Landscape Ecology (2006) 21:917–931
DOI 10.1007/s10980-005-5568-6

Research Article

Currents, landscape structure, and recruitment success along a passive–active dispersal gradient

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Received 19 July 2005; accepted in revised form 30 November 2005

Key words: Cellular model, Dispersal strategy, Habitat shifts, Hydrodynamic currents, Recruitment success

Abstract

There exists a gradient in dispersal behavior from passive to active, which reflects organisms' dependence upon currents vs. self-propelled movement. We asked: Do currents modify organism–landscape interactions to influence recruitment success along this dispersal gradient? Using a spatially-explicit cellular model, we simulated the recruitment success of three generalized dispersal strategies (walkers, swimmers, and drifters) through hierarchically structured benthic landscapes. We evaluated the relative recruitment success (recruited population size, overall area occupied, time to recruit) of the three dispersal strategies in similar landscapes, as well as the consequences of varying the total proportion of habitat suitable for recruitment, and the scale and pattern of habitat patchiness on recruitment success. In the presence of currents, swimmers and drifters generally recruited over larger areas and in less time than walkers. Differences among the dispersal strategies' recruitment success were most pronounced when an intermediate number of good habitat cells (16–48% of landscape) were broadly dispersed across the landscape. Although recruitment success always increased with increasing proportion of good habitat, drifters were more sensitive, and swimmers less sensitive, to these landscape changes than walkers. We also found that organisms dispersing within currents typically responded non-linearly (logarithmically or exponentially) to increasing proportion of total good habitat, whereas walkers more often responded linearly.

Introduction

The absence of evidence defining connectivity between juvenile and adult habitats is a critical missing link in our understanding of marine population dynamics and our efforts to protect these populations (Beck et al. 2001; Gillanders et al. 2003). Hydrodynamic models of passive particles traveling in oceanic currents have provided insight into large-scale population processes and dispersal mechanisms linking adult and juvenile populations (Roberts 1997; Cowen et al. 2000; Gaines et al. 2003). Yet, juvenile mobile marine fauna spend an average of 13 months (range 8 days to 5 years) living and moving among nursery habitats in estuarine, coastal, or backreef environments prior to residing in adult habitat (Gillanders et al. 2003). Many of these species have complex life cycles that include one or more ontogenetic habitat shifts, during which they disperse over distances from a few meters to hundreds of kilometers (Beck et al. 2001; Gillanders et al. 2003), traverse complex habitats, and display strong species-specific habitat preferences (Eggleston 1995; Irlandi and Crawford 1997; Acosta 1999; Dahlgren and Eggleston 2000). The waters hosting these juveniles are characterized by complex, highly variable (both spatially and temporally) hydrodynamic patterns, where wind and tidal currents predominate. In addition, these juveniles are no longer pelagic larvae, but now actively interact with the benthos, seeking shelter and food resources as they move within complex habitat mosaics. High mortality in these environments could result in a decoupling of larval supply and adult abundances, such that high larval recruitment and high density of young juveniles would not serve as an indicator of future adult population density (Beck et al. 2001; Gillanders et al. 2003).

Species' interactions with currents may be described along a gradient from passively drifting (e.g. some insects, marine larvae, and seeds), to selectively using currents to orient or increase dispersal distance (e.g. some fish, marine mammals, and birds), to seemingly ignoring currents (e.g. some amphibians and small mammals). These different dispersal strategies correspond to differences in search area (size and shape) and directionality, and potentially impact the relative influence of landscape composition and configuration on recruitment success. For example, species utilizing currents for propulsion or orientation would be expected to display a more linear search pattern with directional flow and to spend more time dispersing above landscapes rather than through landscapes, relative to species that ignored currents. Species using currents for propulsion would move primarily downstream (e.g. Forward and Tankersley 2001; Gibson 2003; Thomas et al. 2003), while those using chemosensory cues within currents for orientation would likely move upstream (e.g. Schooley and Weins 2003). Despite the potential influence of currents on landscape scale organism dispersal, no study has comparatively evaluated how the potential differences in search area and directionality associated with currents may affect organism–landscape interactions along this passive–active dispersal gradient.

We developed a spatially explicit, cellular automata model to investigate how animal dispersal strategies interact with water currents and benthic landscape characteristics to influence the recruitment success of dispersing marine organisms at spatial scales of one to several hundred kilometers. The model was designed to simulate ontogenetic movement of juvenile species within nearshore, estuarine, or backreef habitats. Our model, however, could equally represent movement of some terrestrial organisms influenced by both aerodynamic currents and landscape composition and structure. We compared recruitment success of virtual dispersers as a function of three different dispersal strategies (walking, swimming, and drifting), and in response to the scale and pattern of habitat patchiness. The dispersal strategy treatments differed in their movement ability (passive vs. active horizontal dispersal), their response to currents (ignoring them vs. utilizing them), and their potential search area (large vs. small). The model was not intended to represent a specific species, but rather to explore the relative advantages of three dispersal strategies' unique dispersal 'footprint' (e.g. search area size, shape, directionality) to recruitment success in diverse landscapes. We measured recruitment success in terms of population size (number of survivors), area (number of landscape cells occupied), and time (number of model iterations). We asked: (1) Do the unique characteristics of the three dispersal strategies result in significant differences in recruitment success within similar landscapes? (2) Does the recruitment success of the three strategies respond similarly to changing landscape characteristics? and (3) What is the relative influence of dispersal strategy and landscape characteristics upon recruitment success?

Many dispersal simulation models have investigated the interacting influences of organism behavior and landscape composition and structure on organism dispersal patterns, recruitment success, and subsequent population dynamics. Most of these studies of dispersal have focused on population dynamics (births, deaths, immigration, and emigration) within and between patches of suitable habitat within a matrix of unsuitable habitat (Fahrig and Merriam 1985; Fahrig 1988; Fahrig and Paloheimo 1988; With and Crist 1995; King and With 2002; Ovankainen et al. 2002; Krawchuk and Taylor 2003; Russell et al. 2003; Schooley and Weins 2003). Our dispersal simulation model differed from past models in several important ways: (1) we incorporated currents as an additional factor influencing organism dispersal, (2) our habitat classification system was unique by departing from traditional ‘good patch’, ‘poor matrix’ habitat designations, and (3) we did not model reproduction due to our focus on recruitment success during ontogenetic habitat shifts rather than metapopulation dynamics. These design differences, discussed in detail below, represented what we perceived to be important distinctions between terrestrial and concomitant marine environments and population dynamics.

Methods

Modeling organism dispersal strategies

Separate models simulated three generalized dispersal strategies: (1) walking, (2) drifting, and (3) swimming (Figure 1). Model organisms from all three strategies shared the same perceptual range, habitat preference and mortality rates (Figure 1). Organisms’ movement iterations were modeled in two stages (active and resting) to simulate the selective tidal stream transport, or diel migration common among marine organisms (review by Forward and Tankersley 2001). When actively dispersing, organisms experienced the hydrodynamic currents as a uniform flow (constant speed and direction) from left to right across all simulated landscapes. Resting organisms sheltered in available benthic habitat and were not influenced by currents (see details below).

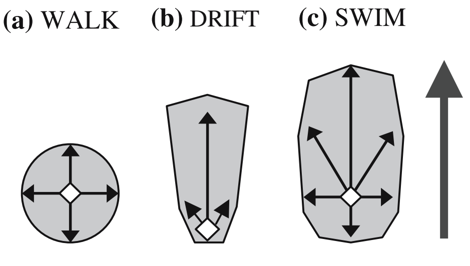
Walkers simulated organisms that move on or just above the seafloor, such as many crustaceans, gastropods, and demersal fish (Figure 1a). Hydrodynamic currents did not influence walkers’ movement direction or range during active dispersal. Instead, the model evaluated the neighboring eight landscape cells and assigned each a relative attraction value based upon habitat quantity and the population density. Cells with abundant recruitment habitat were more attractive to dispersing organisms than cells with sparse recruitment habitat. Similarly, cells below carrying capacity were more attractive than cells at or above carrying capacity. Individuals dispersed among the eight neighbor cells proportionate to the neighboring cells’ relative attraction value. Walkers could move one landscape cell per iteration, in any direction.

The drifter model simulated the strategy of passive horizontal dispersal (Figure 1b). This strategy is common to some species of crustaceans and bivalves, which rise up from the seafloor to

Common Characteristics:

Perceptual range:
8 neighboring landscape cells
Habitat preferences:
- Prefer sites with abundant shelter to sites with sparse shelter
- Prefer sites below carrying capacity to sites at or above carrying capacity

Daily mortality rate:
- $7.87 * 10^{-4}$ when recruited
- $37.88 * 10^{-4}$ while dispersing



Strategy-Specific Characteristics:

	(a) WALK	(b) DRIFT	(c) SWIM
Self-propelled mobility:	Yes, 1 cell	No	Yes, 1 cell
Current influences movement:	No	Yes	Yes
Moves above or through benthos:	Through	Above	Above
Controls movement direction:	Yes	No	Yes
Potential search area per time step:	8 cells	8 cells	16 cells

Figure 1. Three movement behaviors: (a) Walking, where an individual may move in any direction based upon habitat preference; (b) Drifting, where an individual cannot move against or perpendicular to the current; and (c) Swimming, where an individual can move in any direction, however, the current significantly biases potential movement. The dark arrow on the right indicates direction of current flow. The white diamonds represent individual organisms, with the potential movement trajectories identified by the fine arrows. The gray areas indicate the potential search area of the individuals. Notice that the area, shape and perimeter of the search areas vary between movement strategies. The daily mortality rates correspond to annual mortality rates of 0.25 when recruited to good habitat, and 0.75 while dispersing in search of good habitat. Simulated currents flowed from left to right across all landscapes.

move with the currents and then recruit to the seafloor as they pass over suitable substrates (Forward and Tankersley 2001; Gibson 2003). In the horizontal plane of the model, drifters moved only in response to hydrodynamic currents and could not direct their movement towards favorable habitat or away from crowded cells. They did, however, exercise some control over their vertical movement by dropping into unoccupied habitat cells that passed under their passive dispersal trajectory. Most drifters were transported up to two cells in the direction of the current, while a small fraction were moved one cell to the right (10%) or left (10%) of the current, simulating the effects of turbulent mixing.

Swimmers simulated the active dispersal of some fish and crustacean species (Armsworth et al. 2001; Forward and Tankersley 2001; Gibson 2003). The combination of neighboring habitat quantity, population density, and hydrodynamic currents determined a swimmer's dispersal trajectory. Similar to walkers, swimmers' self-propelled movement was limited to one cell in any direction. Swimmers could, however, utilize currents to extend their search distance in the direction of a given currents' trajectory. The model allowed swimmers to move one cell against the current in search of recruitment habitat, however, by moving with the current, individual swimmers could move up to three cells.

Modeling landscape patterns

All landscape cells contained some high quality recruitment habitat, but the relative abundance of high quality recruitment habitat, and therefore the carrying capacity, differed among cells. 'Good' habitat cells held abundant recruitment habitat and could support a recruitment population of 100 individuals. 'Poor' habitat cells contained sparse recruitment habitat and therefore had a carrying capacity of only ten individuals per cell. This quantitative, rather than qualitative definition of good vs. poor habitat differs from most previous, terrestrially oriented, cellular models (e.g. Fahrig and Merriam 1985; With and Crist 1995), and is based on our observations of the ubiquitous distribution of recruitment habitat in both temperate and tropical coastal habitats at intermediate (one to several hundred kilometers) spatial scales (Eggleston and Drew, unpublished data).

We assumed that all individuals could distinguish good and poor recruitment habitat, and that they would prefer the former. A penalty was applied to populations located within both good and poor habitat cells under conditions of overcrowding; all individuals in excess of the carrying capacity experienced a higher mortality rate (see mortality rates below).

We used a hierarchical clustering procedure called 'Curdled' in the software program RULE (Gardner 1999) to generate 252 cells by 252 cells binary landscapes. We elected to use hierarchically structured landscapes because (1) they are considered more realistic representations of natural landscapes than randomly generated patterns (Lavorel et al. 1993), and (2) they allowed us to evaluate the relative importance of changing total proportion of good habitat vs. the arrangement of habitat within the landscape.

In RULE, we specified three landscape generation levels (Figure 2). The coarsest level (Level 1) divided the whole landscape into 49 equal sections and specified that some cells within each section would be classed as good habitat. This ensured that patches of good habitat would be distributed across the entire landscape. Each Level 1 section was then subdivided further into 36 medium scale sections (Level 2). We varied the percentage of Level 2 sections that could contain good habitat from 20% to 80%, in increments of 20%. Finally, each Level 2 section that had been randomly selected to contain good habitat was subdivided into the 36 individual cells. At this finest scale, Level 3, we again varied the percentage of cells classified as good habitat from 20% to 80% in 20% increments.

The total proportion of good habitat (p_{tot}) was the product of the proportion of cells classified as good at Level 3 (p_{fine}) and Level 2 (p_{med}). Thus, we generated 16 landscapes among which the total percentage of cells classified as good habitat varied from 4% to 64%. Early trials during the development of the simulation model assured us that the 252 by 252 cells matrix size was adequate to ensure that none of the dispersing individuals would encounter the landscape edges.

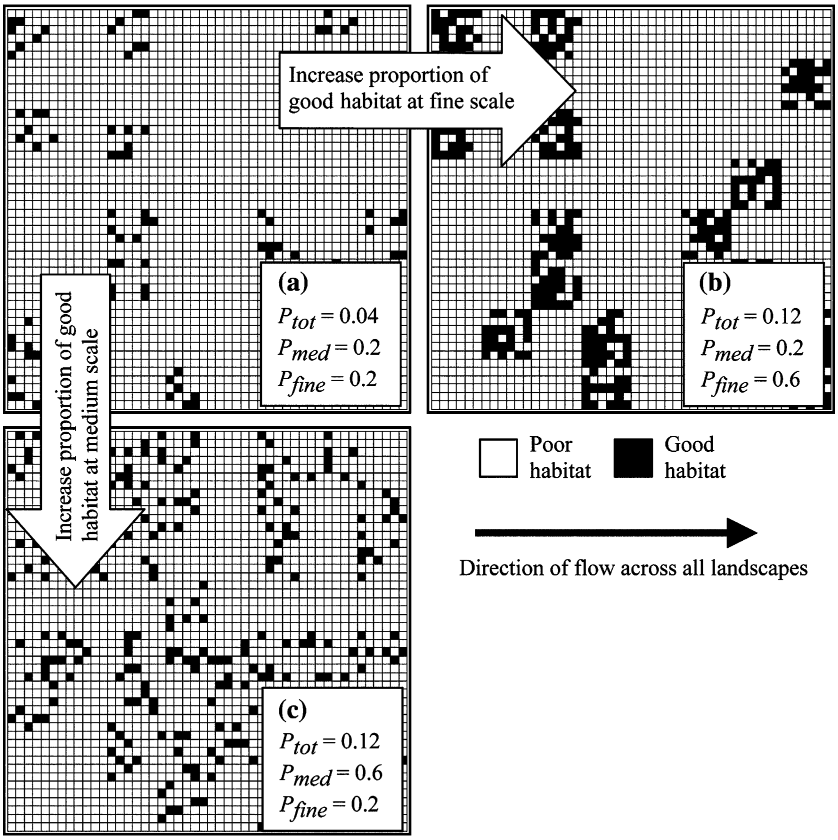


Figure 2. Schematic of 3 of the 16 hierarchically structured cellular landscapes used to manipulate the scale and pattern of habitat patchiness. The dark cells represent areas with abundant settlement habitat and, therefore, high carrying capacity (referred to as 'good' habitat in the text). The white cells indicate areas that offer sparse settlement habitat and limited carrying capacity within the cell's area (referred to as 'poor' habitat in the text). Comparison of the images (a) and (b) illustrates how adding good habitat at the fine scale generated small, tightly clumped patches of good habitat separated from one another by expanses of poor habitat. Alternatively, as shown by comparing images (a) and (c), adding good habitat at the medium scale generated a dispersed pattern with fewer dense patches of good habitat, but also fewer open expanses of poor habitat than observed when habitat was added at fine scales.

Modeling movement, mortality, and recruitment success

We incorporated active and resting dispersal phases into the models to simulate natural dispersal patterns of many marine species, which commonly exhibit directed movement by migrating in response to diurnal and tidal cycles (e.g. Forward and Tankersley 2001). Virtual organisms dispersed only during the active phase and were forced to wait on the seafloor during the resting phase, irrespective of behavioral strategy. As a consequence of this movement pattern, walkers dispersed through the landscape cell-by-cell in a manner similar to traditional, terrestrial cellular dispersal models, while swimmers and drifters experienced a distinct interaction with the landscape. Poor habitat would not necessarily inhibit or redirect the movement of swimmers and drifters, which move over rather than through the landscape cells.

We applied mortality to populations within individual landscape cells at the transition between the resting and active phases of dispersal. During this transition, the model evaluated each landscape cell to locate individuals in excess of that cell's carrying capacity. We assumed that these individuals would lack shelter from predators or sufficient food resources, and would therefore experience a higher mortality rate per iteration (37.88×10^{-4}, equivalent to an annual mortality rate of 0.75). The proportion of the population that had safely recruited into the available recruitment habitat experienced a lower mortality rate of 7.87×10^{-4} per iteration (equivalent to an annual mortality rate of 0.25). The natural mortality rates of marine species are not well known and vary strongly depending upon the species' growth rate and longevity (Froese and Pauly 2003). Our mortality rates corresponded to those of a moderately long-lived fish species (Thompson and Munro 1977). Following the mortality calculations, all surviving individuals in excess of a cell's carrying capacity participated in the next active phase of dispersal by moving according to strategy-specific rules (Figure 1). Therefore, habitat quantity and species density together drove both immigration to and emigration from the individual landscape cells in our model. The model continued to iterate through resting and active phases until all surviving individuals successfully recruited into suitable habitat, herein referred to as 'complete recruitment'. We ran 20 repetitions for each dispersal strategy in each of the 16 landscapes (20 repetitions × 3 dispersal strategies × 16 landscapes; total $N = 960$). Each dispersal and recruitment simulation commenced with a population of 30,000 individuals seeded to a central landscape cell, and continued until all surviving individuals successfully recruited. Only a single spatial location was seeded initially to eliminate potentially confounding effects of inter-population competition and overlap.

Three response variables measured recruitment success: (1) recruited population size, (2) area occupied, and (3) time to complete recruitment. We considered a dispersal strategy highly successful if it enabled a large proportion of dispersing individuals to quickly recruit over a broad extent. Increased survival would reflect a given dispersal strategy's ability to successfully locate high quality habitat while avoiding over-crowded situations. Recruitment over a broad extent would potentially enable the regional population to survive local perturbations, such as disease outbreak or habitat damage. Finally, rapid recruitment to habitats offering safe shelter from predators and high quality resources would allow individuals the best chance to survive and regain the energy expended during dispersal (McCormick 1998; Zollner and Lima 1999).

Data analyses

For models with large sample size and small variance, similar to our own, MANOVA procedures frequently reveal highly significant results for all main and interaction effects, even where observed differences in recruitment success responses are very small and the biological effects of the measured differences are likely trivial (Steidl and Thomas 2001). Therefore, we used the partial R^2 values calculated from a fully factorial MANOVA to estimate the relative influence of behavioral strategy, the proportion of good habitat at fine and medium spatial scales, and their interactions on recruitment success.

We contrasted recruitment success of the three behavioral strategies by fitting linear, logarithmic, and exponential models to the response slopes of recruitment success to increasing proportion of good habitat as an indicator of overall response strength. In this manner, we evaluated the shape of the response of dispersers to increasing the proportion of good habitat at fine scales (while holding the medium scale proportion constant), and medium scales (while holding the fine scale proportion constant), and for the overall total proportion of good habitat in the landscape. Akaike's Information Criterion (AIC) was then calculated to determine the relative fit of the three models (linear, logarithmic, exponential) to the data. AIC weights (Akaike 1973; Myung and Pitt 1997) provides an objective method of discerning which regression model explains more variability in the data while accounting for differences in sample size and the number of model parameters. We interpreted linear responses between recruitment success and landscape structure as indicative of consistent sensitivity to changing proportion of good habitat across all values of available good habitat, while non-linear responses indicated variable responses to incremental changes in the proportion of good habitat.

We pooled the recruitment success data for organisms exposed to increasing proportion of good habitat at medium and fine scales because there was no difference at these scales. For example, the total proportion of good habitat in the landscape could be increased from $p_{\text{tot}} = 0.04$ ($p_{\text{fine}} = 0.20$ and $p_{\text{med}} = 0.20$) to $p_{\text{tot}} = 0.12$, either through the addition of good habitat cells at medium (p_{med} increased to $p_{\text{med}} = 0.60$) or fine (p_{fine} increased to $p_{\text{fine}} = 0.60$) spatial scales (Figure 2). Both scenarios resulted in similar recruitment success response curves; mean recruitment success did not vary significantly according to independent sample *t*-tests. This result of equal means was observed for all simulations with equal total proportion of good habitat but opposite landscape structure. Therefore, we pooled the data based on total proportion of good habitat for all further comparisons of the effects of the three dispersal strategies on recruitment success.

Simulations and model sensitivity analysis

In addition to the dispersal strategy and landscape treatment effects, our model contained two constant parameters that influenced the simulation outcomes: mortality rate and carrying capacity. Past research into the data requirements and sensitivity of spatially-explicit population models indicates that incorrect estimates of parameters such as dispersal mortality can result in significant prediction errors for dispersal success. (Ruckelshaus et al. 1997). Therefore, a sensitivity analysis of the simulation results was conducted to understand how error in mortality rate and carrying capacity would affect the simulation outcome. This sensitivity analysis sequentially examined the influence of a 10% increase and 10% decrease in mortality rate and carrying capacity on recruitment success for each of the original 48 landscape-strategy combinations (Table 2).

Results

Relative recruitment success of the three dispersal strategies

When we measured recruitment success by the population size at complete recruitment (proportion of dispersing individuals that successfully recruit), the strategies that utilized currents (swimmers and drifters) were more successful than the walker strategy, which ignored currents (Figure 3a). Differences among the three strategies were generally greater for the area and time response variables, however, than for population size (Figure 3). Swimmers dispersed over a larger area and occupied more landscape cells than either drifters or walkers, which had much smaller potential search areas during each iteration of the model (Figure 3b). Swimmers also required the fewest model iterations to successfully locate and occupy recruitment habitat (Figure 3c). In comparison, walkers recruited somewhat slower than swimmers, but faster than drifters (Figure 3c). Thus, active dispersers recruited faster than passive dispersers, and organisms with a large potential search area recruited faster than those potentially searching a smaller area.

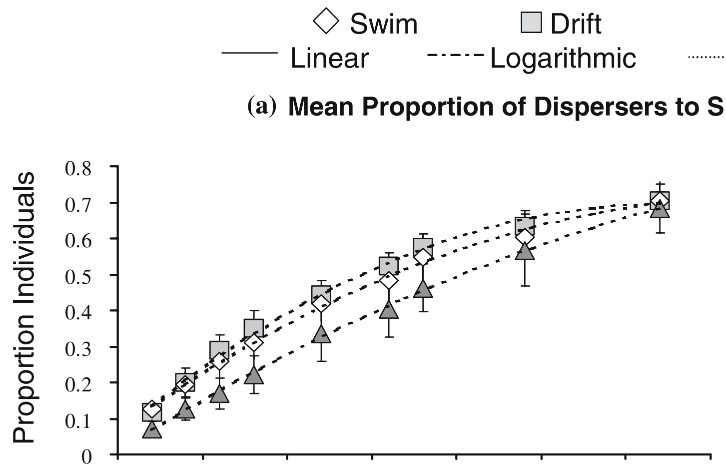
The rank order of the three dispersal strategies generally remained constant for a given response variable regardless of the proportion of good habitat in the landscape (Figure 3). As an exception, while drifters typically occupied more landscape cells than walkers, the opposite was true at the lowest ($p_{\text{tot}} = 0.04$) and the highest ($p_{\text{tot}} \geq 0.48$) modeled proportion of good habitat (Figure 3b).

The magnitude of the differences in recruitment success between dispersal strategies differed depending upon the proportion of good habitat and the response variable measured. Differences among the three dispersal strategies' mean recruited population size were greatest when the landscape presented an intermediate proportion of good habitat (Figure 1a: $0.16 < p_{\text{tot}} > 0.48$). Alternatively, for mean time to complete recruitment and mean area occupied, differences among the dispersal strategies were most pronounced with a low proportion of good habitat (Figure 1b and c: $p_{\text{tot}} < 0.40$). As the total proportion of good habitat increased, the advantage of walker and drifter strategies relative to swimmers, as measured in time and area occupied, diminished rapidly (Figure 3b and c).

Influence of increasing total proportion of good habitat

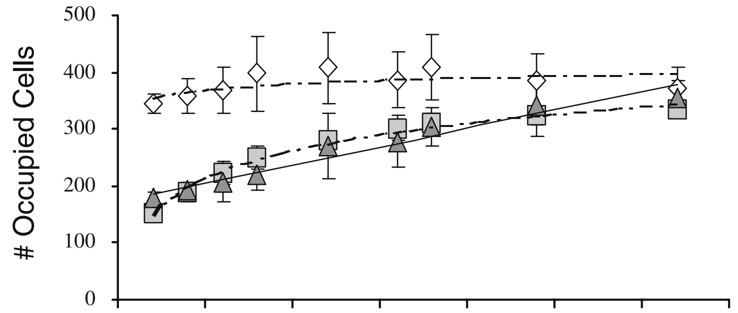
All three behavioral strategies benefited from increasing the proportion of good habitat; however, the strength and shape of the recruitment response curves differed among strategies and recruitment response variables (Figure 3). Overall, drifters were most sensitive (steepest slope) to changes in the proportion of good habitat cover, particularly as the proportion of good habitat increased from low ($p_{\text{tot}} = 0.02$) to moderate ($p_{\text{tot}} = 0.48$) levels, while swimmers were least sensitive. Differences between the strategies were most pronounced for the response variables time and area (Figure 3b and c).

(a) Mean Proportion of Dispersers to Successfully Recruit



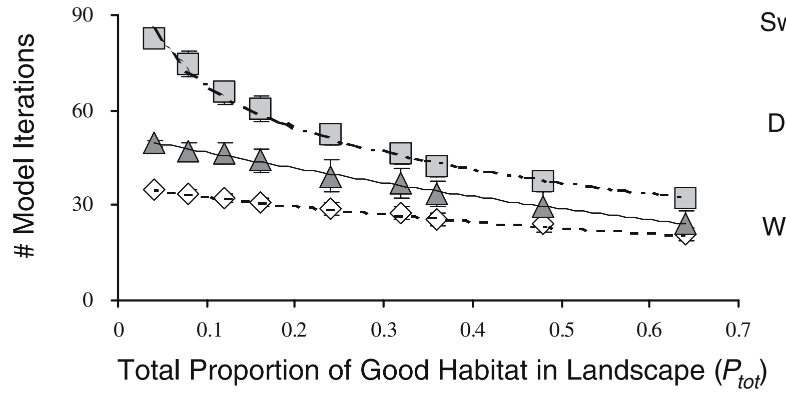
	Model	Adj.R^2	P	AICw
Swim	Exp	0.916	0.000	1.000
	Linear	0.887	0.000	0.000
	Log	0.886	0.000	0.000
Drift	Exp	0.945	0.000	1.000
	Log	0.932	0.000	0.000
	Linear	0.881	0.000	0.000
Walk	Exp	0.884	0.000	0.987
	Linear	0.875	0.000	0.013
	Log	0.814	0.000	0.000

(b) Mean Area Occupied by Successful Recruits



Swim	Log	0.041	0.000	0.596
	Exp	0.047	0.000	0.339
	Linear	0.010	0.044	0.065
Drift	Log	0.885	0.000	1.000
	Exp	0.829	0.000	0.000
	Linear	0.747	0.000	0.000
Walk	Linear	0.662	0.000	0.998
	Log	0.630	0.000	0.002
	Exp	0.497	0.000	0.000

(c) Mean Time to Complete Recruitment



Swim	Exp	0.830	0.000	0.948
	Linear	0.820	0.000	0.052
	Log	0.781	0.000	0.000
Drift	Log	0.938	0.000	1.000
	Exp	0.914	0.000	0.000
	Linear	0.852	0.000	0.000
Walk	Linear	0.758	0.000	0.558
	Exp	0.760	0.000	0.442
	Log	0.685	0.000	0.000

Figure 3. Effects of dispersal strategy (walk, drift, swim) and total proportion of good habitat in the landscape on recruitment success as measured by (a) mean recruited population size (represented as the proportion of dispersers that successfully recruit), (b) mean area occupied by successful recruits, and (c) mean time to complete recruitment. Each series of symbols represents the 9 distinct p_{tot} values obtained from the 16 model landscapes. Individual symbols represent the mean of 20 (p_{tot} = 0.04, 0.36, 0.64), 40 (p_{tot} = 0.08, 0.12, 0.24, 0.32, 0.48), or 60 (p_{tot} = 0.16) model repetitions. Error bars show one standard deviation above and below the mean. The model type, adjusted R^2 values, p-values, and AIC weights are shown in the table to the right of each figure. For each dispersal strategy, the models are listed from best to worst fit based on their AIC weights. The best fitting models are illustrated on the figures.

All strategies' final recruited population size responded positively and exponentially to increasing total proportion of good habitat (Figure 3a). This non-linear response was slightly more pronounced for swimmers and drifters than for walkers, in that: (1) the exponential models for swimmers' and drifters' population responses had higher adjusted R^2 values (adj. R^2 swimmer = 0.916, drifter = 0.945) than the walkers population response (adj. R^2 walker = 0.884), and (2) AIC attributed no weight to the swimmer and drifter linear models, while the walker response could have been described by the linear model (AIC*w* linear = 0.013). Thus, the ability to rise off the seafloor and disperse within currents (swimmers and drifters) resulted in a strong exponential response, in contrast to walkers who showed a more constant increase in final recruited population size over the same range of landscape changes (Figure 3a). Currents and an organisms' ability to behaviorally respond to currents did marginally affect landscape–organism interactions by increasing sensitivity to habitat loss or gain when the total proportion of good habitat in the landscape was low, and decreasing sensitivity when the total proportion of good habitat was high (Figure 3a).

Drifters showed a logarithmic increase of area occupied in response to increasing good habitat, whereas walkers displayed a linear response to the same landscape change. Swimmers displayed a general lack of response (all model adj. R^2 values < 0.047) due to very high variability around the mean number of occupied cells, particularly at intermediate proportions of good habitat (Figure 3b: $0.16 < p_{\text{tot}} < 0.48$). Although, swimmers and drifters experienced similar recruitment success in terms of population size, swimmers settled over a broader because they more successfully encountered and settled within the cells hosting sparse settlement habitat (e.g. the poor habitat cells). Drifters showed a logarithmic decrease in mean time to complete recruitment in response to increasing the proportion of good habitat. The responses of walkers (linear) and swimmers (exponential) were much less pronounced (Figure 3c). Thus, recruitment time for organisms with small search area and the inability to horizontally navigate towards good habitat appears more sensitive to landscape changes than does the recruitment time for organisms with large search areas or directed movement. For both the time and area response variables, a non-linear model best described the responses of organisms utilizing currents (swimmers and drifters), while a linear model best described the walker response (Figure 3b and c).

Relative influence of dispersal strategy and landscape structure on recruitment success

Although all interaction terms in the fully factorial MANOVA were significant, the partial R^2 values revealed that the main effects (behavioral strategy, proportion of good habitat at the coarse scale, and proportion of good habitat at the fine scale) explained most of the variability in recruitment success (Table 1). While landscape characteristics accounted for most of the variation in recruited population size (45% and 38% for coarse and fine scale, respectively), behavioral strategy explained most of the variation in area occupied by recruits (50%) and time to complete recruitment (54%).

Sensitivity analysis

Our model was not overly sensitive to the constant values selected for mortality and carrying capacity (Table 2). In almost all cases, 10% changes in mortality or carrying capacity resulted in < 10%

Table 1. Sum of squares and partial R^2 values from a fully factorial MANOVA testing the main and interaction effects of dispersal strategy, proportion of good habitat at the coarse spatial scale, and proportion of good habitat at the fine spatial scale on recruitment success. R^2 values are shown for all main effects. None of the interaction effects exceeded $R^2 = 0.05$.

Source	DF	Sum of squares	Partial R^2
Recruited population size			
Strategy	2	16192	0.0508
Coarse	3	144393	0.4526
Fine	3	123025	0.3856
Area occupied by successful recruits			
Strategy	2	3347073	0.4995
Coarse	3	788411	0.1177
Fine	3	689005	0.1028
Time to complete recruitment			
Strategy	2	113611	0.5370
Coarse	3	35460	0.1676
Fine	3	31919	0.1509

change in all measures of recruitment success (Table 2). Changing the value of these constants also failed to affect the relative recruitment success of the three dispersal strategies in response to increasing total proportion of good habitat (Table 2).

Discussion

The importance of currents and organism dispersal behavior in connecting distant habitat patches across broad spatial scales is well documented for a variety of terrestrial (e.g. Thomas et al. 2003; Nathan et al. 2005), aquatic (e.g. Nilsson et al. 2002; Elliott 2003), and marine (e.g. Wolanski et al. 1997, Botsford et al. 2001, Carr et al. 2003, Gaines et al. 2003) species. Likewise, regional habitat heterogeneity is recognized as essential to conserve species diversity (Tuomisto et al. 2003; Tews et al. 2004) and, particularly in marine populations, to support some species' complex life-cycles that require multiple habitat types (Acosta 1999; Leslie et al. 2003). Yet, these three factors (currents, behavior, and habitat) are rarely explicitly considered together in the design of dispersal and recruitment studies, or in the evaluation of proposed habitat-based conservation strategies (but see: Schmitt and Holbrook 2002; Schooley and Weins 2003; Nathan et al. 2005). In this study, we quantified the recruitment success of organisms simulating three generalized dispersal strategies within currents flowing across hierarchically structured landscapes that varied in the percentage of available recruitment habitat. We determined that currents modify recruitment success of organisms dispersing through heterogeneous landscapes based on dispersing organisms' behavioral responses to those currents (whether to walk, swim, or drift).

Existing landscape ecology theory predicts decreased sensitivity to landscape structure as organism dispersal range increases, and as the total proportion of good habitat increases (Fahrig and Paloheimo 1988; King and With 2002). Thus, in comparing walkers (small search area, limited dispersal range) in this study, drifters (small area but longer range), and swimmers (larger area and longer range), it was not surprising that organism dispersal behavior in the presence of currents (whether to walk and ignore them, drift passively, or actively disperse within the currents) strongly influenced subsequent recruitment success during ontogenetic habitat shifts. It is important to consider the implications of these differences in the three strategies' recruitment success in the context of conservation and management planning, as well as experimental design and interpretation of recruitment studies.

Spatially explicit population models are often used to predict dispersal patterns among distant habitat patches for such diverse purposes as predicting the spread of invasive species and diseases (With 2002), designing reserve networks that maximize propagule exchange to reduce extinction risk (Cabeza and Moilanen 2003), and postulating the effects of climate change on species distribution patterns (Iverson et al. 2004). Our results support a growing body of evidence demonstrating the importance of incorporating dispersal behavior into such spatially explicit population models (Lima and Zollner 1996; Russell et al. 2003). Models ignoring the role of currents and organisms' behavioral responses to currents would potentially underestimate the time passive drifters require to locate and occupy recruitment habitat, but overestimate the time required by active swimmers. Errors estimating time spent searching for suitable habitat could have significant effects on population models because several parameters, particularly those related to mortality (e.g. predation risk) and condition (e.g. energetic reserves), are often time dependent (Hiebeler 2004; Zollner and Lima 2005). Predictions of the number of successful recruits would also potentially be incorrect, as we found that organism–current interactions increased the number of individuals successfully recruiting to good habitat. Also, although walker-style models would also potentially provide an accurate prediction of the total area occupied by organisms that drifted, they would underestimate the area occupied by organisms that actively dispersed within currents, and thereby potentially underestimate the functional connectivity of the landscape for these species.

The potentially strong influence of dispersal behavior on recruitment success and the tendency of sparse habitat to accentuate the differences in recruitment success among the dispersal strategies point to several situations where knowledge of current–organism behavior could benefit conservation planning and monitoring. The high

Table 2. Summary of sensitivity analyses of a ±10% change in mortality and carrying capacity on mean recruitment success of organisms displaying three different dispersal strategies: (1) walk, (2) drift, and (3) swim.

	Percent change in constant	Settled individuals' mortality AMR (DMR)	Dispersing individuals' mortality AMR (DMR)	Carrying capacity of poor habitat No. of individuals	Carrying capacity of good habitat No. of individuals	Percent change in response variable mean								
						Walk			Drift			Swim		
						Pop	Area	Time	Pop	Area	Time	Pop	Area	Time
Original model	N/A	0.25 (0.000787)	0.75 (0.003788)	10	100	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Mortality rate sensitivity	+10%	0.325 (0.000698)	0.775 (0.003072)	10	100	−3.2	−0.1	−5.0	−9.1	−8.0	−10.0	−2.4	1.4	−7.7
	−10%	0.275 (0.000880)	0.825 (0.004761)	10	100	0.9	−0.5	2.1	2.9	3.2	3.5	0.7	−0.4	2.3
Carrying capacity sensitivity	+10%	0.25 (0.000787)	0.75 (0.003788)	11	110	6.8	4.4	−2.7	6.4	−0.3	−5.2	8.9	5.7	−3.7
	−10%	0.25 (0.000787)	0.75 (0.003788)	9	90	−7.4	−4.9	3.2	−7.7	2.2	5.9	−9.4	−6.4	4.1

Both annual mortality rate (AMR) and the equivalent daily mortality rate (DMR) are presented. Sensitivity analyses of recruitment success to mortality and habitat carrying capacity were evaluated against the original model for each dispersal strategy using the following response variables: (1) mean recruited population size (Pop), (2) mean area occupied by recruits (Area), and (3) time to complete recruitment (Time). The effects of changing mortality and carrying capacity were minor and did not affect the rank order of recruitment success or the strength and shape of the recruitment success response curve with increasing proportion of good habitat in the landscape.

sensitivity of drifters and walkers to habitat loss relative to swimmers, as evidenced by their steep response to increasing proportion of good habitat, suggests that species with these dispersal strategies would serve as the best focal or indicator species where habitat loss was a concern (Lambeck 1997). Likewise, conservationists considering alternative sites for protection may want to place a priority on the habitat essential to species that display walker or drifter behavior due to their sensitivity to habitat loss. Regarding the amount and configuration of habitat protected, several small protected areas would be expected to disproportionately benefit species dispersing actively within currents, as these species disperse and recruit over the largest area and therefore would be least susceptible to habitat fragmentation or localized perturbations. Although recruitment success always increased with increasing proportion of good habitat, the effect was not equal for all three dispersal strategies or among response variables. By actively moving within currents, swimmers potentially search a larger area, more rapidly than either drifters or walkers. As large search areas are known to decrease sensitivity to landscape changes by increasing the probability that the dispersing organism will encounter the desired habitat (Fahrig 1988), swimmers' relative insensitivity to varying the total proportion of good habitat was not surprising. It was surprising, however, that drifters were more sensitive to increasing proportion of good habitat than walkers. Both swimmers and drifters exhibited a more linear search pattern and could travel further into the landscape with each iteration relative to walkers. Increasing dispersal distance typically decreases sensitivity to landscape changes (Fahrig 1988), and linear and 'nearly linear' search patterns, such as our drifter strategy, can be advantageous over strategies that follow a random-walk pattern (Zollner and Lima 1999). In our model, however, the ability to actively navigate towards good habitat ultimately had a greater influence on sensitivity to landscape change than did increasing dispersal distance. This sensitivity to landscape change likely reflected the passive nature of drifter dispersal; although drifters with their long, nearly linear search pattern more frequently encountered good habitat patches, they could not disperse laterally to fully occupy these patches.

The potential for currents to increase the linear distance an organism travels became important, however, when we considered the shape of the recruitment success response curve as we increased the proportion of good habitat. The longer search distances of drifters and swimmers corresponded to non-linear responses for the area occupied by recruits and final population size. For these non-linear responses, increasing the proportion of good habitat from low to intermediate levels was more beneficial than increasing the proportion of good habitat from intermediate to high levels. In contrast, the recruitment success of walkers, which could actively control their horizontal movement but could not utilize currents to extend their search area, increased linearly with increasing proportion of good habitat. Therefore, for walkers, any gain or loss of good habitat had a corresponding effect upon recruitment success.

All dispersal studies, whether terrestrial or marine, face a common challenge: while behavioral decisions are often made in response to fine spatial resolution of environmental cues (e.g. habitat quality or the presence of conspecifics), the cumulative response of these decisions are generally observed at the population and community levels over broad spatial scales. In terrestrial dispersal simulation studies, the challenge of representing fine scale spatial habitat heterogeneity in large scale models has led to the predominance of patch-corridor-matrix model design, where (1) populations reside and reproduce within patches and emigrate to new patches via corridor or matrix habitat, and (2) each landscape cell is considered either suitable or unsuitable for dispersal or reproduction. This patch-corridor-matrix approach has been found effective to predict dispersal pathways and population dynamics for many species, including invertebrates (e.g. Johnson et al. 1992; Firle et al. 1998, Jonsen et al. 2001, Goodwin and Fahrig 2002), vertebrates (e.g. Fahrig and Merriam 1985; Zollner and Lima 1997), and even seeds (e.g. Tewksbury et al. 2002). Alternatively, models of marine organism dispersal emphasize hydrodynamic currents rather than complex benthic habitat mosaics. Although our landscapes did contain hierarchically structured habitat patches, our classification of landscape cells departed from the traditional patch-corridor-matrix model by assuming that all landscape cells within dispersal range would contain at least some habitat suitable for settlement. This classification undoubtedly contributed to the absence of an effect of landscape structure on recruitment success (e.g. increasing the proportion of good habitat at fine scales or at medium scales had the same effect). However, dispersal by currents is thought to reduce marine organisms' response to landscape patchiness by enhancing movement over inhospitable habitat (Darcy and Eggleston 2005), increasing the grain at which dispersing organisms respond to habitat heterogeneity (Kotliar and Wiens 1990), and thus potentially reducing the relevance of traditional patch-corridor-matrix representations of benthic landscape structures to dispersal studies in marine systems.

Our results have important implications for spatial scaling in ecological experiments. Identifying the appropriate spatial scales for population modeling and empirical ecological studies remains a significant challenge. Allometric scaling studies conducted on terrestrial species to relate species size to such factors as home range or mean and maximum dispersal distance (Sutherland et al. 2000), have not typically accounted for the effects of currents. Our model highlights how organism–current interactions could influence these and other scaling relationships of importance in landscape ecology. Currents potentially alter allometric relationships such that smaller, less mobile species would be able to travel further than expected based solely on their size or average movement speeds. Kinlan and Gaines (2003) noted that dispersal by sedentary marine species (whose larvae swim or drift in ocean currents) was typically one to two orders of magnitude greater than estimated maximum dispersal distances of terrestrial plants. A review by Carr et al. (2003) similarly concluded that dispersal distances are much greater in marine systems. The failure of allometric measures to account for currents may help explain why marine experiments modeled after successful terrestrial landscape projects, using similarly spatial scales and similarly species, can fail to measure significant landscape effects on dispersal (Darcy and Eggleston 2005).

In general, our study supports major conclusions from predominately terrestrially oriented simulation literature: both organism behavior and landscapes influence dispersal patterns, and should be considered in conservation management or experimental design, particularly when either behavior (e.g. limited range, limited orientation ability) or landscape structure (e.g. limited suitable habitat or the presence of dispersal barriers) limit dispersing individuals' access to suitable habitat patches. However, our research highlights the need to jointly consider the influence of currents, dispersal behavior, and landscape structure on dispersing organisms' recruitment success wherever currents potentially play an important role in shaping dispersal pathways and subsequent population and community dynamics. The unique dispersal footprints associated with different behavioral dispersal strategies in this study differed in the magnitude and shape of their response to landscape changes. The nature of these differences in recruitment success could not have been predicted by individual search area or distance alone, but rather by the combined effects of currents on organism search area, distance traveled, and directionality of dispersal.

Acknowledgements

This work was funded by an NSF grant (OCE-003253) to D.B.E., an NSF Graduate Research Fellowship to C.A.D. (DGE-0237090), and the Caribbean Marine Research Center (CMRC-01-NRDE-04-03C). We thank P. Zollner, N. Reyns, and two anonymous reviewers for constructive comments on a previous version of this manuscript.

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