



Implications of Macroalgal Isolation by Distance for Networks of Marine Protected Areas

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Abstract: *The global extent of macroalgal forests is declining, greatly affecting marine biodiversity at broad scales through the effects macroalgae have on ecosystem processes, habitat provision, and food web support. Networks of marine protected areas comprise one potential tool that may safeguard gene flow among macroalgal populations in the face of increasing population fragmentation caused by pollution, habitat modification, climate change, algal harvesting, trophic cascades, and other anthropogenic stressors. Optimal design of protected area networks requires knowledge of effective dispersal distances for a range of macroalgae. We conducted a global meta-analysis based on data in the published literature to determine the generality of relation between genetic differentiation and geographic distance among macroalgal populations. We also examined whether spatial genetic variation differed significantly with respect to higher taxon, life history, and habitat characteristics. We found clear evidence of population isolation by distance across a multitude of macroalgal species. Genetic and geographic distance were positively correlated across 49 studies; a modal distance of 50–100 km maintained $F_{ST} < 0.2$. This relation was consistent for all algal divisions, life cycles, habitats, and molecular marker classes investigated. Incorporating knowledge of the spatial scales of gene flow into the design of marine protected area networks will help moderate anthropogenic increases in population isolation and inbreeding and contribute to the resilience of macroalgal forests.*

Keywords: gene flow, marine protected areas, marine reserves, population genetics

Implicaciones del Aislamiento por Distancia de Macroalgas para Redes de Áreas Marinas Protegidas

Resumen: *La extensión global de los bosques de macroalgas está declinando, afectando significativamente a la biodiversidad marina en escalas amplias a través de la influencia que las macroalgas tienen sobre los procesos ecosistémicos, provisión de hábitats y soporte de las redes alimentarias. Las redes de áreas marinas protegidas son una herramienta potencial que puede asegurar el flujo génico entre poblaciones de macroalgas frente a la creciente fragmentación poblacional causada por la contaminación, la modificación del hábitat, el cambio climático, la cosecha de algas, las cascadas tróficas y otros estresantes antropogénicos. El diseño óptimo de una red de áreas protegidas requiere del conocimiento efectivo de las distancias de dispersión para un área de macroalgas. Llevamos a cabo un meta-análisis global basado en datos publicados en la literatura para determinar la generalidad de la relación entre la diferenciación genética y la distancia geográfica entre poblaciones de macroalgas. También examinamos si la variación genética espacial difiere significativamente con respecto a taxones más altos, historia de vida y características de hábitat. Encontramos evidencia clara del aislamiento de las poblaciones por la distancia a lo largo de una multitud de especies de macroalgas. La distancia genética y geográfica estuvo correlacionada positivamente en 49 estudios: una distancia modal de 50–100 km mantuvo una $F_{ST} < 0.2$. Esta relación fue constante para todas las divisiones, ciclos de vida,*

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bábitats y marcadores moleculares de las algas investigadas. Al incorporar escalas espaciales de flujo génico al diseño de redes de áreas marinas protegidas, ayudaremos a moderar incrementos antropogénicos en el aislamiento de la población y a moderar la endogamia, contribuyendo a la resistencia de los bosques de macroalgas.

Palabras Clave: Áreas marinas protegidas, flujo de genes, genética de poblaciones, reservas marinas

Introduction

Networks of marine protected areas (MPAs) are being established worldwide in an effort to conserve species and ecosystems that may be negatively affected by fishing and other forms of anthropogenic stress (e.g., Hoegh-Guldberg 2004; Fernandes et al. 2005; Jones et al. 2007). The central aim of establishing most networks of protected areas is to conserve marine biodiversity and ecological processes, an outcome more easily achieved via conservation of critical and important habitats, rather than directing management responses at species individually. Habitat-forming macroalgae, such as laminarians and fucaleans, comprise an important functional group that benefits from MPAs, mostly through indirect effects whereby predatory fish and lobster populations increase with restrictions on fishing and thus grazing invertebrates are suppressed, which allows recovery of macroalgal forests (Babcock et al. 2010).

Macroalgal forests in turn support high faunal biodiversity in temperate marine waters (Mann 1973). They are foundation species (Dayton 1985) and as such stabilize habitats and facilitate colonization of a variety of marine organisms by providing sanctuary from predators and otherwise harsher environmental conditions. Residing within these forests are many economically and ecologically important species that utilize these habitats as nursery grounds (Tsukidate 1984; Coleman & Williams 2002). Indeed, macroalgal forests are disproportionately important for the conservation of marine biodiversity due to the variety of species they support (Dayton 1985; Poloczanska et al. 2007; Wernberg et al. 2010), and the decline of macroalgal forests in temperate waters worldwide has ecosystem-level implications (Steneck et al. 2002; Thibaut et al. 2005; Wernberg et al. 2012). Human induced stressors, such as the harvesting of kelp and predators of grazers, bottom trawling over low-relief reef, pollution, coastal development, and climate change are some of the causes of decline of macroalgal forest (e.g., Dayton & Tegner 1984; Steneck et al. 2002; Coleman et al. 2008) and the biodiversity they support.

Conservation initiatives are increasingly designed to protect areas so that they may confer greater persistence and resilience in the face of future environmental change. These initiatives rely on the premise that decreasing anthropogenic stressors via regulations (e.g., harvesting and pollution) in MPAs will result in net reduction in the sum of threats, and fewer negative responses to stressors

over which local management strategies have little control (e.g., climate change). Through such actions, MPAs may play a refugial role for marine organisms and help to maintain biodiversity and ecological processes in the face of a changing climate (IUCN World Commission on Protected Areas [IUCN-WPCA] 2008; McLeod et al. 2009).

One effect of climate change that is already noticeable is restructuring of marine communities as species begin to shift poleward with increasing ocean temperatures (Harley et al. 2006; Johnson et al. 2011). Temperate marine ecosystems, such as the macroalgal forests of Southeast Australia, are already being effected by range shifts of invasive species (e.g., the sea urchin [*Centrostephanus rodgersii*]) (Steneck et al. 2002). Such species are capable of decimating whole kelp communities, turning them to urchin barrens, and consequently removing the habitat that a variety of species rely upon for protection, many of which are economically important taxa (e.g., spiny rock lobster [*Jasus edwardsii*]) (Mislan & Babcock 2008). Protecting marine areas mitigates stressors such as recreational activities, pollution, and fishing, resulting in increased population persistence and resilience with climate change within MPAs (Micheli et al. 2012).

An important role of MPAs in an era of changing climate is to ensure long-term maintenance of connectivity among populations (Salm et al. 2006; Almany et al. 2009). Marine park planners should include provision for adequate and ongoing gene flow of key species in the face of increasing anthropogenic stress and habitat fragmentation. Thus, spacing and location of MPAs should reflect the dispersal capabilities of key species (e.g., Roberts et al. 2003; Shanks et al. 2003; Almany et al. 2009), such that connectivity and genetic diversity between reserves is maintained. Species dispersal capabilities have been used to help determine MPA spacing across a variety of species (Sala et al. 2002; Shanks et al. 2003; Palumbi 2004).

Dispersal capabilities of macroalgae are variable and difficult to assess directly due to microscopic propagules and multiple life history stages (Kusumo et al. 2006). Past research has suggested poor dispersal capabilities due to the small size of propagules and the short time they remain in the water column. Most macroalgal propagules apparently remain suspended in the water column for a few hours to a week, whereas marine animal larvae can survive weeks to months (e.g., fish) (Santelices 1990; Reed et al. 1992). Gene flow among macroalgal

populations can also potentially be influenced by a variety of factors such as life cycle (e.g., Loveless & Hamrick 1984; Palumbi 1994; Coleman & Brawley 2005) and habitat (Billot et al. 2003; Kelly & Palumbi 2010).

Most insights into macroalgal dispersal capabilities have been derived from population genetic studies. Quantitatively synthesizing these results through meta-analysis is an important first step toward incorporating macroalgal connectivity into the design or adaptive management of MPA networks.

The presence and nature of a significant relation between gene flow and geographic distance, isolation by distance (IBD), is useful in the context of MPA design because it focuses attention on the critical issue of protected areas spacing. This information can then be incorporated into marine reserve models to optimize and maintain MPA connectivity and in turn help inform policy managers (Sala et al. 2002; Fernandes et al. 2005). We conducted the first global meta-analysis of marine macroalgae to test for IBD. We also aimed to establish whether IBD was general across a variety of factors, including habitat, life cycle, higher taxonomic group, and genetic marker type used.

Methods

To assemble the data set of published studies, we performed a literature search using the Web of Science database (Reuters 2012) in February 2012. We searched for pairwise combinations of the keywords *genetic* and *connectivity* with *algae*. The reference lists of these papers were inspected for relevant studies that may have been overlooked in the original search.

We used a meta-analysis to investigate the influence of various traits and study variables on the presence and slope of IBD. Inclusion criteria for studies were that they reported a correlation coefficient between genetic and geographic distance (r) and a sample size (n). Our search resulted in a total of 24 papers. Because some papers included more than one species or discontinuous marine regions, some studies contributed more than one data point, resulting in an overall sample size of 30 data points. The groupings of variables investigated included life cycle (monoecious, dioecious, alternating generations), habitat (intertidal, subtidal), algal division (Rhodophyta, Phaeophyta, Chlorophyta), and the genetic marker type used (amplified fragment length polymorphism [AFLP], microsatellite, and random amplified polymorphic DNA [RAPD]). The latter can affect the outcome of population genetics studies (e.g., Whitlock & McCauley 1999; Burridge et al. 2004; Weersing & Toonen 2009). We first tested the significance of each grouping on the entire data set (life cycle, habitat, division, and genetic marker),

and then examined the relative strength of each variable within these groups (i.e., monoecious vs. dioecious vs. alternating generations, intertidal vs. subtidal, red vs. brown vs. green algae, and AFLP vs. microsatellite vs. RAPD).

The meta-analysis was undertaken using MetaWin (Rosenberg et al. 2000). A random effects model was used to calculate mean effect sizes (Hyatt et al. 2003), and bootstrap resampling procedures were used to determine confidence intervals (Rosenberg et al. 2000). A standardized effect size was calculated for each study from the correlation coefficient of IBD and sample size. The total heterogeneity within the data set, Q_{TOTAL} (Hedges & Olkin 1985), was also calculated. Significance values were corrected with sequential Bonferroni adjustments (Rice 1989).

Publication bias can arise when a meta-analysis comprises a large number of studies with significant results because researchers have a tendency to publish significant results over nonsignificant results (Dickersin 1990; Scargle 2000). This bias was tested for in our meta-analysis with a funnel plot, as well as a test of correlation between effect size and sample size (Spearman's rank correlation) (Begg 1994).

Because many studies did not present r and p values for tests of IBD and reported only significance, we also examined the presence of IBD with reported F_{ST} values (a measure of genetic differentiation) and the spatial scale of the study. Although this is not necessarily as robust as the meta-analysis (e.g., no accommodation of publication bias or effect size), it provides a coarse analysis for a greater number of studies. Although there are limitations when using F_{ST} as an index of genetic differentiation, it is a suitable choice in many situations (Jost 2008; Heller & Siegismund 2009). Using F_{ST} values, we calculated Rousset's distance measure for each study ($F_{ST}/(1-F_{ST})$) (Rousset 1997) and used this in the correlation. A $\log(x+1)$ of geographic distance was used in this correlation because multiplicative effects were considered more relevant than additive effects. A transformation of $\log(F_{ST}/(1-F_{ST}))+0.05$ was also used in the correlation. Inclusion criteria for studies were that they reported an overall F_{ST} value and were published before 2012. A total of 49 papers met these criteria and, because many assessed population structure within subsets of their study range (e.g., on distinct islands) as well as different species within the one study, our sample size for this analysis increased to 101 data points.

Results

IBD significantly explained macroalgae genetic connectivity across all studies ($Q_{\text{total}} = 585.97$, $df = 29$, $p < 0.05$; Table 1). Further, the correlation test between

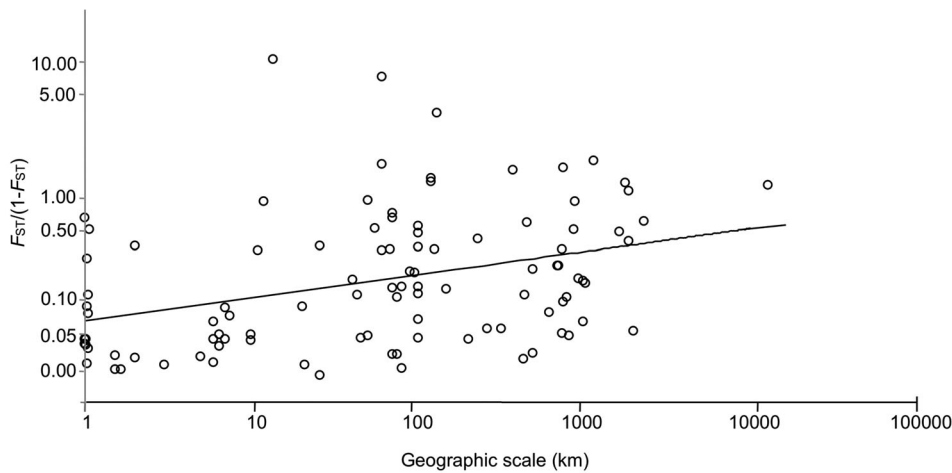


Figure 1. Relation between genetic distance, $\log[(F_{ST}/1-F_{ST})+0.05]$, and geographic distance, $[\log(x+1)]$ ($r^2 = 0.127$ $p < 0.01$) in populations of macroalgae.

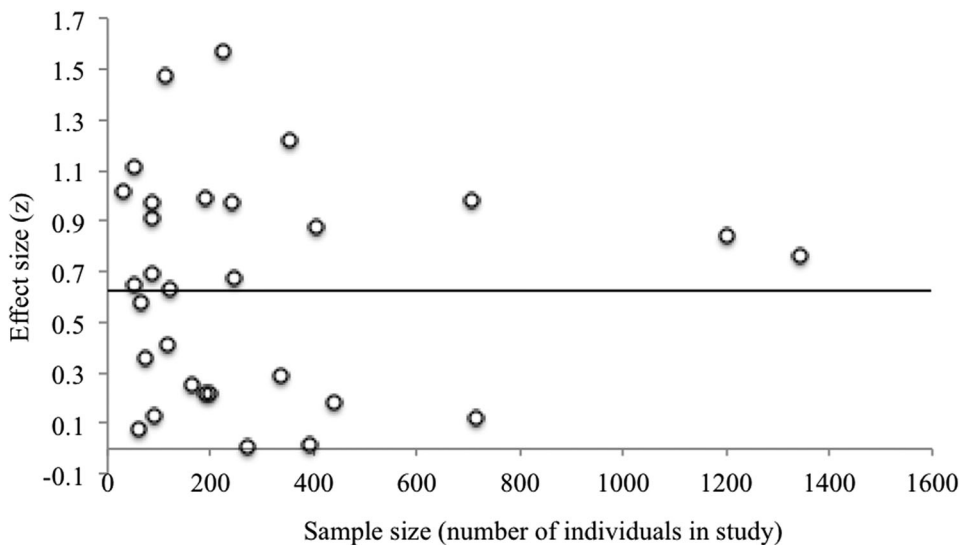


Figure 2. Relation between each study's effect size and sample size included in the meta-analysis, with testing for publication bias (Pearson's correlation test, $r_s = 0.012$, $p = 0.949$; mean effect size $[E = 0.6249]$, horizontal line).

genetic and geographic distance showed that a significant positive correlation was evident across the 49 studies ($r^2 = 0.127$, $p < 0.01$; Fig. 1). Moreover, IBD was general among macroalgae of different divisions, habitats, life cycles, and studies involving different genetic marker types ($p < 0.05$ in all cases; Table 1). A comparison of effect sizes within groupings revealed no significant influence of covariate on IBD prevalence between intertidal and subtidal algae species ($p = 0.436$), among different life cycles (monoecious, dioecious and alternating generations) ($p = 0.506$), among the genetic markers used across studies ($p = 0.358$, AFLP, microsatellite, RAPD), or among algal divisions ($p = 0.344$) (Table 1). This implies that the presence of IBD was independent of the habitat, higher taxa, genetic marker, and life-cycle divisions examined. A Spearman's rank correlation test showed no effect of publication bias ($r_s = 0.012$, $p = 0.949$, Fig. 2). An F_{ST} in the range of 0.1–0.2 was centered around a geographic scale of 50–100 km (Fig. 3).

Discussion

Genetic and geographic distance for macroalgae were positively correlated. This correlation was prevalent regardless of macroalgal division, habitat, life cycle, and molecular marker surveyed. Macroalgal propagules are generally broadcast spawned and are relatively immotile (limited endogenous capacity for movement); dispersal distances are determined primarily by ocean currents, wave action, and other physical vectors of dispersal (Reed et al. 1992; Gaylord et al. 2002; Gaylord et al. 2004). Reproduction is also often tightly cued to environmental conditions including calm periods, low tide, or slack tides, which increases fertilization success (Pearson & Serrao 2006) but may reduce variance in dispersal distances. These characteristics, which are seen in many macroalgal species, may explain why we found evidence of IBD across a multitude of studies and species in our meta-analysis.

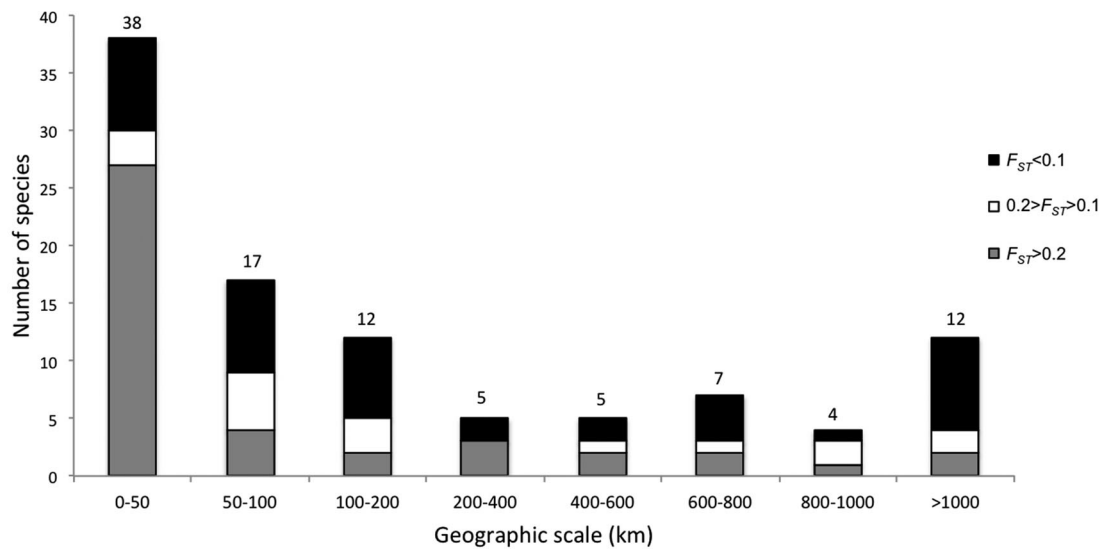


Figure 3. Total number of macroalgae species from all studies grouped into three F_{ST} categories ($F_{ST} > 0.2$, $0.2 > F_{ST} > 0.1$, $F_{ST} < 0.1$), corresponding to their relative geographic distance category to determine the number of studies that showed sufficient gene flow ($0.2 > F_{ST} > 0.1$).

Table 1. Heterogeneity of each group of life-history variables (column 1) and of each individual life-history variable within groups (column 4) in a meta-analysis of macroalgal population isolation by distance ($n = 30$ studies).

Group	Q_{TOTAL}	p	Variable ^a	Q_{total}	p
Habitat	27.526	0.436	Subtidal	476.43	<0.01
			Intertidal	327.75	<0.01
Reproduction	26.23	0.506	Monoecious	58.58	<0.01
			Dioecious	357.79	<0.01
			Alternating	292.54	<0.01
Marker	29.050	0.358	AFLP	79.23	<0.01
			MSAT	950.98	<0.01
			RAPD	108.86	<0.01
			Red	69.95	<0.01
Division	29.36	0.344	Green	41.62	<0.01
			Brown	915.18	<0.01
			All	585.97	<0.01
Total data set					

^aAbbreviations: AFLP, amplified fragment length polymorphism; MSAT, microsatellite; RAPD, random amplified polymorphic DNA.

IBD should be considered in assessing spacing of MPAs. For example, the slope of the IBD correlation can be used to determine the maximum distance for MPA spacing such that F_{ST} will not exceed a certain magnitude, for example, the level that corresponds to approximately one migrant per generation ($F_{ST} = 0.2$) or any other predetermined level of genetic differentiation. A network of MPAs with individual protected areas arranged in such a manner to maintain F_{ST} below 0.2 should result in relatively little population differentiation (Slatkin 1987; Wang 2004). The majority of studies we surveyed exhibited $F_{ST} > 0.2$ at spatial scales of less than 50 km (Fig. 3).

Many studies have used similar distance values to those suggested here (50 km) in MPA planning reports and particle modeling (e.g., Roberts et al. 2001; Almany et al. 2009; California Department of Fish and Game [CDFG] 2009). Studies such as these are theoretically based, with some incorporation of information on larval dispersal distances. We derived similar results based on a synthesis of empirical genetic studies of dispersal distances and population connectivity. This is the first time empirical data for macroalgae have been collated and statistically reviewed in the context of MPA design, an important consideration given the fundamental role that habitat-forming algae play in marine community biodiversity. Similar genetic data exist for a wide range of marine species (e.g., Ridgway et al. 2008; Curley & Gillings 2009; Schultz et al. 2011) and could likewise be incorporated into future planning to achieve more informed decisions that consider connectivity. Recently, the importance of empirical studies in MPA management has been emphasized (Botsford et al. 2009).

Meta-analytical approaches have been criticized, including in the MPA literature (Huntington 2011), for failing to account for publication bias, which occurs when primarily positive results are published, providing a biased sample. No significant effect of publication bias was detected in our meta-analysis. However, studies frequently neglected to report r and p values and instead provided a simple statement about whether the IBD was present or absent, a serious failure in statistical reporting (Gerrodette 2011).

The strength of conclusions about source-sink dynamics within MPA networks will be greatly enhanced when different sources of information are cross-validated. In

addition to studies of genetic distance, the field of meta-population dynamics has advanced rapidly in recent years through genetic marker studies and greatly improved particle dispersal models. A recent study using genetic parentage analysis for 2 fish species in the Great Barrier Reef Marine Park, for example, indicated broad-scale reseeding of adjacent areas from parents living within no-fishing zones (Harrison et al. 2012).

Oceanic particle dispersal modeling provides a further avenue for estimating probabilities of macroalgal gene flow among MPAs and identifying likely source and sink populations (Roberts 1997; Treml et al. 2008; Munday et al. 2009). Through modeling approaches, temporal heterogeneity in dispersal can also be appreciated through hindcasting (Espíndola et al. 2012). Ocean models are, however, rarely accurate in shallow nearshore waters (Roberts 1997; Bode et al. 2006) and should be validated with biological data. In combination, genetic distance information, genetic marker information, and oceanic models incorporating seasonal variability and climate change allow key areas for future MPA protection to be identified, ultimately permitting increased species persistence through time (Munday et al. 2009).

Our finding of an overall pattern of IBD in macroalgae suggests that the spatial distribution of MPAs and unprotected populations is likely to be critical in determining the level of connectivity of macroalgae populations within MPA networks. Given increasing anthropogenic stressors, networks of MPAs should be designed with the intention to maintain dispersal among a network of similar areas and, in addition, serve as sources of genetic material for areas not afforded protection. We found a high proportion of macroalgae displayed $F_{ST} > 0.2$ even at a scale of 0–50 km, indicating that MPAs spaced >50 km apart may be susceptible to genetic isolation. This finding is consistent with modeling studies (e.g., Roberts et al. 2001; Almany et al. 2009; Moffitt et al. 2011). Data obtained from collating IBD values across a range of species can be incorporated in MPA models and help improve the decision making process for MPA managers. This will contribute to the formation of representative and adequately spaced marine reserve networks.

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Supporting Information

A summary of studies used in the meta-analysis (Appendix S1) and correlation between genetic and geographic distance (Appendix S2) are available online. The authors are

solely responsible for the content and functionality of these materials. Queries, other than the absence of materials, should be addressed to the corresponding author.

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