in the Caribbean, and found that up to 50% were recruited locally (i.e. had dispersed less than ~ 60 km and originated from reefs around the island), while others drifted in from more distant sources on other islands.

Markers can also be introduced artificially into calcified structures by dosing eggs with substances like tetracycline which can subsequently be detected as a fluorescent layer in the otolith. These markers enable calculation of the ability of populations to replenish themselves locally. They have helped overturn previous common wisdom that planktonic transport always takes place over long distances for species that spend more than a few days dispersing. By incorporating fluorescent tags into embryonic otoliths, Jones et al (1999) showed that 15-60% of yellowtail damselfish (*Pomacentrus amboinensis*) self-recruited to sites at Lizard Island on the Great Barrier Reef. Using the same technique they estimated that 42% of recruits of panda clownfish (*Amphiprion polymnus,* pelagic larval duration 9-12 days) at Schumann Island, Papua New Guinea, were from larvae spawned on the same reef (Jones *et al.* 2005, 2007). By genetic typing of parental fish, in the same experiment they determined that a third of larvae settled within a two hectare natal area. This represents an extraordinary degree of larval retention that was unexpected given the length of the pelagic larval dispersal phase.

In an area nearby Almany *et al.* (2007), found that in another species of clownfish (*A. percula*) with an 11 day pelagic larval duration, and for a butterflyfish (*Chaetodon vagabundus*) with pelagic larval duration of 38 days, 60% of juveniles had been locally spawned. For these species their natal reef was only 0.3km^2. In both Jones *et al.* (2005) and Almany *et al.* (2007), the nearest reefs from which outside recruits could have originated were 10-20 km away, so 40 – 58% of the fish recruiting to the reefs had travelled at least this distance.

From the perspective of MPA function, a combination of both short and longer distance transport of propagules, as found for these fish species, is ideal. It means that even relatively small MPAs that contain suitable habitat may be able to support self-sustaining populations, while also supplying offspring to areas in fishing grounds or more distant MPAs.

9. Evidence from the spread of invasive species

Invasive species provide an extremely useful window onto realised dispersal distances and the rate of recruitment to sites at increasing distances from a source population. Shanks et al. (2003) reviewed evidence from fifteen species invasions in different parts of the world (in some cases several invasions by the same species). Dispersal distances varied widely, from 0.5 km per year in an alga that disperses as floating fragments, to more than 100 km in several species with planktonic durations in the range of 16 to 80 days. For the shore crab, *Carcinus maenas*, and the seaweed, *Sargassum muticum*, estimates were available from several places and showed dispersal to differ substantially depending on local conditions. For example, in the English Channel, *Sargassum* dispersed an average of 28 km per year, compared to 90 km per year on Atlantic coasts of Europe. The shore crab dispersed twice as far on the Pacific coast of North America (173 km per year) compared to the Atlantic coast (63 km per year).

In a more comprehensive review of marine invasions, Kinlan and Hastings (2005) compiled data on 37 marine plant and animal species, including those reviewed by Shanks et al. 2003). Dispersal distances were broadly in line with the earlier review, ranging from less than a kilometre per year to over 200km per year.

Table 2: Distances dispersed by invasive marine species (from Kinlan and Hastings 2005)

Average spread rate	**Genus and species**	**Type (km/year)[a]**	**Reference (see Kinlan and Hastings and 2005 for details)**
Antithamnionella ternifolia	Red seaweed	64	Maggs and Stegenga 1999
Avrainvillea amadelpha	Green seaweed	0.51	Smith et al. 2002
Balanus improvisus	Barnacle	30[b]	Leppakoski and Olenin 2000; Leppakoski et al. 2002
Botrylloides violaceous	Tunicate	16	Grosholz 1996
Carcinus maenas	Crab	173	Shanks et al. 2003
Caulerpa scalpelliformis	Green seaweed	0.3 (average, N = 3)	Davis et al. 1997
Caulerpa taxifolia	Green seaweed	10.9	Meinesz et al. 1993; Shanks et al. 2003
Cerithium scabridum	Snail	19.4	Por 1978

Average spread rate	**Genus and species**	**Type (km/year)[a]**	**Reference (see Kinlan and Hastings and 2005 for details)**
Codium fragile ssp tomentosoides	Green seaweed	12	Shanks et al. 2003
Dasya baillouviana	Red seaweed	40	Maggs and Stegenga 1999
Elminius modestus	Barnacle	41	Shanks et al. 2003
Ensis americanus	Clam	125	Armonies 2001
Ensis directus	Clam	111	Shanks et al. 2003
Gammarus tigrinus	Amphipod	12[c]	Gras 1971
Gracilaria salicornia	Red seaweed	0.28	Rodgers and Cox 1999
Grateloupia doryphora	Red seaweed	2	Maggs and Stegenga 1999
Hemigrapsus penicillatus	Crab	160	Shanks et al. 2003
Hemigrapsus sanguineus	Crab	33	Shanks et al. 2003
Hemimysis anomala	Shrimp	29.2	Leppakoski and Olenin 2000
Hypnea musciformis	Red seaweed	3.8	Russell and Balazs 1994
Kappaphycus alvarezii	Red seaweed	0.25	Rodgers and Cox 1999
Kappaphycus spp	Red seaweed	0.19	Smith 2002
Kappaphycus striatum	Red seaweed	0.25	Rodgers and Cox 1999
Littorina littorea	Snail	42	Shanks et al. 2003
Lutjanus kasmira	Fish	130	Shanks et al. 2003
Marenzelleria viridis	Polychaete worm	246.7	Leppakoski and Olenin 2000; Leppakoski et al. 2002
Membranipora membranacea	Bryozoan	20	Grosholz 1996
Mytilus galloprovincialis	Mussel	97 (average, N = 2)	McQuaid and Phillips 2000
Mytilus galloprovincialis	Mussel	115	Grosholz 1996
Perna perna	Mussel	235	Shanks et al. 2003
Philine auriformis	Nudibranch	80	Grosholz 1996
Portunus pelagicus	Swimming crab	8.3	Por 1978
Pranesus pinguis	Fish	13.5	Por
Sargassum muticum	Brown seaweed	37.4 (average, N = 3)	Leppakoski and Olenin 2000; Shanks et al. 2003
Tapes philippinarum	Clam	30	Breber 2002
Tritonia plebeian	Nudibranch	50	Grosholz 1996
Undaria pinnatifida	Brown seaweed	0.37	Fletcher and Farrell 1999
Zostera japonica	Seagrass	6	Shanks et al. 2003

[a]Average rate of linear expansion of an invasion front measured from field surveys, unless otherwise noted. Where spread rates varied among distinct directions or time periods in a study, the maximum average rate is reported. Where multiple invasions were studied, the average rate over all invasions is reported. All spread rates represent (presumed) non-anthropogenic spread into suitable habitat.
[b]Minimum rate.
[c]Maximum rate.

Evidence from invasive species also shows that there may be substantial directionality in dispersal. In South Africa, an invasive population of the mussel *Mytilus galloprovincialis* dispersed 55 to 97 km per year from the point of first invasion in a northeasterly direction, but only 12 to 29 km to the southwest (McQuaid and Phillips 2000). Dispersal was clearly influenced by wind-driven currents. More importantly, from the perspective of MPA design, most individuals travelled much less. Ninety percent of individuals were still found within 5 km of the source population after four years.

10. Summary of evidence on connectivity and experience from other places

Table 3 summarises evidence discussed in this report on levels of population connectivity in the sea. Many species disperse less than 10 to 20 km and the scales of their dispersal can be accommodated satisfactorily in MPAs that have minimum dimensions of 10 to 20 km across (see discussion of movements of adults in Section 12 for further development of a rationale for MPA size). For species that disperse further than this, their populations must connect between different MPAs and with populations in intervening unprotected areas to sustain the species at a regional level. Many species will be able to sustain some level of presence in exploited areas between MPAs and these unprotected populations could act as stepping-stones for dispersal between MPAs that are spaced further apart than the dispersal ability of the species. However, for other highly vulnerable species, there may be few individuals and low population viability in unprotected sites. For these species, MPAs must be close enough to exchange propagules directly.

As Figure 10 shows, there are conditions under which populations between MPAs contribute very little to successful reproduction of a species. This may occur where there are strong Allee effects. An Allee effect is the situation where a species' reproductive success is strongly dependent on population density. Below certain critical densities, reproductive success is zero or very low. Such effects are often found in sedentary and sessile species that need to be close together for successful egg fertilisation. At low densities, individuals may be too widely spaced for eggs to be fertilized. One possible example in the UK is the fan mussel (*Atrina fragilis*), a large mollusc that lives half buried in seabed sediments. These have been badly affected by bottom trawling and dredging and at present only appear to occur at densities high enough for successful reproduction in de facto refuges from such gears, such as close to shipwrecks (K. Hiscock personal communication). Allee effects can also occur in more mobile species, such as fish, where individuals are strongly attached to home sites. At low population densities, they may be unable to find suitable breeding partners.

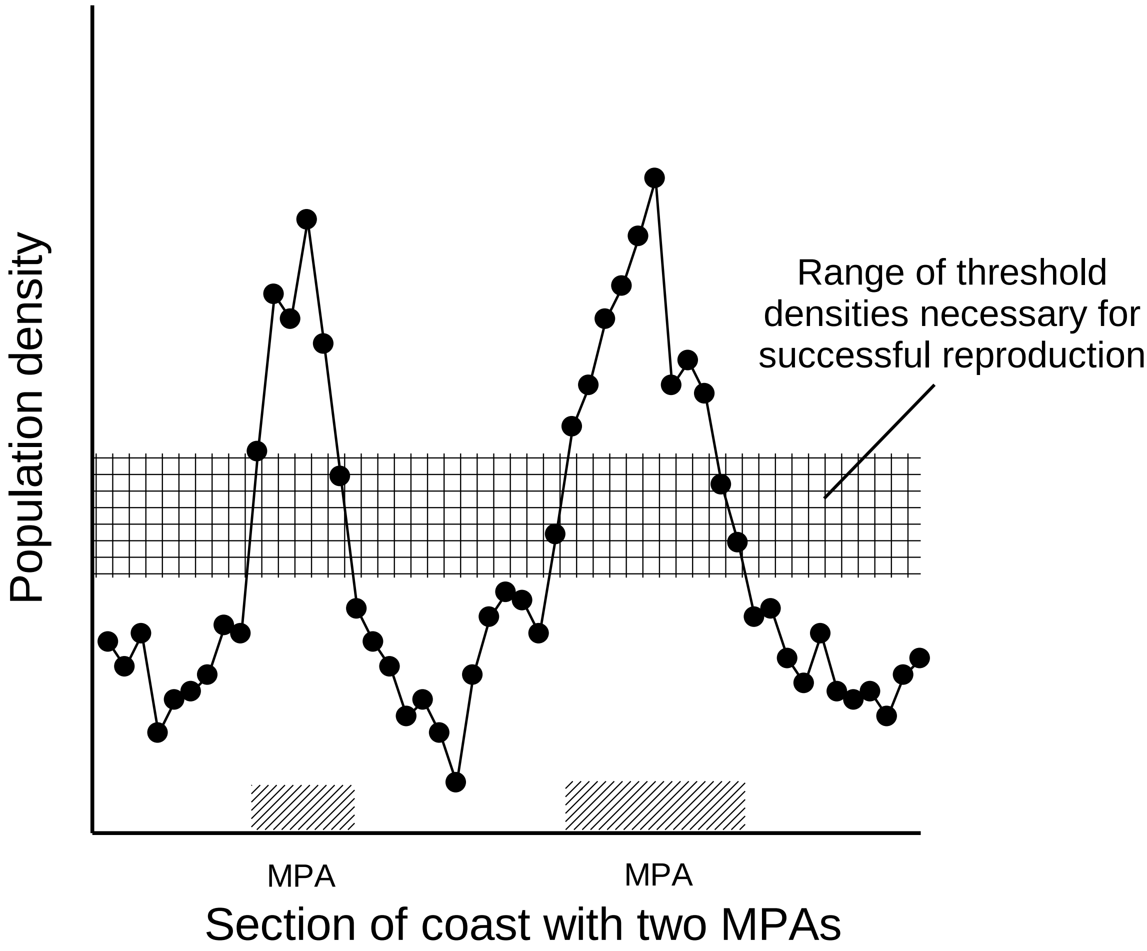


Figure 10: Hypothetical population densities of a marine invertebrate species along an imaginary stretch of coastline with two fully protected MPAs. Due to Allee effects at reproduction, the species can reproduce successfully only above a certain threshold of population density, shown as the checked area in the figure. In this circumstance, such densities are reached only inside MPAs. Although the species exists outside the MPAs, only MPA populations contribute to recruitment. Figure reproduced from NRC (2001).

The evidence from various different sources suggests that for many species, dispersal is limited to distances of a few tens up to 80 km or so. Some species can travel further, reaching distances of 100 to 200 km. **It is therefore recommended, that MPAs in the network should be spaced no further apart than 40 – 80 km. This spacing recommendation applies to waters from the coast to 200 nautical miles offshore, both alongshore and across the continental shelf.** The upper limit of 80 km is particularly warranted given that connectivity levels also depend on the distribution of habitats. For species that are specialists on particular habitats, populations will only be able to connect with those in other MPAs that include those habitats. In places with patchy and rare habitats, the effective spacing of MPAs may be greater than the distances between adjacent MPAs. For example, consider an MPA network that has an average inter-MPA distance of 50 km. For a habitat that is only found in 50% of MPAs, the average separation of protected sites would be 100 km. Hence, connectivity of MPAs in a network will need to be assessed in conjunction with data on habitat distributions. The recommendation above is made in relation to the separation of similar protected habitats, rather than straightforward adjacency of MPAs. A protected nearshore rocky reef habitat, for example, may have little connectivity with an offshore MPA that is within 40-80km, because of low overlap in the habitats and species present.

The connectivity needs of short-distance dispersers should be met by following the recommendation on size of individual MPAs. Protected areas of 10 to 20km across should accommodate the scales of dispersal for many such species. These species are likely to include many that live in nearshore coastal waters, even those with relatively long pelagic durations, because the coastal boundary layer is expected to restrict dispersal below levels suggested by the oceanographic model used in this report (Mitarai et al., 2009).

Although there is some evidence that levels of connectivity vary from place to place around England, a substantial research effort will be necessary to produce reliable evidence of any regional differences that might exist. In the absence of this evidence, applying a 40 to 80 km spacing between MPAs around the country should assure sufficient connectivity for the majority of species. **It is therefore recommended that the same spacing criterion be applied throughout English waters, and indeed is applicable to the whole of UK seas.**

Table 3: Summary of evidence on population connectivity in the sea.

Type of evidence	Findings
Dispersal kernel mapping around the UK presented in this report	Short-duration planktonic dispersers could typically travel 5 to 10 km on tidal currents through passive dispersal; long-duration planktonic dispersers could typically travel 15-25 km on tidal currents. Adding wind-driven residual current flows probably at least doubles the distances travelled.
Particle tracking of Irish Sea fish (Van der Molen *et al.* 2007)	Most eggs and larvae generally dispersed less than 160 km, but modal distances of dispersal (i.e. the distances that were reached by most individuals) were usually between 40 and 80 km.
Location of spawning and nursery areas around UK	Distinct spawning and nursery areas are typically a few tens to a few hundreds of kilometres apart. Many overlap suggesting more limited dispersal.
Particle tracking model for Caribbean fish: Cowen et al. (2006)	Ecologically relevant dispersal distances typically lie between 10 and 100 km.
Genetics: (Palumbi 2003; Kinlan and Gaines, 2003, Kinlan et al. 2005)	Most species dispersed less than 100 km per generation, although some appear able to disperse several hundreds of kilometres. Large numbers of species sampled had estimated dispersal distances in the range 30 – 80 km.
Invasive species: (Shanks et al., 2003; Kinlan and Hastings, 2005)	Generally spread a few tens to less than 200 km per year (but average dispersal is usually at the lower end of this range).
Measured export of larvae from MPAs: (Cudney Bueno et al., 2009; Pelc et al., 2009; Planes et al., 2009)	Export of larvae of fish and molluscs detected to distances of a few to a few tens of kilometres.

11. The importance of unusual dispersal events

So far, much of what has been discussed has examined the potential for dispersal under 'normal' conditions. However, environmental conditions fluctuate on many timescales and the conditions that dispersing organisms experience can depart a long way from average conditions. Unusual dispersal events, although rare, may be very important to population replenishment and connectivity. Rare or periodic events such as storms, or favourable conditions for propagule survival (e.g. certain phases of the North Atlantic Oscillation) may result in strong pulses of population replenishment, or may connect more distant populations (Hedgecock *et al.* 2007a). Unusual oceanographic features such as jet currents formed around frontal areas may do this. For example, a jet current forms between the Irish and Celtic seas on a periodic basis and could move propagules further than under normal current conditions (Horsborough *et al.* 1989).

Genetic evidence indicates that the majority of annual replenishment in some marine populations stems from reproduction by a handful of individuals. This phenomenon, known as 'sweepstakes reproductive success', is thought to result from the chance matching of reproductive activity to highly specific conditions that favour fertilization, the survival of propagules during dispersal and their successful transition to juveniles. For example, Hedgecock *et al.* (2007b) found that all of the settling spat of the European oyster (*Ostrea edulis*) in one season in the western Mediterranean sites sampled appeared to have come from reproduction by no more than 10 individuals.

Other evidence suggests that significant range extensions of species are possible due to rare events that transport large numbers of offspring long distances. For example, Ben Victor of the Ocean Science Foundation in California recorded massive recruitment for a small species of wrasse in the Galapagos Islands during an intense El Niño event (personal communication to Callum Roberts). The wrasse recruited at a density of one fish per square metre and the closest site the fish larvae could have come from was 1000 km away.

There are other examples of rare, long-distance dispersal events, and unusual pulses of recruitment to replenish populations (Ellien *et al.* 2004, Cowen *et al.* 2007). What these events mean for management is that MPAs that have suitable habitat but do not at the time of establishment have resident populations of a species, could benefit from an unusual dispersal or recruitment event at some time after establishment. However, such events should not be assumed in the design of networks of MPAs by increasing inter-MPA spacing above normal levels of connectivity, unless this has already been well documented for a given species in a particular region.

12. Implications of species' movements for marine protected area size

How effective protection from a marine protected area will be for an organism depends on how much time an individual spends inside the protected area. Organisms that are permanent residents in MPAs should gain complete protection if the MPAs are well respected and enforced (except from impacts that cannot be mitigated by MPAs, such as non-point source pollution and climate change). Mobile animals will potentially gain less protection because they may periodically move beyond the borders of the MPA. Species that are more mobile – i.e. move further in terms of absolute distance – will spend longer outside MPAs and will exit them more frequently than species that are more sedentary. The distances that species move offer a guide to the likely efficacy of MPAs of different sizes.

There are many reasons why species move from place to place. They may move among different habitats during development, for example. Many exploited species spend their early lives after settlement from the plankton in juvenile nursery grounds. Around England, these are found predominantly close to coasts and in estuaries (Figure 11). As they grow, there is a tendency for animals to move offshore and into deeper water. Species may also move as juveniles and adults due to competition with other animals for resources. They may undertake seasonal migrations, for example to spawning aggregation or feeding grounds. They may undertake daily movements from resting to feeding areas and back, or may simply move around a home range in search of food.

The use of coastal nursery areas by a wide variety of species provides further evidence that simple oceanographic modelling of the kind presented in this report may not adequately represent scales of connectivity. The POLPRED model does not adequately represent nearshore coastal flows that would be experienced by these species. In such cases, evidence of the kind shown in Figure 11 may better represent the scales of connectivity involved.

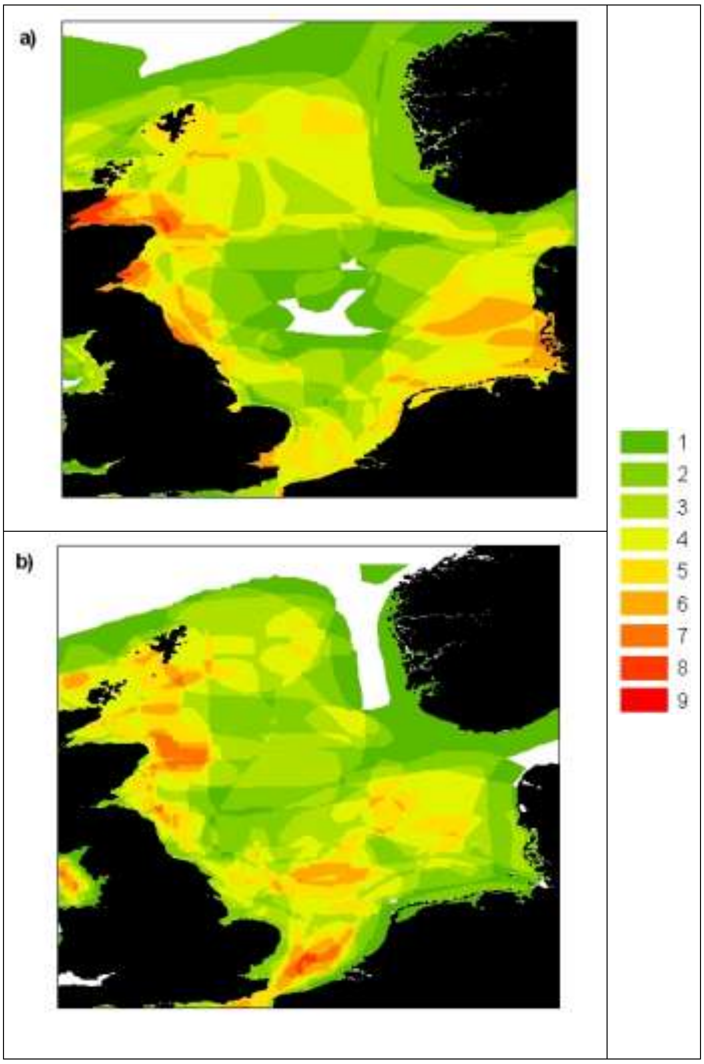


Figure 11: Composite maps of (a) nursery areas for blue whiting, cod, haddock, herring, lemon sole, mackerel, *Nephrops*, Norway pout, plaice, saithe, sandeel, sole, sprat and whiting; (b) spawning areas for cod, haddock, herring, lemon sole, mackerel, *Nephrops*, Norway pout, plaice, saithe, sandeel, sole, sprat and whiting. Reproduced from Roberts and Mason (2008).

For 72 of the species listed in Appendix 1, all of which occur in English waters, typical movement ranges could be estimated based on information on species' life histories, tagging and genetic studies. The analysis was simplified (and thus made tractable) by considering only movements made by mature adults. Hence the ranges shown include movements such as spawning migrations, but do not include habitat shifts through the growth and development of a species. Species were classified into a logarithmic scale of movement distances. This was done because scales of movements differ among individuals of species and from place to place. They also differ according to time of life, and time of year. Species may move little as juveniles but more widely as adults, for example. Or they may be sedentary for much of the year, but migrate to spawning aggregation sites during the reproductive season. If a species fell into more than one movement category, it was classed into the category that reflected the movement propensity of the majority of individuals. The results are graphed in Figure 12.

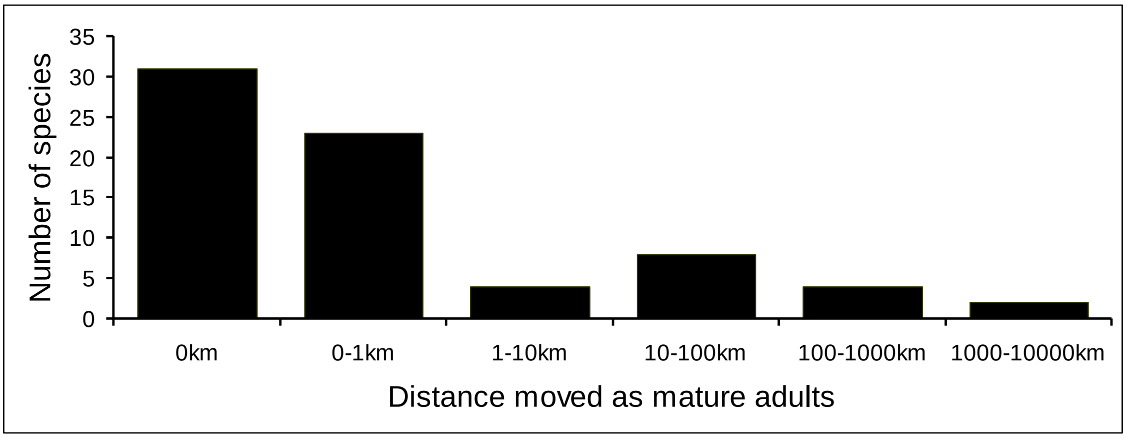


Figure 12: Frequency distribution of organism movements as mature adults. 81% of the 72 species sampled typically move less than 10km as adults. Data on species and their movements are shown in Appendix 1.

Fifty-eight species (81% of the sample) typically move less than 10 km after reaching maturity, and 31 species (43%) do not move at all. This means that many of the species sampled, four out of five, should gain good protection from MPAs that have a minimum dimension of 10 km, if their preferred habitat is found within the MPA. However, for more mobile species, lower levels of protection will be afforded by MPAs of this size. Examples of species with different levels of mobility are shown in Table 4. There are a couple of generalities that this table serves to highlight. The first is that invertebrates tend to have more limited movements than vertebrates, especially those that live within sediments or attached to the seabed. The second is that species associated with the seabed tend to be more limited in their movements than those that inhabit the water column. However, there are many exceptions to these broad observations.

Table 4: Typical movements of a selection of different species found in English waters.

Distance moved					
0 km	**0-1 km**	**1-10 km**	**10-100 km**	**100 – 1000 km**	**1000 – 10000 km**
Bryozoans Seafans Corals Sponges Sea squirts Oysters Mussels Seaweeds Barnacles	Starfish Sea urchins Brittle stars Scallops Dog whelks Polychaete worms *Nephrops*	Lobster Brown shrimp Shore crab Sandeel	Cuttlefish Edible crab Spider crab Cod Sole Lemon sole Anglerfish Sprat Thornback ray Sardine	Plaice Herring Whiting Hake Sea bass Spurdog Scad	Mackerel Basking shark Blue shark

In the rezoning of the Great Barrier Reef Marine Park, one of the 'biophysical operating principles' developed by an expert science panel was that the minimum dimension of no-take zones established during the rezoning should be no less than 20 km in offshore areas, and 10 km in coastal regions (Day *et al.* 2002). It appears from the evidence above that applying a similar principle in English waters would result in good protection for a wide diversity of species.

It should be noted here that just because a species moves beyond the boundaries of an MPA, this does not mean that the MPA will not afford valuable protection to that species. How much protection it gains will depend on the amount of time spent inside the boundaries of the MPA (as well as how much protection the MPA affords to the species, which will be discussed later). For example, a commercially important species that spends 80% of its time within the boundaries of an MPA that is protected from all fishing will be at 80% less risk of being caught than one that inhabits fishing grounds full time, although the distribution of fishing effort around MPAs may alter these figures somewhat. If fishers concentrate effort around the boundaries of MPAs, as is often the case (Murawski et al., 2005), then the protective benefit may be reduced[4]. Furthermore, strategic placement of MPAs into sites where mobile species are at particular risk – such as spawning aggregation sites, nursery grounds or other migration bottlenecks – can provide substantial benefits to those mobile species (Roberts and Sargent 2002).

Finally, it should be noted that 43% of species (31 of 72) in the sample do not move at all as adults (see Appendix 1 for their identities). Many of these sessile species, like corals, have short-lived propagules and limited planktonic dispersal. They must be afforded protection where they exist as there may be limited settlement of young into newly created MPAs without resident populations.

Based on the available evidence of movement propensities of the kinds of organisms found in English waters, it is concluded that MPAs that measure 10 to 20 km in their smallest dimension will provide protection to a wide range of species in English territorial seas. Smaller MPAs than this will still be worthwhile, e.g. of one to 5 km minimum dimension, but they will provide more limited protection to species. However, the network will not be as effective if it consists only of small MPAs as it would be if larger MPAs were also incorporated. **It is recommended that the median size of MPAs in a network within territorial seas should be no less than**

[4] Cross-boundary movements of species may be discouraged by locating MPA boundaries at habitat discontinuities, rather than having them straddle areas of continuous habitat that would facilitate movement outside the MPA,

5 km in their minimum dimension, and that the average size of MPAs in the network should lie between 10 and 20 km in their minimum dimension. In a network with many small sites and some large, the median dimension will be lower than the mean. Following this recommendation will ensure that the network includes a sufficient number of large MPAs as well as accommodating small sites.

Table 4, above, shows that many commercially valuable species of fish and invertebrate that inhabit continental shelves, move quite long distances. If they are to gain adequate protection they will need larger MPAs than the sizes recommended for territorial waters. Fishery closures that protect areas of continental shelf habitat in the United States and Iceland, reviewed in Roberts and Mason (2008), have been effective in promoting recovery of populations of groundfish, including cod (Iceland), haddock, witch and yellowtail flounder. These areas range in size from approximately 1000 to 6000 km^2, equivalent to square MPAs with edge lengths between approximately 32 and 77 km. Based on this experience, **it is recommended that MPAs designed to protect commercially important species in the region 12 – 200 nautical miles from the coast, should have a minimum dimension between 30 and 60 km.**

At this point it should be remembered that species' mobility is but one of several design considerations that influence how large an MPA should be. Others include representation of habitats and species, the viability of protected populations, ease of enforcement, and feasibility, among others. Some of these criteria may be applied with a greater level of certainty in some settings than the mobility criterion outlined above. Hence, in these circumstances it could be more appropriate to assess MPA options primarily on the basis of other criteria.

13. Analyses of species' responses to MPA protection

Movements of animals only offer an approximate guide to whether or not species will benefit from MPA protection. Another source of evidence worthy of scrutiny is the actual effects of MPAs detected in field studies. A search of the primary literature was conducted for studies reporting responses of organisms to protection in marine protected areas by quantitative measures of abundance, biomass, density, diversity and catch per unit effort (CPUE). The responses to protection by taxa, the history and nature of the fishery as well as specific MPA characteristics were extracted from the studies. This information was usually stated in the papers, but where it was not, it was obtained from other studies and internet sources. Figure 13 shows the locations of MPAs used in this study.

13.1 Methods

In most cases, studies investigated the responses of species to the establishment of a marine reserve that was fully protected from fishing, although in a few cases protection was partial, such as from mobile fishing gears like trawls. Studies usually measured abundance, size or biomass, and catch per unit effort or spawning stock biomass were also used occasionally. Often two measures were reported for a species. Therefore it was necessary to combine measured effects into a meaningful overall response. A positive/negative[5] response was assigned when there were

[5] In this analysis, the term 'negative' is used to refer to a fall in the value of a measure. However, it should be kept in mind that 'benefits' of MPA protection go beyond such a simplistic definition. MPAs that shift ecosystems closer to an undisturbed state will alter abundances of species in both upward and downward directions because of the interlinked nature of foodwebs. Hence, recovery of exploited predator species could lead to a reduction in the abundance of their prey species, for example. Hence, some of the responses classified

statistically significant ($p < 0.05$) increases/decreases observed in one or more biological measures. If strong non-significant trends of increase/decrease were observed ($p > 0.05$ to < 0.10), these were categorised as positive/negative trends respectively. If several biological measures showed strong trends in the same direction, this response was assigned to the significant positive or negative categories based on the cumulative effect. Non-significant results ($p > 0.10$) were categorised as null responses. In cases where a significant response (or strong trend) was observed in one biological measure in combination with a null response in a different biological measure, the former outweighed the null response. When two trends seemed to indicate contrary results, categorization of the species was based on assessment of the trends observed: e.g. where abundance decreased but biomass increased, this was classed as an indication of a population growing to larger mean sizes (so a positive response). Conversely, when abundance increased but biomass decreased, it was considered that the mean size was decreasing (so a negative effect). If a species was observed only at the MPA site but not in fished areas (or vice versa), it was categorised as a significant positive trend (or a negative trend).

Species' life-history data were extracted from Fishbase, Cephbase and other online data sources. Movement data were not available for all species, and for some species were inferred from data for closely related organisms.

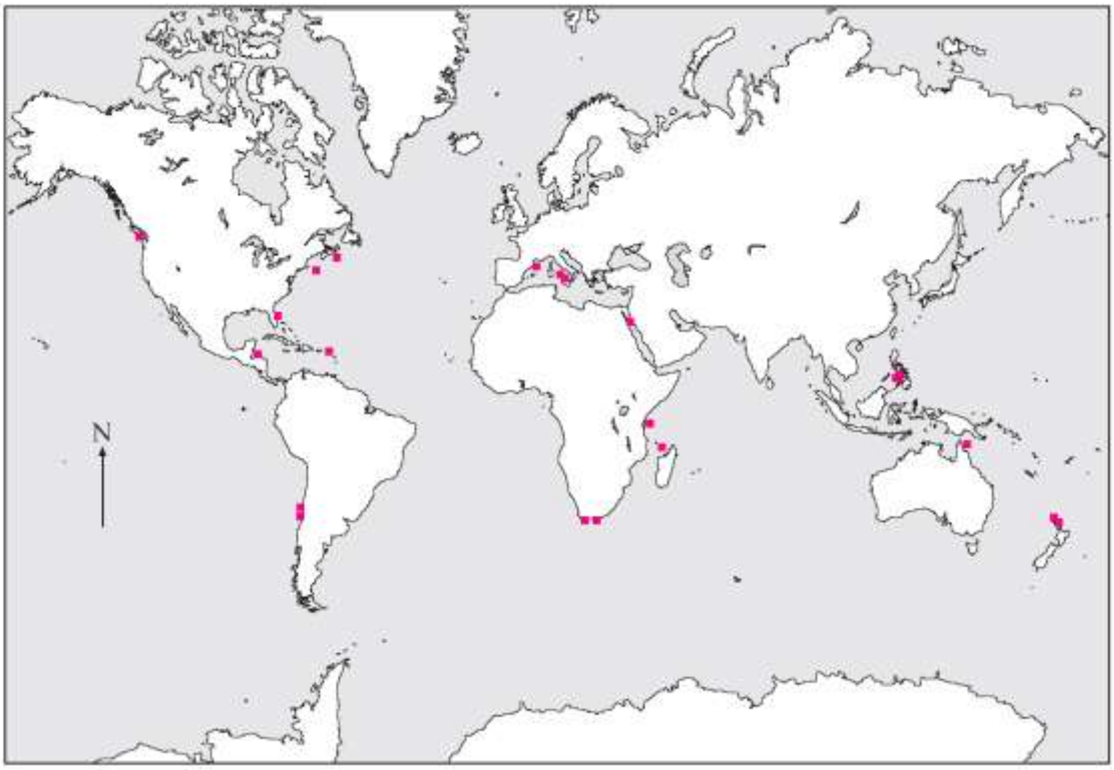


Figure 13: Locations of the 23 marine protected areas included in the study. There were 10 tropical and 13 temperate protected areas in the sample. Several dots in the Philippines and close to Italy overlap.

Approximately 51% of the species in our sample were from temperate marine reserves and other kinds of protected areas (Figure 13, Appendix 2). The remaining approximately 49% were from tropical protected areas. The figures are approximate, since the precise numbers of species included in each analysis varied slightly

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as 'negative' here, may actually be regarded as positive benefits of protection, seen in this light.

depending on information availability. However, there is a close balance of temperate and tropical sites in the sample and the results can be considered informative when considering how MPAs might perform in English waters.

13.2 Results

Figure 14 shows that there is no clear evidence of a fall-off in the effectiveness of MPAs as the adult movement range of species increases. Species showed positive responses to protection across the entire range of movements sampled. All of the four species that moved 100 – 1000 km showed significant positive responses to protection.

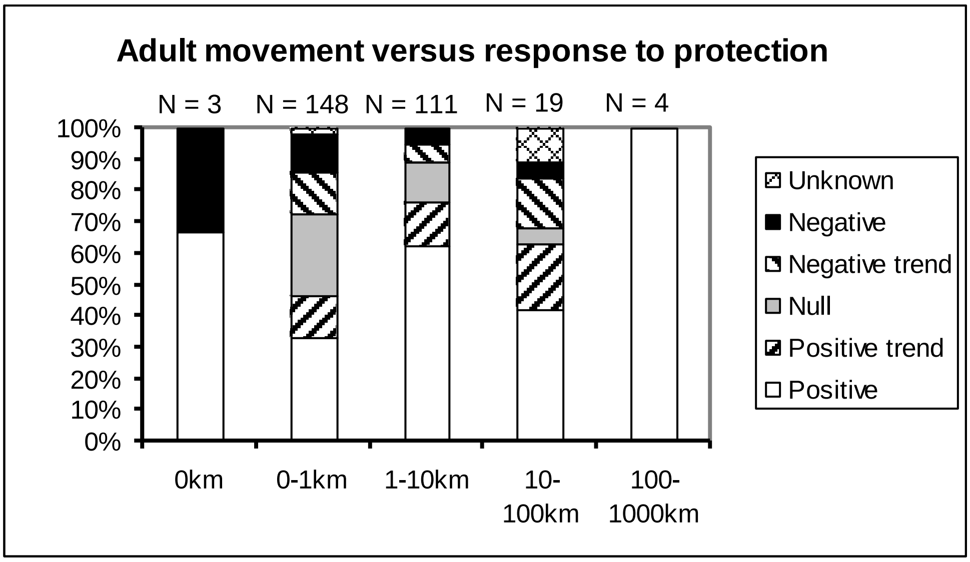

Figure 14: The effects of marine reserves and other MPAs around the world classified by species according to their adult movement propensities. The y-axis shows percentage of responses of each kind, as shown in the legend.

The effect of MPA size on the fraction of species responding positively to protection was also explored (Figure 15). MPA sizes were classed into small (0-10 km^2), intermediate (11-100 km^2), large (101-1000 km^2), and very large (> 1000 km^2). There is a hint from the available data that large and very large MPAs produced more positive responses than intermediate and small MPAs. However, the results should be treated with caution as the sample size from the largest MPAs was low.

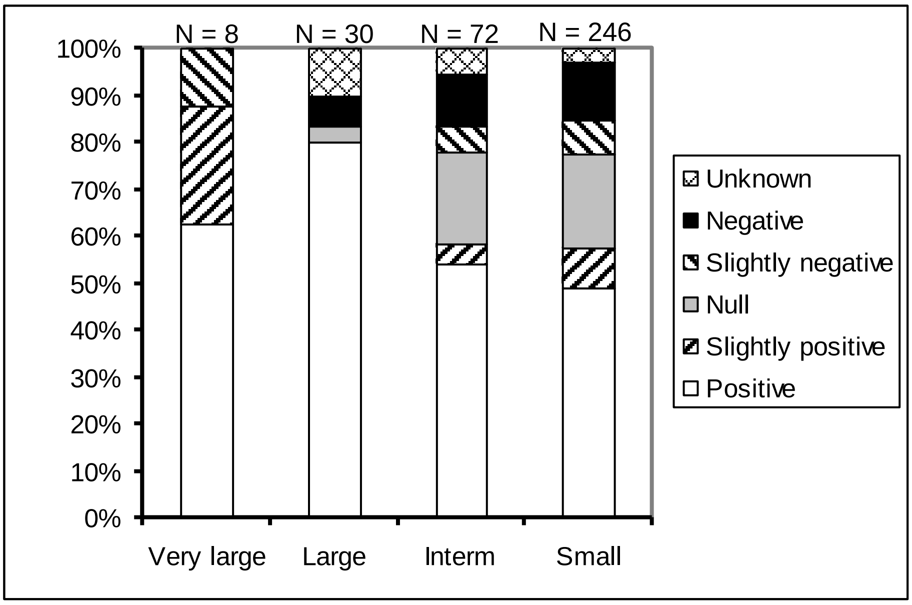

Figure 15: The effects of marine reserves and other MPAs around the world classified by MPA size: small (0-10m km^2), intermediate (11-100 km^2), large (101-1000 km^2), and very large (> 1000 km^2). The y-axis shows percentage of responses of each kind, as shown in the legend.

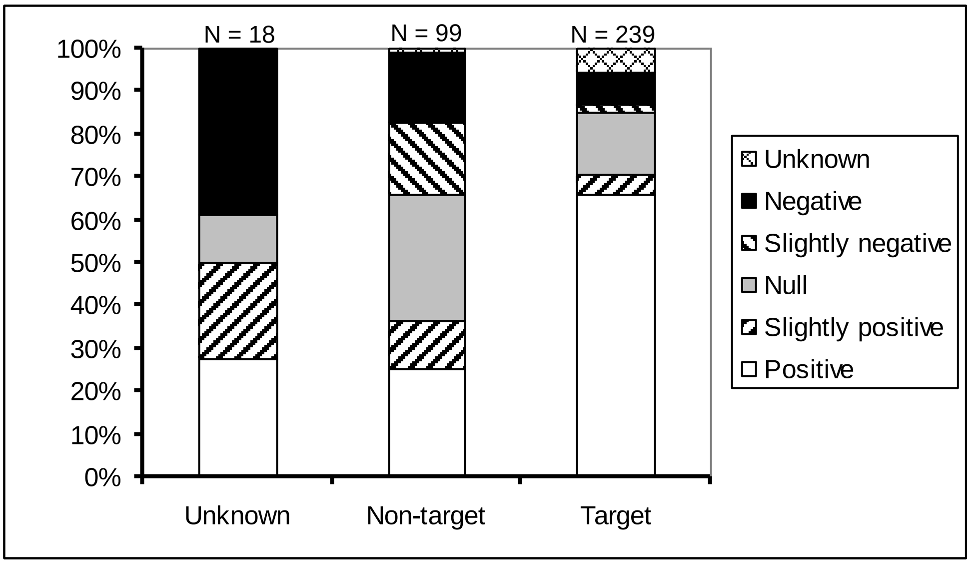

Figure 16: The effects of marine reserves around the world classified by species according to whether or not they are targets of fishing. The y-axis shows percentage of responses of each kind, as shown in the legend.

Two other possible influences on responses of species to protection were explored: (1) whether or not the species was a target of fishing, and (2) the intensity of exploitation in surrounding areas. Figure 16 shows that species that are targets of fishing are around twice as likely to respond positively to MPA protection than those that are not targets. There is also a strong effect of prior fishing on species' responses to protection (Figure 17). Eighty-three percent of species that were moderately exploited showed significant positive responses following protection. Two thirds (67%) of heavily exploited species and 56% of overexploited species showed significant positive responses to protection. The trend of falling numbers of species responding positively with increasing prior fishing intensities may reflect the relatively short time since protection in many of the studies. Some species in more intensively exploited sites may need longer to respond positively than they would in sites with less intensive exploitation where starting population sizes would presumably be higher.

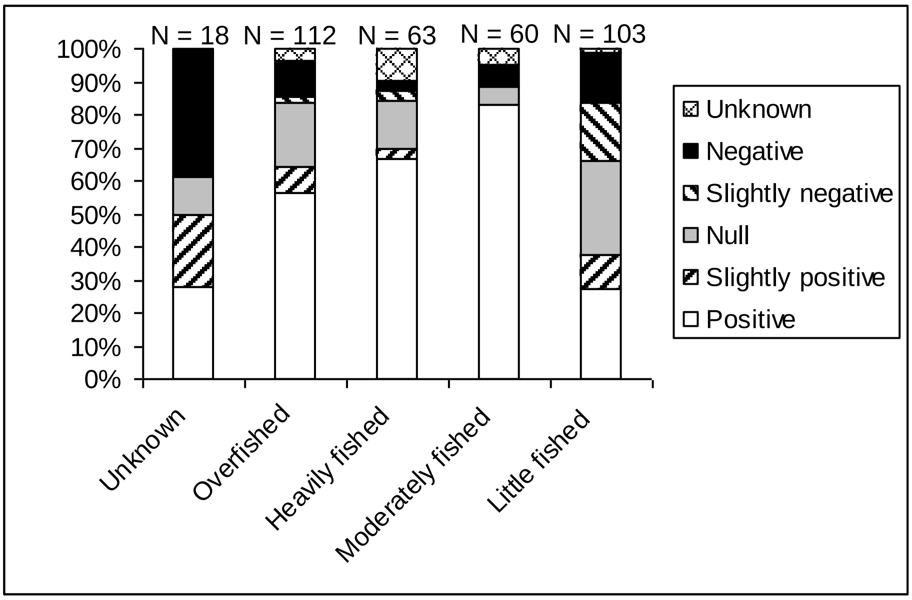

Figure 17: The effects of MPAs around the world on species classified according to the intensity of exploitation prior to MPA establishment. The y-axis shows percentage of responses of each kind, as shown in the legend.

14. Effects of level of protection on connectivity among MPAs

Fishing drives down production of offspring in both target species and many non-target species. In target species, fishing usually selectively removes large individuals, thereby compressing population age structures. Around England, species like cod, for example, have seen their populations change from having 20 to 30 reproductively active year classes 200 years ago, to just one or two today (Roberts 2007). Similar effects are seen in non-target species, including those that form habitat structures, like sponges and seafans, because fishing mortality leads to progressive loss of older, larger individuals. There has also been a concomitant reduction in biomass in both target and non-target species. Reproduction is therefore vested in fewer, smaller individuals than in unexploited populations causing loss of reproductive output. These individuals are younger and less experienced than old animals, probably reducing reproductive success (experienced individuals of most animals breed more successfully than recently matured individuals).

Biomass reductions have typically been of the order of 70 to 95% for most exploited species around England (Christensen et al. 2003, Roberts 2007, Roberts and Thurstan 2008). In combination with compression of age structure, population reproductive output of such species has therefore probably fallen by greater than 90% from levels achieved by unexploited populations (in some cases much more; e.g. oysters, common skate and angel sharks where reproductive outputs are of the order of 100 to 10,000 times less than 200 years ago; Roberts and Thurstan 2008). These reductions will have reduced connectivity among populations through the mechanism shown in Figure 18. Reduced offspring production means that ecologically meaningful levels of population replenishment will occur at progressively shorter distances from the source population. In other words, the tail of the distribution of dispersal distances will contract closer to the source population.

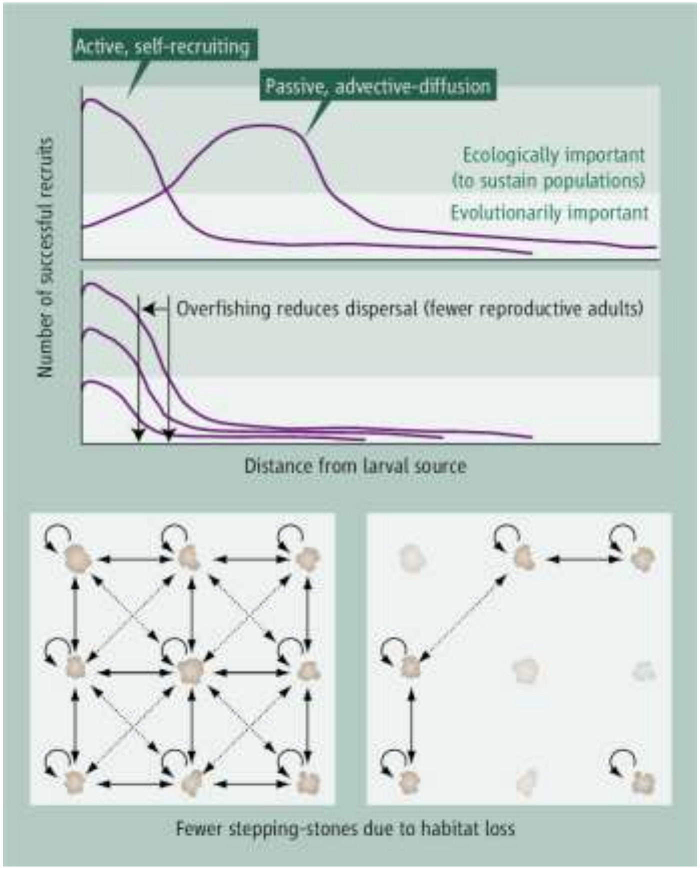

Figure 18: Fishing reduces connectivity among populations by reducing the amount of offspring produced (top graph). This contracts the distance over which populations are able to disperse effectively. Contracting dispersal distances combine with habitat loss and fragmentation (bottom diagrams) to reduce the viability of populations at regional scales, leading to biodiversity loss. MPAs can reverse this process, and the greater the level of protection given to species within them, the greater the expected rebuilding of offspring production. Reproduced from Steneck (2006).

Figure 19 illustrates the effects of increasing the level of protection afforded to an MPA on population reproductive output and connectivity. In this simple model, the benchmark level of reproductive output from an unprotected site is set at 1 million offspring produced. Three levels of protection in MPAs established at this site increase reproductive output by 5x, 10x and 20x respectively, corresponding to increasing strength of protection. The offspring are subjected to 20% mortality per day during planktonic dispersal, which is typical of real mortality rates observed in larval fish (Cowen et al. 2006). The graph shows the number of offspring that remain alive after dispersal periods between 30 and 60 days, which is the period over which larvae of this model species are able to metamorphose into juveniles.

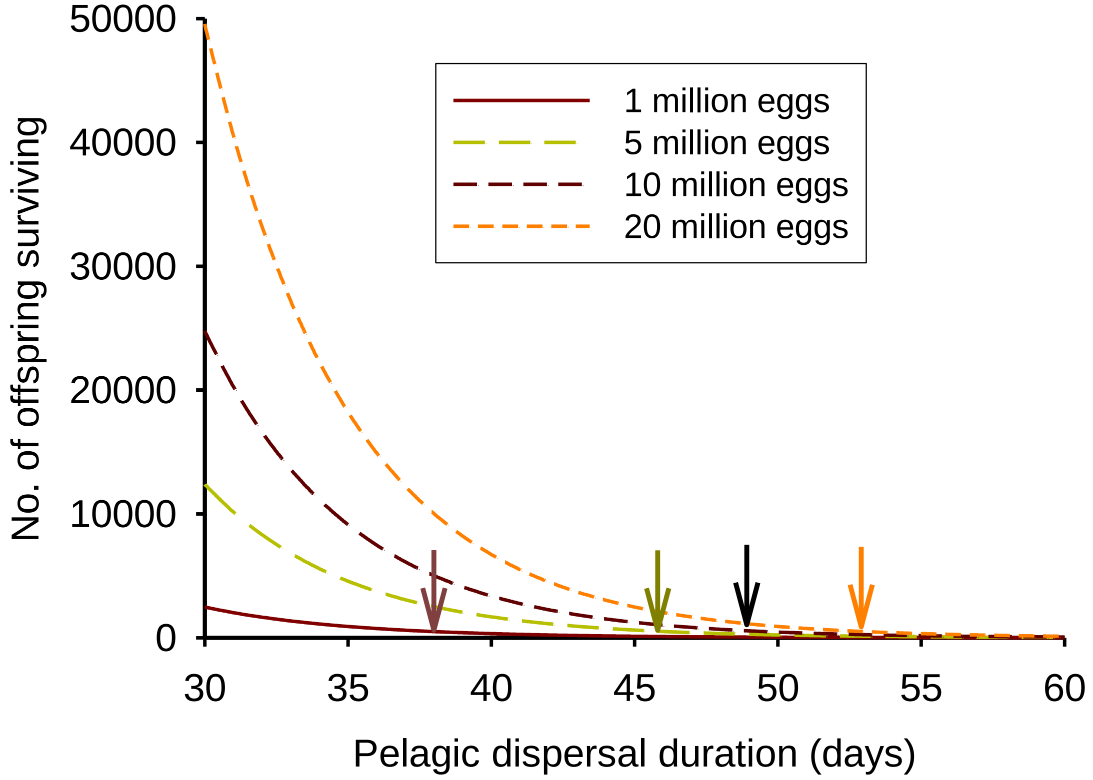

Figure 19: Model of planktonic dispersal from an MPA. The benchmark level of reproductive output from the site without protection is set at 1 million offspring. Three levels of protection in MPAs increase reproductive output by 5x, 10x and 20x respectively, shown by coloured dashed lines, corresponding to increasing levels of protection. The offspring are subjected to 20% mortality per day during planktonic dispersal. The graph shows the number of offspring that remain alive after dispersal periods between 30 and 60 days, which is the period over which larvae of this model species are able to metamorphose into juveniles. Arrows show the times at which the number of surviving offspring drops to 500 for each level of offspring production from the site.

Increases in reproductive output from the MPA translate into similar levels of difference in the number of offspring surviving after a given dispersal period. For example, after 40 days, 6709 offspring survive from 20 million produced, compared to just 335 from 1 million young produced by the benchmark, unprotected population.

These increases in reproductive output should translate into ecologically meaningful replenishment of populations at ever greater distances from the source MPA. The arrows in Figure 19 show the time periods after which there are just 500 young left alive from the original numbers of offspring produced. With a current speed of 2 cm per second throughout the dispersal period (comparable to current strengths seen around parts of the UK), those 500 young would have travelled 66 km from the benchmark population, 79 km from the population with 5x greater egg production, 85 km from the population with 10x greater egg production, and 92 km from the population with 20x greater egg production. According to this model, more highly protected MPAs can therefore supply ecologically meaningful numbers of offspring to more distant sites. In other words, populations will be better connected.

There is some evidence that large, old fish produce better quality eggs than small, young fish (Berkeley *et al.* 2004). These eggs carry bigger oil droplets, and the larvae survive better and grow faster than those from eggs produced by young fish. Better survival in the plankton may increase connectivity among populations by allowing larvae to disperse further. By eliminating most large, old fish from populations (Roberts 2007), fishing reduces likely dispersal distances even more than is implied by reductions in spawning stock biomass. This effect on levels of replenishment can be simulated by adjusting mortality rates in the plankton in the model just described. After a period of decades, highly protected MPAs will develop more extended age structures in populations of resident species compared to less protected MPAs, and the biomass of animals will be made up of greater numbers of large-bodied adults. In the following example, intermediate protection (e.g. from all mobile fishing gears) increases offspring output 10x and eggs and larvae survive 2.5% better than those in the benchmark case. In highly protected MPAs (excluding all exploitation), offspring output is 20x greater and eggs and larvae survive 5% better. After 40 days of dispersal, 335 young remain alive from the benchmark case, 4079 from the MPA with intermediate protection and 10,009 from the highly protected MPA. Again, these differences in survival translate into longer potential dispersal distances. By the time there are only 500 individuals left alive, those from the benchmark case could have dispersed 66 km, those from the intermediate protection MPA 87 km, and those from the highly protected MPA 96 km.

As noted above, the effects of fishing on many non-target species can be similar to those on target species and so similar principles apply. Fishing reduces biomass and compresses age structure of many non-target species populations, leading to lower offspring production and reduced effective dispersal distances. This has impacts on both connectivity and viability of populations. Bycatch (or bykill) species include habitat-forming species that live on the seabed, such as sponges, ascidians, corals, seafans, molluscs and polychaetes. Such species are important to a wide variety of organisms, both exploited and unexploited. Vast areas of the sea around the UK and England have been stripped of habitats formed by invertebrates as a result of bottom trawling (Roberts 2007, Roberts and Thurstan 2008). Much of it was lost over 100 years ago. This habitat loss and fragmentation will have had significant impacts on the ability of many species to persist at a regional scale. These processes limit connectivity by reducing population sizes and eliminating stepping stone habitat patches for dispersal (Figure 18). It is likely, although difficult to prove given the absence of baseline data, that many rarities in English seas were formerly abundant. One such species that has clearly suffered badly and is now only just able to maintain a toehold in UK seas is *Atrina fragilis*, the fan mussel. This mollusc has a large shell up to 48 cm high and lives partially buried in sediments. It has disappeared from trawled areas and now persists in low numbers in a few isolated refuges from trawling. There could be many more species like it, which is why broad-based habitat protection is needed within MPAs, rather than only measures targetted at species that are recognised conservation priorities.

14.1 Loss and rebuilding of resilience

Environmental resilience is the ability of ecosystems to persist in the face of fluctuations and impacts. Resilient systems are less affected by impacts than non-resilient systems, and are able to recover more quickly from catastrophes. They are also better able to sustain ecological processes in fluctuating environments, and from them secure the flow of ecological goods and services of value to people (e.g. seafood production, water purification, carbon uptake, coastal protection). Resilience is critically linked to two things: the variety of life and its abundance. Variety is important because species perform different roles within ecosystems. Maintaining the variety of life provides a foundation for sustaining ecosystem processes. Abundance is important because throughput measures of ecological processes are closely linked to abundance. For example, reducing the abundance of filter feeding invertebrates in estuaries by 90% (as hundreds of years of human impact have done in most English estuaries; Roberts 2007) will have reduced the water filtration and transfer of nutrients from the water column to seabed sediments by similar amounts. It matters not whether the species still exists somewhere in the estuary, these ecosystem processes have been compromised by quantitative reductions in the species that perform the roles.

Environmental resilience is inextricably linked to abundance of species. Population viability is dependent on breeding population sizes and their connectivity, for example. This linkage is recognised explicitly in IUCN Red List Criteria. The degree of vulnerability of a species to extinction rises with falling population sizes and increasing population fragmentation (IUCN Red List, http://www.iucnredlist.org/info/categories_criteria2001). The ability of species to resist the impacts of environmental fluctuations is dependent on population size and age structure. Larger populations have further to fall than small before there is a risk of collapse, and populations with many older animals will be able to see through periods of reduced reproductive success better than populations with few reproductive year classes. They will also be better able to sustain connectivity and gene flow at regional scales than small populations. For all these reasons, large populations are better able to rebound after localised catastrophes than small. Finally, larger populations deliver greater levels and more security of the ecological goods and services that are important to people. It should be clear from this discussion, that impacts from fishing and other sources of anthropogenic harm have greatly reduced environmental resilience in the seas around the UK and England. MPAs are required to help recover this lost resilience.

MPAs have the potential to reverse the attrition of offspring production, thereby extending dispersal distances and connectivity. They can also reduce habitat fragmentation by fostering recovery of degraded habitats, so providing stepping stone habitats for dispersal (Figure 18). However, the degree to which they can achieve these benefits is closely related to the level of protection given to them. A fundamental goal of MPAs is to recover depleted populations and restore the natural balance among populations, but this can only be achieved where species are given genuine protection from the agents causing decline. While many human impacts affect English seas, fishing has had the broadest and deepest effects on marine life (Roberts 2007). To have any chance of creating the conditions for recovery, MPAs must be protected from at least some forms of exploitation. At a minimum this means removing the impacts of mobile fishing gears (trawls and dredges). Mobile gear closures benefit some species (e.g. Murawski et al. 2005, Blyth et al. 2006, Jaworski *et al.* 2006), but they fall well short of the benefits possible from full protection from exploitation. If serious inroads are to be made into the task of recovering populations, reducing habitat fragmentation and rebuilding lost resilience, then highly protected MPAs are essential. Furthermore, the level of regional benefit that they can produce will be closely linked to their coverage.

A simple model shows how level of protection and coverage play out in achieving higher levels of population viability and environmental resilience (Figure 20). In this model, population reproductive output has been reduced by 90%, in line with the reduction in biomass of many of the larger exploited species in English waters since 1900 (Christensen et al. 2003). Fisheries models suggest that managers need to maintain populations at 35% or more of their unexploited biomass to avoid recruitment overfishing and reduce the risk of population collapse (Mace and Sissenwine 1993). What coverage and level of protection of MPAs would be necessary to achieve this?

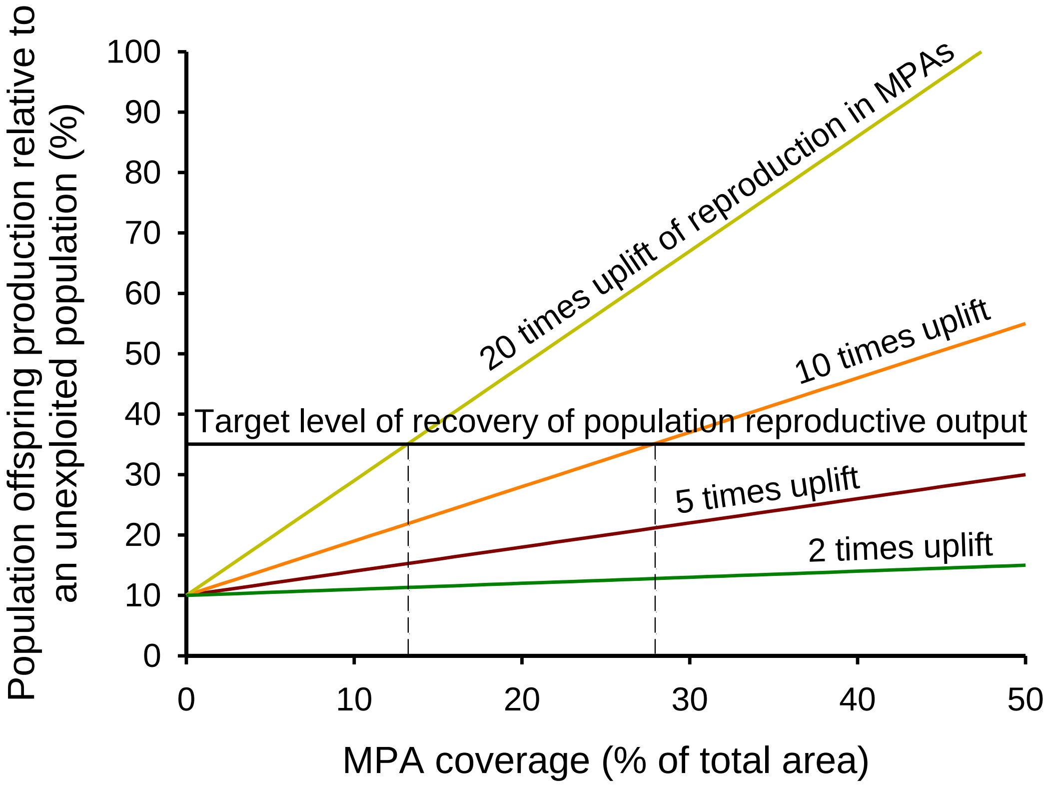

Figure 20: The contribution of MPAs to recovery of reproductive output of a population. The model assumes that fishing has reduced reproductive output of an unprotected population to 10% of the level that would be produced if the population were not exploited. Four levels of MPA protection produce increasing amounts of uplift in reproductive output by protected populations. Lines show the level of coverage of MPAs necessary to rebuild total reproductive output (from animals in MPAs + fishing grounds) to 35% of the level produced by an unexploited population. For simplicity it is assumed that species populations are protected in line with the coverage of protected areas (e.g. 30% of a species population would be protected by 30% coverage of MPAs). See text for further explanation.

Consider first the level of protection given to MPAs. Figure 20 shows four scenarios of uplift in population reproductive output by MPAs. The more highly protected an MPA is, and the greater the fishing intensity outside, the greater the uplift in reproductive output of a protected population. A lightly protected MPA (e.g. one which allows use of static fishing gear only) might double reproductive output of a protected species, while a fully protected MPA that excludes all exploitation might increase it by 20 fold (according to experiences with such marine reserves around the world; Gell and Roberts 2003). With business as usual in surrounding areas (i.e. no improvement in management), the least protected areas could at best produce an increase to 20% of the level of offspring production by an unexploited population, but only with 100% coverage of MPAs. Protected areas that increased offspring production by 5x would achieve the target rebuilding with 63% coverage. MPAs that increased offspring production 10x would require 28% coverage to meet the rebuilding target, and if they increased production 20x, they would meet the target at 13% coverage. 10x and 20x are realistic expectations for increases in reproductive output in depleted species from marine reserves that exclude all, or significant amounts of fishing. What Figure 20 makes clear is that lightly protected MPAs will contribute only modest amounts to region wide recovery of populations and ecosystems and will therefore not increase environmental resilience by much.

14.2 The effects of climate change

Climate change is another key consideration in the development of a network of MPAs. Climate change is expected to alter marine ecosystems in a number of ways. In particular, there will be changes in geographic distribution of species as ranges shift; there will be reductions in the area of intertidal habitats; and there will be alterations in the abundance of organisms in relation to changes in seawater chemistry (ocean acidification). There are also expected to be changes in wave climate, current patterns, dissolved oxygen levels and tidal regimes. These processes may affect the distribution of species and habitats, as well as changing patterns of connectivity among populations. What advice can be offered to ensure that marine conservation and management with MPAs remains effective into the future?

The points made about environmental resilience above apply equally to ensuring resilience in the face of climate change. Other things being equal, larger populations with extended age structures will be better able to survive and adapt to the challenges of climate change. Hence, the use of highly protected MPAs in networks is critical to assuring sufficient resilience across a broad range of species, and the overall benefits will be proportional to the total coverage of these MPAs.

Connectivity patterns will certainly change with alterations in current regimes and shifts in the distribution of species and their habitats. It is possible to make some broad estimates of how species' distributions might change in relation to rising temperatures. The website Fishbase (www.fishbase.org) provides a modelling tool that predicts range shifts of fish in relation to temperature, for example. But these predictions are little more than guesses and cannot be relied upon in any detail. If we cannot predict changing patterns of connectivity, then how can effective networks be designed? The simple answer is to use the method applied in the financial world. Like ecological systems in which many factors affect a species' population, many different factors affect the value of company shares. Few can be predicted with any reliability for more than short periods into the future. Market traders use all kinds of strategies to try to maximise returns from their money. The most reliable is the most straightforward. They build portfolios of shares in many companies to spread risk. A well diversified portfolio balances the ups and downs of financial markets. Little surprise then that the most popular investment funds are index trackers that spread risk by investing in a representative spread of companies listed on any given share price index.

MPA networks can be designed in a similar way to spread risks against changing conditions in the future. The creation of a network can be viewed as developing a well-diversified portfolio of protected sites. The key design principles that can deliver resilience are to (1) represent the full range of habitats in the network, (2) replicate them in multiple MPAs, (3) ensure MPAs are sufficiently close together that they can exchange offspring of longer distance dispersers, (4) ensure that MPAs are large enough to support viable populations of short-distance dispersers, and (5) protect MPAs sufficiently to rebuild populations to higher levels and allow them to develop more natural extended age structures. If there are many MPAs in a network then shifts in current patterns and species' ranges will simply alter the pattern of linkages among protected populations; some links will weaken, others will strengthen. By contrast, a network with few MPAs will be vulnerable to loss of species as conditions change. A network with a higher coverage of MPAs will remain better connected than one with less coverage, as will a network with shorter inter-MPA distances compared to one with widely spaced MPAs. Well-connected networks will help facilitate species' range shifts by providing stepping stone habitats along the way. A network that has a significant fraction of highly protected sites will have stronger and longer connections made among MPAs than one with less highly protected sites. A highly protected network can therefore be expected to fare better under changing conditions.

There is a further effect of climate change that is important in the context of connectivity among MPAs. Warmer sea temperatures may speed up larval development times, provided that there is also sufficient food available to them (O'Connor et al., 2007). If this happens, dispersal distances will decrease, and connectivity of populations among MPAs would fall. This effect puts a premium on using conservative estimates of spacing and of the dispersal distances of marine organisms in planning MPA networks.

The conclusions that can be drawn from the foregoing analyses are as follows:

(1) A network with a significant coverage of highly protected MPAs will afford greater resilience to changing conditions than one with few such MPAs.
(2) The higher the fraction of highly protected MPAs within a network, the better populations will be connected among MPAs.
(3) The higher the fraction of highly protected MPAs within a network, the lower will be the extinction risk for species.
(4) Closely spaced MPAs will provide a higher level of population resilience and reduce extinction risks by more than widely spaced MPAs.

15. Implications of MPA size and spacing for coverage of the network

Recommendations made on the size and spacing of MPAs in this report have implications for the coverage of the resulting network (Figure 21). At one extreme, if all MPAs established were the minimum average size recommended (i.e. 10 km across), and the maximum inter-MPA spacing of 80 km was adopted, then the resulting network would cover 11% of the area of English territorial seas. At the other end of the spectrum, if the largest average size of MPA recommended (i.e. 20 km across) was adopted and the average spacing set at 40 km, then the network would cover 33% of English seas.

There is another design feature of the MPA network that should be considered. As the size of MPAs in the network decreases, so the number of MPAs necessary to fulfil the spacing criterion will increase. This could lead to an impracticably large number of MPAs. Hence, creating fewer, larger MPAs should ease the management burden.

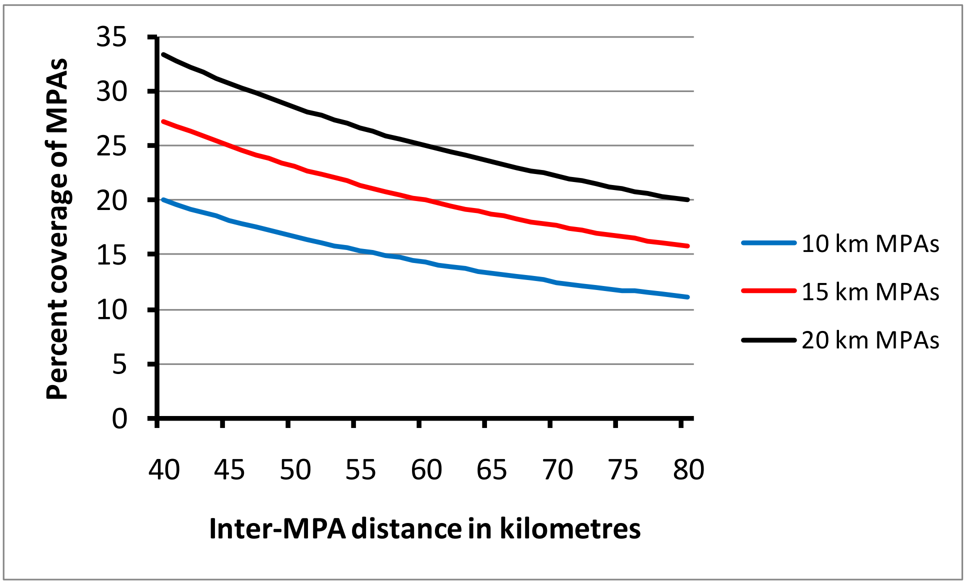

Figure 21: Coverage of MPAs required in English waters for a range of different MPA sizes and spacings.

16. Limitations

The evidence and models presented in this report enable general conclusions to be reached about likely scales of connectivity among populations and habitats protected in MPAs. Some of the evidence used comes from English waters, other evidence from further afield. It is not possible, based on available evidence, to reach any detailed, specific conclusions about actual patterns of connectivity or dispersal for any particular species around England. For several reasons, such information would, in any case, be of limited value for designing an effective, broad-based conservation strategy using MPAs. MPAs are not single-species conservation tools, and the cases in which an MPA is created to benefit only a single species can be expected to be highly unusual. There is a limited scope for the introduction of MPAs into the waters of any country, because of space and cost constraints. It is therefore important to design them with a view to benefiting the widest spectrum of species and habitats that is possible. Furthermore, designing MPAs around detailed knowledge of the present distribution and inferred connectivity of a species may fail to meet that species needs under changed future conditions. A further reason not to use detailed, species-specific knowledge as a guide to designing an MPA network in England is that such data are extremely expensive and time-consuming to acquire. Information of this quality will only ever be available for a small fraction of the species present. Designing networks around their needs risks failing to meet those of less well understood species.

It will be evident from the above that the design of an MPA network represents a compromise. Some species will benefit a great deal from MPAs, others less so. The objective of the advice developed here is to maximise the spread of species that should receive adequate protection from the network. Managers will have to develop complementary measures outside MPAs to protect species for which MPAs offer little protection.

The guidance developed on spacing of MPAs should be considered in relation to particular habitats. Populations of species within MPAs will only connect with others in MPAs that contain suitable habitats for them.

This report considers only ecological aspects of the size and spacing of MPAs. Human factors also play a role in determining the most effective size and configuration of MPAs in a network. Species and habitats will benefit little if an MPA cannot be effectively enforced. MPA size, for example, has an important bearing on enforcement and compliance, as does location. In some places, MPAs may benefit from high levels of local support, in others little. It may be possible to enforce small MPAs in some coastal areas with good surveillance but it would be impossible in others. These considerations will play out in the selection of individual sites as a network is built. The recommendations on size and spacing of MPAs made in this report provide a strategic framework against which candidate sites can be screened and with which the adequacy of network designs can be evaluated. The recommendations are not intended to be applied so rigidly that they would override important practical considerations at a local level.

17. Conclusions and recommendations

Bearing in mind the limitations noted above, the following conclusions are drawn and recommendations made. The available evidence of adult movement propensities of the types of organisms found in English waters, lead to the conclusion that MPAs that measure 10 to 20 km in their smallest dimension will provide protection to a wide range of species in English territorial seas, as they have done in other parts of the world. Evidence of the effectiveness of existing MPAs indicates that smaller MPAs than this will still be worthwhile, e.g. of 1 to 5 km minimum dimension, but they will provide more limited protection to species. However, the network will not be as effective if it consists only of small MPAs as it would be if larger MPAs were also incorporated. **It is therefore recommended that in territorial seas the median size of MPAs should be no less than 5 km in their minimum dimension, and that the average size of MPAs in the network should lie between 10 and 20 km in their minimum dimension.**

Many commercially important species have relatively large ranges of movement. Bigger MPAs will be needed to protect these species in areas beyond territorial waters. **In the region of 12 – 200 nautical miles from the coast, it is recommended that the average and median sizes of MPAs should be between 30 and 60 km in their minimum dimension, if they are intended to protect many commercially important species.** Larger MPAs are also warranted in offshore areas compared to territorial seas to facilitate compliance and enforcement.

MPAs of the dimensions set out above may offer benefits to more mobile and migratory species if they are located strategically in places that are particularly important in these species' life-cycles, such as spawning, nursery grounds and migration bottlenecks. However, complementary management measures will be necessary to protect such species outside MPAs.

Detailed, reliable information about planktonic dispersal characteristics is not available for any species found in English waters. Therefore, the question of how far species can disperse was examined from a number of perspectives and inferences made from them. Sources of evidence examined included duration of planktonic dispersal, oceanography, modelling, chemistry, population genetics, the spread of invasive species, and the proximity of known spawning and nursery grounds. Based on the evidence reviewed, there are many species that can be expected to disperse distances of the order of a few metres up to around 20 km whose movements can be accommodated within MPAs of the sizes recommended above. For species with longer planktonic durations, the distances dispersed per generation lie within the range of approximately a few tens to a hundred kilometres or so. The majority of species disperse less than 80 km per generation. **It is therefore recommended that**

MPAs should be no more than 40 to 80 km apart in the network. This recommendation applies to waters from the coast to 200 nautical miles offshore.

In making the above recommendations, no particular level of protection was assumed within MPAs. However, connectivity and population viability depend on level of protection in MPAs because more highly protected sites will support larger populations and will export more propagules over greater distances. Therefore a lightly protected network will need to have a higher coverage of more closely spaced MPAs than a highly protected network. Furthermore, networks that contain a greater coverage of highly protected sites can be expected to perform better under changing environmental conditions (i.e. climate change) than networks that have few such sites.

Table 5 summarises recommendations on size and spacing of MPAs made in this and other studies.

Table 5: Summary of size and spacing recommendations.

Location/Study	MPA size recommendation	MPA spacing recommendation
California Marine Life Protection Act	10 – 20 km minimum dimension	50 – 100 km apart
Rezoning Great Barrier Reef Marine Park, Australia	20km minimum dimension except close to mainland where 10km	Not set, but applying principles of coverage (at least 20% of each bioregion) and replication (3-4 replicates per bioregion) was felt sufficient to assure connectivity
Shanks et al. (2003) based on species' dispersal distances	4 – 6 km minimum dimension	10 – 20 km apart
This report, UK	An average size of 10 – 20 km minimum dimension in territorial seas, and a median size > 5 km minimum dimension. In offshore waters (12-200 nm) MPAs should have an average and median size between 30 and 60 km in their minimum dimension if they are to be effective in protecting many commercially important species.	40 – 80 km apart

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Appendix 1: List of species included in the study and their attributes

Key to locations: EC – English Channel, IS – Irish Sea, MNS – Mid North Sea, SNS – South North Sea, SWA – South Western Approaches, SWP – South West Peninsula.

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Virgularia mirabilis	7 - 15 days	Sheltered fine sediments from 12-400m deep	0 km	SWP, SWA, MNS, IS, EC.	15
	Alcyonium digitatum	2-10 days	Lower shore to 50m attached to rock, shell etc.	0 km	All	16
	Metridium senile	1 - 6 months	Hard substrate to 100m deep	0 km	All	17

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Caryophyllia smithii	1 - 6 months	Sublittoral rocks and shell etc. to 200m deep	0 km	SWP, EC, MNS.	18
	Cerianthus lloydii	1 - 6 months	Sublittoral sediments to 100 m deep	0 km	All	19
Echinodermata	*Asterias rubens*	87 days	A variety of substrata to over 100 m deep	0 – 1 km	All	20

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Echinus esculentus	45 - 60 days	Rocky areas to > 100m deep	0 – 1 km	All	21
	Ophiothrix fragilis	11 - 30 days	Tideswept rock and coarse sediments from coast to offshore shelf	0 – 1 km	All	22

Phylum	**Species**	**Planktonic duration**	**Habitat**	**Adult Dispersal**	**Location**	**References**
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
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	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Neopentadactyla mixta		Coarse mobile gravel and maerl	0 – 1 km	SWP, MNS.	23
	Antedon bifida	2 -10 days	Shallow sublittoral to 450m but mainly 15-40m	0 – 1 km	SWP, EC, MNS, NS.	24
	Psammechinus miliaris	1-2 months	Bouldery, sheltered intertidal and sea lochs	0 – 1 km	All	25

Phylum	**Species**	**Planktonic duration**	**Habitat**	**Adult Dispersal**	**Location**	**References**
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Amphiura filiformis	1-6 months	Fine muddy sands > 15m	0 – 1 km	All	26, 27
Mollusca	*Ostrea edulis*	11 - 30 days	Estuaries and shallow coasts out to continental shelf on a variety of substrata	0 km	SWP, NS, EC, SNS.	28

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Cerastoderma edule	3 months	Intertidal estuaries and bays in sand, mud or gravel	0 – 1 km	All	29
	Mytilus edulis	20 days – 2 months	Rocky intertidal and shallow subtidal	0 km	All	30
	Pecten maximus	18 days	Sand and gravel over continental shelf	0 – 1 km	SWP, EC, NS, MNS.	31

Phylum	**Species**	**Planktonic duration**	**Habitat**	**Adult Dispersal**	**Location**	**References**
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Nucella lapillus	non-dispersing	Wave exposed rocky shores	0 – 1 km	All	32
	Tenellia adspersa	4-5 days	Intertidal and shallow subtidal; euryhaline	0 – 1 km	EC, SNS, NS.	33
	Octopus vulgaris	2 months	Wide range of habitats		SWP, EC.	34, 35, 36
	Sepia officinalis	None	Offshore to 200m deep	10 – 100 km	All	37, 38, 112

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
Chlorophyta	*Ulva intestinalis*	8 days		0 km	All	39, 40
Ochrophyta	*Ectocarpus sp.*	>4km		0 km	All	39, 41
	Sargassum muticum	germling <25d, <5m; veg 28km	Hard substrate in shallow waters; also estuaries	0 km	SWP, EC	39, 42

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
Chromophycota	*Laminaria digitata*	1 day	Hard substrate to 20m deep	0 km	SWP, SWA, MNS, IS, EC	43, 44
	Ascophyllum nodosum	2-10days	Estuaries to exposed coasts, rocks and boulders	0 km	All	43
	Laminaria hyperborea	>1day	Hard substrate up to 30m deep	0 km	SWP, SWA, MNS, IS, EC	45, 46

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Chorda filum	100-1000m	Low shore rock pools to 5m deep	0 km	All	47
	Saccorhiza polyschides	<1day, <200m	Hard substrate low water to 35m deep	0 km	SWP, MNS, IS	48
Rhodophycota	*Corallina officinalis*	2 days	Mid-tidal to 18m deep	0 km	All	43

Phylum	**Species**	**Planktonic duration**	**Habitat**	**Adult Dispersal**	**Location**	**References**
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Palmaria palmata	<10m	Epilithic and epiphytic, littoral to 20m deep	0 km	All	49
Anthophyta	*Zostera marina*	100-1000m	Sand and fine gravel to approx 4m deep	0 km	All	50
	Zostera noltii	100-1000m	Intertidal mud to shallow sublittoral	0 km	All	50

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
Annelida	*Aphelochaeta marioni*	None	Intertidal and subtidal soft sediments	0 – 1 km	All	51, 52
	Chaetopterus variopedatus	11-21 days	Sediments in low water to continental shelf	0 – 1 km	SWP, SWA, MNS, IS, EC	53
	Owenia fusiformis	30 - 60 days	Sand or muddy sand at or below low water	0 – 1 km	SWP, SWA, MNS, SNS, EC	54, 55, 56

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Arenicola marina	None	Intertidal sand	0 – 1 km	All	57
	Hediste diversicolor	None	Muddy bottoms	1 – 10 km	All	58
	Lanice conchilega	60 days	Intertidal and subtidal sediments	0 – 1 km	All	59, 60
	Sabellaria alveolata	40 -180 days	Lower intertidal sand and rock	0 – 1 km	SWP, SWA, MNS, EC, IS	61, 62

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Polydora ciliata	11 - 30 days	Calcareous sediments from low water	0 – 1 km	All	63, 64, 65
	Pomatoceros triqueter	14 -21 days	Subtidal stones, rocks and shells to 70m deep	0 – 1 km	All	66
	Serpula vermicularis	6 - 60 days	Subtidal stones, rocks and shells to 250m deep	0 – 1 km	SWP, SWA, MNS, IS,	61

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
Arthropoda	*Cancer pagurus*	30 - 180 days	Lower shore to 100m on bedrock and sand	10 – 100 km (mature females)	All	67, 68, 112
	Carcinus maenas	80 days	High water to 60m deep	0 – 1 km	All	69, 70
	Maja squinado	2-10 days	Shallow sublittoral to 50m deep	10 – 100 km	SWP, SWA, EC, IS	71, 72, 112

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Homarus gammarus	14-20 days	Rocky substrates from lower shore to 60m deep	1 – 10 km	All	73
	Nephrops norvegicus	30 - 60 days	Soft sediments from 200-800m; shallower in Firths and sealochs	0 – 1 km	SWP, SWA, IS, MNS	74, 75, 76
	Crangon crangon	30 - 180 days	Sand and mud; middle shore to 150m deep	1 – 10 km	All	77

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Callianassa subterranea	28 days	Soft sediments	0 – 1 km	IS, MNS	78, 79
	Balanus crenatus	11 - 30 days	Cobbles, shells, bedrock etc; lower shore to shallow sublittoral	0 km	All	43
	Chthamalus montagui	11 - 30 days (100-1000m)	High to mid- rocky intertidal	0 km	SWP, SWA, IS, MNS	43

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Chthamalus stellatus	12 - 30 days (100-1000m)	Exposed rocky shores	0 km	SWP, SWA, IS, MNS	43
Chordata	*Gadus morhua (cod)*	90-100 days	Sublittoral to 600m deep	10 – 100 km	All	80, 81, 82
	Pleuronectes platessa (plaice)	100 days	Sand, gravel and mud to 200m deep	100 – 1000 km	All	83

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Solea solea (sole)	35-51 days (eggs 10 days)	Sand and mud to 120m	10 – 100 km	All	84, 85, 112
	Microstomus kitt (lemon sole)	5.5-8.8 days (eggs)	Rocky and stony bottoms 5-400m deep	10 – 100 km	All	86, 87, 112

Phylum	**Species**	**Planktonic duration**	**Habitat**	**Adult Dispersal**	**Location**	**References**
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Limanda limanda (dab)	12 days (eggs)	Sandy bottoms, 1-150m deep; mainly 20-40m		All	88, 89
	Platichthys flesus (flounder)	37 days (eggs 7 days)	Muddy bottom from lower shore to 50m; often in estuaries		All	90, 91, 92
	Clupea harengus (herring)	160 days	Epielagic, 0-200m	100 – 1000 km	All	93, 94, 112

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Merluccius merluccius (whiting)	4 days (eggs)	Demersal, 70-350m	100 – 1000 km	All	95, 96, 112
	Melanogrammus aeglefinus (haddock)	127 days (eggs 13-15 days)	Demersal, 0-250m		All	97, 98

Phylum	**Species**	**Planktonic duration**	**Habitat**	**Adult Dispersal**	**Location**	**References**
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Scomber scombrus (mackerel)	40 days (eggs 2 – 7 days)	Epipelagic	1000 – 10000 km	All	99, 100, 112
	Merlangius merlangus (whiting)	extensive (1 year?)	Demersal mud and gravel to 200m deep	100 – 1000 km	SNS, EC, SWP, IS	101, 102, 103

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Lophius budegassa (black-bellied anglerfish)	3-4 months	Demersal, 300-1000m		SWP, IS	101, 106
	Lophius piscatorius (Anglerfish)	3-4 months	Demersal, 18-550m	10 – 100 km	EC	101

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Ammodytes marinus (sandeel)	2-5 months	Benthopelagic; over soft sediment; nearshore and offshore	1 – 10 km	SWP, MNS	101, 107, 113
	Sprattus sprattus (sprat)		Pelagic; estuaries to 150m deep	10 – 100 km	SNS, EC, SWP, IS	101, 108, 112
	Raja clavata (thornback ray)		Demersal, 10-60m; up to 300m	10 – 100 km	SWP, EC, IS, SNS	109

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Dicentrarchus labrax (sea bass)		Demersal, nearshore to max 70m	100 – 1000 km (juveniles 10 – 100 km)	SWP, EC, IS, SNS	110, 111
	Squalus acanthias (spurdog)		Benthopelagic, inshore and offshore to 1500m	100 – 1000 km	All	112

Phylum	Species	Planktonic duration	Habitat	Adult Dispersal	Location	References
Bryozoa	*Alcyonidium diaphanum*	<1day	Intertidal to offshore rock and shell	0 km	All	1
	Bugula turbinata	<1day	Rock walls of gullies	0 km	All	2
	Conopeum reticulatum	1-6 months	Under boulders/rock shallow intertidal	0 km	All	3
	Electra pilosa		On seaweed etc, intertidal to lower shore	0 km	All	4
	Flustra foliacea	<1day	Coarse sediment and rock in current swept areas	0 km	All	5
	Pentapora fascialis	<1day	Bedrock and boulders in current swept areas	0 km	SWP, IS, MNS, EC.	6
	Victorella pavida	<1day	Attached to submerged rock, stones, plants etc in estuaries and lagoons	0 km	SWP, IS, MNS, EC.	7
Porifera	*Halichondria panicea*		Wave exposed shores attached to algae	0 km	All	8
	Ophlitaspongia seriata	<1day	Wave exposed shores attached to algae	0 km	EC	9, 10, 11
	Mycale macilenta	>2 days	Attached to rock and seaweed to 40m deep	0 km	SWP, IS, SNS, EC.	10, 12
Cnidaria	*Eunicella verrucosa*		Upward facing bedrock	0 km	SWP	13
	Cordylophora caspia	<1day	Low salinity estuaries and lagoons	0 km	SWP, SNS	14
	Sardina pilchardus (sardine)		Pelagic surface to 50m+	10 – 100 km	EC	112
	Trachurus trachurus (scad)		Pelagic-neritic100-200m	1000 – 10000 km	All	

No.	Reference
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94 http://www.fao.org/fi/website/FIRetrieveAction.do?dom=species&fid=2886
95 http://www.fao.org/fi/website/FIRetrieveAction.do?dom=species&fid=2238
96 http://www.fishbase.com/Summary/SpeciesSummary.php?id=30;
97 http://www.fishbase.com/Summary/SpeciesSummary.php?id=1381
98 http://www.fao.org/fi/website/FIRetrieveAction.do?dom=species&fid=2228
99 http://www.fao.org/fi/website/FIRetrieveAction.do?dom=species&fid=2473
100 http://www.fishbase.com/Summary/speciesSummary.php?ID=118&genusname=Scomber&speciesname=scombrus;
101 Strategic Environmental Assessment - SEA2, Technical Report 003 - Fish & Fisheries
102 http://212.219.37.112/gridMap/gridMap.jsp?allDs=1&srchSpKey=NBNSYS0000176425
103 http://www.fishbase.org/Summary/speciesSummary.php?ID=29&genusname=Merlangius&speciesname=merlangus
104 http://212.219.37.112/gridMap/gridMap.jsp?allDs=1&srchSpKey=NBNSYS0000177329
105 http://212.219.37.112/gridMap/gridMap.jsp?allDs=1&srchSpKey=NBNSYS0000178447
106 http://212.219.37.112/gridMap/gridMap.jsp?allDs=1&srchSpKey=NBNSYS0000183686
107 http://212.219.37.112/gridMap/gridMap.jsp?allDs=1&srchSpKey=NBNSYS0000173710
108 http://212.219.37.112/gridMap/gridMap.jsp?allDs=1&srchSpKey=NBNSYS0000178133
109 http://212.219.37.112/gridMap/gridMap.jsp?allDs=1&srchSpKey=NBNSYS0000177627
110 http://212.219.37.112/gridMap/gridMap.jsp?allDs=1&srchSpKey=NBNSYS0000188622
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112 Pawson, M.G. (1995) Biogeographical identification of English Channel Fish and Shellfish Stocks. Fisheries Research Technical Report 99. MAFF Directorate of Fisheries Research, Lowestoft.
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Appendix 2: Sources of data for the study of marine protected area effects

Study	Marine Protected Area	Temperate	Snapshot only	Temporal scale	Before/after comparison	Controls in fished areas	More than one MPA
Alcala & Russ, 1990	Sumilon Island, Phillipines			Yes	Yes[6]	Yes	
Alcala *et al*., 2003	Apo Island, Phillipines			Yes		Yes	
Babcock *et al*., 1999	Leigh MR & Tawharanui Park, New Zealand	Yes	Yes	Yes		Yes	Yes
Bell, 1983	Banyuls-Cerbère, France	Yes	Yes			Yes	
Bennett & Attwood, 1991	De Hoop MR, South Africa	Yes		Yes	Yes	Yes	
Buxton & Smale, 1989	Tsitsikamma Coastal National Park, South Africa	Yes	Yes			Yes	
Castilla & Duran, 1985	Punta El Lacho, Chile	Yes		Yes	Yes	Yes	
Denny *et al*., 2004	Poor Knights Island MR, New Zealand	Yes		Yes	Yes	Yes	
Fernandez & Castilla, 1997	El Quisco & Las Cruces, Chile	Yes		Yes	Yes[7]	Yes	Yes
Ferreira & Russ, 1995	Glow & Yankee reefs, GBR Austalia			Yes (1y)		Yes	Yes
Frank *et al*., 2000	Emerald/Western Bank, USA/Can	Yes		Yes	Yes	Yes	
Johnson *et al*. 1999	Kennedy Space Center, USA	Yes	Yes			Yes	
Letourneur, 1996	Mayotte Island, Indian Ocean		Yes			Yes	
Murawski *et al*. 2000	Georges Bank, USA/Can	Yes		Yes	Yes	Yes	Yes
Pipitone *et al*. 2000	Castellamare, Italy	Yes		Yes	Yes		
Polunin & Roberts, 1993	Hol Chan MR, Belize & Saba Mpark, NL Antilles		Yes			Yes	Yes

[6] Backwards, after the breakdown of protection at Sumilon Island.
[7] At establishment.

Study	Marine Protected Area	Temperate	Snapshot only	Temporal scale	Before/after comparison	Controls in fished areas	More than one MPA
Roberts & Polunin, 1992	Ras Mohammed, Egypt		Yes			Yes	
Roberts, 1995	Saba, NL Antilles			Yes		Yes	
Russ & Alcala, 1996	Sumilon & Apo, Phillipines			Yes	Yes[8]	Yes	Yes
Tuya *et al*. 2000	San Juan Islands, USA	Yes	Yes			Yes	Yes
Vacchi *et al*., 1998	Ustica Island, Italy	Yes	Yes			Yes	
Watson & Ormond, 1994	Kisite Marine National Park, Kenya		Yes[9]	Yes[10]	Yes	Yes	

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[8] Yes only for Sumilon Island, No for Apo Island.
[9] For abundance and size estimates
[10] For biomass estimates.

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