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When is dispersal for dispersal? Unifying marine and terrestrial perspectives

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ABSTRACT

Recent syntheses on the evolutionary causes of dispersal have focused on dispersal as a direct adaptation, but many traits that influence dispersal have other functions, raising the question: when is dispersal 'for' dispersal? We review and critically evaluate the ecological causes of selection on traits that give rise to dispersal in marine and terrestrial organisms. In the sea, passive dispersal is relatively easy and specific morphological, behavioural, and physiological adaptations for dispersal are rare. Instead, there may often be selection to limit dispersal. On land, dispersal is relatively difficult without specific adaptations, which are relatively common. Although selection for dispersal is expected in both systems and traits leading to dispersal are often linked to fitness, systems may differ in the extent to which dispersal in nature arises from direct selection for dispersal or as a by-product of selection on traits with other functions. Our analysis highlights incompleteness of theories that assume a simple and direct relationship between dispersal and fitness, not just insofar as they ignore a vast array of taxa in the marine realm, but also because they may be missing critically important effects of traits influencing dispersal in all realms.

Key words: adaptation, dispersal, complex life cycles, movement, multivariate selection.

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> "... *although some behaviors are specifically 'for' dispersal, others may be for dispersal and finding food, shelter, mates etc. The definition of dispersal as movement only by a specific mode has created much confusion, as it ignores the 'non-dispersal' movement that, over a lifetime, may create as much or more spatial gene flow*"
>
> (Benton & Bowler, 2012, p. 46)

> "*A particular point of discussion is to what extent dispersal is the result of 'special behavior' of which the main function is to disperse* (Van Dyck & Baguette, 2005); *or whether it is a by-product of other movements*"
>
> (Matthysen, 2012, p. 4)

I. INTRODUCTION

Dispersal has pervasive ecological and evolutionary consequences for all living organisms, influencing gene flow and the potential for local adaptation, connectivity among local populations and the dynamics of metapopulations, and the expansion or shifting of species' geographic ranges (Kokko & Lopez-Sepulcre, 2006). Given these important consequences of dispersal, a clear understanding of the selective factors that govern the evolution of dispersal is fundamental to predicting species' responses to environmental variation and rapid change (Kokko & Lopez-Sepulcre, 2006; Baskett, Weitz & Levin, 2007).

Much of the theory on the evolution of dispersal explores the balance between the advantages of spatial displacement between related individuals and the costs of such movement (reviewed in Section III; see also Johnson & Gaines, 1990; Bonte *et al.*, 2012; Starrfelt & Kokko, 2012; Duputié & Massol, 2013). The most widely considered advantages of dispersal encompass (*i*) avoiding competition with relatives, (*ii*) reducing the risks of inbreeding, or (*iii*) spreading risk in spatially and temporally heterogeneous environments. Determining the relative importance of these factors has been the primary objective of recent empirical studies on the evolutionary causes of dispersal (e.g. Matthysen, 2012; Bitume *et al.*, 2013; Bonte *et al.*, 2014). The emerging synthesis of the ecology and evolution of dispersal emphasizes how these selective processes can lead to individual differences in multiple traits and behaviours related to their dispersal patterns, and that the evolution of dispersal can only be understood in the context of multiple life-history traits (Clobert *et al.*, 2009, 2012; Bonte *et al.*, 2012; Stevens *et al.*, 2012; Buoro & Carlson, 2014).

This emerging synthesis principally derives from the biology of terrestrial organisms, and largely omits a marine perspective. Nevertheless, marine biologists have long recognized that the distinctive features of the marine realm may lead to very different selective pressures on the traits that mediate dispersal (Table 1) (Thorson, 1950; Strathmann, 1974; Johannes, 1978; Palmer & Strathmann, 1981). In particular, many marine animals exhibit a biphasic life cycle, where one stage is sessile or relatively sedentary (typically the adult reproductive stage) and the other stage swims or drifts (typically early developmental stages), often feeding while dispersing. Models of the evolution of such marine life cycles typically consider the benefits of sending propagules into the plankton, where growth and survival during early developmental stages may be considerably higher than in benthic habitats (e.g. Vance, 1973; Strathmann, 1974; Christiansen & Fenchel, 1979; Palmer & Strathmann, 1981; Todd & Doyle, 1981; McEdward, 1997; Levitan, 2000; Baskett *et al.*, 2007; Pringle *et al.*, 2014). These models further suggest that advantages of displacement between locations of birth and subsequent reproduction cannot alone account for the maintenance and modification of the traits expected to increase dispersal (Table 1). Such traits relate to feeding, development time, defences, and buoyancy. Thus, whereas the terrestrial literature typically (though see Van Dyck & Baguette, 2005) emphasizes dispersal as a direct adaptation to increase displacement between relatives, the marine literature focuses on dispersal as an incidental by-product of traits selected for other functions and types of movement (e.g. Strathmann, 1974; Johannes, 1978; Hedgecock, 1986; Emlet, McEdward & Strathmann, 1987; Havenhand, 1995; Todd, Lambert & Thorpe, 1998; Pechenik, 1999; Bonhomme & Planes, 2000; Strathmann *et al.*, 2002; Table 1).

The distinction between terrestrial and marine perspectives may be more apparent than real, because dispersal may be both an adaptation and a by-product in both physical realms of life (Toonen & Pawlik, 2001; Van Dyck & Baguette, 2005; Baskett *et al.*, 2007; Krug, Gordon & Romero, 2012; Matthysen, 2012). For example, cilia on marine larvae function as both feeding and locomotory devices. In terrestrial plants, seed size influences germination success and could also influence dispersal distance. Avoiding interactions with kin or spreading risk in heterogeneous environments may be the reason why traits influencing dispersal are linked to fitness (dispersal 'for' dispersal), but not the only reason (in which case, dispersal is considered a by-product). Consequently, inferences and predictions gained from only one perspective may not explain how dispersal responds when there are changes in any environmental factor that influences selection in each system. There is, therefore, a need to integrate our understanding of the direct and indirect causes of selection on the traits influencing dispersal across systems.

Here, we compare and contrast the traits and selective forces influencing the evolution of dispersal in marine and terrestrial systems. From this comparison, a unifying question emerges: when is dispersal for dispersal and when is dispersal a by-product of selection on traits with other functions? We begin by clarifying how dispersal is an emergent property interacting with other types of movement and influenced by an array of traits. We review the theory on the adaptive benefits of dispersal and evaluate when net displacement might be an evolutionary by-product. We then compare the traits that influence dispersal in air and sea water to assess how the physical medium imposes constraints and opportunities for dispersal, movement, and life-history evolution. First in marine and then in terrestrial

Table 1. Hypotheses on the evolution of traits that influence dispersal in benthic marine fishes and invertebrates with pelagic, dispersing offspring

Taxa and context	**Hypothesis**	**Stage of dispersal**	**References**
Benthic marine invertebrates	Dispersal reflects a trade-off between egg size and number: high larval growth and survival in the plankton favours the production of many small, feeding offspring with longer pelagic duration; low larval growth and survival favours large non-feeding offspring with shorter pelagic duration	Departure and transfer	Vance (1973)
Benthic marine invertebrates	The pelagic larval stage in species that release non-feeding, competent larvae is for dispersal and habitat selection	Departure, transfer, and settlement	Strathmann (2007)
Fishes and benthic marine invertebrates	Large scales of dispersal in species with feeding larvae occur as a by-product of selection favouring exploitation of both benthic and pelagic environments	Transfer	Strathmann (1985) and Strathmann *et al.* (2002)
Benthic marine invertebrates	The presence of dispersive larvae reflects the difficulty of losing larvae from the life cycle more than selection for their maintenance	Departure	Pechenik (1999)
Benthic marine invertebrates	Long planktonic durations are: (*i*) evolutionarily stable when larval transport is dominated by stochastic eddies instead of mean alongshore current, and (*ii*) favoured for the additional fecundity that larval feeding in the plankton provides, rather than the additional dispersal they allow	Departure and transfer	Pringle *et al.* (2014)
Reef fishes	The pelagic interval is an emergent property of trade-offs among dispersal-related traits (e.g. egg size–number), which reinforces long-term evolutionary constraints on reducing the pelagic interval	Departure and transfer	Bonhomme & Planes (2000)
Reef fishes and estuarine crabs	Timing of release of gametes and larvae occurs during the largest-amplitude nocturnal tides, enhancing transport of larvae from shallow waters where visual planktivorous fishes are most abundant	Departure	Johannes (1978), Morgan (1990) and Morgan & Christy (1995)
Fishes from coral reefs, mangroves, and tropical seagrass	The timing and location of spawning flushes eggs and larvae away from predators in shallow-water adult habitats, but also enhances the return of planktonic larvae to the natal habitat by local currents	Departure transfer, and settlement	Johannes (1978)
Estuarine crabs	Among species, the distance larvae move from their parents is negatively related to parental investment per offspring and larval defences	Transfer	Morgan (1990)
Coral reef fish	Selection favours larval dispersal because adults live in patchy, unstable environments and cannot move between reefs	Departure and transfer	Barlow (1981)
Coral reef fish	Selection favours larval dispersal because larvae experience patchy and unpredictable survival in the pelagic environment	Transfer	Doherty *et al.* (1985)
Fishes	Dispersal allows larvae to avoid competition for food by allowing larvae to feed at low *per capita* prey densities, which occur in pelagic rather than benthic habitats	Departure	Economou (1991)
California Current fishes and benthic crustaceans	Life-history traits (such as age at maturity, fecundity, larval duration, and timing of offspring release) have evolved to enhance the return of larvae back into the parental population	Departure and transfer	Sinclair (1988) and Shanks & Eckert (2005)

systems, we discuss how the traits and physical medium support the potential for dispersal to evolve as a by-product. We conclude by showing how the framework for analysing multivariate selection in combination with experiments represents a way to address quantitatively the question posed in the title. Rather than covering all aquatic organisms, we focus on benthic marine organisms with a biphasic life cycle, because such life cycles are common in the sea, include a diverse array of taxa, and exemplify the greatest contrast with life cycles in most terrestrial organisms (which have been the focus of previous reviews; e.g. Clobert *et al.*, 2012). Our synthesis stresses a greater emphasis on the ecological causes of selection on traits that influence dispersal, rather than considering all dispersal as a direct adaptation. Such a focus is a requirement for predicting how changing environments influence the way dispersal alters ecological processes.

II. DISPERSAL AS AN OUTCOME OF MANY TRAITS AND DIFFERENT TYPES OF MOVEMENT

Dispersal is an outcome, or an emergent property, of a multi-stage process that includes a departure, transfer, and settlement stage (Bonte *et al.*, 2012; Travis *et al.*, 2012). At each stage, individuals potentially vary in multiple traits and multiple selection pressures can act on this individual variation (Ronce, 2007; Clobert *et al.*, 2009). The traits at each stage potentially have multiple functions (e.g. feeding, escape, exploration, migration, and reproduction) that relate to the overall life history of individuals (Van Dyck & Baguette, 2005; Strathmann, 2007; Benard & McCauley, 2008; Phillips, Brown & Shine, 2010). The outcome of performing these multiple functions manifests as net displacement from where individuals were born to where they reproduce, or would have reproduced had they been successful (Ronce, 2007). This includes the displacement between parents and offspring, as well as between siblings.

It is the combination of multiple processes generating net displacement between locations of birth and subsequent reproduction over the lifetime of individuals (parents or offspring) and lineages that we seek to understand here. Movement away from the location of birth (e.g. departure) would not be considered dispersal if individuals subsequently return to the same location to reproduce (Dingle, 2014). There are two main reasons for defining dispersal by its outcome and attempting to explain net displacement: (*i*) there is no simple definition of dispersal as a behaviour that is universally applicable across taxa and systems, whereas net displacement is a universal outcome, and (*ii*) it is the net displacement between birth and reproduction at the individual level that has important consequences for populations (e.g. population connectivity, gene flow, shifts in geographic ranges, spread rates of invasive species). Understanding net displacement therefore allows a more mechanistic understanding of how the causes of dispersal are linked to their consequences for the ecology and evolution of populations. This definition of dispersal forces us to understand the causes of selection on traits that influence the multiple stages of dispersal that ultimately generate patterns of net displacement, rather than only viewing dispersal as a specific adaptation.

Common patterns of dispersal in nature may not always reflect a direct adaptation for such displacement, even though the traits that cause dispersal are linked to fitness. For example, when movement is passive, displacement depends on the timing and spatial location of release relative to the flow of the medium (wind, currents, or hosts), and the size, mass, and morphology of the propagules. Selection on timing of release and propagule characteristics depends on a variety of factors, such as the temporal availability of resources and offspring size–number trade-offs, in addition to selection for spatial displacement. Furthermore, dispersal is a particular type of movement and is only one of many possible reasons why organisms move (Winkler, 2005; Nathan *et al.*, 2008). The degree to which dispersal is a direct adaptation or a by-product requires consideration of how the phenotypes related to each stage of dispersal affect movement, and the causes of any relationships between dispersal phenotypes and fitness (MacColl, 2011).

Understanding how dispersal-related traits evolve further depends on whether the parent or the offspring controls displacement (Wolf & Wade, 2001). Parents and offspring may have different optimal levels of displacement, creating an arena for parent–offspring conflict (Starrfelt & Kokko, 2010). In mobile animals, dispersal is typically studied empirically from the point of view of the individual that is dispersing (Clobert *et al.*, 2009). In higher plants, dispersal is typically studied from the point of view of the parent spreading its offspring among different sites (Donohue, 1999; Fig. 1). In many animal taxa, especially benthic marine invertebrates and fishes, the genomes of both the parent and offspring can potentially control the expression of traits affecting dispersal (Marshall & Morgan, 2011), which makes it especially challenging to understand whose fitness dispersal influences and therefore when dispersal is an adaptation or by-product. Incorrectly assigning components of offspring fitness to parents can lead to incorrect estimates of evolutionary change in parental traits (Wolf & Wade, 2001).

III. THEORY OF THE EVOLUTION OF DISPERSAL

The theory on the evolution of dispersal (Johnson & Gaines, 1990; Starrfelt & Kokko, 2012; Duputié & Massol, 2013) typically focuses on the question ‘why disperse?’, where dispersal itself is the trait directly under selection, rather than the traits that give rise to dispersal outcomes. In models, the dispersal trait might be realized as the propensity to disperse or not (e.g. the proportion of offspring leaving the nest) or the dispersal distance (mean of the dispersal kernel or the shape of the kernel itself). Existing theory does not yet fully address the more general question of what evolutionary processes contribute to observed

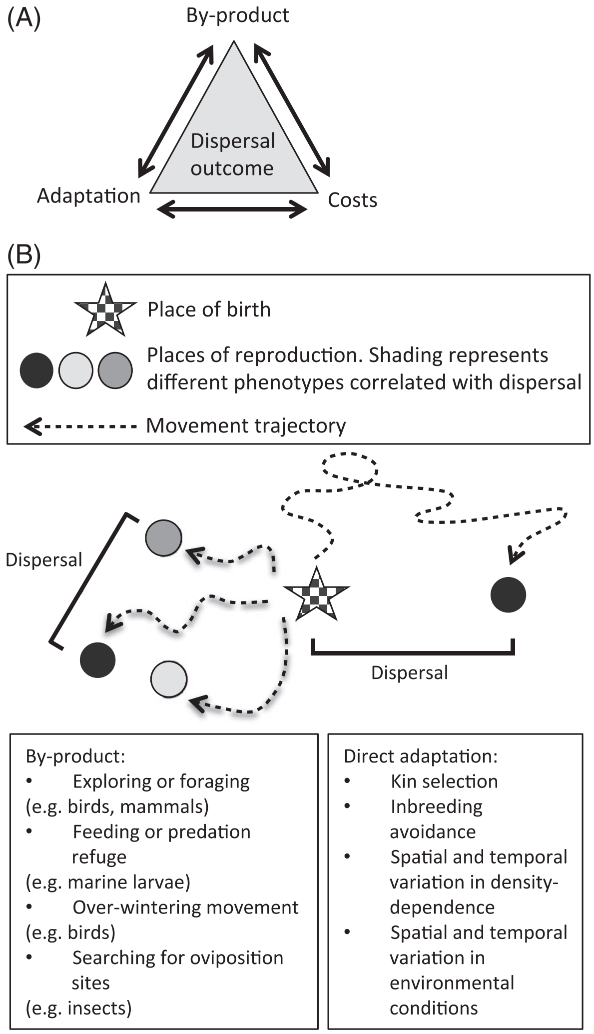

Fig. 1. (A) Dispersal is typically viewed as a balance between the costs and benefits of dispersal (bottom axis of triangle). However, in considering dispersal as an outcome of multiple traits with multiple functions at each of multiple stages, we seek to understand net displacement. Net displacement can be generated, maintained, and modified as an evolutionary by-product of selection acting on other traits that are correlated with dispersal distance. (B) Dispersal is an outcome, or an emergent property, of a multi-stage process determined by multiple traits with multiple functions. The end result manifests as a net displacement of an individual from the place of birth to the place of subsequent reproduction. The spread of sibling offspring from their birthplace to different breeding sites also constitutes dispersal. Dispersal is really just one type of movement phenomenon and different types of movement phenomena are not necessarily independent of one another.

patterns of dispersal. Nonetheless, understanding the existing theory is a prerequisite for asking when dispersal is for dispersal.

Considering the propensity to disperse as the evolving trait, in their seminal paper Hamilton & May (1977) demonstrated the capacity for reduced competition among kin to select for dispersal, even in homogenous landscapes and costs to dispersal. Note that this inclusive fitness benefit of spreading offspring diminishes: (*i*) with increasing spread (more so in two dimensions than in one dimension; Rousset & Gandon, 2002), (*ii*) when population sizes are large or individuals produce many offspring (Comins, Hamilton & May, 1980), (*iii*) when vacant sites are available or the strength of competition varies across space (McPeek & Holt, 1992), or (*iv*) when there are diploid genetic systems, which can also create parent–offspring conflict in optimal dispersal distance (Starrfelt & Kokko, 2010; also reviewed in Johnson & Gaines, 1990; Levin *et al.*, 2003). For dispersal to be selected as a risk-spreading strategy in variable environments, the environment must vary in space as well as time, where that variability might arise intrinsically due to competition with conspecifics as well as extrinsically due to changing environmental conditions (e.g. McPeek & Holt, 1992). The structure of environmental variation also matters: increasing spatial autocorrelation selects for increased dispersal propensity (although see Fronhofer *et al.*, 2014), while increasing temporal autocorrelation selects for a reduced dispersal propensity (e.g. Travis, 2001).

Considering dispersal distance as the evolving trait, the evolutionarily stable dispersal distance increases with increasing spatial autocorrelation and decreases with increasing temporal autocorrelation (Palmer & Strathmann, 1981; Snyder, 2011). Dispersal distances beyond the spatial scale of environmental autocorrelation occur only when environmental conditions vary randomly over relatively short time scales (Palmer & Strathmann, 1981; Snyder, 2011). Kin competition can promote dispersal to distances beyond that which spatial and temporal variation in environmental conditions would predict (Hovestadt, Messner & Poethke, 2001). If all offspring move the same distance, then they will compete with each other after dispersal, leading to reduced fitness of the parent. A parent (or more precisely a genetic lineage) can increase its inclusive fitness if offspring are spread across different locations to reduce competition among relatives. Hence, theory predicts that, in uniform environments, a parent (or lineage) should spread its offspring evenly among all suitable locations leading to a uniform dispersal kernel extending to maximum possible distances (Hovestadt *et al.*, 2012). In variable environments, theory predicts the emergence of 'fat-tailed' dispersal kernels, where most individuals settle relatively close to their natal site but a few individuals are spread out over large distances, representing a combination of risk spreading in variable environments and the fitness benefits of reduced kin competition in small populations when sites are at or near carrying capacity (Hovestadt *et al.*, 2012). Kin competition, therefore, does not just influence whether or not to leave the natal site (Hamilton & May, 1977), but can also influence the shape of the whole distribution of dispersal distances (Hovestadt *et al.*, 2001; Rousset & Gandon, 2002; Starrfelt & Kokko, 2010; see Bitume *et al.*, 2013, for an empirical example). Kin selection is often invoked as a powerful and universal explanation for dispersal propensity and distance (Hovestadt *et al.*, 2012), although large populations, high fecundity, and outbreeding all reduce

Table 2. Broad differences in some characteristics related to dispersal in marine and terrestrial systems

Characteristic	Marine	Terrestrial
Pollinators	Absent/rare	Common
Sessile copulation	Present	Rare
Unprotected female gametes shed	Common	Absent
Gamete dispersal	Commonly centimetres to metres	Potentially hundreds of kilometres in plants
Development or growth during dispersal	Common	Rare
Adaptations for dispersal	Usually absent	Common
Stage of dispersal	Gamete, zygote, embryo, larva, postlarva, adults (e.g. ground fish, rafting invertebrates)	Gamete (e.g. pollen), juveniles (e.g. spiders, vertebrates), adults (e.g. insects)
Sex-biased dispersal	Poorly investigated	Male-biased (e.g. mammals), female-biased (e.g. birds)
Scale of patch extinctions or ephemeral habitat relative to the scale of dispersal of the affected organisms	Typically smaller	Typically comparable

the ability of kin competition to select for increasing dispersal (see Comins *et al*., 1980; Johnson & Gaines, 1990; McPeek & Holt, 1992; Levin *et al*., 2003 and references therein).

While dispersal distance tends to represent the transfer stage, and the propensity to disperse tends to represent the departure stage, the two interact to influence each other in reality (e.g. Table 1). Modern approaches to modelling dispersal evolution typically allow the costs and benefits of the departure, transfer, and settlement stages to interact and co-evolve, which then influences trade-offs with other aspects of life history (e.g. Travis *et al*., 2012; Fronhofer *et al*., 2014). These models show how direct selection for dispersal in one stage can result in evolutionary changes in other stages, including settlement, both directly and indirectly (Stamps, Krishnan & Reid, 2005; Burton, Phillips & Travis, 2010). Importantly, the causes of departure may reveal little, if anything, about how far an individual should move once the decision to depart has been made. Similarly, if the same traits that promote departure, or travelling short distances, also influence long-distance dispersal, then the scale of net displacement could conceivably arise as a by-product of selection for departure. One therefore needs to assess the scales of relatedness, competition, mating, and external environmental conditions that affect fitness relative to the scales at which organisms are capable of moving in their physical medium (Duputié & Massol, 2013).

IV. PHYSICAL DIFFERENCES BETWEEN AIR AND SEA WATER AND THEIR RELATIONSHIP TO DISPERSAL

Realized dispersal not only depends on a suite of organismal traits, but also on how those traits interact with the environment. Air and sea water differ in their constraints and opportunities for movement and balancing life-history trade-offs due to differences in viscosity, density, terminal velocity, specific heat and oxygen supply (Table 2) (Strathmann, 1990; Denny, 1993; Dawson & Hamner, 2008; Vermeij & Grosberg, 2010). In particular, as described below, passive dispersal is relatively ‘easy’ in marine realms, but requires ‘effort’ in terrestrial realms. The opposite is true for active dispersal: active dispersal is relatively more efficient (see Section IV.1 for explanation) in terrestrial animals compared to benthic marine animals with small pelagic larvae.

(1) Density and viscosity of water

The higher density and viscosity of water compared to air determines the relative efficiency of passive and active movement, and hence how selection influences adaptations to increase or decrease dispersal (Strathmann, 1990; Denny, 1993; Carr *et al*., 2003; Vermeij & Grosberg, 2010) (Table 2). Specifically, it is less energetically expensive to remain suspended and move passively in sea water due to its higher viscosity and density. Density and viscosity combine with the properties of the organism (e.g. size and shape) to determine the overall efficiency of movement (buoyancy and passive drag for suspension, the ratio of inertial to viscous forces in locomotion; Denny, 1993). For example, small sizes allow passive dispersal in air (e.g. spores and pollen) (Dawson & Hamner, 2008). However, small body sizes in many species are likely to be selected against for other reasons (e.g. mortality associated with smaller initial size, weaker defences; Strathmann, 1990). Passive dispersal with larger body sizes requires additional structures that increase drag to decrease fall velocities and increase the distance travelled (e.g. the samaras of seeds, the silk thread of ballooning spiders). Thus, sea water is a more efficient medium for passive movement by small early life-history stages (e.g. gametes and larvae), whereas passive dispersal in air requires adaptations to increase drag (Dawson & Hamner, 2008). Passive movement in both sea water and air exposes individuals to the costs of landing in unfavourable habitat, but the additional costs due to predation during movement (see Section IV.2) are arguably higher in planktonic marine larvae compared to terrestrial organisms dispersed by air (Strathmann, 1990).

For active dispersal, swimming is less energetically expensive than flying for a similar-sized organism, but flying is faster (Denny, 1993; Alexander, 1998, 2005). Higher costs are often paid by organisms that spend more time actively dispersing (Bonte *et al.*, 2012). Active dispersal is generally more efficient with larger body sizes, and body sizes need to be larger in sea water to achieve equivalent speed and metabolic cost compared to that in air (Alexander, 1998; Hein, Hou & Gillooly, 2012). The lower specific heat of air reduces metabolic costs at a given temperature for active locomotion in air compared to sea water (Denny, 1993; Vermeij & Grosberg, 2010). Thus, air is a more efficient medium for active movement of larger-bodied juveniles and adults, whereas active movement in sea water by small early life-history stages is energetically inefficient (Alexander, 2005; Dawson & Hamner, 2008; Hein *et al.*, 2012).

(2) Terminal velocities and plankton 'soup'

The slower terminal velocities and higher potential for turbulent mixing to keep particles passively suspended in water underlies the abundance of plankton in sea water and a distinct lack of aerial plankton (although some terrestrial species catch their prey mid-air) (Denny, 1993). The capacity for sea water to support plankton also provides opportunities for novel trophic modes: suspension feeding, or planktivory, is common in the sea, but rare on land. The slower terminal velocities in sea water create risks for pelagic offspring remaining near benthic adult habitats, where floating eggs and larvae can be eaten by higher densities of selective and suspension-feeding planktivores, while at the same time offering opportunities for larvae to feed. So while benthic habitats provide shelter, food, and mates for adult stages of the life cycle, the high densities of planktivores can present hazards to the small, free-swimming early stages of the life cycle and encourage seaward migrations of larvae away from parental habitat to feed (Morgan & Christy, 1995). Overall, the marine plankton creates opportunities for larvae to feed, grow, and develop for days to months without parental care in a medium that is also conducive to passive movement.

(3) Oxygen constraints and desiccation resistance

While externally developing embryos in terrestrial and marine environments experience constraints, such as acquiring oxygen and avoiding desiccation (in the marine intertidal zone), marine embryos are unique in their ability to avoid some of these restrictions by planktonic development. Various means of supplying oxygen to embryos while restricting desiccation have evolved on land, but suspending embryos in the atmosphere does not solve the problem. In the sea, the lower solubility and diffusion rate of oxygen in water restricts oxygen supply to embryos. Oxygen supply limits the size and shape of a mass of embryos in water because the viscosity of water slows flow between embryos and the solubility and diffusion rate of oxygen in water is low (Strathmann, 1985; Fernandez, Bock & Portner, 2000). In many marine taxa, protective brooding of a mass of embryos is restricted to species with small adult size, and thus a small brood mass, or requires substantial parental investment to oxygenate the mass (Fernandez *et al.*, 2000). Larger adults with high fecundity commonly release eggs into the plankton where siblings drift apart, so that embryos present a larger surface area to volume ratio for oxygen supply. Therefore, planktonic suspension, leading to passive dispersal, can also reduce oxygen limitations in marine organisms.

V. TRAITS RELATED TO MOVEMENT IN MARINE AND TERRESTRIAL ENVIRONMENTS

In the sea, where passive dispersal is easier, specific morphological, behavioural, and physiological adaptations for dispersal are rare. By contrast, such adaptations are relatively common on land (Table 2). In terrestrial systems, plant traits associated with dispersal include plant height, growth form, seed mass, and seed morphology (e.g. Thomson *et al.*, 2011). Animal traits associated with dispersal typically include sex, body size, fecundity, longevity, fraction of winged offspring, aggression, exploratory behaviour, or other distinct behaviours (Bowler & Benton, 2005; Bonte *et al.*, 2012; Stevens *et al.*, 2012, 2014; Buoro & Carlson, 2014). Patterns of covariation between such traits and dispersal are often called 'dispersal syndromes' and presumably represent a response to the adaptive value of dispersal or co-adaptation between dispersal and life-history strategies (reviewed in Stevens *et al.*, 2012, 2014; Buoro & Carlson, 2014). Note that the majority of these traits may also influence fitness through means other than dispersal itself, such that their effect on dispersal potentially occurs as a by-product, as well as being 'for' dispersal.

In benthic marine invertebrates and fishes, traits that affect dispersal include possession of a pelagic larval stage, duration of time spent in the plankton, reproductive mode (e.g. broadcast spawning *versus* direct development), adult life span, egg buoyancy, larval behaviours (e.g. vertical positioning in the water column; directed onshore swimming), and the timing and locations of offspring release relative to tides and currents that affect retention and export (Morgan & Christy, 1995; Strathmann *et al.*, 2002). In addition, pelagic durations emerge from many other traits such as: (*i*) developmental rate, which is mediated by water temperature, food availability, and propagule size; (*ii*) obligatory or facultative larval feeding; and (*iii*) the ability to delay metamorphosis once competent to settle (Marshall & Keough, 2008; Shanks, 2009). Therefore, dispersal syndromes in benthic marine invertebrates and demersal fishes (e.g. Shanks & Eckert, 2005; Riginos *et al.*, 2011) potentially arise from traits with direct links to fitness, in which displacement could be a by-product, as well as being 'for' dispersal.

The stage in the life history when dispersal occurs influences selection for dispersal, as well as how the physical environment influences the relative ease of passive movement, the need for active movement, and the opportunities to make informed decisions (Strathmann, 1990; Table 2).

Because sea water is physiologically more benign and much denser than air, it is more hospitable to delicate phases of the life cycle. Gametes, zygotes, embryos, and tiny larvae are often shed into the water and movement potentially leading to dispersal commonly begins with an unprotected early developmental stage in marine life cycles. Even if pelagic larvae encounter suitable adult habitat, dispersal may continue until they reach metamorphic competence. By contrast, air is relatively physically hostile to small, delicate phases of the life cycle, so terrestrial animals commonly retain female gametes on or in their bodies, and fertilization and early development are usually internal. Dispersal of terrestrial animals typically begins as a fully developed and motile juvenile, or an adult capable of reproduction, and ends when breeding habitat is chosen (Bitume *et al.*, 2013). The dispersing airborne stage for terrestrial organisms (e.g. insects and plants) with life cycles analogous to marine life cycles does not as clearly afford the same opportunity for enhanced growth and survival as occurs in the sea. Where complex life cycles occur in terrestrial taxa (e.g. insects), reproduction occurs during the mobile stage. In marine complex life cycles, reproduction commonly occurs during the sedentary stage (although some cnidarians are an exception; Table 2). While plants share a similar lifestyle to benthic marine species in having sessile adults and mobile seeds, seeds often do not grow and feed while dispersing. Moreover, seeds often (*i*) cannot actively control their movement, (*ii*) possess specific adaptations to increase dispersal, and (*iii*) exhibit much smaller scales of seed dispersal relative to the scales of gamete exchange whereby pollen typically moves further in air than sperm moves in water (Kinlan & Gaines, 2003). Therefore, early life-history stages in sea water, compared to mobile stages in air, are less likely to have developed specific adaptations for dispersal, whereas specific adaptations are more often expected for juvenile and adult stages in air (Table 2).

VI. DISPERSAL AS A BY-PRODUCT IN MARINE SYSTEMS

Routine large scales of dispersal in many marine taxa (Kinlan & Gaines, 2003) may simply emerge as an incidental by-product maintained by traits favouring movement between alternative niches, rather than dispersal itself (Vance, 1973; Strathmann, 1974; Hedgecock, 1986; Moran, 1994; Havenhand, 1995; Todd *et al.*, 1998; Pechenik, 1999; Bonhomme & Planes, 2000; Strathmann *et al.*, 2002; Pringle *et al.*, 2014). Three main lines of evidence support this hypothesis: (*i*) there are a variety of selective factors favouring a pelagic stage that are not related to dispersal; (*ii*) selective factors favouring dispersal (see Section III) do not explain the observed scales of dispersal observed in the sea; and (*iii*) pelagic stages often persist even where and when selection should favour limited dispersal.

Most hypotheses for the evolution of a pelagic dispersive larval stage in the sea centre on the advantages of small propagules moving to an environment that offers food and perhaps greater safety (reviewed in Table 1) (Strathmann, 1974; Hedgecock, 1986; Todd *et al.*, 1998; Pechenik, 1999; ; Bonhomme & Planes, 2000; Strathmann *et al.*, 2002). The duration of the pelagic feeding larval stage can reflect a trade-off between the size and number of offspring. Many factors influence this trade-off, such as temperature, developmental time and survival rate, fertilization success, the ability to feed facultatively, generation time, and post-metamorphic effects of offspring size (reviewed in Marshall & Keough, 2008). Larval feeding and growth in the plankton, as well as reduced benthic mortality during early developmental stages, represent separate benefits from those directly related to dispersal, but could affect selection on fecundity, initial size, and size at settlement, which in turn influence pelagic larval duration and patterns of dispersal (Baskett *et al.*, 2007; Dytham & Simpson, 2007 Pringle *et al.*, 2014). Realized dispersal also depends on the timing of offspring release into the water. Selective factors driving the timing of offspring release include matching releases with conditions favourable for fertilization, larval feeding, and growth and survival during development and shortly after settlement (e.g. Todd & Doyle, 1981; Morgan, 1995; Morgan & Christy, 1995; McEdward, 1997; Reitzel, Miner & McEdward, 2004). Photodamage, temperature and salinity stress, and larval stranding also relate to patterns of offspring release into the water column (Morgan & Christy, 1995). Therefore, traits correlated with dispersal may also increase fitness, but depend on selective factors outside direct selection for dispersal, such that the benefits of spreading kin are unlikely to be the major cause of why those traits increase fitness.

Realized dispersal in the sea typically occurs at much larger spatial scales than would be expected from direct selection to reduce interactions among kin or to spread the risk in variable environments (Section III) (Strathmann *et al.*, 2002). Many factors relevant to benthic marine species, such as large population sizes, high fecundity, and broadcast spawning may decrease the evolutionarily stable dispersal rate or distance in kin-selection models, sometimes to zero, because they reduce relatedness within and among populations (Comins *et al.*, 1980; Rousset & Gandon, 2002; Levin *et al.*, 2003). Furthermore, moving a large distance from the natal site does not always guarantee that siblings will in fact drift apart (Ben-Tzvi *et al.*, 2012); recent evidence suggests that kin may still settle in groups after a pelagic duration of several weeks (Veliz *et al.*, 2006; Buston *et al.*, 2009; Bernardi *et al.*, 2012). Therefore, the expectation that the relative ease of passive movement in sea water should allow parents maximally to spread their offspring to reduce competition with relatives and increase long-term inclusive fitness (Hovestadt *et al.*, 2012) is likely far from a complete evolutionary explanation for the large scales of dispersal observed in benthic marine species.

Furthermore, interactions with kin and conspecifics may be beneficial (Grosberg & Quinn, 1986; Toonen & Pawlik, 2001). For example, settling next to siblings may be advantageous in a colonial ascidian because related neighbours are more likely to fuse than unrelated neighbours, effectively increasing their size and competitive ability (Grosberg & Quinn, 1986). More generally, in sessile marine invertebrates, cases of aggregated settlement in sibling larvae (Grosberg & Quinn, 1986; Aguirre *et al.*, 2012) and even sessile animals harming unrelated, non-clonemate, nearby settlers (Ayre & Grosberg, 1996), suggest that there may be advantages to settlement near kin. Even if costs to interactions with kin outweigh the benefits, short scales of dispersal (centimetres to metres) are often enough to reduce this cost (Grosberg & Quinn, 1986), as compared to the larger scales of dispersal that result from a longer pelagic stage that spans suitable and unsuitable habitat. For sessile species (e.g. bryozoans, ascidians, corals, sponges, algae) adults can often move to new locations by rafting on debris or floating after becoming detached during a storm (Johannesson, 1988; Thiel & Haye, 2006), and this rafting may alleviate selection for widespread larval dispersal, regardless of whether rafting is accidental or adaptive (Todd *et al.*, 1998).

For spatial and temporal variation in the environment to favour dispersal at the large scales commonly seen in benthic marine species, environments would have to be spatially autocorrelated over unrealistically large spatial scales (kilometres to tens of kilometres) and change randomly between generations at that spatial scale (Palmer & Strathmann, 1981; Travis, 2001; Snyder, 2011). Long-distance dispersal of planktonic larvae may allow colonization of newly unoccupied sites (Phillips *et al.*, 2010; Kremer *et al.*, 2012; Travis *et al.*, 2012), but unoccupied habitat could probably be obtained within metres to kilometres of parents regularly enough to obviate selection for dispersal over tens of kilometres, as seen in many species with feeding larvae (Palmer & Strathmann, 1981; Shanks, 2009). Given the influence of the physical environment on dispersal, any selection for 'moderate' dispersal distances could give rise to long-distance dispersal as an unavoidable consequence of the traits that have evolved in response to selection for shorter distance dispersal (Strathmann, 1974). Furthermore, closely related species that live in the same habitats, and therefore experience similar spatial–temporal variability can have highly divergent developmental modes (i.e. long-lived pelagic larvae *versus* benthic development), with correspondingly different dispersal potential (Johannesson, 1988; Todd *et al.*, 1998; Krug *et al.*, 2012).

The loss of a pelagic stage in cases where selection should reduce dispersal is rare. For example, general theory (Dytham & Simpson, 2007) and empirical evidence from terrestrial systems (Cody & Overton, 1996) demonstrate selection against dispersal on islands, but many island endemic reef fishes have planktonic larvae with dispersal potentials similar to those of more widespread species (Robertson, 2001). In terms of reducing dispersal, long-term constraints on the evolution and loss of capacity for larval feeding may limit selection on larval duration as a means of adjusting dispersal (Pechenik, 1999; Bonhomme & Planes, 2000). Available evidence suggests that the capacity for larval feeding has originated rarely and once lost is rarely regained (Strathmann, 1985; Pechenik, 1999). Many species in many different habitats have direct development, suggesting that benefits of dispersal can be achieved over relatively small scales without pelagic larvae (e.g. dispersal of adult clams with direct development; Commito *et al.*, 2013). Any costs of dispersal in feeding larvae may be offset by the benefits of growth during transit, but selection appears to favour less dispersal than larvae could achieve by passive drift (Pechenik, 1999; Strathmann *et al.*, 2002).

Furthermore, taxa with pelagic adult stages (e.g. krill, tuna, heteropods, and pteropods) capable of extensive dispersal (ocean-basin scale), may still have long-lived larval forms similar to those in taxa with benthic adult stages (Strathmann, 1985). Analogously, copepods that are pelagic as adults tend to have pelagic larval stages, and copepods that are benthic as adults tend to have benthic larval stages, suggesting that planktonic larval stages most capable of dispersal in benthic species do not persist primarily because of selection favouring extensive dispersal of offspring.

(1) Selection for local retention in marine systems

Selection to limit dispersal may actually be more likely than selection to increase dispersal in marine systems. Weighing costs of dispersal, such as planktonic mortality or transport to unsuitable habitat, against the nutrition and survivorship benefits of a pelagic *versus* benthic larval stage, an offspring size–number trade-off can favour the evolution of a pelagic stage as the optimal strategy (Vance, 1973; Baskett *et al.*, 2007; Pringle *et al.*, 2014). Indeed, it may be adaptive for larvae to move away from parental habitat to develop, but maladaptive for larvae to disperse too widely and settle in distant locations (Table 1; Johannes, 1978; Strathmann *et al.*, 2002; Baskett *et al.*, 2007; Dytham & Simpson, 2007).

If selection favoured increased dispersal in benthic marine species, then extending the duration of small, planktonic life-history stages would be a way to increase dispersal. Longer pelagic durations would lead to larger dispersal distances if larvae were passive, since – all else being equal – coastal currents transport and disperse tiny propagules larger distances with increasing time (Largier, 2003; Nickols *et al.*, 2015). Across species, there is some evidence for a positive relationship between dispersal distance and planktonic duration: marine species with a pelagic larval stage typically disperse further than species with a benthic larval stage (i.e. direct developers with no planktonic period), and species that disperse the greatest distances (modal distances far exceeding 20 km) have long (weeks to months) pelagic durations (Shanks, 2009). However, long pelagic durations do not necessarily relate to large scales of dispersal: some species with pelagic durations of weeks to months can have the same short modal dispersal distances (modal distances <1 km) as species with pelagic durations of hours to days (Shanks, 2009; Buston *et al.*, 2012). Other studies using population genetic measures of dispersal find no strong relationship between pelagic duration and dispersal distance (Weersing & Toonen, 2009; Riginos *et al.*, 2011). Emerging empirical and biophysical models of marine larval dispersal reveal levels of local retention ('larvae returning home'; Burgess *et al.*, 2014, and references therein) more often than expected from the passive drift of small larvae in ocean currents, suggesting active involvement on the part of larvae or adults to limit dispersal (Gerlach *et al.*, 2007). Depending on the spatial scale at which currents and behaviours make local retention feasible (e.g. Burgess, Kingsford & Black, 2007; Nickols *et al.*, 2015), selection for local retention could still give rise to enough displacement between relatives that dispersal-related benefits are fully realized (Strathmann *et al.*, 2002). While methodological issues remain, the available evidence suggests that the traits most expected to increase dispersal (e.g. planktonic duration) do not correlate well with dispersal distance in nature. Such evidence is not consistent with selection for dispersal at the scales seen in nature and suggests that other traits, such as larval and adult behaviours, act to decrease the potential for widespread passive dispersal.

In the marine environment, selection to decrease dispersal can sometimes lead to increased spread in the distribution of dispersal distances as a consequence. When a coastal current producing net downstream movement increases the risk of dispersing to an unsuitable habitat, three adaptations might alleviate this risk: (*i*) shorter pelagic durations to minimize larval loss (Nickols *et al.*, 2015); (*ii*) increased fecundity to reduce the effect of losses, perhaps with correspondingly smaller larvae and a longer feeding stage; and (*iii*) spacing larval release to capture stochastic current reversals and increase net retention (Byers & Pringle, 2006; Pringle *et al.*, 2014). The latter two strategies can lead to greater spread in dispersal distances as a by-product of selection to limit dispersal and increase retention.

In some oceanographic settings, longer larval durations could, in fact, reduce losses from benthic adult habitats (Jackson & Strathmann, 1981; Shanks & Eckert, 2005). If seasonal current reversals occur within feasible larval lifespans, longer pelagic durations can improve the chances of larvae returning to parental populations, which could explain differences in the pelagic durations of benthic crustaceans and fishes in different habitats along the California shelf (Shanks & Eckert, 2005). Similarly, a longer developmental period may also require a longer competency (post-development) period to allow larvae additional time to return to suitable adult habitat after developing in offshore waters, which could further increase the spread of dispersal distance distributions (Jackson & Strathmann, 1981). Therefore, costs of dispersal due to transport to locations with no, or poor quality, settlement habitat could select for a reduced pelagic duration, or cause enhanced dispersal as a by-product of selection on other traits that aid in local retention in coastal currents.

(2) When are traits 'for' dispersal in marine systems?

Traits influencing dispersal in the sea are more likely to be 'for' dispersal when there is in fact little potential for dispersal, such that dispersal occurs over spatial scales relevant to benefits of direct selection. In sessile organisms with overlapping generations, like many plants and marine invertebrates, departure from the parent is critical to avoid parent–offspring competition, particularly for organisms capable of indeterminate growth. Some benthic marine species that brood their offspring release them as free-swimming, competent, non-feeding larvae. These larvae (e.g. most sponge larvae, planulae of some cnidarians, many ascidian tadpole larvae, most bryozoan larvae, and some polychaete larvae) are competent to settle upon release, have very brief dispersal periods (minutes to hours), typically swim immediately upwards towards light or do not respond to settlement cues, and then after some time change behaviour and responses to light and settlement cues for settlement. Such larval behaviours influencing departure may be an adaptation for dispersal; that is, to ensure that larvae do not settle immediately next to their parents or relatives (Toonen & Pawlik, 2001; Strathmann, 2007). Larval behaviours conducive to dispersal variation (e.g. differential responses of competent larvae to settlement substrata) can also exhibit heritable within-brood variation (Toonen & Pawlik, 2001) and are correlated with maternally controlled larval phenotypes (e.g. larval size; Marshall & Keough, 2003; Burgess, Hart & Marshall, 2009; Burgess, Bode & Marshall, 2013). In the case of poecilogony, adult sacoglossan sea slugs (*Alderia willowi*) can alter the dispersal potential of their offspring, both within and among clutches, by producing short-lived non-feeding larvae and long-lived feeding larvae (Krug *et al.*, 2012). Populations produce short-lived non-feeding larvae in summer when their estuarine habitat is seasonally closed off from the open coast and produce long-lived feeding larvae in winter when their estuarine habitat seasonally opens and larvae can escape to colonize other estuaries. Krug *et al.* (2012) suggested that the seasonal shift to long-lived feeding larvae with greater dispersal potential represents an adaptation to colonize ephemeral adult habitat at range margins, rather than a nutritional benefit. Though poecilogony is generally quite rare, it represents a potentially powerful system to test hypotheses about selection for dispersal *versus* other functions (Krug *et al.*, 2012; Knott & McHugh, 2012).

VII. IS DISPERSAL AS A BY-PRODUCT UNIQUE TO MARINE SYSTEMS?

The previous section considers how dispersal-related traits and patterns of dispersal in benthic marine systems may reflect both the direct effects of selection on dispersal *per se*, as well as the indirect effects of selection for other functions, especially feeding, and perhaps even limiting dispersal and promoting retention. Against this background, we now consider how both direct and indirect selective processes may influence the evolution of dispersal-related traits in terrestrial systems.

(1) Plants

Traits that potentially lead to net displacement as an evolutionary by-product in wind-dispersed seeds include seed size and plant height. Smaller seeds tend to be lighter and can travel further in the wind, which can generate positive covariation between seed size and dispersal distance (Ganeshaiah & Shaanker, 1991). Seed size may be selected to increase dispersal, but it also evolves as part of a size–number trade-off where larger seeds are better provisioned and have higher establishment success in demanding environments (e.g. low nutrients or water, or high competition; Ganeshaiah & Shaanker, 1991; Levin & Muller-Landau, 2000; Parciak, 2002). Hence, distance-independent variation in germination success and early survival may cause variation in seed size and therefore variation in dispersal distances (Parciak, 2002). Similarly, seeds from taller plants tend to disperse further than those from shorter plants (Thomson *et al.*, 2011), so that selection on plant height, driven by competition for sunlight, grazing by ground-dwellers, or maximizing pollination (Falster & Westoby, 2003), can indirectly influence the evolution of seed dispersal distance (Travis, Smith & Ranwala, 2010). Thus, while traits that influence seed dispersal, such as morphological structures to increase lift, are clearly connected to direct selection for dispersal, other traits such as seed size and plant height may evolve under the influences of a diverse array of selective forces, with effects on dispersal being, to greater or lesser degrees, by-products.

For animal-mediated seed dispersal, net displacement depends on the traits that influence the attraction of, and retention time on or in, the animal vector (Figuerola & Green, 2002; Russo, Portnoy & Augspurger, 2006; Jordano *et al.*, 2007). The amount of time seeds remain on or in the animal also depends on the characteristics of the seed (Figuerola *et al.*, 2010). For example, the dispersal distance of seeds ingested by frugivores depends on gut passage times (Will & Tackenberg, 2008), which are influenced by seed traits such as pulp mass and seed-coat thickness (Traveset, 1998). Although the evolution of fruits to attract frugivores likely evolved as a way for plants to have their seeds removed from the parental area (i.e. 'for' dispersal), traits that influence gut passage time also increase germination success from scarifying the seed coat, digestion of pulp, or deposition of seeds in faeces (Samuels & Levey, 2005; Traveset, Robertson & Rodríguez-Pérez, 2007) Selection for seed traits that increase germination success could then produce changes in the resulting dispersal kernel that are not directly related to the benefits of increasing displacement (Levin & Muller-Landau, 2000). Overall, while the dispersive stage and mode of transport (e.g. wind or animal) might occur 'for' dispersal in plants, a number of traits that determine seed dispersal distance (e.g. seed size, plant height, seed coat thickness) also have links to fitness independently from that brought about directly by dispersal. In other words, direct selection might drive the existence of dispersal and therefore the departure stage, and by-product selection might have the greatest effect on the transfer stage.

(2) Animals

Dispersal in terrestrial animals can be a by-product of movements associated with resource exploitation (e.g. foraging, exploring, mate-location, or shelter seeking: Stamps *et al.*, 2005; Van Dyck & Baguette, 2005; Winkler, 2005; Salewski & Bruderer, 2007; Mabry & Stamps, 2008; Benton & Bowler, 2012; Matthysen, 2012; Dingle, 2014). These sources of dispersal as a by-product occur in mobile marine animals too. The fact that animals use one type of locomotion for multiple ecological functions confounds interpretations of selection on traits for dispersal (Van Dyck & Baguette, 2005; Winkler, 2005; Salewski & Bruderer, 2007). For example, exploratory movements by great tits (*Parus major*) were positively related to dispersal distance and direction (van Overveld *et al.*, 2014), but it remains unclear whether the advantage of exploratory movements arises from more effective use of an area, which might result in net displacement as a by-product, or from the advantages of net displacement *per se* (van Overveld *et al.*, 2014). In addition to the movement itself, traits that determine the amount of movement (e.g. leg morphology) also influence other activities (e.g. foraging, refuge use, and predator avoidance), such that some aspects of dispersal-associated movement could evolve as an incidental outcome of performing these other functions. For example, allelic variation in a gene underlying larval foraging in fruit flies (*Drosophila melanogaster*) also relates to dispersal distances (Edelsparre *et al.*, 2014). Selection for movement indirectly related to dispersal, such as foraging or exploration, might not only increase displacement distances during the transfer stage, but also influence selection on traits influencing the departure and settlement stages of dispersal (Stamps *et al.*, 2005; Benard & McCauley, 2008; Mabry & Stamps, 2008 Bonte, Hovestadt & Poethke, 2010; Travis *et al.*, 2012; Fronhofer *et al.*, 2014). As with plants, many traits that influence dispersal in animals are clearly linked to fitness through the benefits brought about by dispersal (i.e. 'for' dispersal) (Bonte *et al.*, 2014); however, a number of dispersal-related traits also have direct links to fitness for other reasons (Van Dyck & Baguette, 2005).

VIII. USING MULTIVARIATE SELECTION TO ASK WHEN DISPERSAL IS FOR DISPERSAL

Given the mix of direct and indirect selection acting on the complex suite of traits that influence each stage of dispersal across marine and terrestrial systems, a fruitful way to address the unifying question 'when is dispersal for dispersal' is to apply the framework of multivariate selection (e.g. Lande & Arnold, 1983; Phillips & Arnold, 1989) to describe patterns of selection, then couple this statistical description with experiments to identify the ecological causes of selection (Wade & Kalisz, 1990; MacColl, 2011) (Fig. 2). The multiple traits that influence dispersal at each stage form a multivariate phenotype that experiences manifold selection pressures, where phenotypic and genetic correlations among traits determine how the traits change in response to the environment and selection (Fig. 2). This multivariate perspective mathematically formalizes the potential for selection to have both direct and indirect

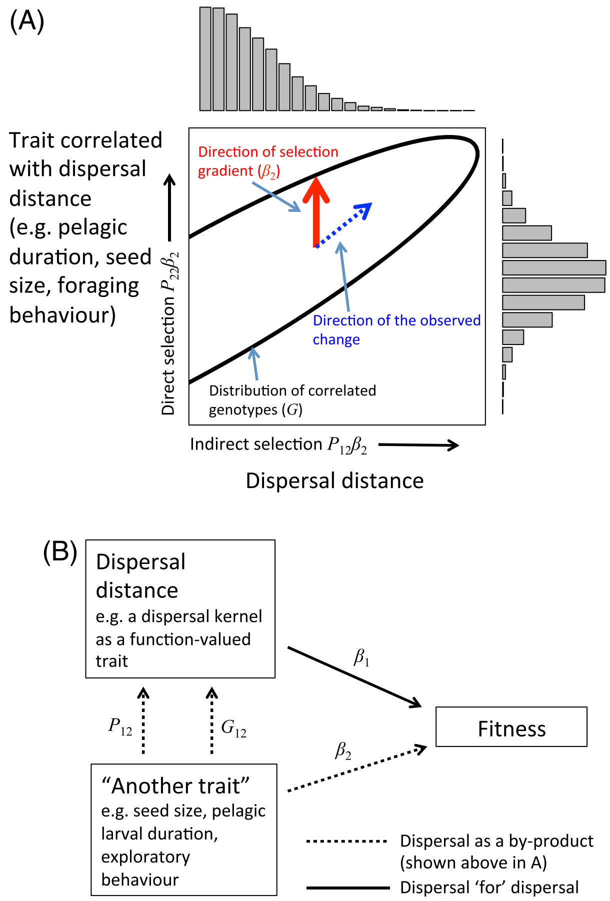

Fig. 2. A framework to address the question 'when is dispersal for dispersal?' (A) The observed evolutionary response of dispersal distance as a by-product of selection on another correlated trait can be represented mathematically as $\Delta z_1 = G_{11}P_{11}^{-1}\,(P_{12}\beta_2) + G_{12}P_{12}^{-1}\,(P_{22}\beta_2)$ (see Section VIII for definitions of parameters). (B) Hypothetical causal relationships (arrows) between a trait, dispersal distance, and fitness. The solid lines show dispersal 'for' dispersal. The dashed lines (situation shown in A) represent dispersal as a by-product. Both the statistical associations between phenotypes and fitness (A) and experimental approaches to identify the causal links between phenotypes and fitness (B) are required to understand the degree to which dispersal is for dispersal.

effects, where some traits in a correlated ensemble are the focus of direct selection for dispersal, and other traits generate and maintain a dispersal outcome as a by-product of indirect selection on traits correlated with dispersal (Fig. 2; Phillips & Arnold, 1989). For example, if we are measuring the relationship between dispersal distance and fitness, and if a second trait is correlated with dispersal distance (e.g. pelagic development time in marine larvae; plant height in wind-dispersed seeds), selection acting only on the second trait can make it appear that that there is a causal association between dispersal distance and fitness, even in the extreme case when dispersal distance is selectively neutral (Fig. 2). Such a correlation highlights the need not only to understand the traits that covary with dispersal (often called dispersal syndromes, which is just the phenotypic co-variation P_{12} in Fig. 2), but also their relationships to fitness and the causes of those relationships, requiring us to move beyond descriptions of dispersal syndromes. A dispersal syndrome should not necessarily imply that all trait correlations are a result of direct selection for dispersal.

Two important points need to be considered when using multivariate selection analyses: (*i*) the statistical approach of multivariate selection analyses can rarely identify the cause of selection without complementary experiments to uncover the causal pathways (Wade & Kalisz, 1990; MacColl, 2011), and (*ii*) components of individual fitness that are measured empirically, such as survival or number of offspring, may not always map in a simple way onto the mathematical measures of fitness, such as inclusive fitness, geometric mean fitness, and harmonic mean fitness, used in models to understand trait evolution in variable environments (Orr, 2009). In the case of measuring fitness of dispersal-related traits, fitness should be assessed in natal and colonized environments and the causes of any fitness variation, as they relate to the phenotypes and behaviours of individuals, their relatedness, the population density, and environmental quality of the different sites, need to be identified and quantified (Stinchcombe *et al.*, 2002; Bonte *et al.*, 2014).

Indirect selection is not merely a practical obstacle to measuring selection in nature, it can also be important for understanding the evolutionary responses to selection. The importance of indirect selection to the evolution of dispersal depends critically on the amount of heritable variation along the trait axis that selection is acting in multivariate trait-space (Fig. 2). In the case of evolution of just two traits, there also needs to be genetic co-variation between dispersal distance and the other trait (Phillips & Arnold, 1989). The observed evolutionary change between generations of dispersal distance (Δz_1) as a by-product of selection on another correlated trait depends on the phenotypic and genetic variation in dispersal distances (P_{11} and G_{11}, respectively), the amount of phenotypic and genetic co-variation between dispersal distance and another trait (P_{12} and G_{12}, respectively), the selection gradient representing the direct effect of selection acting on dispersal distance (β_1), the selection gradient representing the direct effect of selection acting on the other trait (β_2), and can be represented mathematically as $\Delta z_1 = G_{11}P_{11}^{-1}\,(P_{12}\beta_2) + G_{12}P_{12}^{-1}\,(P_{22}\beta_2)$ (in the extreme case when $\beta_1 = 0$; P_{22} is the phenotypic variance of the trait correlated with dispersal; Fig. 2) (adapted from Phillips & Arnold, 1989; see Mitchell-Olds & Shaw, 1987; Wade & Kalisz, 1990; Stinchcombe *et al.*, 2002; Blows & Hoffmann, 2005; Hansen & Houle, 2008; Morrissey, 2014, for a more in-depth discussion).

In addition to dispersal arising from direct and indirect selection, some dispersal is inevitably 'accidental' (e.g. birds displaced by a storm during migration; propagules accidentally attached to the feet of water birds; seeds or larvae passively transported great distances in wind or currents, respectively). If there is no correlation between displacement and the traits of individuals, then such accidental dispersal does not contribute to maintaining and modifying dispersal as an evolutionary by-product (Starrfelt & Kokko, 2012). However, dispersal appearing as an accident can be evolutionarily maintained when it correlates with morphological and behavioural traits of individuals, when such traits are under selection for other reasons, and when there is heritable variation along the dimension that selection acts (Fig. 2). Thus, accidental dispersal could, in some instances, be evolutionarily important.

IX. CONCLUSIONS

(1) The apparent contrast between the dispersal evolution literatures in marine *versus* terrestrial systems likely reflects a difference in the relative importance of direct and indirect causes of selection driving displacement. Direct and indirect causes occur in both physical realms of life, rather than there being a fundamental difference in the importance of dispersal to fitness. Our analysis suggests that direct selection for dispersal has a greater impact on evolutionary changes in dispersal in terrestrial than in marine systems. We also propose that direct selection for dispersal might be more common during the departure than the transfer phase of dispersal.

(2) The question is not whether dispersal provides fitness benefits (it often does), but what is the relative importance of these benefits in explaining evolutionary changes in net displacement that arise through changes in traits that are correlated with dispersal. The traits that influence overall net displacement between relatives also evolve in response to additional selective forces, such as accessing food, reducing predation risk, and optimizing offspring size–number trade-offs. Therefore, the answer to the question ‘when is dispersal for dispersal’ is not one of absolutes, but one of degrees.

(3) The contribution of direct and indirect selection to the overall dispersal outcome is difficult to distinguish, especially when there are parent–offspring conflicts, and in species where the same traits influence not only dispersal, but also foraging, migration, and other aspects of movement (Van Dyck & Baguette, 2005). However, a combination of multivariate selection analyses and experimental approaches presents one promising way forward.

(4) Correlations between traits and patterns of dispersal (dispersal syndromes) are only a starting point and need to be causally linked to fitness to reveal the function of dispersal.

(5) A trait-based approach, focused on selection on traits that influence dispersal, will not only improve our understanding of when dispersal is a direct adaptation *versus* a by-product, but can also advance the integration of theory and data. Theories of dispersal evolution would benefit from considering the evolutionary causes of movement in general as well as additional agents of selection on the multiple traits that influence dispersal specifically. An advantage of focusing on traits that produce movement is that the phenotypes are the targets of selection and are often more easily measured. Measuring dispersal distance in the field is often more difficult, but can also be explored in trait-based models of dispersal evolution (Travis *et al.*, 2010). A trait-based approach that incorporates both direct and indirect selective agents will also be more mechanistic and therefore enhance predictability under novel environmental conditions (Helmuth, Kingsolver & Carrington, 2005; Baskett, 2012), which might be particularly important in the context of climate change given the significant role of dispersal in species responses to changing climatic conditions (Travis *et al.*, 2013).

(6) We join others before us (e.g. Benton & Bowler, 2012; Starrfelt & Kokko, 2012) in advocating an evolutionary focus to the field of movement ecology (Nathan *et al.*, 2008) and a greater focus on studying the causes of selection on the traits correlated with patterns of dispersal to better predict the ecological consequences of changing environments.

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