Marine Policy

Crossing the divide: the challenges of designing an ecologically coherent and representative network of MPAs for the UK

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Abstract

Against a background of international commitments to establish ecologically coherent and representative MPA networks, and the UK Marine Bill which aims to implement these commitments, the larval dispersal potential of 31 rare/scare benthic invertebrates is investigated and it is found that over half have a low dispersal potential (<1km). On the basis of this, interviews with experts and an analysis of relevant literatures, it is argued that the establishment of representative MPA networks may be a reachable objective, as it is scientifically more realistic and thereby more defensible, whilst the aim of establishing ecologically coherent MPA networks may be a bridge too far.

Key words: ecologically coherent, representative, marine protected area, network design, larval dispersal, OSPAR.

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Introduction

There is growing interest in the potential benefits of networks of marine protected areas (MPAs), the World Summit for Sustainable Development calling for a 'representative network' to be in place by 2012 [1]. This target has been adopted by the Convention on Biological Diversity (CBD) and criteria/guidance for selecting MPAs to form such representative networks have been agreed [2]. In Europe the Marine Strategy Framework Directive (MSFD) requires that each member state establishes 'coherent and representative networks' of MPAs by 2020[1]. In the North-East Atlantic the OSPAR Commission recommends that an 'ecologically coherent network' of MPAs be in place by 2010 [3] and guidance [4] and assessment support [5,6] has been produced to support this recommendation, but assessing whether this network will be coherent remains a challenge [7,8] . The UK plans to fulfil these commitments through the Marine Bill, which aims to establish a network of MPAs by 2012 'to conserve the diversity of rare, threatened and representative habitats and species', which 'will be both large enough, and close enough together, to support functioning communities of marine wildlife' [9]. The nature conservation agency for England's MPA Policy includes includes a target to establish a coherent network of MPAs by 2012[2]. Draft guidance states that connectivity amongst MPAs in the UK network should be maximised using the best available science [10].

The OSPAR documents indicate that it is the ecological linkages between MPAs that are the essential basis of a *coherent* network, as without such linkages a given network is not *joined up* and might be better be termed a representative network, in keeping with the WSSD call and the CBD criteria/guidance. Ardron [8] defines an ecologically coherent network of MPAs as one that (i) interacts and supports the wider environment; (ii) maintains the processes, functions, and structures of the intended protected features across their natural range; (iii) functions synergistically as a whole, such that the individual protected sites benefit from each other to achieve the two objectives above; and (iv) (additionally) may be designed to be resilient to changing conditions.

A key challenge is to design networks that are both representative and ecologically coherent, as the UK Government is committed to the WSSD, MSFD and OSPAR MPA network targets, but on what bases might this challenge be addressed? This significantly depends on the scale at which connectivity occurs amongst the features of particular interest when designing MPA networks. This paper is premised on the assumption that such features should include rare and scarce species, contributing to the conservation of such species being an accepted objective of MPAs [11,12] and the presence of such species being an accepted criterion for MPA selection [2].

The success of MPAs depends on connectivity amongst protected areas and spillover into unprotected areas [13] through linkages at various scales. In the past many have assumed that the connectivity of marine ecosystems occurs across such wide scales that such linkages are not an issue [12], but there is growing evidence that this is an unsafe assumption. Kinlan and Gaines [14], for example, assessed the dispersal potential of different marine benthic organisms based on a literature review of genetic isolation-by-distance slopes. These indicate that whilst some taxa of fish have dispersal distances of as much as a 1000 km or more, many invertebrate and macroalgal taxa have dispersal distances of up to five orders of magnitude less, their dispersal distances being measured in units as small as 10s of metres. This implies that linkages between MPAs are an important issue when designing a network with the aim that it should be

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[1] Article 13(4), Marine Strategy Framework Directive (2008/56/EC) <eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2008:164:0019:0040:EN:PDF>
[2] Natural England's MPA Policy
<www.naturalengland.org.uk/Images/Marine%20Protected%20Areas%20Policy%20Dec%202007_tcm6-9280.pdf>

ecologically coherent, as some species have very narrow scale distributions, as revealed by their genetic population structures.

For sessile benthic invertebrates, a key determinant of genetic population structure is the pattern of larval dispersal [15]. This is, in turn, determined by the period of time that the larvae spends in the water column - life history traits [16, 17] and, assuming that the larvae drifts passively, the speeds and directions of the waters into which the larvae are released - hydrodynamics [18]. In combination, these factors are often discussed in terms of source-sink dynamics, the importance of gaining an understanding of which in MPA network design is widely recognised [19]. Gerber et al [20], however, note that very few MPA network design models explicitly include larval dispersal parameters, though Shanks et al [17] have reviewed propagule dispersal distances and applied them in the development of criteria for the design of MPA networks around the US.

Against this background, this paper has two aims. (1) To review the available information on the larval dispersal potential of rare, scarce and/or protected inshore benthic macro-invertebrates found around the UK, assuming that providing for the dispersal of such species should be a factor when designing an ecologically coherent MPA network. (2) To assess expert opinion on the potential bases on which an ecologically coherent network of MPAs around the UK might be designed. This will provide for discussions on the challenges of designing ecologically coherent networks of MPAs and defending related decisions. The empirical work on which this paper is based was undertaken by Carpenter [21].

Methods

(1) *Review of larval dispersal potential*

Rare/scarce benthic macro-invertebrates species were identified using Sanderson's [22] review of inshore (within 3 nm) species, which identified 69 nationally rare (recorded in 8 or less 10x10km squares out of total of 1546) and 124 nationally scarce (recorded in 9-55 such squares) marine flora and fauna species. A further 3 species were considered on the basis that that they are protected under Schedule 5 of the Wildlife and Countryside Act (1981) but not listed as rare/scarce by Sanderson, 16 such protected species also being listed as rare/scarce. Of the total of 196 rare/scarce/protected benthic macro-invertebrates species, the larval dispersal potential of 31 species was assessed by studying life history traits, particularly nutritional mode, site of development and developmental mode, this sample simply being based on those species for which information concerning such traits was available. These species were categorised as having a low, medium and high dispersal potential drawing on the categorisation developed by Dibacco et al. [23] (Table 1). Life history traits were assessed through a literature review, including reports, etc that were kindly made available by the library of the Marine Biological Association Laboratory, Plymouth. Some dispersal potential data was also obtained from the biological traits information catalogue (BioTIC) [24] developed through the Marine Life Information Network (MarLIN).

There is very little information available for such species as this is an under-researched area, so it was often necessary to use information that was available for similar co-familial species. This approach is based on that employed by Carson and Hentchel [25], but they only assigned traits to an unknown species when 80% of known members of a taxon shared the same traits. Due to time and, particularly, information availability limitations, this study took the approach whereby the life history traits information was used for species that are in the same family or genus as the rare/scarce species of interest. Whilst this reduces the reliability of the data, given the lack of life history traits information available for the species of interest, this was the only feasible means of undertaking this preliminary analysis.

Several of the life history characteristics listed in table 1 were particularly used to define categories - nutritional mode of the larvae, time before larval settlement, fecundity, and swimming behaviour. Nutritional modes of marine invertebrate larvae include planktotrophic (feed whilst in the plankton) and lecithotrophic (feed on a yolk reserve) phases, the former tending to have a greater dispersal potential [26]. Low dispersers were particularly straight-forward to categorise as many were 'direct' developers, i.e. species with no intermediate stage of development - a juvenile emerges and typically crawls away from the parent with limited dispersal [23]. Overall, though, it must be recognised that there was an element of judgement to these categorisations.

(2) *Interviews with experts*
Eight experts were interviewed in person (2), by phone (5) or by email (1) in order to assess opinions on the potential bases on which an ecologically coherent network of MPAs around the UK might be designed. These consisted of senior marine specialists in the conservation agencies for England and Wales (3), marine campaigners in NGOs (2), a regional MPA project manager, the MarLIN programme director and an American authority on MPA network design issues. The interviews were undertaken on a semi-structured 'conversation with a purpose' basis [27] and the discussions revolved around various issues related to the design of ecologically coherent networks.

Results/discussion

(1) *Review of larval dispersal potential*
Of the 31 rare/scarce species that were studied, 32% (10) were categorised as having a high (>100km), 13% (4) a medium (1-100km) and 55% (17) a low (<1km) larval dispersal potential (see tables 2-5). Sampling bias has clearly had an influence on these results, as researchers are more likely to study species with a low dispersal potential as these are particularly interesting from a population ecology perspective and this research could yield important information on species which are particularly sensitive to local impacts. It remains, however, indicative to note that more than half of the rare/scarce species assessed had a larval dispersal potential of less than 1km, mainly because they are direct developers or have lecithotrophic larvae, though some have short duration planktonic larvae. There is clearly a link in that one of the reasons species can be rare/scarce is that they have a limited dispersal potential, though there are evidently other reasons as nearly one third of the species assessed had high a high dispersal potential, but the low dispersal potential of many rare/scarce species none-the-less has significant implications for the design of an ecologically coherent MPA network around the UK, assuming that ecological coherence includes providing linkages for such species.

(2) *Interviews with experts*
The finding that many rare/scarce species may have a low dispersal potential was one of the issues discussed in the expert interviews, all of whom considered that whilst it is important to include the larval dispersal potential of rare/scarce invertebrates in MPA network design, this is not a high priority as habitat representativity must be the primary consideration, the presence of rare/scarce species being a secondary criterion for selecting amongst replicates of representative habitats. On the related question of whether ecologically coherent MPA networks can protect rare/scarce species, the interviewees generally considered that they cannot, as many such species have dispersal distances that are less than can reasonably be expected between MPAs in such networks. Some considered that improvements in our knowledge on dispersal distances and source-sink dynamics might provide for more protection for some species through such networks, while others pointed out that wider management measures should continue to provide for the protection of rare/scarce species, as areas outside MPAs could still be a significant residual source of larvae of species with low dispersal potential.

As to whether it is scientifically feasible to rigorously design an ecologically coherent network of MPAs, the majority of interviewees considered that we do not have sufficient knowledge and understanding to do this, given the lack of data on the dispersal potential of species and the complexities and uncertainties of hydrodynamics. It was considered that we do have sufficient information to develop certain 'rules of thumb', such as percentage representativity of different habitats, that could potentially provide for such a network. Such 'rules of thumb' could then be used as parameters in network design programmes such as Marxan [39]. This is the approach taken, for instance, by Richardson et al [40] in a study commissioned by the UK government to inform the development of the Draft Marine Bill. Whilst this study noted that ecological coherence assessment based on the dispersal characteristics of selected species through oceanographic modelling is an area for potential further investigation, such assessments were not undertaken due to data limitations and the complexities of this task. The majority of interviewees considered that ecological coherence assessments are likely to continue to be a major challenge in the near future due to such factors, and that whilst they *may* become feasible in the future, the present emphasis should be on moving forward with the information that is available.

This is similar to the view expressed by Ardron [8] based on the OSPAR Commission's work on how progress towards meeting their target for an ecologically coherent network of MPAs in European seas by 2010 can be assessed [6]. In the face of growing urgency as this deadline approaches, this work has identified three 'fast and frugal heuristics' that can be employed in the data limited situations that prevail for the spatial assessment of ecological coherence - (1) Is the network spatially well distributed, without more than a few major gaps? (2) Does the network cover at least 3% of most (7 of the 10) biogeographic provinces? (3) are most (70%) of the threatened and/or declining habitats and species represented in the MPA network?

In the context of discussions on what constitutes an ecologically coherent network with regards to the larval dispersal distances of rare/scarce species, a key parameter is clearly the maximum distance between MPAs within the network, which is considered by the above spatial distribution heuristic. Whilst Richardson et al's [40] study did not include such a parameter, Roberts et al's [41] recommendation for UK MPA network design is that the maximum spacing distance should be 40-80km, with connectivity for short distance dispersers being provided for within MPAs. Ardron [8] considers that the maximum distance between nearshore MPAs as part of the OSPAR network should be 250km, whilst a recent international review of MPA network initiatives considers the maximum distance between MPAs in regional networks to be 10-100km [42]. One interviewee pointed out that the design of California's MPA network used the rule that designations should be no more than 50-100km apart, though it is worth noting that a similar previous study had identified a maximum spacing distance of 10-20km [17]. The very wide variability amongst these 'rule of thumb' figures on what the maximum distance between MPAs in a 'coherent' network should be illustrates the arguably arbitrary nature of such figures.

Whilst such a distance should be agreed for UK MPAs in order to provide for the design of a network to proceed, it must be recognised that, hydrodynamic linkages of sources-sinks aside, such distances between MPAs would not necessarily provide linkages for those species with a low dispersal potential, other than within MPAs, and even some of those with a medium-high dispersal potential, including rare/scarce species, unless it is assumed that areas between MPAs will provide residual sources of such larvae and/or stepping stones for such species.

This highlights the importance of continuing to provide for a degree of protection for the habitats of rare/scarce species between MPAs, i.e. at a landscape scale, as the 'permeability' of the marine landscape to larval dispersal cannot be taken for granted in the absence of such wider scale protection, particularly with regards to species with a more limited larval dispersal potential. This underlines the argument discussed previously that it is unsafe to assume that the connectivity of marine ecosystems means that linkages between populations of marine species are not an issue. Where the distance between MPAs is greater than the potential dispersal distance of rare/scarce species and the aim is to restore populations of such species that are locally depleted or even extinct within a given MPA, other means of providing linkages will have to be explored, such as translocations of mature individuals to provide a local source of propagules [43]. It also highlights, as stressed by Roberts et al [41], the importance of strictly protecting known populations of vulnerable species with very limited larval dispersal, as restoration of depleted populations through colonisation from long distances away is very unlikely, only connectivity within MPAs being likely.

The pragmatic 'rules of thumb' approach, focusing on parameters such as habitat representativity and maximum distance between MPAs, is understandable in order to avoid network design being stalled in the quest for unfeasibly rigorous approaches given the high degrees of complexity and uncertainty associated with larval dispersal analyses. It is also consistent with arguments that scientific uncertainty is not necessarily an obstacle to conservation initiatives, and that decisions and actions should be taken on an iterative, adaptive basis which recognises scientific uncertainty, rather than delaying actions in the quest for scientific certainty [44]. Meanwhile, it is important that initiatives are taken to improve our knowledge and understanding of marine ecosystems, and to this end the UK MPA Connectivity Partnership was formed in May 2008 to promote cooperation on related research amongst scientists and relevant government departments/agencies.

The Draft Marine Bill [9] proposes adopting such a pragmatic MPA selection approach based on 'best available evidence', but quite how such selections will stand up to challenges by potentially restricted users of a given candidate MPA area remains to be seen. The precautionary principle could be invoked to address such challenges, as it is recognised as an important justification for the designation of MPAs networks [45]. Whilst the documents antecedent to the Draft Marine Bill recognise the importance of the precautionary principle as part of the ecosystem approach [46], the words 'precautionary' or 'precaution' are noticeably completely absent from the Marine Bill, as is a target for the percentage area of UK seas to be protected through MPAs. Instead, it repeatedly stresses the importance of taking an evidence-based approach to decision-making [47]. This will clearly have a bearing on debates concerning the validity of 'rules of thumb' approaches to MPA network design in the face of challenges from potentially restricted users for a given designation proposal, based on any lack of actual site-specific selection evidence, beyond the application of what could be argued to be 'arbitrary rules of thumb', recognising that there are often alternative representative sites.

Conclusions

Against a background of growing calls for the designation of ecologically coherent networks of MPAs, this paper explores the implications of the larval dispersal potential of rare/scare benthic invertebrates for the design of a network of MPAs in the UK, that it is assumed should provide connectivity between sources and sinks for such species if the network is actually to be 'joined up'. The life history traits of 31 such species were investigated and it was found that 32% (10) had a high (>100km), 13% (4) a medium (1-100km) and 55% (17) a low (<1km) dispersal potential. Accepting a degree of sampling bias and that this sample is small and may not be representative, it is none-the-less indicative that a significant number of species have low dispersal potentials, particularly rare/scarce species. The view of interviewed experts is that 'rules of thumb', particularly habitat representativity, are more important in network design than the dispersal potential of certain species and related hydrodynamic assessments of source-sink dynamics. Given the complexity of and uncertainty over source-sink dynamics, it was considered that major challenges to designing MPA networks on this basis would remain for the foreseeable future.

The 'rule of thumb' of maximum distance between MPAs is also considered. It is argued that such distance 'rules of thumb' are somewhat arbitrary, and stressed that species with larval dispersal potentials of less than such distances would not be protected through such networks, therefore such networks could not be considered to completely coherent. This highlights the need for wider landscape-scale habitat protection measures, as it is unsafe to assume that the connectivity of marine ecosystems means that linkages between populations of marine species are not an issue. Where the distance between MPAs is greater than the potential dispersal distance of certain species, other means of providing linkages will have to be explored, such as translocations, as it is likely that connectivity will only occur within MPAs unless landscape scale connectivity can be assured.

On this basis it could be argued that ecologically coherent MPA networks might be more accurately described as representative networks, as it is difficult, if not impossible, to demonstrate that a given MPA network is ecologically coherent, given the complexity of marine ecosystems, related uncertainty and, on the basis of the knowledge that is available, the fact that such MPA networks cannot provide for the connectivity of populations of species with limited larval dispersal potential. If the establishment of ecologically coherent MPA networks is to be a policy aim, then thresholds of connectivity must be agreed on the basis of which it can be assessed whether a given MPA network fulfils this aim.

Ecological coherence can be considered as a continuum, the position along which can be determined by agreed heuristics that essentially represent 'rules of thumb', including the spatial distribution of the MPAs and the presence of no more than a few large gaps [6, 8]. It is, however, argued that this is too vague and arbitrary and represents a tautology, whereby fulfilment of the policy aim of ecological coherence is evaluated through constructed heuristics that are politically realistic, in that they could potentially provide for a rather sparse network to be judged to be coherent, but are ecologically unrealistic, in that they are of little relevance to the actual extent and degree of connectivity within a given network, particularly for species with a limited larval dispersal potential. Furthermore, if such heuristics only provide for a given network to be assigned a position along a continuum, from very likely to very unlikely to provide for ecological coherence [6,8], the question remains open as to when a given network's position along this continuum constitutes fulfilment of the policy aim. As such, it is concluded that the aim of establishing ecologically coherent networks of MPAs, such as that set by the OSPAR Commission, is not a relevant and practical policy aim that can be objectively evaluated. The aim of establishing representative networks, such as that set by the WSSD and adopted by the CBD, the properties of which include ecological connectivity but are not based on this [2], is more realistic and practical.

The pragmatic 'rules of thumb' approach is understandable in order to move forward with MPA network design in the face of complexity and uncertainty, whether in the context of ecologically coherent or representative MPA networks. The Draft Marine Bill is likely to adopt such a pragmatic approach but quite how such selections will stand up to challenges by potentially restricted users of a given candidate MPA area remains to be seen. The tensions within the Draft Marine Bill between using the best available evidence and taking an evidence-based approach will clearly have a bearing on related debates. The precautionary principle could be invoked to address such tensions, but whilst this principle featured in documents preparatory to the Marine Bill, the emphasis of the current Bill is on an evidence-based approach to decision-making. This will clearly have a bearing on debates concerning the validity of 'rules of thumb' approach to MPA network design in the face of challenges to such designations. Whilst the science behind the design and evaluation of ecologically coherent networks is developing, it is clear that even the best designed networks will not provide for the connectivity of species with low dispersal potential and that the translation of such science, which is likely to involve arguably arbitrary 'rules of thumb', into legally and politically defensible decisions will continue to pose major challenges that can realistically only be partly addressed by improvements in scientific knowledge.

Whilst it is recognised that the design and evaluation of representative MPA networks poses similar challenges, it is argued that this approach to network design is legally and politically more defensible as it is scientifically more realistic. The establishment of representative MPA networks may be a reachable objective, but ecologically coherent MPA networks may be a bridge too far.

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http://dx.doi.org/10.1016/j.marpol.2009.02.006

Nutritional mode	
Lecithotrophic (L)	Pertaining to development stages (e.g. larvae) that feed on a yolk reserve. Marine benthic invertebrates of this category tend to produce small quantities of large eggs which develop into clumsy larvae rather unfit for locomotion
Planktotrophic (H)	Pertaining to development stages that feed on plankton. Characteristic of invertebrates that brood a large number of small eggs. It is the most common form of development in marine benthic invertebrates.

Site of development	
Pelagic (H)	Pertaining to larvae that develop in the open sea.
Planktonic (H)	Pertaining to larvae that development in the water column
Neritic (M)	Pertaining to larvae that develop in the near-shore water column
Benthic/Demersal (L)	Larvae that develop on or in the substratum.
Aplanktonic (L)	Larvae that develop in the substratum (e.g. brooded in capsules)

Developmental Mode	
Indirect development (H)	Development that includes free-living larval stages or spores. Most common mode of dispersal in marine invertebrates and increased their likelihood of dispersal
Direct development (L)	Describes species with no intermediate stage of development; a juvenile emerges and typically crawls away from the parent with limited dispersal

Table 1. Marine invertebrate and fish larval dispersal development patterns and hypothesised relationships to connectivity: (H) high, (M) moderate or variable, or (L) low. After Dibacco et al. [23].

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Dispersal category	Number of species	No. literature sources used
High (>100km)	10 (32%)	5
Medium (1-100km)	4 (13 %)	1
Low (<1km)	17 (55 %)	9
Total	31 (100%)	15

Table 2 – Summary of dispersal categorisations for rare, scarce and protected species for which life history traits data were available.

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Species	Life history traits	Source
Polychaeta		
*Armandia cirrhosa**#	Armandia species recorded to have a pelagic planktonic stage of three weeks to several months.	A
Mollusca		
*Callista chione** Smooth venus	Larvae from several species in the family Veneridae observed by Thorson (1946) were found in the plankton. Larvae seen to be quite large in the plankton.	B
Pholadidea loscombiana+ Burrowing bivalve	Larvae from several species in the family Pholadidae observed by Thorson (1946) found in the plankton. Larvae grow to be quite large in the plankton.	B
*Jujubinus striatus** Sea snail	Species from the sub-family Gibbulidae, which share the same family Trochidae as *Jujubinus striatus*, are known to have a pelagic stage.	B
*Acanthocardia aculeata** Spiny cockle	Larvae from species of the family Cardidae observed by Thorson (1946) all appeared in the plankton in various stages of development suggesting a longer length of time in the plankton.	B
*Bittium simplex** Sea snail	*Bittium reticulatum* produce larvae which are found in all stages of development in the plankton. Large masses of 'Bittium' plankton are found.	B
Crustacea		
*Bathynectes longipes** Crab	Three species in the family Portunidae studied: six stages to pelagic development with a particularly long pelagic planktonic life.	B
*Clibanarius erythropus** Hermit crab	Larval development consists of four zoea stages and one megalopa stage. Megalopae of greater than 10 days old change their swimming behaviour and become less active staying close to the bottom.	C
Cnidaria		
*Amphianthus dohrnii** Sea anemone	*Amphianthus inornata* has planula larvae with the potential to be swept long distances by water currents	D
*Obelia bidentata** Hydroid	*Obelia longissima* has a medusoid stage lasting 7 -30 days. Obelia species, with their long-lived pelagic planula larvae, have significant dispersal potential by larval stages. Dispersal is potentially unlimited given the ability of hydroids to raft on floating objects as colonies or resting stages.	E, F

Table 3. Species with high (>100km) dispersal potential. Nationally *rare/+scarce/#protected. Sources: A. Carson and Hentchel [25]; B. Thorson [28]; C. Harms [29]; D. Bronsdon [30]; E. BIOTIC [24]; F. Stepanjants [31]

Species	Life history traits	Source
Crustacea		
Achaeus cranchii⁺ Crab	Two species from the family *Inachidae* produce planktonic larvae.	A
Cnidaria		
Edwardsia ivelli[*#] Ivel's sea anemone *Edwardsia timida*[+] Burrowing anemone *Scolanthus callimorphus** Worm anemone	Free-swimming lecithotrophic pelagic larvae seen in *Edwardsia beautempi* (family *Edwardsiidae*). Eggs are laid and fertilized in the water. In laboratory settings the larvae swim about for as much as a month before settling.	A

Table 4. Species with medium (1-100km) dispersal potential. Nationally [*]rare/[+]scarce/[#]protected. Source: A. Thorson [28]

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Species	Life history traits	Source
Polychaeta - *Ophelia bicornis**	Short pelagic stage.	A, B
Alkamaria romijni#	*Ampharetidae* species are known to have direct larval development; dispersal potential 10 -100m	C, D, E
Mollusca - *Doris sticta*+ Sea slug	Larvae of species of *Dorididae* are likely to have short if any planktonic development.	D
*Atagema gibba** Sea slug	Larvae of species of *Dorididae* are likely to have short if any planktonic development.	D
*Tenellia adspersa**# Lagoon sea slug	Switch from capsular metamorphic to pelagic lecithotrophic development has been seen in individuals that have been starved for up to 7 days. Dispersal potential 10 - 100m.	C, F
*Thyasira gouldi**# Northern hatchet shell	Fertilized eggs are 'pumped' out and being quite dense, sink down onto and stick to the sediment. Consequently eggs are rarely dispersed by water currents. Dispersal potential <10m.	C
*Paludinella littorina**# Sea snail	Direct developer which lays few eggs; may have poor powers of dispersal and where they disappear from a site the chances of re-colonization from neighbouring populations are low.	G
*Truncatella subcylindrica** Looping snail	Each egg capsule laid contains one egg and they are attached singly to pieces of detritus in the habitat in which the adults live. Dispersal potential <10m.	C
Crustacea *Gammarus insensibilis*# Lagoon sand shrimp	Direct developer.	C
Cnidaria - *Balanophyllia regia*+ Gold and scarlet star coral	*Balanophyllia elegans* possess demersal larvae which do not appear to swim. In laboratory tests larvae dispersed a mean distance of 0.5m before attaching.	H
Nematostella vectensis+ # Startlet anemone	Ciliated planulae larvae alternate between swimming and resting;; settle after 2-10 days.	C, I
Eunicella verrucosa# Pink sea fan	Larvae are most likely lecithotrophic with short life span. Colonies seem to take time to colonize wrecks that are distant < 1km from existing populations. Larval dispersal potential 100 - 1000m	C
Parerythropodium coralloides+ Soft coral	*Alyconium digitatum* in the family *Alcyonaria* spawns large yolk rich eggs rich. These float and develop active swimming planulae that settle after a few days to a week.	D
Anthopleura thallia+ Gaucus pimplet	*Bolocera tuediae* of the family *Thenaria* produce large, unwieldy larvae, rich in yolk with 25 day pelagic life. Swim very slowly in irregular directions and remain near the bottom.	D
*Phellia gausapata** Sea anemone	*Sarcatia troglodyte* & *Sagartia elegans* (family *Thenaria*) produce larvae with a short pelagic life (5-7 days) that seem to be able to feed on phytoplankton.	D
*Leptopsammia pruvoti** Sunset coral	Lecithotrophic larval setting time 1 day. Dispersal potential <10m.	C
Bryozoa *Victorella pavida** # Trembling sea mat	Lecithotrophic larval settling time < 1 day.	C

Table 5. Species with low (<1km) dispersal potential. Nationally *rare/+scarce/#protected. Sources; A. Wilson [32]; B. Dales [33]; C. BIOTIC [24]; D. Thorson [28]; E. Young [34]; F. Chester [35]; G. Killeen & Light [36], H. Gerrodette [37], I. Hand and Uhlinger [38].