DISPERSAL IN A METACOMMUNITY

QUANTIFYING DIPSERSAL IN A METACOMMUNITY AND UNDERSTANDING ITS ROLE IN LOCAL COMMUNITY STRUCTURE

By

LUANA SCIULLO, BSc.

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AUTHOR: Luana Sciullo, BSc

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ABSTRACT

Dispersal has been long recognized as an important process in metacommunity dynamics, allowing isolated communities to interact with each other through the movement of individuals. Metacommunity theory and its four models (species-sorting, mass-effects, patch-dynamics and neutral) emphasize the significance of dispersal in the structure and composition of local community. Therefore, quantifying movements of individuals between patches is necessary to understand how systems will respond to varying degrees of connectivity and resulting species interactions. Many studies that have attempted to quantify dispersal, particularly of aquatic invertebrates, found conflicting results with respect to the intensity with which dispersal occurs. Moreover, investigations of invertebrate dispersal from aquatic habitats have neglected to consider the influence of multiple factors such as life cycle stage, species, and external environmental features on dispersal rate via three vectors (wind, overflow, and animal transport). Colonization experiments have largely emphasized the importance of dispersal in influencing species richness, abundance and diversity but have yet to demonstrate direct comparisons between composition of dispersing species and local community structure. I investigated dispersal of aquatic invertebrates in a rock pool metacommunity, its possible influencing factors (species, life stage and the surrounding rock pool environment), and potential impact on species composition in local communities. To explore this, I used a combination of dispersal interception traps, colonization experiments and long term biotic community surveys. I found dispersal occurs both rapidly and in high abundance across rock pools, particularly using wind and flow vectors, with minimal influence of connectivity, vegetation and ocean on dispersal rate. Although species and life cycle stages were highly variable and differed in their dispersal intensity, a high degree of similarity existed between composition of dispersing species and local community structure. Regional processes (i.e., dispersal), despite its unpredictability, is important for species assemblage and local community composition and necessary in the colonization of newly created habitats.

Key Words: *dispersal, vectors, metacommunity, local community, colonization, regional processes*

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Introduction

BACKGROUND

Species dispersal has been of longstanding interest to the field of ecology, ecosystem dynamics and evolution. Reasons for dispersal commonly involve a combination of potentially interacting factors such as resource limitation, prevention of inbreeding or kin competition, and poor habitat quality (Bowler & Benton 2005, Clobert *et al.* 2001, Hansson 1991). These factors have the ability to influence individual survival and dictate the ability for species to persist in a given area. Therefore, the movement out of one patch and into a more suitable habitat nearby is often necessary.

One of the earliest accounts of dispersal was Charles Darwin's (1859) simple observation that juvenile molluscs could effortlessly latch onto waterfowl and potentially disperse over large geographic distances. Although Darwin did not directly observe the physical movement of these individuals across habitats, he drew attention to the potential for dispersal – a process investigated for a wide range of species and environments. Since then, studies of dispersal have transitioned from focusing solely on the likelihood of dispersal to tracking and quantifying movement of different taxa, including birds (Lehnen & Rodewald 2009, Rhim & Son 2009, Serrano & Tella 2003, Sharp *et al.* 2008), mammals (Cittadino *et al.* 1998, Long *et al.* 2005, Zedrosser *et al.* 2007), plant seeds (Wenny 1999, Wenny 2000), insects (Mercader *et al.* 2009, Roland *et al.* 2000), aquatic invertebrates, and others.

The movement of organisms between habitats not only involves an "in transit" period, but is thought to occur in a sequence of highly connected phases. In practice, it is often cumbersome to observe and track individuals (particularly smaller species) through all phases of dispersal. These phases include: (1) emigration out of one habitat, (2) transit to another habitat, during which a species cross some uninhabitable or life threatening space, and (3) successful arrival to and establishment in a new habitat (immigration) (Bowler & Benton 2005, Clobert *et al.* 2001, Ims & Yoccoz 1997) (Figure 1-1).

Dispersal between habitat patches is difficult for many species whereby movement across far distances or through a terrestrial space can result in mortality. Aquatic invertebrate dispersal (emigration, transition, immigration) can be influenced by various factors at each stage. For example, the initial movement out of a patch may be impeded or assisted by variations in wind, air temperature and moisture (Higler 2004, Nathan *et al.* 2005), or shape/size of the patch or patch edge (Hanski 1999, Ims & Yoccoz 1997). Population density and interactions with other species may also influence the ability to emigrate out of an unsuitable habitat (Hanski 1999). The modes of dispersal used by aquatic invertebrates may also influence emigration rate. For example, dispersal via water flow may be affected by the frequency or volume of discharge (Plachter 2004). Individuals that have successfully left the habitat and are in transition to another are also faced with multiple factors that affect survival. The distance travelled (Hanski 1999), time spent locating a suitable habitat (Gaines & Mcclenaghan 1980, Higler 2004), features of the surrounding environment and predation (Gaines & Mcclenaghan 1980, Weisser 2001) all pose an increasing threat on the successful transition of invertebrates between locations. Immigration into a new habitat does not necessarily imply successful colonization and integration into the new community. This is dependent upon various factors, including: similarity of the new habitat to the original patch, influence of resident species on the survival of the arriving individual (i.e., predation, competition), and species life history traits that may impede or promote successful integration into the community (Gaines & Mcclenaghan 1980, Higler 2004, Ims & Yoccoz 1997) (Figure 1-1). Due to the obvious difficulty involved in quantifying this process, the study of dispersal has been more focused on the *movement* stage of organisms across populations or between habitats (Bilton *et al.* 2001, Bohonak & Jenkins 2003, Bowler & Benton 2005), which can occur at various life cycle stages (Gaines & Mcclenaghan 1980, Havel & Shurin 2004).

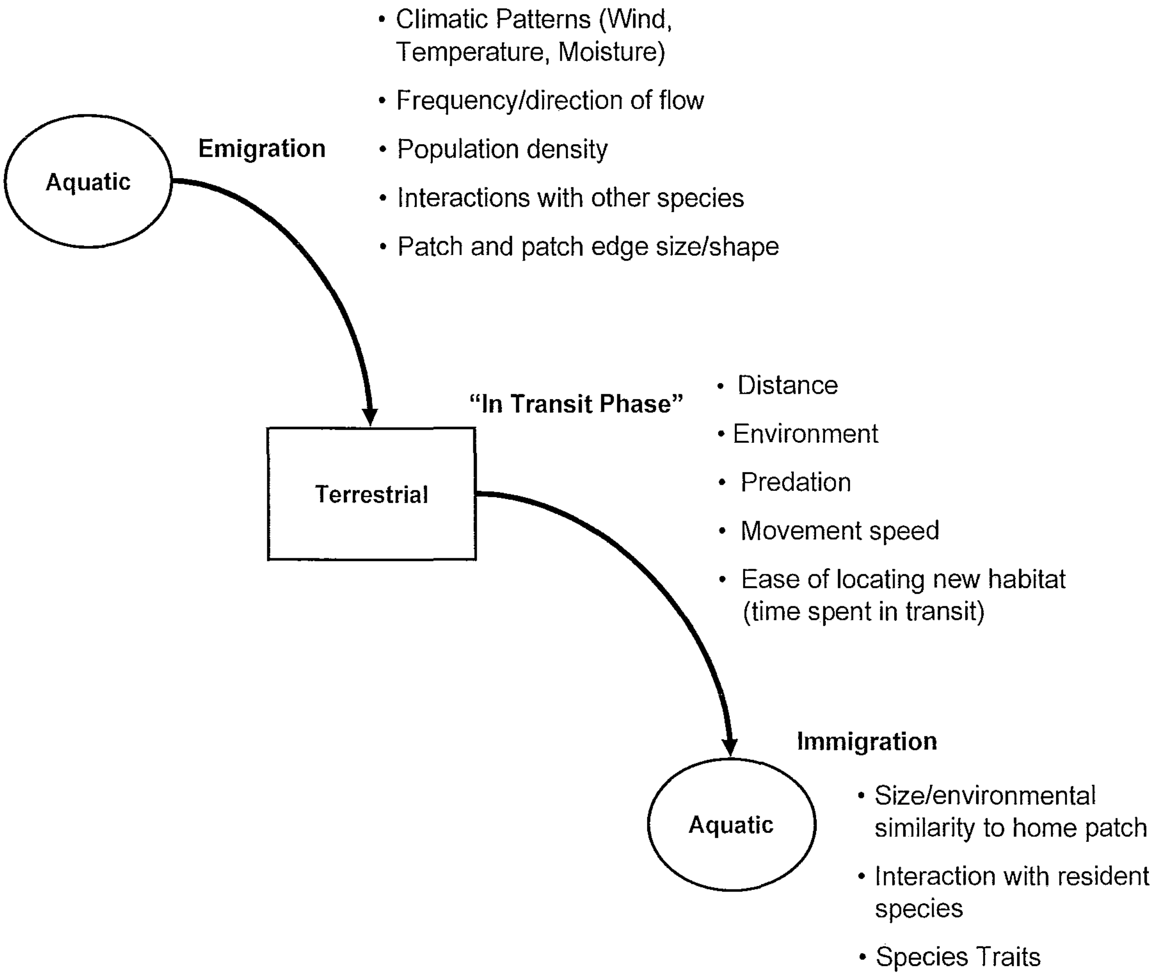

Figure 1-1. Three-stage process of dispersal between aquatic habitat patches across an inhospitable terrestrial space. Some potential factors that may affect aquatic invertebrate dispersal success at each stage are indicated.

Dispersal in a Metacommunity

Species dispersal is particularly important to the study of metacommunities which are defined as local communities (inhabiting an array of habitat patches) that are connected to each other through the simultaneous dispersal and exchange of species (Gilpin & Hanski 1991, Leibold *et al.* 2004, Wilson 1992). Dispersal remains an important component of highly fragmented and heterogeneous systems as it allows for exchange of individuals between otherwise isolated communities. This makes multi-species dispersal cornerstone to metacommunity theory (Leibold *et al.* 2004). Naturally occurring metacommunities exist in a wide range of landscapes and spatial scales, including chains of oceanic islands, fragmented forests or mountains, lakes/ponds, coral reefs and even rock pools (Leibold et al. 2004). Understanding to what degree dispersal occurs in these systems is important for classification into one of the four models of metacommunity. These metacommunity models include: species-sorting, mass effects, patch-dynamics and the neutral model. Each of the above models are defined based on two highly important processes: (1) intensity of species dispersal between habitat patches and, (2) species interactions once together in the new environment (Table 1-1) (Leibold & Miller 2004, Leibold *et al.* 2004). Therefore, understanding to what degree dispersal occurs across local communities in any environment regardless of spatial scale is crucial in applying the metacommunity theory and its principles to real life systems.

Table 1-1. Summary of four metacommunity models and the influence of environment and species dispersal ability on community structure.

Model	*Patch Characteristics*	*Dispersal and Interactions*
Species-sorting	Patches are heterogeneous (environmentally different)	Species reside in patches in which they are best adapted to environmental conditions. Dispersal influence is weak as the environment determines community structure.
Mass-effects	Patches are heterogeneous (environmentally different)	Dispersal rate is high and has the potential to influence population abundances.
Patch-Dynamics	No environmental differences among patches	Variation in species ability to disperse to a new patch and compete for resources once there. Allows for coexistence as a result of competition-colonization trade-off.
Neutral	No environmental differences among patches	Species have the same ability to disperse and are present in all patches.

Impacts of Dispersal

Local communities that constitute a metacommunity may run the risk of local extinction due to stochastic events (e.g., drought) that create sudden changes to their environment (Caughley 1977). Many local communities are constantly faced with random changes that can occur to their surrounding environment. In order for populations to survive these sudden changes, species have developed mechanisms to cope. Certain species, for example, have evolved the ability to alter either genetically or phenotypically when challenged by drastic habitat changes, which may prevent populations from becoming locally extinct (Caughley 1977). Dispersal is another form of adaptation to drastic environmental change, whereby species are able to leave unsuitable habitat patches – or reach patches that have returned to suitable conditions – in order to re-establish populations (commonly referred to as the *rescue effect*) (Bohonak & Jenkins 2003, Bowler & Benton 2005, Brown & Kodric-Brown 1977, Hanski 1999). If dispersing individuals are able to colonize and reproduce following immigration, gene flow may occur between habitat patches (Bilton *et al.* 2001, Gaines & Mcclenaghan 1980). This in turn can influence other factors including local population dynamics and genetic variability in the new community (Clobert *et al.* 2001, Hanski & Gilpin 1997). The impact of dispersal on gene flow between isolated populations, however, is often questioned in the literature. Movement between habitat patches does not always result in the movement of genetic material as well (Bohonak & Jenkins 2003). De Meester *et al.* (2002) suggested that gene flow between populations (even in the presence of high dispersal) will be small since the large population sizes of resident species will prevent the integration of new genetic material brought in by the dispersers. This process was termed the "Monopolization Hypothesis" and may even be further exacerbated by the presence of dormant forms (such as ephippial eggs) that are usually in high abundance, able to rejuvenate at any time (De Meester *et al.* 2002). Therefore, although dispersal may be present, an inability for species to integrate into a well established community prevents the flow of genetic material between populations (De Meester 1996, Okamura & Freeland 2002).

Although it is clear that dispersal of species may indeed be a beneficial process preventing populations from becoming locally extinct, the movement of individuals between patches may also be detrimental to populations as well. Abundant dispersal that occurs on a short time scale can also increase the likelihood of extinction. High dispersal between habitat patches combined with limited local interaction may, in some cases, homogenize local communities (Jenkins 1995, Kneitel & Miller 2003, Mouquet & Loreau 2002, Mouquet & Loreau 2003). In such instances, populations from different habitat patches may be equally vulnerable to changes in the environment, which may lead to multiple extinctions across patches (Heino *et al.* 1997).

The dispersal of species is also known to interact with other processes to influence local community structure. Dispersal is considered a regional scale process, whereby species immigration and colonization occurs among habitat patches throughout a metacommunity (Bohonak & Jenkins 2003, Havel & Shurin 2004, Jocque *et al.* 2007). Several other processes are also at work in association with dispersal, and together can influence the structure of communities. Factors such as predator-prey dynamics, inter-specific competition, and environmental conditions of the habitat are all considered local processes (Bohonak & Jenkins 2003, Jocque *et al.* 2007) (Figure 1-2). Understanding the degree to which regional (dispersal) or local (biotic) factors influence community structure, however, is a difficult task. In aquatic systems, dispersal has been found to interact with environmental conditions (Cottenie & De Meester 2003, Cottenie & De Meester 2004) as well as biotic interactions (Caceres & Soluk 2002, Cadotte *et al.* 2006, Cohen & Shurin 2003, Hauzy *et al.* 2007, Kneitel & Miller 2003, Shurin 2000, Shurin & Allen 2001) in structuring local community. Often however, the degree to which dispersal is an influencing factor in community structure is dependent upon its rate as well as the system under study.

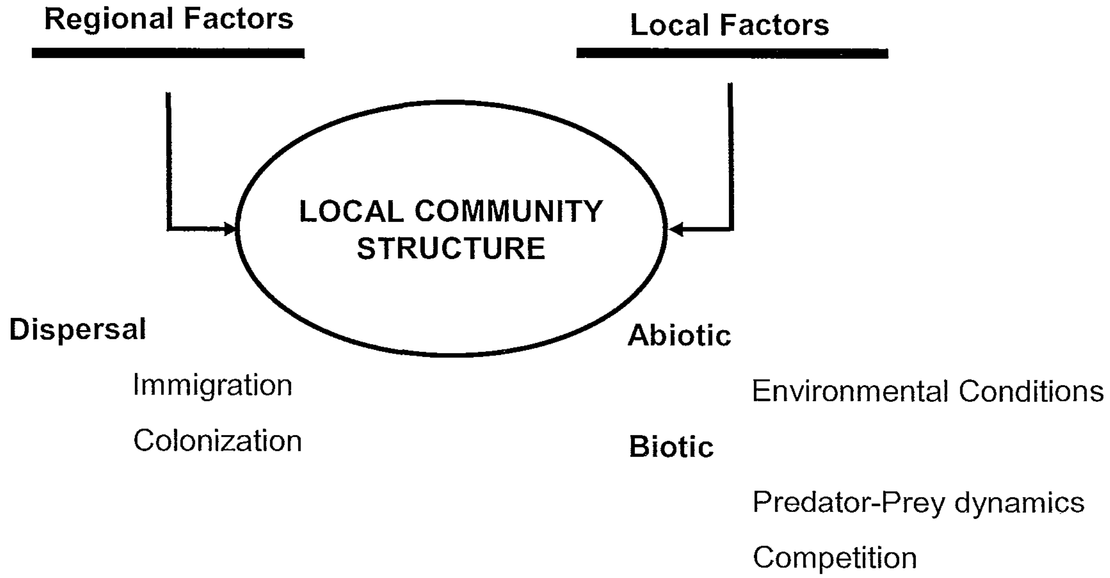

Figure 1-2. Summary of local and regional factors involved in the structure and composition of local communities.

Mechanisms of Aquatic Invertebrate Dispersal

Aquatic metacommunities have become model systems for studying dispersal, in part due to their relatively small, distinct habitat patches (e.g., ponds, lakes, rock pools) and large populations of short-lived, rapidly reproducing invertebrate species (Bohonak & Jenkins 2003). Accordingly, these systems are ideal for studying metacommunities as they allow evaluation of invertebrate movement and population dynamics from only a short study period. Ongoing efforts as well as debate focused on the frequency and intensity with which invertebrates disperse, and their involvement in structuring local aquatic communities, continues to exist in the literature. Some have suggested that all aquatic invertebrates *can* easily disperse in large abundance (Brooks & Dodson 1965, Lampert & Sommer 1997), resulting in many cosmopolitan species (Darwin 1859, Pennak 1989). Others have implied a lack of reliable data to suggest this (Bohonak & Jenkins 2003), or inferred that most research focuses on the dispersal vectors and the ability for these vectors to intercept propagules. Quantifying dispersal of aquatic invertebrates becomes complex simply due to their small body size, making it much more difficult to follow the trajectory of individuals compared to other large bodied organisms (Bohonak & Jenkins 2003, Nathan 2001). Despite these challenges and opposing viewpoints, a considerable attempt to quantify dispersal of aquatic invertebrates in a metacommunity has been made, and continues to be an important area of ecology. Below I comment on the three potential vectors of dispersal used by aquatic invertebrates that I considered in my study, namely: overflow, animal transport, and wind transport.

Overflow

Connecting channels, rivers or streams which link otherwise isolated aquatic systems represent one important vector of dispersal utilized by species that lack the ability to actively disperse (via flight). For example, rock pools in Botswana that are linked to one another via channels were found to disperse a large number of both eggs and larvae from an anostrocan species (*Branchipodoposis wolfi)* through rain overflow (Hulsmans *et al.* 2007). Michels *et al.* (2001) and Van de Meutter (2006) found similar results in a series of ponds in Belgium linked to each other through various rivulets. While both intercepted a large number of propagules, Michels *et al.* (2001) found the dispersers to have minimal influence on the new community, implying that dispersing individuals were unable to survive. Overflow dispersal estimates in South African rock pools in conjunction with precipitation data suggested that, on average, 4,088 invertebrates were being transported on an annual basis via each individual channel (Vanschoenwinkel *et al.* 2008b). These parallel results may suggest that overflow dispersal may be a significant factor in the transfer of individuals and species. However, the relationship between flow dispersal intensity and its ability to influence already established communities requires greater consideration.

Animal

Animal vectors have also long been thought to aid in dispersal of invertebrates, with much work focusing on retrieving dispersing individuals from the animal vector itself. For example, ectozoochory was observed in waterfowl found to be carrying both live and dormant invertebrate forms on their feet or plumage (Maguire 1959). Others found eggs to be capable of hatching from animal faeces, implying the successful transport of propagules through the digestive tract (endozoochory) (Figuerola *et al.* 2003, Frisch *et al.* 2007, Green *et al.* 2008). Larger mammals, including the wild boar (*Sus scrofa)* in French wetlands, carried viable eggs of several species (including copepods, cladocerans and ostracods) on their bodies (Vanschoenwinkel *et al.* 2008c). Smaller organisms have also been observed carrying invertebrates across aquatic habitat patches.

Examples include reptiles and amphibians transporting bromeliad ostracods and annelids (Lopez *et al.* 1999), pond dwelling salamanders ingesting fairy shrimp eggs *(Branchinecta coloradensis)* (Bohonak & Whiteman 1999), and even flying aquatic insects (*Notonecta maculata*) transporting *Daphnia* ephippia (Van de Meutter *et al.* 2008).

Contrary to general observations that infer a high capacity for invertebrate dispersal via animal vectors, one particular colonization experiment by Cohen and Shurin (2003) used newly created pools to show that animal transport was *not* an important vector involved in dispersing zooplankton. They utilized various size screens to seal pool openings, thereby impeding the entrance of animal vectors, but found no significant change in the ability of zooplankton to colonize (Cohen & Shurin 2003). Similarly, Vanschoenwinkel *et al.* (2008b) concluded animal vectors to be of limited importance for transporting invertebrates as compared to overflow and wind. Invertebrates that move across aquatic habitats via animals are difficult to intercept as certain vector species can migrate across large geographic distances (i.e., waterfowl), and may carry small-bodied, inconspicuous invertebrates that can be deposited at any point along the voyage.

Wind

Wind is known to displace not only propagules but dried sediment as well. Wind tunnel experiments performed by Graham and Wirth (2008) found that cysts inhabiting both disturbed and undisturbed sediments could move several meters when exposed to low wind speeds. These results suggested that displacement of branchiopod cysts can take place in naturally occurring potholes exposed to similar wind conditions across the Colorado Plateau. In another study that quantified dispersal directly in the field, Vanschoenwinkel *et al.* (2008a) intercepted over 800 propagules, predominantly dormant forms or diapausing eggs, using wind socks arranged throughout a system of rock pools in South Africa. In the same study area, both wind socks and sticky surface paper collected over 4,000 propagules (Vanschoenwinkel *et al.* 2009). Unlike overflow, however, the literature is inconsistent in reporting rates of propagules dispersal by wind. Both Jenkins and Underwood (1998) and Brendonck and Riddock (1999), for example, reported very low numbers of wind dispersing invertebrates from ponds and rock pools, respectively. The importance of wind as a vector of invertebrate dispersal in aquatic metacommunities is the most debatable of dispersal mechanisms. Not only must propagules be successfully lifted by wind currents from one patch, but they must also be transported across unsuitable habitat. In many cases this unsuitable habitat is terrestrial and deposition of the individual here will invariably result in mortality (Vanschoenwinkel *et al.* 2009). The inconsistency of results for all three putative dispersal vectors suggests that other external factors may be at work during the movement of individuals.

RESEARCH QUESTIONS

The dispersal of aquatic invertebrate species via wind, flow and animal vectors, although has been well studied, continues to produce confounding results with respect to the frequency and intensity with which movement occurs. The importance of each vector in dispersing species between habitat patches may vary depending on study site and surrounding environmental conditions such as connectivity between habitats, weather patterns, or the presence of major landscape features. Moreover, many of the studies discussed above, although successfully intercepted propagules, have failed to investigate various other factors that are potentially influencing dispersal rate. Since dispersal involves an "in transit" period whereby mortality is often high, investigating the "non-habitat" space surrounding suitable patches is very important and requires greater attention to better understand its impact on inter-patch dispersal. Species traits (life cycle stage and body size) may also play an important role in the successful movement between patches. Simply quantifying dispersal via vectors will not provide an accurate portrayal of dispersal in a metacommunity and other potentially influencing factors must also be considered.

All three stages of dispersal work in conjunction with one another in relocating individuals to new habitat patches, which can in turn contribute to the structure and dynamics of local communities. Dispersal of species is an important factor in structuring local communities as it is capable of increasing local species richness (Cadotte *et al.* 2006, Kneitel & Miller 2003) and abundance of individuals (Ives *et al.* 2004). Moreover, species dispersal that occurs at a slow rate can be particularly influential to local community structure (Jenkins & Buikema 1998), and even more so in newly created habitats in which communities are in their early stages of development (Louette & De Meester 2005). Although studies have explored the relationship between local and regional processes in structuring communities, none have performed direct comparisons in terms of relative species abundance between a long term established local community and dispersal. Since dispersal is responsible for providing new individuals to habitats, similarity in species composition between local and dispersing communities may exist. However, to what degree composition of dispersing organisms reflects the local community is still relatively unknown. In general, my thesis assumes an integrative approach and involves a three part investigation of dispersal. This comprehensive investigation allows us to obtain a better understanding of both the factors influencing dispersal in a metacommunity and its potential impacts on a local scale. I aimed to address/discuss the following questions:

I. **Dispersal Quantification** – Which vector(s) are more dominantly used for invertebrate dispersal among local rock pool communities, and is species/life stage an important factor in determining vector efficiency?

II. **Influence of Environment and Landscape** – How do external environmental factors (i.e., proximity to dense vegetation and the open ocean) and the degree of 'patchiness' in the system (i.e., distance between local communities) influence the rate of dispersal?

III. **Consequences of Dispersal** – Does a relationship exist between the composition of dispersing animals and the local community that is their potential interceptor?

Or could other local processes (abiotic factors, biotic interactions etc.) be at work dictating the successful colonization and integration of species? If so, could these processes be more important for community structure than dispersal alone?

RESEARCH STRATEGY

To examine the questions outlined above, I combined both field experiments and long term biotic community datasets across multiple years to perform a comprehensive exploration of dispersal in a metacommunity. To quantify dispersal occurring across rock pools, I constructed vector traps (wind, flow, animal) specifically designed to intercept propagules during their "in transit" phase. Multiple pools (24 in total) were chosen in three zones of the rock pool landscape: near vegetation, near the ocean, and an intermediate space. I used these distinct zones to investigate the influence of external environmental features on the dispersal rate of various species/life stages. Vector traps were left in the pools for 11 days in order to quantify dispersal on a short term time scale. For comparisons in dispersal rate between species and life cycle stages and the influence of vegetation/ocean zones, I used an array of both parametric and nonparametric tests where fitting (i.e., if data did not conform to the assumptions of parametric tests, then equivalent nonparametric tests were performed). I also aimed to determine if short term dispersal was reflective of long term local community composition by using two sets of data. First, a long term biotic community dataset from 49 rock pools across 11 years was used in the assessment of similarity between dispersing organisms and established local communities. Second, I used data from a colonization experiment that was performed in 2004. That experiment provided data on composition of successful colonizers into newly created rock pool habitats. Using these colonization experiments I was able to determine the influence of dispersal on the structure of communities over several stages of the colonization process and community development.

STUDY SYSTEM

The data collected for my thesis was obtained from a naturally occurring rock pool metacommunity, close to the Discovery Bay Marine Laboratory, on Jamaica's northern coast (Figure 1-3 and Figure 1-4). The system consisted of approximately two hundred and thirty freshwater, brackish, and saline rock pools, formed as a result of weather erosion on an exposed fossil coral reef. This weathering also created channels and depressions that allow for connectivity of neighbouring pools during overflow. Periods of intense sunlight and heat mean that pools can be subjected to drying events and are thus considered temporary habitats during the dry season, able to regenerate again during periods of precipitation. This rejuvenation occurs particularly during the Jamaican rainy season (May to June, September to November). Over shorter time scales, stochastic events (such as drought) lead to the temporary extinction of local communities, common even more so in shallower pools that face desiccation (Therriault & Kolasa 2001).

The rock pool metacommunity is sandwiched between two geographical features: dense vegetation (predominantly mangrove trees [*Rhizophora mangle*], as well as

Jacquinia sp., *Croton* sp. and *Strumfia* sp. bushes) and the Caribbean Sea. Low lying bushes and shrubs are also found densely packed between rock crevices as well growing directly within certain pools. All pools are filled through precipitation (supplying freshwater). Those pools located amongst vegetation tend to have lower salinity, while others closer to the sea receive more saltwater inputs as a result of tidal water or wave spray. Although each individual pool is considered to be a local community separate from other pools, they continue to exist together on a highly connected shelf. A sufficient amount of pool overflow allows for the exchange of pool water (and consequently any organisms that reside therein) to occur through a set of passageways. Channels, grooves and depressions in the rock surface maintain varying degrees of connectivity among discrete habitats – rock pools – that are home to the coastal rock pool metacommunity.

The Jamaican rock pool system has been under study for several years, with annual biotic and abiotic surveys being conducted from 1989 to 2002 on 49 rock pools (usually during January of each year). For this study, I used short term dispersal experiments, colonization experiments as well as long term biotic community surveys – all performed using a number of rock pools in the area. Individual pools can vary considerably from one another in biotic, abiotic and physical characteristics (volume, surface area, elevation, edge morphology) despite their close proximity to one another and exposure to similar climatic conditions (Romanuk & Kolasa 2001, Romanuk & Kolasa 2002, Schuh & Diesel 1995). For this study, 24 pools were chosen for dispersal quantification with varying environmental characteristics (Table 1-2). Studies conducted in this system have found a range of small-bodied, short-lived taxa, including: Turbellaria (7 species), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (21), Copepoda (8), Cladocera (4), Decapoda (crab) larvae (1), Decapoda (shrimps) (3), Amphipoda (1), Isopoda (1), and Insecta (18) (Kolasa & Romanuk 2005).

Table 1-2. Mean temperature, salinity, dissolved oxygen (DO), pH and physical characteristics of 24 rock pools. Pools 4-48 measured from 1989-2006 (DO% from 2007 only); pools 106-19200 measured in 2002, 2006-2007. Symbol ---- indicates absent data.

Pool	Length (cm)	Width (cm)	Cavity Depth (cm)	Temp °C	Salinity (ppt)	DO %	pH
4	89.3	44.6	18	24.8	9.9	188.8	8.3
9	71.4	45.3	31	24.9	12.3	63.3	8.2
10	63.5	28.5	19	24.8	8.1	196.7	8.6
15	34.6	20.7	8	25.6	12.7	207.0	8.7
17	28.1	17.3	21	25.3	19.9	141.4	8.1
20	88.9	52.0	21	25.9	15.7	230.9	8.7
23	61.6	40.5	19	26.0	18.2	122.0	8.6
27	42.2	31.6	22	25.8	16.1	179.8	8.6
28	56.1	31.4	15	25.0	11.3	160.5	8.8
48	28.6	18.7	33.5	25.2	15.8	129.1	8.5
106	43.3	33.8	9	26.8	7.2	20.1	9.5
108	31.7	22.5	10	25.8	7.8	60.9	8.9
117	49.6	33.9	13	25.3	----	29.9	7.7
125	35.7	15.6	25.5	24.7	12.4	93.8	8.3
139	41.9	37.6	10	25.4	5.3	61.9	8.5
142	40.5	30.0	13	25.5	0.9	87.7	9.3
143	45.6	25.5	9	26.9	2.9	36.3	9.0
179	31.2	17.6	----	27.6	2.6	123.4	8.5
184	52.5	18.1	----	28.7	0.9	191.2	9.3
1183	28.4	16.1	----	25.7	0.7	10.1	8.3
1431	23.0	16.2	----	25.9	3.0	-32.5	8.2
14200	53.9	33.5	----	33.0	1.0	226.1	8.9
17200	35.2	22.8	----	28.5	2.5	201.7	9.6
19200	99.6	37.3	----	28.9	1.0	166.7	9.4

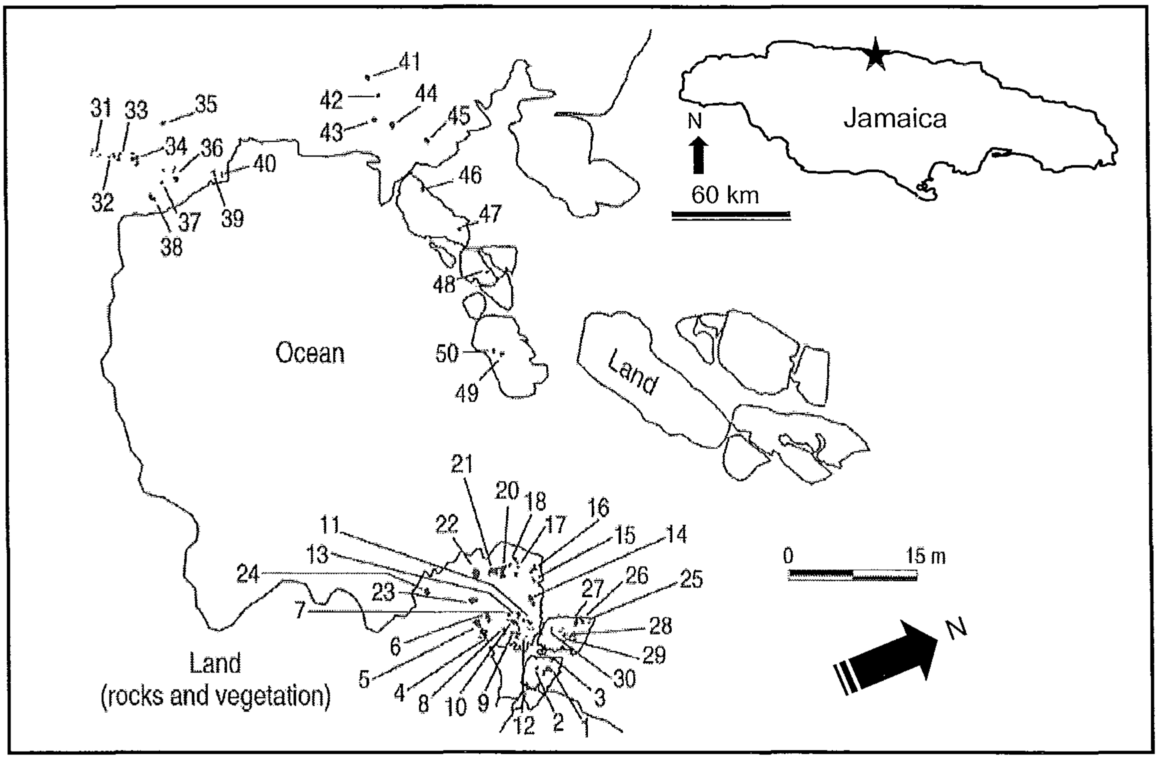

Figure 1-3. Map of rock pool study site on the northern coast of Jamaica near the Discovery Bay Marine Lab (indicated by a star in the upper map). Numbered pools indicate the 49 rock pools used in annual abiotic and biotic community surveys. Figure modified from Pandit *et al.* (2009).

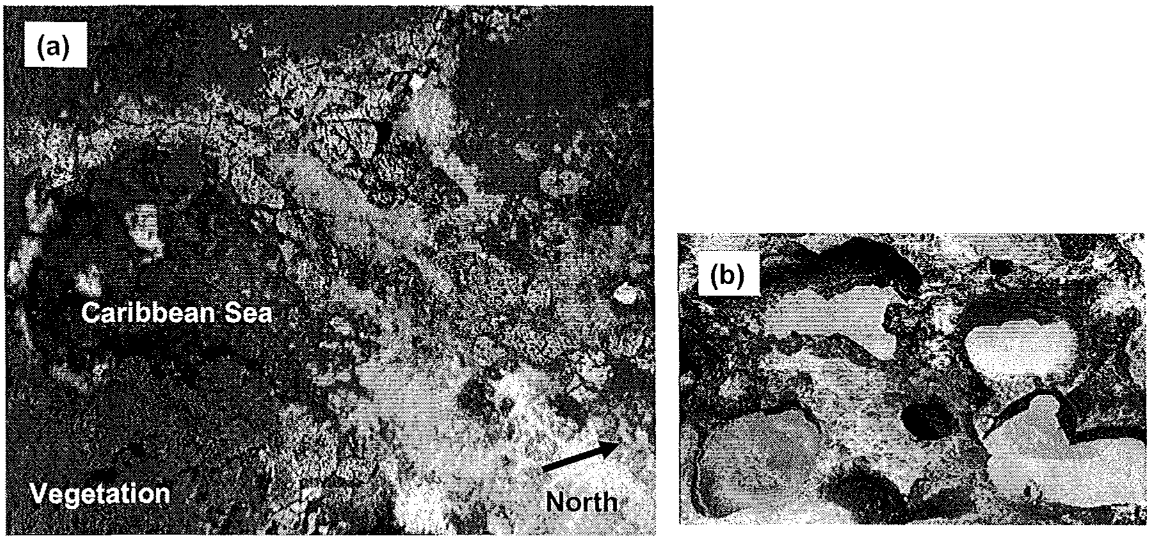

Figure 1-4. (a) Aerial photograph of rock pool study site showing regions of dense vegetation and the Caribbean Sea, and (b) Close up photograph of 4 typical rock pools in the area showing grooves and depressions in the rock.

THESIS OUTLINE

My thesis comprises four sections. Chapter 1 includes a detailed introduction providing information regarding dispersal in a metacommunity and its potential impacts on local communities. Also in this chapter is a review of the relevant literature and a summary of previous work on dispersal of aquatic invertebrates. Throughout Chapter 1, areas of the literature requiring further investigation are also mentioned. Finally, an outline of the three part exploration into dispersal in a rock pool metacommunity is included, along with the research approach used.

Both Chapters 2 and 3 contain papers that are in preparation for publication, and as a result some information (particularly introduction and methods) may be overlapping from other sections of this thesis, which was necessary in order for each paper to stand alone. Chapter 2 contains the article entitled: "Takeoff and landing: investigating the colonization and dispersal ability of aquatic invertebrates in a Jamaican rock pool metacommunity." In this paper, I aimed to address the question of how and at what rate do species disperse using three vectors and how various external factors can influence this rate (species, life cycle stage, surrounding environment).

Chapter 3 contains the article: "Linking local community structure to the dispersal of aquatic invertebrate species in a rock pool metacommunity." In this chapter, I explore the relationship between short term dispersal and long term community composition in rock pools, as well as the influence of dispersal on various stages of community development. Furthermore, I conclude by discussing the relative importance of regional (dispersal) and local (biotic interactions) processes in structuring local communities.

Chapter 4 contains an overall summary of results as well as concluding thoughts. The strengths and limitations of this work are presented along with its implications and potential future directions.

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Chapter 2

Takeoff and Landing: investigating the colonization and dispersal ability of aquatic invertebrates in a Jamaican rock pool metacommunity

This chapter is in preparation for submission for publication.

RATIONALE AND OBJECTIVES

The goal of this chapter is to investigate dispersal of aquatic invertebrates in a metacommunity by using both colonization experiments and intercepting individuals moving via dispersal vectors (wind, animal, overflow). Dispersal of invertebrates and the intensity at which it occurs is a very complicated phenomenon to study, and much of the literature shows conflicting results in terms of species dispersal rates. The objective of this study is to determine which species and life stages disperse among habitat patches (rock pools), at what rate, and via which vector(s). The environment that surrounds the rock pools and its potential role in influencing dispersal intensity is also included in this investigation. Since dispersal is an important component in any habitat and is responsible for providing local communities with new recruits, quantifying it is essential for determining how the movement of species can influence community composition. Through the use of artificial pools and specially designed vector-specific traps, I found:

- Multiple species were able to abundantly disperse throughout the metacommunity using all three vectors and were capable of early colonizing artificial pools; however,
- The number of dispersers intercepted from different taxa and life stages in vector and artificial pool experiments was highly variable; and
- The surrounding environment (dense vegetation, ocean and connectivity to neighbouring pools) was not important in determining dispersal intensity.

These results suggest that dispersal is a highly fluctuating process, whereby the species and life stages most abundantly dispersing may be a reflection of those currently dominating the rock pool community. The results of this study provide a basis for a future study (Chapter 3) that will investigate the link between dispersal and local community composition.

ABSTRACT

Dispersal is an important component of metacommunities, providing a link between otherwise isolated local communities. Aquatic invertebrates are known to colonize new communities and can disperse using wind, overflow and via an association with larger bodied animals. We investigated the colonization and dispersal of aquatic invertebrate species over an 11 day period in a naturally occurring Jamaican rock pool metacommunity. We used artificial pools and constructed traps to intercept individuals dispersing via the 3 methods. We also investigated the influence of external environmental factors on dispersal intensity and colonization ability, including the influence of a dense mangrove forest and the nearby Caribbean Sea. We found artificial pools to be rapidly colonized by a total of 531 individuals from 20 species; with individuals representing mainly Ostracoda and Copepoda juveniles (~65.5%). All 3 dispersal vectors were able to carry propagules: overflow transported 65.0 ± 23.14 [mean ± SE] individuals, wind 11.58 ± 2.96, and animal vectors 0.42 ± 0.23 individuals. Contrary to our assumptions, we did not find any influence of vegetation or ocean proximity on vector dispersal intensity, nor were distance to neighbouring pools or pool perimeter significant predictor variables. Our findings emphasize the high capacity of aquatic invertebrates to disperse across rock pools. Moreover, according to these results we expect overflow to have a high potential to disperse a large number of individuals under certain circumstances. Our results also suggest that dispersal of invertebrates in this site does not occur from a given point-source (i.e., from one particular pool), but instead is better represented by an equal ability for dispersal to occur from any patch ("propagule rain" concept). Despite the strong presence of juveniles in our samples, a high degree of variability in dispersal abundance among pools implies that the intensity at which certain life stages and species disperse is uneven. It is likely therefore, that dispersal intensity of different species and life stages may be a reflection of the current pool community.

Key Words*:* *dispersal, colonization, vectors, metacommunity, life cycle stage, rock pool, wind, overflow, propagule rain, aquatic invertebrate*

INTRODUCTION

Many aquatic environments are known to be spatially disconnected from one another, with few or no connecting elements between them. For example, lakes, ponds and rock pools each have distinct boundaries, separated from each other by an inhospitable terrestrial landscape (Hanski & Gilpin 1997, Leibold *et al.* 2004). Isolated environments such as those listed above are known as a metacommunity. In these regions, habitat patches host local communities physically separated from one another but still highly connected through species dispersal (Bohonak & Jenkins 2003, Leibold *et al.* 2004, Wilson 1992). Dispersal is an essential component to the life history of many organisms (Gaines & Mcclenaghan 1980) and is particularly important in heterogeneous environments, allowing for the continued survival of populations (Allen 2007) and preventing them from local extinction (Brown & Kodric-Brown 1977). It becomes increasingly evident that the degree at which dispersal is taking place between habitat patches should be considered when investigating concepts such as gene flow (De Meester *et al.* 2002, Gaines & Mcclenaghan 1980, Hulsmans *et al.* 2007), structure of local communities (Cottenie & De Meester 2005), and community assembly (Belyea & Lancaster 1999).

Due to the spatial separation of habitat patches in a metacommunity, obtaining accurate measurements of dispersal is often difficult, particularly for aquatic invertebrates (Havel & Shurin 2004). Despite the complexities involved in dispersal quantification, aquatic invertebrates have been found to disperse through several methods, one of which includes large animals. Waterfowl are capable of dispersing dormant life stages, ephippial eggs and even adult forms of aquatic invertebrates (Figuerola *et al.* 2003, Frisch *et al.* 2007, Green *et al.* 2008, Green & Sanchez 2006, Proctor 1964). Other large bodied animals, including the wild boar (Vanschoenwinkel *et al.* 2008c) and muskrat (Peck 1975), have the potential to transport aquatic organisms over varying distances. Despite the obvious difficulty involved in investigating the role of aquatic insects as dispersal vectors, evidence of their abilities to disperse small bodied organisms and their eggs has also been explored (Schlichting & Sides 1969, Van de Meutter *et al.* 2008). It becomes clear that animals may be an important vector for dispersal; however assessing their contribution as compared to other modes of transportation is often difficult.

Wind is another vector that has been quantified (Caceres & Soluk 2002, Graham & Wirth 2008, Vanschoenwinkel *et al.* 2008a), however its ability to successfully move individuals into suitable habitat has come into question (Bilton *et al.* 2001, Bohonak & Jenkins 2003). Regardless of this, wind (i.e., eddies, turbulence) has been associated with the movement of insects, birds, seeds and pathogens (Nathan *et al.* 2005), and may also be related to invertebrate movement. Flow of water via connecting channels or streams has also been found to disperse individuals (Michels *et al.* 2001, Shurin & Havel 2002, Vanschoenwinkel *et al.* 2008b), however the relative efficiency of this vector may vary depending on the species in question (Elliott 2003).

The capacity for species to successfully disperse is linked closely to their colonization of nearby habitat patches. Colonization of newly created habitats by aquatic invertebrates has been frequently studied in ponds (Frisch & Green 2007, Jenkins & Buikema 1998), pools (Cohen & Shurin 2003, Louette & De Meester 2005), and mesocosms (Caceres & Soluk 2002). Investigating both colonization and dispersal together provides a greater understanding of both the capability for species to enter the transport phase (dispersal) and their ability to successfully survive once landing in a new community. The relationship between ability to disperse and the capacity to survive once in a new community is often not straightforward, and varies considerably between species (Jenkins 1995).

Despite a recent surge in research quantifying the dispersal of aquatic invertebrates, several potential influencing factors have yet to be investigated. Numerous experimental studies have noted differences in dispersal capacity between taxa (Louette & De Meester 2005, Van de Meutter *et al.* 2006, Vanschoenwinkel *et al.* 2009), however, these differences were studied for only one specific mode of dispersal at a time (i.e., wind or flow). Considering the influence of multiple factors like taxonomy, life cycle stage and body size is important when determining the principal vector(s) used by different species/life stages for dispersal in an aquatic metacommunity. External environmental factors and connectivity between patches may also influence the likelihood of successful movement of individuals. Distance, for example, and its influence on dispersal rate has been considered in several different metacommunity settings such as rock pools

(Vanschoenwinkel *et al.* 2009), wetlands (Vanschoenwinkel *et al.* 2008c) and colonization experiments (Caceres & Soluk 2002, Cohen & Shurin 2003). A small number of studies have also briefly hinted at the presence of nearby vegetation impacting the dispersal of species via wind (Brendonck & Riddoch 1999, Vanschoenwinkel *et al.* 2008b, Vanschoenwinkel *et al.* 2009). These studies, however, have focused solely on small, spatially-variable patches of vegetation. Other landscape features that could influence a metacommunity, such as the presence of *dense* vegetation or proximity to an ocean ecosystem, have not been taken into consideration when investigating vector dispersal rate. Since dispersal is a necessary means for providing new recruits into isolated habitat patches which can in turn influence community structure, factors such as those listed above have the potential to promote or impede the movement of species. Connectivity between habitats and the surrounding environment are important as they may influence dispersal intensity between patches and consequently be indirectly involved in community structure.

The purpose of this study is to quantify the dispersal of aquatic invertebrates in a naturally occurring rock pool metacommunity with specific focus on the contribution of three different vectors and on the difference in dispersal rate due to taxonomic identity. The main method of obtaining data was by intercepting individuals during dispersal. We used artificial rock pools to examine the total dispersal and early colonization patterns of invertebrate species (Experiment 1). We also investigated dispersal of species via three known vectors: overflow, animal, and wind (Experiment 2). We suggest that (1) disperser species or life stage, (2) degree of connectivity or distance between habitat patches, and (3) presence of major geographical or environmental features surrounding the rock pools (which could either promote or impede dispersal), can influence dispersal intensity. We propose that these factors must be taken into consideration when examining dispersal in aquatic metacommunities as they may be important in determining the ability of species to arrive successfully to new habitats and colonize. Utilizing both colonization and dispersal vector experiments allowed for a better understanding of how aquatic invertebrates dispersed and with what intensity different species and life stages moved throughout the rock pool metacommunity. Moreover, by using a unique field site that is surrounded by both a dense mangrove forest and the Caribbean Sea, we were able to determine how the surrounding rock pool environment altered dispersal.

METHODS

Study Site

This study was conducted in a rock pool metacommunity located in Discovery Bay on the northern coast of Jamaica (18°28'N, 77°25'W) (Romanuk & Kolasa 2005). The site is comprised of 230 temporary rock pools surrounded by grooves and depressions in the fossilized rock that maintain a degree of connectivity between habitat patches. The site is unique in the sense that it is surrounded by a dense red mangrove stand (as well as *Jacquinia* sp., *Croton* sp. and *Strumfia* sp. bushes) and the Caribbean Sea. Pools located closer to the sea are exposed to ocean splash and have a greater degree of salinity than pools located near vegetation. Small organisms such as amphipods, isopods and crabs inhabit the rock pools, and few species of waterfowl are observed throughout the area.

For this study, a total of 24 pools were selected to quantify patterns in multi-species dispersal. Eight pools each were randomly chosen from three distinct regions: (1) a vegetation zone (pools situated approximately 1 meter or less from dense vegetation); (2) an ocean zone (<1 meter from the ocean); and (3) an intermediate zone (≥1 meter from both vegetation and ocean) (Figure 2-1). Three additional dried pools were randomly chosen from each zone for quantifying total dispersal (i.e., non-vector specific) and colonization. Computer mapping software ArcView GIS 3.2 was used to determine pool dimensions (length, width) and distance to vegetation, ocean and neighbouring pools. Distance of pools to the vegetation zone was measured from the midpoint of each pool to the closest region of dense vegetation. The ocean zone was defined as the location on the rock surface where water levels were at their greatest (i.e., during high tide), and pool distance to this zone was measured using pool midpoint. Pool perimeter measurements were obtained using image processing software, ImageJ (Abramoff *et al.* 2004). Chosen pools ranged in size from 16 to 100 cm in length and width (mean length = 49.0 ± 20.9 cm [SD], mean width = 28.8 ±10.5 cm). Pool edge perimeter was on average 165.6 ± 75.2 cm. To quantify potential for connectivity between pools, the distance between each study pool and its three nearest neighbours were obtained and mean distance was calculated. Distance of the neighbouring pools was on average 69.3 cm with an average perimeter of 120.5 cm.

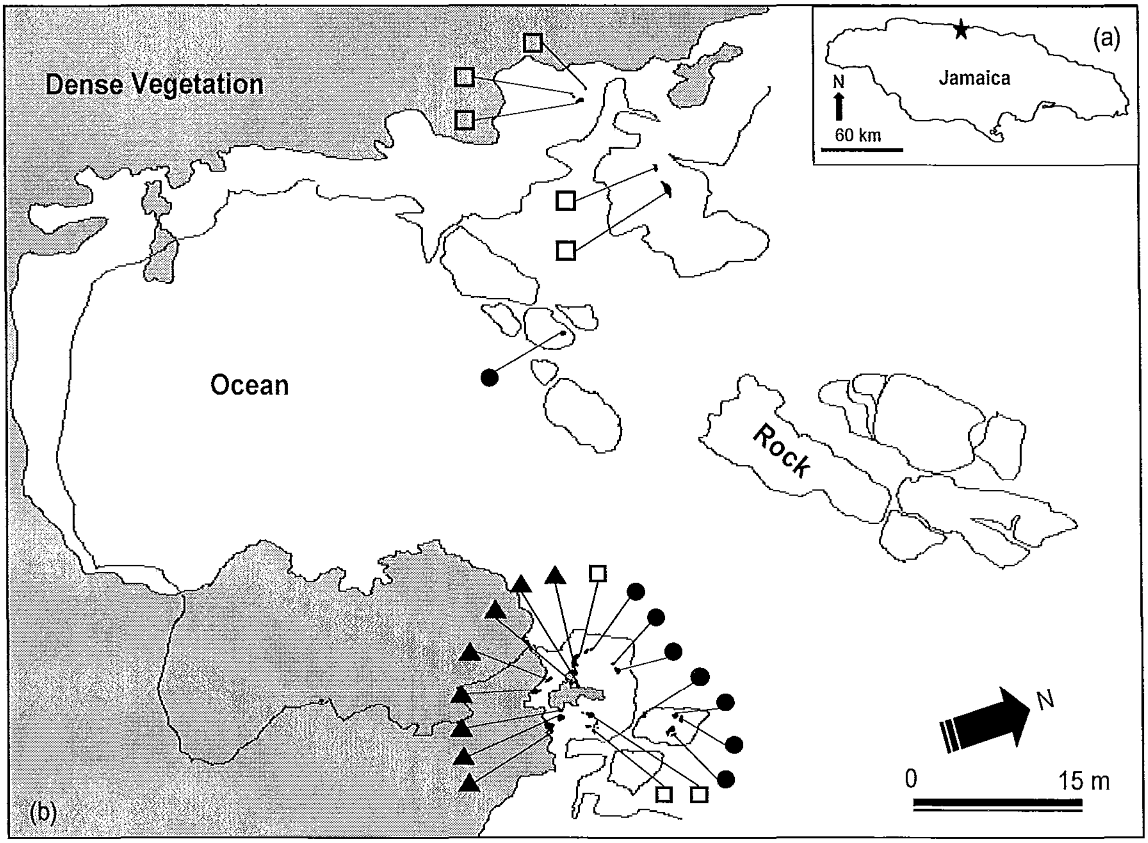

Figure 2-1. Study site and experimental metacommunity at Discovery Bay, Jamaica. (a) Approximate location of the Discovery Bay Marine Lab, University of the West Indies, Jamaica indicated by a star on the northern coast; (b) Aerial view of the field site with 24 rock pools outlined and their respective zones (▲-Vegetation Zone ☐ - Intermediate Zone ● - Ocean Zone). Shaded grey areas indicate regions of dense vegetation and low lying bushes/shrubs.

Sampling Design

Dispersal into Artificial Pools

Total dispersal experiments were carried out in order to observe which species are first to arrive to newly created patches and which can coexist during this earlier period of colonization. In order to assess this, new artificial pool environments were created using three dry pools chosen in each zone (vegetation, intermediate, ocean). The inside cavity of each pool was lined with two layers of a plastic covering to ensure contents could not spill through. Pools were then filled with 500 ml of freshwater and 100 ml of filtered rock pool water allowing for some bacteria and algae to remain for colonizing invertebrates to consume and survive until samples collected. Pools were left for just under three days and samples taken on the third day. This time range permitted only a brief period for dispersal and colonization to occur, thereby providing a snapshot of what a rock pool community may resemble during the early stages of succession. The contents of each bag was collected, filtered through a 63-µm net, preserved in 50% ethanol, and stored in 50 ml vials. Artificial pools were then reset and the process repeated every three days for a total of three collection cycles.

Dispersal Rates of Three Vectors

Between 25 May and 4 June, 2009, we employed three sets of trapping containers in 24 rock pools to determine how many and what kind of organisms disperse using the three dispersal modes (wind, water, animal) in the metacommunity. The trapping protocol for each vector is described below.

Overflow Transport

Overflow dispersal was assumed to occur only after a rain event, dispersing invertebrates through outflow of excess rock pool water. Only pools with a high degree of unidirectional connectivity (i.e., distinct channels leading from one pool to another) were chosen for the installation of overflow traps. These pools possessed a sufficiently defined outflow channel and were at a slightly higher elevation than neighbouring pools receiving overflow. This selection of pools ensured the one-way movement of overflow water and dispersing organisms between discrete source and sink populations. Overflow dispersal traps consisted of a thin, plastic tube (approximately 9.5 mm internal diameter) that led into the neighbouring pool. The tube intake opening was moulded to the mouth of the pool using water resistant clay. Dispersal tube lengths varied based on the distance between pools. Outflow was captured in a sealed bag on the terminal end of the tube. Upon the completion of the trial, the volume of water collected in each bag was measured and filtered into vials. Due to the fact that precipitation was insufficient during the sampling period, a rain event was simulated. To best mimic a natural rain event, water was carefully added to pools during early morning hours by allowing freshwater to trickle off the rocky surface into the targeted pools until overflow occurred. It was assumed that regular rain events predominantly disperse individuals residing in the water column or surface layers, and that disruption of bottom sediments and therefore benthic organisms only occurs during torrential rain storms in particularly shallow pools. Therefore, the *gradual* flooding of the pool technique that we employed corresponds best to common, low-intensity rain events.

Animal Transport

Three types of organisms were identified as possible animal vectors: amphipods, isopods and crabs since they frequently visit the rock pools as well as the adjacent ocean. In doing so, these organisms may be picking up eggs or larval stages of other pool invertebrates and carrying them in their guts or gill chambers to new sites (Kolasa & Romanuk 2005). Larger vertebrate species (i.e., water birds, reptiles and amphibians) visit the rock pools rarely or not at all (*personal observation*) and were not included in our study.

To trap these animals and capture any smaller, dispersed organisms, containers (approximately 7 cm height and 228 cm^2 aperture area) were filled with freshwater and placed adjacent to each pool. To distinguish between propagules arriving by air and those brought in by animals, two types of traps were used. One trap (referred to as "open") was left completely open to the outside environment and allowed animal dispersers to enter. The other trap or "control" was fitted with a 500-μm Nitex netted lid, excluding larger organisms to allow only wind dispersing propagules to enter. A systematic difference between these two kinds of traps could be attributed to accessibility of one type only to animal vectors. Contents of all containers were inspected every other day.

Wind Transport

Traps for invertebrates dispersing by wind consisted of replicated water-filled pea cups (approximately 7 cm height, 120 ml volume and 28 cm^2 aperture area) placed to float inside each pool. Each wind trap comprised 4 joined containers and was surrounded by Styrofoam wedges for floatation (Figure 2-2). Two containers placed opposite each other were half filled with freshwater (labelled A and B), while the other two (C and D) were half filled with rock pool water, filtered by a 63-µm netting. Constant water levels within wind traps were maintained by replenishing water after a daily inspection.

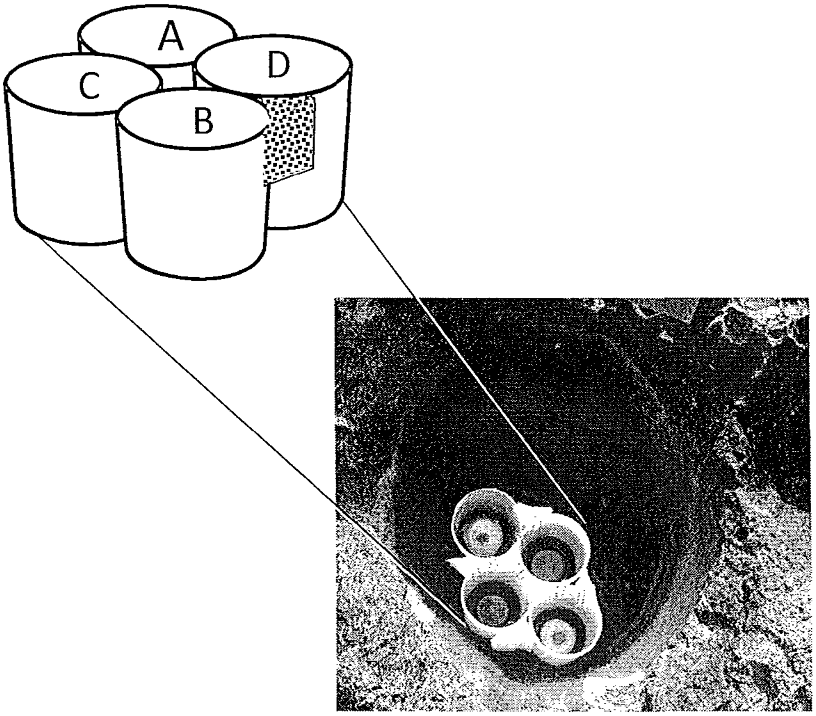

Figure 2-2. Construction and example of a typical wind trap. Metal clips kept individual pea cups together and surrounding Styrofoam (stippled) allowed the group to float. Containers A and B had freshwater, C and D had filtered rock pool water.

All three trap types (for wind, water and animal transport) were fitted into each of the 24 pools. Inspection of dispersing invertebrates was done using a magnifying glass (2.5X and 5X magnification) and collected in the morning every other day. Organic debris (i.e., leaf litter) or insects blown/washed into traps were recorded and digital photos taken. The field site was inspected daily in order to adjust and record any vector traps that had become displaced due to strong winds or high tide. Traps were also periodically refilled during periods of extreme heat when evaporation rates were high. In order to prevent cross contamination, all equipment (filter nets, vials, etc.) were thoroughly rinsed between pool and vector sampling. All collected samples were stored in either 25 ml (wind, animal) or 50 ml (overflow) vials using 50% ethanol. Following each collection, all traps were reassembled/refilled (if necessary) and placed in their respective locations.

Invertebrate Identification

Following both experiments, all samples were returned to the laboratory for counting and identification of organisms using a compound and light stereomicroscope. Invertebrates were identified using identification keys constructed over 20 years of sampling the Jamaican rock pool biotic communities. Individuals were identified to species level, with the exception of a few, which could only be identified to genus or family. Life cycle stage of dispersers was determined as juvenile, adult or larvae (insect larvae only). Both ostracod and copepod individuals that had not reached adult stages at the time of collection (i.e., nauplii or small bodied ostracods) were identified only as juveniles of their specific taxa. Eggs occurred rarely, but when found they were separated and identified solely as ephippia or unknown eggs. Following identification, species were aggregated into six taxonomic groupings to be used in further analyses. These taxa included: Copepoda, Ostracoda, Branchiopoda (Cladocerans), Insecta (fly, mosquito or beetle larvae), Rotifera, and Others (annelids, turbellarians, nematodes and decapod larvae).

Statistical Analysis

Dispersal into Artificial Pools

Species richness (S) of each artificial pool was defined as the total number of different species identified. The Shannon Diversity Index (H') was used to calculate community diversity using the statistical software package Primer version 6.1.6 (PRIMER-E Ltd. 2006). The software used the following formula for H':

$$H' = \Sigma\, pi \ln (pi)$$

where pi is proportion of individuals of the ith species among all species present in the artificial pools.

We used a Factorial ANOVA to assess whether any significant differences existed across (i) the three sampling periods, and (ii) the three zones, for mean number of dispersers, mean species richness and mean diversity. In this model, both sampling day and zone were used as categorical variables. In order to comply with normality and homoscedasticity assumptions of the ANOVA, mean number of dispersers was log x+1 transformed. Significant Factorial ANOVA results were then further analyzed using Tukey *post-hoc* tests which tested for pairwise differences that existed between sampling days, zones and day x zone interactions. The data analysis software Statistica 7.0 (StatSoft Inc. 2004) was used for all Factorial ANOVAs and *post-hoc* tests.

To assess whether certain life cycle stages dispersed to artificial pools more readily than others, a Kruskal-Wallis ANOVA by ranks test was used with absolute abundance values and *post-hoc* multiple comparisons tests were performed. The dispersal abundance of each stage was also analyzed across dispersal zones to determine if pool location (vegetation, intermediate, and ocean) may have led to selective dispersal of certain life cycle stages. To do this, three separate Kruskal-Wallis ANOVA by ranks tests were performed, with abundance of life cycle stage (juvenile, adult and larva separately) as the dependent variable and zone as the categorical independent variable (Statistica 7.0). Multiple comparisons *post-hoc* tests were performed to assess which zones were significantly different in terms of abundance of dispersers at each life stage.

Dispersal Rates of Three Vectors

I. Dispersal Quantification

Several samples were removed from further analyses, including two wind dispersal traps that were found overturned on one sampling day as a result of weather. Mean abundance of dispersers and species richness for the wind vector was obtained for all four pea cups combined for each pool on each sampling day. To assess the efficiency of larger animals as dispersal vectors, both total dispersal abundance and species richness were compared between open and control animal traps. A non-parametric Mann-Whitney U Test was used for this comparison (chosen because abundance data showed major departure from normality). The mean number of dispersers and mean species richness for each vector are reported in this paper; however these are not directly comparable across vectors due to differences in vector dispersal quantification techniques used.

To assess if the abundance of each dispersing life cycle stage varied among pools, the number of juveniles and adult dispersers were each summed across all sampling days for each pool. A ratio of juveniles to adults was then calculated for each pool (for each separate vector) and both means and standard deviations were calculated. Utilizing both mean and standard deviation values for juvenile and adult ratios provided an overview of how variable vectors were in dispersing each life cycle stage. To test the effect of overflow volume on dispersal rate, linear regressions were performed using overflow volume (independent variable) and abundance of dispersers/species richness (dependent variables). Abundance of dispersers was transformed (log x+1) to ensure a normal distribution of residuals. Due to extreme heat, several natural pools into which traps were placed had become relatively dry and were therefore recorded as either 'dry' or 'wet' prior to manual pool overflow. An independent samples t-test was used to assess the difference in abundance of dispersers per ml of overflow (log x+1 transformed) and number of species per ml between dry and wet pools following overflow treatment.

The abundance of each of the six taxonomic groups was compared within each mode of dispersal to investigate the influence of the vector itself on the movement rate of each taxa. Because dispersal vectors were quantified using methods that could not be mutually converted (i.e., traps differed in size, shape, or method of interception.), a comparison of absolute abundance values across vectors was not possible. Instead, we used relative abundance of each taxa for each vector to allow for such comparisons. Among taxa comparisons within each vector was accomplished using a non-parametric Kruskal-Wallis ANOVA by ranks test followed by multiple comparisons *post-hoc* tests. All statistical analyses were completed using Statistica 7.0.

II. Influence of Environment & Landscape

In order to investigate the influence of distance from ocean or vegetation on dispersal intensity, the total number of dispersers and species for each vector over the sampling period was compared across the predefined spatial zones (vegetation, intermediate and ocean). For overflow dispersal, a multivariate analysis of variance (MANOVA) tested whether abundance and species richness together were influenced by pool location. In order to meet normality assumptions for overflow dispersal, abundance of dispersers was transformed (log x+1). Analysis for wind and animal vector dispersal used a nonparametric Kruskal-Wallis ANOVA by ranks test for both abundance of dispersers and number of species. All MANOVA and Kruskal-Wallis tests were performed using Statistica 7.0.

Since dispersing invertebrates were previously classified into six taxonomic groups, we used the total abundance of each group to determine if the overall dispersing community differed between the three respective zones. A non-parametric Analysis of Similarities (ANOSIM) test was used, based on Bray-Curtis measure of similarities. The dispersing community (using the six taxa as variables) were compared altogether across the three zones. An ANOSIM test provided a non-parametric alternative to a multivariate analysis of variance because it allowed for comparisons of multiple dependent variables (in this case, abundance of each taxa) across the three zones by using permutations. From permutations, a test statistic (Global R) is computed based on both within group and between groups similarity ranks, which varies between -1 and 1 with an associated probability value. Global R values approaching 1 imply that within group similarities are greater than between groups and thus helps to decide whether treatment effects are meaningful. Non-parametric ANOSIM tests were completed using Primer version 6.1.6. We also performed Kruskal-Wallis ANOVA by ranks tests (Statistica 7.0) on each of the six taxa independently (using total number of dispersers from each taxa across the entire sampling period) in order to assess if dispersal intensity was influenced by pool location for each *individual group.* These separate univariate tests were completed to ensure that one or more taxa did not predominantly influence the statistical results obtained from the multivariate ANOSIM.

As wind dispersal of invertebrates may potentially be influenced by external environmental factors, we performed a multiple regression analysis to assess if both mean abundance of dispersers and mean species richness were influenced by four predictor variables: (1) distance to the vegetation; (2) distance to the ocean; (3) mean distance to three nearest neighbouring pools; and (4) mean perimeter of three nearest pools. Mean number of dispersers was transformed (log x+1) to meet normality assumptions. Multiple regression analysis for mean species richness was completed after transforming all variables (species richness, vegetation/ocean distance, neighbour distance and pool perimeter) into log x+1 form in Statistica 7.0. To assess whether abundance and species richness of animal vectors were linearly correlated with vegetation/ocean distance and neighbouring pool distances, we performed non-parametric Spearman Rank correlation tests (Statistica 7.0). As animal vectors (i.e., larger invertebrate organisms) typically reside in neighbouring pools, mean distance to three nearest pools was used as a predictor variable as were vegetation and ocean distance. All statistical analyses and data transformations are listed below (Table 2-1).

Table 2-1. Summary of statistical analyses performed for each experiment.

Experiment	Investigate	Data Treatment	Test
Dispersal into Artificial Pools	Abundance (N), species richness (S), diversity (H') across sampling days and zones	N → log x+1 transformed	Factorial ANOVA and Tukey *post-hoc*
	Abundance of life cycle stages (juvenile, adult, larva) overall and across zones	Absolute values	Kruksal-Wallis ANOVA by ranks and multiple comparisons *post-hoc*
Dispersal Quantification	Animal transport intensity (open versus control traps)	Absolute values arranged in blocks according to zone	Mann-Whitney U Test
	Variability in dispersal of life stages (juvenile, adult)	Abundance of each group summed across all days per pool (for each vector)	Mean and standard deviation values of juvenile to adult ratios
	Volume overflow and dispersal intensity (N and S)	N → log x+1	Linear Regression
	Influence of dry and wet pools on dispersal abundance and richness	N → log x+1	Independent samples t-test
	Within vector comparison of taxa dispersal intensity	- Sum of individuals in each taxa across all sampling days (per pool) - Calculated relative abundance	Kruskal-Wallis ANOVA by ranks and multiple comparisons *post-hoc*
Influence of Environment	Influence of zone (vegetation, intermediate,		

and Landscape	ocean) on: Overflow N, S	N → log x+1	MANOVA
	Wind N, S and Animal N,S	Sum N, S across all sampling days per pool	Kruskal-Wallis ANOVA by ranks and multiple comparisons *post-hoc*
	Overall dispersing community (6 taxa groups) across zones (for each vector)	Sum of individuals in each group across all sampling days	ANOSIM
	Individual taxa group comparison across zones	Sum of individuals in each group across all sampling days	Kruskal-Wallis ANOVA by ranks and multiple comparisons *post-hoc*
	External factors influencing intensity of wind dispersal (N, S)	N → log x+1 S, vegetation/ocean distance, neighbour distance and perimeter → log x+1	Multiple Regression Analysis
	Influence of vegetation, ocean and neighbour distance on animal dispersal intensity	Untransformed	Spearman Rank Correlation

RESULTS

Experiment 1 – Dispersal into Artificial Pools

Over the course of three sampling periods, artificial pools were colonized by a total of 531 invertebrates from 20 species. Colonizers were dominated by ostracods (51.4%) and copepods (36.2%) and consisted of adult, juvenile and larval forms (Table 2-2). Eggs of an unknown species (85 individuals), ephippia (1), amphipod (10) and isopod (1) specimens were also present.

Mean number of dispersers differed significantly between sampling periods (Factorial ANOVA, $F_{2,18} = 7.277$, $p = 0.004$) and zone (Factorial ANOVA, $F_{2,18} = 9.291$, $p = 0.001$) (Table 2-3). A greater mean number of dispersers were found in pools sampled on the first date than on sampling dates 2 and 3 (Table 2-4, Figure 2-3a). More individuals colonized pools located in the vegetation and intermediate than ocean zone (Table 2-4, Figure 2-3a). Species richness, however, was not significantly different between sampling dates (Factorial ANOVA, $F_{2,18} = 2.904$, $p = 0.080$), although did vary between sampling zones (Factorial ANOVA, $F_{2,18} = 4.761$, $p = 0.021$) (Table 2-3). More species colonized pools in the vegetation and intermediate zones as compared to the ocean zone (Table 2-4, Figure 2-3b). Diversity of pool communities (Shannon Index, H'), however, was similar across sampling dates and only marginally significant among zones (Factorial ANOVA, $F_{2,18} = 3.163$, $p = 0.066$) (Table 2-3). Nonetheless, a general trend of greater diversity in vegetation and intermediate zones is evident (Figure 2-3c).

Table 2-2. Abundance, N, and percent of dispersers colonizing artificial pools (subdivided into taxa and life stages).

Colonizing Taxon	Life Cycle Stage	Species	Abundance	% of Total
Ostracoda				**51.4**
	Adult	*Cypricercus* sp.	17	3.2
		Candona sp.	7	1.3
		Potamocypris sp.	22	4.1
	Juvenile	Unidentified	227	42.7
Copepoda				**36.2**
	Adult	*Orthocyclops modestus* (Herrick)	21	4.0
		Nitocra spinipes (Boeck)	25	4.7
		Paracyclops fimbriatus (Fischer)	23	4.3
		Unidentified copepod species	3	0.6
	Juvenile	Copepod nauplii	120	22.6
Branchiopoda	**Adult**	*Alona davidii*	4	**0.8**
Insecta				**2.3**
	Larva	Dipteran (Dolichopodidae) sp.	3	0.6
		Dipteran sp.	1	0.2
		Culex sp.	2	0.4
		Midge	5	0.9
		Pyralid caterpillar	1	0.2
Rotifera	**Adult**	Rotifer	5	**0.9**
Other				**8.5**
	Larva	*Sesarma miersi*	39	7.3
	Adult	Tardigrade	1	0.2
	Juvenile	Unidentified shrimp	1	0.2

	Adult	Oligochaete Unknown species 1 Unknown species 2	2 1 1	0.4 0.2 0.2

Table 2-3. Factorial ANOVA on the influence of sampling date and zone for mean number of dispersers (log x+1), mean species richness and mean diversity (Shannon Diversity Index, H'). Significant p values are in bold.

Source	**df**	**SS**	**MS**	**F**	**p**
No. of Dispersers (Logx+1)					
Sampling Date	2	2.468	1.234	7.277	**0.004**
Zone	2	3.151	1.575	9.291	**0.001**
Sampling Date x Zone	4	0.583	0.145	0.860	0.506
Error	18	3.052	0.169		
Total	26	9.254			
Species Richness					
Sampling Date	2	18.074	9.037	2.904	0.080
Zone	2	29.629	14.814	4.761	**0.021**
Sampling Date x Zone	4	6.148	1.537	0.494	0.740
Error	18	56.000	3.111		
Total	26	109.851			
Shannon Diversity (H')					
Sampling Date	2	1.421	0.710	1.975	0.167
Zone	2	2.276	1.138	3.163	0.066
Sampling Date x Zone	4	1.212	0.303	0.842	0.516
Error	18	6.476	0.359		
Total	26	11.385			

Table 2-4. *Post-hoc* test results (Tukey) complementing Factorial ANOVA tests (Table 2-3). Only significant differences are reported. Values in parentheses are means ($\bar{x}$ for sampling date and zone type). Symbol ≠ represents statistically different number of dispersers between dates and zones.

Source	**Factorial ANOVA p**	**Tukey *Post-hoc* Test Significant Differences**	**p**
No. of Dispersers (Log x+1)			
Sampling Date	0.004	Date 1 ≠ Date 2 ($\bar{x}$ = 1.31, 0.67)	0.011
		Date 1 ≠ Date 3 ($\bar{x}$ = 1.31, 0.66)	0.010
Zone	0.001	Vegetation ≠ Ocean ($\bar{x}$ = 1.04, 0.40)	0.011
		Intermediate ≠ Ocean ($\bar{x}$ =1.19, 0.40)	0.002
Sampling Date x Zone	0.506	Vegetation Date 1 ≠ Ocean Date 2 ($\bar{x}$ = 1.68, 0.20)	0.008
		Vegetation Date 1 ≠ Ocean Date 3 ($\bar{x}$ = 1.68, 0.28)	0.006
		Intermediate Date 1 ≠ Ocean Date 2 ($\bar{x}$ = 1.39, 0.20)	0.046
		Intermediate Date 1 ≠ Ocean Date 3 ($\bar{x}$ = 1.39, 0.28)	0.036
Species Richness			
Sampling Date	0.080	------	p>0.05
	0.021	Vegetation ≠ Ocean	0.039

Zone		($\bar{x} = 3.66, 1.44$) Intermediate ≠ Ocean ($\bar{x} = 3.66, 1.44$)	0.039
Sampling Date x Zone	0.740	------	p>0.100
Shannon Diversity (H')		------	
Sampling Date	0.167	------	p>0.100
Zone	0.066	------	p>0.100
Sampling Date x Zone	0.516	------	p>0.100

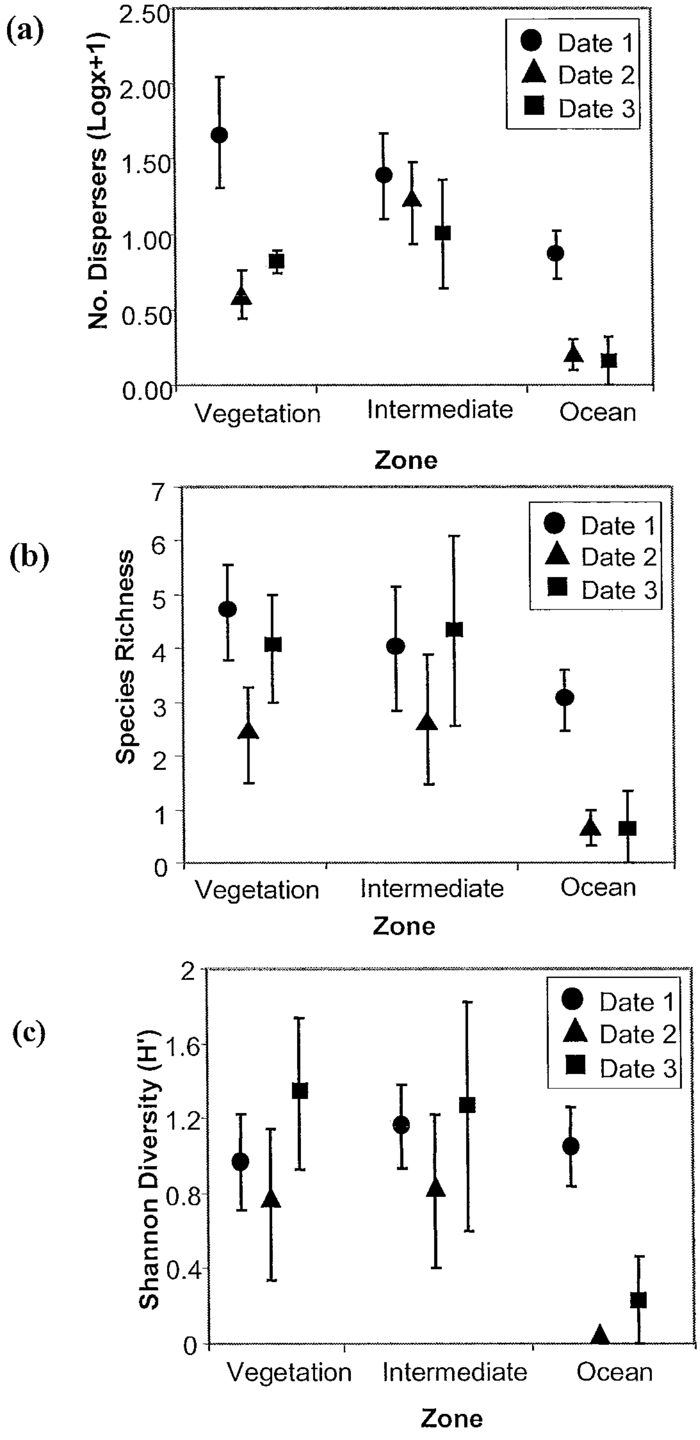

Figure 2-3. Influence of zones (x axis) on (a) mean number of dispersers (log x+1), (b) species richness and (c) diversity (Shannon Index, H') in artificial pools at three different sampling periods: (● Date 1, ▲ Date 2, ■ Date 3). Bars indicate standard errors.

Invertebrates collected from artificial pools included juveniles (65.54%), adults (24.86%) and larvae (9.60%). We found each life stage contributed differently to dispersal intensity (Kruskal-Wallis ANOVA by ranks test, H = 16.39, p = 0.0003). Specifically, the abundance of larvae differed significantly from juveniles (p = 0.011) and adults (p = 0.0006) (multiple comparisons, *post hoc* tests). Adult and juvenile contributions to dispersed numbers also differed among habitat zones (Kruksal-Wallis ANOVA by ranks test, H = 6.667, p = 0.035 and H = 8.265, p = 0.016 respectively), but larvae did not (H = 4.453, p = 0.107). More juveniles and adults were seen in vegetation and intermediate zones (Figure 2-4), however the only significant difference was between the intermediate and ocean zone pools (multiple comparisons, *post hoc* tests) (Table 2-5).

Table 2-5. *Post-hoc* multiple comparisons analysis (Kruskal-Wallis ANOVA by ranks) for overall abundance of juvenile and adult dispersers from colonized pools in each sampling zone. Significant p values are in bold.

	Vegetation		**Intermediate**		**Ocean**	
	Juvenile	*Adult*	*Juvenile*	*Adult*	*Juvenile*	*Adult*
Vegetation			0.815	1.00	0.280	0.117
Intermediate	0.815	1.00			**0.016**	**0.056**
Ocean	0.280	0.117	**0.016**	**0.056**		

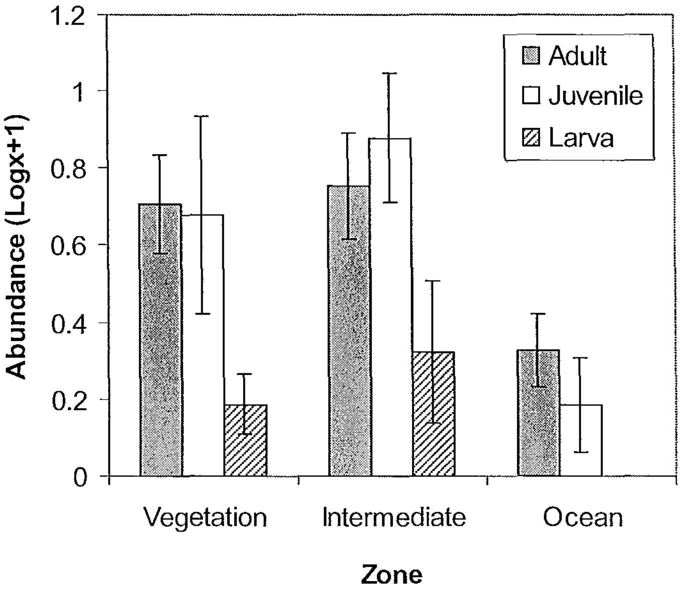

Figure 2-4. Mean abundance (log x+1) of adult, juvenile and larval dispersers collected from artificial pools in vegetation, intermediate, and ocean zones. Bars indicate standard error values.

Experiment 2 - Dispersal Rates of Three Vectors

I. Dispersal quantification

1,912 aquatic invertebrates were caught in traps among rock pools during the eleven day sampling period. Dispersers included individuals from 22 species, further classified into six taxa: Copepoda, Ostracoda, Branchiopoda (Cladocerans), Insecta (fly, mosquito and beetle larvae), Rotifera, and Others (Table 2-6). Several other propagules were also dispersing among pools, including terrestrial mites (3 individuals), dormant eggs of an unidentifiable invertebrate species (21), ephippia (17) and one unidentified snail. Overall, dispersers represented juveniles (copepod nauplii and small bodied ostracods; 55.0%), adults (42.9%) and larvae (insects; 1.6%).

Table 2-6. Abundance of dispersers collected amongst all dispersal vectors subdivided into six taxa. Percentage of total dispersal of each taxa is shown in parentheses.

Dispersing Taxon	Dispersing Species	Abundance
Copepoda (46.6)		
Adult	**Cyclopoida (Order)**	
	Orthocyclops modestus (Herrick)	63
	Paracyclops fimbriatus (Fischer)	100
	Harpacticoida (Order)	
	Nitocra spinipes (Boeck)	129
	Metis sp.	1
Juvenile	**Copepod Nauplii**	598
Ostracoda (36.3)		
Adult	**Podocopida (Order)**	
	Cypricercus sp.	180
	Cypridopsis sp.	4
	Candona sp.	18
	Potamocypris sp.	30
Juvenile	**Unidentified**	463
	Cladocera (Suborder)	
Branchiopoda (3.1)		
	Ceriodaphnia rigaudi	28
	Alona davidii	31
	Diptera (Order)	
Insecta (1.4)		
	Fly larvae (Dipteran sp., Dolichopodidae sp.)	8
	Mosquito Larvae (*Culex* sp.)	15
	Ceratopogonidae (Biting Midge)	1
	Coleoptera (Order)	
	Beetle Larvae	3
Rotifera (11.5)	Rotifer sp.	220
	Annelida (Phylum)	
Other (1.1)		
	Oligochaete	1
	Polychaete	6
	Decapoda (Order)	
	Sesarma miersi	3
	Turbellaria (Class)	

		Gieysztoria reggae	2
	Nematoda (Phylum)		8

Invertebrates in the rock pool metacommunity dispersed using all three vectors with varying intensities (Figure 2-5), however mean abundance and species richness were not directly comparable across vectors due to obvious differences in quantification methods as previously discussed. A single overflow event dispersed on average 65.0 ± 23.14 individuals and 3.88 ± 0.40 species [mean ± SE]. Wind dispersal vectors intercepted approximately 11.58 ± 2.96 individuals and 1.83 ± 0.34 species. Animal vector traps were successful at capturing larger animal species suspected of dispersing small bodied invertebrates, including Amphipoda (9 individuals) and Isopoda (1). Amphipods and isopods dispersed 0.42 ± 0.23 individuals and 0.25 ± 0.12 species. Abundance and species richness of dispersers caught in opened animal traps did not significantly differ from control group (sealed traps) (Mann-Whitney U Test, U = 7146, p = 0.73 each), implying that large invertebrate carriers contributed little to dispersal of rock pool fauna.

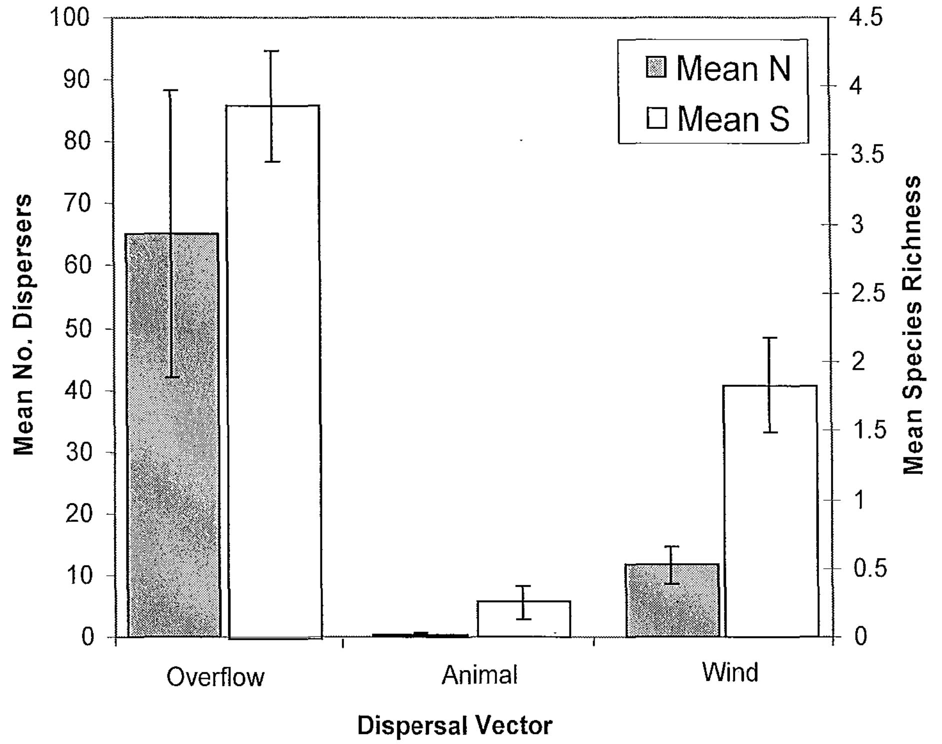

Figure 2-5. Mean number of dispersers (N denoted by grey bars) and mean species richness (S denoted by white bars) intercepted in each dispersal vector during the study period. Means here are reported only and not comparable across vectors. Bars indicate standard error.

The mean ratio of juvenile to adult dispersers in each of the 24 rock pools varied among pools within the same vector. Overflow carried on average 1.91 ± 5.43juveniles to adults (mean ± standard deviation), animal vectors dispersed 0.41 ± 0.52, and wind vectors intercepted 3.9 ± 4.16. The high reported standard deviation values with respect to all vectors reflect that the abundance of juveniles or adults dispersing via any of the three vectors is highly variable.

Several pools were relatively dry (with some degree of dampness) prior to re-hydration and overflow treatment. Various species were still found to disperse from these drier pools, including Ostracoda (juvenile and adult), Cyclopoida, Harpacticoida, Rotifera, Nematoda, Polychaeta, and Cladocera species. More invertebrates (per ml) were found to disperse from previously hydrated pools than from pools classified as dry (Independent samples t-test, $t = -2.03$, $df = 22$, $p = 0.05$). Conversely, overflow from wet pools dispersed on average a greater number of species per ml than dry pools, however this was not significantly different ($t = -1.34$, $df = 22$, $p = 0.19$) (Figure 2-6). Volume of overflow and number of dispersers was only marginally significantly correlated (Simple Linear Regression, $F_{1,22} = 4.24$, Adjusted $R^2 = 0.12$, $p = 0.05$), while species richness was not correlated with flow volume ($F_{1,22} = 2.55$, Adjusted $R^2 = 0.06$, $p = 0.12$).

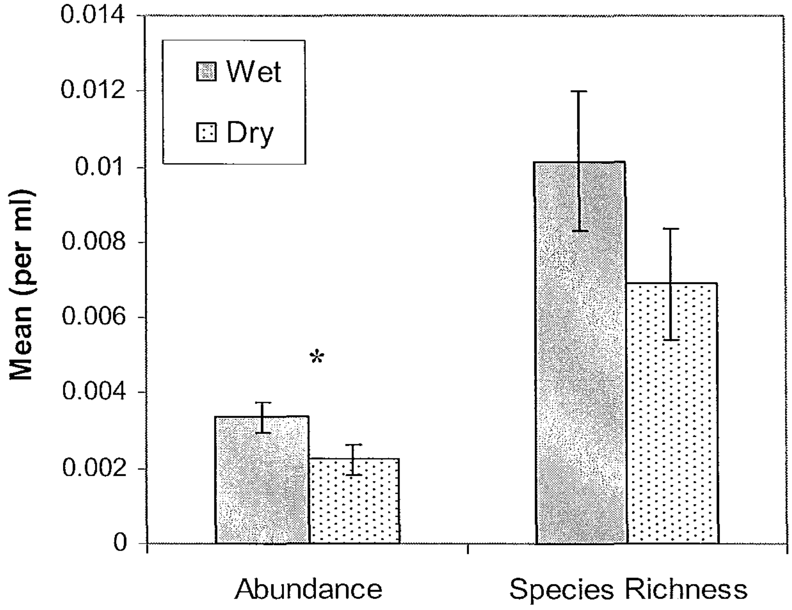

Figure 2-6. Mean abundance of dispersing invertebrates per ml (log x+1 transformed) and mean species richness per ml intercepted during pool overflow. Bars indicate standard error; (*) indicates marginally significant difference for abundance (p = 0.05), but not species richness (p = 0.19) between wet and dry pool types.

Abundance of the six dispersing taxa groups differed *within* each of the dispersal vectors for overflow and wind (H = 50.13, p <0.001 and H = 49.79, p<0.001 respectively), however no differences were found for animal vectors (Kruskal-Wallis ANOVA by ranks test, H = 8.32, p = 0.14) (Table 2-7, Figure 2-7). The number of dispersing copepods was significantly different from other taxa (Branchiopoda, Insecta, Rotifera and Other) in overflow dispersal (Kruskal-Wallis multiple comparisons, *post-hoc* test, p<0.001 each). Copepods dispersing via wind also differed in abundance from Branchiopoda, Insecta, Rotifera and Other (Kruskal-Wallis multiple comparisons, *post-hoc* test, p<0.01 each) (Table 2-7). Although Ostracoda were abundant in most traps, they did not significantly differ from other taxa irrespective of vector considered. Considerable variability (i.e., many traps with no ostracods) may have attributed to this statistical result.

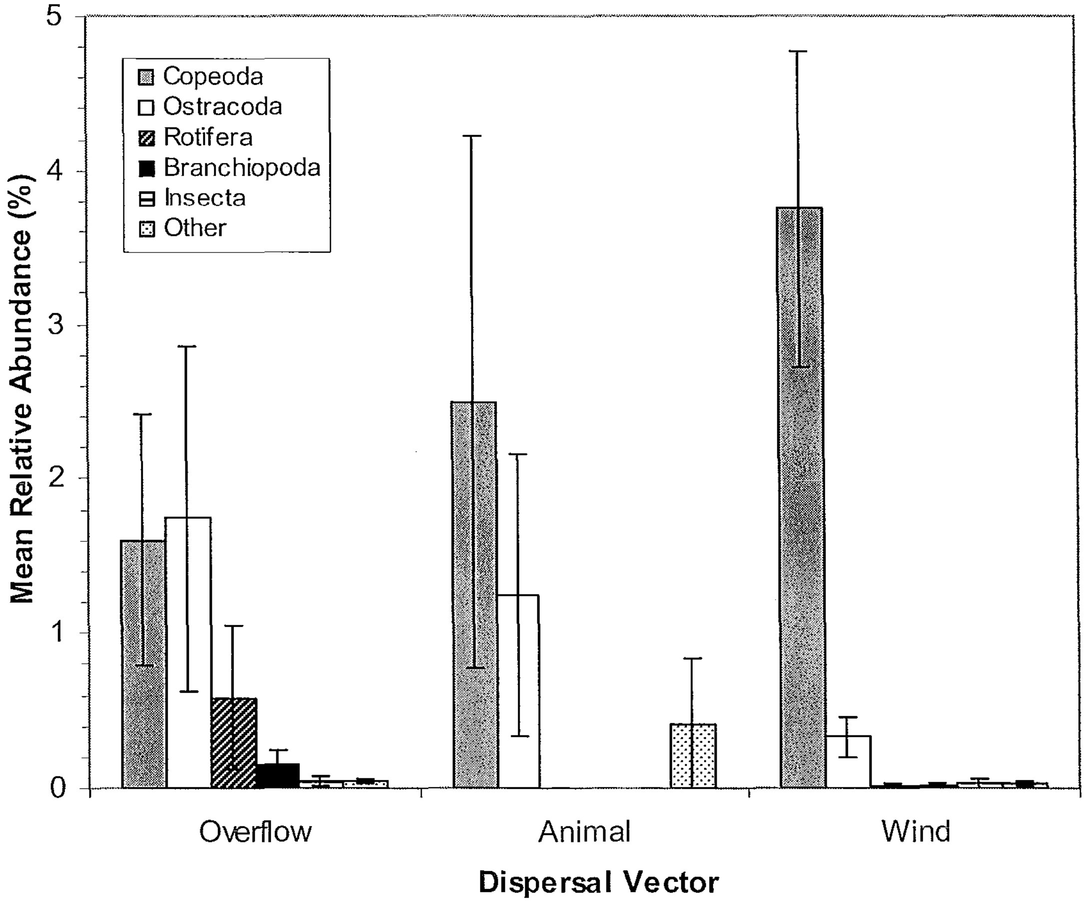

Figure 2-7. Mean relative abundance (for each dispersal vector) of 6 dispersing taxa. Bars indicate standard error values.

Table 2-7. *Within* vector comparison of the relative abundance for 6 taxa using non-parametric Kruskal-Wallis ANOVA by ranks. Symbol > indicates the more abundantly dispersed taxa. Statistical significance values are in bold.

Vector	**Test Statistic (H)**	**p**	**Multiple Comparisons *Post-Hoc* Test Significant Differences**	
Animal	8.32	0.14	N.A	
Overflow	50.13	**<0.001**	Copepoda > Branchiopoda	**p<0.0001**
			> Insecta	**p<0.0001**
			> Rotifera	**p<0.001**
			> Other	**p<0.0001**
Wind	49.79	**<0.001**	Copepoda > Branchiopoda	**p=0.002**
			> Insecta	**p=0.002**
			> Rotifera	**p=0.002**
			> Other	**p=0.005**

II. Influence of Environment and Landscape

Neither the abundance of dispersers nor number of species being transported via overflow differed between vegetation, intermediate and ocean zones (MANOVA, Wilks lambda = 0.81, $F_{4,40} = 1.11$, $p = 0.37$) (Figure 2-8). A similar pattern was also true for wind dispersed invertebrate abundance and species richness (Kruskal-Wallis ANOVA by ranks, H = 0.29, p = 0.87 and H = 0.19, p = 0.91, respectively). Aquatic invertebrates transported by isopods and amphipods were consistently low in both abundance of dispersing individuals and number of species across all three zones (Kruskal-Wallis ANOVA by ranks, H = 0.57, p = 0.75 and H = 0.58, p = 0.75, respectively) (Figure 2-8). The across zone comparisons above were completed for each individual vector; between vector comparisons across zones were not suitable for the data retrieval methods used.

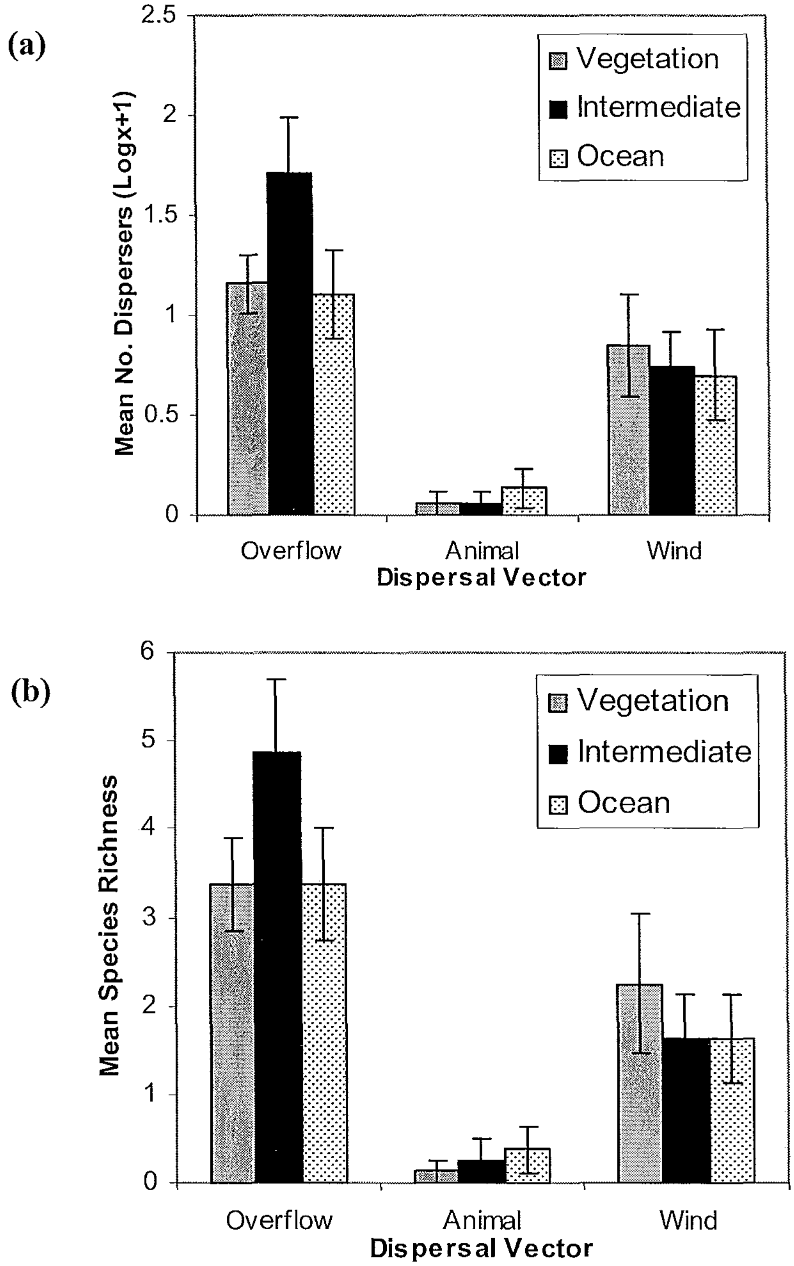

Figure 2-8. Within vector comparison of (a) mean number of dispersing invertebrates (log x + 1), and (b) mean species richness amongst three spatial zones for each dispersal vector. Bars indicate standard error.

The overall composition and abundance of dispersers (i.e., all six taxa together) did not differ between the three habitat zones for overflow (ANOSIM, R = -0.039, p = 0.73), animal (R = 0.20, p = 0.50) and wind vectors (R = 0.01, p = 0.37) (Table 2-8). Similarly, the abundance of each *individual* taxa group was also not significantly different among zones for each dispersal vector (Kruskal-Wallis ANOVA by ranks test, p>0.05) (Table 2-8).

Table 2-8. Comparison of abundance for all dispersing taxa (ANOSIM, Global R values reported) and individual taxa (Kruskal-Wallis ANOVA by ranks, H values reported) amongst three habitat zones (vegetation, intermediate, ocean). ANOSIM results based on 999 permutations.

Vector	Comparison Level	Analysis	Taxa Group	Test Statistic (Global R or H)	p
Overflow	Overall dispersing community	ANOSIM		-0.039	0.73
	Individual Taxa Group	Kruskal-Wallis ANOVA by Ranks	Ostracoda	1.18	0.55
			Copepoda	3.86	0.15
			Branchiopoda	0.89	0.64
			Insecta	2.29	0.32
			Rotifera	1.29	0.53
			Other	1.74	0.42
Animal	Overall dispersing community	ANOSIM		0.2	0.50
	Individual Taxa Group	Kruskal-Wallis ANOVA by	Ostracoda	1.05	0.59
			Copepoda	2.28	0.32
			Branchiopoda	0.00	1.00

		Ranks	Insecta	0.00	1.00
			Rotifera	0.00	1.00
			Other	2.00	0.37
Wind	Overall dispersing community	ANOSIM		0.01	0.37
	Individual Taxa Group	Kruskal-Wallis ANOVA by Ranks	Ostracoda	1.71	0.43
			Copepoda	1.23	0.54
			Branchiopoda	2.00	0.37
			Insecta	2.00	0.37
			Rotifera	2.00	0.37
			Other	1.05	0.59

The abundance of dispersers intercepted during wind transport was not affected by any external environmental variables, including proximity to the vegetation or ocean, mean distance to three nearest neighbours and mean perimeter of nearest pools (Multiple Regression Analysis, overall $R^2 = 0.07$, $F_{4,19} = 0.36$, $p = 0.83$). Similarly, the mean number of species intercepted during wind transport was not affected by any of the suspected predictor variables (overall $R^2 = 0.15$, $F_{4,19} = 0.82$, $p = 0.53$). Although mean perimeter of the three (nearest) neighbouring pools appeared as the most important variable in predicting both the mean number of dispersers (18.5%) and mean number of species (30.4%), it was not statistically significant ($p = 0.44$ and 0.19, respectively) (Table 2-9). Invertebrates dispersed by animal vectors were unaffected by location in terms of both abundance of dispersers and number of dispersing species for vegetation (Spearman Rank Correlation, $p = 0.48$ and $p=0.41$, respectively), ocean ($p = 0.87$ and $p=0.84$), and mean distance to three nearest neighbour pools ($p = 0.28$ and $p=0.23$) (Table 2-10).

Table 2-9. Multiple regression analyses for mean number of dispersers (log x+1) and mean number of species (log x+1) intercepted via wind.

Mean No. Dispersers (logx+1)			**Mean No. Species (logx+1)**		
Measurement Factor (cm)	**Beta (β)**	**p**	**Measurement Factor Log x+1 (cm)**	**Beta (β)**	**p**
Vegetation Distance	-0.113	0.79	Vegetation Distance	0.188	0.45
Ocean Distance	0.075	0.77	Ocean Distance	0.161	0.51
Mean Distance Neighbour	0.011	0.98	Mean Distance Neighbour	-0.005	0.98
Mean Perimeter Neighbour	0.185	0.44	Mean Perimeter Neighbour	0.304	0.19

Table 2-10. Spearman rank correlation values for mean number of dispersers and mean number of species intercepted by animal vector traps.

	Mean No. Dispersers			**Mean No. Species**		
Factor	**Spearman R**	**n**	**p**	**Spearman R**	**n**	**p**
Vegetation Distance	0.153	24	0.48	0.176	24	0.41
Ocean Distance	0.034	24	0.87	0.044	24	0.84
Mean Distance Neighbour	0.231	24	0.28	0.252	24	0.23

DISCUSSION

Dispersal into Artificial Pools

Our study revealed a high capacity for dispersal and successful early colonization of aquatic invertebrates to artificial pools in the Jamaican rock pool metacommunity. Small bodied taxa such as Ostracoda and Copepoda (specifically, Cyclopoida and Harpacticoida) accounted for the greatest number of colonizers. This high abundance of copepods corroborates with other studies that found these species to have a high dispersal and colonization capacity. For example, Frisch and Green (2007) found cyclopoids to be the earliest and most abundant colonizers in newly created ponds over a nineteen day period. Similarly, Caceres and Soluk (2002) as well as Jenkins and Buikema (1998), found that mesocosms and ponds were colonized by copepod and rotifer species first. Rotifers in particular, were abundant dispersers and early colonizers in experimental ponds (Jenkins 1995). Our study found few rotifers colonizing artificial pools, however this discrepancy may not necessarily be due to an inability to adequately disperse across our study system, since rock pools are situated close to one another and distance is unlikely to be a factor. Instead it is possible that rotifer species may have unknowingly passed through filtering nets due to their much smaller body size than other rock pool species sampled.

Aquatic invertebrate species have differing abilities to disperse between habitat patches (Caceres & Soluk 2002, Cohen & Shurin 2003) as was evident in this study. The most abundant species collected during early colonization of artificial pools may simply reflect the natural rock pool metacommunity, which includes various Copepoda and Ostracoda species. Artificial pools in this study were not found to have similar species dispersal rates across all sampling dates (i.e., more colonizers were present in pools during sampling date 1 than dates 2 and 3). The variation in the number of dispersers over time may indicate that aquatic invertebrate movement across habitat patches may be influenced by other variables. For example, variation in invertebrate dispersal intensity across rock pools in South Africa was attributed to both wind direction and wind speed (Vanschoenwinkel *et al.* 2008a). Although wind patterns were not quantified in this study, it is likely that environmental conditions (particularly fluctuations in climate) have the potential to influence the intensity with which invertebrates disperse. This in turn should be an area of focus in future rock pool metacommunity dispersal studies, as fluctuations in weather patterns may influence successful dispersal and consequently be involved in community structure.

Invertebrate juveniles were found to colonize artificial pools in high abundance, including copepod nauplii and small bodied ostracods. As these individuals are frequently in the water column and are unlikely to survive exposure to dry conditions, we infer two potential mechanisms of dispersal. First, the high abundance of copepod and ostracod juveniles may simply have been the outcome of a few fertilized adult females dispersing into pools. Due to the rapid generation cycles, eggs of adult females may have hatched and grown to nauplii or juvenile stages just before pools were sampled (Frisch & Green 2007). Second, exposed sediments from neighbouring dry pools have the potential to hold invertebrate eggs and other dormant structures capable of withstanding long periods of harsh environmental conditions, including desiccation (Brendonck & De Meester 2003, Hairston 1996). These dormant forms may have passively dispersed from the surrounding dried sediment via wind to more suitable habitats (i.e., the artificial rock pools) where they had a greater potential to hatch (Brendonck & De Meester 2003). A study on South African rock pools for example, found that the number of dried pools (in which sediment was exposed to air) was an important factor influencing both the abundance of dispersers and species intercepted via wind (Vanschoenwinkel *et al.* 2008a). Moreover, due to the small size and shape of invertebrate eggs it is possible that these structures may be more easily dispersed via wind gusts or animal vectors. For example, Vanschoenwinkel *et al.* (2009) found a high number of copepod eggs dispersing via wind at high altitudes and related this to their relatively small size (70-100 μm). Despite this however, it cannot conclusively be argued that smaller bodied passively dispersing individuals (including eggs) are always the furthest dispersed compared to their larger bodied adult counterparts (Jenkins *et al.* 2007, Vanschoenwinkel *et al.* 2009). Due to the difficulty involved in tracking small bodied individuals (particularly eggs), the influence of invertebrate body size on dispersal intensity or colonization ability is still relatively unknown (Rundle *et al.* 2007).

Despite the short duration of this study, we found aquatic invertebrates in the rock pool metacommunity to have a high capacity to colonize new habitat patches. This is not necessarily always the case however, as several have argued that dispersal and colonization of newly created habitats are neither rapid (Jenkins & Buikema 1998) nor a steady occurring process (Bohonak & Jenkins 2003). The results of our study however concur with others that have found colonization to occur relatively quickly as a result of a high dispersal ability by various species (Cohen & Shurin 2003, Frisch & Green 2007, Louette & De Meester 2005). These conflicting results do not necessarily imply that dispersal must be either a rapid *or* slow process. Instead, it is probable that variations in dispersal and colonization rates amongst studies may be the result of environmental, landscape and climatic variations that exist in different field sites. Furthermore, interactions with other species (both in the original patch and during the in-transit phase) may impact the rate of invertebrate movement. If so, the influence of the surrounding environment and interactions with other species must be taken into consideration when addressing the issue of aquatic invertebrate dispersal and colonization ability of various taxa.

Dispersal Rates of Three Vectors

Aquatic invertebrates of various species and life stages were able to disperse in considerable numbers by air, water, and animal transport. It is difficult, however, to determine which method is most efficient at dispersing individuals across habitat patches as the techniques used to determine dispersal rate in each vector were very different from one another. Although juvenile forms were consistently more abundant than adult forms across all modes of dispersal, they showed a high degree of variability, even within a given vector. It is possible that the number of dispersers of any particular life stage changes as a function of the dominant population cycle in a given pool. Rock pool environments fluctuate in terms of their abiotic components and community composition (Jocque *et al.* 2010). There may exist certain periods of time whereby communities are dominated by juvenile forms due to a recent surge in female reproduction. Conversely, periods following long term desiccation maybe marked by a surge in hatching of dormant eggs that were produced prior to the drought and were able to survive in the sediment (Altermatt & Ebert 2008). As a result, the high observed variation in the number of juvenile to adult dispersers captures the unpredictability of the pool community and reflects the variability in life stage dispersal in space and time.

Although vectors did vary in their capacity to disperse individuals, the high abundance transported via overflow shows that this vector may be important in dispersing organisms when it occurs. Flow appears to move organisms in large periodic pulses as compared to the two other modes that, while variable, appear to operate more continuously. Overflow in particular, has a high capacity to move many individuals of multiple species. Michels *et al.* (2001) estimated that approximately 7,000 zooplankton on an hourly basis disperse throughout a series of ponds in Belgium connected via rivulets. The high dispersal through flow may even correlate with the movement of invasive species between isolated aquatic bodies (Shurin & Havel 2002) as well as potential gene flow (Hulsmans *et al.* 2007).

Although we observed a high number of dispersers transported by overflow, we found no correlation with flow volume. A similar pattern was observed in Belgium ponds where Van de Meutter *et al.* (2006) found no influence of discharge volume on dispersal intensity despite the high number of macroinvertebrates from various families that were dispersing via rivulets. Moreover, intensity of precipitation, although assumed to be a potential factor influencing overflow dispersal, was also not correlated with dispersal rate in other systems (Vanschoenwinkel *et al.* 2008b). Possibly, the pool community itself and the frequency with which it is overflowed may be important in influencing dispersal rate. A lack of correlation between flow volume and dispersal rate may also be attributed to differences in the initial water levels in experimental pools (some pools were completely filled while others were relatively damp or entirely dry). In particular, rock pools that experience recurrent instances of desiccation are characterised by fewer species, diversity and abundance compared to pools that do not frequently dry up (Therriault & Kolasa 2001). Species are unable to withstand periods of desiccation unless they possess dormant life stages and as such, these species will be missing from pools that dry frequently. Therefore fewer individuals will likely disperse from damp or dry pools irrespective of their volume of discharge.

Wind also emerged as an important dispersal mechanism to transport invertebrate species, despite the fact that efficiency for wind to carry propagules is often debated. Nevertheless, some studies found wind to be a major factor in metacommunity dispersal (Vanschoenwinkel *et al.* 2008a, Vanschoenwinkel *et al.* 2008b, Vanschoenwinkel *et al.*

2009), and others in the colonization of newly created habitats (Louette & De Meester 2005). These results are in contrast to other dispersal studies that argue wind is an inefficient mode of transport and its role is overestimated (Jenkins & Underwood 1998). Low success rates in intercepting propagules suspended in air is insufficient to conclude that dispersal via wind plays a negligible role. Brendonck and Riddoch (1999) for example, although were unable to intercept wind dispersing individuals, still argued that anostracan eggs have a high potential to be carried by wind. This was due to the fact that such eggs are likely to be easily lifted by wind currents due to a lack of protruding external structures that would otherwise result in wind resistance. Although wind dispersal may not be the primary mode of transportation for aquatic invertebrates, it can still contribute to dispersal depending upon the system as well as species involved.

Animal vectors in this study carried the fewest number of individuals and species. Although many have suggested that birds in particular are likely to disperse dormant invertebrate eggs (Figuerola *et al.* 2003, Frisch *et al.* 2007, Green *et al.* 2008), the Jamaican rock pool site is not frequently visited by waterfowl and therefore it is unlikely that their role is important. Similarly, other larger animal taxa such as reptiles and amphibians (Lopez *et al.* 1999) or large mammals such as the wild boar (Vanschoenwinkel *et al.* 2008c) are capable of dispersing invertebrates, however the intensity of dispersal by these vectors is inconsistent and its success depends upon the survival of dormant eggs as well as their ability to hatch following deposition. The vector species in our study (amphipods, isopods) were observed both throughout the site and within traps; however the abundance of aquatic invertebrates in these traps was low. The limited dispersal via these animal vectors could have two potential reasons: firstly, it is possible that amphipods and isopods did carry small bodied invertebrates on their bodies or within gill chambers, however were simply not deposited into the traps. Secondly, a larger abundance of amphipods or isopods may be required to transport enough small bodied invertebrates for the study to detect them. These possibilities point out to the difficulty involved in estimating individuals dispersed by animal vectors, and continues to be a challenge faced by dispersal studies.

Despite our previous assumptions, external environmental factors and connectivity between patches had no detectable influence on abundance or species richness of dispersers for any of the studied vectors. This contrasts others studies that found dispersal rates of aquatic invertebrates to typically decrease with increasing distance from source populations (Allen 2007, Vanschoenwinkel *et al.* 2008b, Vanschoenwinkel *et al.* 2009). Unlike these systems in which single source populations were more easily identified, the Jamaican rock pool metacommunity is a highly clustered environment in which all pools are located in close proximity to one another (typically pools are within 1 meter of each other). In this scenario, identifying distinct sources and sinks is difficult as it is likely that multiple pools are providing dispersing individuals. This potentially random movement of individuals can be viewed as “propagule rain,” whereby the chance of trapping a disperser is similar across all habitat patches (Resetarits *et al.* 2005), and no single rock pool is responsible for providing dispersing individuals.

Moreover, the lack of influence of both dense vegetation and the ocean may be attributed to the fact that the distance between the two zones was likely too small to see the effect of either on dispersal rate. It is possible that a larger metacommunity in which major geographic features were much farther apart from each other would better show their influence on dispersal rate. Although neither vegetation nor ocean distance appeared to affect any of the vectors, artificial pools in vegetation and intermediate zones were generally colonized by more individuals. The design of the vector traps may have been an influencing factor, as traps did not cover the entire surface area of their corresponding pools and therefore dispersal rates may have been underestimated sufficiently to undermine the power of the statistical tests.

Summary and Conclusions

It is evident that species in this system have a high ability to disperse via both overflow and wind vectors, with limited influence of larger animal species. Moreover, the intensity of dispersal via these various modes is highly variable and is likely dependent upon the current structure and dynamics of the pool community. Despite the high potential for dispersal in this system, it is crucial to investigate its possible impacts on local communities. Successfully intercepting propagules during transport does not necessarily infer their survival or integration into new habitat patches, as individuals must be able to survive amongst resident species and successfully reproduce. Future research in this area should therefore attempt to investigate the relationship between dispersal and local community structure. The intensity of dispersal and its potential role in the assembly of communities should also be investigated as it may function in conjunction with other important factors including abiotic and biotic interactions.

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Chapter 3

Linking local community structure to the dispersal of aquatic invertebrate species in a rock pool metacommunity

This chapter is in preparation for submission for publication.

RATIONALE AND OBJECTIVES

The previous chapter showed that aquatic invertebrates abundantly dispersed among rock pools via multiple vectors (wind and flow in particular), with limited influence of the surrounding environment on dispersal rate. Many studies have also found that dispersal can play a role in community structure and development. However, the degree of similarity in terms of species composition between dispersal and the local community has not been well studied. The goal of this paper is to move one step forward in this investigation of dispersal and determine the influence of population movements on the composition of local communities. Colonization of newly created habitats is accomplished through the dispersal of individuals between habitat patches and subsequent recruitment/survival. Therefore, I also aim to compare the composition and abundance of dispersers to multiple stages of rock pool community development. Using dispersal quantification (Chapter 2), colonization experiments and biotic surveys, I examined the possible relationships that exist between the composition of dispersers and the structure of the local community. Overall, I found:

- Short term dispersal and local community composition (in terms of species relative abundance) was remarkably similar
- A select number of species were much more pronounced in dispersal vectors than in rock pool communities and vice versa, suggesting a potential competition-colonization trade-off

- Composition and abundance of dispersing species was most similar to the later stages of community development, in which passive dispersers were most pronounced in both dispersal traps and rock pool communities.

These results suggest the potential for dispersal to be a very important factor influencing the composition of local communities. Furthermore, this study emphasizes the role that species movements can have on community development during the later stages of the colonization process.

ABSTRACT

Dispersal allows species to immigrate and emigrate to and from different habitat patches and is an important factor in determining community composition. Species richness, abundance and diversity are all influenced by dispersal (Cadotte *et al.* 2006, Cottenie & De Meester 2004, Ives *et al.* 2004, Kneitel & Miller 2003). The impact of species movements at the metacommunity level, however, is poorly understood, particularly at the scale of component local communities. The goal of this study was to evaluate the influence of dispersal on local community composition in a natural rock pool metacommunity. Short term dispersal was quantified over an 11 day period by intercepting propagules dispersing via overflow and wind. The identity of dispersing organisms was then compared to natural local communities in the rock pools. Additional colonization experiments that used newly created rock pool habitats aimed to assess what stage of the colonization process (early versus late) most corresponds to dispersal patterns. Overall, we found a high degree of similarity in relative species abundance and composition between dispersers and the local rock pool community in each of the 11 years for which data were available. On average, the composition and abundance of dispersing species was approximately 54.1 ± 9.3 % (mean ± SD) similar to the established pool community (Minimum = 38.42% in 1994 and Maximum = 70.23% in 1998). A select number of species, however (i.e., certain cyclopoid species), were disproportionately more abundant in vectors than in the pool community. This may have been the result of a competition-colonization trade-off, whereby inferior competitors may compensate by investing more in dispersal. Other species (i.e., harpacticoids) exhibited the reverse relationship, being more dominant in pools but less abundantly dispersed, which indicates a greater ability to compete once in the pools. Patterns in dispersed species were also found to be most similar to the later stages of colonization, during which passively dispersing species were most abundant. Flow and wind transported more passive than active dispersers, indicating the importance of such vectors in relocating individuals to new habitats and impacting community structure during the later stages of community development. The results of this study indicate a similarity between short term dispersal and long term local community composition, however, we stress that dispersal (a regional process) although important, must work in conjunction with local processes in structuring communities.

Key Words: *Dispersal, vectors, local process, regional process, competition-colonization, trade-off, local community structure, metacommunity, aquatic invertebrate*

INTRODUCTION

The intensity at which individuals move into new habitat patches is important in understanding the impact of dispersal on community structure. Dispersal can be an important process influencing aspects of local community such as species richness, diversity and abundance (Cadotte *et al.* 2006, Cottenie & De Meester 2004, Ives *et al.* 2004, Kneitel & Miller 2003), while also being a central factor involved in the colonization of newly created habitats (Caceres & Soluk 2002, Louette & De Meester 2005) and assembly of communities (Belyea & Lancaster 1999). Understanding how and at what rate dispersal occurs has become important in the study of multiple areas of ecology. For example, recognizing the significance of dispersal has become crucial in understanding how invasions of exotic species occur (via human related or natural means), since movement of invasive species can dramatically alter the structure of ecosystems (Boudreau & Yan 2003, Caraco *et al.* 1997, Irons *et al.* 2007, Schooler *et al.* 2006, Yan *et al.* 2002). Moreover, the movement of individuals can be important in ensuring the survival of populations in the presence of stochastic events that could result in species extinction (Bowler & Benton 2005, Brown & Kodric-Brown 1977). Understanding how the influx of species into a new habitat patch is related to the local community can provide insight into the relative importance of dispersal in structuring community dynamics.

The processes that are involved in both bringing species together and allowing them to coexist in a suitable environment are often complex and generally difficult to discern. Typically, two main processes have been found to play a significant role in community structure – local and regional. However, the relative importance of each is difficult to assess. Local processes are typified by the interactions occurring between species at small, localised spatial scales (i.e., within a single habitat patch), such as predator-prey relationships and competition for resources (for example, food or habitat space) (Bohonak & Jenkins 2003, Cottenie & De Meester 2004). Local abiotic conditions (pH, salinity, temperature etc.) can also influence the ability for species to survive, thereby interacting with biotic components to structure the local community (Bohonak & Jenkins 2003). Regional processes involve the movement of species between habitat patches (Jocque *et al.* 2007), transmitting individuals to either already existing communities or, as colonizers, to newly created habitats. Regional factors, such as fragmentation and degree of connectivity between habitats, therefore, will influence species ability to disperse (Bohonak & Jenkins 2003, Jocque *et al.* 2007). Such factors further complicate the capability to determine the relative importance of regional processes on community structure. Some studies support the importance of local factors in shaping communities (Cottenie & De Meester 2003, Jocque *et al.* 2007, Shurin 2000), while others have shown the significance of dispersal and colonization (Kneitel & Miller 2003).

Dispersal of individuals into new environments interacts closely with the ability for those environments to filter out species that are incapable of surviving to reproduce and integrate into the community. Dispersal occurring at a high rate means that individuals are easily capable of reaching a given patch. For example, many aquatic invertebrate species have been found to colonize new environments rapidly or move between habitat patches in high abundance (Louette & De Meester 2005, Vanschoenwinkel *et al.* 2008a, Vanschoenwinkel *et al.* 2009). Not all of these individuals are capable of surviving, however, and thus local processes such as predation, competition or the environment filter out species that are poor competitors (Cottenie & De Meester 2004, Jenkins & Buikema 1998, Shurin 2000). Conversely, the influence of these local processes becomes delayed when dispersal rate is low (Jenkins 2006, Jenkins & Buikema 1998). In this case, not all species are quickly able to reach the new habitat patch due to a limited dispersal ability or minimal connectivity between patches. The patch will then encompass only a small community of species that were successful at dispersal, thereby minimizing the influence of local processes on community structure (Bohonak & Jenkins 2003, Jenkins 2006, Jenkins & Buikema 1998). A limited number of species capable of quickly dispersing into the community means that species interactions are reduced (i.e., competition, predation) and the onset of local processes (biotic interactions) becomes delayed (Jenkins & Buikema 1998). It is evident that neither dispersal nor local scale interactions are sole determinants of structure in local communities, but instead both processes are interlinked and their impact on communities dependent upon each other (Palmer *et al.* 1996).

Several studies have attempted to quantify dispersal of aquatic invertebrates in order to understand the colonizing ability and dispersal efficiency of species via various vectors (Allen 2007, Brendonck & Riddoch 1999, Caceres & Soluk 2002, Jenkins & Underwood 1998, Louette & De Meester 2005, Maguire 1963, Michels *et al.* 2001, Van de Meutter *et al.* 2006, Vanschoenwinkel *et al.* 2008a, Vanschoenwinkel *et al.* 2008b). The relationship and similarity between the composition of dispersers and the established local community, however, has not been investigated and warrants further examination to better understand how much dispersal may influence community composition. The purpose of this study is to quantify dispersal of aquatic invertebrates in a rock pool metacommunity via wind and flow, and evaluate the potential effectiveness of dispersal in structuring local communities. This was accomplished through a combination of short term dispersal and colonization experiments, as well as long term biotic community surveys which took place annually for 11 years. We aimed to compare composition of dispersers in terms of species abundance to various stages of colonization and to the local communities in long established rock pools. A further goal was to assess the degree of similarity between local community and dispersal and to examine the potential role of regional processes (i.e., dispersal across habitat patches within a metacommunity) in local community composition.

METHODS

Study Site

This study took place in a natural rock pool metacommunity located near the Discovery Bay Marine Laboratory on the northern coast of Jamaica (18°28’N, 77°25’W)

(Romanuk & Kolasa 2005) (Figure 3-1). Rock pools were formed through long term weathering of an exposed fossil reef. Pools are typically filled through precipitation, however, frequent drying due to high temperatures make them ephemeral in nature. Abiotic parameters of pools vary considerably across space and seasons, indicating a highly heterogeneous system. For instance, while pools are typically brackish, some are more saline than others depending on their proximity to the bordering Caribbean Sea where they receive inputs from ocean splash. Rock pools are close in proximity to one another and are separated by no more than 5 meters in distance. Hydrologic connectivity between pools is accomplished through interconnected channels that allow for movement of aquatic invertebrates via pool overflow. A wide array of invertebrates inhabit the rock pools, including: Turbellaria (7 species), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Copepoda (6), Cladocera (4), Decapoda larvae (4 crab, 3 shrimp), Amphipoda (1), Isopoda (1) and Insecta (18). A total of 44 rock pools were chosen for either dispersal quantification, whereby propagules were intercepted during transport (24 pools), or colonization experiments (20 pools). Selected pools typically had a length of 49.0 ± 20.9 cm [mean ± SD] and a width of 28.8 ±10.5 cm, and were on average 76.6 ± 80.1 cm above sea level.

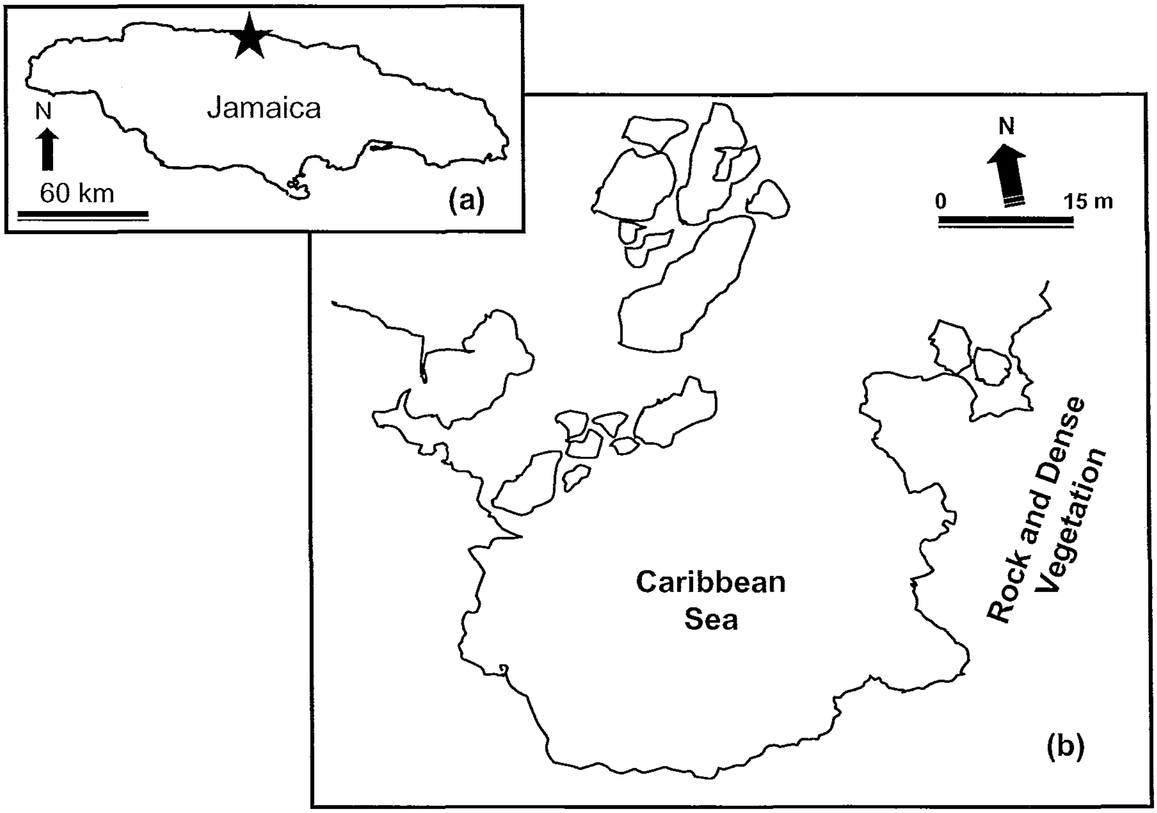

Figure 3-1. (a) Location of study site on the northern coast of Jamaica, Discovery Bay Marine Laboratory, and (b) layout of study area including rock pools and dense mangrove vegetation surrounded by the Caribbean Sea.

Sampling Design
Dispersal Vector Quantification & Biotic Community Sampling

Dispersal quantification experiments were conducted in 24 randomly chosen rock pools between 25 May and 4 June, 2009 by intercepting individuals dispersing via wind and pool overflow. Invertebrates dispersing via flow were mobilized by artificially flooding pools using freshwater since there was insufficient rainfall necessary to capture a natural overflow event. Flooding was simulated by trickling water onto the rocky margins and into the pools to ensure gradual overflow and prevent sediment disturbance. To intercept flow-dispersing species, a narrow plastic tube (9.5 mm internal diameter) was moulded to the mouth of the pool with a sealed plastic bag on the end to capture outflow and dispersing invertebrates (Figure 3-2a). Pools were artificially flooded once during the experiment and samples were filtered through a 63-μm net. Specimens were stored in 50 ml vials using 50% ethanol.

Wind dispersing species were intercepted in 4 small pea cup containers (7 cm height, 120 ml volume and 28 cm^2 aperture area) clipped together, and surrounded by Styrofoam for buoyancy (Figure 3-2b). Each wind trap was filled with freshwater and filtered rock pool water, and placed floating within each pool. Cups were inspected periodically to ensure evaporation was minimal, and refilled with water as needed. Wind traps were left in pools for the full duration of the experiment and were inspected for the presence of aquatic invertebrates and sampled every other day. Samples were collected and filtered through a 63-µm net. Specimens were stored in 25 ml vials using 50% ethanol.

Biotic community data for the rock pool system was collected annually for eleven years (1989-1994, 1996-1998, 2001 and 2002), during December or January for 49 rock pools. During invertebrate sampling, contents of the pools were thoroughly stirred to homogenize the community and a 500 ml sample was retrieved and filtered through a 63-µm net. Specimens were stored into 50 ml vials using 50% ethanol. Samples were then taken to the laboratory for counting, following the protocol outlined in Therriault (2002). Species were identified to species, genus or family level using a dissecting microscope.

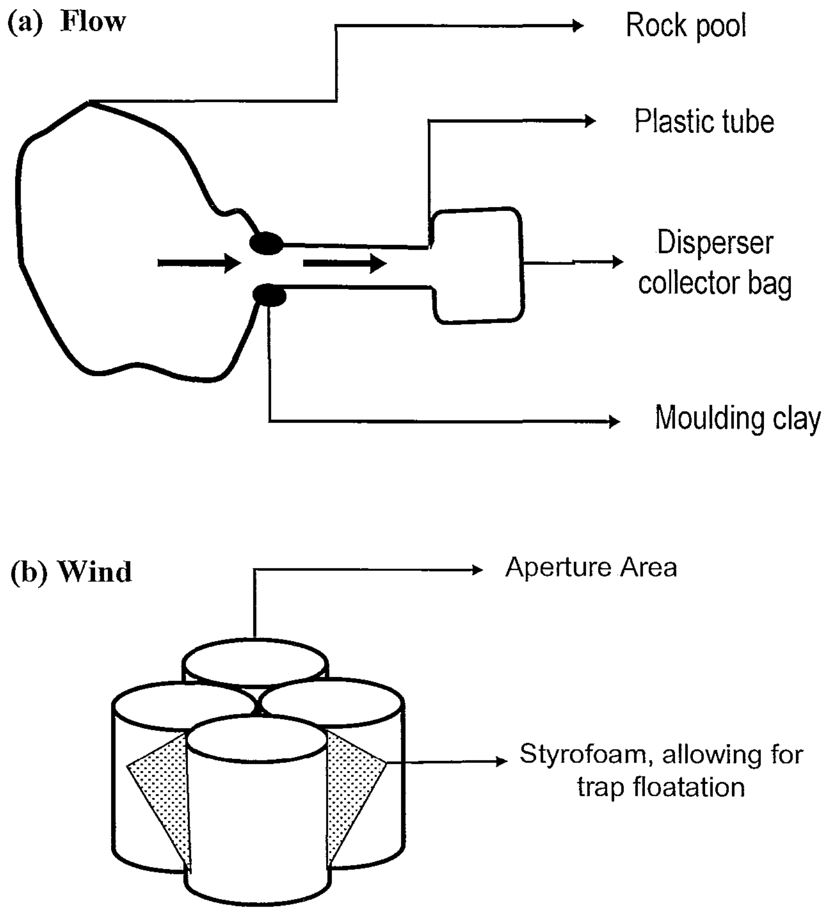

Figure 3-2. Typical structure of (a) flow trap, and (b) wind trap fitted into pools for dispersal quantification. Direction of flow is indicated by arrows in (a).

Stages of Colonization

To investigate the sequence of species arrival in natural rock pools, data was compiled from colonization experiments performed in June 2004 (courtesy; Dr. April Hayward). For the experiment, twenty rock pools were randomly selected in order to create new habitats for species to colonize. Contents of the pools were drained and their interior thoroughly scrubbed and washed with both freshwater and saltwater to ensure no live individuals or dormant eggs were left remaining in the sediment. Rock pools were filled with equal parts of distilled and tap water and left for 30 days. Pools were sampled every six days for a total of five sampling periods (hereafter referred to as stage 1-5). The entire content of each one of the pools was thoroughly stirred to homogenize the community. A 500 ml beaker was used to obtain biotic samples which were then filtered into vials using a 63 μm mesh netting. Samples were preserved in 50% ethanol and invertebrates were later identified using a dissecting microscope to species, genus or family level.

Statistical Analysis

To determine if short term dispersal composition was similar to the typical rock pool communities, species dispersal rates were compared to community data from 49 rock pools surveyed over eleven years. To control for differences in temporal scale and methodology, relative abundances (%) were calculated for each species in both the rock pools (for each year) and all dispersal vectors (cumulated across flow and wind vectors). The degree of similarity between dispersal and rock pool communities for each year was assessed using Bray-Curtis measures as calculated by Primer version 6.1.6 (PRIMER-E Ltd. 2006). Patterns in the similarity between dispersers and local community were further examined within each of the eleven years. Best fit equations for relative species abundance in pools and vectors were determined using TableCurve 2D version 5.01.03. The mean relative abundance of each species across all eleven years was also calculated and compared to the relative abundance from dispersal vectors, and best fit equations/curves were determined. To assess which species were most variable in abundance between dispersal vectors and the actual rock pool community, the relative abundance of species in each separate vector (flow and wind) was subtracted from the relative abundance of species in the rock pools for each year. The mean difference (for each species) between the dispersal vector and pool community across all eleven years was then calculated to determine the degree of disparity existing between dispersal and community composition.

The relationship between the composition of dispersers (for flow and wind vectors) and local community composition at different stages of the colonization process was investigated. For this, the sum of individuals from each species across all 20 pools at each of the 5 stages of colonization (i.e., each of the 5 sampling periods) was taken and relative abundance values calculated. Species abundance in each vector was also converted into a relative abundance and the similarity between vectors and each stage of colonization was calculated using Bray-Curtis similarity measures in Primer version 6.1.6. From these results, the stage of colonization that was most similar to dispersal in terms of species composition could be assessed.

RESULTS

Overall, short term dispersal was found to be an accurate reflection of long term community composition. There was a relatively high degree of similarity between the composition of dispersers and rock pool community, both within each sampling year as well as across all years (Figure 3-3). Although different functions were fitted to the dispersing and pool community (Table 3-1, Appendix A), best-fit lines showed similar trends in species abundance. The degree of similarity varied somewhat from year to year (Figure 3-4); however dispersers were on average 54.1 ± 9.3 % [mean ± SD] similar to the resident community. The identities of the most variable (or outlier) species were quite consistent across years suggesting some regularity in community dynamics over time. In particular, consistently large differences between dispersal and pool relative abundance in several species of cyclopoids and ostracods (CycS and Ost5A) suggested a high capacity for dispersal but a minimal ability for survival once in the pools. Conversely, other species appeared to have a minimal ability to disperse including harpacticoids, cladocerans, ostracods and nematodes (Harp, Daphn, Ost6, Nema), but were consistently the most abundant species in pools (Figure 3-3).

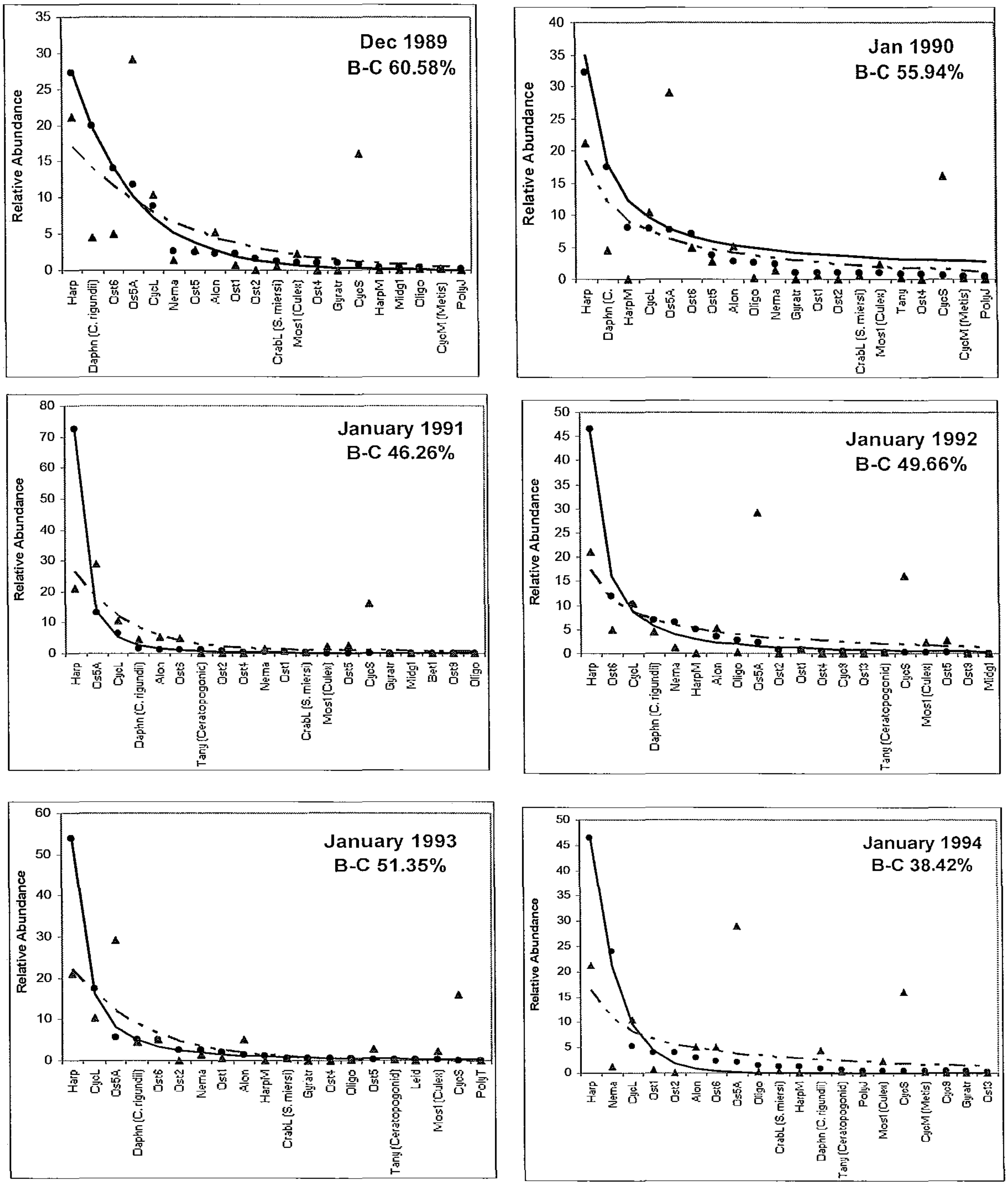

Figure 3-3. Mean relative species abundance and best fit lines from dispersal ▲ ------- and rock pool ● —— communities based on sampling year (ordered by ranked mean relative abundance). Bray-Curtis similarity measures (B-C) indicated above.

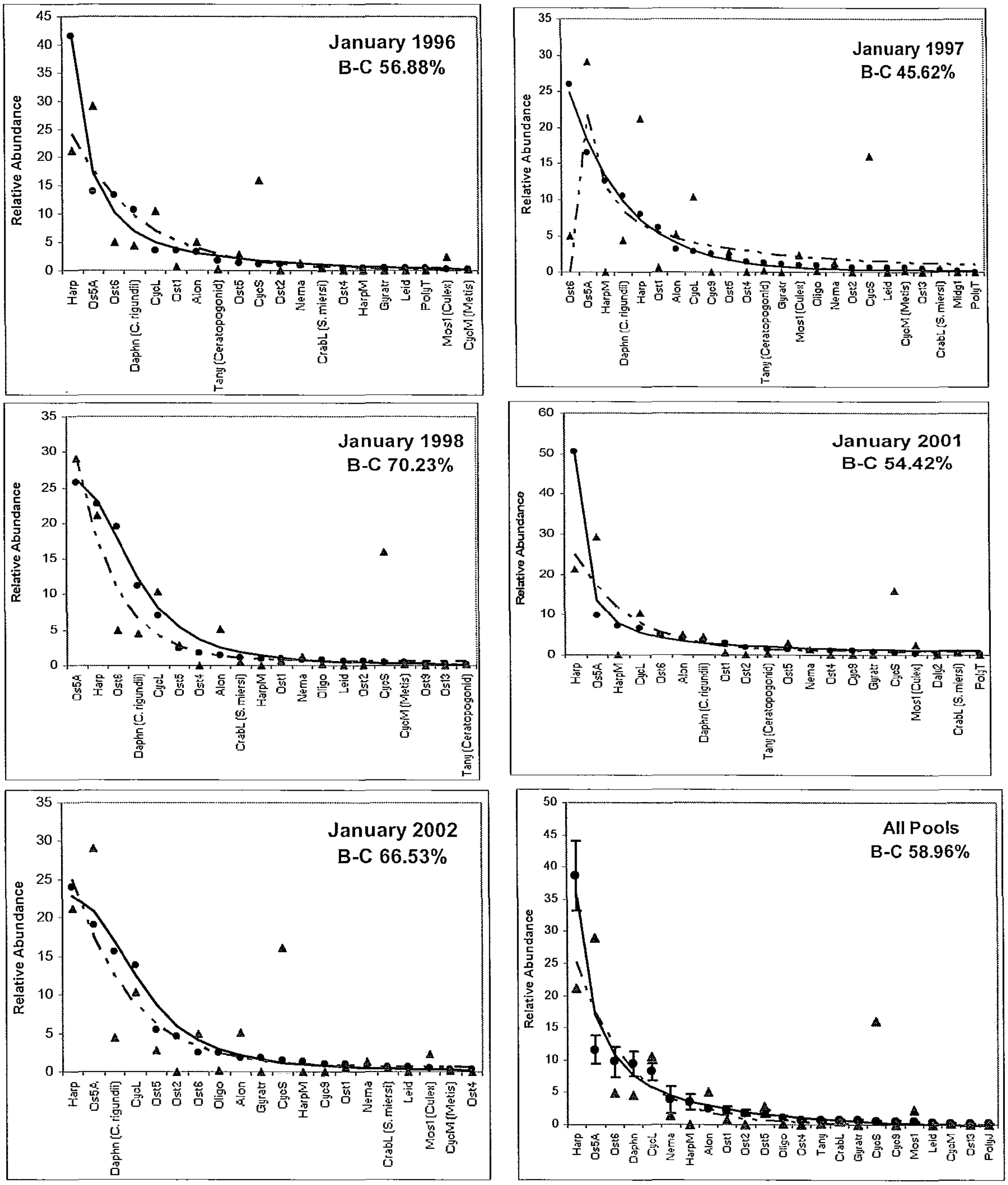

Figure 3-3 continued. Mean relative species abundance and best fit lines from dispersal ▲ ---- and rock pool ● —— communities based on sampling year (ordered by ranked mean relative abundance). Final figure (lower right) compares overall mean relative abundance in pool communities with dispersal abundances (bars indicate standard error).

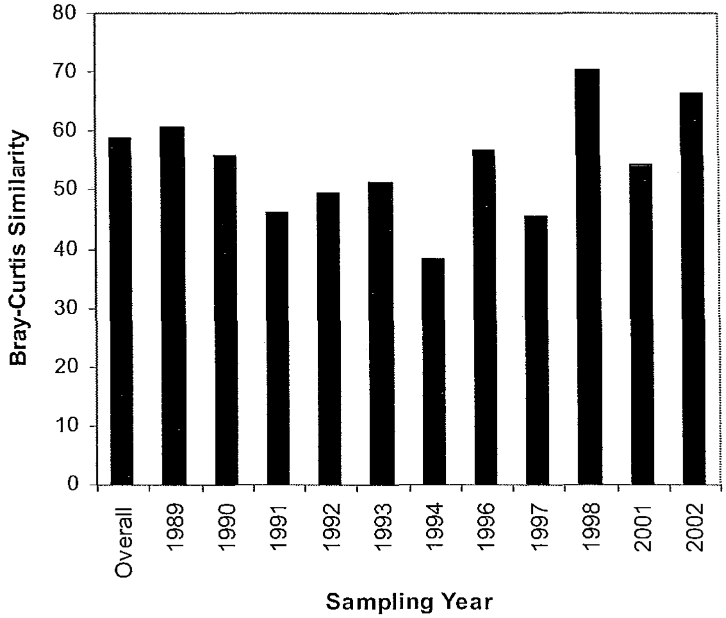

Figure 3-4. Bray-Curtis Similarity measures between composition of dispersers and rock pool community in each sampling year and across all years (overall). Minimum = 38.42% (year: 1994), Maximum = 70.23% (year: 1998).

Although most species were similar in relative abundance between dispersal and rock pool community, this relationship varied for several species and also occasionally differed among dispersal vectors (Figure 3-5 and Figure 3-6). For example, the ostracod species Ost5A dispersed abundantly via flow, but despite the intensity with which it likely reached the rock pools, still appeared unable to successfully integrate into the community and survive (Figure 3-5). Interestingly, Ost5A dispersal via wind was so limited that its abundance was much greater in the rock pools than in the traps (Figure 3-6). Similarly, despite the high dispersal of cladocerans (Alon) by flow, this species was unable to maintain a similar high abundance once in the rock pools (Figure 3-5). It is important to note, however, that despite the differences in abundance of these particular species between dispersal and pool communities, the degree of difference overall was still relatively low (the maximum mean difference in relative dispersal abundance was 39.75 for CycS, see Figure 3-6).

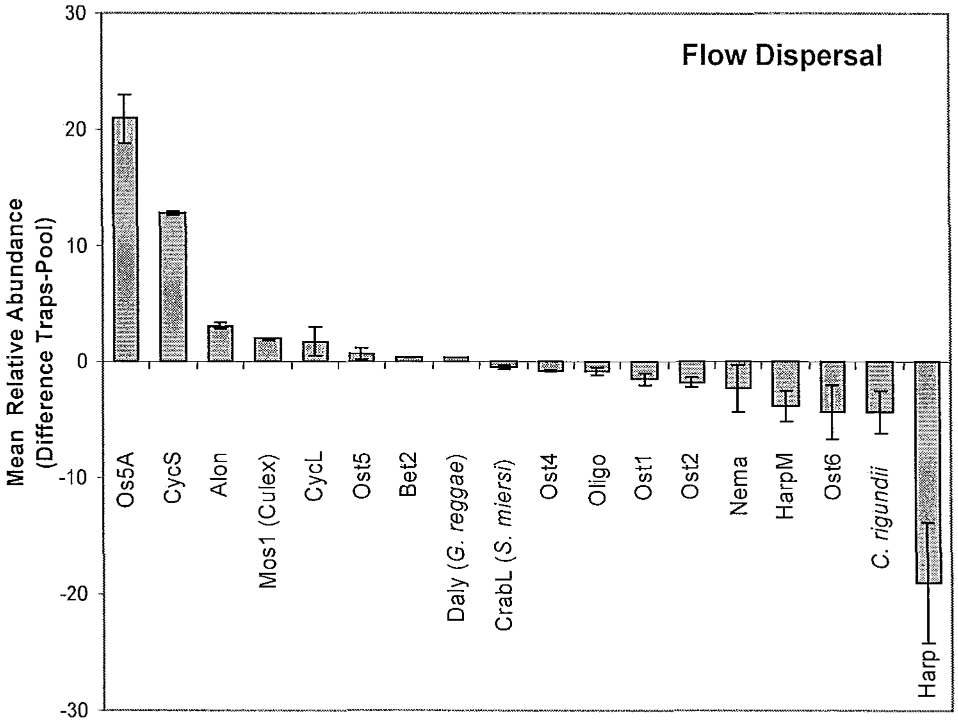

Figure 3-5. Difference in mean relative abundance for each species between flow dispersal and rock pool community. Bars indicate standard error values.

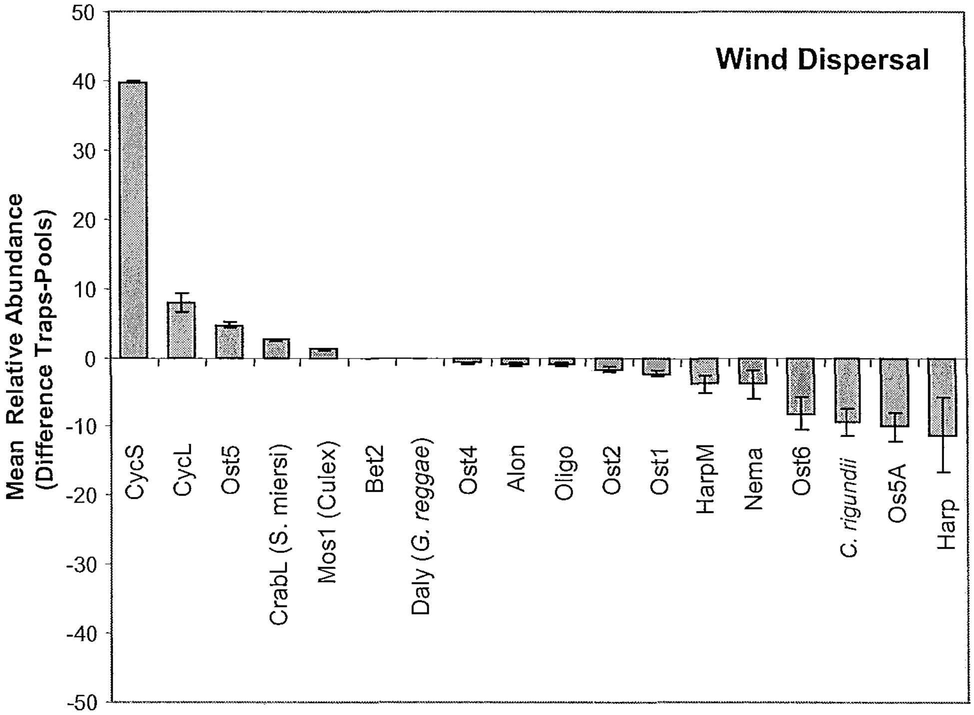

Figure 3-6. Difference in mean relative abundance for each species between wind dispersal and rock pool community. Bars indicate standard error values.

Rock pools colonized over a 30-day period showed differences in community composition between early and late stages of development. Several species that were found to most rapidly disperse to pools (and therefore in highest abundance at sampling periods 1 and 2) were almost entirely eliminated from pools by colonization stage 5, including crab (CrabL) and midge (Midg1) larvae (Figure 3-7). Conversely, harpacticoids and cladocerans (Harp and Daphn) gradually increased in their abundance in pools through time, becoming more pronounced amongst other species by stages 4 and 5. In general, later stages of colonization found more species established. For instance, only three species colonized rock pools at stage 1, but a total of 14 species were present by colonization stage 5. The dispersing community in both wind and flow vectors was most similar in composition to the later stages of colonization (stages 3-5) (Figure 3-8). This similarity was at least in part due to the high number of species present (species richness) in both dispersal vectors and during later stages of colonization in the rock pools.

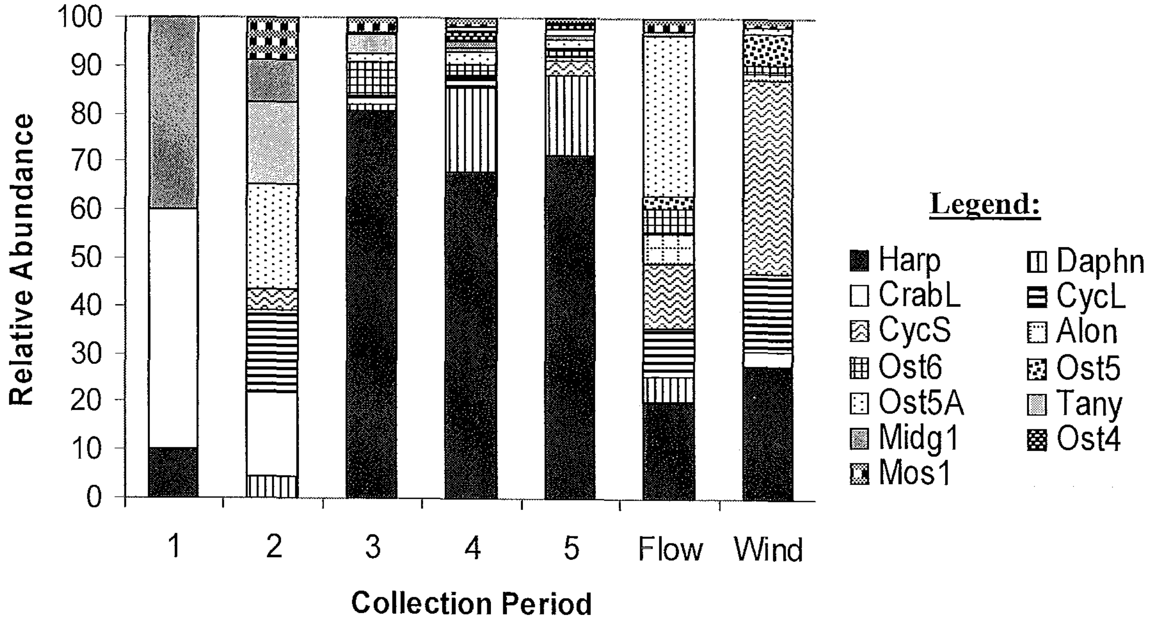

Figure 3-7. Comparison of species relative abundance throughout the stages of colonization (collection period 1-5) to dispersal vector intensity (flow and wind).

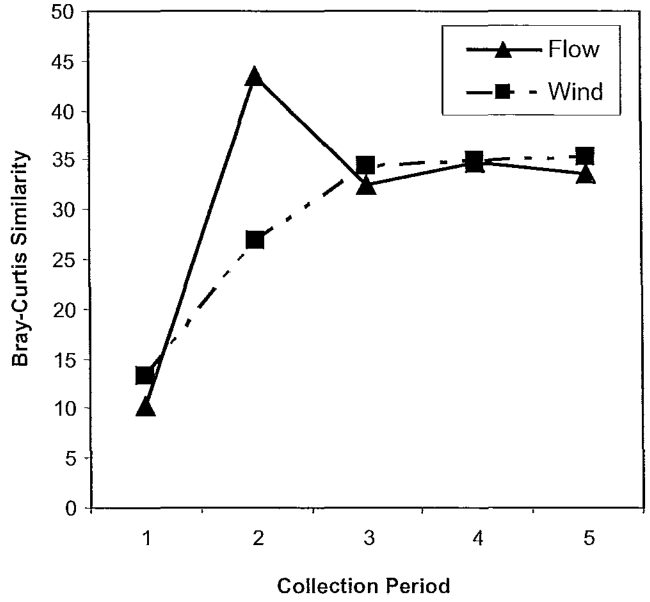

Figure 3-8. Similarity (Bray-Curtis) between dispersal and rock pool community at various stages of colonization.

DISCUSSION

Local communities can be highly dynamic, therefore, understanding the relative influence of regional and local processes in shaping community structure is a difficult task (Bohonak & Jenkins 2003). The results of this study show similarities exist between dispersal and established pool communities, suggesting that long-term community composition reflects short-term dispersal (a regional process that occurs across the rock pool metacommunity). The dispersal of species has also been found to influence community structure in other studies, not only by increasing mean abundance of individuals in a new habitat (Ives *et al.* 2004) but also by increasing species richness, particularly during early stages of colonization (Cadotte & Fukami 2005). Kneitel and Miller (2003), for example, found positive effects of dispersal on both species richness and population abundance in invertebrate communities that developed on the leaves of pitcher plants. Movement of aquatic invertebrate species is also important in structuring newly created pond communities where, despite the similarities in environmental conditions among ponds, divergent communities were formed due to a variation in dispersal/colonization ability of species (Jenkins & Buikema 1998). In this case, dispersal was important in structuring local communities even when it occurred at a low rate.

Despite the overall similarities found between the rock pool community and dispersal, there were several species with a high ability to disperse that were not as equally pronounced in the pools. For example, dispersal by the cyclopoid species, CycS was high; however its presence in the pools remained low relative to other species. The variation in pool versus dispersal abundance may be attributed to two possible mechanisms. Firstly, this may be explained by the overriding influence of local factors in structuring pool community when in the presence of high dispersal. Local processes become a dominant force dictating the structure of a community when dispersal occurs at a high rate and in a short period of time, whereby more individuals are immigrating into a new patch than are becoming extinct (Cohen & Shurin 2003, Jenkins & Buikema 1998, Shurin 2000). In this case, the arriving individuals become controlled by biotic processes such as competition for resources and predator-prey interactions (Jenkins & Buikema 1998). Local factors are necessary for determining species survival and community composition during periods of intense dispersal. Without this process it is likely that all patches in a metacommunity will develop into identical communities, whereby the most easily and abundantly dispersed species will be present in all locations resulting in community homogenization (Jenkins 1995, Kneitel & Miller 2003).

The inability for highly dispersed species in this study to successfully integrate into the rock pool community may also have been the result of a "competition-colonization trade-off" that allow species with differing abilities to disperse and compete to coexist in a single patch. This process involves an evolutionary trade-off between dispersal and competition, whereby poor competitors compensate by being efficient dispersers, capable of quickly colonizing new sites (Tilman 1994). Tilman *et al.* (1997) used a modeling study to show that in the presence of disturbance, species considered to be good competitors were unable to survive random stochastic events and were the first to become extinct. On the contrary, species with high survival rates and a rapid ability to disperse (colonize) were able to survive longer and quickly reestablish populations despite their lack of competitive abilities (Tilman *et al.* 1997). It is possible that several species in this study (for example certain cyclopoid species) fit this model by having a high capacity for dispersal, therefore able to reach the rock pools rapidly and in large abundance. Once in these pools, however, it is possible that abundantly dispersed species were unable to compete with dominant resident species that were more capable of exploiting limiting resources.

Other species in this study (for example harpacticoids) dispersed infrequently via each vector but were still a dominant presence in the pools. It is likely that slow-dispersing individuals of any species allocate less energy to movement across habitat patches, and more towards competition for resources (Ehrlen & van Groenendael 1998). The competition-colonization trade-off, however, is not likely to be the result of only one process. The varying ability for species to disperse across fragmented landscapes and the interactions between these species once together in the new habitat seems to imply that a combination of both regional and local processes are involved. The persistence of species with superior competitive abilities in rock pools may initially lead one to believe that these individuals are at a greater advantage than those with a poor ability to compete, as the former is able to persist and thrive in the community. This is not always the case, however, as colonization experiments show species ability to colonize and survive in the community to be dependent upon the development stage of the community and conditions of the environment (Caceres & Soluk 2002)

In this study, the later stages of colonization had an increasing similarity to dispersal vectors, which may be attributable to a fundamental difference in dispersal ability between active and passive dispersers. Unlike stage 1 of colonization, which contained crab larvae capable of dispersing actively, the dominating species in later stages were mainly passive dispersers (harpacticoid, cyclopoid, *Ceriodaphnia*) that rely on external forces to transport them. Both flow and wind vectors were also found to carry predominantly passively dispersing species, with only a limited number of active dispersers (i.e., crab larvae). The similarity in composition of species between dispersal vectors and later stages of colonization indicates the effectiveness of flow and wind in transporting otherwise slow dispersing species to newly created habitats. The passively dispersed "vector" species in this study, although requiring a greater amount of time to locate and establish into a suitable habitat patch, did very well in terms of survival and population growth once present. Therefore, the ability for vectors to transport passively dispersing invertebrate species is important to the structuring of local communities during later stages of colonization.

Flow and wind were both effective at transporting different aquatic invertebrate species across habitat patches, which has also been the case in similar studies that quantified passive dispersal in a metacommunity (Michels *et al.* 2001, Van de Meutter *et al.* 2006, Vanschoenwinkel *et al.* 2008a, Vanschoenwinkel *et al.* 2008b). Species intercepted in this study also displayed clear differential abilities and strategies for dispersal, where certain species dispersed more effectively than others via different vectors. This observation indicates that not all species have the same ability to move between habitat patches and that the rate of colonization of new communities is variable (Caceres & Soluk 2002, Cohen & Shurin 2003, Jenkins & Buikema 1998, Louette & De Meester 2005). Additionally, choice of observed dispersal vector itself may be important in assessing what rate species move into new habitats and how this can influence local community structure. For example, Ost5A was overrepresented in flow dispersal compared to pool communities, but underrepresented in wind dispersal. This ostracod species may be more effectively dispersed via flow and therefore invest more energy in this mode of dispersal.

In this study, the rock pool community was well represented by the dispersing community, indicating the importance of regional factors (i.e., movement of individuals) on the structure of local communities. Other studies, however, have found regional processes to be overpowered by biotic and environmental factors that dictate species dynamics. Environmental conditions, for example, may be very influential on community structure (Cottenie & De Meester 2003, Cottenie & De Meester 2004, Vanschoenwinkel *et al.* 2007), and abiotic conditions in the receiving patch are inhospitable to some species. Therefore, not all species that disperse to a given location will survive, but only those that are best adapted to specific habitat conditions (Leibold *et al.* 2004). In some cases, despite the high rate of movement of individuals and the highly connected nature of habitat patches, dispersal of species is still a minor influence on local community structure. For example, Michels *et al.* (2001) found zooplankton dispersal intensity to be high between connected ponds, however movement of these individuals between habitats had a minimal impact on the local community (<0.05 % influence) which may have been the result of environmental or biotic factors. Although the influence of local processes are important to the distribution of species and structure of communities, the role of dispersal in the colonization of new sites (Caceres & Soluk 2002) and influence on species richness (Cottenie & De Meester 2004) or species abundance (Warren 1996) cannot be negated. A stable relationship can exist between dispersal and local processes, creating a system with more shared than partitioned dynamics. The composition of dispersal and rock pool communities in this study is likely similar because invertebrate exchange between pools is balanced by suitable local conditions allowing propagules to survive.

Despite the clear similarity between dispersal and rock pool communities, several limitations to this study existed. Temporal scales for both the dispersal experiment and local community surveys were very different: dispersal was quantified during only an 11 day period, while pool communities were assessed annually across multiple years. Dispersal is likely to be a highly variable phenomenon, with fluctuations occurring across multiple time scales including daily, seasonal and yearly variations. Therefore, using a snapshot of dispersal (i.e., quantifying dispersal in a small period of time or on only one occasion), though providing a great deal of information, may not necessarily be an accurate representation of average dispersal (or its magnitude of variation) in the rock pool metacommunity. Furthermore, the spatial scale of sampling both dispersal and the local community in this study were inconsistent. Not all rock pools quantified for dispersal were included in the 49 rock pools that were annually sampled for biotic community. Therefore, it is still possible that the degree of similarity between dispersal and local community may have resulted differently had the same pools been used for both quantifying dispersal and sampling community composition.

Conclusions

Although similarities existed between dispersal and local communities, we cannot conclusively determine which of these two processes (regional versus local) is most influential in structuring local invertebrate communities in the rock pools. We can, however, conclude that regional processes are very strongly expressed in the rock pool metacommunity and are likely to be a highly important factor involved in determining species composition in pools. Furthermore, dispersal via flow and wind is important in the movement of passively dispersing species to newly created habitats and thus is influential to the later stages of community development. Since metacommunities are complex systems, it is likely that multiple factors (dispersal, predation, competition, and environment) work in combination when structuring communities. The influence of local or regional processes may vary based on the type of community under investigation and the time period at which the investigation is taking place (i.e., the relative impact of local and regional processes on communities may fluctuate based on season) (Caceres & Soluk 2002). Even random stochastic events, such as disturbance, has the potential to influence the relative importance of these two processes on community structure (Palmer *et al.* 1996, Shurin 2000).

As previously discussed, the temporal and spatial scale varied considerably between dispersal quantification and surveys of the rock pool community. Future research in this field should investigate the similarity between dispersal and local communities within a similar time scale. Also, relating dispersal influx or efflux from a given patch is best compared to the local community within that actual patch, which can provide a more direct comparison of the influence of dispersal on community composition. Understanding the influence of the competition-colonization trade-off that occurs amongst coexisting species is necessary to understand how species traits and life history influence the relative importance of regional processes on community composition. The results of this study emphasize the importance of dispersal in determining the composition and structure of local communities, while also reinforcing the need to examine systems in terms of regional *and* local processes. The complexity associated with metacommunities reflects the reality that dispersal will rarely be the sole contributor influencing local community structure, and will likely interact with many other processes.

Appendix A

Table 3-1. Summary of curvilinear functions fitted to both dispersing community and pool community relative abundances and their respective R^2 values

Year	**Group**	**Function Type**	**Fitted Function**	**Adjusted R^2**
Overall	Pool	Linear	$y = a+b/x$	96.4
	Trap	Exponential	$y = a*\exp(-x/b)$	55.6
1989	Pool	Exponential	$y = a*\exp(-x/b)$	98.8
	Trap	Exponential	$y = a*\exp(-x/b)$	41.5
1990	Pool	Linear	$y = a+b/x$	98.4
	Trap	Linear	$y = a+b/x^{0.5}$	34.7
1991	Pool	Power	$y = ax\hat{}b$	99.9
	Trap	Exponential	$y = a+b*\exp(-x/c)$	64.5
1992	Pool	Linear	$y = a+b/x^{1.5}$	98.4
	Trap	Linear	$y = a+b/x^{0.5}$	29.6
1993	Pool	Power	$y = ax^b$	99.6
	Trap	Exponential	$y = a*\exp(-x/b)$	51.9
1994	Pool	Exponential	$y = a*\exp(-x/b)$	97.9
	Trap	Linear	$y = a+b/x^{0.5}$	23.4
1996	Pool	Power	$y = a+bx^c$	97.8
	Trap	Exponential	$y = a*\exp(-x/b)$	65.2
1997	Pool	Exponential	$y = a+b*\exp(-x/c)$	99.1
	Trap	Linear	$y = a+b/\ln x$	41.1
1998	Pool	Linear	$y^{-1} = a+bx^3$	98.6
	Trap	Exponential	$y = a+b*\exp(-x/c)$	74.7
2001	Pool	Linear	$y^{-1} = a+bx$	98.7
	Trap	Exponential	$y = a+b*\exp(-x/c)$	57.7
2002	Pool	Linear	$y^{-1} = a+bx\hat{}^3$	97.7
	Trap	Exponential	$y = a+b*\exp(-x/c)$	63.2

Table 3-2. List of scientific species names and their corresponding codes.

Code	**Species Scientific Name**
Alon	*Alona davidii*
Bet2	Beetle larvae (genus species, unidentified)
CrabL	*Sesarma miersi* Rathburn
Cyc9	Copepod (genus species, unidentified)
CycL	*Orthocyclops modestus* (Herrick)
CycM	*Metis* sp.
CycS	*Paracyclops fimbriatus* (Fischer)
Daly (*G. reggae*)	*Gieysztoria raggae*
Daphn (*C. rigundii*)	*Ceriodaphnia rigaudi* Richard
Dipter	Dipteran larvae
Gyratr	*Gyratrix hermaphroditus*
Harp	*Nitocra spinipes* Boeck
HarpM	Copepods (genus species, unidentified)
Leid	*Leidigia leidigi*
Midge1	Chironomid
Mos1	*Culex* sp.
Nema	Nematode sp.
Oligo	Oligochaete sp.
Ost1	*Heterocypris* sp.
Ost2	*Cytheromorpha* sp.1
Ost4	*Candona* sp.
Ost5	*Cypricercus* sp.
Os5A	*Cypridopsis cf. mariae* Rome
Ost6	*Potamocypris* sp.
PolyT	Polychaete T
PolyJ	Dorsovilleid polychaete
Tany	Tanypodid sp.

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Chapter 4

Conclusions

CONCLUSION

Summary and Conclusions

This thesis dissertation took on an integrative and comprehensive approach in the investigation of dispersal and its effects in a rock pool metacommunity. Although previous studies have quantified dispersal of aquatic invertebrates across habitat patches (Michels *et al.* 2001, Vanschoenwinkel *et al.* 2008a, Vanschoenwinkel *et al.* 2008b), the research presented here took into consideration multiple aspects of dispersal that have been previously neglected. In quantifying dispersal, my study took into account the role of species type and life cycle stage in dispersal intensity via wind, flow and animal vectors. Moreover, this study was one of the first to include an investigation into the impact of two major geographic features surrounding the metacommunity (dense vegetation and ocean) on dispersal rate. Finally, I was able to link the movements of species to community composition, relating dispersal rate to the structure of local communities by combining short term dispersal and colonization experiments with long term biotic community surveys.

Through this study, I concluded that species in this system have a high capacity to both disperse and colonize newly created habitats mainly through wind and flow vectors, with minimal influence of external environmental features (connectivity between pools or the presence of vegetation or the ocean). Although juvenile forms were most capable of dispersing, a high degree of variation in the number of dispersers existed between pools, even within a given vector. This suggests dispersal in this metacommunity is not a constantly occurring phenomenon, but instead may be an unpredictable process governed by the current conditions of the pool community itself. My conclusion that aquatic invertebrate species are abundantly dispersed throughout a metacommunity is in sync with others that have found dispersal and colonization to occur rapidly, particularly via wind and flow (Cohen & Shurin 2003, Frisch & Green 2007, Louette & De Meester 2005, Michels *et al.* 2001, Van de Meutter *et al.* 2006, Vanschoenwinkel *et al.* 2008a). Other studies, however, have refuted this concept and argue that these organisms are unable to disperse as rapidly as is claimed through dispersal studies (Bohonak & Jenkins 2003, Brendonck & Riddoch 1999, Jenkins & Buikema 1998, Jenkins & Underwood 1998). These confounding results may be a product of the system itself, suggesting that aquatic invertebrates are not *always* abundantly dispersed, but vary based on species and habitat. The rock pool study site is a densely packed system where pools are very close in proximity to one another. Accordingly, it is possible that dispersal between habitat patches (rock pools) is more successful for the species in this metacommunity, since dispersal distance between suitable habitats is small. This may indicate that invertebrate eggs, dormant life stages or fully grown adults are able to successfully disperse among rock pools and survive, resulting in similar species composition between communities and dispersers.

This study found that the movement of species between habitat patches also had an effect on local community structure as was indicated by the high degree of similarity between dispersal and local communities. A small number of species, however, were disproportionately represented in vectors and pool communities – a pattern which suggested the potential for a competition-colonization trade-off taking place in this system. Highly dispersed species underrepresented in pool communities suggested an efficient ability to disperse but a limited ability to compete and integrate into the community. These results indicate both dispersal and local scale processes are important for structuring communities. Local factors, including environmental conditions or interaction between coexisting species, must therefore also be taken into consideration when attempting to relate dispersal to community composition (Cohen & Shurin 2003, Cottenie & De Meester 2003, Cottenie & De Meester 2004, Hauzy *et al.* 2007).

The need to quantify dispersal and understand the potential factors that can enhance or impede it is necessary for the study of metacommunity theory. The four metacommunity models (patch-dynamics, species-sorting, mass effects and neutral) are all classified and defined based on the degree to which species move between habitat patches (Leibold & Miller 2004, Leibold *et al.* 2004). For example, metacommunities in which dispersal is abundant and therefore influences local community composition follows the mass-effects model (Leibold *et al.* 2004, Mouquet & Loreau 2002, Mouquet & Loreau 2003). Differing species in a system exhibiting mass-effects would only be able to coexist locally through variation in dispersal and competitive abilities (Leibold *et al.* 2004). Species that are poor competitors (compared to others) in a particular patch would be easily able to disperse into another patch where conditions are more suitable. As a result, composition of species will be similar on a regional scale (i.e., across all habitat patches), but differ in each local community (Mouquet & Loreau 2002). In this study, although the impact of abiotic factors on the presence or absence of species was not investigated, dispersal rate was high and a correlation between the relative abundance of dispersing species and pool species was evident. This may suggest the presence of mass-effect, whereby local community structure is influenced by a high degree of connectivity and dispersal among rock pools (Leibold *et al.* 2004). Accurately fitting a metacommunity model to a particular system, however, is not a simple process due to the dynamic nature of systems that vary spatially and temporally in terms of abitoic and biotic components. Moreover, community dynamics and species traits are so complex that often, multiple metacommunity models may be applied to a single system (Leibold *et al.* 2004). A study conducted by Pandit *et al.* (2009) showed that a fundamental difference in the response of generalist and specialist species to the influence of local and regional processes resulted in multiple metacommunity models accurately representing the system based on the degree of species specialization. Since the abundance of generalists was most influenced by regional factors, both patch dynamics and the neutral model were most fitting to this community. The abundance of specialists, however, was more impacted by local processes and therefore best modelled by either mass-effects or species sorting (Pandit *et al.* 2009). Therefore, fitting the most appropriate model to a natural metacommunity would require not only knowledge of dispersal intensity but also an understanding of how species and communities react to local and regional processes.

Limitations and Future Directions

This study quantified dispersal via flow, wind and animal vectors and found a high capacity for dispersal. There were several important factors that were not included in this investigation which may prove to be important in aquatic invertebrate movement in a metacommunity. Fluctuations in weather patterns, for example, may be important in influencing population distribution of species. Wind patterns may be important for dispersing propagules, as shown by Vanschoenwinkel *et al.* (2008a) who found wind direction to influence invertebrate movement in a South African rock pool metacommunity. Graham and Wirth (2008) found branchiopod cysts to be easily transported from sediment even at low wind speeds. Greater intensity winds, therefore, may more efficiently dislodge dormant propagules from sediment thereby allowing wind-borne dispersal. Alternatively, erratic wind patterns and intense rain events may dislodge propagules from the sediment but deposit them into inhospitable habitats resulting in increased mortality. If this should occur, high dispersal of species accompanied by a high mortality rate may suggest dispersal to be a process whose inefficiency prevents populations from growing (Caughley 1977). Understanding to what degree weather patterns can influence dispersal, however, can only be accomplished through regular interval interception experiments performed across multiple seasons. Future studies, therefore, should investigate seasonal variation in dispersal intensity along with how this variation may influence local community structure.

Certain species life history characteristics may also play an important role in successful dispersal between habitat patches, and consequently influence local community dynamics. Abiotic components of the environments were not taken into consideration in this study (i.e. pH, salinity, temperature etc.), all of which may dictate an individual's ability to not only disperse but also survive once having colonized the pools. Although the results presented in this dissertation clearly show the intensity at which species move between habitats, we did not investigate the influence of species traits or the local environment on their dispersal ability or survival once there. Grantham *et al.* (2003) for example, showed that the potential for larvae of marine macroinvertebrates to disperse depended upon both their initial environment and life history characteristics. In this sense, it is important for future research to investigate abiotic conditions of habitats as well as emigration and recruitment rates of different species to determine what degree environmental conditions of the home patch influence dispersal/recruitment ability.

Conservation Implications

Modification of natural landscapes as a result of anthropogenic influences has resulted in fragmentation of habitats, impacting species populations (Saunders *et al.* 1991). Habitat range for many species is reduced, and large populations become subpopulations with lowered abundance and minimal connectivity between optimal habitat (Travis & Dytham 1998). Successful dispersal of species, however, may be able to provide links between smaller populations, preventing local extinction (Brown & Kodric-Brown 1977). This is the case for several different species, including large predatory vertebrates (Sweanor *et al.* 2000) or birds (Serrano & Tella 2003) of which local populations have a high capacity for extinction if not for dispersal to neighbouring patches. This ensures that populations are more protected against extinction than they would be in isolated patches where dispersal is inhibited (Brown & Kodric-Brown 1977). Tracking and quantifying species movements between patches is thus necessary to understand the impact of habitat fragmentation and the loss of connectivity on the survival and success of populations (Bowler & Benton 2005), particularly with respect to endangered species (Simberloff 1988).

The results presented in this thesis dissertation indicate the high dispersal capacity of pelagic aquatic invertebrate species. Small bodied species that reside in the pelagic zone of the rock pools were seen to disperse more abundantly than large bodied benthic species. This indicates the ease with which certain aquatic invertebrates can disperse between water bodies, an important aspect to consider when implementing management plans to control the spread of aquatic invasive species. Moreover, the results presented here show the relevance of dispersal and its interaction with local processes in structuring communities, as well as its potential for preventing local extinction events. Small scale studies performed in easily manipulated systems such as this are necessary in deriving general patterns and principles of dispersal in fragmented landscapes (such as how varying rates of species movements influence community composition). Although the aquatic invertebrates in the rock pools are not at risk species, quantifying their dispersal to understand the impacts on community structure is necessary in order to improve metacommunity theory and accurately apply it to both large scale systems and higher order species. Understanding how, when and in what quantity species disperse between subpopulations is essential in the planning and implementation of conservation initiatives for the protection against extinction of endangered species.

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