Vol. 393: 1–12, 2009
doi: 10.3354/meps08287

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published October 30

OPEN ACCESS

FEATURE ARTICLE

Population genetics, larval dispersal, and connectivity in marine systems

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ABSTRACT: Population connectivity plays significant roles on both evolutionary and ecological time-scales; however, quantifying the magnitude and pattern of exchange between populations of marine organisms is hindered by the difficulty of tracking the trajectory and fate of propagules. We explored biophysical correlates of population substructure to determine how well pelagic larval duration (PLD) correlates with population genetic estimates of connectivity in a sample of 300 published studies drawn pseudo-randomly from about 1600 hits on electronic searches. In direct contrast to the general expectation of a strong correlation, we find that average PLD is poorly correlated ($r^2 < 0.1$) with genetic structure (F_{ST}). Furthermore, even this weak correlation is anchored by non-pelagic dispersal, because removal of the zero PLD class (direct developers) from the analysis resulted in a non-significant relationship between F_{ST} and PLD. For species in which minimum, maximum, and mean PLDs were available, it is noteworthy that both minimum and maximum PLDs are better correlated with F_{ST} than the mean larval duration, which has been used in all such previous studies. A 3-way ANCOVA reveals that genetic marker class (allozymes, microsatellites, and mitochondrial DNA sequences), as opposed to habitat or swimming ability, explain most of the variation in F_{ST} ($F = 7.113$, df = 2, $p = 0.001$), with higher values of F_{ST} obtained from mtDNA than with either microsatellites or allozymes (which were not significantly different). Our meta-analysis refutes recent reviews and conventional wisdom that PLD is a good predictor of the magnitude of gene flow and geographic scale of population structure in marine systems.

KEY WORDS: Genetic structure · Pelagic larval duration · PLD · Isolation-by-distance · Marine reserve design · *F*-statistics

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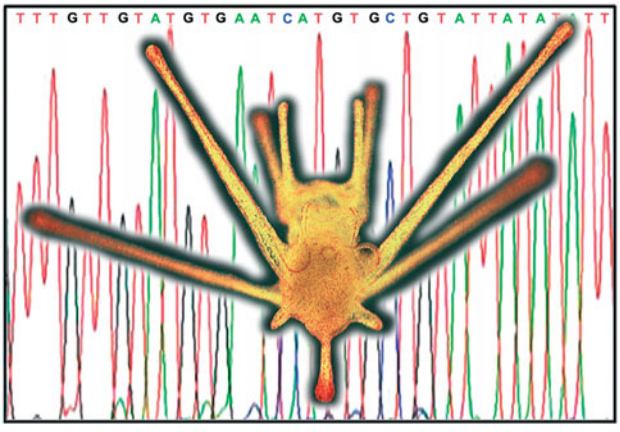

DNA sequences are used to infer patterns of larval dispersal in organisms such as the heart urchin *Brisaster latifrons*.

Image: Michael Hart

INTRODUCTION

Dispersal plays a fundamental role in structuring populations, and the wide range of dispersal strategies found among terrestrial and marine species is presumed to have wide-reaching micro- and macroevolutionary ramifications (Jablonksi 1986, Bohonak 1999, Kinlan & Gaines 2003, Bullock et al. 2006). Ideally, dispersal is quantified by tracking large numbers of individuals and observing their movements, but it is often not possible to obtain direct measurements of movement of tiny propagules, such as seeds and larvae. Consequently, patterns of dispersal remain poorly understood for many species, despite the importance of dispersal in shaping ecological processes and

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informing conservation and management decisions (Cowen et al. 2006, Fogarty & Botsford 2007). For example, a common theme in the recent literature on marine reserves is that reserve configuration needs to reflect the dispersal of individuals among populations; however, there is far less agreement about how dispersal distance and the magnitude of exchange actually should be estimated (e.g. Halpern & Warner 2003, Palumbi 2003, Dawson et al. 2006, Treml et al. 2008).

The dispute about how to quantify dispersal kernels is due in part to the challenge of studying dispersal of individuals directly, because most macroscopic marine species have a bipartite life cycle in which sessile or sedentary adults produce tiny planktonic propagules that are virtually impossible to track with current technology (Bradbury & Snelgrove 2001, Levin 2006). The small size and weak swimming ability of most marine larvae have been used to argue that they are oceanographically advected from their natal populations by ambient currents and that their dispersal potential is determined primarily by the length of their pelagic stage (Scheltema 1971, Grantham et al. 2003).

These intuitive arguments have been the basis for a number of reviews, which find a strong correlation between dispersal potential and population connectivity in a limited number of species (e.g. Waples 1987, Doherty et al. 1995; reviewed by Bohonak 1999). Expanding on this practice, recent meta-analyses have shown a strong positive correlation between dispersal potential, estimated as mean pelagic larval duration (PLD), and realized dispersal. For example, Shanks et al. (2003) surveyed 25 species for which dispersal could be observed directly, experimentally, or through the progressive spread of alien species and found that the more time propagules spend in the water column, the further they tend to be dispersed ($r^2 = 0.60$). Likewise, Siegel et al. (2003) showed a very strong correlation ($r^2 = 0.80$) between the length of the pelagic larval phase and the mean absolute dispersal distance estimated using a population-genetic modeling approach. These studies appear to corroborate the conventional wisdom and long-standing hypothesis that longer planktonic larval durations confer greater dispersal ability (e.g. Jablonski 1986, Doherty et al. 1995, Bohonak 1999) and that knowledge of PLD can be used as a reasonable proxy for realized dispersal distance. In contrast, a number of studies indicate that factors such as larval behavior (Warner & Cowen 2002, Leis 2006, Woodson & McManus 2007) and mesoscale oceanography (Wing et al. 1998, Bradbury & Snelgrove 2001, Diehl et al. 2007) are responsible for a significant amount of larval retention and/or self-recruitment. Likewise, many population genetics studies report exceptions to the rule of decreased population subdivision in species with relatively long PLDs (e.g. Todd 1998, Taylor & Hellberg 2003, Rocha et al. 2005, Baums et al. 2006, Bowen et al. 2006). The abundance of such counter-examples does not fit well with the extremely strong correlations between PLD and dispersal found in previous analyses which indicate that from 60 to 90% of the variation in dispersal distances is explained by the length of the pelagic developmental period (e.g. Siegel et al. 2003, Shanks et al. 2003, Kinlan et al. 2005).

Such strong correlations ($r^2 = 0.60$ to 0.90, depending on the study) would imply that the majority of studies support the expectation that increased PLD would result in increased gene flow and, consequently, decreased levels of population genetic structure. In reading the literature, however, no such obvious pattern emerges among population genetic studies of marine species, and we wondered how representative the specific studies included in previous analyses were of marine connectivity in general. Our study therefore sought to randomly survey the published literature to determine how broadly applicable and predictive PLD is for population genetic structure in marine organisms. To this end, we surveyed 300 publications drawn pseudo-randomly from the published literature, which we then used to assess whether PLD and the degree of genetic population differentiation (F_{ST}, ϕ_{ST}) are significantly correlated for marine taxa with pelagic larvae.

In addition to evaluating PLD, we also explored other potential correlates of gene flow that have not been considered in previous meta-analyses. The impacts of various biophysical mechanisms on larval transport and settlement are well documented for some species (e.g. Gilg & Hilbish 2003, Baums et al. 2006, Galindo et al. 2006), but these factors are largely absent from models used for designing marine reserves (but see Mace & Morgan 2006). Additionally, different classes of genetic markers (e.g. allozymes, microsatellites, and mitochondrial DNA sequences) are often used interchangeably to estimate population differentiation, but there are many reasons to question exact values of quantitative estimates of dispersal based on genetic differentiation (Hutchison & Templeton 1999, Whitlock & McCauley 1999), and it is widely agreed that quantitative results from different classes of genetic markers are rarely directly comparable (Grosberg & Cunningham 2001, Bazin et al. 2006). Therefore, we include these factors explicitly in our analysis and ask (1) How well does PLD predict population genetic structure in marine organisms overall? (2) In addition to the length of pelagic development, do estimates of gene flow among species vary by habitat, genetic marker class, or larval swimming ability?

METHODS

Literature survey. We sampled peer-reviewed literature from queries on the ISI Web of Science search engine, spanning publications from January 1980 to June 2007. Key words and phrases used in the search queries included combinations of the following terms: marine, genetic structure, population structure, population genetics, larval dispersal, marine dispersal, population connectivity, genetic, and gene flow. The searches resulted in >1600 hits, not all of which pertained specifically to gene flow among marine organisms, and after culling to this subject area, we began to collect literature pseudo-randomly until we reached 300 papers for inclusion in our study. This final number was determined by a 1 yr time limit to accumulate, read the papers, and compile a database of the metadata for analysis. These 300 papers were then filtered according to the following criteria (modified from the selection criteria of Kinlan & Gaines 2003), which ultimately left us with data on 130 species drawn from 87 of those 300 studies. The selection criteria were that each study included must have (1) surveyed a minimum of 3 subpopulations, (2) reported a global or overall F_{ST} or ϕ_{ST} value for the study, (3) examined an organism for which an estimate of PLD is available, (4) included species with sessile or sedentary adults, (5) surveyed multiple loci, if using nuclear data (allozymes or microsatellites), and (6) included species for which sexual reproduction was the primary mode of propagation. From these papers, we created a database that included overall F_{ST}, PLD (minimum, maximum, and mean), genetic marker type, larval horizontal swimming ability, and habitat (Supplement 1, available at www.int-res.com/articles/suppl/m393p001_app.xls or by request from the authors).

Definitions and data categorization. Wright's (1951) hierarchical *F*-statistics partition population-wide genetic variance (F_{IT}) into population substructure (F_{ST}) and non-random mating (F_{IS}) components. F_{ST} is the fixation index, which in an idealized system ranges from 0 to 1, where 0 represents uniform allele frequencies among subpopulations and 1 indicates that each of the subpopulations is fixed for an alternate unique allele (Hartl & Clark 1997). Under specified models, the magnitude of population substructure can be used to infer the amount and direction of gene flow among populations (Wright 1951, Hutchison & Templeton 1999, Palumbi 2003). Although this framework has some substantial practical limitations (Whitlock & McCauley 1999, Jost 2008), F_{ST} continues to be a valuable tool for exploring the magnitude of gene flow among populations, as evidenced by the ubiquity in the literature (Hutchison & Templeton 1999, Neigel 2002, Palumbi 2003). Throughout this paper, F_{ST} refers to the global or overall F_{ST} of all sampled populations in the included studies.

Habitats were defined according to their biological and/or geophysical properties. 'Reefs' refer to any organo-sedimentary subsurface feature that forms a relief from the surrounding seafloor, that lies in close proximity to islands or continents (in contrast to seamounts), and which hosts biological communities that are unique in comparison to nearby assemblages. Intertidal organisms occupy any substrate that occurs within the zone demarcated by the highest and lowest tide lines. Subtidal habitat is defined as the total region extending from the intertidal out to 100 km from shore or from the surface to 200 m in depth (whichever occurs first and exclusive of reefs), because subdividing from 0 to 30 m depth and from 31 to 200 m depth, to reflect different hydrography between these 2 habitats (Shanks & Eckert 2005), resulted in an insufficient sample size. Estuaries were also excluded from the analysis due to low sample size.

Vertical positioning of larvae in the water column and orientation to environmental cues are likely to be important contributors to patterns of larval dispersal (Warner & Cowen 2002, Woodson & McManus 2007), but data were unavailable for most species; therefore, we used a number of studies on the horizontal swimming ability of larval fishes and invertebrates to classify relative larval mobility (Table 1). We tested whether larval swimming ability affects population

Table 1. Ranges of reported horizontal swimming velocities for larvae of various taxa. SP: Subphylum

Phylum	N	Swimming velocities (cm s^{-1})	Category of swimming ability	Source
Porifera	1	0.05–0.33	Weak	Chia et al. (1984), Maldonado & Young (1996)
Cnidaria	19	0.04–3.0	Weak	Chia et al. (1984)
Echinodermata	13	0.01–0.03	Weak	Chia et al. (1984)
Arthropoda	9	0.6–33	Strong	Phillips & Olsen (1975), Chia et al. (1984)
Mollusca	24	0.02–0.08	Weak	Hidu & Haskin (1978), Chia et al. (1984)
Chordata (SP Urochordata)	4	0.3–6.0	Weak	McHenry (2005)
Chordata (SP Vertebrata)	77	1.8–65.5	Strong	Leis & Fisher (2006)

connectivity by dividing taxonomic groups into 2 broad categories (weak and strong swimmers) based on the range of reported horizontal swimming velocities within these taxa (Table 1). We categorized larvae that were capable of maximum horizontal swimming velocities of ≤6 cm s^{-1} as relatively weak swimmers, while strong swimmers are those capable of maximum speeds >20 cm s^{-1}. There were no taxonomic groups reported with maximum swimming speeds between 6 and 20 cm s^{-1} (Table 1); therefore, these 2 groupings reflected a natural break in the data, with non-overlapping categories of larval mobility. Clearly, this method would not account for taxa that demonstrate ontogenetic shifts in swimming ability, e.g. crab zoea are weak horizontal swimmers in contrast to crab megalopae. We examined maximum swimming speeds because such detailed life-history information on ontogenetic swimming ability was only available for a small fraction of the species that we surveyed. Organisms with demersal development or crawl-away larvae that do not exhibit any swimming behavior were classified as weak swimmers.

Effects of study scale and PLD on F_{ST}. All data were log-transformed prior to analyses. Because both F_{ST} and PLD can include values of zero, we added 1 to each value prior to transformation, so that the log-transformed values would equal zero, i.e. log(F_{ST} + 1) and log(PLD + 1). We first explored whether F_{ST} values among different species are sensitive to the maximum geographic scales of the individual studies. For example, 2 studies on the same species may result in different estimates of F_{ST} (and inferences about dispersal ability), depending on the geographic proximity of the populations sampled. To test for this potential bias, we performed a regression analysis of F_{ST} against geographic scale, tried standardizations of both geographic scale (F_{ST} per kilometer) and genetic differentiation (F_{ST} / (1 – F_{ST})), and attempted to bin studies by geographic scale and location. We similarly evaluated various measures of PLD (average, minimum, and maximum) as potential predictors of F_{ST} to determine which is best correlated with estimates of gene flow.

Effects of additional factors on F_{ST}. We first confirmed that our log-transformed data met the assumptions of normality and homogeneity of variance before performing an analysis of covariance (ANCOVA) to examine the relationship between gene flow and habitat, genetic marker class, and larval swimming ability. We used each of the statistically significant correlates of F_{ST} as covariates in an ANCOVA to determine if F_{ST} differed among genetic markers, habitats, or larval swimming abilities. We also ran a pairwise general linear model analysis to examine each of the individual factors and the interactions among them.

Among the selected studies, little or no data were available for some combinations of terms: specifically, estuarine species were poorly represented, and weakly swimming reef organisms studied via mtDNA were absent from our sample of the literature, and were not considered in the analysis. We dealt with the issue of this missing cell by generating Type IV sums of squares to compare treatments for which data were available (Shaw & Mitchell-Olds 1993). The results of the ANCOVA were thus valid for 17 of the 18 total possible combinations between the different markers, habitat types, and swimming abilities. Sequential Bonferroni tests for multiple comparisons of means were performed to determine the effects of significant treatment terms. All statistical analyses were conducted using SPSS Version 15.0 (SPSS Inc.), and a plot of observed versus predicted residuals did not reveal any patterns that would bias the results or interpretation of the regression model (data not shown).

RESULTS

Effects of study scale and PLD on F_{ST}

Among our sample of 300 pseudo-randomly selected studies from the literature, the 87 which met all 6 selection criteria provided data on 130 species (Supplement 2; Supplements 2 to 6 are available at www.int-res.com/articles/suppl/m393p001_app.pdf), some of which were studied multiple times, resulting in 149 individual data points. Additionally, data on 26 of the 32 species studied by Kinlan & Gaines (2003) met the selection criteria and were also included in the data set.

Global F_{ST} was poorly correlated with geographic study scale (r^2 = 0.02, p = 0.07; Table 2). Consistent with previous reviews (e.g. Bohonak 1999, Siegel et al. 2003), PLD was negatively correlated with F_{ST}, regardless of whether the average, minimum, or maximum PLD was used (Fig. 1, Table 2). It is noteworthy, however, that the predictive power of PLD on F_{ST} is uniformly low (r^2 ranged from 0.097 to 0.175) in comparison to previous analyses, and there is considerable scatter in the data across the entire range of PLDs (Fig. 1). Including the geographic scale of study and standardizing the reported F_{ST} by geographic distance did not change this result. The relationship between log average PLD and log F_{ST} per kilometer was actually slightly decreased relative to the values not standardized (r^2 = 0.082, p > 0.05; data not shown). Likewise, although the magnitude of correlation is slightly different in each analysis, the same overall pattern is seen whether comparisons are standardized by F_{ST} / (1 – F_{ST}), geographic scale of study, or by binning studies by geographic scales (r^2 ranged from 0.0004 to 0.1223; Supplement 3; www.int-res.com/articles/suppl/m393p001_app.pdf).

Table 2. Predictors of overall population genetic structure (F_{ST}). PLD: pelagic larval duration

Effect	N	r^2	p	Equation
Geographic study scale (km)	149	0.023	0.067	$y = 0.019x - 0.011$
All PLD data[a] (d)				
Average PLD	149	0.097	0.000	$y = -0.037x + 0.094$
Minimum PLD	95	0.164	0.000	$y = -0.047x + 0.103$
Maximum PLD	95	0.175	0.000	$y = -0.046x + 0.113$
Non-zero PLD data only[a] (d)				
Average PLD	135	0.028	0.053	$y = -0.023x + 0.073$
Minimum PLD	80	0.095	0.006	$y = -0.041x + 0.095$
Maximum PLD	81	0.090	0.007	$y = -0.043x + 0.109$

[a]Minimum and maximum PLD data were only available for a subset of the organisms surveyed

Species with direct development or crawl-away larvae have a pelagic duration of zero because they actually lack a pelagic larval stage entirely. Therefore, we also regressed F_{ST} against non-zero PLD data to examine the effects of non-pelagic dispersal. We found that the significant negative relationship between F_{ST} and average PLD was anchored by the non-pelagic species; when removed, the relationship became non-significant (p = 0.053) for average PLD (Fig. 1, Table 2). Although removal of species that lack a pelagic stage does not change the significance of the correlation between minimum or maximum PLD and F_{ST}, the proportion of variation explained in the non-zero PLD analysis is roughly half that in the complete data set (Fig. 1, Table 2).

Effects of additional factors on F_{ST}

Minimum and maximum PLDs were significantly correlated with F_{ST}; however, there were insufficient data to develop ANCOVA models using these measurements of PLD (Table 2). Therefore, as with previous studies, we used average PLD, and incorporated that as a covariate in the ANCOVA model to separate the variation in F_{ST} attributable to PLD (r^2 = 0.028, Table 2) from that of marker type, habitat, and larval swimming speed. The 3-way ANCOVA with non-zero PLD species explained 47% of the variability in F_{ST} (Table 3; full model output for species with and without pelagic larval development is presented in Supplement 4; www.int-res.com/articles/suppl/m393p001_app.pdf). Larval swimming ability and habitat type were not significant terms in the model; in contrast, differences in F_{ST} among the classes of genetic markers were significant (Table 3). Further investigation via post hoc comparisons indicated that significantly higher values of F_{ST} were reported in studies using mtDNA than in those using either of the nuclear markers (allozymes and microsatellites), which were not significantly different from one another (Table 4). Finally, the general linear model analysis was consistent

Table 3. Analysis of covariance of biophysical factors on reported population genetic structure for marine taxa with a pelagic larval stage (n = 129). PLD: pelagic larval duration; bold print: significant p-values

Factor	Type	Levels or transformation	*F*	df	p
Mean non-zero PLD (d)	Covariate	Log-transformed to linearize	9.464	1	**0.003**
Marker	Independent	Allozyme, microsatellite, mtDNA	7.113	2	**0.001**
Habitat	Independent	Reef, subtidal, intertidal	0.996	2	0.372
Larval horizontal swimming ability	Independent	Weak (≤6 cm s^{-1}), strong (>20 cm s^{-1})	0.001	1	0.974

Table 4. Bonferroni-adjusted pairwise comparisons of mean F_{ST} values by marker type. *p = 0.05

Marker (I)	Marker (J)	Mean difference (I – J)	SE	Significance[a]	95% CI for difference[a] Upper	Lower
Allozyme	Microsatellite	0.003	0.016	1.000	−0.036	0.042
	MtDNA	−0.062*,[b]	0.016	0.001	−0.102	−0.022
Microsatellite	Allozyme	−0.003	0.016	1.000	−0.042	0.036
	MtDNA	−0.065*,[b]	0.020	0.004	−0.113	−0.017
mtDNA	Allozyme	0.062*,[c]	0.016	0.001	0.022	0.102
	Microsatellite	0.065*,[c]	0.020	0.004	0.017	0.113

[a]Adjustment for multiple comparisons: Bonferroni
[b]An estimate of the modified population marginal mean (J)
[c]An estimate of the modified population marginal mean (I)

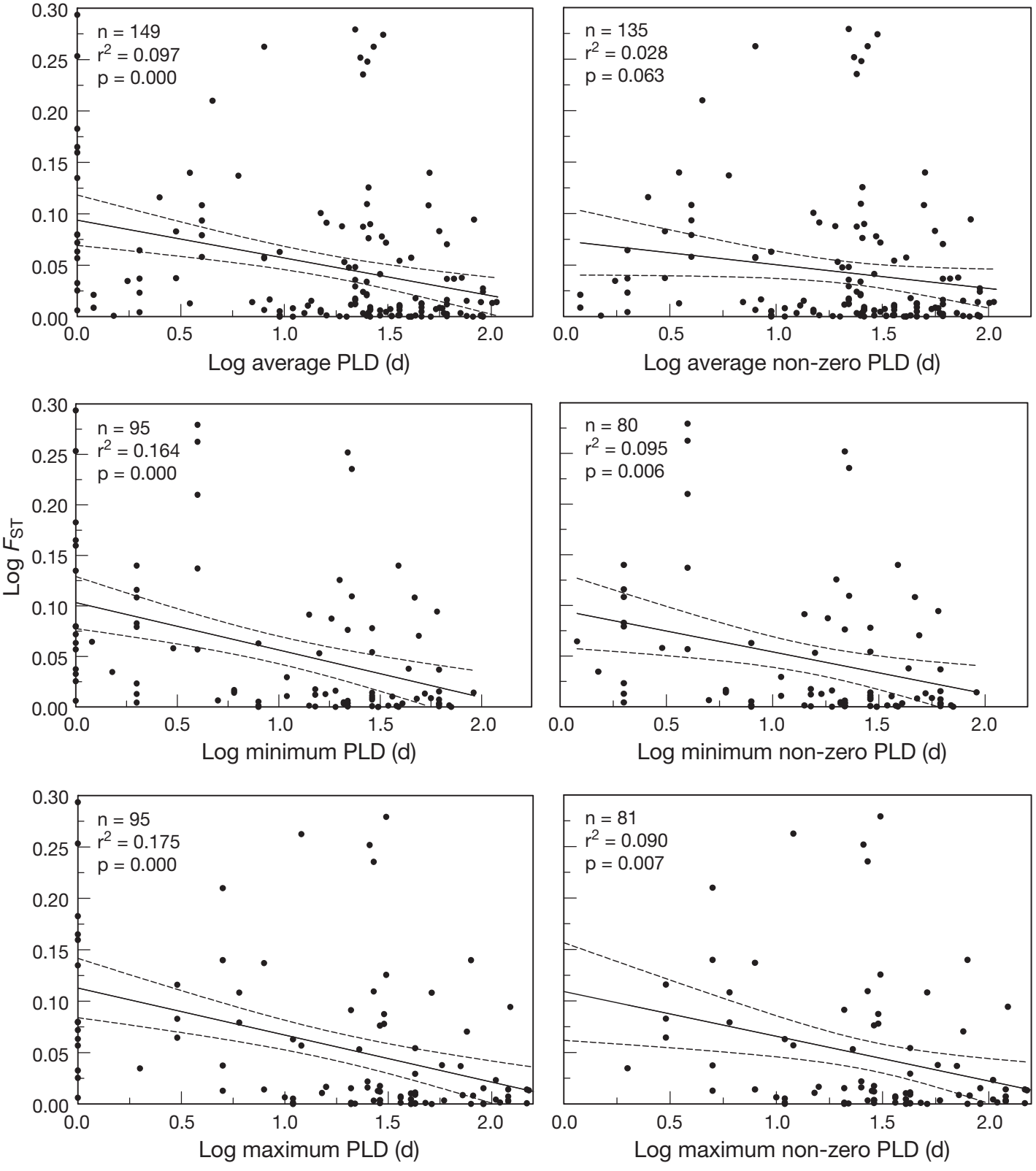

Fig. 1. Overall population genetic structure (F_{ST}) versus 3 measures (average, minimum, and maximum) of pelagic larval duration (PLD) for a range of marine vertebrate and invertebrate fauna. The plots on the right share the same *y*-axes as those on the left but exclude species that lack a planktonic larval stage. The 95% confidence intervals for each regression line are plotted as dotted lines around the solid best fit line

with the full ANCOVA (Supplements 3 & 4; www.int-res.com/articles/suppl/m393p001_app.pdf).

DISCUSSION

The ability to resolve the pattern and magnitude of demographic exchange among populations is important to our understanding of the evolutionary and ecological processes of speciation, adaptation, persistence, and population dynamics. Management and conservation efforts can be greatly informed by considering explicitly how landscape and ecological factors shape the genetic diversity and structure of populations. Such direct comparisons are difficult in complex 3-dimensional environments, where the 'landscape' is dominated by water or atmospheric circulation patterns directing the dispersal pathways of microscopic propagules (e.g. Baums et al. 2006, Galindo et al. 2006, Schueler & Schlunzen 2006). A number of advances have been made in developing tools to quantify population connectivity in marine environments, including natural and artificial tags (Warner & Cowen 2002) and spatially explicit physical models of larval dispersal (e.g. Cowen et al. 2000, Baums et al. 2006). However, the complexity of marine hydrodynamics and the variation in life-history strategies within and among species continues to make accurate estimates of connectivity notoriously difficult to obtain (Warner & Cowen 2002, Levin 2006). In the absence of quantitative estimates of larval exchange among locations, it is very appealing to use PLD as a proxy for the dispersal potential of benthic organisms (Kinlan & Gaines 2003, Lester et al. 2007), but an unbiased sample drawn from the literature reveals only weak correlations between any available measure of PLD and F_{ST} (r^2 ranged from 0.028 to 0.175).

PLD and larval development

A commensurate increase in gene flow with prolonged PLD is an intuitive expectation that has been supported by several earlier reviews (e.g. Bohonak 1999, Shanks et al. 2003, Siegel et al. 2003), yet our results contrast starkly with previous findings that from 60 to 90% of the variation in dispersal is explained by PLD. What mechanisms may account for the weak correlation that we found between population connectivity and planktonic duration? First, our broad sampling of the literature may inject considerably more noise into the relationship than selective inclusion has in previous studies. We believe that noise is an important reality, and our study indicates that, while a tight relationship between pelagic duration and dispersal may hold in some specific cases, the extrapolation of those findings to a general rule for marine organisms is inappropriate; our data show that PLD is a poor predictor of larval exchange in the vast majority of cases and explains <10% of the variation in population structure observed across a random sample of published studies to date. We caution readers not to interpret this finding as showing that there is no relationship between pelagic duration and dispersal potential. Other studies have demonstrated a clear relationship for specific taxa (e.g. Waples 1987), and we found some significant correlations in our study as well; however, the strength of the correlations is far lower (less than half) than reported in previous surveys based on more selective data sets. We argue that our analysis captures a realistic representation of the literature and that patterns of connectivity in marine systems are in fact noisy and difficult to predict based on simple life-history characters.

A second complication likely derives from the average PLD reported in the literature often being poorly estimated for at least some of the taxa under consideration. Fish possess otoliths and other calcified tissues that record their growth over time, but the near absence of analogous structures in invertebrates requires that researchers rear invertebrate larvae under laboratory conditions to estimate their planktonic periods. There are many who question whether such artificial rearing experiments provide a realistic estimate of field development times and larval behaviors (e.g. Bradbury & Snelgrove 2001, Leis 2006). Third, the length of the planktonic larval stage is a plastic life-history trait that can vary by an order of magnitude or more for some species (Toonen & Pawlik 2001, Addison & Hart 2004). Such variation in PLD can occur due to behaviors such as delayed metamorphosis (reviewed by Pechenik 1990) or larval responses to environmental stochasticity (Woodson & McManus 2007). Finally, the expectation that dispersal potential is determined primarily by hydrodynamic diffusion for the length of the pelagic larval period is rooted in the implicit assumption that larvae are largely passive particles, an assumption that has now been invalidated for many marine taxa (reviewed by Warner & Cowen 2002, Leis 2006).

While most of the invertebrate taxa surveyed here are unable to swim effectively against ambient currents as meroplankton (Table 1), the majority of larvae are quite capable of overcoming vertical current velocities (reviewed by Chia et al. 1984, Warner & Cowen 2002). Larvae also possess a variety of sensory structures that enable them to orient to environmental cues (e.g. temperature, light, and salinity), which in combination with vertical swimming behavior allow them to actively position and maintain themselves within a particular water mass (e.g. Pineda 1999; reviewed by

Sponaugle et al. 2002). Vertical positioning within the water column has been demonstrated by numerous taxa to maximize residence time near food sources, mitigate advection away from and/or aid in transport towards suitable settlement habitat, and for predator avoidance (e.g. Woodson & McManus 2007; reviewed by Warner & Cowen 2002). The coupling of larval orientation behaviors with mesoscale oceanography provides an elegant example of effective adaptation and habitat utilization; however, such complex biophysical interactions, which are often temporally variable, make the task of discerning useful predictors of population connectivity difficult (e.g. Wing et al. 1998, Diehl et al. 2007).

Effects of PLD on F_{ST}

Inferring dispersal potential from the length of pelagic larval development is attractive; both conventional wisdom and several previous reviews suggest that PLD is a reasonable approximation of dispersal potential in the field (e.g. Bohonak 1999, Kinlan & Gaines 2003, Shanks et al. 2003, Siegel et al. 2003, Kinlan et al. 2005). Such studies have been cited as 'indisputable evidence of the tight coupling between hydrodynamics and realized dispersal' (Treml et al. 2008, p. 21), and form the basis for a variety of management and conservation efforts, such as the design of marine protected area networks in the Pacific (e.g. Lester et al. 2007, Treml et al. 2008). However, the absence of a general proportional decrease in genetic structure with PLD in numerous species, myriad biophysical mechanisms for retention and self-recruitment (reviewed by Leis 2006), and the wealth of available studies sampled for our meta-analysis here, all refute a strong predictive link between PLD and population connectivity (inferred from F_{ST}).

We specifically considered the effect of maximum, minimum, and mean estimates of PLD on realized gene flow between populations (as measured by global F_{ST}) drawn from a sample of 300 of the >1600 published studies in the literature. Consistent with previous reviews, we found a statistically significant negative correlation between PLD and F_{ST}, but the variation explained by this relationship varies considerably (r^2 ranges from 0.10 to 0.18, $p < 0.01$) depending on which estimate of PLD is used (Fig. 1). All previous studies used mean PLD in their analyses, which we find to be the worst correlate of population genetic structure compared to either the minimum or maximum estimated PLD. More importantly, the significance of the relationship between PLD and genetic structure is driven largely by the presence or absence of a pelagic stage rather than the length of pelagic duration per se, because removal of the zero PLD class from the analysis results in a non-significant relationship between mean PLD and population genetic structure (Fig. 1). Interestingly, the only analysis that employed direct estimates of dispersal (e.g. based on visual observations of larval release and settlement, or of larval spatial distributions) found a bimodal distribution in dispersal, with larvae being either restricted (<1 km) or dispersed (>20 km), and removal of the zero PLD class resulting in a non-significant relationship between PLD and dispersal (Shanks et al. 2003). Likewise, in the Siegel et al. (2003) study, there is a cluster of low-PLD points that suggest a bimodal distribution, although they did not emphasize that pattern in their analysis. Both our data and that compiled by previous authors indicate that even short dispersal periods substantially reduce population structure in comparison to demersal or directly developing species. It is important to emphasize that these data do not indicate that time in the plankton is irrelevant. The presence or absence of a pelagic phase appears to be the primary driver of significance in our analysis, but there remains a slight trend across the range from very short to very long pelagic duration, even with mean PLD, and correlations using both minimum and maximum PLDs are always significant regardless of whether the zero PLD class is included or not (Fig. 1). Our primary finding is that mean PLD, however, has very little predictive value for population structure, and, even for the minimum and maximum pelagic durations, which remain significant upon removal of the non-pelagic dispersal category, PLD uniformly accounted for <10% of the variation in F_{ST}.

Our finding that PLD is weakly correlated with population structure across a broad range of marine taxa is clearly at odds with the very strong correlations reported in the previous analyses outlined above (e.g. $r^2 = 0.80$; Siegel et al. 2003). Additionally, while the minimum and maximum larval durations are not always known for an organism (these data were available for only ~50% of species), our results indicate that it is more informative to use the tails of the larval duration distribution than average PLD in models estimating dispersal and gene flow. For example, Lester & Ruttenberg (2005) found that PLD was a good predictor of range size ($r^2 = 0.257$) and concluded that this resulted from Indo-Pacific fishes with a long maximum PLD being able to cross the Eastern Pacific Barrier. The disparity between our results and those of previous publications (Bohonak 1999 and studies that rely on the model presented in Palumbi 2003, including Kinlan & Gaines 2003, Siegel et al. 2003, Kinlan et al. 2005, and Lester et al. 2007) likely has a variety of explanations. First, some previous reviews included only phylogenetically, geographically, and demographically

controlled comparisons (e.g. Bohonak 1999), and we were concerned that this may introduce a publication bias, because researchers seeking to test this relationship in such a controlled manner are naturally inclined to select taxa for which they expect the relationship is likely to hold. Second, we have drawn our pseudo-random sample of 300 studies from all hits in our search as opposed to a specific investigator-selected set of <35 studies in previous analyses. Third, Palumbi (2003) outlines a suite of serious issues with comparing estimates of dispersal based on low F_{ST} values in high-gene-flow species and advocates an isolation-by-distance (IBD) simulation approach over an estimate of population differentiation based on a summary statistic such as F_{ST}. The primary issue is that a statistical association between genetic differentiation and dispersal potential is not expected if the error in estimating F_{ST} is of the same magnitude as the difference among populations; this situation is particularly likely for marine species with high gene flow and low differentiation, where patterns observed in many published data sets are similar to noise generated by sampling variance (Waples 1998). Under such conditions, the reported advantage for this IBD slope-tuning approach is that, because sample sizes of individuals and loci can be standardized among comparisons, sampling artifacts can be minimized and biologically relevant signals can be separated from error variance noise (Palumbi 2003). While we agree with the intent, the largest source of sampling variance in comparisons of population differentiation derive from differences in genetic diversity among populations rather than sample sizes of individuals or loci, and such effects are greater in pairwise than in global F_{ST} comparisons. None of these previous analyses have controlled for genetic diversity variance, which is the primary source of noise in making these comparisons (Hedrick 2005, Jost 2008). In an effort to minimize this particular source of error variance in our analyses, we have used global F_{ST} rather than a model-based IBD slope-tuning approach. Further, Bradbury & Bentzen (2007) argued that Palumbi's (2003) IBD slope-tuning model, which is the basis of dispersal estimates in the studies by Kinlan & Gaines (2003), Siegel et al. (2003), Kinlan et al. (2005), and Lester et al. (2007), is highly inaccurate because of the particular suite of simplifying assumptions in the model. These assumptions include a single-locus, 2-allele system, a linear slope between genetic and geographic distance, and a 1-dimensional stepping-stone array of N identical populations in a circular array. A comparison of dispersal estimates generated by the Palumbi model, with direct measures of dispersal, revealed that IBD-slope-tuning model estimates of dispersal varied by as much as from 38 to 380% (Bradbury & Bentzen 2007). The calculation of dispersal distance from F_{ST} in the IBD-slope-tuning model from a single-locus, 2-allele idealized system—which is minimally affected by biases from within-population marker diversity—is particularly problematic because real data cannot calculate any F_{ST} value greater than the mean within-population heterozygosity (Hedrick 2005). This diversity effect is particularly critical for the highly polymorphic markers typically used to infer connectivity and can introduce highly non-linear biases into estimates of dispersal compared to this idealized model (the smaller the F_{ST}, the greater the possible error). The importance of these issues is highlighted by our reexamination of the 32 species used in previous studies: without the model, these same studies revealed no significant correlation ($r^2 = 0.006$, $p = 0.670$) between F_{ST} and PLD, as opposed to a highly significant correlation ($r^2 = 0.802$) when using the IBD-slope-tuning approach (Kinlan & Gaines 2003, Siegel et al. 2003). Finally, we have explicitly considered a number of biophysical factors in our study that have not been included in previous analyses, including (1) genetic marker class, (2) mesoscale oceanography, and (3) larval swimming ability, which we discuss in the following subsections.

Effects of genetic marker class on F_{ST}

Of the 3 biophysical factors that were considered in our analysis, only the genetic marker class was a significant term in the ANCOVA. Although allozymes, mtDNA, and microsatellites are frequently used interchangeably in the literature, many have questioned the validity of this practice (e.g. Grosberg & Cunningham 2001, Ballard & Whitlock 2004, Bazin et al. 2006). Across all studies surveyed, we found that values of population structure estimated from different markers are not equivalent. Our study also included 6 species, which were surveyed with each class of marker, and the rank value of F_{ST} values was consistent with our overall findings. Thus, arguments that direct comparisons of F_{ST} values among studies are unreliable and unjustified when values are derived from multiple marker classes appear well-founded.

A number of mechanisms may be responsible for the higher F_{ST} values and increased resolution that we found among the mtDNA studies. First, the uniparental inheritance of haploid mtDNA reduces effective population size (N_e) to one-fourth that of biparental, diploid nuclear markers. Consequently, mtDNA experiences increased rates of genetic drift and thus approaches alternate fixation more quickly (and exhibits higher F_{ST} values) than nuclear loci (Ballard & Whitlock 2004). Second, the disparity in the results of mtDNA and the 2 classes of nuclear markers may be attributed to differences in the inherent characters of the markers,

such as mutation rate, degree of polymorphism, time required to reach equilibrium, or selective pressure (reviewed by Ballard & Whitlock 2004), although considerable debate remains on the severity of this issue (e.g. Bazin et al. 2006, Wares et al. 2006). Lastly, the differences in estimates of genetic structure obtained with mitochondrial versus nuclear markers may be a statistical consequence of standardization, as outlined below.

Although there are many caveats to any quantitative estimate of connectivity based on F_{ST} (Whitlock & McCauley 1999), overall F_{ST} appears to be a robust indicator of the relative influence of genetic drift and gene flow in the approach of populations to alternate fixation (Hutchison & Templeton 1999, Grosberg & Cunningham 2001, Neigel 2002). Several recent publications have pointed out that the maximum calculable F_{ST} is inversely proportional to the mean within-population heterozygosity (Hedrick 2005, Meirmans 2006) and, therefore, does not accurately measure population differentiation (Jost 2008). Thus, for highly polymorphic genetic markers, such as microsatellite loci, the maximum calculable F_{ST} is reduced far below 1 (Hedrick 2005), and, counter to the intuition that more polymorphic loci will reveal finest population structure, F_{ST} values are actually constrained to be lower as allelic diversity becomes higher. This effect may explain why highly polymorphic microsatellites routinely showed lower F_{ST} values than mtDNA in this survey. Although it is possible to standardize F_{ST} values to account for marker heterozygosity (Hedrick 2005, Meirmans 2006) or to estimate genetic population differentiation directly (Jost 2008), we were not able to apply any of these adjustments to our analysis because the standardizations require raw data that were invariably unreported in published studies. However, if standardization were the primary issue to consider, one might expect a correlation between the relative ranks of average marker polymorphism (microsatellites > mtDNA > allozymes) that does not match the pattern from our survey (mtDNA > microsatellites = allozymes). Our results imply that additional factors, such as the 4-fold reduction of population size of mitochondrial relative to nuclear markers, time to equilibrium, or an interaction between factors such as effective population size, marker heterozygosity, and relative resolving power of loci, are responsible for the observed pattern.

Conclusions

Many terrestrial and marine organisms have propagules that are extremely difficult to track directly (reviewed by Bohonak 1999, Bullock et al. 2006, Levin 2006). This difficulty has resulted in the widespread appeal of proxies for estimating mean dispersal of tiny propagules in nature. Although recent efforts in landscape genetics have provided greatly improved understanding of dispersal of terrestrial vertebrates, similar efforts to incorporate complex 3-dimensional atmospheric and oceanographic conditions lag behind (Baums et al. 2006, Galindo et al. 2006, Schueler & Schlunzen 2006, Pringle & Wares 2007, Treml et al. 2008). The intuitive connection between PLD and dispersal potential, bolstered by recent studies indicating a strong correlation between the two, has resulted in the length of the planktonic larval stage being used as a convenient measure of dispersal potential for benthic organisms, both historically and in a growing number of ecological (e.g. Lester et al. 2007), management (e.g. Treml et al. 2008), and evolutionary (e.g. Jablonski 1986) studies. In contrast, there is also a large body of literature documenting high genetic partitioning among organisms with long larval durations or little structure in species with short pelagic periods (e.g. Todd 1998, Taylor & Hellberg 2003, Bowen et al. 2006). In reading the literature, there appeared to be as many exceptions as conformants to the rule, and this was at odds with the extremely strong correlations reported in previous studies. Thus, we undertook the present study to synthesize a large volume of genetic-structure and life-history data across a broad range of marine taxa to test whether the link between PLD and estimates of population connectivity were really as general and predictive as has been suggested in some recent studies. Our results indicate that PLD is, at best, a poor predictor of connectivity and that the variability among realized dispersal is too great to use PLD as a predictive proxy for conservation or management.

There are at least 2 obvious sources of error in this relationship, and either (or more likely both) may be responsible for the poor correlation between PLD and F_{ST} reported here. On the side of PLD, factors such as uncertainty in the duration of pelagic development, larval behavior, and mesoscale oceanography can all influence realized larval dispersal. On the side of population genetic structure, issues such as sampling design, marker type, the extended time scale over which F_{ST} reveals genetic connectivity, and F_{ST} standardization can all confound the relationship between PLD and population genetic structure from which connectivity is inferred. The high degree of scatter in these analyses indicates that our understanding of marine connectivity remains superficial and that the general acceptance of PLD as a reliable predictor of population connectivity across broad taxonomic lines is clearly unfounded. We argue instead that accurate estimates of dispersal and population connectivity in complex 3-dimensional environments will need to

consider the interplay of important biophysical, behavioral, and developmental factors through time and within the framework of standardized estimates of fine-scale genetic differentiation to ultimately consider dispersal in a realistic manner from the perspective of the organism rather than from that of the researcher.

Acknowledgements. This work was supported by funds from the National Science Foundation (OCE-0623678), Sea Grant (R/EL-43), the Hawaii Institute of Marine Biology—Papahānaumokuākea Marine National Monument Research Partnership (NMSP MOA 2005-008/66882), and the University of Hawaii, Department of Oceanography. K.W. especially thanks C. Smith, M. McManus, and B. Bergen for support and guidance while serving on her MS committee, and B. Bergen, A. Taylor, and C. Bird for assistance with statistical analyses. C. Smith, M. McManus, B. Bergen, K. Selkoe, B. Halpern, B. Bowen, S. Karl, C. Bird, C. White, Z. Forsman, and members of the ToBo Laboratory provided valuable discussion and feedback on this project and earlier versions of the manuscript, for which we are grateful. We also thank Steven Morgan, Alan Shanks, and the 3 anonymous referees who provided detailed reviews, which helped to clarify this presentation and improve the manuscript. This is HIMB contribution #1365 and SOEST #7817.

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Editorial responsibility: Steven Morgan, Bodega Bay, California, USA

Submitted: September 29, 2008; Accepted: August 27, 2009
Proofs received from author(s): October 5, 2009