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INVITED REVIEWS AND SYNTHESES

A synthesis of genetic connectivity in deep-sea fauna and implications for marine reserve design

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Abstract

With anthropogenic impacts rapidly advancing into deeper waters, there is growing interest in establishing deep-sea marine protected areas (MPAs) or reserves. Reserve design depends on estimates of connectivity and scales of dispersal for the taxa of interest. Deep-sea taxa are hypothesized to disperse greater distances than shallow-water taxa, which implies that reserves would need to be larger in size and networks could be more widely spaced; however, this paradigm has not been tested. We compiled population genetic studies of deep-sea fauna and estimated dispersal distances for 51 studies using a method based on isolation-by-distance slopes. Estimates of dispersal distance ranged from 0.24 km to 2028 km with a geometric mean of 33.2 km and differed in relation to taxonomic and life-history factors as well as several study parameters. Dispersal distances were generally greater for fishes than invertebrates with the Mollusca being the least dispersive sampled phylum. Species that are pelagic as adults were more dispersive than those with sessile or sedentary lifestyles. Benthic species from soft-substrate habitats were generally less dispersive than species from hard substrate, demersal or pelagic habitats. As expected, species with pelagic and/or feeding (planktotrophic) larvae were more dispersive than other larval types. Many of these comparisons were confounded by taxonomic or other life-history differences (e.g. fishes being more dispersive than invertebrates) making any simple interpretation difficult. Our results provide the first rough estimate of the range of dispersal distances in the deep sea and allow comparisons to shallow-water assemblages. Overall, dispersal distances were greater for deeper taxa, although the differences were not large (0.3–0.6 orders of magnitude between means), and imbalanced sampling of shallow and deep taxa complicates any simple interpretation. Our analyses suggest the scales of dispersal and connectivity for reserve design in the deep sea might be comparable to or slightly larger than those in shallow water. Deep-sea reserve design will need to consider the enormous variety of taxa, life histories, hydrodynamics, spatial configuration of habitats and patterns of species distributions. The many caveats of our analyses provide a strong impetus for substantial future efforts to assess connectivity of deep-sea species from a variety of habitats, taxonomic groups and depth zones.

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Introduction

The deep sea (>200 m) is Earth's largest ecosystem, comprising 90% of the habitable volume and 63% of the surface area, yet is the most understudied environment on the planet. Deep-sea ecosystems are particularly poorly represented in biodiversity surveys due in part to the monetary cost and technological infrastructure required to obtain good sample coverage. In addition, the paucity of taxonomic information for deep-sea fauna hinders accurate species identification, which limits inferences about geographic distributions, ecology, evolutionary history and connectivity. Based largely on morphological data, deep-sea species are thought to have larger geographic ranges than shallow-water species (e.g. Sibuet 1979; Etter & Rex 1990; Allen & Sanders 1996; Young *et al.* 1997; Carney 2005). This idea, combined with the misconception that the deep sea is a largely homogeneous environment with few obvious barriers to dispersal, has led to the long-standing notion that deep-sea organisms probably disperse over larger distances than shallow-water species (e.g. reviewed in Rex & Etter 2010).

As anthropogenic impacts on the world's oceans increase, this paradigm becomes increasingly critical to test. With resources in shallow water becoming depleted, exploitation is steadily moving into deeper waters. For example, trawl fisheries, which have major effects on biogenic seafloor structure (e.g. Watling & Norse 1998), as well as targeted and bycatch species (e.g. Dayton *et al.* 1995; Myers & Worm 2003) now extend to depths of at least 3000 m (Ramirez-Llodra *et al.* 2011; Watson & Morato 2013). Exploration leases have been granted for mining of seafloor manganese nodules at abyssal depths in the Pacific and Indian oceans, as well as for mining of cobalt-rich manganese crusts on seamounts and polymetallic sulphide mining near hydrothermal vents (ISA 2014, Mengerink *et al.* 2014). Global phenomena such as climate change and ocean acidification are also threats to the deep-sea ecosystem as a whole (e.g. Guinotte *et al.* 2006; Mora *et al.* 2013).

Because of these increasing impacts, international efforts have begun to focus on the protection of deep-sea fauna and habitats (e.g. Mengerink *et al.* 2014) through the designation of vulnerable marine ecosystems or VMEs (e.g. FAO 2009, Parker *et al.* 2009), development of regulations to define these sensitive ecosystems and introduction of strategies such as 'move-on' rules to minimize impacts when they are encountered (reviewed in Ardron *et al.* 2013). There are also significant efforts underway to establish high-seas marine reserves with a goal of protecting deep-sea habitats, which largely lie in international waters (O'Leary *et al.* 2012; Wedding *et al.* 2013;).

Marine reserves play increasingly important roles in protecting vulnerable habitats in shallow water. In designing reserves, a number of factors are considered including habitat representation and replication, patterns of species richness and endemism, risk spreading, protection of unique areas, and reserve location, size and spacing (reviewed in Green *et al.* 2014). One of the primary considerations for size and spacing and many of the other design factors is connectivity. Connectivity in turn is determined by many components, perhaps the largest of which is the dispersal of the organisms in question.

Dispersal is a key phase in the life cycle of many marine organisms and influences a wide variety of demographic, ecological and evolutionary processes with far-reaching implications for conservation and management of marine resources. The scale, intensity, direction and frequency of dispersal among populations determine connectivity. Quantifying the scale over which populations are connected is a key to understanding the relative importance of various ecological processes, to identifying the appropriate scales of environmental influence in driving population dynamics and to determining how local communities might respond to environmental change (Kinlan *et al.* 2005; Gaines *et al.* 2007). Because of the vital importance of understanding connectivity, considerable effort has focused on quantifying dispersal in shallow water. However, very little is known about dispersal distances or connectivity in the deep ocean.

A number of methods have been developed to estimate dispersal and connectivity among populations in marine ecosystems including biophysical transport models, trace-element signatures and various genetic techniques (reviewed in Levin 2006; Thorrold *et al.* 2007; Cowen & Sponaugle 2009; Lowe & Allendorf 2010; Leis *et al.* 2011; Simmonds *et al.* 2014). Numerical models of physical transport processes simulate larval dispersal and have been widely used to estimate connectivity of near-shore organisms (e.g. Cowen *et al.* 2006; Siegel *et al.* 2008; Xue *et al.* 2008; Watson *et al.* 2010; Kendall *et al.* 2013), but few studies have explored

this approach in deep water (e.g. Yearsley & Sigwart 2011; Young *et al.* 2012; Mullineaux *et al.* 2013; Hilário *et al.* 2015). Elemental fingerprints of calcified structures have also been used extensively to estimate dispersal in shallow water (e.g. Swearer *et al.* 1999; Thorrold *et al.* 2001; Becker *et al.* 2007; Carson *et al.* 2010, 2013; Fodrie *et al.* 2011; Lopez-Duarte *et al.* 2012), but thus far they have not been applied in the deep sea. Genetic approaches have long been used to estimate dispersal and should provide the best estimates in the deep sea because geographic patterns of genetic variation are readily available for many deep-sea taxa and the theoretical underpinnings for inferring dispersal from phylogeographic data are well developed (Rousset 1997; Kinlan & Gaines 2003; Palumbi 2003; Pinsky *et al.* 2010; Wright *et al.* 2015).

Genetic approaches for estimating dispersal are based on the relationship between population differentiation (usually measured as F_{ST} or one of its relatives) and geographic distance between sampled populations as determined in an isolation-by-distance (IBD) framework. The slope of the relationship between F_{ST} and distance, the IBD slope, is used to estimate dispersal distance (Rousset 1997; Kinlan & Gaines 2003; Palumbi 2003; Pinsky *et al.* 2010; Wright *et al.* 2015). Although caveats exist around the use of IBD for estimating dispersal (Bradbury & Bentzen 2007; Jenkins *et al.* 2010, Meirmans 2012), it nevertheless is an important tool that can be used to obtain empirical estimates of average dispersal distances, when applied carefully in a meta-analytic context on large data sets (Kinlan & Gaines 2003). Until data from other methods become more widely available for deep-sea fauna, genetic estimates of dispersal offer the best possibility for a synthetic understanding of dispersal distances in the deep sea.

Here, we estimate dispersal distances of deep-sea taxa following the approach applied in shallow water to address two goals. One is to provide a first-order estimate of the range of dispersal distances in the deep sea, to lay the groundwork for deep-sea reserve design. Dispersal distances may be influenced by many factors related to various aspects of life-history strategies (e.g. adult mobility, developmental mode, larval mobility), which in turn can be related to the ecology and phylogenetic history of the species. Any of these could be confounding factors in our analyses. Thus, we address the relationship of these factors to assess how they might affect dispersal distances of deep-sea species. The second goal of our study is to compare the range of dispersal distances in the deep sea to recent reviews of dispersal distances in shallow water (Kinlan & Gaines 2003; Selkoe & Toonen 2011), to test the paradigm that deep-sea species are capable of larger dispersal distances.

Methods

Literature survey

We used the search terms 'deep sea' and 'population genetic' in Google Scholar to identify papers for analysis. Additional papers were added from the literature collections of the authors and from the reference sections of the papers obtained through the search. We included all papers available for deep-sea taxa at the time of compilation (August 2013), regardless of life-history strategy, marker type, habitat or benthic vs. pelagic. Species were considered deep-sea taxa if their depth range began or extended below 200 m.

We excluded studies for which data were available from fewer than three study sites. We also excluded studies for which no information was provided on geographic locations of sampling unless a map was provided that allowed us to estimate distances among samples, or where authors replied to requests for geographic coordinates when no map was available. Many early studies provided data on total allele frequencies by locus and population, but we could not determine a reasonable way to calculate F_{ST} from these studies, and therefore, they were also excluded. Studies using RAPDs were also excluded given the difficulty in interpreting them in population studies (Sunnucks 2000). Based on an examination of caveats to the IBD method in P. Beerli, B. P. Kinlan, R. J. Etter, P. A. Ribeiro, S. von der Heyden, A. R. Baco (in prep), we also chose to exclude studies that had data only as hierarchical AMOVA or 'Global F_{ST}' values.

Of the 267 papers obtained from the original search, 51 papers representing 42 species (Table 1) had data that were useable for our study and resulted in a positive IBD slope (see *IBD slope* and *Methods Concerns and Caveats* sections below for explanation).

IBD slope

The isolation-by-distance (IBD) slope can be estimated as the slope of the regression line of pairwise population differentiation (measured as F_{ST} or one of its relatives) and geographic distance between sampled populations (Wright 1943). Few of the available studies calculated IBD slopes, and among those that did, the slope equations were often not reported. Thus, we used the pairwise F_{ST} values provided in the paper along with pairwise geographic distance to calculate the IBD slope using the online version of GENEPOP 4.2 (http://genepop.curtin.edu.au/; Raymond & Rousset 1995; Rousset 2008). Option 6 of GENEPOP was used to obtain the IBD regression slope value (using the subroutine ISOLDE) as well as the option '*P*-value' for the Mantel test for each study.

Table 1 Summary of results of the literature review. Number of papers by marker type is calculated as number of papers using only that marker type, with papers using multiple markers included as 'multiple types of markers'. Mean study scale was calculated as mean of mid-point of range of each study

	Total	Vents	Inverts	Fishes
Initial collections of papers*	267	34	70	163
No. with frequency data only or no geographic information, or AMOVA or global F_{ST} only*	210	18	57	135
No. useable but with negative slopes*	6	0	0	6
Final no. of papers used in this study, with usable data or data obtained from authors and non-negative IBD slope*	51	16	13	22
No. species**	42	15	11	16
No. allozymes	7	4	2	1
No. microsatellites	15	2	3	10
No. mtDNA	14	2	6	6
No. other type of nuclear marker	4	2	0	2
No. multiple types of markers	11	6	2	3
Mean geographic study scale (km)	1912	1907	1796	2041

*Calculated as number of papers, regardless of number of species in the paper.
**Calculated as number of species, regardless of if there was more than one paper on the same species.

Kinlan & Gaines (2003) pointed out the need for a conversion of haploid mitochondrial F_{ST} values to accurately compare with data from diploid nuclear markers. Thus, all F_{ST} values derived from mitochondrial data were converted prior to calculation of IBD slopes using the following equation, updated by BPK to correct a typographical error in Kinlan & Gaines (2003):

$$F_{\mathrm{STdiploid}} = F_{\mathrm{STmt}}/(4 - 3F_{\mathrm{STmt}}). \quad \text{(eqn 1)}$$

For studies providing geographic coordinates of sampling locations but not geographic distances, pairwise geographic distances were calculated as great circle distances using the spherical law of cosines in Microsoft Excel. For studies that only provided a map, the iMap program (http://www.biovolution.com/imap/) was used to derive great circle distances between sampling locations. For simplicity, in all cases, a straight-line distance was calculated regardless of landmasses or substrate availability at the appropriate depth.

After calculating dispersal estimates, we removed all studies that resulted in a negative IBD slope. We retained all studies that had a positive slope value even if the *P*-value from the Mantel test was not significant. This formed the basis of what we will hereafter call the 'All' data set (dispersal estimates for all studies, markers and geographic scales for which a positive IBD slope was found). In our analyses, we also distinguished those studies with nonsignificant *P*-values from studies with statistically significant *P*-values; the latter is referred to as the 'SigMantel' data set. To balance considerations of type I and type II errors, we considered any slope with a Mantel test *P*-value ≤ 0.10 to be significant. Type II error (low power) could create a bias against long dispersal distances, because long dispersal distances lead to small IBD slopes that are more difficult to detect. There is no reason to expect that type I error would cause a similar bias; thus, we reasoned that an alpha level of 0.10 was likely to have a net effect of reducing biases due to low power. All other statistical analyses used the conventional $P < 0.05$ for significance.

Derivation of dispersal distance from IBD slope

We used the method of Palumbi (2003) as implemented in Kinlan & Gaines (2003), hereafter referred to as the PKG method, to estimate dispersal distance using the following equation, fit to simulation results

$$\text{PKG dispersal distance} = 0.0016(\text{IBD Slope})^{-1.0001}. \quad \text{(eqn 2)}$$

This method, as described in the original references, makes a variety of assumptions including an effective population size (N_e) of 1000 individuals. The IBD slope is based on raw F_{ST} values vs. raw geographic distance in kilometres.

An alternative approach to estimating dispersal distance from IBD slope is that of Rousset (1997). P. Beerli, B. P. Kinlan, R. J. Etter, P. A. Ribeiro, S. von der Heyden, A. R. Baco (in prep) conducted an in-depth comparison of the PKG method to the Rousset method and concluded that the PKG estimates of the range of dispersal distances are likely closer to the truth than any estimate that assumes a constant density and found a strong log-linear relationship ($R^2 = 0.978$, $P < 0.0001$) between PKG and Rousset estimates so the results should be qualitatively similar. The PKG method also provides data that can be compared to existing syntheses of shallow-water dispersal distances. Thus, the Rousset (1997) method is not incorporated into our synthesis.

Method concerns and caveats

Error distributions, outliers and definition of filtered data sets. The mathematics relating IBD to dispersal distance (Rousset 1997), and the variability and stochasticity of

the dispersal process itself (Siegel *et al.* 2008), lead to a log-normal error distribution wherein the variance increases with the mean. Thus, log-transformation is essential to properly analysing and interpreting dispersal distance data, particularly when data span many orders of magnitude. Averages and other linear statistics applied to the untransformed, arithmetic-scale values of dispersal will result in bias – often extreme bias – towards large dispersal distances. As one of the goals of our study is to bracket the ranges of dispersal distances for a variety of deep-sea taxa, we must take particular care to mitigate the effects of bias and outliers on the tails of distributions.

We thus adopt several statistical strategies to account for and limit the impact of error in IBD dispersal estimates on our conclusions. Log_{10}-transformation was used to normalize distributions and homogenize variance prior to all statistical analyses *and* all summary statistic calculations. Means, confidence intervals and other quantities reported on the kilometre scale have all been back-transformed from the log_{10} scale. Two important implications of this are as follows: (i) all means reported are geometric means unless stated otherwise, and (ii) confidence intervals are asymmetrical on the arithmetic scale, with the upper confidence interval wider than the lower interval. We report all major results on the log_{10} scale (orders of magnitude) or as geometric means (i.e. back-transformed means calculated on the log scale), and all error estimates in orders of magnitude (log_{10} scale), as multiplicative factors (e.g. a difference of 0.7 orders of magnitude is equal to a factor of about 5×), or as asymmetrical back-transformed intervals. We do report minima and maxima of estimates in tables, statistics that are highly sensitive to uncertainty, but also examine the 10–90th percentile ranges, which are less sensitive to the influence of outliers and error and provide a more conservative estimate of the range.

We analysed two data sets: the 'All' data set described above, and a subset of the 'All' data set that eliminates cases with nonsignificant Mantel *P*-values ('SigMantel' data set). Analysis of both data sets together provides a better perspective on patterns in the data than analysis of either data set alone. On the one hand, nonsignificant IBD slopes in the All data set could lead to over- or underestimates of dispersal distance and increased error variance. Yet, elimination of nonsignificant IBD slopes creates a bias against inclusion of the longest dispersal distances, due to the low statistical power – coupled with the massive geographic scale, high numbers of samples and validity of the drift-migration equilibrium assumption – required to detect those long average dispersal distances. By analysing both data sets, we can obtain estimates of the range of deep-sea dispersal scales ranging from the smallest, most conservative estimate (from the SigMantel data set) to a larger estimate less affected by bias against longer dispersal distances, but likely at the cost of increased error. Moreover, we can utilize the greater statistical power afforded by the larger sample size of the All data set to examine patterns in dispersal distance with respect to a variety of taxonomic, life-history and study factors, but temper our conclusions by examination of the same patterns in the SigMantel data set.

Life history and study data compilation

For each of the 51 papers included in our final synthesis, we extracted taxonomic data, information on as many habitat and life-history parameters as possible, marker type and the genetic structure statistic (GSS) used (F_{ST}, G_{ST}, R_{ST}, etc.), which are included in the data summary Table S1 (Supporting information). These were used as factors for comparing dispersal estimates. The specific factors with sufficient data across all studies were as follows:

The factor 'Taxon' had three categories – fishes, invertebrates from chemosynthetic ecosystems (hereafter referred to as CE inverts) and invertebrates from nonchemosynthetic ecosystems (hereafter referred to as NCE inverts). This factor was used because the vast majority of available studies were either of fish, which are likely to be more mobile than invertebrates and therefore to have different dispersal estimates, or of species found at hydrothermal vents, highly specialized habitats that may have constraints on dispersal compared to the general deep sea (Audzijonyte & Vrijenhoek 2010; Vrijenhoek 2010).

The factor 'Phylum' was simply the Phylum of the organisms on which the study was based.

The factor 'Marker' was the type of marker used for the study, that is allozymes, mitochondrial DNA (mtDNA), microsatellites, AFLPs, SNPs and other nuclear markers. This was included because previous studies comparing genetic estimates of dispersal to estimates based on pelagic larval duration found that mtDNA provided higher F_{ST} values than allozymes or microsatellites (Weersing & Toonen 2009).

The factor 'Adult Habitat' included four categories 'Benthic Hard' was used for species associated with hard substrate habitats, regardless of whether they were chemosynthetic. 'Benthic Soft' was defined as soft-substrate habitats regardless of chemosynthetic influence. 'Demersal' was used for species associated with the seafloor, although they may not be directly attached or burrowing. Finally, 'Pelagic' was used for species that were associated with the water column.

The factor 'Adult Mobility' included three categories. 'Sessile' was used for taxa that were attached, 'Sedentary' was used for taxa that are not attached but are

largely sedentary (e.g. anemones, crinoids, bivalves). 'Swimmer' was used for highly mobile species.

The factor 'Adult Depth Zone' was based on the midpoint of the adult depth range for each species and, due to the distribution of the data points, was only divided into two broad depth zones: <2000 m and 2000–4000 m.

Based on the small number of species with direct developing larvae in our data set, for larval types, we used a 'Larval Feeding Type' factor consisting of 'Feeding' (planktotrophic larval types) and 'Nonfeeding' (direct developing and lecithotrophic larval types). Designation was based on the classification of larval type given in the paper or another paper on the same or closely related species.

'Larval Dispersal' was split as 'Benthic' for larvae that crawled along the substrate, 'Pelagic' for larvae that spent most of their time in the water column, and 'Demersal' for larvae which dispersed near the seafloor.

The factor 'Ocean Region' was based on the region of the study rather than the full range of the species.

The factor 'Genetic Structure Statistic' (GSS) indicates the statistic used, and also, in the case of $F_{ST,}$ whether the method was of Hudson (1992) or Weir & Cockerham (1984). A comparison of the Hudson (1992) and Weir & Cockerham (1984) methods for deriving F_{ST} indicated no difference ($P = 0.18$), and so they were combined as F_{ST} in further analyses. Comparisons to additional metrics are outlined below.

Statistical analyses of final data set

All statistical analyses were carried out in JMP 11.0.0 (SAS Institute, Cary, NC, USA). To test for differences in dispersal distance estimates among various divisions of the data (see *Life History and Study Data Compilation*), one-way analyses of variance (ANOVAS) were used. ANOVAS were conducted using the SigMantel data set and then separately for the All data set. Homogeneity of variances was tested using Levene's test. All statistical analyses and summary statistics were calculated on $\log_{10}$-transformed data. Log-transforms are appropriate both for theoretical reasons – important underlying relationships are linearized by a log-transform (Rousset 1997 and Table S1, Supporting information) – and for statistical reasons, that is to account for the extreme heterogeneity in variances of dispersal estimates on the untransformed scale. A Tukey–Kramer HSD test was used to make pairwise comparisons among different categories within each factor. Results using the PKG equation were selected for these analyses because this allowed us to make direct comparisons to the existing shallow-water data (Kinlan & Gaines 2003). The response variable in our analyses is the $\log_{10}$-transformed dispersal distance in kilometres estimated using the PKG method.

Our analyses revealed differences in dispersal distances among the deep-sea taxa related to many of the life-history parameters as well as depth and GSS. However, a close examination of Figs S1–S10 (Supporting information) suggests much of this difference may be driven by taxonomic biases, in particular the greater dispersal distances of the fishes relative to the nonchemosynthetic invertebrates. For most of the significant ANOVAS, fishes dominated the data points in the class that had significantly larger dispersal estimates. Thus, we repeated all of the ANOVAS using just the NCE Inverts portion of the All and SigMantel data sets and again with just CE and NCE Inverts in both data sets.

Statistical analyses of shallow vs. deep

To test whether deep-sea species have broader dispersal ranges than shallow-water taxa, we also compared our results from the PKG method to the combined results of Kinlan & Gaines (2003) and Selkoe & Toonen (2011). For the Kinlan & Gaines (2003) data set, we used their supplementary material, which included dispersal distances derived in the same way as in this study, and we used only data on fishes and invertebrates, removing the two deep-sea species that were also a part of our study. For the Selkoe & Toonen (2011) data set, we used only their 'IBD data set' reduced to just fishes and invertebrates, removing the 7 studies that overlapped with either our study or Kinlan & Gaines (2003). Their supplemental material included IBD slope data, so we converted their values to dispersal distance using the PKG equation (eqn 2). To compare our data to these two data sets, we combined our deep-sea CE inverts data with our NCE inverts data, resulting in a deep-sea 'invertebrate' data set that was congruent with the other studies. Two-way ANOVAS using type II sums of squares were carried out on both SigMantel and All data sets to test for differences due to factors of 'Depth' and 'Taxon', with depth as shallow vs. deep, and taxon divided into fishes and invertebrates. Tukey's HSD pairwise comparisons were made following the two-way ANOVA.

A number of recent studies have compared pelagic larval durations to genetic estimates of dispersal (e.g. Selkoe & Toonen 2011). We chose not to make this comparison because a concurrent synthesis focuses specifically on pelagic larval duration in deep-sea taxa (Hilário *et al.* 2015).

Results

Literature survey and included data

Our literature survey produced 267 papers on population genetics and phylogeography of deep-sea species

(Table 1). Of these 57 had data in the format needed to obtain IBD slopes. Six of these had negative IBD slopes, resulting in 51 papers representing 42 species, including 15 species from chemosynthetic ecosystems, 16 fishes and 11 nonchemosynthetic ecosystem invertebrates. The publication dates of the papers spanned from 1987 to 2013. A list of the papers and their included data is provided in Table S1 (Supporting information).

A number of studies had positive IBD slopes but nonsignificant Mantel tests. Previous studies have shown that the spatial scale of the study as well as the number of populations used in the study can influence whether a statistically significant Mantel was obtained (Weersing & Toonen 2009; Jenkins *et al.* 2010; Selkoe & Toonen 2011). Thus, to determine whether these might confound our analyses, we tested whether the IBD slopes or the Mantel *P*-values were influenced by these variables (Fig. 1).

IBD slopes decreased as a function of maximum geographic distance indicating that smaller IBD slopes occurred in studies that covered a broader geographic range. This is not surprising or inappropriate, as it is important to match the study scale to the scale over which IBD is expected (Rousset 1997), and also because large geographic scales of sampling are required to detect very small IBD slopes. Importantly, there was no relationship between Mantel *P*-value and maximum geographic distance of the study. Weersing & Toonen (2009) and Selkoe & Toonen (2011) found no relationship between F_{ST} and geographic range of the study, although Selkoe & Toonen (2011) did find that pelagic larval duration correlated better with IBD slope at smaller dispersal scales (<650 km).

The number of populations influenced the Mantel test *P*-value but not the IBD slopes (Fig. 1). Significant

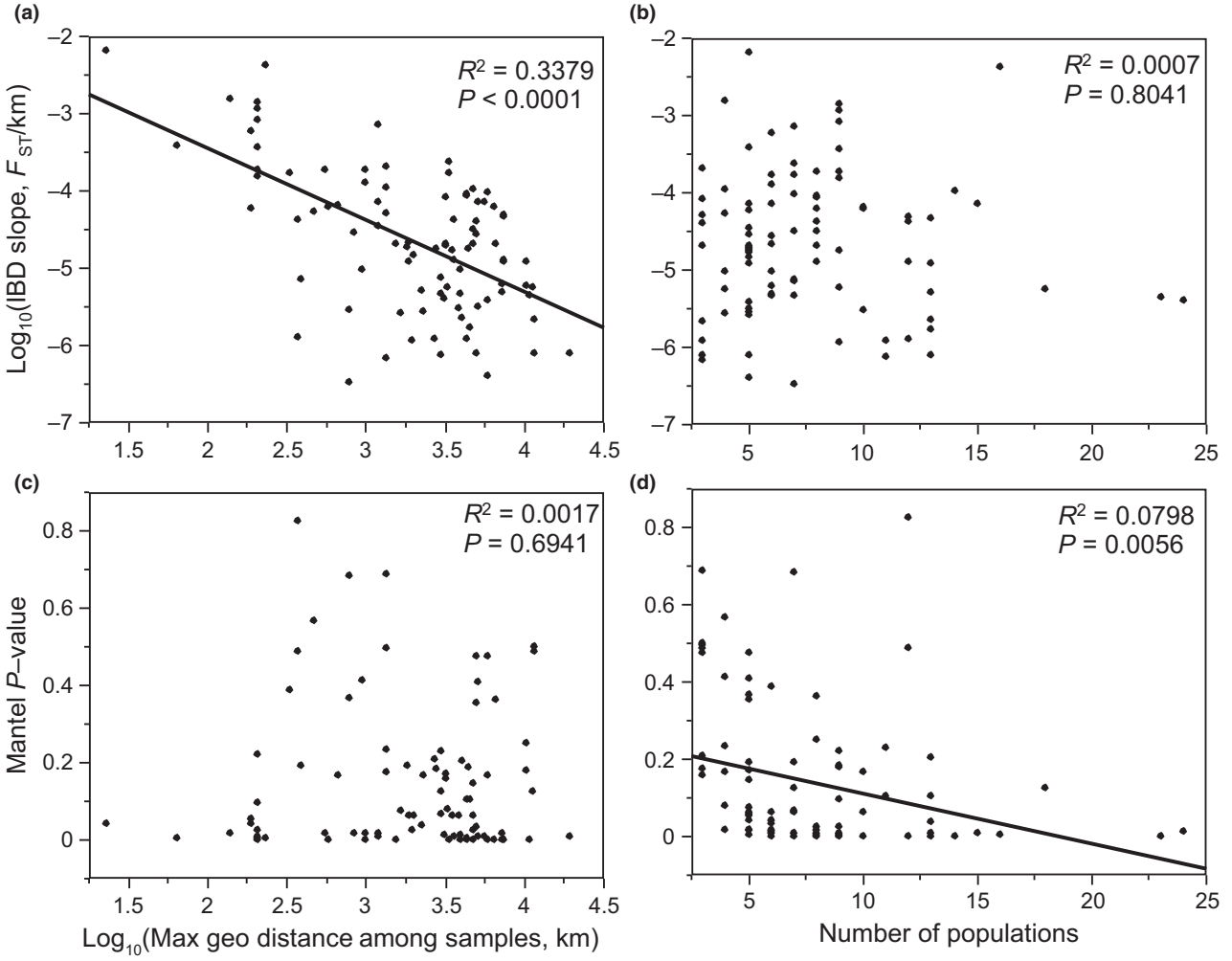

Fig. 1 Pairwise comparisons of IBD slope (a, b) and Mantel test *P*-value (c, d) to assess potential bias by geographic scale of study area (a, c) or number of populations (b, d). R^2 and *P*-values for linear regression are as shown. For $P < 0.05$, regression lines are plotted. Regression equations are as follows: (a) $Log_{10}(F_{ST}/km) = -1.576934 - 0.9300371 * Log_{10}$[Max Geo Distance Among Samples, km]; (d) Mantel *P*-value = 0.2388225–0.0128103*Number of Populations.

Mantel tests were more likely with a greater number of populations, as has been found in previous studies, although the number of populations explained little of the variance in our analysis ($R^2 = 0.0798$).

Variation within a species by marker and scale

Of the included papers, there were a number that used more than one type of genetic marker on the same species within the same study (Table 2, Fig. 2). In some cases, the dispersal estimates from different markers for a given species resulted in dispersal distances that were similar (e.g. *Ifremeria nautilei* in Thaler *et al.* 2011). On average, multiple estimates for a given species ranged over 0.93 to 0.97 orders of magnitude (a factor of 6–8×) based on the SigMantel (Tables S2 and S3a, Supporting information) and All (Table S3b, Supporting information) data sets, respectively. However, in some cases,

Table 2 Summary of dispersal estimates for species that were included in more than one study and/or for which more than one type of marker was used, using the All data set and the PKG method. Species with a value in the 'geometric mean' column had more than two studies and/or markers. A more detailed species-level summary of variability in the All and SigMantel data sets can be found in Tables S2 and S3 (Supporting information).

Species name*	Taxon	# studies	# estimates†	Markers‡	GSS used§	Min. PKG dispersal estimate (km)	Geometric mean PKG dispersal (km) (for >3 rows)	Max. PKG dispersal estimate (km)	Max. geographic range of studies (km)
Coryphaenoides rupestris	Fishes	2	2	S	F	534		1405	1947–3853
Gadus morhua	Fishes	5	8	A, S, N, SNPs	F, G	15	83	334	1564–7253
Hoplostethus atlanticus	Fishes	2	2	MT, S	F, P	229		2028	393–19 553
Pagellus bograveo	Fishes	1	2	MT, S	F	74		132	1856
Scomber scombrus	Fishes	1	2	MT – 2 different genes	F	424		3908	5857
Deminucula atecellana	NCE Inverts	3	11	MT, N – multiple introns	P	0.4	4.4	287	65–11 234
Desmophyllum dianthus	NCE Inverts	1	2	MT, N – multiple introns	F	131		277	10 191
Lophelia pertusa	NCE Inverts	2	5	S	F, R	0.243	21	134	23–7505
Alvinocaris sp.	CE Inverts	1	2	MT, S	F, P	728		2081	11 456
Bathymodiolus sp.	CE Inverts	1	4	A, MT	F	8	138	347	3009–3586
Bathymodiolus thermophilus	CE Inverts	1	2	A, MT	G	7		1252	70
Ifremeria nautelei	CE Inverts	1	2	MT, S	F, P	19		77	228
Lepetodrilus elevatus	CE Inverts	2	2	A, N	F, G	10		80	333–3189
Ridgeia piscesae	CE Inverts	2	4	A, MT	F, G, P	9	13	31	465–998
Riftia pachyptila	CE Inverts	4	6	A, MT, AFLPs, N	F, G, P	26	81	352	3968–6551
Rimicaris exoculata	CE Inverts	2	2	M, S	F	505		1303	2688–5074

*Only species in the All data set for which more than one dispersal estimate was available from multiple studies and/or multiple markers are included here. For similar summaries for All and SigMantel data sets, see Tables S3a and b (Supporting information), respectively. Species that had multiple estimates arising solely from multiple spatial scales within a study are not included here, but are shown in the full by-species variability summaries in Table S3.

†The number of estimates included in summary statistics may exceed the number of studies if estimates were derived at multiple spatial scales for some studies and/or markers. See Table S3 (Supporting information).

‡Marker Type, MT – mitochondrial DNA, N – nuclear DNA, S – microsatellites, A – allozymes, AF – AFLPs, SNP – SNPs.

§GSS – Genetic Structure Statistic – Coded as type of Fst metric employed in the paper. F – Fst, R – Rst, P – Phist, G – Gst.

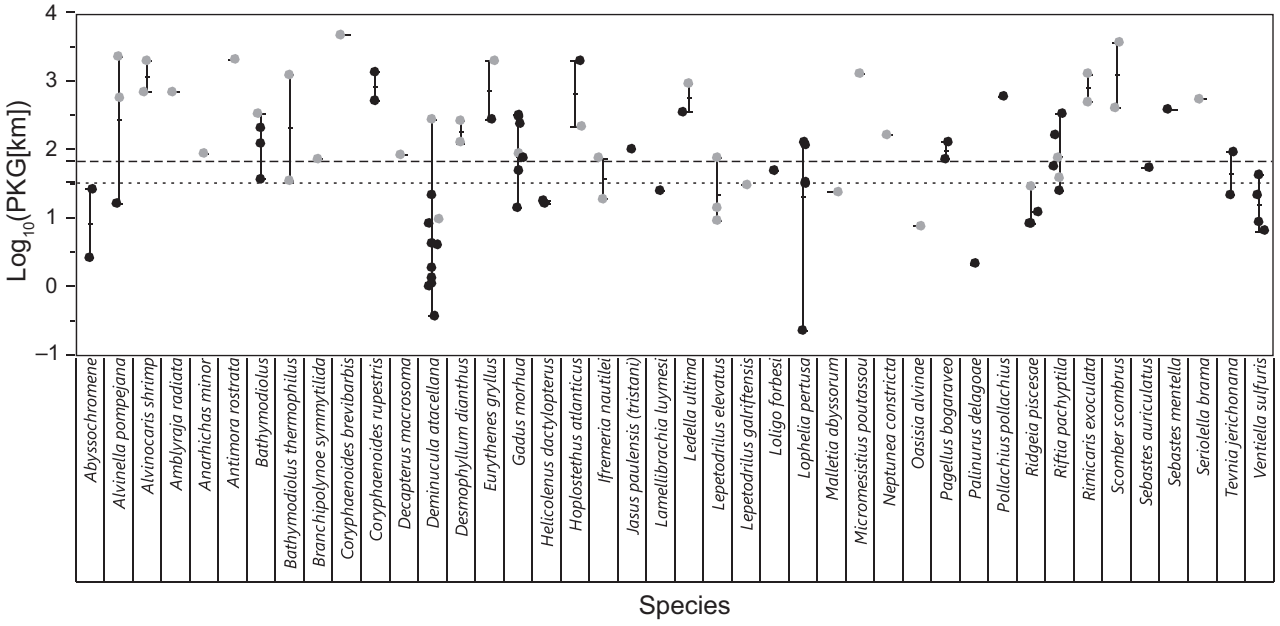

Fig. 2 Variability of $\log_{10}$-transformed PKG genetic dispersal distance estimates within and among species in the All data set. Mean-quartile-range plots are overlaid on points. Points that are only in the All data set are plotted as grey circles; points in the SigMantel data set are plotted as black circles. Points have been jittered horizontally so all points can be seen. For summary statistics by species, see Tables 2 and S3 (Supporting information).

the estimates differed by more than 2 orders of magnitude (Table 2, Fig. 2 and Table S3a,b, Supporting information; e.g. *Deminucula atacellana*, *Lophelia pertusa*). In all cases, we kept the estimates from all markers regardless of the disparity.

A number of papers included taxa that exhibited strong genetic breaks over the geographic range of the study. Previous compilations of IBD estimates of dispersal (Kinlan & Gaines 2003; Selkoe & Toonen 2011) excluded taxa with genetic breaks or divided them into different groups of populations (based on the conclusions of the respective paper) and recalculated IBD slopes for the group of populations on either side of the putative break. We included IBD estimates for all populations together (regardless of the genetic break) as well as for the populations split into groups on either side of the putative break. We included these because estimates across multiple scales may provide a fuller characterization of potential dispersal (which might differ at different scales and in different locations), do not arbitrarily divide populations based on differing levels of divergence (not all papers divided populations equitably or used the same criteria for identifying a genetic break) and allow us to bracket the likely range of dispersal scales for each taxon. Moreover, restricting our estimates to subsets without divergence could lead to either an underestimate or overestimate of true dispersal scales, depending on the circumstances. Genetic breaks occur for a variety of reasons (e.g. physical barriers, recent localized disturbances that create population bottlenecks in a subset of samples, geographic differences in selection, lack of migration-drift equilibrium across all scales) that might be unrelated to the distances larvae can disperse. In general, a genetic break caused by nondispersal-related mechanisms would be expected to result in an underestimate of dispersal distance, by inflating the IBD slope. However, statistical sampling issues could just as easily lead to overestimating dispersal by partitioning populations on either side of a break. For example, Jenkins *et al.* (2010) show that the ability to detect an IBD slope is affected by the number of populations, with high numbers of populations more likely to result in statistically significant signals of IBD. Also, Selkoe & Toonen (2011) and our own results (Fig. 1) show that the spatial scale of the study could bias dispersal estimates. Audzijonyte & Vrijenhoek (2010) also found that the ability to detect an IBD signal in some studies was a function of statistical power and gaps in sampling. As such, if we only included populations on either side of a 'genetic break', then nonsignificant or negative IBD slopes may well be a result of lower statistical power, another outcome could be the bias against detection of IBD for relatively long dispersal scales.

Thus, 15 of the 42 species have data rows for 'all populations' as well as rows for a subset of the populations based on conclusions of their respective papers (Table S1, Supporting information). Estimates of

dispersal distance for a given species varied by 0.25–2.87 orders of magnitude (mean = 0.97 or a factor of 9.38×) in the All data set, and 0.16–2.74 orders of magnitude (mean = 0.93 or a factor of 8.42×) in the SigMantel data set when all spatial scales were included (Table 2, Fig. 2, Tables S2 and S3a,b, Supporting information). However, consistent with the discussion above, there was not a consistent pattern of the 'all populations' having a higher (three studies) or lower (eight studies) dispersal estimate than a subset. Without a consistent result, there was not a way to further screen these studies. Therefore, we felt it reasonable to include the estimates at all geographic scales.

There was also not a consistent signal of the 'all populations' or the subsets having a statistically significant Mantel test, with eight of the studies having at least one scale with a nonsignificant *P*-value, including the two studies with the greatest range of values (Hurtado *et al.*2004; Teixeira *et al.* 2011). For these eight studies, the scale(s) with nonsignificant *P*-values are excluded from the SigMantel data set.

Range of dispersal estimates for deep-sea studies and comparison of methods

The dispersal estimates we obtained ranged from 0.24 to 4856 km, more than 4 orders of magnitude, with a 10–90th percentile range of 4.3–1320 km and a geometric mean of 69.7 km based on the PKG method applied to the All data set (Table 3). The SigMantel data set, on the other hand, spanned 3.92 orders of magnitude and had a smaller geometric mean (33.2 km), consistent with the expected lower power to detect significant IBD for longer dispersal scales.

Dispersal estimates by Taxon

The results of the one-way ANOVAs for the All data set and for the SigMantel data set are given in Table 4 and Fig. 3. The results based on subsets of the data after removal of fishes are also given in Table 4. Scatterplots of the complete data set for each comparison, colour coded by taxonomic group to aid in identification of potential confounding taxonomic factors, are provided in Figs S1–S10 (Supporting information).

We tested whether dispersal distance differed among fishes, invertebrates and invertebrates inhabiting chemosynthetic ecosystems. Fishes had the largest geometric mean dispersal distance at 234.6 km with a range of 15–4856 km (10–90th percentile range of 17 km to 2269) based on the PKG method using the All data set (Table 3). The geometric mean dropped to 134.8 km for the SigMantel data set. The ANOVA was significant for both data sets (Table 4, Fig. 3), with fishes having a

Table 3 Summary of dispersal estimates from IBD slopes, by data set (All, SigMantel) and taxonomic group (Fishes, CE Inverts and NCE Inverts).

			PKG dispersal distance estimate (km)*						Maximum–Minimum		90–10th percentile	
Data set	Taxon Group	N	Minimum	10th %ile	Geometric Mean (Upper 95% CI, Lower 95% CI)	Median (25%ile, 75%ile)	90th %ile	Maximum	Range (km)	Range (Orders of Magnitude)	90–100%o Range (km)	90–100%o Range (Ord. of Mag.)
All Dataset	All taxa	95	0.243	4.29	69.7 (45.2, 107)	76.9 (17.2, 347)	1320	4856	4855	4.30	1316	2.49
	Fishes	28	14.956	17.00	234.6 (122.6, 449)	280.5 (75.4, 680)	2269	4856	4841	2.51	2252	2.13
	CE Inverts	38	6.658	8.63	67.6 (38.7, 118)	42.8 (18.7, 242)	1257	2356	2350	2.55	1248	2.16
	NCE Inverts	29	0.243	1.06	22.5 (9.0, 57)	27.8 (2.4, 150)	367	2028	2028	3.92	366	2.54
SigMantel	All taxa	56	0.243	1.76	33.2 (19.4, 57)	33.9 (8.8, 133)	377	2028	2028	3.92	375	2.33
Dataset	Fishes	17	14.956	14.96	134.8 (59.6, 305)	131.8 (31.1, 462)	1512	2028	2013	2.13	1497	2.00
	CE Inverts	8	6.658	8.31	34.6 (19.0, 63)	25.9 (11.5, 103)	225	352	345	1.72	217	1.43
	NCE Inverts	2	0.243	0.47	0.3 (3.8, 28)	8.5 (1.6, 74)	249	367	367	3.18	249	2.72

*All summary statistics were calculated on $\log_{10}$-transformed dispersal estimates and back-transformed to kilometre for reporting only

Table 4 Summary of *P*-values for one-way ANOVAs investigating effects of life-history and study-related factors on Log_{10}(PKG dispersal estimate in km) using the All and SigMantel data sets. Means and standard errors are shown graphically in Fig. 3. The last four columns explore the effect of excluding fishes and including/excluding invertebrate taxonomic groups on conclusions.

				Screening for taxon dependence of conclusions			
Factor	*P*-value All taxa All data set	*P*-value All taxa SigMantel data set	Notes based on Tukey's HSD pairwise comparisons	*P*-value NCE Inverts only All dataset	*P*-value NCE Inverts only SigMantel dataset	*P*-value CE and NCE Inverts only All dataset	*P*-value CE and NCE Inverts only SigMantel data set
Taxon	**<0.0001**	**0.0002**	All: **Fishes > NCE, Fishes > CE**, [CE > NCE, $P = 0.06$] SigMantel: **Fishes > NCE**, [Fishes > CE, $P = 0.06$], [CE > NCE, $P = 0.09$]	na	na	**0.0325**	**0.0446**
Phylum	**0.0022**	**0.0038**	All and SigMantel: **Chordata > Mollusca**, [Chordata > Arthropoda, $P = 0.08$]	0.4445	0.352	0.4109	0.4465
Marker type	**0.0267**	0.2562	All: **S > N**, [MT > N, $P = 0.08$] SigMantel: no significant differences	0.2941	0.3172	0.0945	0.2093
Ocean	0.5253	0.3496	No significant differences	0.0883	0.5918	0.15	0.0697
F_{ST} Metric/GSS	**0.0104**	**0.0475**	All: ***F* > *P*** SigMantel: ***F* > *P***	0.1238	0.362	**0.0303**	0.079
Adult habitat	**<0.0001**	**0.0007**	All: **Benthic Hard, Demersal and Pelagic > Benthic Soft**; Benthic Hard, Demersal, Pelagic not different from each other. SigMantel: **Benthic Hard and Demersal > Benthic Soft**; Pelagic not different (only because $n = 1$)	0.3577	0.2159	**0.0215**	**0.0146**
Adult mobility	**0.0001**	**0.0025**	All: **Swimmer > Sessile and Sedentary**; sessile and sedentary not different SigMantel: **Swimmer > Sedentary**; swimmer and sessile not different; sessile and sedentary not different	0.2797	0.2541	0.2285	0.2261
Larval feeding type	**<0.0001**	**0.0002**	All and SigMantel: **Feeding > Nonfeeding**	0.9882	0.5098	**0.0045**	0.169
Larval dispersal	**0.0055**	**0.0003**	All and SigMantel: **Pelagic > Demersal**; no other significant differences	0.17	0.5173	0.1676	**0.0374**
Adult depth zone	**0.0083**	**0.0183**	All and SigMantel: **<2000 m depth range >2000–4000 m depth range**	0.5281	0.2667	0.7759	0.9272

Values and text in bold indicate statistical significance at $P < 0.05$.

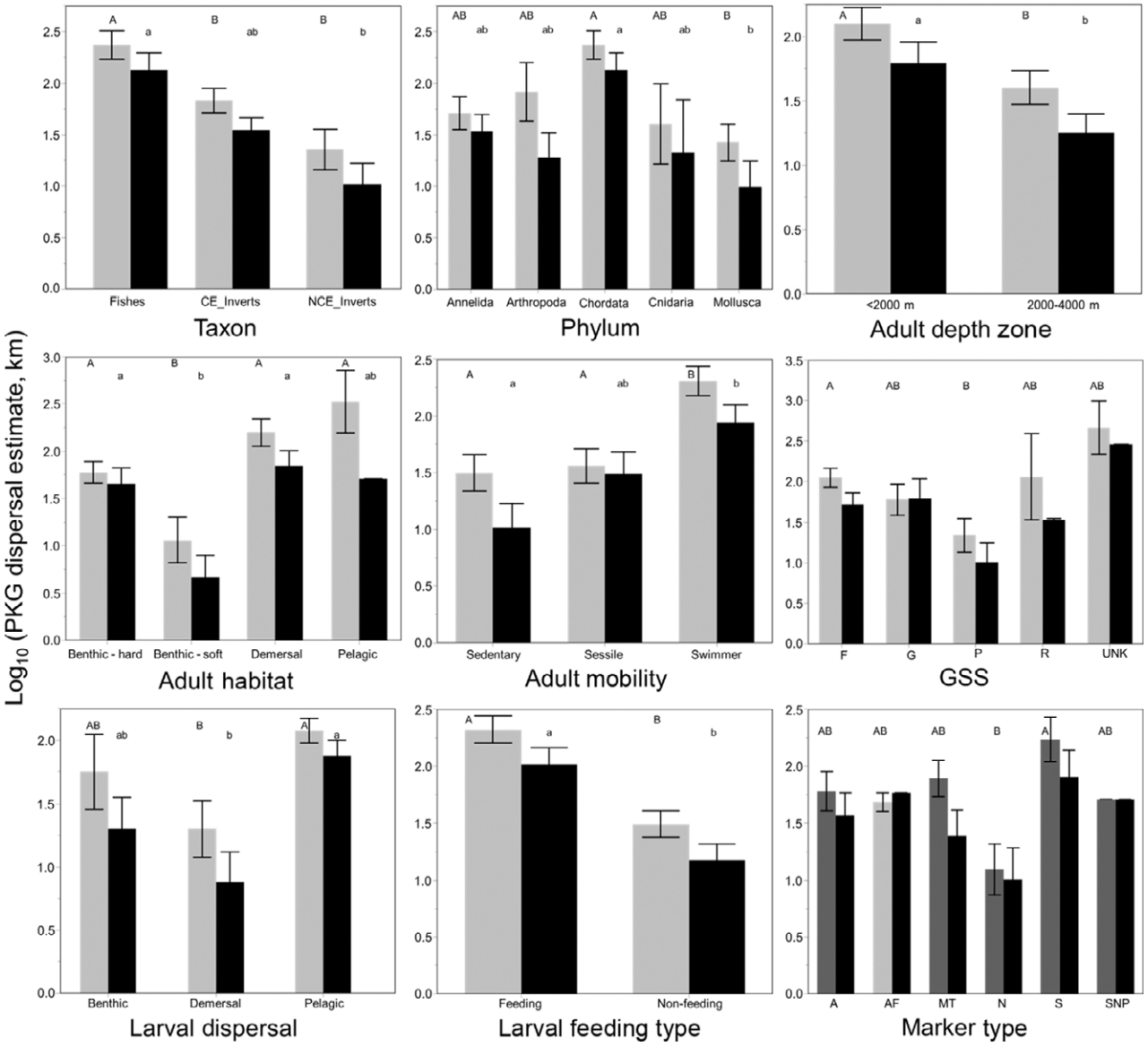

Fig. 3 Results of one-way ANOVAs of potential life-history and study-related variables on $\log_{10}$-transformed PKG estimates of dispersal distance in km. Bars indicate the mean $\log_{10}$(PKG dispersal distance, km) for a given category, with shaded bars for data from the All data set, and filled bars for data from the SigMantel data set. Letters above the bars indicate significance as determined by Tukey's HSD post hoc pairwise comparisons, with uppercase corresponding to the tests on the All data set and lowercase to the SigMantel data set. Missing letter indicates no significant difference at $P < 0.05$ level. Error bars correspond to ±1SE. For an explanation of each factor and category, see Methods. For *P*-values of each test, see Table 4.

significantly larger dispersal distance than both CE and NCE Inverts for the All data set and significantly larger than NCE Inverts in the SigMantel data set. When fishes were excluded, CE Inverts had significantly greater dispersal distances than NCE Inverts in both All and SigMantel data sets (Tables 3 and 4).

These differences were similar to the 'Phylum' test (Fig. 3), which indicated significantly smaller dispersal scales for the Mollusca as compared to the Chordata in the All and SigMantel data sets. These two phyla may be driving the difference in the Taxon categories; when fishes are excluded, there is no significant difference by Phylum (Table 4).

Dispersal estimates vs. life history, habitat and data type

We did not have sufficient replication within any of these categories to conduct multiway ANOVAs, so each of the life-history parameters as well as marker type and type of GSS was analysed as one-way ANOVAs. There was not a difference in dispersal estimates among

oceans (Table 4). In contrast to previous studies (Weersing & Toonen 2009), estimates of dispersal distances were not broadly affected by marker type, with statistical significance of this factor varying depending on data set analysed and taxa included (Table 4). Significant differences emerged only for the All data set and were driven by the differences in microsatellites vs. nuclear markers based on Tukey–Kramer pairwise comparisons (Table 4, Fig. 3). Type of GSS was significant for both data sets with Tukey–Kramer HSD pairwise comparisons indicating dispersal estimates in studies that used F_{ST} were larger than those that used Φ_{ST}, except when NCE inverts were analysed separately (Table 4, Fig. 3).

Dispersal estimates differed among categories for the Adult Mobility and Adult Habitat factors (Fig. 3, Table 4). For Adult Habitat in the All data set, Benthic Soft had a lower dispersal scale than Benthic Hard, Demersal and Pelagic. For the SigMantel data set, the Pelagic class was reduced to a single data point, and Benthic Soft had shorter dispersal distances than Benthic Hard and Demersal. This pattern held for both data sets and the data sets analysed without fishes, but not for the NCE inverts analysed alone (Table 4). Within the Adult Mobility factor, Swimmers typically had larger dispersal estimates than sedentary species, but this was driven primarily by fishes (Table 4).

Species with feeding larvae had significantly larger dispersal estimates than those with nonfeeding larvae in both data sets (Fig. 3, Table 4). In terms of Larval Dispersal, species with pelagic larvae were generally more dispersive than species with demersal larvae (Table 4, Fig. 3). Both dispersal and feeding patterns are to some extent affected by the inclusion of fish (Table 4).

Finally, the test of Adult Depth Zone indicated that deeper (2000–4000 m) species had shorter dispersal than shallower (<2000 m) deepwater species for both data sets (Table 4, Fig. 3). However, analyses of taxonomic subsets revealed that this pattern was entirely driven by fishes, which occurred primarily in the shallower (<2000 m) group.

Deep-sea dispersal distances vs. shallow water

To assess whether the range of dispersal distances we obtained for the deep sea was comparable to shallow-water taxa, we used data from two recent reviews of dispersal distances in shallow water (Kinlan & Gaines 2003; Selkoe & Toonen 2011). Because there were no data from shallow-water chemosynthetic ecosystems in the shallow-water data sets, we pooled our CE and NCE invert data into a deep-sea invertebrate data set for purposes of the shallows vs. deep comparison.

The results of a two-way ANOVA comparing our deep-sea dispersal estimates (SigMantel data set) to shallow-water estimates indicated that taxon ($P < 0.0001$) and depth ($P = 0.0105$) were significant, with no interaction ($P = 0.4683$) (Fig. 4, Table 5). Fishes had greater mean dispersal than invertebrates and deep-sea taxa had greater dispersal distances than their shallow-water counterparts (Fig. 4). However, an important note with these analyses is that the ANOVA is unbalanced with 39 shallow fish, 69 shallow inverts, vs. only 17 deep fishes and 39 deep inverts. To parse out the independent contributions of each taxon to the overall depth differences, we examined the Tukey's HSD results. Dispersal distances were not different between depths within taxonomic groups. That is, there was no difference in shallow vs. deep fish or in shallow vs. deep invertebrates (Fig. 4), which suggest that the unbalanced taxon sampling may be driving the depth differences, or that the Tukey's HSD has insufficient power to detect the difference within taxon. The All data set analysis indicated a stronger difference between taxa and depth (Table 5), but is problematic because the shallow estimates were restricted to significant IBDs while the deep estimates were not. We included them for completeness.

Discussion

Marine reserves play increasingly important roles in protecting vulnerable habitats (e.g. Palumbi 2001; Lester *et al.* 2009). Only recently, however, has the design of marine reserves begun to focus away from coastal areas, for example to seamounts (Clark *et al.* 2011), offshore islands (Lombard *et al.* 2007), pelagic habitats (Game *et al.* 2009) and the deep sea (Wedding *et al.* 2013). One of the critical parameters included in reserve design is the demographic connectivity of a diverse suite of species (e.g. Wright *et al.* 2015). With anthropogenic impacts advancing into deeper waters, there has been an increased focus on the protection of deep-sea ecosystems (e.g. Mengerink *et al.* 2014), but efforts are hampered by a lack of data on the scales of connectivity in deep-sea habitats (e.g. Hilário *et al.* 2015). Connectivity is influenced by dispersal distances, and here, we compiled a synthesis of dispersal distance estimates among deep-sea taxa derived from IBD slopes.

Range of dispersal distances in the deep sea

Using the PKG method on our All data set, we found a range of dispersal distances for deep-sea species that span more than four orders of magnitude. Removing studies with nonsignificant Mantel tests still leaves a range of 3.9 orders of magnitude, from hundreds of metres for both the scleractinian coral *Lophelia pertusa* and the protobranch

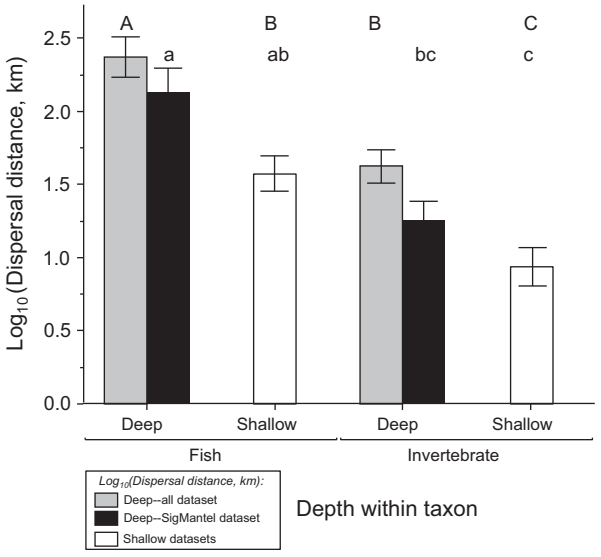

Fig. 4 Results of two-way ANOVA for comparison of $\log_{10}$(PKG dispersal estimates, km) for shallow-water to deep-sea species (Table 5 provides ANOVA results). Error bars correspond to ±1SE. Letters above the bars indicate significance as determined by Tukey's HSD post hoc pairwise comparisons, with uppercase corresponding to the tests on the All data set and lowercase to the SigMantel data set. Missing letter indicates no significant difference at $P < 0.05$ level. The shallow-water estimates represent the combined results of Kinlan & Gaines (2003) and Selkoe & Toonen (2011) with overlapping studies removed. The deep water estimates represent our All data set. 'Invertebrates' for the deep sea are the combined chemosynthetic ecosystem and nonchemosynthetic ecosystem invertebrate groups from this study.

bivalve *Deminucula atacellana* (Table S1, Supporting information) to almost 5000 km for some of the more mobile fish species. Dispersal distances differed among a number of taxonomic, life history and study parameters. Caveats of the method are discussed in P. Beerli, B. P. Kinlan, R. J. Etter, P. A. Ribeiro, S. von der Heyden, A. R. Baco (in prep).

Dispersal distances were generally greater for deep-sea fish relative to invertebrates (Tables 3 and 4 and Fig. 3). The tendency for fish to have greater dispersal abilities might reflect their ability to disperse at both the adult and larval stages, whereas many of the invertebrates disperse only as larvae (Kinlan & Gaines 2003). Many of the CE inverts are crustaceans that are highly mobile as adults, which may also account for the similarity in dispersal scales for fish and CE inverts when the All data set was considered.

Comparison to other studies in terms of life history, habitat and data type

GSS. The differences in dispersal estimates for different metrics of population genetic structure were likely due to an uneven distribution of taxa among the different metrics. For example, F_{ST} included more fish, which tend to have larger dispersal estimates. In fact, only three fish were measured with Φ_{ST} (including the species with the smallest dispersal estimate) while ten were measured with F_{ST} for the SigMantel data set, and the disparity was much greater when all data were included (three vs 18). The disparity in the relative number of fish measured by each metric likely accounts, at least in part, for the greater distances estimated for F_{ST} relative to Φ_{ST}. That said, the pattern remains when fish are excluded, albeit with a smaller difference and less significance (Table 4).

The dispersal distance difference between F_{ST} and Φ_{ST} might also be caused by the difference in the interpretation of the allele frequencies and counts. In calculations of F_{ST}, every allele is unique and counts; thus, with microsatellite data, one chooses the scenario that all alleles are equal and different and thus many alleles are used to calculate the relationship between geographic distance and genetic distance; in contrast, Φ_{ST} uses a distance matrix with distances that are calculated from the multilocus haplotypes taking into account similarity of alleles and is therefore more similar to R_{ST} than to F_{ST} (Michalakis & Excoffier 1996). As a result, values of Φ_{ST} are more similar when alleles are similar. This different interpretation of the data would lead to smaller dispersal distance estimates for Φ_{ST} based on IBD analyses.

Adult habitat. A priori one would expect species with demersal or pelagic adults to have greater dispersal abilities than benthic species because they are by definition likely to be more mobile. Our results generally reflect this expectation, regardless of the inclusion of fishes (Fig. 3, Table 4). However, the statistical significance may be driven by the small dispersal distances for those species from Benthic-Soft habitats (Fig. 3).

The lower dispersal distance of soft-substrate benthic species may be influenced by some factor related to finer-scale habitat type. While many of the Benthic-Soft substrate species were molluscs, the phylum with the lowest mean dispersal distances, and most were lecithotrophs, lecithotrophs were also represented in the chemosynthetic ecosystem data set and there was no difference in dispersal estimates by phylum in either of the reduced data sets. Perhaps, the comparative scarcity and patchiness of hard substrate in the deep sea favours a larger dispersal distance for deep-sea invertebrates endemic to hard substrate habitats. We are not aware of any other studies comparing the dispersal abilities of hard- vs. soft-substrate species.

Adult mobility. Dispersal can occur during the adult phase when organisms are more powerful swimmers,

Table 5 Two-way ANOVAs of effects of depth (deep sea, shallow) and taxon (fish, invertebrates) on genetic dispersal estimates (PKG method, Log_{10}-transformed) using (a) the SigMantel data set and (b) the All data set to represent deep sea taxa. Shallow-water taxa are represented by the combined results of two previous studies (Kinlan & Gaines 2003; Selkoe & Toonen 2011), as described in *Methods*. To reduce effects of unbalanced sample sizes among groups, type II sums-of-squares were used in construction of F-tests. Note also that the same shallow water data sets are used in (a) and (b), and the SigMantel data set is a subset of the All data set; thus, the two ANOVAs presented in (a) and (b) are not independent

Source	Effect	SS	d.f.	MS	*F*	*P* > *F*	Significance
(a) ANOVA using All data set for deep sea taxa							
Model		44.21	3	14.74	18.17	**<0.0001**	***
	Taxon	20.96	1	20.96	24.16	**<0.0001**	***
	Depth	26.19	1	26.19	30.19	**<0.0001**	***
	Taxon*Depth	0.14	1	0.14	0.16	0.6926	ns
Error		172.67	199	0.87			
Total		216.88	202				
(b) ANOVA using SigMantel data set for deep sea taxa							
Model		24.84	3	8.28	9.68	**<0.0001**	***
	Taxon	18.65	1	18.65	21.81	**<0.0001**	***
	Depth	5.74	1	5.74	6.71	**0.0105**	*
	Taxon*Depth	0.45	1	0.45	0.53	0.4683	ns
Error		136.87	160	0.86			
Total		160.60	163				

Asterisks indicate significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$
Values in bold indicate statistical significance at $P < 0.05$

which can influence connectivity among populations and scales of gene flow. Not surprisingly, adult mobility had a significant effect on dispersal scales in our data. Dispersal scales were greater for those classified as swimmers relative to sedentary or sessile adults (Table 4, Fig. 3). Although similar comparisons have not been made in other syntheses of dispersal data, those studies have compared fishes to invertebrates. This is, of course, confounded because both fish and invertebrates can have adults that are either swimmers or sedentary. Nevertheless, fishes had larger dispersal scales relative to invertebrates for Kinlan & Gaines (2003) but not for Selkoe & Toonen (2011). In general, we expect that species with adults that swim will have greater dispersal scales than sedentary or sessile adults because dispersal is mediated at both the larval and adult stages. Surprisingly, when the analysis was restricted to invertebrates, dispersal distances did not differ among mobility categories. This may indicate that swimming in invertebrates is insufficient to significantly alter dispersal mediated by the larval phase, at least for those invertebrates sampled in our data.

Larval feeding mode. Marine species with direct developing and lecithotrophic larval stages that do not feed during dispersal tend to invest more resources into each offspring and generally produce fewer eggs and larvae. As such, lecithotrophic larvae tend to have shorter PLDs than planktotrophic larvae, and direct developing larvae effectively have PLDs of 0 (Strathmann 1985), which may translate into more genetically structured populations and a more distinctive pattern of isolation by distance. Indeed, for coastal marine species, direct developers are generally more genetically structured with stronger signals of isolation by distance than species with planktonic larvae (Kelly & Palumbi 2010; Wright *et al.* 2015). Analysis of our All data set reveals that, as in shallower waters, deep-sea species with feeding larvae had significantly larger (0.82 orders of magnitude, a factor of 6.6) dispersal distances than those with nonfeeding larvae (Table 4, Fig. 3, $P < 0.0001$; effect remains significant in SigMantel data set, $P = 0.0002$), although it should be noted that direct developers were represented by very few data points ($n = 7$), so the 'nonfeeding' category was dominated by lecithotrophs, and planktotrophs were absent below 3000 m. Kinlan & Gaines (2003) also found that invertebrates in their predominantly shallow-water data set with nonfeeding larvae had smaller genetic dispersal estimates (mean ≈ 30 km) than invertebrates with feeding larvae (mean ≈ 100 km), values broadly consistent with our findings for deep-sea taxa.

Previous studies suggested egg type as an explanatory variable in population genetic structure of fishes, as species with larger, benthic eggs exhibited higher F_{ST} values than those species with pelagic eggs (Riginos *et al.* 2011). The taxonomic distribution of our species with feeding larvae differed from our nonfeeding group, with the former dominated by fishes. Only one fish study was recorded for larval type in the

nonfeeding category. This may have somewhat biased our results, as egg and larval type are probably closely linked with other larval life-history characteristics (such as swimming ability and PLD). However, the relationship between larval feeding type and dispersal distance remained significant when fishes were excluded from the All data set, although not for the SigMantel (Table 4).

Larval dispersal. Dispersal distances were greater for species with pelagic eggs and larvae relative to those with demersal larvae. Pelagic larvae are more likely to disperse above the benthic boundary layer where currents are generally stronger, which might increase their capacity to disperse. Likewise, larvae that stay close to the bottom may exhibit homing behaviour driven by chemical cues (e.g. Kingsford *et al.* 2002; Adams *et al.* 2012). However, the differences might also be confounded by the uneven representation of taxa and other life histories among the dispersal categories. Our pelagic species were mainly fishes and species from chemosynthetic ecosystems, while our demersal species were largely NCE invertebrates (Fig. S9, Supporting information). In fact, dispersal distances did not differ in the analyses that excluded fish, except for the CE and NCE Inverts analysis of the SigMantel data set ($P = 0.0374$; Table 4). The Pelagic category also included numerous planktotrophic species while the demersal species were all lecithotrophic, which tended to have smaller dispersal scales than planktotrophs (see feeding vs nonfeeding). PLDs are generally longer for planktotrophs relative to lecithotrophs (O'Connor *et al.* 2007), which should translate into greater dispersal distances (Siegel *et al.* 2003; Bradbury *et al.* 2008; Young *et al.* 2008), although evidence for a general correlation between PLD and dispersal distance or other metrics of dispersal scale (e.g. IBD slope) has been mixed (Siegel *et al.* 2003; Shanks 2009; Weersing & Toonen 2009; Selkoe & Toonen 2011; Faurby & Barber 2012) and is likely confounded by differences in oceanographic factors (eddies, current speeds, tidal circulation, vertical structure), larval/juvenile behaviours, and the shifting relative importance of advection and diffusion as PLD increases.

Deep-sea vs. shallow-water dispersal distances

Historically, it was thought that marine populations in general would be very well connected because of their long-lived larvae and subsequent transport by ocean currents (e.g. Scheltema 1986). This paradigm has shifted over the last decades because we now understand that many marine species have significant genetic structure, and even some species with long-lived larvae exhibit behaviours that increase retention in their natal habitat and constrain dispersal (e.g. reviewed in Cowen & Sponaugle 2009).

So too there has been a paradigm that dispersal distances might increase with depth because the deep sea has vast areas of relatively homogenous habitat and many species have enormous geographic ranges, often encompassing entire oceans or multiple oceans (e.g. reviewed in Rex & Etter 2010). If the existing paradigm of larger dispersal distances in the deep sea holds true, then deep-sea marine reserves would need to be designed at different spatial scales than they are in shallow water.

Our analyses indicated a small, albeit statistically significant difference among shallow vs deep taxa. Although statistically significant, the size of the difference (0.3–0.6 orders of magnitude) is less than even the typical variation of genetic dispersal estimates for the same taxon in the same environment. Thus, it is either (i) an artefact of some underlying sample bias, or (ii) a real but relatively small difference. If real and general, then this small but consistent difference between average dispersal distances in deep vs shallow habitats may be interesting theoretically, if it can be independently confirmed.

This suggests that connectivity in the deep sea, on average, occurs on comparable to slightly larger spatial scales than in shallow water. Different scales of connectivity for different taxonomic groups and depths may have broad implications for ecology, evolution, management and conservation of deep-sea ecosystems. These results also provide the first broad, quantitative community perspective on connectivity in the deep sea. General arguments for greater dispersal in the deep sea based on range size did not provide any estimate of what scales of connectivity might be, and recent syntheses have raised doubt on theoretical and empirical grounds as to whether a relationship between dispersal distance and range size should be expected at all (Lester *et al.* 2007). Likewise oceanographic simulations of deep-sea dispersal struggle with large uncertainties due to poor sampling of physical parameters in the deep sea and a lack of empirical data for calibration and groundtruthing of models (e.g. Young *et al.* 2012; Sala *et al.* 2013; Etter & Bower 2015; Hilário *et al.* 2015). Our database of genetic estimates of dispersal from IBD will help to advance such simulation work, which may in turn help to make our models of IBD in marine systems more realistic.

A variety of factors could lead to increased dispersal distances in the deep sea, and still other factors could act to constrain those increases. Reasons to expect a correlation between depth and mean dispersal distance include changes in PLD and oceanography. For

example, several recent studies found that PLDs increase with depth (Bradbury *et al.* 2008; Hilário *et al.* 2015). All else being equal, longer PLDs should translate into greater dispersal distances, suggesting dispersal might increase with depth. However, as noted above (see 'Larval Dispersal'), a variety of factors can disrupt any expected correlation between PLD and dispersal distance (Shanks 2009; Weersing & Toonen 2009; Selkoe & Toonen 2011; Faurby & Barber 2012). Longer PLDs for deep-sea taxa may not always translate to greater dispersal distances, simply because current velocities typically decrease dramatically with depth (e.g. Hogg & Brechner Owens 1999; Bower & Hunt 2000a,b; Toole *et al.* 2011) and therefore deep-ocean currents transport particles much more slowly than wind-driven surface currents, reducing dispersal potential for passively dispersing larvae. For example, recent simulations of passive larval dispersal in the deep Gulf of Mexico indicated dispersal distances were lower in deeper currents (Young *et al.* 2012). For similar PLDs, larvae dispersed further at 100 m depth compared to those at 500 m depth, and currents at 500 m depth are strong compared to most currents in the very deep sea, particularly in the benthic boundary layer within ≈ 100 m of the seafloor (Gage & Tyler 1991)). Consequently, an increase in PLDs with depth is likely partly offset by oceanographic factors that limit dispersion per unit time. This interplay may help to explain the relatively modest difference in dispersal distance between deep and shallow taxa. More studies of the interaction between PLD changes, temperature and oceanography with depth are needed to explore this issue.

The decreasing temperature and current speed with increasing depth might also lead one to expect a continued change in dispersal estimates with increasing depth *within* the deep sea (O'Connor *et al.* 2007), but this is not what our results suggest. In fact, we found the opposite pattern: dispersal distances of deep-sea taxa were smaller, on average, in the 2000–4000 m depth zone compared to the <2000 m depth zone. This difference was almost entirely driven by the decrease in fish species in our data set; when fish are excluded, there is no significant change in dispersal distances with depth in the deep sea. Fish were primarily present above 2000 m with most <1000 m. The lack of invertebrate planktotrophs below 3000 m likely also contributed. Given the strong taxonomic patterns in dispersal distance in our data set, it is likely that shifts in major taxonomic groups sampled with increasing depths play a large role in influencing changes in overall average dispersal distances with depth, which might lead to complex, system-dependent patterns. The lack of a clear trend could also be due to the oceanographic factors discussed above or could result from an interplay of other factors with oceanography – food availability, larval survivorship, larval behaviour and distribution of suitable habitat can all modify effective dispersal distances and could act to mitigate the longer PLDs expected at colder temperatures. Recent estimates of passive larval dispersal based on physical transport processes within the deep sea (1500–3200 m) revealed little difference in mean (or median) dispersal distances with depth, especially over longer time periods that would be more comparable to genetic estimates (Etter & Bower 2015). More precise estimates of dispersal (e.g. by fusing genetic, PLD and simulation approaches) and more equitable sampling with respect to taxa, life-history characteristics and developmental mode will be necessary to rigorously test how dispersal scale might change with increasing depth

Challenges and caveats of approach

While the methods used here provide the best available first-order estimate of the range of dispersal distances in deep-sea taxa and broad, relative patterns among groups, we found many caveats that are worth discussing to improve future studies. The first is that we were able to use less than one-fifth of the available deep-sea population genetic studies in our analyses because of the way in which data were reported. We recommend future studies at a minimum include geographic positions for each of their study stations and pairwise F_{ST} (or relevant GSS) in the paper.

Another significant caveat of the approach of using genetic estimates of dispersal lies in the difference found between different studies and/or markers that targeted the same species. Of the 17 species that had multiple studies or markers, 3 of them had a two or more order of magnitude difference in dispersal estimates (Table 2). Two of these were at the extreme low end of the range of dispersal values found: *Deminucula atecellana* and *L. pertusa* had an estimated dispersal distance of <1.0 km for at least one study or marker and a ~3 order of magnitude difference in dispersal estimates (Table 2).

Some disparities are expected to arise simply due to error in regression estimates of IBD slopes, which are then fed into a nonlinear formula for dispersal distance. The natural scale for comparison of dispersal estimates is logarithmic, so a small amount of error variance in the IBD slope translates to an asymmetrical confidence interval when dispersal estimates are back-transformed to the arithmetic scale. On the arithmetic scale, the upper confidence interval (longer dispersal distances) will always be substantially larger than the lower confidence interval (shorter dispersal distances). Thus, seemingly large discrepancies in dispersal estimates on the

arithmetic scale could be generated by relatively small errors in estimation of IBD slope. An additional statistical explanation for disparities in dispersal estimates for the same species may have to do with different results being produced by different numbers of populations being sampled in different studies. Jenkins (2010) demonstrated that the power to detect a statistically significant IBD slope is related to the number of populations sampled; the standard error of the IBD regression slope is also surely higher for small numbers of populations. We too found a significant correlation of Mantel test *P*-value with number of populations studied (Fig. 1). Thus, the disparity of multiple studies for a given species may in part be attributed to the difference in the number of populations sampled between studies and attendant differences in error variance.

Several mechanistic factors may also contribute to disparities in dispersal estimates. First, variance in dispersal estimates among studies conducted on the same species but in different geographic areas may reflect different oceanographic conditions and habitat arrangements.

A second possible mechanistic explanation may be related to marker types used in the studies. It has been well established that different markers evolve at different rates, for example mtDNA vs nuclear DNA, and this has been found to affect dispersal estimates in compilations of dispersal distances (e.g. Selkoe and Toonen 2011). However, we compensated for this using eqn (1) and found no significant difference in marker type in our ANOVA, nor have others who also accounted for the rate difference (Bradbury *et al.* 2008). A controlled study of the effects of different mutation rates in different markers on the IBD slope for a given species sampled from the same set of populations has not been directly addressed. In our study, we had five species in which more than one marker type was used on the same species from the same set of populations (Table 3). Two of these used both mtDNA and microsatellites (Thaler *et al.* 2011; Teixeira *et al.* 2013) and found a 0–1 order of magnitude difference in estimates of dispersal distances. Another study, by Jennings *et al.* (2013) used one mitochondrial gene and four nuclear loci (two introns and two noncoding anonymous fragments). Dispersal estimates using the PKG approach varied from 1 to 10 km for the different loci, with the multilocus estimate of 1.95 km. Two other studies used the mitochondrial regions cyt b and D-loop, to investigate genetic structure in *Scomber scombrus* (Nesbo *et al.* 2000) and *H. dactylopterus* (Aboim *et al.* 2005). While in the first case, dispersal estimates for each of those genes were 424 and 3068 km, respectively, in the second, these were 17 and 19 km. The disparity in dispersal estimates among markers might reflect systematic differences in rates of evolution, neutrality or degree of drift-migration equilibrium among marker types. Based on the degree of variation in estimates for a single species, we recommend that future studies estimating dispersal scales from genetic data use multiple marker types and as many populations as possible. Simulations and analytical studies that characterize the error structure of IBD slope estimates and related dispersal estimates under realistic marine population conditions would also be valuable.

It is important to consider the possible impact of nonequilibrium population structure on our results. A variety of factors can disrupt or prevent establishment of drift-migration equilibrium over all or part of a species range. For example, greater habitat fragmentation and resulting local or regional extinction/recolonization events may be more common in the deep sea compared to shallower habitats and could result in systematic differences in the degree to which populations have approached drift-migration equilibrium. Such a systematic difference would lead to large differences in the magnitude of *individual values of Fst* for deep vs. shallow taxa. However, IBD *slope* estimates are relatively insensitive to nonequilibrium conditions (Slatkin 1993). Slatkin (1993) showed analytically and via simulations that the geographic extent over which IBD can be found increases approximately with the square root of time (number of generations), but the IBD slope converges on its equilibrium value much more quickly (within as little as 1–10 generations, given model assumptions used in simulations). Subsequent simulation studies bear this result out (e.g. Bradbury & Bentzen 2007). Thus, if IBD is detected, the slope calculated over the portion of the species range where IBD exists is robust to nonequilibrium conditions. Our use of Mantel *P*-values to assess statistical significance of IBD over a given study extent is thus expected to reduce any impact that systematic differences in equilibrium might cause in dispersal distance estimates.

Another important caveat is the uneven distribution of species among the various categories (taxa, life histories, habitats) in our analyses, which confounds the interpretation of how the different taxa, life histories or habitats might influence dispersal. For example, we tested whether dispersal distances differed among larvae dispersing in pelagic, demersal or benthic realms. Dispersal distances were greater for pelagic larvae, but this was confounded because all the fish were pelagic and fish had larger dispersal distances than invertebrates. So it was unclear whether the greater dispersal for pelagic larvae was because pelagic larvae disperse greater distances or because the demersal and benthic strategies did not include any fish. Similarly, the benthic larvae were all direct developers, whereas the pelagic and demersal forms included both lecithotrophs and

planktotrophs, but no direct developers. Thus, developmental mode might also confound any interpretation of the difference between pelagic, demersal and benthic larvae. While we consider the statistical analyses of the different taxa, life histories and habitats to be valuable, the results should be interpreted cautiously because of the uneven distribution of species among the different categories.

One final consideration is the low levels of representation of the many different deep-sea habitat types. Although we obtained a first-order estimate of the range of dispersal distances in the deep sea, it is important to emphasize the small number of species from most habitat types in our data set. Probably, the best-studied ecosystems are hydrothermal vents. The least studied are nonchemosynthetic ecosystem invertebrates, with only 11 species sampled. However, even the deep-sea fishes were only represented by two species at depths >2000 m. In general, given the paucity of data for deep-sea taxa, there is an urgent need for more population genetic studies of deep-sea species in general, and an emphasis should be placed on targeting nonhydrothermal vent habitats and invertebrates at all depths.

Conclusions and implications for conservation and spatial planning of deep-sea reserves

Conservation planning for the deep sea is probably the most complex of any ecosystem on this planet, given its remoteness and the paucity of knowledge for the many different and unique habitats. Further, parts of the deep sea are under national jurisdiction, but the vast majority is in international waters, crosses international boundaries and has little organized governance. Conservation policies must consider both national and international laws and regulations as well as the needs of various stakeholders such as mining or fishing sectors. The deep sea is also extremely vulnerable and faces mounting pressures related to resource extraction, pollution and climate change (e.g. Mengerink *et al.* 2014). The design of individual reserves and networks of reserves is crucial to maintain parts of the deep sea as functioning and viable ecosystems that can act as buffers to future change scenarios. As identified previously, dispersal and connectivity are important considerations when planning reserve networks. Our study is the first to estimate dispersal for a large swath of deep-sea species and to compare this to existing data of shallow-water taxa.

Using identical methods, dispersal ranges estimated for the deep-sea fauna were comparable to or slightly larger than those for shallow water. The small difference between average dispersal distances in deep vs shallow habitats is not of great relevance for planning and conservation in the deep sea because it does not exceed the range of variation within either data set. In fact, what is more surprising about our results is the similarity to results from shallow-water systems, suggesting that shallow-water MPA design principles may translate more easily to the deep sea than previously thought. These results imply that the scales of dispersal and connectivity used in designing marine reserves for the deep-sea fauna are likely to be similar to or slightly larger than those used in shallow water. The spatial scale of any reserve or network should be sufficiently large to ensure a significant level of self-recruitment across taxa from within the reserves, as well as adequately spaced to enable external recruitment (Botsford *et al.* 2003, 2009; Gaines *et al.* 2003, 2010; Palumbi 2003; Wilhelm *et al.* 2014). Of course, other factors such as taxonomic diversity (reflected in varying dispersal capabilities), life histories and habitats must also be considered when establishing the nature, location and scale of a reserve or a reserve network (Kinlan *et al.* 2005). Buffer zones from mining activities, which can impact reserves (Wedding *et al.* 2013), should also be considered.

Reserve size and spacing suggested by our study may prove particularly difficult for patchy habitat types such as chemosynthetic ecosystems and seamounts. Many of these are smaller in areal coverage and spaced further apart than the mean dispersal distance found in this study. Although patchily distributed, these habitat types already experience some of the highest deep-sea impacts from trawl fisheries and may experience significant impacts in the near future through mining for polymetallic sulphides and cobalt-rich manganese crusts. The growing pressure on seabed mineral resources is driving a need to develop environmental management plans for potential mining areas. Benthic communities in most of these areas remain poorly understood, making it difficult to predict the scale and extent of future impacts. Habitat loss due to mining could lead to important changes in ecological connectivity patterns that help sustain deep-sea metapopulations. These habitats should be a particular focus of future connectivity studies and recommendations should reflect their special needs. At the same time, research should not be limited to these habitats, as the many caveats of our analyses provide a strong impetus for substantial future efforts to assess connectivity of deep-sea species from a variety of habitats, taxonomic groups and depth zones.

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Authorship order is by level of contribution. ARB conceived the study, and – all authors compiled papers, analysed the data and wrote the manuscript.

Data accessibility

All data used in this synthesis are included in Table S1 (Supporting information). The original data that these results were derived from are available in the cited papers.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Scatterplot of all data points within each category in the Translated Marker factor.

Fig. S2 Scatterplot of all data points within each category in the Ocean factor.

Fig. S3. Scatterplot of all data points within each category in the Taxon factor.

Fig. S4 Scatterplot of all data points within each category in the Phylum factor.

Fig. S5 Scatterplot of all data points within each category in the Genetic Structure Statistic (GSS) factor, coded as Type of F_{ST} metric employed in the paper.

Fig. S6. Scatterplot of all data points within each category in the Adult Habitat factor.

Fig. S7 Scatterplot of all data points within each category in the Adult Mobility factor.

Fig. S8 Scatterplot of all data points within each category in the Larval Feeding Type factor.

Fig. S9 Scatterplot of all data points within each category in the Larval Dispersal factor.

Fig. S10 Scatterplot of all data points within each category in the Adult Depth Zone factor.

Table S1 Summary of data used for this study.

Table S2 Number of dispersal estimates for each species included in the All and SigMantel datasets.

Table S3 Summary of variability of $\log_{10}$(PKG Dispersal Estimate [km]) by taxon for the a) SigMantel b)All dataset.