IMPORTANCE OF DISPERSAL IN CORAL REEF FISHES

by
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ABSTRACT

Among vertebrates, coral reef fishes are a spectacularly diverse group currently threatened by different forms of human activities. Such a situation has added impetus to the understanding of ecological processes that regulate their diversity. The aim of this dissertation is to assess the role of dispersal in processes that maintain the diversity of coral reef fishes at levels of integration ranging from populations to communities. I started by reviewing existing information of dispersal in coral reef fishes and showing that critical methodological artifacts, biases and alternative interpretations limit any conclusion on the extent to which reef fish populations are "open" or "closed" systems. I then used a variety of approaches and databases to show that during the process of dispersal species interchange propagules among populations (Chapters 2, 3, 4) likely affecting the dynamics of their populations, the geographical extent of their range (Chapter 5) and their presence in communities within the range (Chapter 6). These broad effects of dispersal on diversity patterns suggest that the maintenance of coral reef fish diversity will strongly depend on the extent to which conservation strategies warranty the connectivity that maintain such patterns. This thesis is one of the first attempt to unify principles for the development of a paradigm to apply dispersal theory to different levels of biological organization at different spatial scales.

CO-AUTHORSHIP

Several people have been critical to the development of this thesis and therefore their contribution has been acknowledged in the form of co-authorship in several of the papers produced from this. In all these articles I have been the sole "designer" of ideas and analyzer of data and main writer. My contribution to other aspects of the development of articles such as data collection and writing has varied because of the contribution of others. Their specific contributions are acknowledged below:

Peter Sale: Peter has been crucial to the translation from "spanglish" of most of the papers of this thesis. Our discussions were also important to the development of several null models that I constructed for Chapters 3 and 6.

Ross Robertson: Ross is senior staff at the Smithsonian Tropical Research Institute in Panama. He provided the maps of distribution of most fishes in the Tropical Eastern Pacific from which I got data on species ranges used in Chapter 5. He also contributed to the writing of the paper produced from that chapter.

Paul Chittaro: Paul has been my "partner in crime" in different parts of my work. Together we planned the collection of the data used in Chapter 3. My discussions with him have also been illuminating in the development of several ideas mainly those contained in Chapter 6.

Russell Hepburn: Russ provided data on genotypes of new recruits that I used in Chapter 3. He also instructed me in laboratory protocols that I used for the collection of the adult genotypes analyzed in that Chapter.

Daniel Heath: He is the director of the laboratory that I used for the collection of data for Chapter 3. He also commented on the paper of that chapter.

Jake Kritzer: He commented on the paper from Chapter 6 but also instructed me in the creation of macros that have been used in several of my null models.

Stuart Ludsin: He commented on the paper from Chapter 6.

Derek Hogan: He helped on the collection of field samples used in Chapters 3 and 4.

Paolo Usegglio: He helped on the collection of field samples used in Chapters 3 and 4.

DEDICATION

This thesis is one of the end results of a life of efforts and

sacrifices by my parents Rosa Eugenia and Orlando.

I dedicate this thesis to both of you.

opportunity to develop myself and I am very thankful for that. I also have to thank the members of my committee Jon, Jan and Brian for comments, suggestions, and overall discussions.

The happiness of a man influences his work. And in this regards many, many friends have always been by me. Some few of these are: Paul, Paolo, Derek, Russ, Jake, Stu, Sarah, Chelsy, Misan, Nancy (both Macdonald and Barkley), Fercho, Sacha, Felipe, Juancho, Pili, Michel, and others from that combo; and obviously the ones sharing my heart: Paola, Ibon, and Valeria. During the last part of my career, Audrey has also been important in my motivation to work.

To finish with this section I want to acknowledge all the animals with which I lived while I grew up (observing their behaviors captivated my interest for nature) but also the ones I work with and all those that I have sacrificed for the purpose of this and other projects.

Somebody said…or maybe I just made it up…a man's work is the reflection of his surroundings. I have to say that with the culmination of this thesis I feel like I have had one of the best surrounds in terms of people, animals and environments. For all that thanks God.

STATEMENT OF ORIGINALITY

I declare that all the content in this thesis is original, and that all the research related to it is a product of my own imagination, and that any ideas or quotations from the work of other people, published or otherwise, are fully acknowledged in accordance with the standard referencing practices of the discipline.

TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER 6

CHAPTER 7

LIST OF TABLES

CHAPTER 3

CHAPTER 5

CHAPTER 1: General introduction

A central aim of ecology is to identify processes that shape patterns in biodiversity. These diversity patterns exist at a range of small and large geographical scales and are observed at different integration levels (e.g. populations, communities, ecosystems). The diversity of scales and integration levels has led to the generation of specialized fields in ecology such as population ecology, community ecology, and biogeography among others. Such specialization has been needed for the understanding of highly complex systems but has precluded broad assessment of hypotheses across scales and integration levels (Nee 2002). Such limitation in our broad understanding of biological systems has led to the emergence of a relatively new discipline: macroecology (Nee 2002). One of the main aims of this field is the search for general processes underlying diversity patterns found across scales and integration levels (Blackburn and Gaston 2002). Some examples of such unifying principles include the "Neutral Theory" proposed by Hubbell (2002) and the "Metabolic Theory" proposed by Brown et al. (2004). Both of these "theories" argue to explain several ecological patterns ranging from population to ecosystem scale based on dispersal and energy use alone, respectively. As can be seen, the birth of this new ecological field has not been without alternative arguments. This thesis is intended to build up a unification of principles on the importance of dispersal on several diversity patterns observed in coral reef fishes.

Dispersal is one of the most studied yet least understood concepts in ecology and evolution. Even its definition is not clear, varying among researchers, disciplines and taxa (Clobert et al. 2001). For the specific purpose of this thesis dispersal is defined as the movement of individuals away from a starting point (Mora and Sale 2002), which in reef fishes will be their natal reef. In coral reef fishes, as in many benthic marine

organisms, dispersal occurs mainly during the larval period (Johannes 1978, Barlow 1981). The adaptive reasons of this pelagic phase early in life have been widely discussed. They include advantages of reducing mortality by reef-dwelling predators (Johannes 1978), reducing extinction caused by local disturbances (Barlow 1981) and increasing survival by using oceanic resources that may be limited on reefs (Doherty et al. 1995). Regardless of the evolutionary causes for a pelagic larval period in reef fishes, it is clear that this is the stage most prone to dispersal (but see Mora et al. 2001, for dispersal of adults associated with floating debris). Because the pelagic larval phase is a constituent part of the life cycle of coral reef fishes, any factor associated with this relatively short phase can have profound consequences for several fundamental aspects of coral reef fish biology (e.g., Sale 2002). These include the replenishment of local populations (Caley et al. 1996), range expansions (Jones et al. 2002) and the structure of local communities (Chapter 6). However, such a comprehensive macroecological analysis of diversity patterns in relation to dispersal is still lacking.

This dissertation is a first attempt toward such macroecological analysis in a specific group of vertebrates: marine fishes. The following chapters are expected to provide evidence on the importance of dispersal on diversity patterns observed in coral reef fishes at different spatial scales and levels of integration. I start by describing patterns of dispersal in reef fishes through a review of current knowledge (Chapter 2) and through the collection of empirical data in a specific species of reef fish (Chapter 3). I found that dispersal can be a very variable process and that energetic "penalties" do not seem to apply to larvae that disperse long or short distances (Chapter 4). I discuss how

such variability could account in part for the strong variability in patterns of recruits observed in reef fish populations.

Following the chapters on dispersal among reef fish populations, I determined the extent to which dispersal correlates with species distribution on geographical scales (i.e. range size). In Chapter 5, I assess the effect of dispersal in range size indirectly through the constraining effect of habitat patchiness on dispersal. I assumed that habitat patchiness limits dispersal, and therefore expect range size to decline among species whose habitats increase in patchiness.

If dispersal is enough to connect populations within a species range, then one should expect that species be present within most communities encompassing its range. In turn, this could explain macroecological patterns of species richness and assembly of local communities. In Chapter 6, I determined the extent to which dispersal after speciation explains such macroecological patterns in reef fishes from the Indian and Pacific Oceans. I finalized this dissertation with an integrated discussion of the previous results (Chapter 7).

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CHAPTER 2: A review about dispersal in coral reef fishes

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Dispersal is one of the most important life-history traits involved in the evolution and persistence of species (Shulman 1998, Planes 2002, Victor and Wellington 2000, Caley et al. 1996). The flow of individuals among spatially discrete populations can deeply determine genetic structure and processes of speciation (Rosenblatt and Waples 1986, Doherty et al. 1995, Lacson 1991, Shulman and Berminghan 1995), affect the input and posterior size of local adult populations (Doherty and Williams 1988), extend the geographic range of species (Victor 1991) and influence the structure of local communities (Mora et al. 2003). Such connectivity is also a vital parameter for the successful design of conservation strategies based on protected areas (Robert 1997, Cowen et al. 2000, Sale 2002). However, delineating patterns of dispersal for demersal and benthic marine organisms with pelagic larvae remains a major challenge, both because the dispersing organisms are minute and difficult to track, and because dispersal is driven by multiple complex factors. Because of the potential for transport of propagules by currents, early work assumed that larval dispersal was largely passive, with an extent that was dependent on patterns of water movement and duration of larval life. Thus, local populations were expected to be replenished largely by larvae derived from elsewhere (Ehrlich 1975, Johannes 1979, Schetelma 1986, Roberts 1997, Williams et al. 1984)

Fish of coral reefs typically have larval lives that are measured in weeks or months, but their larvae are capable behaviorally of participating actively in their own dispersal [Kingsford et al. 2002, Leis and McCormick 2002, Armsworth 2000, Armsworth et al. 2001). These attributes are compatible with various patterns of dispersal (Armsworth et

al. 2001), but reef ecologists have increasingly tended to emphasize that fish larvae remain in the vicinity of the natal reef (e.g., Warner and Cowen 2002). Whereas the view in the late 1970s was that reef-fish populations were broadly open, the consensus has shifted to view them as substantially closed (e.g., Warner and Cowen 2002 and associated paper). This change relies on a variety of evidence, including physical oceanography near reefs (Cowen 2002), larval behavior (Kingsford et al. 2002), tagging studies (Jones et al. 1999, Swearer et al. 1999) and genetic patchiness among geographically separate populations (Planes et al. 1998, Planes 2002, Taylord and Hellberg 2003). It is also supported by some recent models of dispersal (Cowen et al. 2000), and conforms to theoretical expectations that marine populations must achieve closure by developing life histories that retain offspring as 'members' of the reproductive unit (Sinclair 1988, Strathmann et al. 2002). Here, I critically analyze the evidence concerning dispersal in reef fish, identifying limitations in techniques and in data interpretation. At present, these limitations prevent an accurate assessment of the extent to which reef fish populations are replenished by local or exogenous recruits.

Scales of dispersal

The description of any system depends largely on the chosen dimensions of space and time. At biogeographical spatial scales, all populations are closed, whereas at meter scales, any population of organisms with pelagic larvae is likely to be open. Whereas most of the ecological investigations of fish on coral reefs were done at single local sites in the 1970s, it is now common to do research at sets of sites 10s of km apart (Jones et al. 1999, Swearer et al. 1999); some studies are undertaken on scales of 100s of km or more

(Planes et al. 1998, Bernardi et al. 2001). Therefore, the change in emphasis concerning the degree of openness of reef fish populations might be due partially to a shift in the scale at which they are routinely viewed. Nevertheless, although spatial and temporal scales at which studies are done can have important effects on how ecological patterns and processes are perceived, this is not the main limitation in studies of larval dispersal in reef fish.

Evidence for dispersal in reef fish

Tagging studies

By using tags to differentiate larvae from different populations, two studies have provided quantitative evidence for self-recruitment in coral reef fish. Over three months, Jones et al. (1999) used tetracycline to tag ~10 million embryos of the damselfish *Pomacentrus amboinensis* around Lizard Island, Great Barrier Reef, Australia. Analysing the otoliths of 5000 recaptured late-stage larvae; they found 15 tagged larvae and calculated that between 15% and 60% of the recruits to that island were locally produced. Unfortunately, this imprecise estimate means that this population might be either almost entirely open (85% of recruits from elsewhere) or moderately closed (60% of recruits produced in situ). In addition, their estimate of self-recruitment might also be biased upwards. Most effort for collection of larvae was done on the windward side of the island, a location where a retentive convergence zone occurs owing to complex patterns of water flow (Milicich 1994, Leis 1986). A broader distribution of sampling effort around Lizard Island might have led to a lower estimate of retention.

The other study of larval tagging, by Swearer et al. (1999), was based on the assumption that larvae developing in coastal waters have distinctive signatures (e.g., in growth and otolith microchemistry) compared with larvae developing in less productive open water. During three summer months in 1992, Swearer and colleagues found that ~70% of *Thalassoma bifasciatum* wrasse recruits to St Croix, US Virgin Islands, presented signatures of coastal development. They suggested that these were evidence that larvae remained close to home and were recruited to the natal population. One limitation, noted by the authors, is that, if the time spent in open water was minimal, larvae might have coastal signatures, despite coming from outside St Croix, (conversely, animals produced and settled locally might have off-shore signatures after spending most of their larval life in off-shore waters). Based on the minimum number of days necessary for a larva to produce a coastal signature, Swearer and colleagues predicted that up to 50% of larvae with coastal signatures might have been produced on upstream reefs (i.e. elsewhere in the Lesser Antilles). This estimate implies that, during those three summer months, as few as 35% of the recruits of this wrasse to St Croix might be produced locally. This study also shows that during the autumn of 1992, most recruits to this island presented signatures of open ocean development. Rates of recruitment in the sites sampled by Swearer et al. tend to be similar during summer and autumn [~1.1 and 0.95 fish m2 respectively (Caselle and Warner 1996)]. Thus, the overall extent of retention might be less than that implied by Swearer and colleagues.

Overall, the study by Jones et al. (1999) confirms, and that by Swearer et al. (1999) strongly suggests, that these local populations of reef fish retain some larvae, but might also receive significant recruitment from other locations. The generalization of

these results requires additional studies, which should involve a range of hydrographical regimes, including simpler coastlines with long-shore currents (Palumbi 1999). Although these two studies have motivated renewed interest in reef fish dispersal, their results provide only tentative support for retention as the motor driving the replenishment of reef fish populations.

Genetic comparisons

Variation in genetic markers, such as allozymes and mitochondrial DNA (mtDNA) among sub-populations (commonly quantified using fixation Index Fst) has been used to track patterns and levels of migration in reef fish (Shulman 1998, Planes 2002). However, several aspects of genetic studies become crucial when addressing questions of reef fish demography. Demographic studies require, for instance, that markers are able to drift distinctively among populations at temporal scales that are relevant to population replenishment (usually months). Allozymes and mtDNA are, however, not very sensitive to drift, particularly in large populations and over short periods (Avise 1994). Results based on allozymes and mtDNA are usually interpreted as a reflection of long-term processes, not on timescales that are relevant to population demography (Shulman 1998, Avise 1994). Microsatellites are promising markers that are not yet used for demographic studies of reef fish. They present high levels of polymorphism, and are probably neutral to selection. Their high rates of mutation also make them suitable for tracking genes on ecological timescales (Shulman 1998, Avise 1994, Hellberg et al. 2002).

In interpreting genetic data, it is also important to consider the forces that are influencing genetic structure. A common assumption is that genetic structure reflects a

balance between gene flow and drift. Yet, selection can be a major force maintaining genetic differentiation even when gene flow is occurring (Williams et al. 1973). In coral reef fish, rates of mortality are high, with up to 70% occurring during the first few days after settlement (Mora and Zapata 2002). This mortality is, in many cases, associated with variations in attributes, such as body condition (McCormick 1998), size (Mora and Zapata 2002), and possibly speed (Leis and Carson-Eward 2001), and with habitat characteristics (Beukers and Jones 1997), suggesting that there might be substantial and differential selection among populations at and shortly after settlement. In fact, comparative studies between allozymes (selective markers) and mtDNA (neutral markers) show different results (Avise 1994, Shullman 1998, Planes 2002) suggesting that there are effects of selection on allozymes and raising caution when interpreting data based on these markers [currently 73% of the available data for reef fish (Planes 2002)]. Thus, genetic differentiation might support the existence of closed populations (genetic differences arising through drift) or open ones (genetic differences arising because of differential selection in spite of gene flow). Genetic differences might also suggest the existence of barriers to dispersal, even though populations on each side of the barrier remain otherwise open (Davis et al. 1981, Terry et al. 2000).

At equilibrium (no selection included), as few as 1–10 effective migrants per generation will eliminate genetic differences between populations with 95% confidence (Shulman 1998, Planes et al. 2002). Thus, genetic similarity among populations might suggest either that populations are broadly open (with substantial migration), or largely closed (genetic similarities arising because of the exchange of only a few individuals). Although the growing numbers of genetic studies on coral reef species suggest that

dispersal is not usually as extensive as has been believed (Planes 2002), answers using

genetic data are not yet conclusive. More studies, particularly with rapidly evolving

markers, are needed.

Larval behavior

Recent studies have highlighted the fascinating and diverse spectrum of behavior in reef

fish larvae. Larvae of coral reef fish have good swimming abilities and sensory systems

that enable them to control their dispersal (Appendix 2.1, Leis and Stobutzki 1997,

Armsworth 2000, Stobutzki 2000, Armsworth et al. 2001, Kingsford et al. 2002, Leis and

McCormick 2002). However, it is not yet known whether they do this, and if they do,

whether they use their abilities to enhance retention or dispersal. Although there is a clear

need to include larval behaviors when modelling larval dispersal (Armsworth 2000,

Armsworth et al. 2001, Stobutzki 2000, Wolanski et al. 1997), it is also clear that larval

behavior (and other biological data) exhibits substantial interspecific variability. For

instance, the pelagic period ranges among species from >100 to <10 days, and a handful

of species lack it completely (Leis 1991, Leis and McCormick 2002). Swimming abilities

also vary broadly among species (Appendix 2.1). Furthermore, swimming abilities,

sensory systems and behaviors, such as vertical migration (Appendix 2.2), all develop

during the larval period (Leis 1991, Fisher et al. 2000, Job and Bellwood 2000, Leis and

McCormick 2002), so that even species with appropriate dispersal behavior achieve this

capability at different ages, and have a period of passivity early in their life. Given the

large set of physical oceanographical features with advective and retentive characteristics

(Appendix 2.3), this behavioral variability ensures that the extent to which larvae are

retained will vary among locations (because of spatial differences in oceanographical

conditions), and among species within a locality (because of interspecific variability in

responses to the physical environment). Recognition of this cross-species and cross-

locality variation must be part of the debate on the nature of dispersal in reef fish

(Bellwood et al. 1998, Roberts 1998, Sale and Cowen 1998).

Dispersal models

In the absence of a direct way to track reef fish larvae through their entire pelagic phase,

modeling approaches have been used to infer patterns of larval dispersal (Roberts 1997,

Cowen et al. 2000, Schultz and Cowen 1994). By considering the complex set of

variables affecting the larval period (Figure 2.1), models can be used to explore the

importance of particular features, and to make predictions about larval dispersal.

Nevertheless, a characteristic common to most models to date is the omission, or gross

simplification in modelling of many factors affecting the larval period, with the result

that model outputs cannot yet be assumed to predict dispersal accurately. Roberts' (1997)

model, for instance, has been strongly criticized, because it did not include larval

behaviors, such as swimming ability (Bellwood et al. 1998) or vertical migration (Sale

and Cowen 1998). Schultz and Cowen (1994) included larval duration as a variable in

their model, but did not consider larval swimming abilities. Capable swimmers could

either enhance or reduce advection effects owing to other model components (Armsworth

2000). Cowen et al. (2000) included values for diffusion based on passive particles, but

the larvae of many reef fish species have demonstrated some ability to aggregate actively

in the pelagic environment (Leis and McCormick 2002, Warner et al. 2000). In this case,

the pattern of diffusion could be very different to that modeled under passive dispersal (Okubo 1980). Cowen et al. (2000) also had to estimate larval mortality rates. Although larval mortality is generally assumed to be high, there are very few empirical data available. That larvae of reef fish can be collected several 100 km away from the nearest reef (Leis 1984, Victor 1987, Clarke 1995) proves that some fish larvae survive and do disperse far into the ocean, in numbers that are sufficient to show up in small plankton nets (Victor and Wellington 2000). The model developed by Cowen et al. does not show this, which suggests either that the model might be unrealistic or that the distribution of larvae in open waters is far patchier than has been supposed.

The difficulty of simulating the complex world in which larvae move (Figure 2.1) explains many of the discrepancies between empirical data and model predictions. For instance, Roberts (1997) predicted a general pattern of larval dispersal over long distances, based on very simple models of long-term average surface currents in the Caribbean. This pattern was directly contradicted by the known pattern of spread of the *Diadema* pathogen in this region (Lessios et al. 1984) suggesting that, because the pathogen was presumably passively dispersed, even a model of passive dispersal requires more detailed hydrodynamics than that used by Roberts (Sale and Cowen 1998). Cowen et al. (2000) built a more complex physical model of circulation in the eastern Caribbean coupled to estimates of larval mortality and diffusion, and predicted that the concentration of larvae falls essentially to zero at a distance of only 140 km from the larval source. They argued that this indicates that substantial dispersal of larvae is unlikely, although other studies have shown that long-distance dispersal does sometimes occur (Leis 1984, Victor 1987, Clarke 1995). The problem of modelling the physical

environment adequately is also shown in a recent study that compared local

concentrations of coral larvae observed around Bowden Reef (Great Barrier Reef) with

concentrations predicted from a model of dispersal using the local hydrography (Oliver et

al. 1992). Coral larvae are passively dispersed at the surface, yet this study found

virtually no correlation between these two data sets. Modelling is an important technique

that is capable of yielding novel insights, but we need to be aware of the limitations of

models, and of our limited knowledge of the factors that they model.

Evolutionary advantages of dispersal

Selection is the major force driving life-history traits of species. A trait is usually favored

by selection due to the "advantages" (in terms of survival and reproduction) that it

provides. Rationally one can presume the existence of a given trait (e.g., retention or

dispersal) based its "advantages". The problem, however, is that there is not a clear

unique advantages for either retention or dispersal. Retention has been speculated to be

favored by selection because it increases the chance of the larvae of finding places where

fish can survive and reproduce as noted by the fact that their parents reproduced in that

particular reef (Strathmann et al. 2002). Yet retention might also increase the risk of

inbreeding and competition among relatives (Cloberg et al. 2001). Similarly, high levels

of self-recruitment might be speculated to be necessary for local population maintenance

(Cowen et al. 2001). However, if the rate of foreign recruits is not enough to populate

distant locations then species might be overexposed to extinction as result of localized

disturbances (Cloberg et al. 2001). Costal waters might provide better food supply for

larvae, and therefore, keeping close to shore might favor larval growth. This, however,

does not provide a disadvantage for dispersal because larvae can still disperse long-distances along continental shores. Dispersal might also reduce exposure of recruits to parasites infecting local populations, but it might also be the case that it results in exporting larvae from areas with no parasites to areas with many (Strathmann et al. 2002). The evolution of dispersal is complex and unfortunately there many alternative arguments for its "benefits", which are notoriously difficult to reject. It might also be the case that neither retention nor dispersal are deterministic but rather a stochastic trait (Cloberg et al. 2001).

Other approaches

The temporal link between local production of propagules (spawning) and subsequent recruitment has also been used to deduce the pattern of dispersal leading to recruitment at particular locations. The rationale for this approach is that, if larvae are exogenous, local patterns of spawning will not be correlated with local recruitment, whereas if larvae are self-recruited, patterns of spawning and recruitment should be coupled (Danilowicz 1997). Although the relation between spawning and recruitment has been explored extensively (Meekan et al. 1993), using this relationship to infer the pattern of dispersal is novel (Danilowicz 1997). Examples showing coupling or lack of coupling between spawning and recruitment are broadly reported (Meekan et al. 1993); however, what these tell us about dispersal is unclear. Coupling of spawning and recruitment patterns might result when spawning is synchronized closely over a broad spatial scale, even if recruits are dispersed widely. Such large-scale synchrony in reproduction might occur for reef fish that spawn at similar times [i.e. specific moon phases (Robertson et al. 1988)] at

many locations. Neither does decoupling inevitably imply broad dispersal. Danilowicz and Sale (1999) used a model to show how plausible patterns of mortality during larval life can decouple local production and subsequent recruitment even when recruitment is entirely endogenous. The presumed link between spawning and recruitment will not easily advance our understanding of dispersal.

Observations of colonization of previously unoccupied areas [e.g. Eastern Pacific localities by Indo–Pacific species during El Niño events (Robertson and Allen 1996)], or of recruitment of fish after rafting in association with floating objects (Mora et al. 2001), demonstrate larval advection and prove the existence of open populations. Because of the long distances travelled in these cases, these events might have an important role in determining genetic connectivity and/or processes of speciation in reef fish. However, because these sorts of events are rare [i.e. annually in the case of drifting (eg. Mora et al. 2001) and every several years in the case of El Nino (Robertson and Allen 1996)], they probably do not contribute markedly to the replenishment of fish populations. Conversely, the existence of endemic species on remote archipelagos confirms that at least some fish populations achieve sufficient local recruitment to maintain their densities (Robertson 2001). Of course, endemic species might still be structured as open systems within the local region in which they occur (Danilowicz 1997).

Passive drifters have been used extensively to suggest potential trajectories of larval transport. They reveal considerable complexity in the paths that are possible when several drifters are released simultaneously at a single site. However, because such devices ignore larval behaviors, and because these behaviors are considerable in many

species (Appendix 2.1), drifter studies seem unlikely to be useful in defining paths travelled by larvae.

Conclusion and future directions

Among reef fish ecologists, the perception of reef fish populations as broadly open systems has shifted to a currently widespread emphasis on the retention of larvae at natal reefs. This dramatic shift has been made with important but as yet limited new evidence. Our review of evidence concerning reef fish dispersal shows that these limitations are serious and that, at present, the answer to whether reef fish populations are open or closed must be regarded as unknown. We can go further and state with confidence that there is not one answer. Different species in different places will be structured into more or less open populations depending on the capabilities of the species, the physical features of its environment, and the spatial and temporal scales at which the question is posed.

Our uncertainty about patterns of larval dispersal reveals a crucial gap in knowledge of coral reef fish. Apart from the intrinsic interest in the capabilities of these animals, if marine protected areas (MPAs) are to have any impact on conserving these species, or the management of fisheries based upon them, we need to know more about the spatial and temporal scales at which populations function, and the extent of connectivity among populations. Otherwise, there is no biological basis on which to decide the size, positioning, or number of MPAs that are required to protect these species.

In addition to new work using microchemical, genetic and other novel tagging approaches for defining the scales (both in space and time) and extent of larval dispersal among populations, major efforts are required to expand our knowledge of the behaviors that are actually used, and the cues to which reef fish respond during their larval period. The work completed is a good beginning, and the challenges in extending it are many, but scientists and funding agencies must see this as a crucial area of research and support it accordingly. Finally, we need to encourage multi-investigator, multidisciplinary approaches combining physical oceanography, larval behavior, tagging studies and sophisticated modeling approaches, because this gap in knowledge cannot be filled by one approach alone.

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Figure 2.1. Factors affecting larval dispersal. The path taken by a larva might lead to it returning to the natal reef or dispersing to a more or less distant site. The path taken is determined by a mix of factors, which act synergistically over the larval period to determine the dispersal of each member of a larval cohort. Where and when eggs or larvae enter the water column, their quality, and the food resources and predators that they encounter will affect survival, condition and growth rates. Condition and growth rates will determine the development of swimming and sensory abilities, and these will determine how larvae respond to the physical environment and to any cues from reefs. We can predict considerable variation among cohorts and locations in the paths travelled, as well as among species, but we cannot yet do much more. We lack information on most of the factors operating.
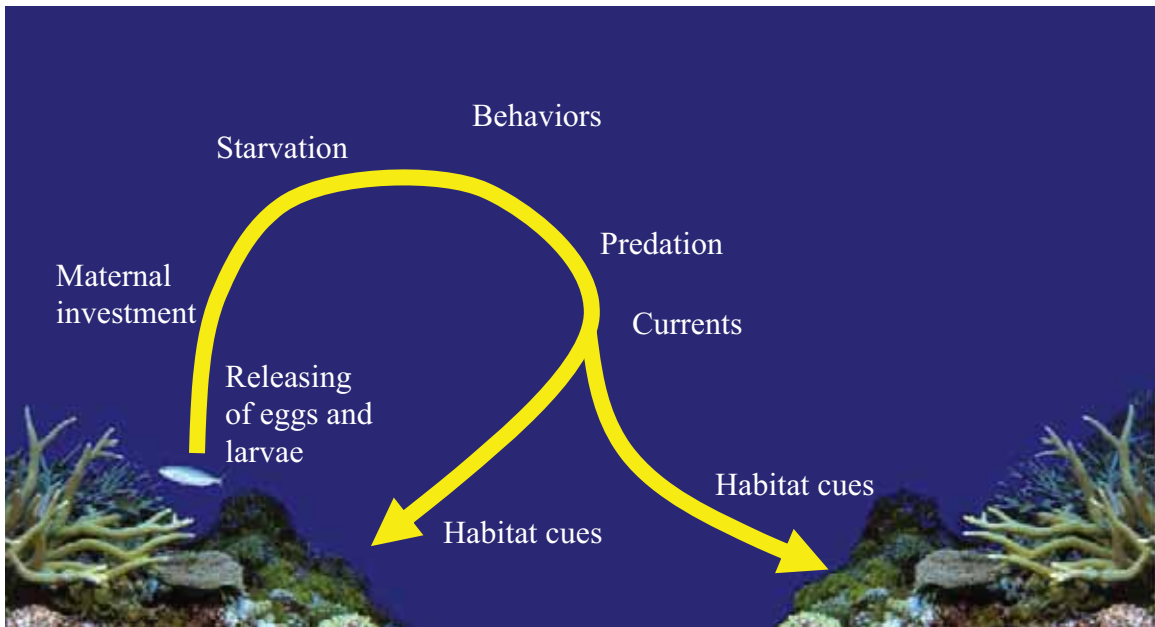
Appendix 2.1. Navigation by reef fish larvae: what do we really know?

Late-stage larvae can orient toward different reef stimuli (Leis and McCormick 2002) and are capable of independent movement [they can swim at field speeds of between 5 and 50 cm s^{-1}, 20 cm s^{-1} on average (Leis and Stobutzki 1997), and long enough to cover between 4 and 200 km before exhaustion depending on the species (Leis and Stobutzki 1997, Dudley et al. 2000)]. It seems probable, therefore, that reef fish larvae can navigate over large distances and towards reefs (Leis and Stobutzki 1997, Dudley et al. 2000, Leis and McCormick 2002, Fisher et al. 2002). However, there are several problems with this conclusion.

1. How reliably can fish orient towards reefs? Reef sound has been suggested to be the most probable stimulus for orientation (Montgomery et al. 2001, Leis et al. 2002, Myberg and Fuiman 2002). Reef sounds are measurable at least 10 km from a reef (Montgomery et al. 2001), but physiological evidence suggests that larval hearing is not sufficiently acute to detect them (Myberg and Fuiman 2002), and field results show little behavioral response at distances of >1 km (Leis et al. 2002). During the first pelagic day (when the eggs or larvae still lack swimming abilities), at a common current of 20 cm s−1, a larva could be carried as far as 17 km away from a reef; thus, early in their life, larvae could be transported far from cues with which to locate reefs, especially the natal reef, and would therefore be unable to navigate. In addition, the ability to detect a cue does not automatically mean that the cue can be used reliably to determine a direction to find its source (Montgomery et al. 2001).

2. What is the true extent of their swimming abilities? Laboratory studies have shown that late-stage larvae of many reef fish species are good swimmers, but how well do these skills transfer to natural conditions? First, published records of distances swum might be biased. They might overestimate abilities, because, in nature, it is unlikely that a larva will swim until exhaustion, as they do in the laboratory. They might also underestimate abilities, because the larvae are not fed during most experiments [one recent study shows that feeding does enhance swimming ability in one species (Fisher and Bellwood 2001)]. There are also several reasons to believe that larvae do not swim continuously in the field. Swimming represents an energetic cost (Stobutzki 1997), which has negative effects on survival subsequent to settlement and recruitment (McCormick 1998). Movements of larvae (e.g. when they are swimming) are also a cue for predators that detect the movements and turbulence of their prey (Nielson and Perry 1990). Finally, significant displacement might increase the chance of encounters with predators.

3. Are ecologists of reef fish overestimating the importance of swimming capabilities to dispersal? Fisher and Bellwood (2002) have recently found that the sustainable swimming time decreases exponentially with increasing speed. They suggest that the abilities of larvae to avoid advection are limited to speeds below a threshold that can be maintained for a period of between 12 and 48 h. This is 7 cm s^{-1} in the late-stage larvae of the damselfish *Amphiprion melanopus* or 50% of its U-crit (maximum swimming speed maintained for 2–5 min). U-crit in late-stage larvae of other species is 30 cm s^{-1} on average [n=five species, (Fisher et al. 2000, Stobutzki and Bellwood

1994] and 4.7 cm s^{-1} in newly hatched larvae [n=three species (Fisher et al. 2000)]. This suggests that currents of 7 cm s^{-1} that last more than 12–48 h might not be overcome by late-stage larvae of *A. melanopus*; for other species, on average, late-stage larvae might be able to overcome currents slower than 15 cm s^{-1}, whereas early-stage larvae might cope with currents of only 2.4 cm s^{-1}. A substantial component of the spectrum of current speeds that are likely to be encountered by larvae (5–60 cm s^{-1} is usual) will be too strong to be actively resisted, even if the larvae could orient themselves to swim against it.

4. There are also problems inherent to behavioral research, because behavior is a particularly labile characteristic of an animal's phenotype. Are larvae that were caught, held overnight and then placed into experimental apparatus or back in the ocean with divers in attendance likely to behave as they do naturally?

5. Our final concern is about data interpretation. At present, all larval behaviors have been analysed with reference to dispersal. However, navigation to locate settlement places is just one, although the final crucial, objective of a larva during its pelagic stage. Larvae must also swim and orient towards food and away from predators.

Appendix 2.2. Vertical migration of larvae and consequences for larval dispersal

Reef fish larvae have been suggested to respond behaviorally to vertically stratified flows in ways that result in retention close to shore and to the source population (Appendix C, Cowen 2002). This suggests that vertical migration is a response to different current directions at different depths. Certainly, many other physical or biological stimuli (e.g., light, temperature, food availability and predation) have been proposed to explain vertical migrations in fish larvae (Nielson and Perry 1990, Hendrix et al. 2001, Diebel et al. 2000) and, in these cases, resulting horizontal displacement because of vertical migration would be random, depending on local currents.

There are two ways in which vertical migration could result in predictable horizontal transport. Either the species lives predominantly in regions where vertically stratified flows are a widespread and consistent feature that reliably transport water at specific depths towards shore, or the animal has the capacity to measure current directions and act accordingly. In the first case, evolution of a fixed pattern of vertical migration is probable, regardless of the cue used, and results in reliable transport (perhaps back to the natal shore). In the second case, more flexible migration behavior could be used, the larva positioning itself in the layer of water travelling in the preferred direction. Although, this second case is seductive, it requires much of the larva. There are no fixed references in the pelagic realm, so the larva would need the equivalent of a geographical positioning system plus knowledge of where to go. Such a navigation system might exist, but there is not yet evidence for it. Still, the recent discoveries of a magnetic receptor in a fish (Diebel et al. 2000), and geomagnetic orientation in several vertebrates, suggest that there might be a common and sophisticated mechanism of

orientation among these animals (Brown 2001). Even if vertical migration is an adaptive

response used by larvae to return home, it does not appear to be a widespread adaptation

among reef fish. Vertical distributions are diverse among species. Some species can be

homogeneously distributed throughout the water column (Hendriks et al. 2001), whereas

others present aggregated distribution at particular depths, sometimes depending upon the

thermocline (Nielson and Perry 1990, Leis 1991). Finally, premises about vertical

migration require some caution, because they are based on quite limited field studies of

larval distributions. Reliable data about larval distributions are few because reef fish

larvae are usually sparse, they are difficult to sample, no sampling device can capture all

developmental stages (Leis 1991), and few studies have used multiple sampling devices.

Most standard sampling designs also appear to underestimate the abundance of larvae in

offshore locations (Clarke 1995).

Appendix 2.3. Oceanographic features and potential consequences for larval dispersal

Although oceanographers cannot yet specify the patterns of water movement in close proximity to complex topography, such as reefs, there is a range of small to mesoscale oceanographic features that provide opportunities for predictable transport of larval fish.

Eddies (rotary currents) can form downstream of reefs and can aggregate buoyant particles and prevent broad dispersal. Within such eddies, reef fish larvae have been found in large abundance at some locations [e.g., Florida Keys (Lee et al. 1994), Hawaii (Lobel and Robinson 1986) and Johnston Atoll (Boehlert et al. 1992)] but not at others [e.g., Myrmidon Reef, Great Barrier Reef (Williams and English 1992)]. Such eddies also vary in their persistence (e.g., a few days at Johnston Atoll or several months in the Florida Keys), further suggesting that the influence of eddies on larval dispersal will vary.

Upwelling systems are probably important if the larvae exhibit vertical migrations. An upwelling occurs usually where winds move superficial water in an offshore direction and as a result deep water flows in an opposite onshore direction. By descending in the water column, advected larvae can be returned to the reefs. However, because reef fish species vary in vertical migration behavior (Appendix 2.2), the effects of upwellings on patterns of larval dispersal are species-specific. Moreover, because similar physical processes can result in downwellings (when superficial waters move onshore), an inflexible larval response to depth can also result in advection.

Surface slicks resulting from convergence zones created by complex interactions involving the thermocline, internal waves, opposing currents and winds might also affect

larval dispersal (Kingsford and Choat 1986). Converging currents can accumulate organisms around slicks that flow in the direction of the wind. Such circumstances can act to accumulate diffused larvae offshore into aggregate lines that flow onshore (Kingsford and Choat 1986), or alternatively prevent diffusion of eggs and larvae and move them from onshore to offshore localities.

Currents flowing along the coast can disperse larvae of a given population along the coast reinforcing advection or can generate peripheral eddies that entrain fish larvae and favor retention (Hutchins and Pearce 1994, Limouzy et al. 1997, Possingham and Roughgarden 1990).

CHAPTER 3: Connectivity among populations of a Caribbean reef fish

Introduction

Dispersal is an important but poorly understood aspect of the biology of marine species with pelagic larvae (Sinclair 1988, Hanski 1999, Clobert et al. 2001, Leis 2002, Mora and Sale 2002, Palumbi 2003). As the concern over anthropogenic impact on marine species grows (Hutchins 2000, Jackson et al. 2001), understanding dispersal has become particularly critical for the success of fishery management and conservation policies (Palumbi 2003 Roberts 1997, Cowen et al. 2000, Sale 2002). In reef systems, however, the extent to which populations are connected through larval dispersal is unclear. While early studies assumed larval dispersal to be passively determined by mean field currents (e.g., Roberts 1997) so that populations would be open to the immigration of larvae from elsewhere (Ehrlich 1975, Johanness 1979, Scheltema 1986), recent work has provided evidence of some degree of self-recruitment (Jones et al. 1999, Swearer et al. 1999), suggesting that populations can be closed (Warner and Cowen 2002 and associated papers). Here we use an approach that assigns new recruits to their natal populations based on comparison of their genotypes and therefore allows tracking their pattern of dispersal and connectivity among reefs.

Methods of assignment of new recruits to natal populations

In coral reef fishes and other marine organisms, the reproduction of benthic and sedentary adults produces numerous planktonic and potentially highly dispersive larvae. Since dispersing larvae will have genotypes very similar to those of their natal population, one can determine the population from which new recruits are most likely derived by matching their genotypes to reference genotypes for different populations in a

given region. Reference populations are obtained by analysis of adults collected at different sites within the region. Here we apply this approach to the bicolor damselfish (*Stegastes partitus*) in the MesoAmerican Barrier Reef System (MBRS) (Figure 3.1). We use the genotypes of 647 new recruits collected at 38 sites along the MBRS and of 200 adults collected at 20 of those sites (Figure 3.1) (see Appendix 3.1).

Testing of assignment methods

Several tests are available that will assign individuals to their most likely natal population on the basis of their genotypes (Waser and Strobek 1998, Cornuet et al. 1999, Bank and Eichert 2000, Piry et al. in press). Most of these tests, however, vary in their reliability depending on the particular conditions of the studied system [e.g., levels of genetic structure, polymorphism of the markers, sample sizes, number of markers used, departure from Hardy-Weinberg equilibrium (Cornuet et al. 1999)]. Therefore, evaluation of the reliability of the results of such tests is critical, particularly in cases like ours, where not all potential parental locations were sampled.

To evaluate the reliability of the different tests, we used the genotypes of 60 *S. partitus* embryos collected while they were still being cared for by their parents at two of the sampled sites in Turneffe Atoll and Banco Chinchorro (five embryos per clutch, six clutches per site) (Figure 3.1). We expected the different tests to assign these embryos to their respective natal sites in Turneffe and Banco Chinchorro. We used the 24 different combinations of assignment tests in Geneclass (Piry et al. in press) (i.e. eight different criteria based on Frequency, Bayesian or Distance methods, each with three different Monte-Carlo algorithms) plus the likelihood method available in Whichrun (Bank and

Eichert 2000). The results indicate that assignment was more accurate for many methods than if embryos were assigned randomly (Figure 3.2). However, there remained large errors in assignment. On average, embryos from Turneffe were assigned to locations 58 km away from their natal reef while embryos from Banco Chichorro were assigned to locations 87 km away.

There are several factors that could account for this error in assignment, including the limited number of microsatellite loci (N=8), the low parental sample sizes and the low levels of genetic differentiation among populations (e.g. Fst<0.1 among pairs of adult populations). However, we found that when most tests agree upon the location of an embryo's origin, this location was relatively close to its actual natal site (Figure 3.3). When more than 21 tests similarly assigned an embryo to a given location, this location was on average 19 km and 47 km away from the actual natal site in Turneffe and Banco Chinchorro, respectively (overall error=25.8 km, SE=5.8). An average error of 25.8 km represents 5.7% of the spatial domain analyzed in this study suggesting that the degree of consensus among assignment tests (i.e. more than 21 tests) is a reliable criterion of successful assignment for our system.

Connectivity among populations inferred from assignment methods

Out of 647 new recruits used, only 62 were assigned to natal populations using the set criterion (Table 3.1). The frequency distribution of dispersal distances of these recruits shows a peak of larvae settling at distances <30 km away from their natal sites (i.e. 27% of the recruits), few dispersing for the entire scale of the studied system (i.e. ~1.6% of the

recruits dispersing >360 km) and interestingly a second mode of recruits settling at
intermediate distances (i.e. ~180 km, ~21% of the recruits) (Figure 3.4a).

We are aware of two potential factors that could affect this pattern of dispersal
distances: 1) a bias that could arise if in our sampling design some distances between
natal and recruitment sites were more common than others, and 2) the error with which
our criterion assigned new recruits to their natal populations. We corrected for the bias by
subtracting the entire set of distances between natal and recruitment sites in our design
(solid line in Figure 3.4a) from the raw data on dispersal distances. The resulting
histogram (Figure 3.4b) shows clearly that in comparison to the set of distances in our
design there was a greater proportion of new recruits dispersing both small (<30 km) and
intermediate distances (~180 km). Similarly, the gap between those two peaks of
dispersal distances was characterized by a lower proportion of recruits than expected by
the set of distances in our design (Figure 3.4a-b). In short, the bimodal pattern of
dispersal distances is not an artefact set by the spatial distribution of our sampled sites.
To assess the effect of the assignment error we use the mean assignment error identified
previously in the assignment of the embryos (i.e. 25.8 km) to generate a normal
distribution of distances around 0 km that was used to simulate 95% confidence limits
around the dispersal distances of the 62 new recruits. The resulting distribution (dotted
lines in Figure 3.4a-b) shows that the precision of the assignment criterion is sufficient to
confirm that the bimodal pattern of dispersal distances is real.

Directions of larval dispersal were predominantly northeast and southwest with few
larvae dispersing northwest or southeast (Figure 3.4c, Figure 3.1). We remove any
sampling bias from this pattern by subtracting the frequency distribution of directions

between all natal and recruitment sites in our sampling design from the observed

frequency distribution of dispersal directions. The resulting distribution (Figure 3.4d)

shows that the peak of dispersal northeast and southwest of the natal reef is due mainly to

the northeast-southwest orientation of the MBRS (Figure 3.1). Nevertheless, this analysis

indicates a deficit of larvae dispersing southwest and an excess dispersing northeast

(Figure 3.4d), which could be due to the predominant northeastern flow of the Caribbean

current in the MBRS (Sheng and Tang 2004, Thattai et al. in press).

In the analyzed recruits the average pelagic larval period, quantified as the number

of daily growth rings between the core and the settlement mark in the otoliths, was 29

days (SD+/- 3.1). In the MBRS, the mean northeastern flow of the Caribbean current is

~50 cm s^{-1} (Sheng and Tang 2004, Thattai et al. in press). Assuming passive dispersal, a

simplistic model of this current can put these recruits at locations ~1253 km away from

their natal reef at the end of their larval life. Our results show that this is hardly the case

and suggest that larval dispersal is affected by a more complex interaction of factors.

Recent studies have shown that the Caribbean current does sometimes generate a low

speed gyre in the lower part of the MBRS (Sheng and Tang 2004, Thattai et al. in press),

and there is extensive evidence for vortexes leeward of islands, stratified water flows,

and small peripheral eddies in similar current systems (Cowen 2002, Mora and Sale

2002, Sponougle et al. 2002). This contrast between small-scale retentive hydrodynamic

processes and advective ocean currents likely plays an important role in determining the

bimodal shape of dispersal distances. However, the variety of trajectories of dispersal

observed in this study (Figure 3.4c), and the fact that larvae from the same or nearby sites

showed different dispersal paths (Figure 3.1, Table 3.1) suggest that the effect of larval

behavior must also be considerable. Given that these hydrodynamic features vary in space and time (Cowen 2002, Mora and sale 2002, Sponougle et al. 2002, Sheng and Tang 2004, Thattai et al. in press) and that larval behavior varies within and among species (Leis 2002, Mora and Sale 2002) it is clear that we should expect substantial heterogeneity in patterns and scales of dispersal among reef fishes (Kinlan and Gaines 2003). The tremendous variation in recruitment patterns (as the final result of dispersal) usually observed in coral reef fishes (Doherty and Williams 1985) could also be explained by such variability in dispersal patterns.

Resolving the issue of connectivity among populations of marine species is of intrinsic interest not only for fundamental science but also for the effective management and conservation of these species. Our study suggests, at least for the bicolor damselfish within the MBRS, that population dynamics can depend on both local (~30 km scale) and regional (180 km scale) sources of recruits. These data also point to the fact that management decisions aimed at the conservation of reef fishes in the MBRS will require international partnerships among the countries having jurisdiction in this system if they are to be effective.

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Figure 3.1. Patterns of connectivity among reefs of the MesoAmerican Barrier Reef System (MBRS). For display purposes, connectivity is shown among clusters of sites. The heads of the arrows were scaled by area to the percentage of new recruits arriving at a given cluster from different source clusters. The sampled sites are indicated with stars for embryos, filled and open circles for new recruits, and open circles for adults.
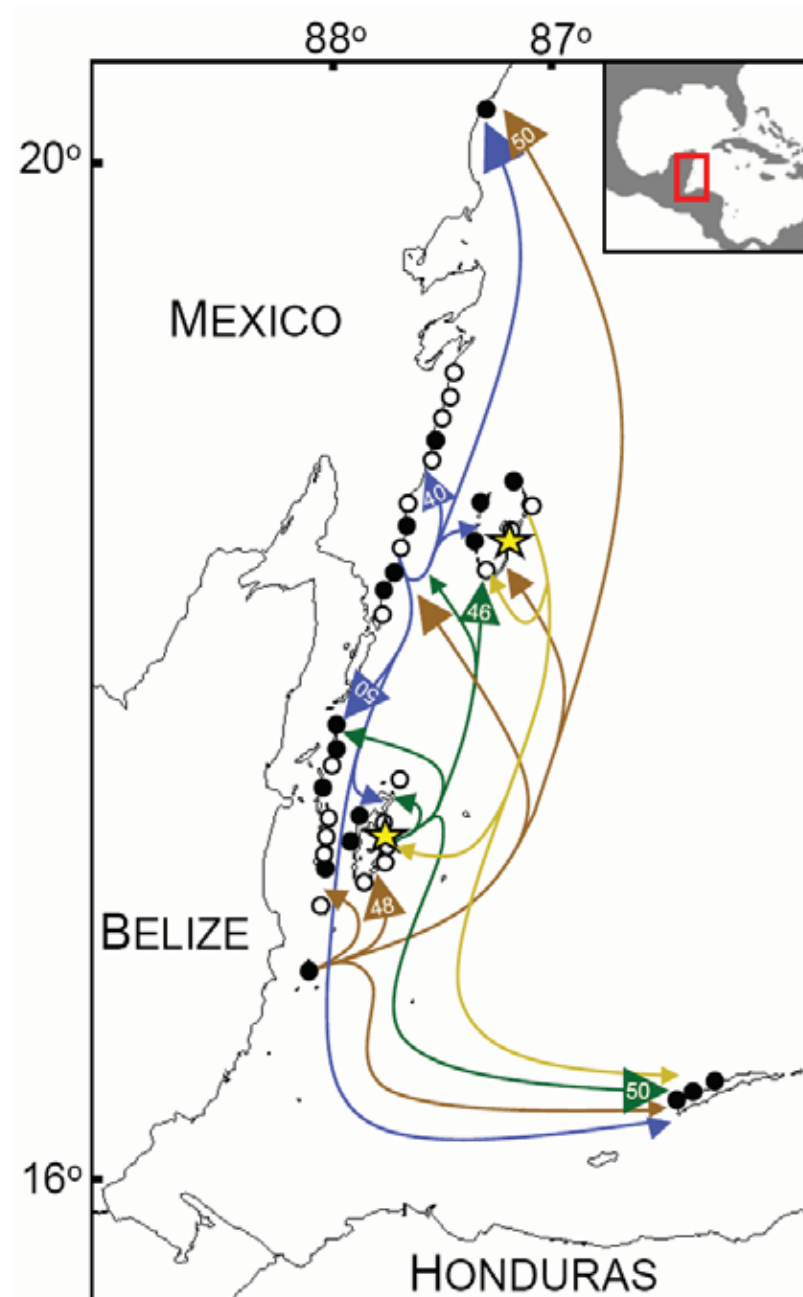
Figure 3.2. Validation of assignment tests. Here we use the genotypes of embryos collected at two sites in Turneffe Atoll (a) and Banco Chinchorro (b) and expect the different methods to assign these embryos to their actual natal sites. The assignment error for each test was quantified as the distance between the natal site of each embryo and the site to which it was assigned by the given test. We also performed a null model that quantified the distance between the natal site of each embryo and any randomly selected site from our sampled sites. 95% confidence levels of 500 replications of this null model are indicated with dotted lines. The criteria of the different tests are indicated directly on the graph while the names of the three Monte-Carlo algorithms are indicated as C (Cornuet), R (Rannala) and P (Paetkau).

Figure 3.3. Consensus among tests in the assignment of embryos from Banco

Chinchorro (open bars) and Turneffe Atoll (filled bars). Note that as the consensus

among tests increases the assignment error decreases. Bold vertical lines indicate 95%

confidence levels of the null model described in Figure 3.2.
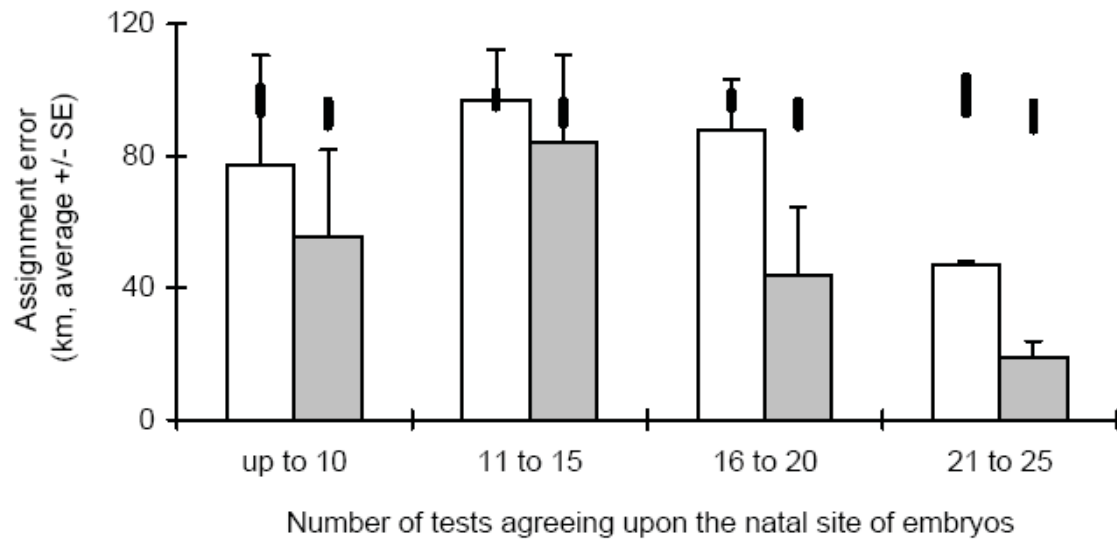
Figure 3.4. Frequency distribution of dispersal trajectories of new recruits in the MBRS. The continuous line in each plot indicates the respective distribution of distances and directions between natal and recruitment sites in our sampling design. Panels (b) and (d) remove any sampling bias in the observed distributions of dispersal distances and directions by subtracting from them the respective distribution of distances and directions in our sampling design. Negative values in the resulting distributions indicate a deficit of new recruits dispersing at those distances (b) or directions (d). The potential effect of assignment error on the distribution of dispersal distances was taken into account by adding to each of the 62 distances of dispersal a random distance drawn from a normal distribution centered on 0 km, and containing 50% of the observations between +/- 25.8 km (i.e. the average assignment error). Confidence levels (95%) based on 500 repetitions of this procedure are shown as dotted lines in plots a-b.
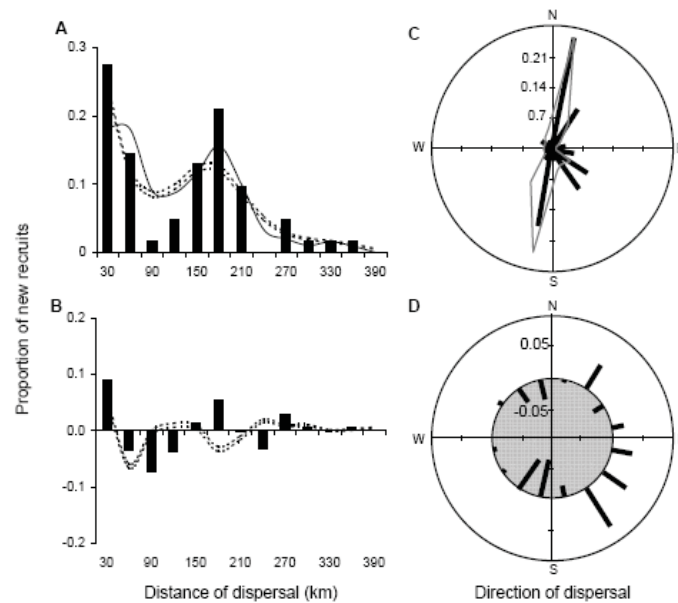
Table 3.1. Data on distance and direction of dispersal of new recruits whose natal populations were reliably identified. Locations in the Belize (BBR) and Mexican Barrier Reef (MBR) were enumerated from South to North while sites in Turneffe Atoll (TA) and Banco Chincorro (BC) were enumerated clock wise starting at the northern locations (see Fig. 1). Sites at Rodatan (RO) were enumerated from west to east.

Number of tests that agree in the location	Location of hatching	Location of recruietment	Distance of dispersal (km)	Direction of dispersal (degrees)
21	BBR-2	MBR-1	127.1	8.8
22	BBR-2	MBR-2	137.2	8.8
22	BBR-2	RO-1	180.6	115.3
21	BBR-2	BC-6	184.1	21.2
21	BBR-2	TA-3	33.2	43.2
21	BBR-2	BC-5	169.5	21.7
22	BBR-4	TA-4	24.9	82.4
22	BBR-4	TA-4	24.9	82.4
22	BBR-4	BC-4	144.9	29.1
22	BBR-5	BBR-8	32.8	2.1
21	BBR-5	MBR-3	120.1	14.1
21	BBR-5	MBR-6	150.4	13.5
21	BBR-5	TA-5	24.6	140.2
22	BBR-5	TA-6	8.2	93.1
22	BBR-5	TA-5	24.6	140.2
23	BBR-5	TA-4	24.8	108.5
22	BBR-6	TULUM-1	315.9	11.8
21	BBR-6	TA-3	28.8	117.2
22	BBR-6	TA-5	33.4	151.6
21	BBR-6	TA-6	13.7	141.6
21	BBR-6	TA-2	23.9	94.9
22	BBR-8	TA-3	43.4	144.8
22	BBR-8	BC-5	115.9	33.7
21	BC-2	BC-5	26.3	236.6
22	BC-3	RO-1	256.9	159.4
25	BC-3	TA-2	136.8	204.2
24	BC-4	BC-2	34.4	33.4
22	MBR-10	BBR-9	151.7	198.1
22	MBR-10	MBR-12	20.1	15.7
22	MBR-11	BBR-1	250.3	193.3
21	MBR-11	TA-1	168.0	187.7
22	MBR-12	RO-3	337.9	162.3
21	MBR-4	TA-2	118.6	183.0
21	MBR-6	MBR-2	40.1	195.4
23	MBR-6	MBR-3	30.3	191.0
22	MBR-6	TULUM-1	176.0	9.6
21	MBR-6	TA-1	119.9	181.6
22	MBR-6	TA-2	138.7	184.2
21	MBR-6	TA-4	155.1	184.0
21	MBR-6	TA-4	155.1	184.0
21	MBR-6	BC-5	33.6	117.1
21	MBR-6	RO-2	286.0	153.8
21	MBR-8	MBR-2	60.2	197.7
22	TA-1	RO-3	190.3	139.1
22	TA-2	RO-1	182.8	128.2
22	TA-2	BC-5	128.6	18.7
22	TA-2	BC-6	143.2	18.4
22	TA-2	TA-7	11.2	278.3
21	TA-2	BC-2	150.3	25.1
21	TA-3	BBR-4	27.9	253.3
23	TA-3	MBR-10	188.8	7.2
21	TA-3	MBR-11	198.4	8.0
22	TA-3	RO-2	170.0	128.7
21	TA-3	TA-1	30.4	10.1
21	TA-3	TA-7	18.2	315.0
22	TA-3	TA-7	18.2	315.0
22	TA-3	TA-5	18.9	213.4
22	TA-3	TA-2	11.6	351.8
22	TA-3	BC-2	160.3	22.8
21	TA-3	RO-1	174.5	125.6
22	TA-4	BC-3	152.2	21.8
22	TA-4	BC-2	165.7	22.8

Appendix 3.1. Sampling collections

This chapter included collection of adults and new recruits from 38 different locations from the MBRS. Their geographical positions are provided below. 10 adults were collected from each of 20 of these locations and between 10 and 25 new recruits from each of the 38 locations. All collections were done during the summer of 2003. New recruits were collected with clove oil and hand nets and adults with spear guns. All samples were preserved in 95% ethanol until they were analyzed in the laboratory.

Geographical coordenates where embrios (E), juneviles (J), and adults (A) were collected.

LOCATION	Site	Site code	LAT (DEGREES)	LONG (DEGREES)	GROUP COLLECTED
Tolum	1	TO1	20.23	87.45	J
Turneffe	1	TA-1	17.59	87.75	J , A
	2	TA-2	17.42	87.81	J , A
	3	TA-3	17.32	87.79	J , A
	4	TA-4	17.27	87.81	E , J , A
	5	TA-5	17.17	87.89	J , A
	6	TA-6	17.34	87.95	J
	7	TA-7	17.44	87.91	J
Banco Chinchorro	1	BC-1	18.75	87.29	J
	2	BC-2	18.66	87.23	J , A
	3	BC-3	18.55	87.30	E , J , A
	4	BC-4	18.40	87.40	J , A
	5	BC-5	18.52	87.43	J
	6	BC-6	18.65	87.40	J
Belize Barrier Reef	1	BBR-1	16.89	88.06	J
	2	BBR-2	17.10	88.00	J , A
	3	BBR-3	17.30	88.04	J
	4	BBR-4	17.24	88.04	J , A
	5	BBR-5	17.35	88.03	J , A
	6	BBR-6	17.44	88.03	J , A
	7	BBR-7	17.54	88.05	J
	8	BBR-8	17.64	88.02	J , A
	9	BBR-9	17.70	88.01	J
	10	BBR-10	17.78	88.00	J
Mexico Barrier Reef	1	MBR-1	18.23	87.83	J , A
	2	MBR-2	18.32	87.81	J
	3	MBR-3	18.40	87.77	J
	4	MBR-4	18.49	87.75	J , A
	5	MBR-5	18.58	87.73	J
	6	MBR-6	18.67	87.72	J , A
	8	MBR-8	18.84	87.65	J , A
	9	MBR-9	18.92	87.62	J
	10	MBR-10	19.00	87.58	J , A
	11	MBR-11	19.09	87.54	J , A
	12	MBR-12	19.18	87.53	J , A
Rodatan	1	RO-1	16.38	86.48	J
	2	RO-2	16.34	86.57	J
	3	RO-3	16.27	86.60	J

Appendix 3.2. DNA Analyses

DNA was extracted from caudal fin clips using the Wizard$^®$ Genomic Purification Kit

(Promega Madison, WI) following the manufacturer's protocol. Eight microsatellite

markers developed for *Stegastes partitus* (Williams et al. 2003) were used in this study.

Polymerase chain reactions (PCR) were carried out in reactions with 10X PCR Buffer (10

mM Tris-HCL (pH-8.4) 50mM KCL), 2.5 mM $MgCl_2$, 200 μM dNTP's, 0.05 μg of each

primer, 0.5 units DNA Taq polymerase, and 50-100 ng of genomic template DNA (25 μL

total reaction volume). PCR's were performed on an MJ Research Tetrad DNA Engine

model PTC-0225 (MJ Research Waltham, MA) with the following reaction profile: 2

minute initial denaturation (94^oC); followed by 35 cycles of 1 minute denaturation

(94^oC), 1 minute annealing, 1 minute extension (72^oC); 3 minute concluding extension

cycle (72^oC). Amplifications were analyzed using a CEQ 8000 automated DNA

sequencer (Beckman-Coultier, Fullerton, CA). Approximately 5% of all PCR reactions

were replicated to verify repeatability.

     Two of the eight markers were not in Hardy-Weinberg equilibrium but their

removal did not improve the assignment of the embryos to Turneffe and Banco

Chincorro. In addition to this, distance-based methods are less affected than frequency

and Bayesian methods by departures of Hardy-Weinberg equilibrium (Cornuet et al.

1999). Therefore, we include the entire set of eight loci in our full analysis.

Appendix 3.3. Null models

Null model for the assignment of embryos to their natal populations

The results of this model are expected to provide a background of comparison for the reliability of assignment of the different assignment tests. In this section different assignment tests were used to assign embryos of known origin to potential natal populations based on their genotypes. The reliability of the methods was evaluated by comparison of the actual assignment distances (i.e. the distance between the natal site of
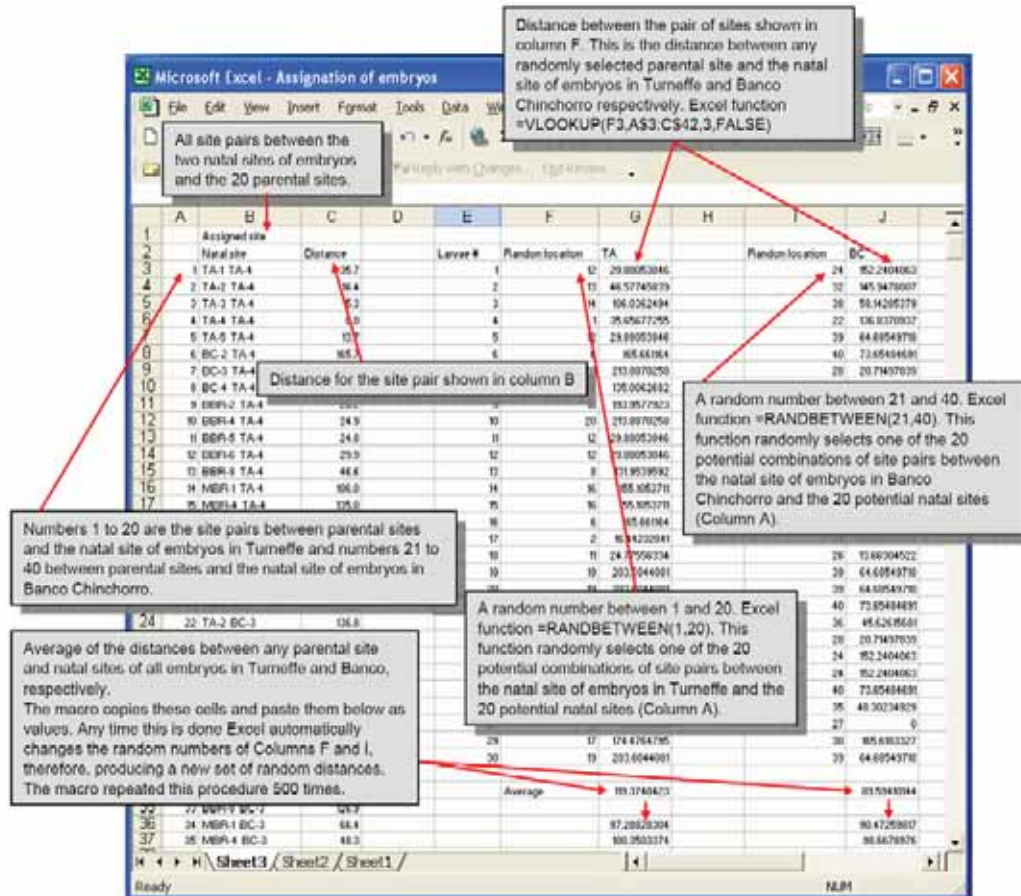
Window 3.3.1. Description of the model for random assignment of embryos from Turneffe and Banco Chinchorro among parental sites.

each embryo and the site to which it was assigned by each of the different methods) and

null distances. Null distances were determined with a null model in which each embryo

was assigned to a site randomly drawn from the 20 potential parental sites. The outcomes

of 500 repetitions of this model are shown as 95% confidence limits in Figure 3.2. The

model was designed in Excel (see window 3.1) and repetitions done with a macro (see

window 3.2).
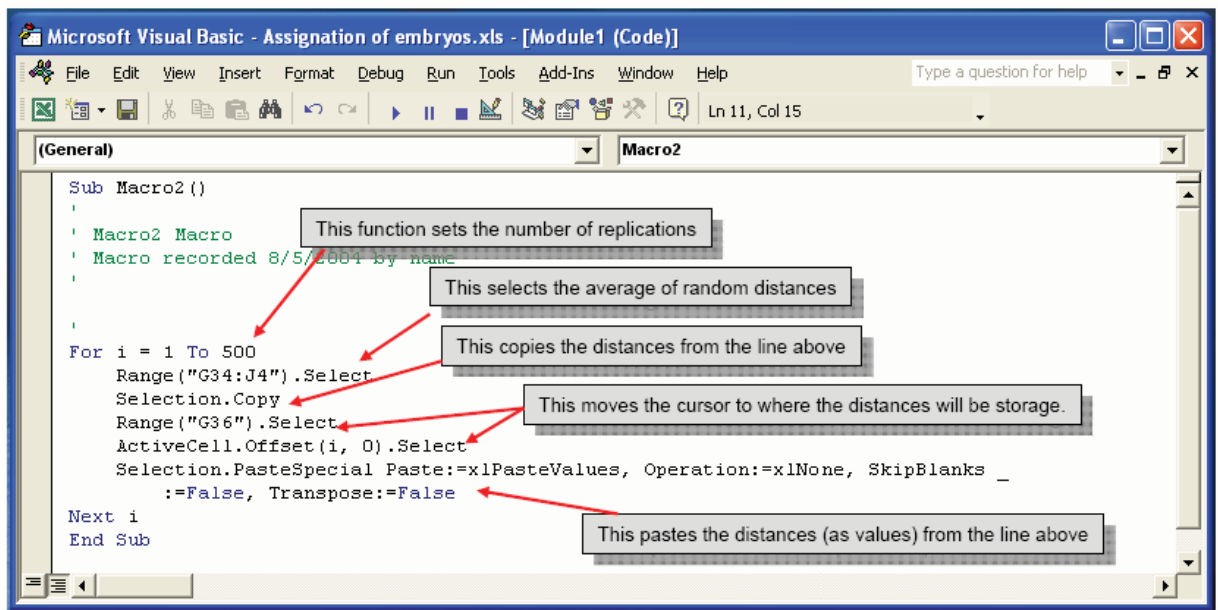
Window 3.3.2. Description of the macro for random assignment of embryos from Turneffe and

Banco Chinchorro among parental sites

Null model for the inclusion of the assignment error

From the assignment of embryos with known origin it was found that the best criterion of

assignment still contained an average error of 25.8 km. This model assesses the extent to

which such error affected the pattern of dispersal distances observed. Here I generated a

normal distribution of distances with 0 mean and with 50% of the observations being

between +/- 25.8 km. This distribution was generated in Excel with the *Data Analyses*

tool (See window 3.3). From the raw data of this distribution I randomly took distances

that were added to the actual dispersal distances of the 62 new recruits analyzed. After
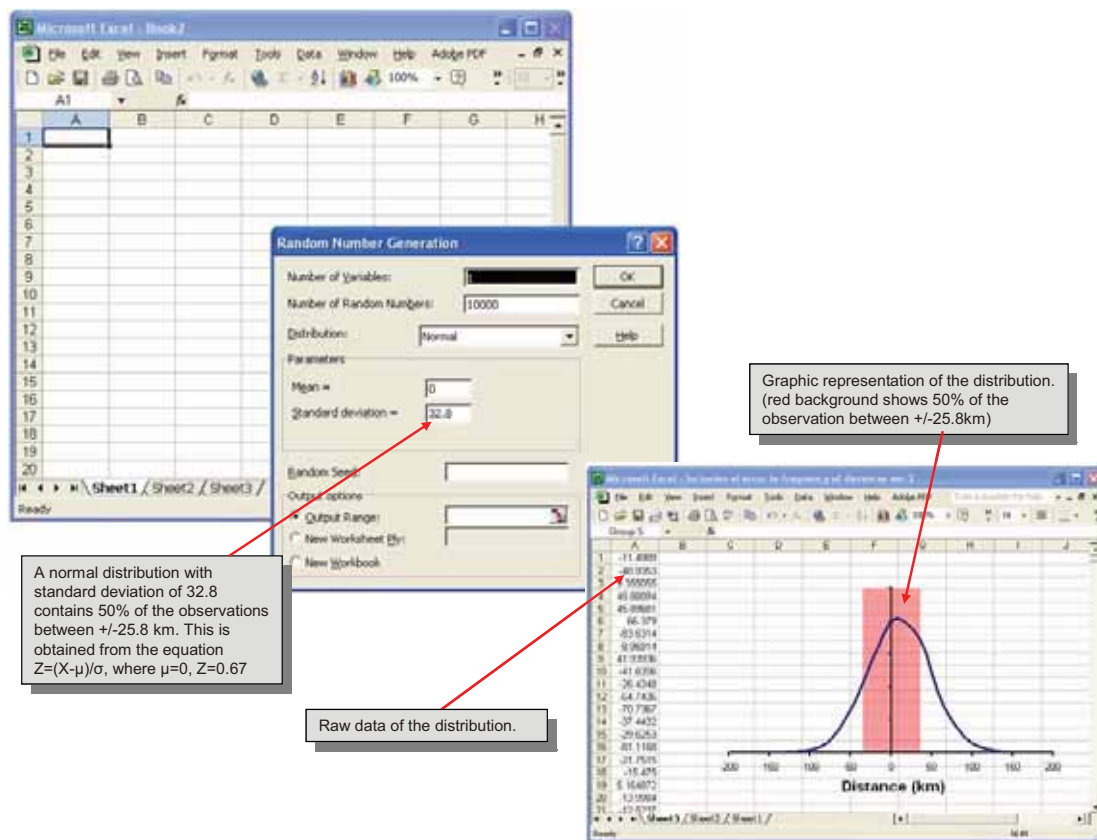
Window 3.3.3. Description of the process for obtaining of the normal distribution of random

distances.

addition of the random distances the frequency distribution of dispersal distances was

quantified again. This model was done in Excel (see description in Window 3.4) and

repeated 500 times (see description of macro in Window 3.4).
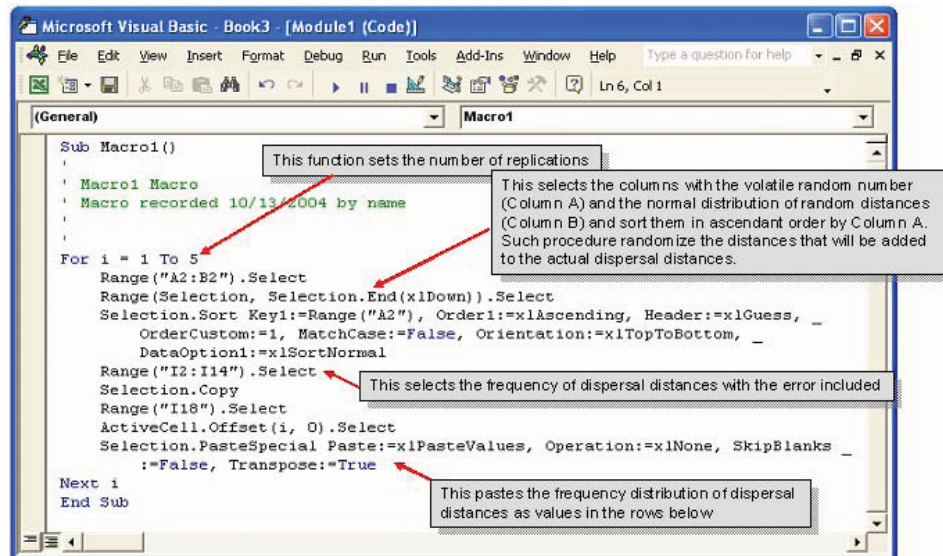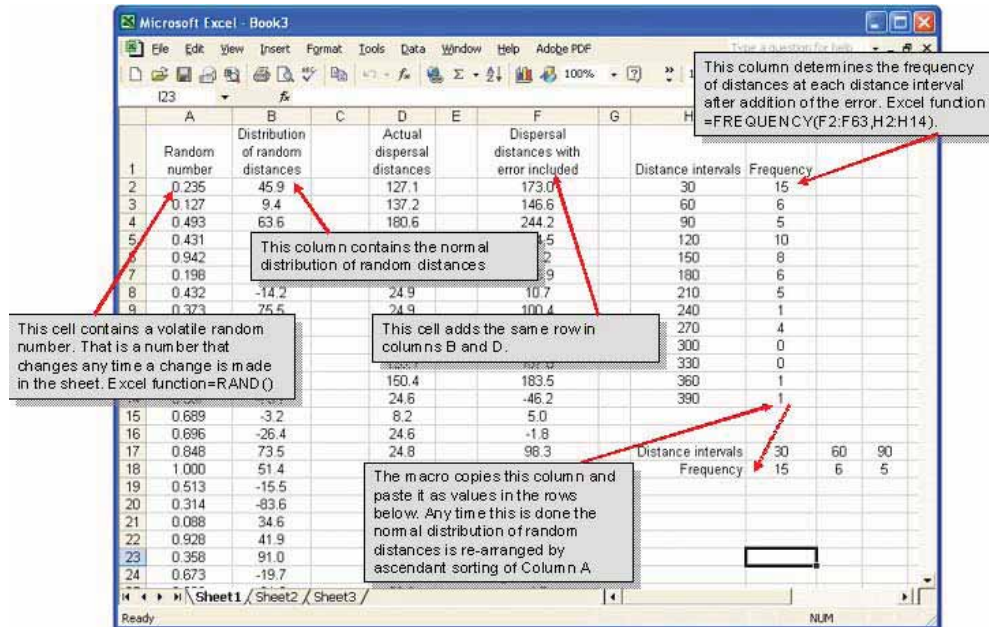
Window 3.3.4. Description of the model (upper window) and macro (lower window) for inclusion of the assignment error in the dispersal distances of the 62 new recruits.

Appendix 3.4. Discussion on the assignment tests

Deriving valid concepts about the causes and consequences of dispersal depends largely on our ability to reliably estimate dispersal. Unfortunately, there are few methods that are reliable and those often give answers at very small scales (e.g. mark/recapture experiments) (see chapter 2, and also Bilton et al. 2001, Nathan et al. 2003). This calls for exploration and/or inclusion of new methodologies for the study of dispersal. In this Chapter, I introduced a new method for assessing dispersal in reef systems, which is based on the assignment of new recruits to natal populations based on their genotypes. This assignment methodology has been used only recently to assess questions of dispersal in other systems (see review by Waser and Strobeck 1998, Cornuet et al. 1998). The promising nature of this methodology has led to a proliferation of different statistical programs (e.g. Structure, Geneclass, Whichrun, Arlequin, Spassing, and others). Although the underlying principles of many of these programs are the same or only slightly different their reliability remains poorly tested (see review in Berry et al. 2004). In one such test, using larvae from known natal sites, I found that most tests perform poorly when used alone (Figure 3.2). However, we noted that when combined, the consensus of assignment tests did reduce the assignment error to an average of 25.7 km or ~5.7% of the spatial domain of the study site (Figure 3.3.). Based on theoretical data, Cornuet et al. (1998) have previously pointed out that several factors may cause such lack of accuracy. The most important of these are low genetic differentiation among populations and low parental sample size. Note that the levels of genetic differentiation among populations can be a function of the number of markers and their polymorphism.

61

In the bicolor damselfish, levels of inter-population genetic structure have been found to be significant ($F_{st}>0.1$) at scales of less than 1 km (Lacson et al. 1989). Based on this, five loci and a parental sample size as low as 10 individuals per population are assumed, based on theoretical data, to be enough for assignment reliability of up to 100% (Cornuet et al. 1999). As shown in this Chapter, an a priori use of this information can lead to very unreliable assignments. Therefore, several problems need to be addressed before assignment tests can achieve higher power in the study of larval dispersal of reef fishes. First, this Chapter points to the lack of generality of patterns of inter-population genetic structure. The bicolor damselfish in our study site did not have the levels of genetic structure it showed in the Florida Keys. The reasons for such differences may be due to the use of different genetic markers [microsatellites (here) vs allozymes (Lacson et al. 1989)]. The fact that allozymes are codifying versions of genes means that they suffer strong selection, which in turn may cause stronger spatial variations in genetic structure than that observed with microsatellites (See chapter 2). Another factor may be variation in landscapes: the Florida Keys are patchier than the MBRS. Dytham (2003) has suggested, based on a model, that habitat patchiness can reduce dispersal. Such limitation in dispersal by habitat patchiness may well be an explanation for variations in patterns of genetic structure among regions with different patterns of habitat continuity. Finally and perhaps more importantly is the temporal variation of such spatial structure. Lacson and Morizot (1991) repeated the same sampling in the same places studied by Lacson et al. (1989) three years later [~two generations between the collection done by Lacson et al. 1989 and that of Lacson and Morizot 1991] but found no genetic structure at all (Fst<0.014). That is almost a 10 order variation in the levels of genetic structure in only

three years. Regardless of the cause(s) of this striking change in pattern, it is clear that the reliability of assignment tests will vary temporally suggesting that pilot studies may not be that useful.

Another issue in regard to assignment tests is how many individuals represent a good sample size of the parental populations. At present, decisions on sample size are obtained from theoretical studies and might not be appropriate for real conditions in natural populations (Cornuet et al. 1999). The cost of extraction and amplification of genetic markers certainly limits the number of individuals for which one can obtain genotypes. Therefore, determining optimal sample size needs to be a priority for the appropriate use of assignment tests. Perhaps the best solution will be to sample adult populations massively at many locations and then accumulate adult genotypes until embryos get reliably assigned to their natal reefs. Once such reliability in the assignment of embryos has been reached one would expect that the samples of genotyped adults would be sufficiently large for reliable assignment of new recruits from unknown sources. It is also important to mention that sample size could be reduced if the number of markers is increased and if their variability is high (Cornuet et al. 1999). New techniques for amplification of multiple markers in single PCR (multiplexes) may prove to be useful in reducing costs.

CHAPTER 4: Is larval dispersal energetically expensive? A case study with the

bicolor damselfish *Stegastes partitus*.

Introduction

The life cycle of most reef fishes and other marine benthic organisms includes a widely dispersive larval stage. It is well recognized that this dispersive stage can have tremendous effects on the ecology (i.e. Caley et al. 1994) and evolution (i.e. Clobert et al. 2001) of species, and on the effectiveness of conservation policies (Sale 2002, Palumbi 2003). Despite its importance larval dispersal is still poorly understood in marine systems. Such lack of knowledge arises mainly from the complexity of the system being studied, which includes minuscule propagules suffering high initial mortality and moving in vast parcels of dynamic water. Such complexity has precluded direct tracking of dispersal through mark-recapture experiments (but see Jones et al. 1999) and led to the use of more indirect approaches to achieve that task (reviewed in Mora and Sale 2002, Warner and Cowen 2002 and associated papers). Since indirect approaches to study larval dispersal can not be fully tested, because of the lack of empirical data, there has been considerable reservation about the reliability of their results (e.g. Bellwood et al. 1998, Colin et al. 2003, but also Chapter 2). This chapter focuses on a line of thinking that infers the existence of specific forms of dispersal (i.e. short- or long-distance dispersal) due to selection by energetic costs (Bourret et al. 1979, Swearer et al. 1999, Strathmann et al. 2002).

Recent studies have shown that larval growth is a trait that is highly selected for in reef fishes (Booth 1995, Searcy and Spounaugle 2001, Bergenius et al. 2002, Shima 2002, Wilson and Meekan 2002, Vigliola and Meekan 2002). These studies have found, consistently among different species and regions, that larvae with good physiological condition (often quantified as somatic growth) survive the pelagic period and the

transition to their benthic life more often than larvae in poor condition. In addition, condition (as somatic growth) has been shown to have a genetic basis (Conover and Munch 2002, Planes and Romans 2004) suggesting that any factor that influences larval growth may have profound evolutionary implications. Dispersal has been argued to be one of these factors with high potential effect on larval growth. On the one hand, it is suggested that extensive dispersal favors larval growth since it reduces the energetic expenses associated with maintaining position in a specific location (Bourret et al. 1979 cited in Bonhomme and Planes 2000). On the other hand, dispersal is assumed to have a negative effect on larval growth due to shortages in food supply that larvae may experience when dispersing in less productive open water (Swearer et al. 1999, Strahmann et al. 2002). The hypothesis by Bourret et al. (1979) predicts that there will be selection for long-distance dispersal while that of Swearer et al. (1999) predicts that there will be selection against long-distance dispersal and for mechanisms favoring retention. Underlying these hypotheses is a relationship between larval growth and dispersal, which is expected to be positive according to Bourret et al. (1979) but negative according to Swearer et al. (1999).

In this chapter, I quantify larval growth (obtained from the analysis of the microstructure of the otoliths) for the 62 new recruits of *Stegastes partitus* from which data on dispersal trajectories were obtained in chapter 3. The availability of data on larval growth and dispersal distances for a set of new recruits allows for the first time a test of the importance of dispersal on larval growth.

Materials and Methods

Study species

The bicolor damselfish (*Stegastes partitus*) is a common coral reef fish throughout the Caribbean (Wilson and Meekan 2001, 2002). Its life cycle, which includes benthic eggs, planktonic larvae and a sedentary adult phase is common to many other coral reef fishes. Con-familiars of this species are also widely distributed in tropical seas suggesting that the results of this study could be comparable to other species.

Study site

The Mesoamerican Barrier Reef System (MBRS) running down the Caribbean coast of Mexico, Belize and Honduras is among the largest reef systems in the world and the largest one in the Atlantic Ocean. Patterns of current circulation in this region are known mainly through meso-scale hydrodynamic models based on temperature data (see review by Thattai et al. in press). From these models it is clear that there is a predominant northwest water flow along the MBRS and a low speed anticyclonic eddy that appears intermittently in the Gulf of Honduras (Sheng and Tang 2004, Thattai et al. in press). Other oceanographic attributes of this region, especially at small scales, are not well described but it seems that sites across this region can be interconnected at both small and large scales (Chapter 3). Therefore, dispersal within this region can be variable enough to test the hypothesis on the effects of dispersal on larval growth.

Analysis

Data on larval growth was obtained through the analysis of otolith microstructure for the 62 new recruits for whom dispersal distances were available (from Chapter 3). In the

bicolor damselfish patterns of band accretion of the otoliths have been shown to be daily (Robertson et al. 1988) and to grow in step with the body of the fish (Figure 4.1 and also see Wilson and Meekan 2002). Therefore, otoliths can be used as recorders of somatic growth at different life stages. For the purpose of this chapter, I measure growth rate for the entire larval phase (bands between the core and the settlement mark) and specific time intervals of that larval phase [i.e. first two days (as this is the time larval growth is likely sustained by food reserves from the yolk sac, Wilson and Meekan 2002) and subsequent four-day intervals for the length of the larval phase]. In this Chapter, I correlate the average increment width during the entire larval period and during each interval, with the distance of dispersal of the analyzed recruits to assess any interaction between dispersal and larval growth.

In chapter 3, I showed that the dispersal distances of the new recruits that are analyzed here may contain an assignment error of +/-25.8 km. To assess the extent to which such error affects the relationship between larval growth and dispersal I performed a null model that assesses the correlation between growth and dispersal distances that contain such error. First, I generated a normal distribution of distances with average of 0 and standard deviation of 37.5 (this distribution contains 50% of the observations between +/-25.8km) (This is the same distribution described in Appendix 3.3 and Window 3.3). From this distribution I selected distances randomly and added them to the actual dispersal distances of the 62 new recruits and then correlate these with larval growth of the entire larval phase and of specific time intervals. Such procedure was repeated 100 000 times to ensure that enough contrasts of dispersal distances were used and that the results of any correlation are reliable.

Otolith preparation

The measures of larval growth were done as follow: one sagittal otolith was selected for each fish and mounted on a glass slide using thermoplastic cement. Otoliths were mounted at the edge of the slide and their distal end was ground with lapping films (30 to 0.1 µm) until near proximity of the core. Otoliths were then flipped over and polishing was continued to produce a thin transverse section of the otolith that incorporates the nucleus. Increment width for bands within the larval period was measured along the longest radius of the otolith using a compound microscope at 400X magnification and a video camera with digital analysis software (SigmaScan Pro version 5).

Results

Data on early life history were obtained for 57 of the 62 individuals for which estimates of dispersal distances were available. The pelagic larval period of these recruits ranged between 23 and 38 days (mean = 30.2, SD = 3.1) and they settled at otolith radius of 250 µm (SD=24, CV=9.6%). Otolith growth through the larval phase was on average 8.4 µm per day but varied among intervals of the larval period (Figure 4.2). Dispersal of the analyzed recruits was poorly correlated with growth whether evaluated during the entire larval phase (Figure 4.3b) or any interval of the larval period (Figure 4.4). To further assess the consistency of this result we compared the larval growth of recruits in the two modes of dispersal distances described in Chapter 3 (i.e. <30 km and 150-180 km) but found that average larval growth was not significantly different (mean=8.4 vs. 8.5 µm d^{-1} respectively, t-test: t = -0.03, p<0.97; U-test: Z=-0.04, p<0.96) neither was it significant within specific intervals of their larval period (Figure 4.5). The effect of the assignment

error in such results also was negligible as the few correlations for which the assignment error led to significant correlations were very weak (Figure 4.6 and vertical lines in Figure 4.4). In contrast, dispersal correlated significantly with the duration of the larval period (Figure 4.3a) although such correlation was weak ($r=0.082$, $p<0.03$). The best predictor of variations in larval growth was the variation in the length of the pelagic period (Figure 4.3.C). Older recruits were often the ones growing least well ($r=0.60$, $p<0.0001$, this probability was adjusted based on the Monte-Carlo simulation described below). Since the growth ratio of this correlation includes a common variable with the duration of the larval period (i.e. days) there is the possibility that this correlation is spurious (see Bird and Duarte 1989). To account for this possibility we perform a Monte-Carlo simulation that correlate the PLD of the individuals vs an estimation of growth based on the length of the otolith divided by a random PLD. The probability of the actual correlation was adjusted based on the proportion of resulting slopes larger than the slope of the actual correlation (see Bird and Duarte 1989 for a similar example).

Discussion

The extent to which dispersal is selected by energetic "penalties" and the direction of these penalties has been unclear. By energetic penalties I refer to deleterious changes in larval growth, due to energetic consequences of dispersing short or long distances (see introduction). At present, two alternative hypotheses have been proposed concerning the effects of dispersal on larval growth. One suggests that extensive dispersal occurs in unproductive water of the open ocean and therefore, dispersal results in a detriment of

body condition (Swearer et al. 1999). The other hypothesis argues that short-distance dispersal is associated with energetic costs due to the need to remain in a specific location despite the movement of the water mass (Bourret et al. 1979, in Bonhomme and Planes 2000). If either one of these two hypotheses is correct, then there will be a significant relationship between dispersal distance and larval growth. In an attempt to inspect this relationship, I found no indication of a significant correlation either positive or negative between dispersal distance and larval growth among new recruits of the bicolor damselfish in the MBRS. This result suggests that dispersal may not necessarily incur energetic penalties as opposed to the hypotheses proposed by Bourret et al. and Swearer et al.

Different studies have also shown that several critical factors other than dispersal can account for variations in larval growth. For instance, Wilson and Meekan (2002) found that nearly 50% of the variation in larval growth of *S. partitus* larvae can be explained by variations in temperature alone, which also corroborates experimental studies on the importance of temperature on larval growth (Fukuhara 1990). Food distribution in the pelagic environment is considered to be patchy (Doherty et al. 1985) which could also add to unpredictable variations in larval growth. Even maternal investment in egg production is known to affect early growth (McCormick 1999). The results of this chapter in combination with the empirical work about factors influencing larval growth suggest that the effects of dispersal on larval growth may be less than previously thought.

When considering the energetic expenses associated with different forms of dispersal (i.e. short-or long distance dispersal) it is important to remember that there are several mechanisms by which dispersal can be achieved without any energy expense. For instance, long distance dispersal can be achieved within inshore water along continental shores without larvae being exposed to unproductive open waters and likely shortages in food supply. Even long-distance dispersal across open water gaps may not lead to deterioration in body condition if larvae travel within bodies of rich waters (Doherty et al. 1985). Similarly, larvae can maintain position in specific locations through the interaction of stratified waters and vertical migration, which can be far less energetically expensive than active swimming (Cowen 2002).

Reef fish ecologists have devoted significant effort to the development of a theory of dispersal as a deterministic process, which has resulted in extensive discussions upon whether dispersal in coral reef fishes is localized or extensive (e.g. see Chapter 2). However, such discussions have failed to recognize the large variation in life histories within and among species and in hydrodynamic processes in space and time, altogether highlighting the potential for high variation in dispersal paths among and within species. The lack of energetic expenses associated with specific forms of dispersal (this chapter) suggests that dispersal can be a stochastic process rather than a deterministic one, and that a simplistic perception of dispersal as localized or extensive will fail to recognize the extreme complexity of dispersal in coral reef fishes.

The primary goal of this chapter was to analyze the effect of dispersal on larval growth. However, the data of this chapter also allow discussion on another important

aspect of the ecology of reef fishes (i.e. the time of settlement). Factors that determine the time of settlement in coral reef fishes have been of wide interest to ecologists as these can explain recruitment patterns and influence post-recruitment survival (Doherty and Williams 1985, Cowen and Sponaugle 1997). From the study of these factors it seems that the time of settlement is determined by a trade-off between favorable times for settlement (e.g. lunar and tidal cycles) and body traits at those times (i.e. size or age). In the bicolor damselfish we found that size at settlement was relatively stable (~250 µm otolith radius, CV~9.6%) and that larval growth was negatively related to the length of that period (Figure 4.3c). This highlights the potential for a body size constraint for the time of settlement. One potential explanation for the negative relationship between PLD and growth is that larvae with slower growth may delay their settlement in order to achieve an appropriate settlement size. However, the fact that size at settlement was rather fixed suggests that excessive growth in the plankton may also be selected against. In short, there is the possibility that the time of settlement in the bicolor damselfish is regulated by directional selection for a specific settlement size. In the one hand, there could be selection against small settlers on reefs (one factor being strong predation by small and often very abundant predators; Hixon and Carr 1997) while on the other hand large larvae may be selected against in the plankton as these are more visible to pelagic predators.

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Figure 4.1. Relationship between otolith width and body size in *Stegastes partitus*.
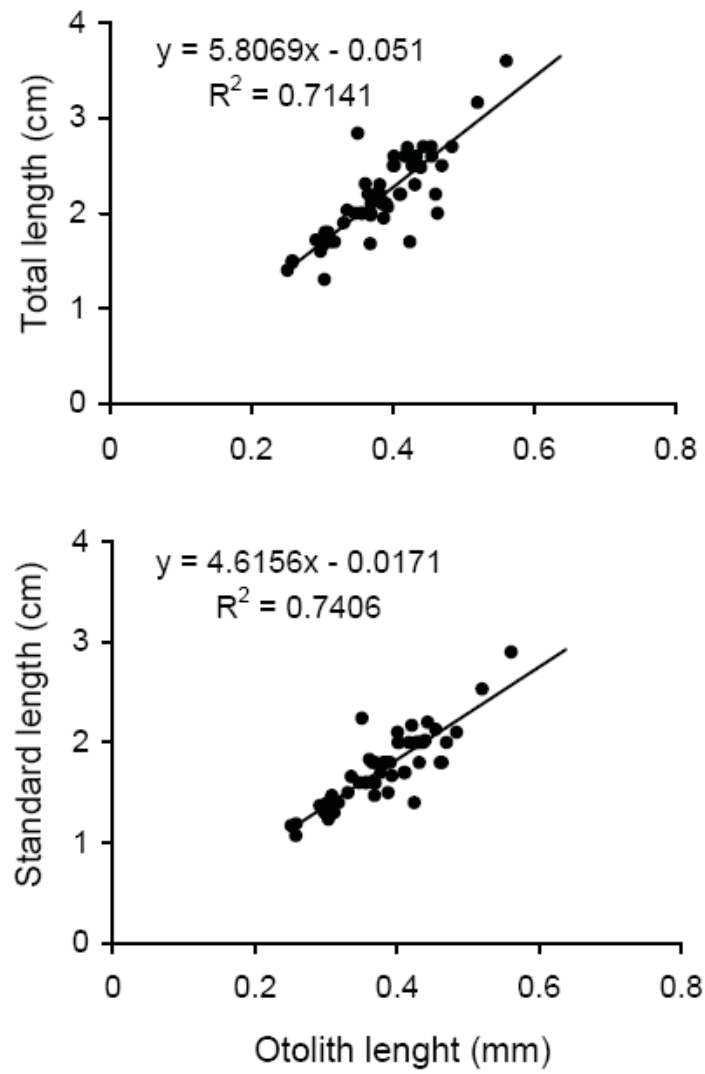
Figure 4.2. Variations in larval growth through different intervals of the larval period.
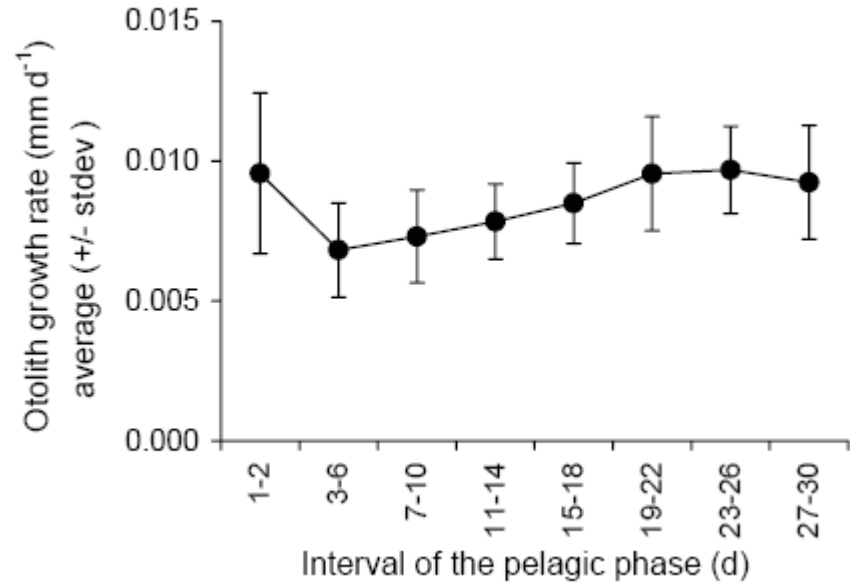
Figure 4.3. Pairwise comparisons between pelagic larval period, distance of dispersal and growth in new recruits of *Stegastes partitus*.
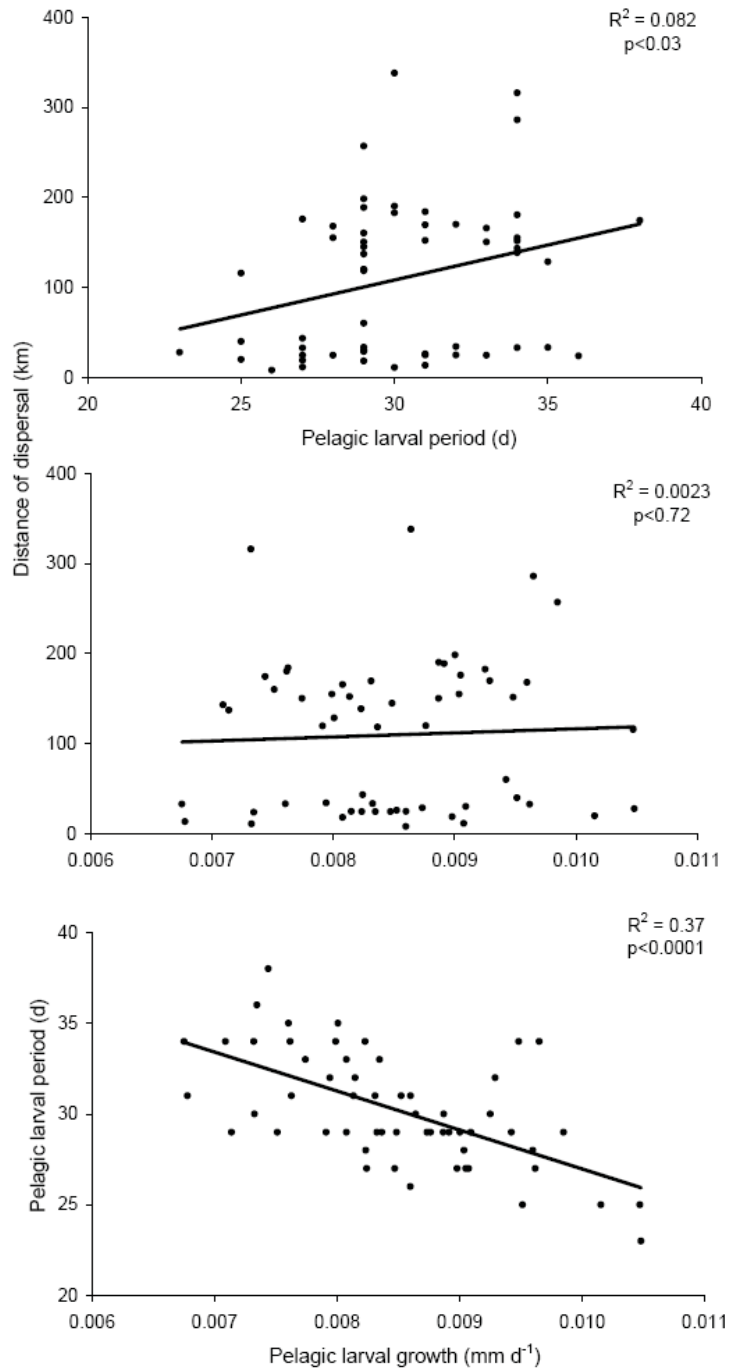
Figure 4.4. Ontogenetic variation in the correlation between specific larval growth periods and dispersal in new recruits of *Stegastes partitus*. Vertical lines represent the maximum and minimum coefficient of correlation of 100 000 regressions in which dispersal was adjusted to accommodate the assignment error. Only 1% and 0.4% of the correlations at growth intervals of between 15-18 d and 27-30 d were significant at $p<0.05$.
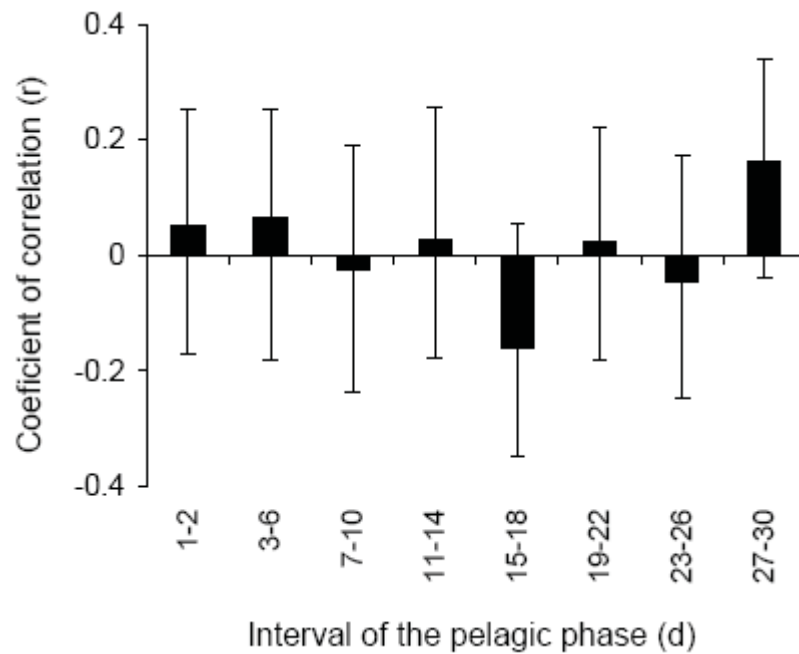
Figure 4.5. Comparison of larval growth among recruits with two distinctive dispersal distances. Although larval growth was significantly variable through the larval period (F=4.05, p<0.0001) such pattern was consistent between the two groups of recruits (i.e. Tukey contrast between the two dispersal groups were not significantly different at p<0.05 in any interval of the larval period).
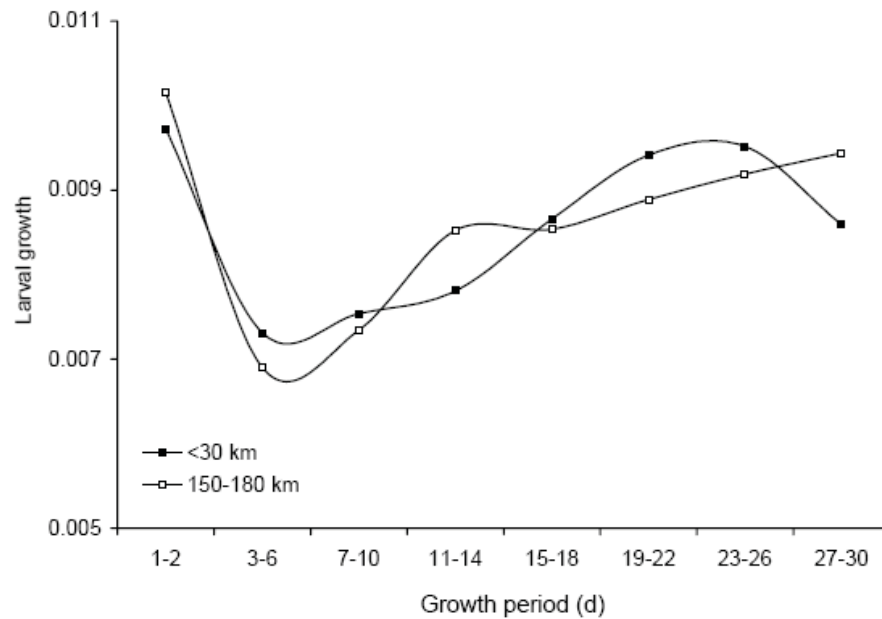
Figure 4.6. Results of the null model for inclusion of assignment error in the regression between growth and dispersal. None of the 100 000 simulated regressions were significant at $p<0.05$ (Shadow area in lower panel).
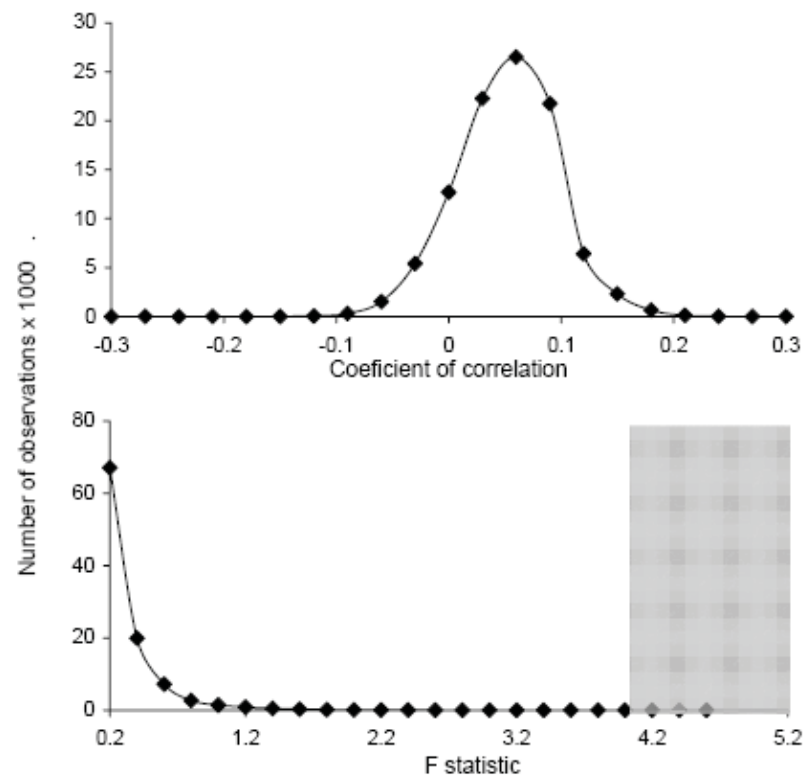
CHAPTER 5: Importance of dispersal on range size

A modified version of this chapter was published with the title:

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the endemic fish fauna of the Tropical Eastern Pacific. Journal of Biogeography 31, 1-10

Introduction

One of the most important biological attributes of a species is the size of its geographic range. Range size strongly affects and reflects processes of speciation and extinction (reviews by Lawton 1993, Gaston 1994, 1996, 2003, Rosenzweig 1995, Chown 1997, Gaston and Blackburn 2000, see also Jablonski and Roy 2004, Hawkins et al. 2000), may influence the geography of species diversity (Stevens 1989) and will affect faunal resilience to ongoing global changes in the environment (Gaston 2003). Therefore, understanding of the factors that determine species ranges is critical for both fundamental science and appropriate design of conservation strategies (Gaston 2003). However, while extensive taxonomic and field work have led to comprehensive databases and relatively good descriptions of species' ranges in several taxa, the factors determining their ranges remain largely elusive (see reviews by Brown et al. 1996, Jones et al. 2002, Gaston 2003).

Ecologists studying coral reef fishes have focused primarily on dispersal abilities of larvae as the main determinant of range size (Brothers and Thresher 1985, Thresher and Brothers 1985, Thresher et al. 1989, Wellington and Victor 1989, Stobutzki 1998, Victor and Wellington 2000, Jones et al. 2002, Zapata and Herron 2002). Such interest in dispersal abilities of larvae is due to the fact that reef fishes are largely sedentary after settlement, and the colonization of patchily distributed reefs is, therefore, most likely during the larval period (but see Mora et al. 2001 for evidence of juvenile and adult dispersal by rafting). However, quantitative studies within several families have failed to demonstrate any significant relationship between estimates of larval dispersal (e.g. pelagic larval duration, swimming abilities) and range size (Thresher and Brothers 1985,

Thresher et al. 1989, Wellington and Victor 1989, Stobutzki 1998, Victor and

Wellington 2000, Jones et al. 2002). Such lack of correlation between dispersal and range

size has been associated mainly with methodological problems due to low sample sizes

and incorrect quantification of range size (Victor 1991).

In this Chapter I use a rather different approach to assess the effect of dispersal on

range size. Here I assume that dispersal among patches of suitable habitat reduces as the

distance between patches increases (also see Cloberg et al. 2001) and if indeed dispersal

affects range size, then one should expect range size to increase as the habitat of species

becomes less patchy. I tested this hypothesis by comparing the range size of species that

are known to live in habitats with different levels of patchiness. Here I used a

biogeographical database of shore fishes from the Tropical Eastern Pacific (TEP), which

includes information on range size and habitat use for almost the entire fish fauna of that

region (Robertson and Allen 2002). I consider two levels of habitat patchiness: isolation

and fragmentation. Isolation represents the separation between the oceanic islands and

the thin continental shelf of the TEP (Figure 5.1), and between the islands themselves;

and habitat fragmentation the continuity of major habitats types (reefs, soft bottom, the

nearshore water mass) along the coastline of the TEP. The effects of these factors were

assessed by comparing Range Size Frequency Distributions (RFD) among species found

at oceanic islands and/or the continental shore, and among species restricted to each

continental habitat type.

Methods

Location

The TEP (Figure 5.1) includes the west coast of the Americas between about 32°N and

8°S, plus five isolated oceanic islands and island groups – the Revillagigedo group

(400km from the tip of Baja), Clipperton (1,100 km from central Mexico), Cocos (480km

from Costa Rica), Malpelo (400km from Colombia) and the Galapagos archipelago

(1000km west of Ecuador). All of these islands originated from oceanic volcanoes, and

were never connected to the mainland (see Robertson, 2001). Hence their shallow-water

shorefish faunas are derived entirely by long-distance dispersal. The continental coastline

has a very narrow continental shelf and an uncomplicated form with a roughly

longitudinal orientation (Figure 5.1). Within the TEP, rocky shores are common along all

but two large sections of coastline that consist entirely of sand and mud, and lack any

reefs: a 1,000 km section from southern Mexico to El Salvador, and a 370km section in

the south-eastern Gulf of California. These reef-less stretches of shoreline, which are

known as the Central American Gap and the Sinaloan Gap, respectively, act as barriers to

the distributions of some shallow reef-fishes (Hastings 2000). In contrast, there are no

analogous large barriers in the TEP likely to affect the distributions of either demersal

soft-bottom fishes or coastal-pelagic fishes.

Data

Thanks to 150y of research that culminated in a recent series of regional and subregional

guides (e.g. see Allen and Robertson 1994, Fischer et al. 1995, Grove and Lavenberg

1997, Thomson et al. 2000), the shorefish fauna of the TEP is now probably as well

defined as that of any equivalent tropical region. Latitudinal range-size data used in this paper are taken from a database of current information (based on 1000+ citations) on the range limits of all known shallow-water shorefishes (those living in <100m of water) in the TEP (see Robertson and Allen 2002). That database includes information on 1,195 fishes, among which ~80% of the species that are resident in the TEP are endemic to it. The remainder include species that occur elsewhere in the tropical Pacific, species known in the region only from vagrant individuals, species primarily found in the temperate parts of the eastern Pacific that penetrate the fringes of the TEP, and a handful of species introduced from the Atlantic (e.g. migrants through the Panama Canal). Here we consider only TEP endemics (n=827 species), in order to assess patterns of variation in range-size in a large suite of species that have been subject to the influence of a common set of geographic factors and a common history of exposure to the region's physical environmental regime.

Analyses

We examined the frequency distributions of range sizes among components of the TEP-endemic fauna in three ways: First we compared species that differ in terms of the extent to which their distributions likely are affected by habitat isolation and have demonstrably different capacities to live in a variety of environments. We considered three groups of species: those restricted entirely to the oceanic islands (hereafter insular species), fishes restricted to the continental shore, and those found on at least one oceanic island as well as the continental shore. Because the oceanic islands of the TEP are well isolated, from each other as well as from the mainland, we predicted that insular species should have

small ranges and the most strongly right-skewed RFD. Because species common to both continental shores and oceanic islands have demonstrated both the dispersal power to overcome insular isolation barriers and the capacity to live in a range of environments, we predicted that their ranges should tend to be large and their RFD left-skewed. Finally, we expected that continent-only species would have an RFD intermediate between these two extremes because they are less restricted by habitat discontinuities than are insular species but are less successful than continent + island species at dispersing across oceanic barriers and/or surviving in different environments.

The second analysis is based on all species found on the continent and assesses range variations along gradients of habitat fragmentation. Here I analyze the following assemblages of species: (i) demersal species that are restricted to reef habitats (rock and coral), (ii) demersal species restricted to soft-bottom habitats (sand, gravel and mud), and (iii) coastal-pelagic species that live in the nearshore water column. It should be noted that coastal-pelagics include both species that have large, vagile adults and live in open water (e.g. scombrids and carangids) and small, less mobile species that live closer inshore, including in estuaries (e.g. atherinids, engraulids, clupeids, some sciaenids). Species with multiple habitat associations were not included in this analysis. The expectation is that, if the large gaps in the distribution of shallow reef habitats do generally limit the distributions of reef-fishes, then their ranges should tend to be smaller than those of either demersal soft-bottom or coastal-pelagic species. Further, because adults of many coastal-pelagics are more mobile than those of demersal species, that capacity should add to dispersal capabilities arising from any pelagic larval stage

possessed by many members of both groups; hence, coastal-pelagics should have larger ranges than demersal species if dispersal ability is a major determinant of range size.

These predictions were tested as follows: (i) by making statistical comparisons of RFDs of the different groups of species, and (ii) by comparing the actual RFDs of those groups with a null RFD. In each case a null RFD was derived by randomly selecting a similar number of species to the analyzed group from the entire pool of species for the first analysis and from the pool of continentally-occurring species for the second analysis. In each case the randomization procedure was repeated 1000 times to generate the 95% confidence limits of the null distribution.

Results

The entire endemic fish fauna of the TEP exhibited a right-skewed RFD (Table 5.1), as species with the smallest ranges are the largest group. However, there was a second, smaller and broader mode present toward the large-range end of the distribution (Figure 5.2a-b). This bimodality is more evident in the log-transformed RFD (Figure 5.2c). There were statistically significant differences in median range-size among insular, continental and continent + island species (Kruskal-Wallis ANOVA, H=295.4, p<0.001). A non-parametric multiple comparison test for unequal sample sizes (Zar 1996) showed all pairwise comparisons to be significantly different at p< 0.001. Insular species had a strongly right-skewed RFD (Figure 5.2d-f), the smallest median range-size (Table 5.1), and more small-range species and fewer large-range species than expected due to chance (Figure 5.2d-f). Continental species had a relatively homogeneous RFD (Figure 5.2 g-i), an intermediate median range-size (Table 5.1), and differed from the null model by

having fewer smallest-range species and more middling-range species (Figure 5.2. g-i). Species found on both the continent and oceanic islands had a strongly left-skewed RFD (Figure 5.2j-l), the largest median range-size (Table 5.1), and fewer small-range species and more widely-distributed species than expected due to chance (Figure 5.2j-l). It should be noted that, while the domain for continental species is 40 degrees of latitude, that for insular species is only ~20 degrees. Hence insular species cannot have ranges greater than about half the potential maximum range of continental species. To take this difference into account we repeated the analysis described above using relative range sizes (i.e. range-size as a percentage of the domain, which were 40 and 20 degrees, respectively, for continental and insular species). The results and patterns of this comparison of relative range-size were the same as those for the comparison of absolute range-size (See Figure 5.2).

Continentally-occurring species with different patterns of habitat usage also exhibited statistically significant differences in median range-size [Kruskal-Wallis ANOVA, H=23.7, p<0.001; all pairwise comparisons (Zar 1996) were significantly different at p<0.002, except coastal-pelagic vs soft-bottom, where p=0.02]. Coastal-pelagics had the largest median range-size and reef-fishes the smallest, while soft-bottom species were intermediate in that regard (Table 5.1). Based on the null models, the coastal-pelagic group had an excess of species with large ranges and a deficit of species with small ranges (Figure 5.3a-b); soft-bottom species showed no statistically significant departures from the null distribution (Figure 5.3c-d); and reef-fishes included an overabundance of small-range species and reduced numbers of large-range species (Figure 5.3e-f).

Discussion

Supporting evidence on the importance of dispersal determining the geographical range

of marine fishes is largely lacking (see review in Jones et al. 2002). Here I report

variations in range size among fish species using habitats with different degrees of

patchiness that are consistent with dispersal being an important determinant of range size.

In a first analysis, it was shown that range size increases along gradients of isolation

ranging from oceanic islands to continental shores and the interaction between the two.

It is very likely that the predominance of species with very small ranges (equivalent to

single islands or island clusters) among insular habitats is due to a constraining effect of

isolation on dispersal. Oceanic islands are characterized by retentive hydrodynamic

processes (Mora and Sale 2002, Sponaugle et al. 2002), which likely assists in local

closure of species' life cycles (Robertson 2001) but also can restrict gene flow and led to

the formation of species with small ranges at oceanic islands. In contrast, habitats along

the continental shore of the Americas lack such level of isolation and therefore species

there can easily achieve large ranges. The importance of dispersal and habitat isolation on

range size is further supported by the fact that continental+oceanic species had the largest

ranges. These species can disperse along continental shores but also have capabilities for

long-distance dispersal as shown by their presence at oceanic islands separated by large

barriers.

In a second analysis, range size of the continental fish fauna of the TEP varied

among species using habitats fragmented at different levels. There was a shift in the

mode of the distribution from small ranges in reef-fishes to a uniform distribution in soft-

bottom species, to large ranges in coastal-pelagic fishes. Similar habitat-related variation in RFD structure has been reported for benthic vs pelagic invertebrates and fishes from both sides of the Atlantic Ocean (Macpherson 2003). Again it is likely that these differences arise through a combination of declining effects of large-scale habitat fragmentation and increasing dispersal ability along this hierarchy. Reef-fishes are those most strongly affected by habitat fragmentation. At the other extreme, the nearshore waters used by coastal-pelagics are continuous throughout the region and those fishes often have more mobile adults with better dispersal capabilities than adults of the other two groups. Soft-bottom fishes are more sedentary than many coastal-pelagics, but have habitat that is more continuously distributed throughout the TEP than is that of reef-fishes. Taken together these patterns support the view that both life-history characteristics associated with dispersal-potential and habitat fragmentation can act as important determinants of range-size.

The interaction between habitat patchiness and dispersal seems to play a major role in determining variations in range size among fishes of the TEP. However, environmental tolerances are also known to affect species ranges (Gaston 2003) and may contribute to the patterns observed here. In the TEP, as in other tropical regions, the maximum possible extent of each species occurrence likely is set by their thermal tolerances and strong gradients in temperature at the edges of tropical regions (Jones et al. 2002, Mora and Ospina 2002, Mora et al. in review). The TEP has perhaps the most dynamic environment of any tropical region, due to an abundance of large seasonal upwelling areas and to frequent, intense and widespread effects of El Niño events (e.g. see Glynn and Ault 2000). Although the isolation of the TEP also has an effect, stresses

of this environmental regime are largely responsible for the depauperate coral fauna and paucity of coral reefs in the region (Glynn and Ault 2000). These events also produce both local mortality of shorefishes and temporary changes in their ranges (Mora and Ospina 2001, 2002, Victor et al. 2001). While this regime should have selected for broad environmental tolerances among continental species, and promote large ranges, regional geography evidently has had a stronger effect on range-size, as continental species in general do not have large ranges [at least not as large as the size of the TEP domain (i.e. 40 degrees of latitude)]. Only the group least affected by continental barriers, coastal-pelagics, has a large-range peak in its RFD, suggesting that this group is the one most constrained at the northern and southern boundaries of the TEP likely by the effects of thermal tolerances.

Range-size can have strong effects on the large-scale geography of species diversity (Colwell and Lees 2000, Jetz and Rahbek 2002, Mora and Robertson in review), as well as the design of conservation strategies (Rodrigues et al. 2004). This paper shows patterns consistent with range size being affected by dispersal, which in turn can be affected by the patchiness of suitable habitats. Potential implications of this work include the need for distinction of species with different habitat uses when addressing questions about the determinants of large-scale diversity patterns, and the potential effect of increasing habitat deterioration (Bryant et al. 1998) on the diversity of coral reef fishes.

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Figure 5.1. The Tropical Eastern Pacific biogeographic region. The continental-shelf

area is shown in black along the coastline.
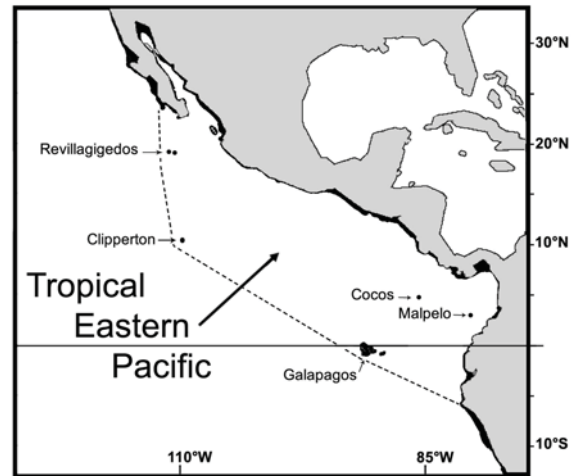
Figure 5.2. Range-size frequency distributions (RFDs) of the marine fishes endemic to the Tropical Eastern Pacific. The RFDs of the entire fauna and components thereof are shown on untransformed (left panels) and log-transformed (right panels) scales. Dotted lines indicate the 95% confidence limits of a null distribution (see methods for details). The untransformed and long-transformed latitudinal RFDs of the reef-fish fauna of the Indo-central Pacific (m,n) are added for comparison (Data from Mora et al. 2003, with the exclusion of TEP endemics). The RFDs of ranges standardized to domain size are shown for comparison (center panels; see text). Dotted lines indicate the 95% confidence intervals of a null model (see methods for details).
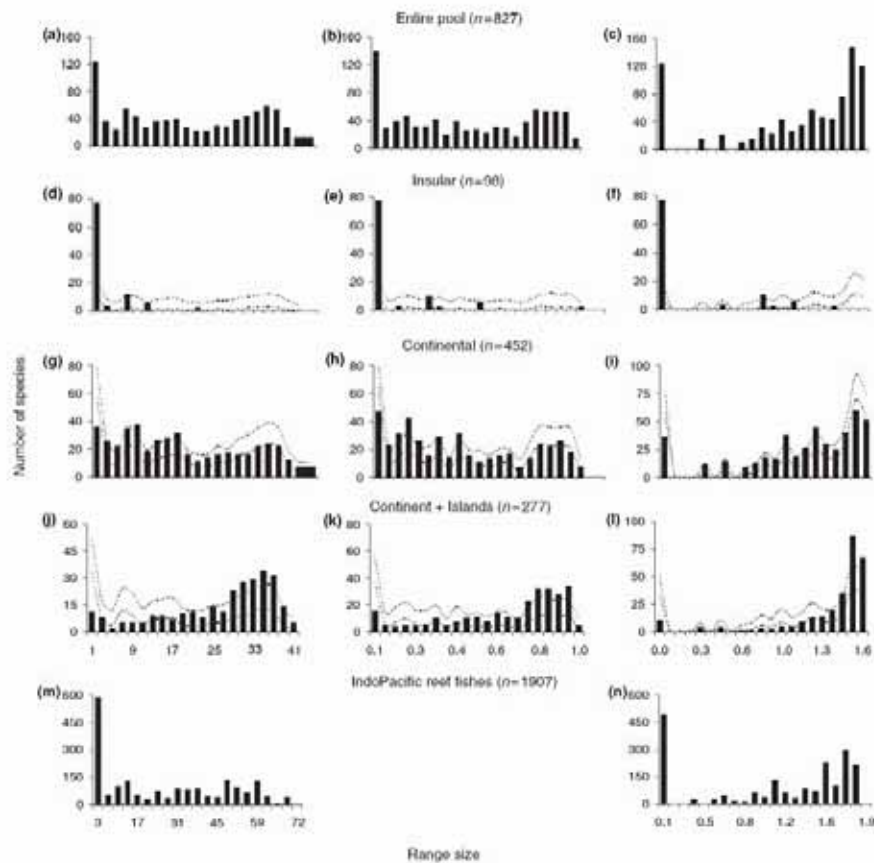
Figure 5.3. Range-size frequency distributions for fishes using different habitats on the continental shore of the Tropical Eastern Pacific. Left: untransformed patterns; Right: log-transformed range sizes. Dotted lines indicate the 95% confidence intervals of a null model (see methods for details).
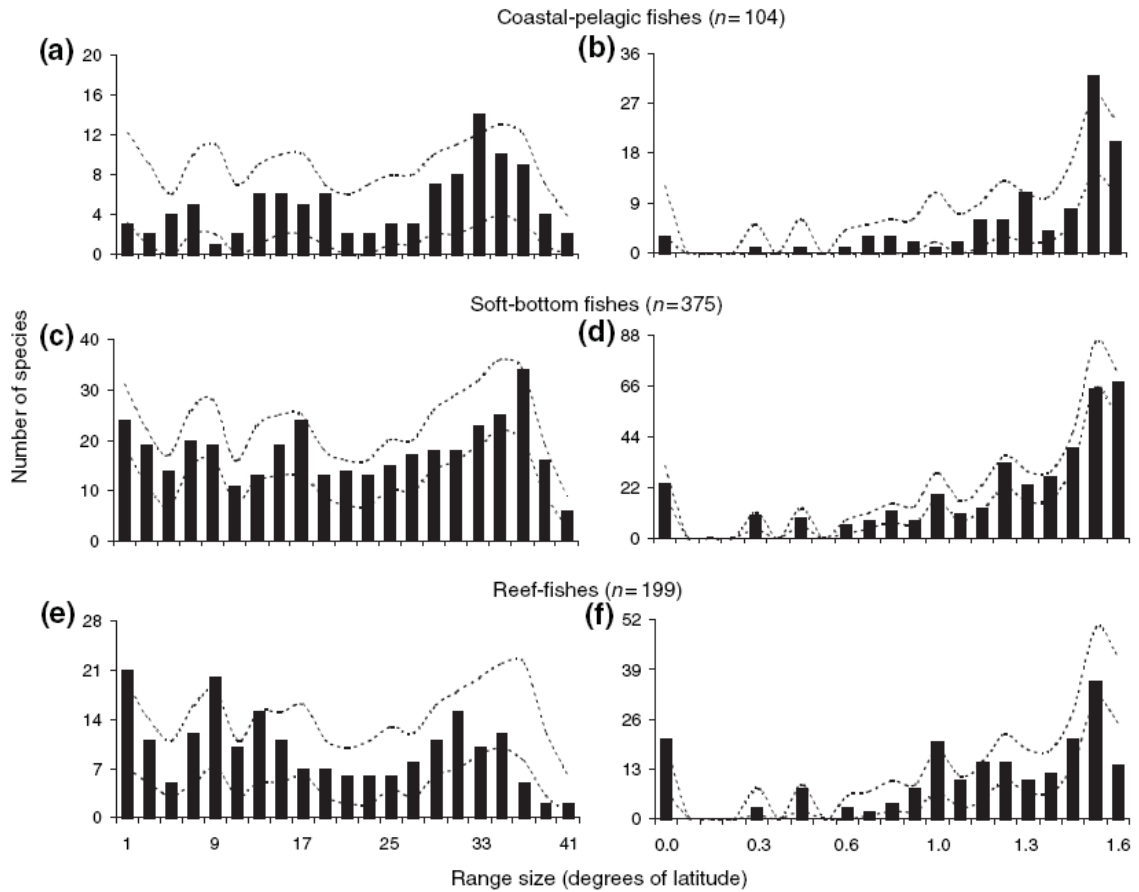
Figure 5.4. Range-size frequency distributions of the reef- and non-reef components of the endemic fish fauna of the TEP. Left: untransformed patterns; Right: log-transformed range sizes. Dotted lines indicate the 95% confidence intervals of a null model (see methods for details).
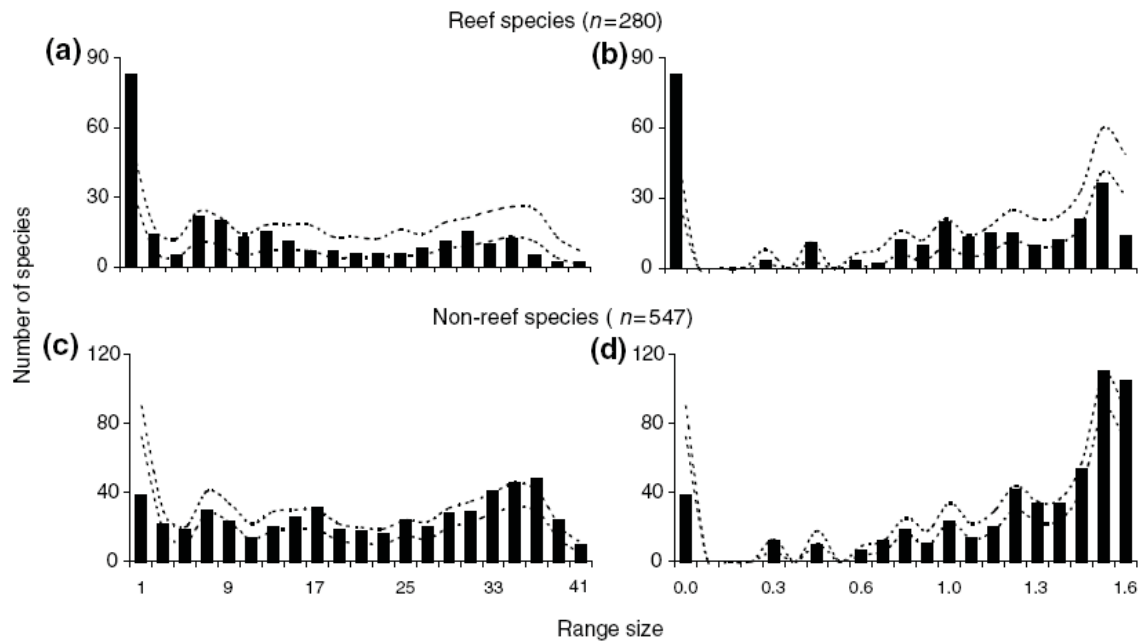
Table 5.1. Statistical descriptors of range-size frequency distributions of the entire endemic fish fauna from the Tropical Eastern Pacific, and components thereof. The range-size frequency distribution of Indo-Pacific reef-fishes (data from Mora et al. 2003) is included for reference. The skews of all log-transformed distributions were significantly different from the log-normal distribution at $p<0.05$.

	n	Untransformed				Log-transformed			
		Mean	Median	Kurtosis	Skew	Mean	Median	Kurtosis	Skew
Endemic TEP fishes									
Entire fauna	827	18.5	17.0	−1.5	0.1	1.1	1.2	−0.4	−1.0
Continent + islands	277	26.0	30.0	−0.2	−0.9	1.3	1.5	5.3	−2.4
Continent only	452	17.4	15.0	−1.2	0.3	1.1	1.2	0.3	−1.0
Islands only	98	2.5	1.0	11.0	3.1	0.2	0.0	1.1	1.6
Coastal-Pelagic	104	23.9	28.5	−1.0	−0.5	1.3	1.5	3.7	−1.9
Soft-bottom	375	20.7	21.0	−1.3	−0.1	1.2	1.3	0.9	−1.3
Reef	199	17.3	15.0	−1.3	0.2	1.1	1.2	0.3	−1.1
All reef fishes	280	13.0	9.0	−1.0	0.7	0.8	1.0	−1.5	−0.3
Remaining diversity	547	21.4	23.0	−1.3	−0.2	1.2	1.4	1.1	−1.4
Indo-Pacific reef-fishes	1907	24.1	21.0	−1.3	0.4	1.0	1.3	−1.3	−0.6

CHAPTER 6: Importance of dispersal on the community structure of coral reef fishes

Introduction

A central aim of ecology is to explain the heterogeneous distribution of biodiversity on earth. As expectations of diversity loss grow (Roberts and Hawkins 1999, Chapin et al. 2000, Roberts et al. 2002,), this understanding is also critical for effective management and conservation (Dayton 2003). Although explanations for biodiversity patterns are still a matter for intense debate (Gaston 2000), they have often been considered to be scale-dependent (Keddy and Wiher 1999, Cornell and Karlson 2000). At large geographical scales, biogeographers have suggested that variation in species richness results from factors such as area, temperature, environmental stability, and geological processes, among many others (Gaston 2000, Cornell and Karlson 2000, Bellwood and Hughes 2001, Veron 1995, Colwell and Lees 2000, Bellwood and Wainwright 2002, Harmelin-Vivien 2002, Rosenzweig 1995). From the species pools generated by these large-scale processes, community ecologists have suggested that local-scale assembly of communities is achieved through processes such as competition, predation, recruitment, disturbances and immigration (See review in Doherty et al. 1991). Here we analyse hypotheses on speciation and dispersal for reef fish from the Indian and Pacific oceans and show how dispersal from a major center of origination can simultaneously account for both large-scale gradients in species richness and the structure of local communities.

Determination of diversity patterns for the Indian and Pacific Oceans

Using a geographical database of species distributions (see Appendix 6.1), we determined large-scale patterns in species richness for reef fish in the Indian and Pacific oceans. From a center of high diversity in the Indonesian and Philippine region (IPR),

species richness decreases steadily along both latitudinal and longitudinal axes (Figure 6.1a-b). Although these patterns are similar in shape to those that one would expect from the mid-domain effect (the pattern expected if species ranges were randomly distributed between geographical boundaries, Colwell and Lees 2000), the overall patterns, and particularly the high number of species in the IPR, result from a nonrandom distribution of species (Figure 6.1a-b).

Tests of hypotheses about speciation and dispersal in the Indian and Pacific Oceans

Three major, yet different, hypotheses invoking speciation and dispersal have been suggested to explain these large-scale patterns. The Center-of-Origin hypothesis suggests that the IPR is a major center of speciation from which species disperse to marginal locations (Veron 1995, Bellwood and Wainwright 2002, Planes 2002). The Center-of-Overlap hypothesis proposes that the high diversity in the IPR is due to the overlapping of faunas from several biogeographic provinces (Veron 1995, Bellwood and Wainwright 2002, Planes 2002). Finally, the Center-of-Accumulation hypothesis states that speciation occurs in multiple areas peripheral to the IPR and that species extend their ranges to the IPR via prevailing currents (Veron 1995, Bellwood and Wainwright 2002, Planes 2002). A variant to Center-of-Accumulation holds that after extending into the IPR, many species have suffered range reductions through the loss of populations marginal to the IPR (Bellwood and Wainwright 2002). While Center-of-Overlap predicts dispersal in all directions within the provinces, Center-of-Accumulation (including its variant) predicts unidirectional dispersal towards the IPR.

The Center-of-Overlap and the Center-of-Accumulation hypotheses state that only the tails of species' ranges extend into the IPR. Consequently, most species should have their range midpoints marginal to the IPR, resulting in bimodal or multi-modal distributions. However, plots of species mid-ranges (both longitudinal and latitudinal) show non-random unimodal distributions with peaks coinciding with the geographical position of the IPR (Figure 6.1c-d). These distributions rule out these two hypotheses and provide support for Center-of-Origin, and to some extent, for the variant of the Center-of-Accumulation hypothesis because range reductions through loss of peripheral populations would shift mid-ranges towards the IPR, and if extensive, this could result in a unimodal distribution of mid-ranges.

The Center-of-Origin and the Center-of-Accumulation (including its variant) hypotheses predict different places of species origination. While Center-of-Origin predicts speciation within the IPR, Center-of-Accumulation predicts speciation in locations marginal to the IPR. To discern between these predictions, we analyzed the geographic pattern in reef fish endemism. We presume that centers of endemism contain a preponderance of recently derived species that are yet to expand their ranges (neo-endemics) and thus provide insights into areas where species most likely originate. It is reasonable to expect that paleo-endemic species, if present, will represent only a small proportion of endemics. Paleo-endemic extinction rates should be high because of their small ranges and longer exposure to factors causing extinction. The IPR stands out as the major center of endemism in the Indian and Pacific Oceans (Fig. 2), a result reported previously for fish as well as for other taxa (Roberts et al. 2002). Hughes et al. (2002) reported lower levels of endemism for the IPR, however, it is important to note that

different criteria to define endemism was used and that most of their data for the IPR was limited to non-judged personal observations). Our result supports the IPR as a major center of speciation and confirms the expectation of the Center-of-Origin hypothesis. Additionally, Springer (1982) has argued that large-scale extinctions have not occurred marginal to the IPR casting doubt on the variant of the Center-of-Accumulation hypothesis.

Our analysis also demonstrates that other minor centers of endemism exist, which might contribute to regional species pools. Most of these minor centers are, however, geographically isolated or in places where current direction is predominately from tropical to temperate latitudes (Roberts et al. 2002) (Figure 6.2). Thus, species generated in these outlying centers of origin likely would not contribute significantly to species pools in other communities. By contrast, the IPR occurs in a highly interconnected area that may facilitate species migration or dispersal to marginal locations. That the IPR harbors among the highest number of islands per unit of geographical area makes it a place where allopatric speciation might be frequent, especially when considering patterns of recent geological sea level change. Whatever the ultimate causal factor, the IPR appears to be a center of species origination and a source of species for reef fish communities in the Indian and Pacific oceans.

Effect of dispersal after speciation on diversity patterns

The notion that reef fishes originate in the IPR and disperse to marginal communities leads to two testable predictions about patterns in reef fish biodiversity: 1) both the

longitudinal and latitudinal gradients of species richness, as one moves away from the IPR, are due to variation in dispersal abilities; and 2) this process will supply the species structuring communities marginal to the IPR. To test the first prediction, we correlated data on species richness for all locations analyzed with the mean pelagic larval duration (PLD) of the species inhabiting those locations. This analysis was restricted to labrids and pomacentrids, the only families for which extensive information on PLD exists (see Methods). We found, as expected, that species richness in both families was negatively correlated with distance from the IPR (Figure 6.3a-e), and that mean PLD for these families increased with increasing distance from the IPR (Figure 6.3b-f) (see also Bonhomme and Planes 2000). Consequently, species richness was negatively correlated with mean PLD at local sites (Figure 6.3c-g). These results indicate that species richness declines as one move away from the IPR, likely owing to limitations in dispersal. Using multiple regression analysis, we found that 57 and 60% of the geographical variation in species richness of Labridae and Pomacentridae, respectively, was explained by PLD and distance from the IPR.

Interestingly, we also found that communities at high latitudes were usually outliers in the relationship between PLD and species richness. The geographical variation in species richness explained by PLD increases when the latitudinal scope of the analysis is reduced (Fig. 3d-h). We presume that shallow-water habitats, which are poorly interconnected in longitude due to deep-water gaps between islands and coasts, but continuous in latitude due to the margins of the continents, make PLD more critical for expansion in longitude than for expansion in latitude. Additionally, sharp barriers (e.g, current and temperature shifts) may limit species expansion at high latitudes regardless of

PLD (Gaylord and Gaines 2000). This suggests that PLD gains additional importance for species distribution and richness where geographical isolation is predominant and that due to the geography of the Indian and Pacific oceans the extent to which different processes regulate local communities may vary geographically. Likely communities at lower latitudes are assembled primarily by distance to, and the abilities of species to disperse across open water from the IPR, whereas extreme abiotic factors may cause local extinctions at higher latitudes.

If the IPR is a center of origin and a source of species to reef fish communities in the Indian and Pacific oceans, and, if local processes affect local diversity only minimally, then reef fish communities throughout this region should have a large number of species in common with the IPR. Indeed, we found that ~86% of the species comprising reef fish assemblages in the Indian and Pacific oceans were species present in the IPR, a result that differs from expectations based on random assembly (Figure 6.4). Moreover, local speciation seems to have a minor role structuring marginal communities given that only ~2% of the species in any community were endemics (Figure 6.4). These results suggest that speciation in and dispersal from the IPR play a major role in assembling communities in the Indian and Pacific oceans. That is, dispersal governs which species from the IPR are capable of reaching communities at marginal locations. The fact that the total number of species present in any location is almost equal to the number of species that it shares with the IPR suggests that no location contributes as much to the overall alpha diversity of the Indian and Pacific oceans as does the IPR.

Concluding remarks

The distribution of biodiversity on Earth can be described in terms of a few well documented, and intriguing, small- to large-scale patterns. Our findings recognize a major link between the evolutionary processes regulating these patterns. That is, the processes of speciation, extinction and dispersal that yield large-scale patterns of species richness also appear to determine which species are present within local assemblages. Given the importance of the IPR to the overall structure of reef fish assemblages in the Indian and Pacific oceans, it certainly should be a target for strategic management and protection. This study also highlights the need for protection of sites marginal to the IPR if the connectivity that maintains broad diversity patterns is to be properly conserved.

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Figure 6.1. Geographical patterns in reef fish biodiversity in the Indian and Pacific oceans. Latitudinal (a) and longitudinal (b) clines (solid lines) were defined as the number of species whose geographical ranges included a point in latitude or longitude, respectively. Distributions of mid-latitudinal (c) and mid-longitudinal (d) ranges (open bars). The effects of geographic constraints on such patterns [the mid-domain effect (Colwell and Lees 2000)] were tested by running a null model in which the ranges (for a-b) and mid-ranges (for c-d) were randomly allocated between boundaries. These boundaries were the 'hard' limits imposed by the coasts of Africa and America in longitude and the 'soft' limits implied by the 37°N and 32°S latitude where tropical organisms show striking reductions in species richness (Gaylord and Gaines 2000). Dotted lines correspond to the maximum and minimum values after running the model 1,000 times.
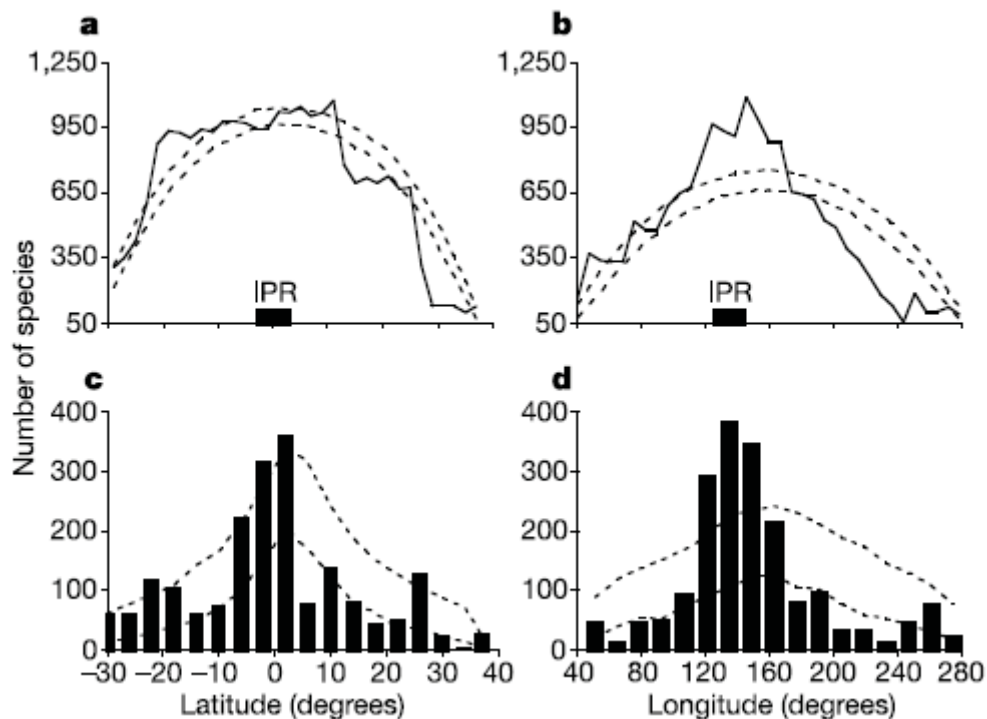
Figure 6.2. Geographical pattern of reef fish endemism in the Indian and Pacific oceans. Endemic species were defined as those species restricted to a single location in the database. Numbers in the graph indicate the number of endemic species at each location. To simplify the figure, we combined endemic species of nearby locations into a single number. These locations are enclosed with a red line.

Figure 6.3. Pairwise comparisons of species richness, pelagic larval duration (PLD), and distance from the Indonesian and Philippine Region in Labridae and Pomacentridae. For Labridae (a: r=-0.73, *P*<0.001; b: r=0.70, n=62, *P*<0.001; c: r=-0.64, n=62, *P*<0.001) and Pomacentridae (e: r=-0.69, *P*<0.001; f: r=0.72, *P*<0.001; g: r=-0.67, *P*<0.001). The sample size in all correlations, except b and c, was 63 locations between 29ºN and 29ºS. Panels d and h show the coefficients of determination for regression analyses between species richness (dependent variable) and mean PLD (independent variable) for 12 latitudinal intervals (d: Labridae: r=-0.92, *P*< 0.001; and h: Pomacentridae: r=-0.90, *P*<0.001). The extent to which the latitudinal pattern in coefficient of determination was a statistical artifact was tested by simulating the regressions for each latitudinal interval, using the same number of locations, but randomly selected from all latitudes. Dotted lines are 95% limits of confidence for coefficients of determination of 1,000 regression analyses for each of the 12 latitudinal intervals.
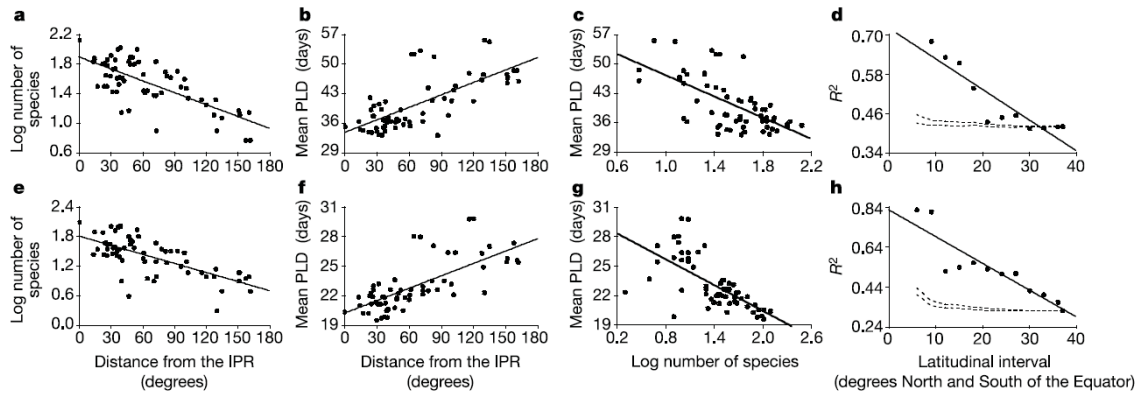
Figure 6.4. Contribution of IPR species (filled circles) and endemic species (open circles) to local reef fish assemblages in the Indian and Pacific Oceans. The extent to which the number of IPR species at local communities is due to chance was assessed by determining the number of IPR species in communities randomly generated from the total species pool (species entered to communities with equal probability and without replacement). The upper and lower limits of the number of IPR species in 1000 iterations for each community are presented (broken lines).
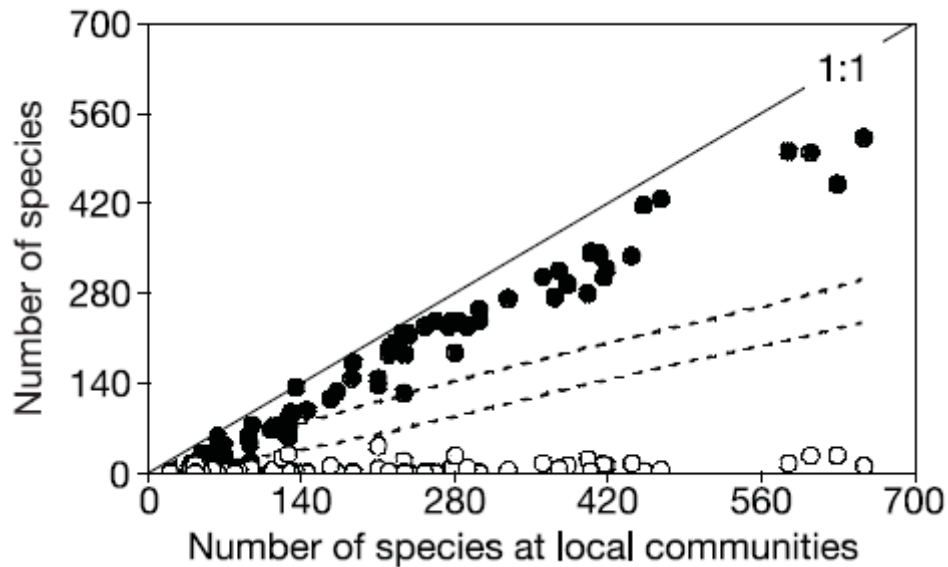
Appendix 6.1. Database.

Analyses were based on the presence/ absence of 1,970 reef fish species in 70 locations in the Indian and Pacific oceans. These species belong to the families Labridae, Pomacentridae, Serranidae, Blenniidae, Apogonidae, Chaetodontidae, Acanthuridae, Scaridae, Holocentridae, Lutjanidae, Pomacanthidae, Scorpaenidae, and Lethrinidae. These families are among the most diverse, best known taxonomically, and represent >70% of the total species expected at any community. Due to the high covariation in species richness among families (Bellwood and Hughes 2001), these families are a good indicator for the remaining diversity of species. The database includes all data from the 63 locations used by Bellwood and Hughes (2001). Data for the following locations were added: Philippines, Madagascar, Easter Island, Cook Islands (all from www.fishbase.org), Cocos Keeling (Allen and Smith-Vaniz 1994); Gorgona Reef (Zapata and Moralez 1998); and Korea (http://ricos.cnu.ac.kr/~kocofish/list/elistintro.htm). Data for the following locations were updated: Galapagos (Grove and Lavenberg 1997); Gulf of California (Thompson et al. 1999); and Malpelo (C. Mora pers. obs). All species records were corrected for synonymy and other taxonomic problems using The Catalog of Fishes (http://www.calacademy. org/research/ichthyology/catalog/fishcatsearch.html). More than 300 species were duplicated in the original database as a result of synonymy, misspelled names or misallocation of species to families.

Pelagic larval durations were obtained for 95 labrid species and 116 pomacentrids. These species represent 28 % of all labrid species and 42% of the pomacentrids. Data were obtained from Bonhomme and Planes (2000), Victor (1986), Victor and Wellington (2000), and Wellington and Victor (1989).

Appendix 6.2. Mid-domain model.

Patterns in species richness and mid-ranges in the Indian and Pacific Oceans were compared with patterns arising from the random placement of ranges within the boundaries of those oceans (i.e. the so-call mid-domain effect). A model for the mid-domain effect was constructed by randomly placing species ranges between the boundaries of these oceans' domains to the extent possible without placing ranges' edges beyond the limits of the domains (after Colwell and Lees 2000). After the random placement of the ranges, species richness and mid-ranges were quantified at specific intervals of latitude or longitude as the total number of species whose ranges and mid-ranges were included in those intervals, respectively. This model was constructed in Excel (see window 6.2.1) and repeated 1000 times with the use of a macro (see window 6.2.2). 95% limits of confidence of these repetitions are shown in Figure 6.1.
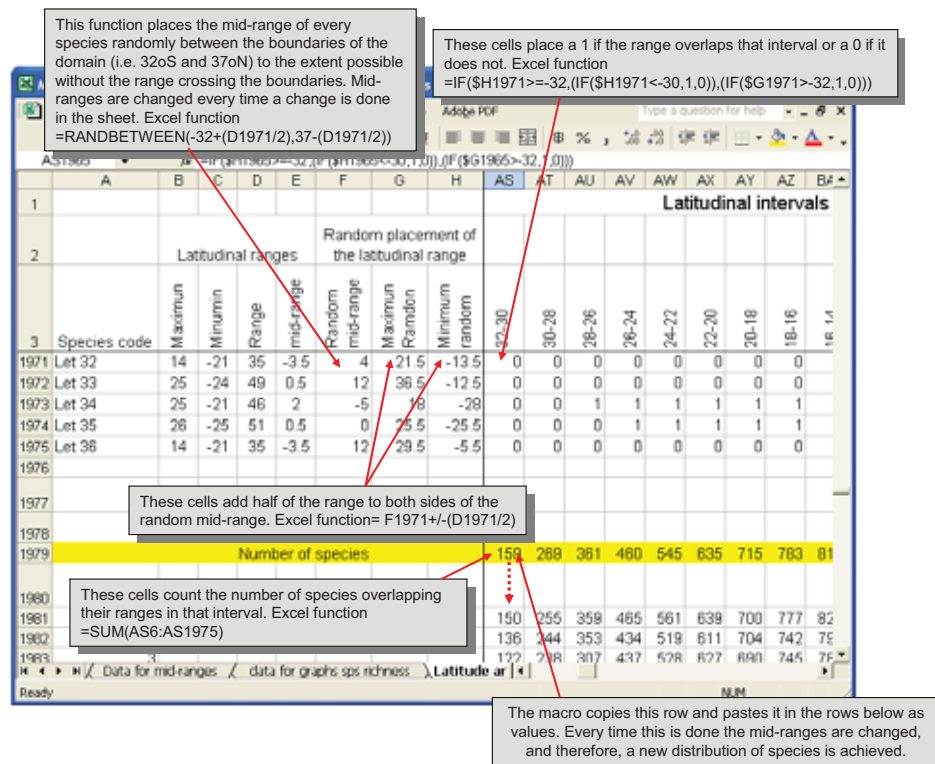
Window 6.2.1. Description of the mid-domain model

121
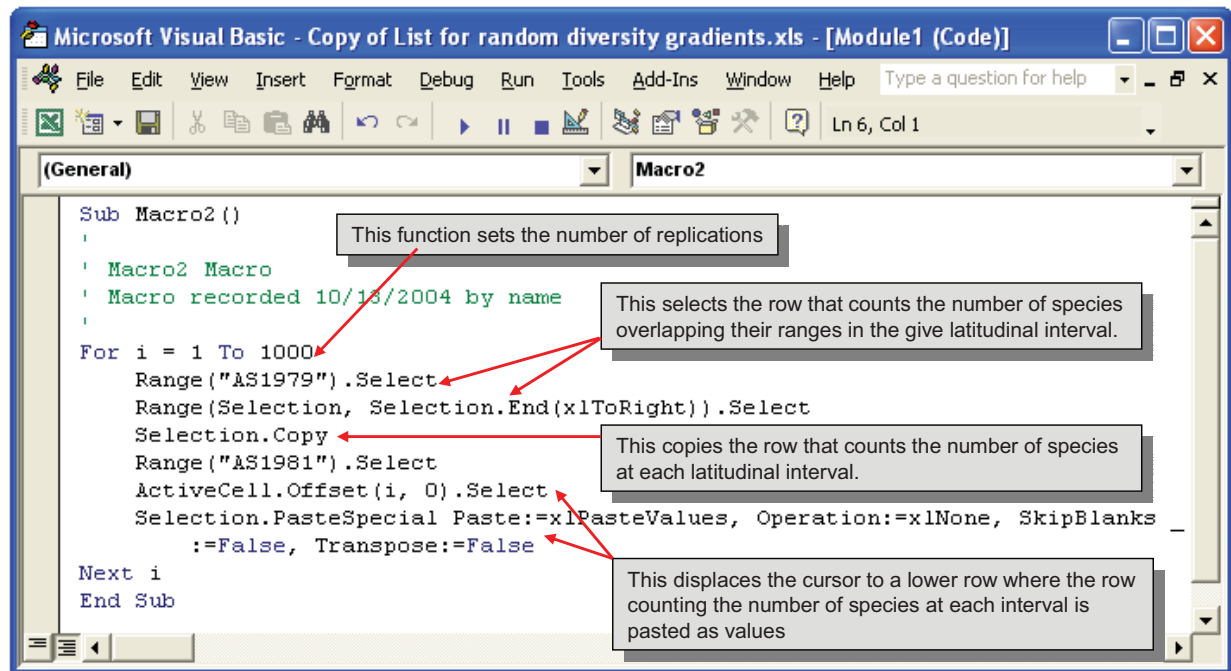
Window 6.2.2. Description of the macro for the mid-domain model.

Appendix 6.3. Null model for the composition similarity between the IPR and communities from the Indian and Pacific Oceans.

In Figure 6.4, I reported a large number of species in common between the IPR and communities of the Indian and Pacific Oceans. I used this pattern, in addition to other evidence, to support the idea that species originate in the IPR and then they disperse, which in turn seems to affect the number and identity of species present in communities marginal to the IPR. Here I develop a null model that tests whether the pattern in commonness of species between the IPR and marginal communities could be due to chance alone. For this model, I assembled communities, of similar size to those found in these Oceans, by randomly drawing species from the total pool of species and determining the number of those species that were in common to the IPR. This model was done in Excel (see window 6.3.1) and replicated 1000 times with a macro (see
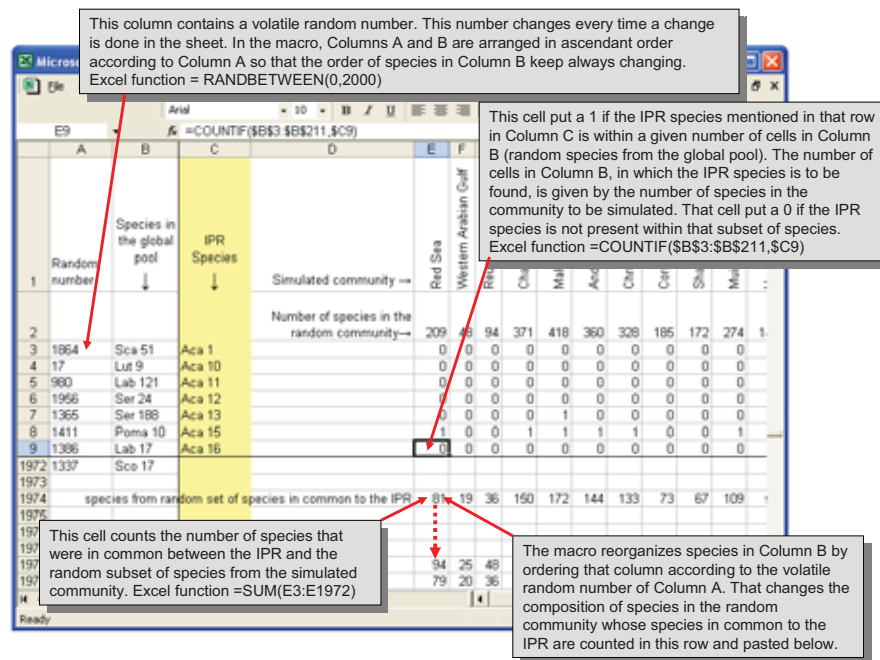
Window 6.3.1. Description of the model for the composition similarity between the IPR and communities from the Indian and Pacific Oceans.

window 6.3.2). The 95% confidence limits of these replications are shown in Figure 6.4.


```
Microsoft Visual Basic - model sp in common to the IPR (version 1).xls - [Module3 (Code)]

File   Edit   View   Insert   Format   Debug   Run   Tools   Add-Ins   Window   Help      Type a question for help

(General)                                                    Macro1

    Sub Macro1()
    '
    '   Macro1 Macro
    '   Macro recorded 10/14/2004 by name
    '
    For i = 1 To 1000
        Range("A1972:B1972").Select
        Range("B1972").Activate
        Range(Selection, Selection.End(xlUp)).Select
        Selection.Sort Key1:=Range("A3"), Order1:=xlAscending, Header:=xlGuess, _
            OrderCustom:=1, MatchCase:=False, Orientation:=xlTopToBottom, _
            DataOption1:=xlSortNormal
        Range("E1974").Select
        Range(Selection, Selection.End(xlToRight)).Select
        Selection.Copy
        Range("E1978").Select
        ActiveCell.Offset(i, 0).Select
        Selection.PasteSpecial Paste:=xlPasteValues, Operation:= _
            :=False, Transpose:=False
    Next i
    End Sub
```

This function sets the number of replications

This selects the columns with the volatile random number (Column A) and the global pool of species (Column B) and sort them in ascendant order by Column A. Such procedure randomizes the species considered in the simulated community.

This selects and copies the row containing the number of species in common between the IPR and the different simulated communities

This pastes the row containing the number of species in common between the IPR and the different simulated communities as values in the rows below

Window 6.3.2 Description of the macro for the composition similarity between the IPR and communities from the Indian and Pacific Oceans

CHAPTER 7: General Discussion

Introduction

Coral reef fishes form one of the most diverse and abundant assemblages of vertebrates to be found anywhere in the world. Their diversity, however, is under high threat as a result of human activities arising from overfishing, habitat deterioration, global warming and others (Dudley et al. 1995, Jackson et al. 2001, Roberts et al. 2002, Hughes et al. 2003). This situation has added particular impetus to the need for understanding of the processes underlying their diversity if they are to be properly protected (Sale 2002, Palumbi 2003, Dayton 2003). However, our understanding of ecological patterns is still limited and has often been controversial. For instance, population and community ecologists have argued for decades on the importance of ecological factors such as competition, predation and recruitment in determining the size of local populations and communities (reviews by Doherty et al. 1991, Jones et al. 1991). Similarly, biogeographers have argued over the importance of environmental factors such as area, temperature, environmental stability and random processes in determining spatial variations in the number of species (see Jones et al. 2002, Gaston 2003, Willig et al. 2003, Mora and Robertson in press). As the agreement within disciplines is still lacking an across-discipline assessment of processes seems still quite remote.

Several theoretical concepts have recently raised the possibility that single mechanisms could account for diversity patterns observed in nature. For instance, Hubbell's (2002) neutral theory suggests that everything being equal variations in local populations and the dispersal of their propagules could account for a wide variety of patterns of distribution and abundance of species. Similarly, Brown et al. (2004) suggests that an organism's metabolism and use of energetic resources shape a wide variety of

patterns; patterns that Hubbell also suggests could be accounted for by his neutral theory. This mode of ecological assessment of diversity patterns (i.e. through single mechanisms) will encourage ecologists to revise the procedures of comparative analyses in ecology and to re-evaluate the functional interpretations of ecological patterns (Bell 2001). Because there already exist different concerns about the importance of specific processes (e.g. dispersal vs. metabolism) their testing becomes critical to our understanding of ecological patterns. Here I provide evidence for the importance of dispersal in several ecological patterns of coral reef fishes.

In coral reef fishes, the existence of a pelagic larval period makes dispersal an obligate step in their life cycle. This step will lead to 1) the openness of local populations so that their dynamics could be regulated by non-local factors, 2) the potential for range expansions and 3) the interconnection of populations within communities encompassing the species' range. It will also determine the extent of a species' resilience to threats arising from overfishing, habitat deterioration, global warming and other disturbances (explained at the end of this Chapter). Such a broad potential effect of dispersal makes its study critical to our understanding of diversity patterns and their conservation. However, regardless of the system [e.g. terrestrial (Clobert et al. 2001), freshwater (Bilton et al. 2001) or marine (Leis 2002, Mora and Sale 2002)] dispersal has been difficult to study because dispersing propagules are often minute and move in vast spaces. In coral reef fishes, the existence of complex behaviors of the dispersing propagules has also added further difficulties to the study of dispersal (Chapter 2). There is an interesting paradox: dispersal seems to be a critical ecological process but we do not know much about it.

Scales of larval dispersal

Deriving valid concepts about the consequences of dispersal depends largely on our

knowledge of the scales of larval dispersal. However, the spatial scales of dispersal in

coral reef fishes are unclear as they are in other systems (reviewed by Cloberg et al.

2001; Bilton et al. 2001). Genetic models suggest that reef fishes disperse at the scales of

tens of km (Palumbi 2003, Kinlan and Gaines 2003). Hydrodynamic models suggest that

dispersal may be at the scales of hundreds of km (Roberts 1997), and there are a few

empirical data suggesting that they may even disperse at scales of thousands of km

(Victor 1987, Clarke 1995, Mora et al. 2001). Data in chapter 3 highlight the diversity of

scales of dispersal shown by larvae of the bicolor damselfish in the MBRS providing a

basis for contrasting arguments about the openness of reef fish populations and scales of

dispersal (see Chapter 2). I also found that dispersal does not affect larvae energetically

to an extent that will affect their pelagic or benthic survival (Chapter 4), suggesting that

dispersal has the potential to be a highly heterogeneous process in the bicolor damselfish.

This is only to be expected considering the variety in larval behaviors, their ontogenetic

development, and the variety of hydrodynamic processes and of topographies in which

reef fishes and their propagules live. For the same reasons it is also expected that the

dispersal patterns observed in the bicolor damselfish will differ from those of other

species or even within this species in different places and times as shown in comparisons

of *S. partitus* in the Florida keys (Lacson et al. 1989, Lacson and Mozori 1991, see

discussion of Chapter 3). It is likely that such intra- and inter-specific heterogeneity of

dispersal distances will have an important role in explaining both the strong temporal and

spatial variation in recruitment patterns commonly observed in coral reef fishes, and the

strong contrast in genetic structure among populations of different species within the same geographical systems (e.g. Doherty et al. 1995).

Dispersal and range size

Explaining failure of previous studies

Variations in dispersal distances are likely to account to some extent for the inter-specific variation in geographical ranges observed among reef fishes. This interaction between dispersal and range has been of wide interest among reef fish ecologists. However, quantitative studies on species within several families have failed to demonstrate any relationship between estimates of larval dispersal (e.g. pelagic larval duration, swimming abilities) and geographic range (Thresher and Brothers 1985, Thresher et al. 1989, Wellington and Victor 1989, Stobutzki 1998, Victor and Wellington 2000, Jones et al. 2002). Victor (1991) suggested, as the causes for such lack of correlation between dispersal and range, inaccurate measurement of geographic range, small sample sizes, and poor accounting for larval behaviors. Two explanations for such lack of correlation are evident from this thesis. Geographical ranges are often based on the most extreme locations where species have been found. Colonization of such extreme places will be done by the few individuals that disperse extensive distances (i.e. the right hand tail of the frequency distribution of dispersal distances; Figure 7.1; Chapter 3). The low frequency of these individuals in natural populations suggests that sample sizes have to be enormous to collect the few individuals whose dispersal may influence range size. Sample sizes in studies analyzing the relationship between dispersal and range size are usually a few tens of individuals with most species being represented by less than ten and

a handful only one or two individuals (Thresher and Brothers 1985, Thresher et al. 1989, Wellington and Victor 1989, Stobutzki 1998, Victor and Wellington 2000). This suggests that small sample size could be one of the major limitations of these studies. From Chapters 5 and 6, it was also clear that geography affects dispersal (i.e. dispersal is constrained as habitat patchiness increases) and therefore range size will be constrained by dispersal only on those fronts where isolation is extreme. Failing to account for geographical variations in the levels of habitat isolation may be another reason for the poor correlation between dispersal and range as most previous studies have considered the range to be rather uniform in geography.

What causes the size and shape of species ranges

The size and shape of the geographical distribution of species is very likely determined by the extent to which geographical attributes challenge species traits [i.e. assuming that ecological interaction such as predation and competition are of minimum effect; as may be the case at such large scales (e.g. Karlson et al. 2004, Chapter 6)]. The results from Chapter 5 provided some insights into the species traits that are challenged by the specific geography of a particular tropical region [i.e. the Tropical Eastern Pacific (TEP)]. In that chapter, I found that range size decreases among species whose habitats increase in isolation. I suggested that this pattern arises from increasing difficulties, in terms of dispersal, for connection among patches of habitats increasing in separation. However, this chapter also points out that when dispersal is facilitated by habitat continuity species will expand their ranges until other traits start being challenged. Note for instance that pelagic species from the Tropical Eastern Pacific (TEP) did have their

ranges constrained within that region despite the fact that their habitat was continuous

outside that region (i.e. their habitat is continuous throughout the entire coast of the

Americas). It is well known that the boundaries of the TEP are set by strong changes in

temperature determined by westward shifts in the polar currents of Peru and California

(Gaylord and Gaynes 2001, Mora and Robertson 2005, in press). In the case of pelagic

species from the TEP, it is likely that dispersal expands species ranges until species

encounter thermal conditions outside their levels of thermal tolerance.

The extent to which dispersal and thermal tolerances influence species ranges

may also apply to fishes from the west Pacific and Indian Ocean. In these oceans, the

geographical distribution of most species is known to be wider in longitude than in

latitude (Jones et al. 2002). This pattern also holds for the species of reef fishes that I

analyzed in Chapter 6 (see Figure 7.2). The flat shape of species ranges in these oceans is

very likely determined by the rectangular shape of a geographical domain that could be

set by thermal tolerance and dispersal. The tropical region of these oceans is set at ~30°S

and 30°N also by changes in temperature (e.g. Veron 1994). If dispersal allows full

covering of such domain then species ranges in latitude may be expected to be about 60

degrees in width from North to South. In contrast, in a east-west direction there is a ~250

degrees expanse between the eastern coast of Africa and the western cost of America that

lacks drastic changes in temperature but which is very patchy in habitat (see Figure 6.2).

That means that in longitude species can expand their ranges without encountering

physiological boundaries but may lack the continuity of habitat required to cover the

entire expanse of this longitudinal domain. One interesting aspect of the pattern shown in

Figure 7.2. is that species with dispersal capabilities to cover more than 60° of longitude

are almost fully distributed in the 60° of latitude that are set if drastic changes in temperature are encountered. This could be explained if species disperse similarly in latitude and longitude but their ranges start being considerably truncated in latitude as they likely face conditions of thermal intolerance.

Dispersal and macroecological patterns in community assembly

If dispersal expands the distribution of species to the extent to which geographical attributes such as isolation and thermal conditions allow, then variations in dispersal among species may explain gradients in the number of species and macroecological patterns of species coexistence within communities (assuming that role of local ecological factors such as predation, competition, and others is minimum). I test these hypotheses in Chapter 6 by determining the extent to which dispersal after speciation determines the number of species and assembly of local communities. Critical to these hypotheses is to find out the places where species originate. In the Indian and Pacific Oceans, patterns of endemism and distribution of species mid-ranges suggested that the central expanse of the Indonesian and Philippine Region (IPR) is one of the main areas for the origination of species (Chapter 6). Brings (2003) and Gaston (2003), support this hypothesis suggesting that such center of biodiversity may exhibit high rates of origination because of the high number of islands which may enhance allopatric speciation and because of a positive "feedback" in which high levels of speciation encourage more speciation. That is based on the argument that the chance for a species to speciate is an inverse function of its range (Jablonski and Roy 2003).

Dispersal from the IPR may produce clines in the number of species that should be related to variations in dispersal capabilities. The support for this idea was striking as dispersal capabilities among species of two reef fish families increased with increasing distance from the IPR, which in turn was related to latitudinal and longitudinal clines in the number of species from the IPR (i.e. across communities there was a negative relationship between their species richness and the dispersal capabilities of their members; Figure 6.3). Also striking is the fact that the strength of such relationship increased as narrower tropical bands were analyzed. This declining effect of dispersal on the number of species as latitude increases is very likely due to the fact that physiological factors are kicking in, limiting the distribution of species at high latitudes (as I point out above). The data from this chapter also point to a critical role of dispersal from the IPR in the structure of local communities as all communities within those oceans have a strong similarity of species with the IPR. In short, local assemblages of reef fishes in the Indian and Pacific Oceans are shaped in large part by which species have been able to reach them from the IPR. On a regional scale, patterns in species richness have likewise been shaped by how many species have reached the different locations.

Fitting of results in an overall ecological context

The results shown so far conform well to an increasing body of research that suggests that local communities are unsaturated and open to the immigration of species from regional pools (i.e. species in local assemblages are not much different to a random subset of the species present in the regional pool) (e.g. Caley and Schluter 1997, Karlson et al. 2004). Such pattern has been shown in a wide variety of terrestrial and aquatic

marine and fresh water systems (reviewed in Gaston and Blackburn 2000, Gaston 2003) and has been explained to arise from a minimal effect of local ecological factors and of dispersal supplying propagules for the sustaining of populations at regional scales (e.g. Caley and Schluter 1997). One of the main contributions of this thesis to that body of work is the understanding of how such regional pools are generated.

Ecology lacks a formal general theory to account, in a simple fashion, for the patterns of diversity that we observe in nature (Bell 2001, Brown et al. 2004). This thesis is an attempt to unify principles for the development of a paradigm to apply dispersal theory to different levels of biological organization at different spatial scales. In such a macroecological attempt I have shown that during the process of dispersal, species interchange propagules among populations (Chapters 2, 3, 4) affecting their dynamics and spatial patterns of genetic structure, the geographical extent of their range (Chapter 5) and their presence in communities within that range (Chapter 6). This provides one of the first empirical demonstrations for a specific taxon of a single mechanism to account for a range of seemingly disparate patterns.

The generality of dispersal in shaping multiple macroecological patterns in other systems is still to be tested. At present, there is a lack of such unifying macroecological studies, which is mainly due to the relatively recent interests of assessing specific processes across patterns (Bell 2001, Hubbell 2002, Brown et al. 2004) and the subdivision in different ecological disciplines of the study of diversity patterns. Note for instance that some of the most outstanding recent macroecological books (e.g. Gaston and Blackburn 2000, Gaston 2003) analyze macroecological patterns and their potential processes independently. Although theoretical examples suggest that the effect of

dispersal can be widespread (e.g. Hubbell's neutral theory) empirical data supporting this contention on the diversity patterns for a specific taxon are largely lacking. Nevertheless, the life cycle of coral reef fishes resembles that of other organisms like marine and freshwater invertebrates and even some plants. They share adult stages that are highly sedentary and occupy patchily distributed habitats, and early life stages that are often very dispersive. These similarities suggest that the multi-pattern effect of dispersal shown in reef fishes may be common to other organisms.

Implications for conservation

Coral reef fishes are a highly threatened group of vertebrates. They not only have most of their diversity concentrated in areas where human threats are intensified (Roberts et al. 2002) and conservation resources are minimal (Hughes et al. 2003), but in addition most species have small ranges (Hawkins et al. 2001, Chapter 5), which expose them to extinction by relatively small-scale disturbances. It has been widely claimed that proper protection of such diversity will depend on the extent to which we understand the processes that generate and maintain such diversity (Dayton 2003, Palumbi 2003). The results shown here concerning the importance of dispersal on reef fish diversity highlight some of the potential mechanisms by which human activities will threaten this diversity. Note for instance that total habitat loss will increase distance between suitable patches, which in turn can reduce dispersal and constrain species ranges exposing them to extinction by small-scale disturbances. Partial habitat loss as well as overfishing will reduce local stocks and therefore the amount of propagules that replenish local populations. Finally global warming will displace thermal "niches" geographically and

the extent to which species will cope with this threat will depend on their capabilities to disperse into more benign habitats. The combined effect of these threats is still unknown but it will very likely be synergistic as dispersal capabilities to respond to global warming may be challenged by habitat isolation (which will be increased by habitat loss) and the number of propagules (which will be reduced by the effects of partial habitat loss and overfishing). This highlights the need for more detailed information on the scales in which populations and communities are connected and for conservation strategies that warrant the connectivity that maintains diversity patterns in reef fishes.

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Figure 7.1. Frequency distribution of dispersal distances. The frequency distribution of dispersal distances in ecological systems has been speculated to be right-skew (continuous line) (after Clobert et al. 2001) but the bicolour damselfish deviates from this pattern by having a second mode of dispersal distances at intermediate distances (dotted line).
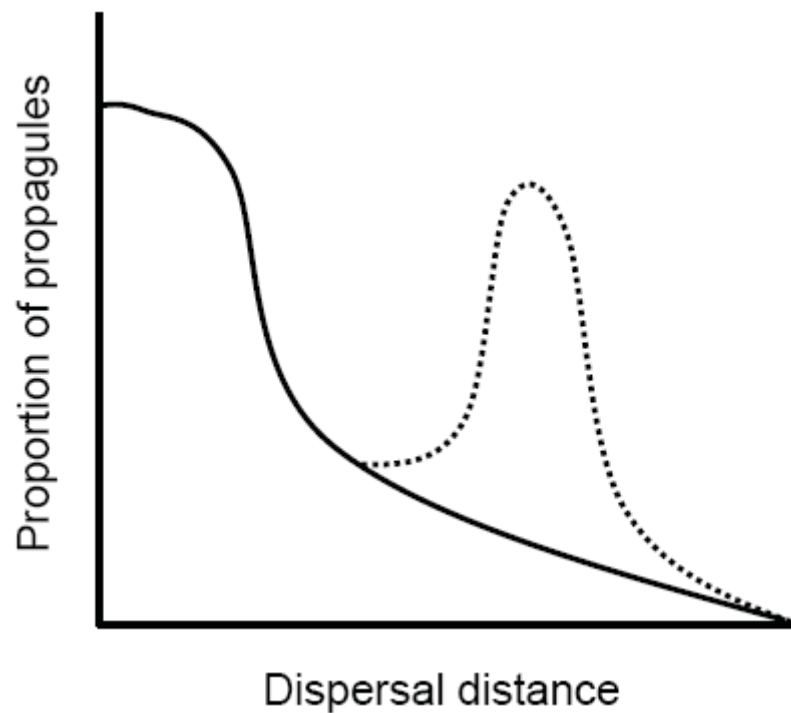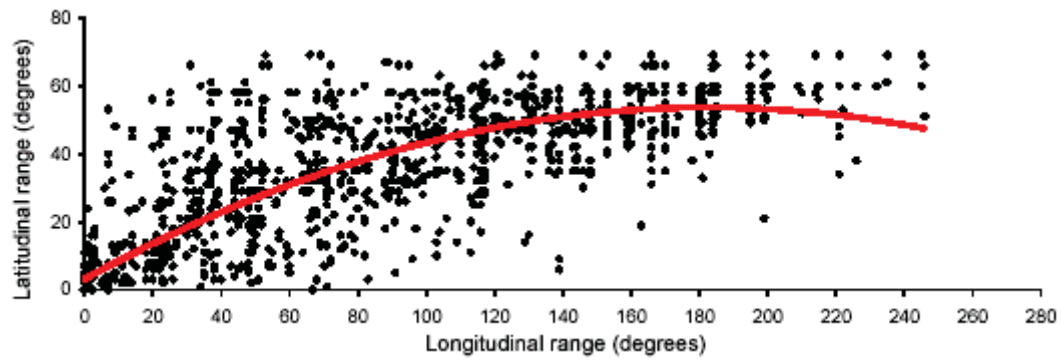
Figure 7.2. Comparison between latitudinal and longitudinal range size of reef fishes from the Indian and Pacific Oceans.

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