

Dispersal and spatial dynamics in marine populations: Predicting MPA effectiveness through examination of local-scale recruitment patterns

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Abstract

The historical assumption of broad-scale dispersal and connectivity in marine species has recently been challenged by studies that have demonstrated localized recruitment in some taxa. Accordingly, the efficacy of spatial management tools such as marine reserves, once thought to be of limited value for many commercial species because of presumed cosmopolitan population structure, requires re-examination. The variability of dispersal patterns as a function of region and latitude suggest the need to develop predictive models of dispersal under different life history and environmental scenarios. Given this variability, it is not surprising that direct estimates of dispersal have been elusive; and indirect genetic approaches have therefore been commonly utilized. Here we contrast single and multitaxa approaches using both direct and indirect measures of dispersal. First, direct observations of spatial patterns during the life history stages of Atlantic cod allow us to predict dispersal distances through their life history. Second we use a genetic approach based on isolation by distance (IBD) to examine dispersal potential in 97 species of marine and anadromous fishes. Despite a prolonged planktonic period in Atlantic cod (months) we observe significant local recruitment to coastal embayments within 50-100 km of spawning location. Patterns of decreasing abundance with increased geographic distance are observed in planktonic eggs, larvae, and demersal juveniles, with the majority of individuals located < 30km from spawning site. Genetic IBD patterns suggest slightly broader dispersal on the scale of 100's of kms for most marine species with much reduced dispersal in anadromous species. Strong similarities are observed between predictions based on genetic patterns and those based on life history traits, suggesting that model species could serve as proxies for species with similar life history strategies. These measures provide a means by which to critically assess recruitment potential within reserve boundaries for multiple species with differing life history strategies, allowing for predictive estimates of reserve efficacy for entire marine communities.

Introduction

Marine protected areas (MPAs) can be an effective mechanism to conserve marine species and their critical habitat (Lubchenco et al. 2003). The continued failure of single-species management, as evident in the global state of many marine fisheries (Myers and Worm 2003), has led to increased interest in ecosystem approaches, including MPAs, by fisheries scientists and managers (Browman, and Stergiou 2004). Despite the exponential increase in scientific publications dedicated towards design and implementation of MPAs since the mid-80s (Conover et al. 2000), many fewer publications have attempted to evaluate MPA efficacy (Sale et al 2005).

Evaluation of marine reserve efficacy is most convincing using Before-After-Control-Impact (BACI) approaches (Sale et al. 2005). BACI designs use repeated sampling in and outside the designated area both before and after establishment of the reserve in order to quantify MPA performance. Evaluation criteria may include relative changes in density, biomass and growth of target species. This design is especially well-suited for MPA evaluation because it can take advantage of temporal replicates when spatial replication is either impossible or impractical (e.g., Randomized Intervention Analysis; Carpenter et al. 1989; Laurel et al. 2003). Unfortunately, such analyses require baseline data prior to management intervention. Because many, if not most, MPAs have been established based on political criteria (Halpern 2003) rather than strong biological data, new *post-hoc* analytical techniques must be developed for evaluating marine reserve efficacy.

For any reserve to be successful, it must be large enough to allow the species to persist within its boundaries (Fig 1i), irrespective of its population status outside the reserve. For this reason, the realized dispersal distribution of marine species (e.g. Fig 1i.) is considered to be the most important biological factor in reserve design (Botsford et al. 2003; Palumbi 2003). The dispersal range of a given species ultimately determines the degree of spill-over from the reserve (Fig. 1i),

whether the reserve will be self-seeding (Fig 1i, line C), or whether the reserve will need outside input of new recruits in order for the species to persist. There are no steadfast rules for minimum necessary reserve size for each species, although modeling studies indicate that species persist when the size of the reserve exceeds 1.5 times the organism's mean dispersal distance (Hastings and Botsford 2003). However, direct estimates of dispersal have been notoriously elusive and the sensitivity of dispersal patterns to environmental differences linked to regional and latitudinal influences suggest the need to develop predictive models of dispersal under varied conditions. Therefore, understanding the mechanisms of variable dispersal in marine organisms is a primary step towards evaluating the efficacy of marine reserves (Sale et al. 2005).

In an attempt to address this objective, we utilize direct and indirect approaches in order to contrast single and multi-species approaches in examining dispersal. Direct observations of spatial pattern through the different life history stages of Atlantic cod in the Northwest Atlantic allow us to predict dispersal distances for each life history stage. But data sets that permit this type of direct comparison are relatively rare. Indirect genetic approaches may provide a realistic estimate of dispersal patterns, though they may slightly overestimate dispersal potential (Bradbury unpublished data). Here, we use an indirect genetic approach based on isolation by distance (IBD, see Palumbi 2003) to examine dispersal potential in 97 species of marine and anadromous fishes.

Atlantic Cod in the Northwest Atlantic

Atlantic cod possess a combined pelagic egg and larval stage duration of approximately 70 – 100 days, depending on water temperature. Given this duration and coastal currents around Newfoundland, dispersal distances are predicted to be as much as 1000 km or more. In fact, potential dispersal distance during the pelagic egg stage may exceed several hundred kilometres (Bradbury et al. 2000). The highly mobile adult stage is characterized by offshore migrations that

may cover several hundreds of kms (e.g., Rose 1991). Similar scales of egg and larval drift have been described along the continental shelf (e.g., Pepin and Helbig 1997). Previous examinations of conservation strategies such as MPAs have suggested that the size required in order for the MPA to be effective was logistically intractable (Guenette et al. 2000). However, recent shifts in spatial pattern following the collapse of northern cod have redistributed the remaining spawning groups to coastal embayments. Because most of the remaining spawners are confined to relatively discrete, isolated patches, it is possible to use recruit density patterns within adjacent inshore nursery grounds as a measure of dispersal pattern. Within Placentia Bay, we observe a decrease in cod recruit density in inshore nursery grounds with increasing distance over a spatial scale of 10-100 km (Fig 1.ii) and with a mean dispersal distance of 25 km (Fig 1.ii). This data suggests that despite much wider dispersal potential, actual dispersal may be much more localized. Moreover, this pattern strongly supports the utility of small-scale (<100km) marine reserves in protecting these populations, which is in sharp contrast to recommendations based on pre-collapse distributions and inferred dispersal patterns.

Isolation by Distance and Dispersal Estimation

Genetic methods provide an alternative to direct field measurements of dispersal and often provide data that is sufficient to resolve migratory or dispersal phenotype and infer rates of gene flow and dispersal in environments where such interpretation would otherwise be impossible (e.g., Hellberg et al. 2002). Genetic differentiation may be regulated largely by gene flow or straying (Bohonak 1999), and magnitude of differentiation is often proportional to the degree of isolation (Slatkin 1994). Examination of the degree of isolation by distance in measurements of genetic markers provides insight into dispersal and migratory patterns that would otherwise be unattainable. In order to estimate dispersal, we applied the equation from Kinlan and Gaines (2003) for IBD slope and dispersal distance to 97 IBD relationships for marine fish collected from the literature (See references in Ward et al., 1994, DeWoody et al. 2000). Using this

approach we estimated mean dispersal distance at ~69 km for marine fish, compared to ~46 km for anadromous fish (Fig 1iv).

Summary

Here we demonstrate how *post-hoc* analytical techniques may be developed for evaluating marine reserve efficacy through the quantification of dispersal patterns. Direct techniques such as measuring abundance, chemical tagging, and the use of trace elemental composition of shells and otoliths provide the best picture of dispersal patterns. However, these techniques have been rarely utilized and rarely is this type of information available. In contrast, genetic isolation by distance data is readily available for many species and may be used in conjunction with modeling studies to estimate average dispersal patterns over many generations. These indirect estimates are undoubtedly less informative than direct approaches because genetic techniques are sensitive to small numbers of migrants and historical patterns, both of which may reduce the ability to resolve small-scale patterns (e.g., Thorrold et al. 2000). Thus, genetic approaches may not detect important population structure that is critical for effective management, and may overestimate actual dispersal on ecological time scales. It is worth noting that the measured dispersal distance in cod in Placentia Bay Newfoundland was of the same order of magnitude as the average IBD estimate for marine fish.

Given that scales of dispersal in marine fish may be localized and discrete, measures of specific dispersal patterns are essential in evaluating MPA efficacy. Measured dispersal distributions provide a realized estimate of the proportion of recruits of the total population settling within reserve boundaries or within the network of reserves. Because MPA efficacy is dynamic and strongly linked to various biological and environmental parameters, realistic measures of dispersal are critical if the influence of environmental or habitat characters on reserve success are to be decoupled and therefore predicted. Moreover, the range of life histories and dispersal

potential in a given MPA may be diverse. Reserve efficacy may be higher in some species than others if the MPA is designed to provide protection for species with a given dispersal pattern. Ultimately, the success of a reserve or network of reserves will depend on its careful evaluation and monitoring over time for species with a range of life history strategies, and the willingness to modify reserve boundaries and characters accordingly.

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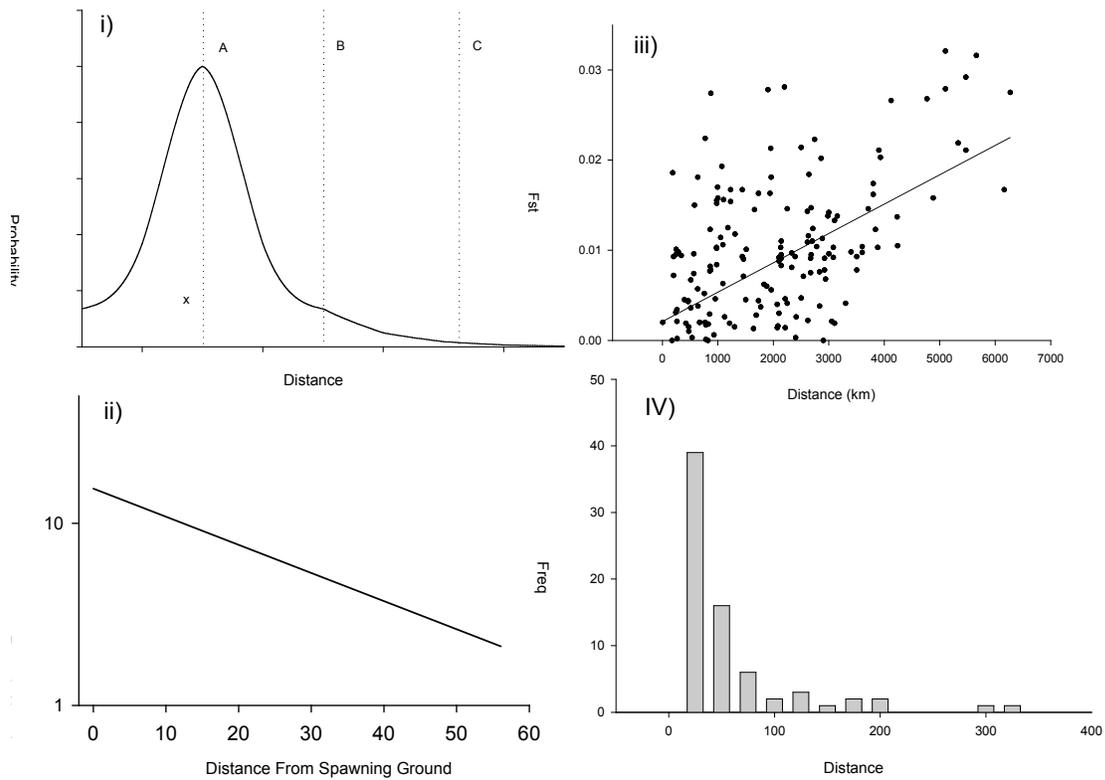


Figure 1. Dispersal in marine organisms. Panel I) represents a model dispersal distribution based on Botsford et al. (2001) and several reserve boundaries (a-c). II) Measured dispersal relationship for Atlantic cod from Bradbury et al. (2005), III) Genetic isolation by distance (IBD) relation for Deepwater Redfish from Roques et al. (2002). IV) estimated average dispersal distances for 97 species of marine fish based on genetic IBDs and mean measures of F_{st} from published sources (See Ward et. al. (1994) and Palumbi (2003)).