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commentary

Biogeography and complex traits: dispersal syndromes, in the sea

How dispersal potential manifests as realized migration (*sensu* Wright 1931) is a core question that links pattern and process in biogeography, ecology and evolution. It is a question that cannot be answered by knowing about dispersal alone; the answer requires understanding how traits of organisms influence dispersal potential, how abiotic and biotic environments filter dispersers, and how interactions between organisms and environments determine dispersal routes (e.g., Johnson and Black 1994, Siegel et al. 2003, Shanks 2009). A new paper by Luiz et al. (2013), investigating determinants of range size in reef fishes, emphasizes that understanding the relationship between dispersal potential and migration also may require understanding the traits of non-dispersive phases.

Luiz et al. (2013) report that the characteristics of generally non-dispersive adult phases correlate strongly with differences in range size, which historically have been considered the consequence of differences among dispersive larval phases (e.g., Lester et al. 2007). The significance of this initially counter-intuitive finding is that it greatly enriches recent discussion of dispersal that, after decades focusing on the influence of pelagic larval duration (PLD), has, as the authors put it, “yielded mixed results” (Luiz et al. 2013:16498) By analogy, consider how the state of knowledge about dispersal in terrestrial plants might look if we studied fruits alone and not other diverse aspects of dispersal syndromes, such as the animals involved (e.g., Beaudrot et al. 2013).

Luiz et al. (2013:16500) find that the individual and combined effects of adult body size (independent effect [IE] = 36%), nocturnality (IE = 26%), and schooling behavior (IE = 16%) “are more important in determining the size of geographic ranges than larval dispersal potential” (IE = 13%; Table 1). They suggest that these adult characteristics provide key advantages in terms of increased establishment success by decreasing predation risk and reducing Allee effects. The result and inference make sense (Figure 1). Population

genetic theory has long recognized the bipartite—dispersal and establishment—nature of migration (e.g., Marshall et al. 2010). Similarly, without dispersal and establishment, there can be no meaningful expansion in range size.

The same suite of population theory, however, also highlights a weakness in the inference that correlation with adult traits means the dominant effects are in “population establishment *after* propagule arrival” (Luiz et al. 2013:16499); emphasis added). For example, adult body size tends to correlate with fecundity and with longevity in many fishes (Beverton 1987, Winemiller and Rose 1992, Hixon et al. 2006:306, Juan-Jordá et al. 2013; see also Figure 1a–d). Thus, although the fecundity advantage of large-bodied species may sometimes be counteracted by greater abundance of small-bodied species, complex relationships between body size and abundance (White et al. 2007) mean that larger fish can be both more fecund and equally or more abundant than smaller fish (e.g., Munday and Jones 1998). Thus, the advantage of body size may accrue via post-dispersal processes and/or via increased lifetime output of larvae. The total effect size of dispersal potential—considering lifetime larval production, PLD, and Luiz and colleague’s preferred dataset—is therefore greater than 13% and possibly as large as 49% (i.e., 13.3% + 36.0%; Table 1), which could turn their conclusion upside-down. Moreover, if a substantial effect of body size is mediated via larval production, their justification for excluding the high-PLD trans-Pacific fishes is limited and the total effect size of dispersal could be as high as 62% (i.e., 24.8% + 37.6%; Table 1), though this would require that other correlated factors, such as young-of-year growth, contribute little. Consequently, despite the advances made by Luiz et al. (2013)—a dataset including ~3–5% of marine fishes, an alternative perspective, and application of mixed models—we remain uncertain about the relative importance of factors influencing migration and range size in this dataset and across

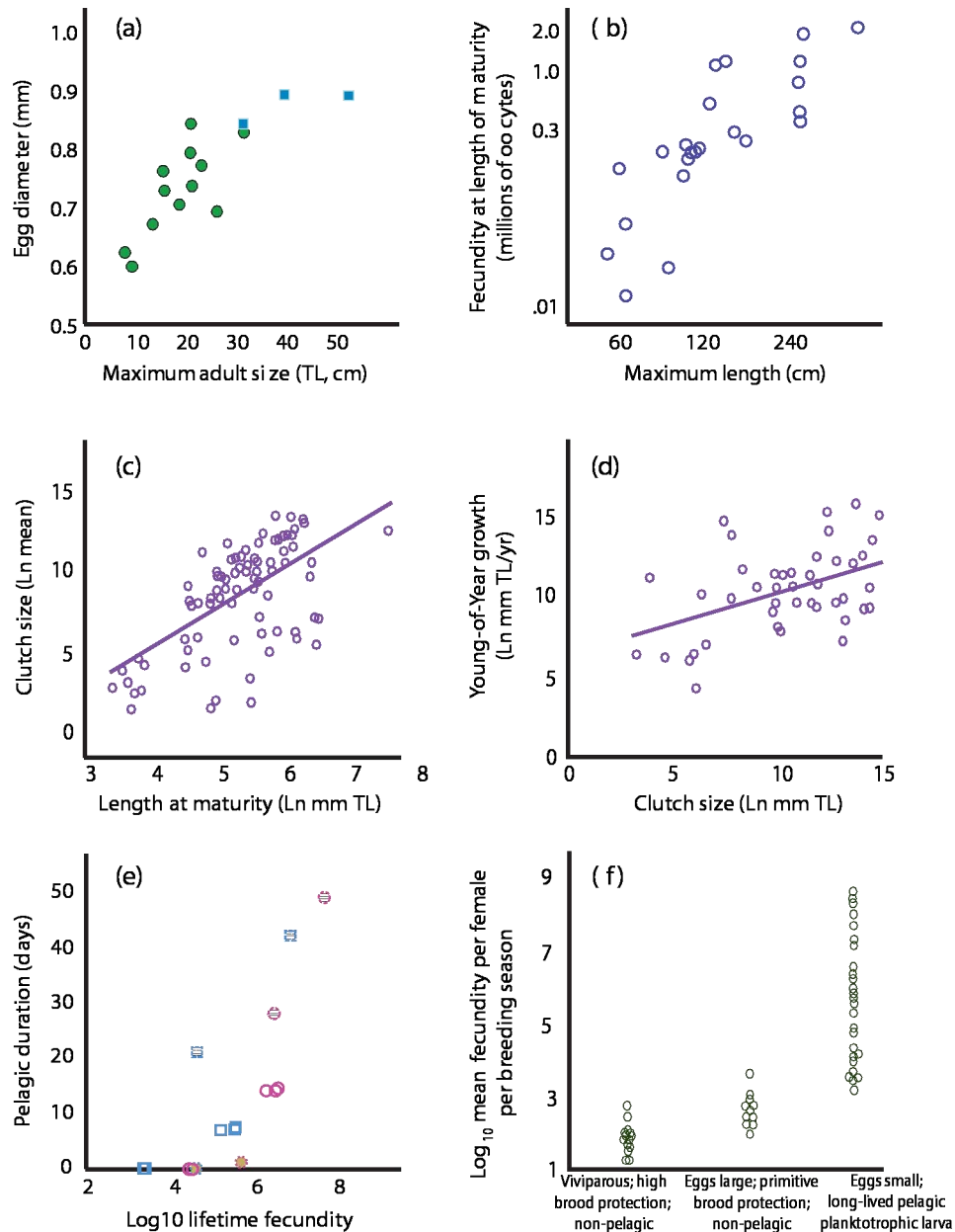


Figure 1. A few examples of possible components in dispersal syndromes, drawn from across a diversity of taxa, predominantly fishes (a–d) and invertebrates (e–f). **(a)** Egg diameter is positively correlated with maximum adult total length (TL) in angelfishes, $r = 0.83$, $p < 0.001$; green circles = Indo-West Pacific species, blue squares = western Atlantic species. Redrawn from Figure 5 of Thresher and Brothers (1985). **(b)** Batch fecundity is positively correlated with maximum length in tunas, mackerels, and bonitos, $r = 0.81$, $p < 0.001$; in these taxa length is positively correlated with longevity (from Figure 1 of Juan-Jordá et al. 2013). **(c)** Fecundity is positively correlated with length at maturity in marine fishes, $\text{Ln}(\text{clutch}) = 2.34 \cdot \text{Ln}(\text{length}) - 2.24$, $r^2 = 0.35$. Redrawn from Figure 2 of Winemiller and Rose (1992). **(d)** Young-of-year growth—mean increment in millimeters total length during the first year following hatching or independent life for viviparous fishes—is positively correlated with clutch size in marine fishes, $\text{Ln}(\text{YoY}) = 0.10 \cdot \text{Ln}(\text{clutch}) + 3.63$, $r^2 = 0.35$. Redrawn from Figure 2 of Winemiller and Rose (1992). **(e)** Pelagic duration is positively correlated with lifetime fecundity across an alga (dotted lines, shaded), five gastropods (solid lines; datapoints for two pairs of taxa with the same pelagic duration and fecundity are jittered), and two barnacle species (dashed lines, hatched), $r = 0.87$, $p = 0.005$. Both factors are strongly correlated with population genetic structure. Redrawn from Appendix D of Dawson et al. (in press). **(f)** The number of eggs produced per female per breeding season of fifty-three marine benthic invertebrates—decapods, echinoderms, molluscs, nemerteans, polychaetes, prosobranchs—with different types of development; redrawn from Thorson (1950). That relationships exist in these six published datasets does not mean that the same relationships exist in other datasets, but establishes the general need to consider correlations within complex traits forming “dispersal syndromes” (Ronce and Clobert 2012, Dawson et al. in press), and their potential effects in specific analyses such as that of Luiz et al. (2013).

Box 1. As the way we think about bio-physical structure in the sea changes, our vocabulary evolves to reframe concepts more clearly and to convey complex ideas more easily. Thus, *dispersal* and *migration* both refer to spatial movements but have long distinguished the latter's inclusion of establishment or gene flow. Here are several other examples that have been influential in the past decade, and a couple of more recent suggestions.

Connectivity: the exchange of individuals among locations. See Riddle et al. (2008) for a brief history of the term, which was brought to prominence by Cowen et al. (2000) and has since become a central topic in marine ecology (Cowen & Sponaugle 2009).

Chaotic genetic patchiness: genetic heterogeneity that does not follow a simple consistent pattern, but forms a shifting, ephemeral patchiness among sites and between years (Johnson and Black 1982, 1984). Employed relatively rarely through the 1990s, the term has surged in popularity since the mid-2000s as larval dispersal has become part of a bigger picture (e.g., Hellberg 2009, Toonen & Grosberg 2011). Similar to *eurymixis* which emphasizes complexity, rather than unpredictability, and transient heterogeneity as a source of adaptive variation in a dynamic environment (Dawson et al. 2011).

Dispersal syndrome: patterns of covariation of life-history, behavioural, physiological, and/or morphological traits associated with dispersal (Clobert et al. 2009, Dawson 2014)

Filters: environmental changes that inhibit the movement of individuals of different species, and therefore their genes, to different extents depending in part on the strength and nature of the filter, and in part on the attributes of the entity being filtered (Carlquist 1965, and many others). Filters may occur individually or co-occur and emphasize multi-faceted links between ecological processes and evolutionary patterns more than the related terms 'breaks' and 'barriers' in the sea (Dawson et al. 2006).

Seascape: analogous with landscape; the environment, particularly through which marine organisms move. Used in scientific literature as early as Sieburth (1975), the term remained rare for two decades (DiSalvo et al. 1988, Bartlett & Carter 1991) before entering the mainstream (e.g. Jackson & Sheldon 1994). Merrel (1994) provides an intriguing metaphor rethinking Wright's adaptive landscape as an undulating surface on which interactions between environmental and biotic factors are in continuous motion.

other taxa. Luiz et al. (2013) will help usher in new perspectives, broader and more detailed datasets, and more life-like conceptual and analytical frameworks (Box 1).

Migration is the result of interactions between complex traits and complex environments. We likely need commensurately sophisticated approaches to infer processes from patterns that vary spatially, phylogenetically, and temporally. If we wish to understand how dispersal potential manifests as realized migration we need to reframe the question, adopt meaningful study designs, collect new data, and make nuanced inferences (Hart and Marko 2010, Dawson 2014). We must approach analyses understanding that there are many covariates—including body size, longevity, fecundity, egg size, developmental mode, time

Table 1. Significant variables ranked according to their independent effects (IE %) after adjustment for the ratio between the species range size and region size and (a) excluding or (b) including trans-Pacific (tP) species. From Table 1 of Luiz et al. (2013). Variables that are, or are potentially, closely allied with dispersal potential are italicized.

Variable	(a) IE % excluding tP species	(b) IE % including tP species
<i>Body size</i>	36.0	37.6
Nocturnal	25.9	19.4
Schooling	16.2	13.9
<i>PLD</i>	13.3	24.8
Region	8.3	4.2

Box 2. A few examples of potentially useful variations on commonplace dispersal syndromes:

- the primary planktonic stage of most medusozoans is juvenile-mature, rather than larval as in the majority of other meroplankton.
- Geographic variation in the suite of environmental drivers of different traits (Marshall et al. 2012) may assemble different syndromes.
- Poecilogeny (e.g. Krug and Zimmer 2004)

to maturity, behavior—that may contribute to marine dispersal syndromes (e.g., Shanks et al. 2003). Among the ~0.5 million marine species, there also may be many exceptions; finding cases that break or vary predominant dispersal syndromes may help tease apart the influences of components in complex traits (Box 2).

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References

- Bartlett, D. & Carter, R.W.G. (1991) Seascape ecology – the landscape ecology of the coastal zone. *Ekologia*, 10, 43–53.
- Beaudrot, L., Rejmanek, M. & Marshall, A.J. (2013) Dispersal modes affect tropical forest assembly across trophic levels. *Ecography*, 36, 984–993.
- Beverton, R.J.H. (1987) Longevity in fish: some ecological and evolutionary considerations. In: *Evolution of longevity in animals: a comparative approach* (ed. by A.D. Woodhead and K.H. Thompson), pp. 161–185. Plenum, New York, NY.
- Carlquist, S. (1965) *Island life: a natural history of the islands of the world*. Natural History Press, New York.
- Clobert, J., le Galliard, J.-F., Cote, J., Meylan, S. & Massot, M. (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12, 197–209.
- Cowen, R.K. & Sponaugle, S. (2009) Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 2, 443–466.
- Cowen, R.K., Lwiza, K.M.M., Sponaugle, S., Paris, C.B. & Olson, D.B. (2000) Connectivity of marine populations: open or closed? *Science*, 287, 857–859.
- Dawson, M.N. (2014) Natural experiments and meta-analyses in comparative phylogeography. *Journal of Biogeography*, 41:52–65.
- Dawson, M.N., Barber, P.H., González-Guzmán, L.I., Toonen, R.J., Dugan, J.E. & Grosberg, R.K. 2011. Phylogeography of *Emerita analoga* (Crustacea, Decapoda, Hippidae), an eastern Pacific Ocean sand crab with long-lived pelagic larvae. *Journal of Biogeography*, 38, 1600–1612.
- Dawson, M.N., Hays, C.G., Grosberg, R.K., & Raimondi, P.T. (in press) Dispersal potential and population genetic structure in the marine intertidal of the eastern North Pacific. *Ecological Monographs*, <http://dx.doi.org/10.1890/13-0871.1>
- Dawson M.N., Waples, R.S. & Bernardi, G. (2006) Phylogeography. In: *Ecology of California Marine Fishes* (ed. by L.G. Allen, M.H. Horn, & D.J. Pondella II), pp. 26–54. University of California Press, Berkeley.
- DiSalvo, L.H., Randall, J.E. & Cea, A. (1988) Ecological reconnaissance of the Easter Island sublittoral marine environment. *National Geographic Research Reports*, 4, 451–473.
- Hart, M.W. & Marko, P.B. (2010) It's about time: divergence, demography, and the evolution of developmental modes in marine invertebrates. *Integrative and Comparative Biology*, 50, 643–661.
- Hellberg, M.E. (2009) Gene flow and isolation among populations of marine animals. *Annual Review of Ecology, Evolution, and Systematics*, 40, 291–310.
- Hixon, M.A. & Webster, M.S. (2006) Density dependence in reef fish populations. In: *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. by P.F. Sale), pp. 303–326. Academic Press, Burlington, MA.
- Jackson, J.B.C. & Sheldon, P.R. (1994) Constancy and change of life in the sea. *Philosophical Transactions of the Royal Society of London B*, 344, 55–60.
- Johnson, M.S. & Black, R. (1982) Chaotic genetic patchiness in an intertidal limpet. *Marine Biology*, 70, 157–164.
- Johnson, M.S. & Black, R. (1984) Pattern beneath the chaos: the effect of recruitment on genetic patchiness in an intertidal limpet. *Evolution*, 38, 1371–1383.
- Juan-Jordá, M.J., Mosqueira, I., Freire, J. & Dulvy, N.K. (2013) Life in 3-D: life history strategies in tunas, mackerels, and bonitos. *Reviews in Fish Biology and Fisheries*, 23, 135–155.
- Krug, P.J. & Zimmer, R.K. (2004) Developmental dimorphism: consequences for larval behavior and dispersal potential in a marine gastropod. *Biological Bulletin*, 2004,

- 233–246.
- Lester, S.E., Ruttenberg, B.I., Gaines, S.D. & Kinlan, B.P. (2007) The relationship between dispersal ability and geographic range size. *Ecology Letters*, 10, 745–758.
- Luiz, O.J., Allen, A.P., Robertson, D.R., Floeter, S.R., Kulbicki, M., Vigliola, L., Becheler, R. & Madin, J.S. (2013) Adult and larval traits as determinants of geographic range size among tropical reef fishes. *Proceedings of the National Academy of Sciences of the USA*, 110, 16498–16502.
- Marshall, D.J., Monro, K., Bode, M., Keough, M.J. & Swearer, S. (2010) Phenotype-environment mismatches reduce connectivity in the sea. *Ecology Letters*, 13, 128–140.
- Marshall, D.J., Krug, P.J., Kupriyanova, E.K., Byrne, M. & Emler, R.B. (2010) The biogeography of marine invertebrate life histories. *Annual Review of Ecology, Evolution, and Systematics*, 43, 97–114.
- Merrell, D.J. (1994) *The adaptive seascape: the mechanism of evolution*. University of Minnesota Press, Minneapolis.
- Munday, P.L. & Jones, G.P. (1998) The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: An Annual Review*, 36, 373–411.
- Riddle, B.R., Dawson, M.N., Hadly, E.A., Hafner, D.J., Hickerson, M.J., Mantooth, S.J. & Yoder, A.D. (2008) The role of molecular genetics in sculpting the future of integrative biogeography. *Progress in Physical Geography*, 32, 173–202.
- Ronce, O. & Clobert, J. (2012) Dispersal Syndromes. In: *Dispersal ecology and evolution* (ed. by Clobert, J. and Baguette, M.) pp. 119–139. Oxford University Press, New York.
- Shanks, A.L. (2009) Pelagic larval duration and dispersal distance revisited. *Biological Bulletin*, 216, 373–385.
- Shanks, A.L., Grantham, B.A. & Carr, M.H. (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13, S159–S169.
- Sieburth, J.M. (1975) *Microbial seascapes: a pictorial essay on marine microorganisms and their environments*. University Park Press, Baltimore.
- Siegel, D.A., Kinlan, B.P., Gaylord, B.P. & Gaines, S.D. (2003) Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series*, 260, 83–96.
- Thresher, R.E. & Brothers, E.B. (1985) Reproductive ecology and biogeography of Indo-West Pacific Angelfishes (Pisces: Pomacanthidae). *Evolution*, 39, 878–887.
- Toonen, R.J. & Grosberg R.K. (2011) Causes of chaos: spatial and temporal genetic heterogeneity in the intertidal anomuran crab *Petrolisthes cinctipes*. In: *Phylogeography and population genetics in Crustacea* (ed. by S. Koenemann, C. Held & C. Schubart), pp. 73–106. CRC Press, Boca Raton.
- Winemiller, K.O. & Rose, K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 2196–2218.
- White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007) Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, 22, 323–330.
- Wright, S. (1931) Evolution in Mendelian populations. *Genetics*, 16, 97–159.

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