HOME RANGE RELOCATION: HOW HABITAT QUALITY, LANDSCAPE CONNECTIVITY AND DENSITY AFFECT MOVEMENTS IN CORAL REEF FISH

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THESIS ABSTRACT

Short-term immigration via home range relocation has important implications for metapopulation dynamics, sustainable harvest and pest control strategies, and conservation in populations experiencing high localized mortality. Despite its importance, no suitable theory is available to predict immigration in response to harvest near an adjacent protected area. There is also little information about the factors that influence the magnitude of immigration. I developed a compensatory immigration model to predict the effect of harvesting on immigration under different assumptions about the factors limiting immigration. The model predicts that immigration from protected areas can contribute importantly to total yield and population recovery in the harvest area and can strongly affect demography in the protected area. Immigration and total yield can show complex non-linear relationships with harvesting as the size of the protected area, initial rate of replacement, mobility and behavioral interactions vary. I carried out field experiments to validate the model and assess the relative influence of limiting factors to immigration (*i.e.* population size in the protected area, the relative habitat quality and functional connectivity between the harvest and protected area). I used longfin (*Stegastes dienaceus*) and dusky damselfish (*S. adustus*) as a model system. I first examined functional connectivity by translocating damselfish to investigate which habitat or social features represent a barrier to movement during homing. Small sand gaps constitute a partial barrier to movement, but the effect of sand gap width varies with reef configuration, and fish minimize travel over conspecific territories. I carried out replicated, experimental, incremental reduction of damselfish populations to examine the mechanisms behind home range relocation at the scale of the territory and to evaluate immigration at the landscape scale. At the territory scale, the probability that a territory would be recolonized decreases with local density. Territories tend to be reoccupied by individuals of the same species, sex and size as the original occupant, but territories occupied by larger individuals are more likely to be recolonized. At the landscape scale, models assuming a constant but partial replacement of removed individuals predict immigration much better than models that include either no replacement or complete replacement. In several sites, the best fitting model also included parameters describing density dependence that changed in direction and magnitude with cumulative harvest. Total yield and the proportion of removed individuals replaced by immigrants were correlated with the combined effects of relative habitat quality and connectivity of replicate sites. Overall, my thesis proposes and tests a new compensatory immigration model to predict immigration from protected to harvested areas and suggests that variation in mobility, habitat quality, functional connectivity and behavioral interactions must be considered when predicting the effects of immigration in a harvesting context on metapopulation dynamics, sustainable harvest and conservation.

RÉSUMÉ DE LA THÈSE

Dans les populations qui sont soumises à une forte mortalité locale, l'immigration à court terme - via la relocalisation du domaine vital - a d'importantes implications pour la dynamique des métapopulations, l'exploitation soutenable des ressources, la lutte contre les espèces introduites et invasives et la conservation. Malgré son importance, il n'existe pas de théorie prédisant l'immigration dans une zone exploitée à partir d'une zone protégée adjacente. Il existe aussi très peu d'information sur les facteurs influençant l'intensité de l'immigration. J'ai développé un modèle d'immigration compensatoire afin de prédire les effets d'une réduction locale de la densité sur l'immigration en utilisant des scénarios hypothétiques qui varient dans l'inclusion de facteurs limitant. Le modèle prédit que l'immigration peut contribuer significativement à la récolte totale et à la récupération des populations exploitées et peut affecter la démographie dans la zone protégée. L'immigration et la récolte totale sont reliées de façon complexe et non-linéaire avec l'exploitation cumulative en relation avec la taille de l'aire protégée, le taux initial de remplacement des individus récoltés, la mobilité et les interactions comportementales. J'ai entrepris des expériences sur le terrain afin de valider le modèle et d'estimer l'influence relative de facteurs limitant à l'immigration (*i.e.* la taille de la population dans la zone protégée, la qualité de l'habitat relative et la connectivité fonctionnelle entre la zone exploitée et la zone protégée). J'ai utilisé la demoiselle noire (*Stegastes dienaceus*) et la demoiselle brune (*S. adustus*) et leur habitat comme système modèle. J'ai examiné en premier lieu la connectivité fonctionnelle en relocalisant des demoiselles afin d'investiguer quelles caractéristiques de l'habitat ou caractéristiques sociales peuvent représenter une barrière au mouvement lors du comportement de retour au territoire (*ang.* « homing »). Les petites étendues de sable constituent une barrière partielle au mouvement mais l'effet de la taille de l'étendue de sable varie en fonction de la configuration des récifs. Les poissons minimisent les mouvements au-dessus des territoires de leur conspécifiques. J'ai également entrepris une réduction expérimentale, incrémentée et répliquée de populations de demoiselles qui a servi à examiner les mécanismes régissant la relocalisation du domaine vital à l'échelle du territoire et l'immigration à l'échelle du paysage. À l'échelle du territoire, la probabilité qu'un territoire soit recolonisé diminue avec une réduction de la densité. Les territoires ont tendance à être recolonisés par des individus de la même espèce, du même sexe et de taille comparable à celle de l'occupant original. Les territoires occupés initialement par les individus les plus gros ont une probabilité plus forte d'être recolonisés. À l'échelle du paysage, les modèles qui assument un remplacement constant mais partiel des individus récoltés ont un meilleur support statistique que les modèles incluant soit un remplacement incomplet ou une absence de remplacement. Dans plusieurs sites où la densité à été manipulée, le modèle ayant le meilleur support statistique incluait également des paramètres modélisant de la densité dépendance (*i.e.* changement de direction et d'intensité en relation avec la récolte cumulative). La récolte totale et la proportion des individus récoltés qui étaient remplacés par les immigrants étaient corrélées avec l'effet combiné de la qualité de l'habitat et de la connectivité fonctionnelle. En conclusion, ma thèse propose et test un modèle d'immigration compensatoire prédisant l'immigration d'individus habitant les aires protégées vers les zones exploitées. Ce modèle considère la variation de la mobilité, la qualité de l'habitat, la connectivité fonctionnelle et les interactions comportementales afin de prédire les effets de l'immigration dans un contexte d'exploitation soutenable et de conservation à l'échelle de la métapopulation.

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PREFACE

THESIS FORMAT AND STYLE

This is a manuscript-based thesis, consisting of a collection of papers of which I am the primary author. All chapters have either been published or are intended for publication. The style of each chapter is that of the scientific journal for which it has been prepared. The four manuscripts and associated journals are as follows:

CHAPTER 1. Turgeon, K., Robillard, A., Grégoire, J.Duclos, V. and D. L. Kramer. 2010. Functional connectivity from a reef fish perspective: Behavioral tactics for moving in a fragmented landscape. *Ecology* 91:11, pp. 3332-3342.

CHAPTER 2. Turgeon, K. and D. L. Kramer. (*In prep.*) Density and habitat quality influence home range relocation in a coral reef fish: Implications for spillover from marine protected areas. Intended journal: *Behavioral Ecology*

CHAPTER 3. Turgeon, K. and D.L. Kramer. (*In prep.*). Modeling migration between harvested and protected populations. Intended journal: *American Naturalist*

CHAPTER 4. Turgeon, K. and D.L. Kramer. (*In prep.*). Spillover in an experimental model fishery: Influence of density, habitat quality and functional connectivity on immigration from protected to harvested areas. Intended journal: *Ecology*

Although the four aforementioned chapters represent the bulk of my doctoral research, I also did an extensive literature search on experimental population reductions that will be the subject of a synthetic review of migration in vertebrate populations (*in preparation*). The synthesis is not included as a chapter in the thesis but has been partially integrated in the *General Introduction*. The methodology used to select the articles and the complete references are presented in *Appendix I.1*.

CONTRIBUTION OF CO-AUTHORS

With advice from my supervisor, Donald L. Kramer, and from my supervisory committee, I conceived the conceptual framework and sampling design of my research project. I collected all the data, with the help of a large team of volunteers and paid assistants working under my supervision during three consecutive summers. The exception to this was the translocation experiment to test functional connectivity from a reef fish perspective (*Chapter 1*). Audrey Robillard, Vanessa Duclos (2007) and Jacinthe Grégoire (2006) participated in developing the conceptual framework and were responsible for the data collection as part of their independent research projects, carried out while working as my field assistants, supported by Prof. Kramer and directly supervised by me. They are co-authors in *Chapter 1*, which is now published in the journal *Ecology*. I selected and performed all statistical analyses and interpreted the results. I am the primary author on all manuscripts associated with this thesis and was responsible for writing all parts of them. D. L. Kramer is a co-author on all manuscripts and has contributed substantially to the conceptual development of all chapters and provided extensive editorial feedback on each manuscript. The research funding came primarily from an NSERC Discovery Grant to D. L. Kramer, supplemented by an NSERC Strategic Grant in which he was a co-investigator (M. Jenkin, York University, P.I.).

ORIGINAL CONTRIBUTIONS TO KNOWLEDGE

Contributions from chapter 1: Functional connectivity in coral reef fishes

- By using translocation experiments in a marine landscape context, I quantify for the first time, functional connectivity for a marine organism in its natural environment.
- I provide the first direct empirical evidence that open sand is a partial barrier to movement for a small coral reef fish by quantifying the probability of crossing sand gaps of variable width. I also provide some of the first evidence for the effect of habitat configuration (*i.e.* spatial distribution of habitat patches) on the width at which sand gaps become partial barriers.
- I present the first demonstration, by a detailed visual tracking of homing trajectories, that a social habitat feature (*i.e.* distribution of conspecifics) is not a barrier to movement but influences microhabitat use during homing.
- I propose a new conceptual framework to compare barriers to movement, by using barrier width and steepness scaled to body size and home range size, which facilitates comparisons of functional connectivity among habitats and taxa.

Contributions from chapter 2: Density and habitat quality influence relocation

- I define and distinguish for the first time territory shifts and territory relocations and show that their occurrence and frequency change with local density, potentially explaining the increasing rate of immigration in response to harvest at high density.
- I present some of the first evidence that the density of remaining individuals in a harvest area influences the probability that a territory will be reoccupied and provide the first evidence that the pattern in the probability of recolonization with decreasing density changed if a vacant

territory was recolonized via territory a shift (*i.e.* recolonization by a close neighbor that still use a portion of its original territory) or a relocation (*i.e.* recolonization by neighbor that abandoned its original territory of from a fish from distant location).

- I present the first support for the hypothesis that habitat selection plays a role in spillover by showing that shifts and relocations occur more often toward territories previously held by larger original occupants, which are assumed to be of higher quality. The redistribution of the population in order to occupy higher quality territories with declining density is a pattern predicted by the ideal free and ideal despotic distribution hypotheses but that has been rarely tested using experimental decreases in density.

Contributions from chapter 3: Modeling migration in response to harvest

- Inspired by the formulation of the original Beverton-Holt stock-recruitment function, I develop a flexible and easy-to-apply compensatory immigration model that predicts immigration from protected adjacent area in response to local harvesting and its effects on the metapopulation (*i.e.* protected adjacent area and harvest area).
- Inspired by the limitation approach, my compensatory immigration model is the first that allows the empirical evaluation of the relative effects of different limiting factors on immigration. This is made possible by using a function that can increase in complexity by adding parameters that are related to different limiting factors to immigration (*i.e.* initial rate of replacement of removed individuals that could be influenced by habitat quality and functional connectivity and density dependence from behavioral interactions) and one variable (initial population size in the protected area). With this model, I also present the first formulation that the rate of immigration can change in direction and magnitude in response to harvest (*i.e.* negative and then positive density dependence over the

removal sequence) as a result of behavioral interactions in both the harvest and protected areas and a limited number of migrants in the protected area.

- My model shows for the first time that the effect of variation in the size of protected populations, in the rate of replacement of removed individuals and in the strength of density dependence contribute importantly and result in some novel non-linear predictions of total cumulative immigration, total proportional yield and to some important changes in population size in protected area.

Contributions from chapter 4: Spillover from reserves in an experimental model fishery

- I present the first strong, direct empirical evidence of spillover in response to an incremental and localized harvest in a coral reef fish.
- I provide the first direct empirical evidence for density-dependent movement in coral reef fish and one of the first for any natural population of vertebrates by showing that the rate of immigration varies in magnitude and direction with density *(i.e.* negative and positive density dependence).
- I present a novel use of the limitation approach by being the first to apply it to an immigration function. This allows me to evaluate for the first time the relative effects of three potential limitations to immigration (population size in the protected area, rate of replacement of removed individuals, effect of behavioral interactions leading to density dependence) on a natural population.
- I provide the first study with adequate replication to show a synergistic effect between landscape functional connectivity and relative habitat quality on the rate of replacement and total yield in an experimental population removal experiment.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my supervisor, Donald L. Kramer, for his encouragement, dedication and support throughout my Ph D. As Edward O. Wilson wrote in his influential work, Biophilia (1984)[1]: *"The ideal scientist can be said to think like a poet, work like a clerk, and write like a journalist".* This quote summarizes well the guidance offered by Don during my Ph.D. Don helped me to develop my creativity, as well as my independent and logical thinking. He also taught me the importance of rigor and clarity when it is time to communicate our exciting discoveries. Enjoy your well deserved retirement in Victoria with Vanessa!

I would also like to thank my supervisory committee members, Frédéric Guichard and Lauren Chapman for their support, guidance and valuable advice. After each supervisory committee meeting, I had an incredible boost of energy and motivation to go forward in the development of the thesis. I also want to thank Brian Leung, Michel Loreau and Andrew Gonzalez for their statistical and modeling advice. I hope I successfully incorporated your constructive suggestions into my thesis.

I have some special thanks for incredible people who help me in the past and allowed me to go through this thesis with useful tools in my ecological toolbox. These days, we should update Wilson's quote by adding "[…] *and analyze like a statistician*". Thanks to Marco Rodriguez (M.Sc. Advisor) who convinced me that stats can be a lot of fun and a very useful tool. Thanks also to Jean Morin and Olivier Champoux (Meteorological Service, Environment Canada) who both trained me with GIS software and spatial modeling and made me realize how cool spatial ecology is! Thanks also to Frédéric Guichard (McGill University) who taught me how to catch my first wave to surf in the complex ocean of theoretical ecology. Thanks to Andrew Beckerman and Owen Petchey (University of Sheffield) who gave an inspiring workshop "R.4. All crash course" that helped me to use R and

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[1] Wilson, E.O. 1984. Biophilia. Harvard University Press. Cambridge MA. 157 pp.

understand programming in the late stages of my Ph.D. Special thanks to Don Thomas (1954-2009) who gave me my first opportunity as a research assistant, believed in my research ability and encouraged me to develop my curiosity. This thesis would never have existed without all these tools in my ecological toolbox. Thanks to all of you!

Even if diving twice a day, every day, and looking at fish behavior in warm turquoise water in Barbados sounds like an amazing holiday, these bunch of dedicated people know that it can be hard work! Thanks to Alexandre Ménard (*a.k.a.* "the volunteer", 2005) Émilie Castonguay (2005), Jacinthe Grégoire (2006), Beth Hall (2006), Joanie Lussier (2006), Vanessa Duclos (2007), Kiyoko Gotanda (2007), Audrey Robillard (2007), Bridget Spelke (2007), Sylvain Theleme (2007) and Sébastien Rouleau (2006, 2007) for being such great field assistants. This thesis would not exist without your support, hard work and enthusiasm toward my data collection and toward your own independent projects. You also taught me a lot about project supervision and mentorship. Thanks also to Dominique Roche (2005), Angélique Dupuch (2008, 2009), Katleen Robert (2008), Sandra Warrens (2008) Jason Bueckert (2009), Marc Delpine (2009) and Eve Desplats (2010) who helped during a couple of days in the winter and spring to gather some additional data. Thanks to Issei Massunaga and Caitlin Foster who 'worked like clerks' to help me with data entry and otolith cleaning and storing.

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GENERAL INTRODUCTION

IMPORTANCE OF IMMIGRATION IN POPULATION BIOLOGY

Many organisms live in spatially structured habitats that can be described as a mosaic of patches rich in resources, such as food, refuges and mating opportunities, and patches that offer few resources and risks such as predation and agonistic interactions. Immigration is one process, in addition to birth, death and emigration, contributing to the regulation of population size and dynamics in heterogeneous landscapes (Diffendorfer 1998, Hanski and Gilpin 1997, Wiens et al. 1993). In metapopulation theory, the long term persistence of local populations in the metapopulation is achieved mainly through immigration which is assumed to be influenced by the size and isolation of local populations (Hanski 1998, Hanski and Gilpin 1997). In source-sink dynamics, local populations of the metapopulation are assumed to vary in quality. Local populations in which birth rate is higher than death rate are self-sustaining source populations and produce surplus that should immigrate to neighboring populations (Pulliam 1988). Local populations in which birth rate is smaller than death rate and in which emigration rate is smaller than immigration rate are known as sinks and can only persist via immigration (Brown and Kodric-Brown 1977, Dias 1996, Pulliam and Danielson 1991). Based on these theories, immigration is likely to be a dominant process for population recovery following localized mortality (Debinski and Holt 2000) and for genetic mixing among isolated local populations (Saccheri et al. 1998).

IMMIGRATION AND METAPOPULATION MANAGEMENT

In many populations targeted by hunters and fishers, harvest takes place in only part of the area occupied by the population as a result of legal protection (*e.g.* protected areas, national parks or reserves) or as a result of natural features that limit access to harvesters such as distance from roads for terrestrial animals (Novaro et al. 2005) or distance from boat launches for aquatic animals (Stuart-Smith et al. 2008). This creates a mosaic of areas that are harvested and areas that are not harvested at the landscape level. Areas that are not harvested will hereafter be called ‘protected areas’.

Populations in harvest areas are suggested to recover in the short term by a net immigration of individuals from protected areas (Almany et al. 2007, DeMartini 1993, Jonzén et al. 2001, McCullough 1996, Novaro et al. 2005, Polacheck 1990). Immigration from protected areas can benefit harvested populations if it allows the replacement of individuals in the short term by rapid movements stabilizing population size and can benefit harvesters by increasing total yield. This effect, called ‘spillover’ in marine protected area literature (Gell and Roberts 2003, McClanahan and Mangi 2000, Roberts et al. 2001, Russ and Alcala 1996), is an expected tangible benefit from the protected area for local fishers. Immigration can also have strong beneficial effect by restoring populations impacted by natural (*e.g.* fires, floods, droughts, landslides, and hurricanes; Adams and Warren 2005, Albanese et al. 2009, Woodley et al. 1981) and/or anthropogenic (*e.g.* poisoning, chemical spills and habitat destruction; Greathouse et al. 2005), disturbances that could partly or completely eliminate a population or community.

Despite its benefits, immigration into harvested populations can be detrimental to metapopulation viability if it creates significant demographic changes in the protected area (Amarasekare 2004, Gundersen et al. 2001). For example, if population size in the protected area declines as a result of emigration, harvesters will have an impression of a growing or a stable population in the harvest area because it will benefit from immigration but the metapopulation will be well into decline before harvesting pressure is reduced. Immigration can also strongly affect species that need significant protection or have slow life history traits (*e.g.* large carnivores; Loveridge et al. 2007, Robinson et al. 2008, Woodroffe and Ginsberg 1998). For example, if harvesting is performed close to a protected area boundary, immigration may expose individuals that were well within the core of a protected area via the ecological ‘vacuum effect’ or a ‘domino effect’ which may weaken the potential of even very large protected areas to protect small populations (Woodroffe and Ginsberg 1998).

Immigration can also affect negatively population control operations of pest species. The goal of pest control management is to bring the number of individuals of a given population below some critical threshold, mainly to minimize damage to crops (Nakata and Satoh 1994), contact with human in the case of large predators (Robinson et al. 2008) or contact with other species in the case of disease transmission (Tuyttens, Delahay, et al. 2000) and predation (Efford et al. 2000, Ji et al. 2004). Immigration from adjacent area can result in counterproductive efforts if removed individuals are replaced quickly in the short term. For examples, a rodenticide experiment to reduce damage to crops by gray red-backed voles (*Clethrionomys rufocanus*) resulted in a higher density in the treated area after the removal operation (Nakata and Satoh 1994) and a badger (*Meles meles*) culling operation resulted in a higher rate of disease transmission between badgers and cattle in United Kingdom due to a higher rate of movement and immigration from the adjacent populations (Rogers et al. 1998, Tuyttens, Macdonald, et al. 2000, Tuyttens, Delahay, et al. 2000).

Because immigration in response to localized mortality can have both beneficial and detrimental consequences for the viability of harvested and protected populations (Gundersen et al. 2001, Woodroffe and Ginsberg 2000), and for management of populations in pest control operations and harvesting (Halpern et al. 2009, Nakata and Satoh 1994, Tuyttens and MacDonald 2000), we need to understand which mechanisms lead to immigration and to understand which factors can affect its magnitude.

MECHANISMS LEADING TO IMMIGRATION: IMPORTANCE OF HOME RANGE RELOCATIONS

Daily movements within the home range, seasonal migration and ontogenetic habitat shifts, which are independent of the variation in density in the harvest area, can expose individuals from the protected area to harvesting and can be a mechanism leading to immigration. Metapopulation models have proposed another mechanism leading to immigration. Individuals produce in surplus in the protected areas are expected to immigrate into harvest areas in response to variation in density. This process is mainly thought to be dominated by larval dispersal in aquatic organisms (Gerber et al. 2003, Pelletier and Mahevas 2005, Roberts et al. 2001) or by juveniles performing long distance natal dispersal in birds and mammals (McCullough 1996). However, there is accumulating empirical evidence that immigration into harvest area can be dominated by rapid, short distance home range relocation of sexually mature individuals and subadults in a variety of taxa (*e.g.* Hannon 1983, Loveridge et al. 2007, Lowry and Suthers 2004, Manuwal 1974, Stickel 1946).

Home range relocation, which consists in a permanent change in space use (Robertson 1988), is an understudied movement because rarely observed and therefore thought to be elusive and rare in nature (Clobert et al. 2001, Sale 1978, Stenseth and Lidicker 1992). Home range relocation has been sometimes described as breeding dispersal or home range shift in mammals and birds literature (Greenwood 1980, Cockburn 1992, Wauters and Dhondt 1993). Natal dispersal (*i.e.* movement between the natal area or social group and the area or social group where the first breeding takes place) differs from home range relocation by being usually long distance movement, strongly biased toward juveniles and pre-reproductive individuals, sometimes sex-biased and costly in terms of other fitness-related traits such as survival (Aars et al. 1999, Stenseth and Lidicker 1992). Natal dispersal is also expected to show seasonal patterns (Clobert et al. 2001, Greenwood and Harvey 1982, Matthysen 2005).

By means of a literature review on density manipulation and removal experiments, I found that home range relocations have been observed in many taxa and are likely to be more common than previously thought. This literature review will be part of a synthesis on migration in vertebrate populations (Turgeon and Kramer, *in prep.*). The goal of this synthesis is to quantify the frequency and magnitude of immigration as a compensatory mechanism to localized mortality in vertebrate populations and to extract key factors influencing the magnitude of immigration. I found 44 articles, including 118 studies meeting certain criteria of selection. Articles from this review will be the source of some figures and discussion in this Introduction (see *Appendix I.1* for the methodology used for the literature search and database construction and for a list of articles).

Net immigration in harvested populations, via home range relocations, may represent one of the most important processes for population recovery and regulation in the short term. Home range relocation has received significant attention in the coral reef fish literature. They have been particularly well investigated in small damselfish species with experiments designed to answer questions related to reef recolonization (Hourigan 1986), territoriality and competition (Sale 1976, Itzkowitz 1991, Williams 1978, Waldner and Robertson 1980), costs of establishing a home range (McDougall and Kramer 2007) and habitat selection (Cheney and Côté 2003, Meadows 1995, 2001). Relocations have also been observed in other reef fish (Chateau and Wantiez 2009, Lowry and Suthers 2004, Robertson 1988, Zeller et al. 2003) in some freshwater fish (Albanese et al. 2009, Berra and Gunning 1970, Crook 2004, Sheldon and Meffe 1995) and in a variety of terrestrial taxa, predominantly in birds and mammals (see *Appendix I.1*). Many studies have revealed a significant population recovery from immigration following harvesting (Fig. I.1). In these studies, populations were reduced from 23% to 100%, and recovery based on the number of harvested individuals was around 84.5% over a period of time varying from 7 days to 1 year, excluding recruitment from reproduction. Nevertheless, 77% of the studies observed only partial replacement of removed individuals (*i.e.* less than a 100% replacement; Fig. I.1), suggesting that some factors may limit immigration following localized mortality.

FACTORS INFLUENCING IMMIGRATION IN RESPONSE TO HARVEST

To predict immigration in response to harvest, we need to know which factors affect home range relocation at the individual level and how this could be translated into immigration at the population and metapopulation levels. Previous research has identified seven main factors that are likely to influence immigration by either quantifying their effects on immigration or by only mentioning potential effect on immigration (Fig I.2a). I grouped the main limiting factors to immigration into four broader categories. Categories are 1) inter- and intraspecific characteristics, 2) density and population size, including density in both the harvest and the protected areas (*i.e.* vacancy creation and availability of neighbors) and behavioral interactions that could lead to density dependence, 3) physical properties of the landscape (*i.e.* relative habitat quality and landscape functional connectivity) and 4) temporal and seasonal patterns (Fig. I.2a).

Inter- and intraspecific characteristics

The ability to perceive and acquire information about variation in habitat quality and population densities and to move successfully in the landscape is likely to vary greatly among species (interspecific variation) and among individuals within a species (intraspecific variation), and this should affect immigration. Much research has quantified the effect of at least one factor related to inter- or intraspecific variation or recognized its importance as an influence on immigration (Fig. I.2a). The most common interspecific factor is the species mobility, and the most common intraspecific factor is the age/dominance of the individuals within a population.

Interspecific variation. Animals are suggested to get information about adjacent areas if they are located within their perceptual range, which is defined as the information window to which an animal can potentially respond (Zollner and Lima 1997). Perceptual range is known to be correlated with species body size and mobility (Zollner and Lima 1997, 1999, Mech and Zollner 2002, Schooley and Wiens 2003, Pe'er and Kramer-Schadt 2008). Species mobility should be a primary limiting factor to immigration. Mobile species are likely to perceive landscape heterogeneity at a larger scale than do more sedentary ones (Fahrig and Paloheimo, 1988; With and King, 1999) and should thus have a higher probability of detecting vacancies and immigrating to a harvested population. Not surprisingly, species with high mobility have an increased probability of recovering quickly following a perturbation compared to less mobile species (*Appendix I.1*).

Intraspecific variation. Within a species, habitat selection theories predict that dominant individuals will occupy high-quality habitat due to their competitive superiority (van den Assem 1967, Both and Visser 2000). Low-quality habitat should contain subordinate, younger, or weaker conspecifics that have not acquired the size, strategy, or status needed to occupy high-quality sites. These subordinate individuals can benefit the most from prospecting for potential vacancies in a context of harvesting because leaving a territory for prospecting may be costly for individuals that have already acquired high quality territory (Sikkel and Kramer 2006). Many studies have revealed that immigrants are mainly composed of subadult and young sexually mature individuals (see *Appendix I.1*) or of non-territorial floaters already present in the local breeding population (Greenwood and Harvey 1982, Kokko et al. 1998, Newton 1998) and rarely of dominant individuals.

Density and population size

Whether or not a harvest area can be recolonized by immigrants originating from a protected area may depend on density and behavioral interactions in both the harvest and protected areas that could influence immigration rate via density dependence.

Population size in the harvest area - A local reduction in density might affect immigration via density-dependent habitat selection. Under the Ideal Free Distribution (IFD; Fretwell and Lucas 1969), individuals are assumed to be highly mobile, able to assess the suitability of all habitat patches and make the best selection among them. If density decreases in a given patch, this patch becomes more attractive because its realized suitability increases. Individuals should thus redistribute themselves as a function of respective realized suitabilities among patches. In territorial species, individuals may be constrained in their movements in saturated habitat by a low availability of suitable territories (Emlen 1994), and vacancy creation should thus elicit intense competition and result in rapid replacement of removed individuals (Komdeur 1992, Newton 1992).

A local reduction in density (*i.e.* creation of vacancies) in the harvest area is one of the most frequently quantified factors to explain the occurrence of immigration (Fig. I.2a). However, the magnitude of the removal (*i.e.* number of individuals removed from the local initial population) and the removal strategy (*i.e.* number of removal events over time as either one single massive removal comparable to the strategy used in population control of pest and invasive species or many successive removals sometimes including immigrants more comparable to what we could observe in harvesting from a sustainable management perspective) can also strongly affect immigration. In the majority of density-manipulated studies, the removal strategy is strongly biased toward a massive initial removal (Fig. I.3c). In these studies, the magnitude of removal, varying from 23% to 100%, was positively related to population replacement by immigration (Generalized linear mixed model; t-value = 3.718; p-value < 0.001, n = 82 studies; 32 articles used as a random factor; *Appendix I.1*). Unfortunately, a large proportion of the studies that manipulated density lacked controls (*i.e.* independent groups or sites that are practically identical to the treatment group or site, except for the variable of interest being tested; Fig. I. 3a), and this reaches 91% if we consider hunting-fishing and population control studies only. Studies without controls cannot provide strong support for the effect of density reduction on immigration because they lack information about net immigration in the absence of harvesting in their respective systems.

Population size in the protected area - Immigration may also depend on the availability of potential migrants in the adjacent protected area. Intuitively, a limited number of potential migrants in adjacent areas should limit the number of immigrants that could move into the harvest area. High density populations in adjacent areas have been recognized as an important factor favoring rapid and high recolonization of the depleted area in rodenticide studies (Grodzinski et al. 1966, Stenseth and Lidicker 1992) and in fish recolonization studies (Beckley 1985, Gundermann and Popper 1975). However, strong and direct evidence for the effect of population size in the protected area on immigration in response to harvest is rather limited (Fig. I. 2a; *Appendix I.1).* To quantify the effect of the size of the population in the protected area, the provenance of the migrants has to be known. This could be achieved by marking individuals either in the adjacent area or in the harvest area. Very few density-manipulation studies have marked individuals (but see Efford et al. 2000, Gundersen et al. 2001, Henderson et al. 1985, Krebs 1971, Loveridge et al. 2007, Nakata and Satoh 1994, Rosatte et al. 2007, Stickel 1946, Tuyttens, Macdonald, et al. 2000). These studies seem to indicate that high abundance of potential migrants in the adjacent area resulted in higher immigration but the interpretation is limited by a very small number of replicates.

Some studies have suggested that the size of the population in the protected area could also affect the rate of immigration via a depletion of the ‘pool’ of potential migrants in the adjacent area. In rodenticide studies, the probability of capture is fairly constant during the first 3-4 days of removal, followed by a declining probability (Grodzinski et al. 1966, Stenseth and Lidicker 1992). These studies suggest that the effect of harvesting on adjacent protected area first affects individuals close to the boundary between the harvest and protected area. As density decreases in the harvest area, the effect of harvesting can go deeper into the adjacent area (Vacuum effect or Domino effect; Ji et al. 2001; Loveridge et al. 2007; Efford et al. 2000). However, the effect of harvesting is likely to decrease as distance between the boundary of a local harvest area and the adjacent area increases. We should thus expect a lower probability of detection of vacancies in the harvest area with increasing distance from the boundary, which should result in a lower probability of immigration per individual over time. Interestingly, this 'effective distance' has been quantified in the red-backed vole (*Myodes rufocanus*), where 90% of voles located within 30 m from the edge of a depleted area made single-direction movements toward it and 50% of voles located at greater distance did not (Nakata and Satoh 1994). The effective distance has been estimated to around 400 m in great tit (*Parus major*; Krebs 1971) and 100 m in brushtail possums (*Trichosurus vulpecula*; Efford et al. 2000).

Behavioral interactions and density dependence – The rate of immigration into the harvest area can be density-dependent as a result of scramble competition, territoriality and other habitat-related behavioural interactions in both the harvest and protected area that are often density-dependent (Sutherland et al. 2002). Despite considerable theoretical interest in density-dependent movement to regulate population size (Stenseth and Lidicker 1992, Saether et al. 1996, Travis et al. 1999), empirical evidence of density-dependent movement in vertebrate is strongly limited (Lambin et al. 1998, Bowler and Benton 2005, Matthysen 2005). As a consequence, most population models still consider movement to be density-independent (Doak 1995, Hanski and Gilpin 1997) or use diffusion-like assumption to model migration (Neubert 2003). Among the density-manipulated studies considered in the review, only 5% quantified the potential effect of behavioural interactions on density-dependent immigration and only six (10%) mentioned the potential of behavioural interactions as a limiting factor (Fig. I.2a). Indeed, more than 75% of the studies do not have the potential to detect density dependence because they used a massive single removal strategy (Fig. I.3c).

Negative density dependence (*i.e.* increasing rate of immigration with decreasing density) can occur following the creation of vacancies in the harvest area when density is high. This can happen if residents of the harvest area were constrained to inhabit a smaller than optimal territory and expand their territories temporarily or permanently or shift their territory location when space becomes available, as expected under an optimal territory size model (Hixon 1981, Schoener 1974). This behavior limits the space available for territory establishment for potential immigrants from adjacent area. Also, individuals from adjacent areas may choose not to immigrate to areas of high population density because an immigrant in a high density area would experience higher levels of aggression than it would if it did not move, as suggested by the social fence hypothesis (Hestbeck 1982).

Positive density dependence (*i.e.* decreasing rate of immigration with decreasing density) can occur if large and dominant individuals are removed preferentially and initially from the population at high density and replaced by several smaller ones as in the case of species that are the object of trophy hunting (*e.g.* large carnivores; Loveridge et al. 2007, Robinson et al. 2008). Positive density dependence may also be observed if immigrants compress their territories compared to original territory occupants of the harvest area (Knapton and Krebs 1974). Furthermore, when density is greatly reduced in the harvest area, the rate of immigration can decrease if individuals from the protected area are less likely to immigrate as suggested by the conspecific attraction hypothesis (Stamps 1991, Danielson and Gaines 1987) or if the adjacent protected area is diluted enough so individuals no longer experience density-dependent effects such as small territory size or high costs of aggression (Kramer et al. 1997, Rosenzweig 1981, 1991).

Physical properties of the landscape

In heterogeneous landscapes, moving organisms encounter habitat patches that differ in quality and risks (*e.g.* predation risk and agonistic interactions), and this heterogeneity can affect both the probability of moving in the landscape but also the trajectory used. Physical properties of the landscape such as variation in habitat quality and functional connectivity have been recognized to influence the magnitude of immigration.

Differences in habitat quality between the harvest and protected area - Costs and benefits related to habitat quality and movement may represent key factors for understanding the mechanisms leading to home range relocation and immigration. There should be strong selection for individuals that can recognize high habitat quality and move accordingly. However, individuals should only relocate their home range when the benefits of the new home range clearly outweigh those of the current location and the costs of moving (Kramer et al. 1997). Because prospecting and moving in a heterogeneous landscape can be costly due to energetic expenditures, higher risks of predation and agonistic interactions (Wiens 2002, Zollner and Lima 1999), animals may not relocate if the benefits are too low or if they cannot obtain information about the availability of alternative habitats. Habitat quality of the harvest area relative to the protected area should be a limiting factor to immigration.

Some empirical evidence and theoretical models on birds, monkey and fish suggested that movement (*e.g.* higher turnover rates and immigration) are related to habitat quality (Winker et al. 1995, Isbell et al. 1998, Bélanger and Rodríguez 2002), but very few density-manipulation studies (12%) have quantified habitat characteristics (*e.g.* food abundance, availability of cover) or possible indices of habitat quality (*e.g.* variation in body size within a population) that are susceptible to affect immigration in response to harvest (Fig. I. 2a, *Appendix* I.1). A higher percentage of studies (22%) have recognized the importance of habitat quality. In many taxa, vacancies created in territories held by dominant and large individuals are recolonized faster and/or at a higher rate than those held by small and subordinate individuals, which is indirect evidence of the effect of habitat quality on immigration. This pattern has been observed in large carnivores (Loveridge et al. 2007; Robinson et al. 2008), small mammals (Lin and Batzli 2001; Jacquot and Solomon 2004), various bird species (Newton 1992, 1998, Studds and Marra 2005) as well in reef fish species (Cheney and Côté 2003, Lowry and Suthers 2004, McDougall and Kramer 2007, Waldner and Robertson 1980). Some studies have observed that in the presence of vacant territories in suboptimal habitat, breeding age individuals remained non-territorial (Krebs 1970, Manuwal 1974, Komdeur 1992, Ens et al. 1992) suggesting that waiting for a vacancy in higher quality habitat will give higher pay-offs in the long term than moving into a low quality habitat and breeding immediately.

Landscape functional connectivity - Functional connectivity (*i.e.* the degree to which the landscape facilitates or impedes movement among patches; Taylor et al. 1993) is an organism-based emergent property of the landscape, combining a description of its physical structure with the response of a species to that structure (Taylor et al. 2007, Tischendorf and Fahrig 2000). Functional connectivity is influenced by intra- and interspecific characteristics (*e.g.* mobility, perceptual range, size, sex and state; Lima and Zollner 1996, McDonald and St. Clair 2004, Pither and Taylor 1998) and by extrinsic factors such as the total travel distance (Rothermel and Semlitsch 2002), landscape configuration (*i.e.* spatial distribution of habitat; Gillies and St. Clair 2008), and quality of the matrix (Baum et al. 2004, Bender and Fahrig 2005). In metapopulation studies, patch size (Stamps et al. 1987, Hill et al. 1996, Andreassen and Ims 2001, Bowman et al. 2002, Cantrell et al. 2002), patch isolation (Hanski and Gilpin 1997, Hanski 1998, 1999) and edge effects between two contrasting habitats (Murcia 1995, Ries et al. 2004, Stamps et al. 1987) can also affect functional connectivity and may affect the rate of immigration and ultimately limit the number of immigrants that can detect and reach vacancies the harvest area. Evidence for the effect of functional connectivity on immigration in response to harvest is very limited; fewer than 10% of the studies quantified the effect of barriers or partial barriers to movement, and 37% mentioned the importance of landscape connectivity as a limiting factor to immigration.

Translocations and gap-crossing experiments have contributed greatly to our understanding of functional connectivity in terrestrial animals by identifying the width of a barrier to movement. From these studies, we know that open habitat in forest represents a partial barrier for many birds (Desrochers and Hannon 1997, Bélisle and Desrochers 2002, Creegan and Osborne 2005, Bosschieter and Goedhart 2005, Awade and Metzger 2008, Lees and Peres 2009) and mammals (Kozakiewicz and Jurasińska 1989, Bowman and Fahrig 2002, Bakker and Van

Vuren 2004) and low complexity substratum such as sand impede movements of reef fishes and other marine organisms (Brock et al. 1979, Ogden and Ebersole 1981, Barrett 1995, Chapman and Kramer 2000, Meyer and Holland 2005, Afonso et al. 2009).

Effects of multiple limiting factors

Realistically, limiting factors may interact synergistically or additively to affect immigration in response to harvest. Very few density-manipulation studies have performed well-controlled experiments (Fig. I.3a), with adequate replication (Fig. I.3b), to test for the effect of multiple limiting factors and their interactions on compensatory immigration (*Appendix I.1*; Fig. I.2b). Although, nearly 70% of the articles quantified the effect of at least two limiting factors on immigration, very few examined the potential for interactions among factors due to a lack of replication or controls (but see Haynes and Cronin 2004, 2003, Lin and Batzli 2001).

AVAILABLE THEORIES TO PREDICT IMMIGRATION IN RESPONSE TO HARVEST

Various theories dealing with either regulation of population size following localized mortality (*e.g.* sustainable harvesting and harvest theory), density-dependent habitat selection (*e.g.* ideal free distribution and related hypothesis; Fretwell and Lucas 1969, Rosenzweig 1981) or population dynamics in spatially heterogeneous landscape (*e.g.* metapopulation ecology and source-sink dynamics) can be helpful to develop a set of predictions concerning immigration following localized mortality.

In sustainable harvesting, harvest quotas are based on whether mortality due to harvesting is additive to the natural mortality or is compensated by density dependence processes such as enhanced per capita reproduction and survival by a higher availability of resource with declining density (Hilborn et al. 1995, Sinclair and Pech 1996, Rosenberg et al. 1993, Caughley and Sinclair 1994). This theory deals with density dependent regulation but assumes that migration (*e.g.*

emigration and immigration) between protected area and harvest area does not contribute to the recovery of harvested populations (Hastings and Botsford 1999).

Under density-dependent habitat selection like the ideal free distribution model (Fretwell and Lucas 1969), individuals are assumed to be distributed uniformly among discrete patches that are characterized by their “suitability”. This theory assumes that individuals are highly mobile and are able to assess the suitability of all patches and make the best selection among them. As density increases, high suitable habitats become less suitable and lower habitat suitability patches become equally attractive. As a result individuals should redistribute themselves to equalize the suitability among patches. Many models, mainly in fisheries, used analogous assumptions to the ideal free distribution with some extensions to model movement among marine protected area and fished area (Gerber et al. 2003, Guénette et al. 1998, MacCall 1990, Pelletier and Mahevas 2005, Walters 2000, Walters et al. 1999). However, even if this theory deals with movements following declining density, it assumes very high mobility of organisms and cannot deal with a change in the rate of immigration in relation to density (*i.e.* density dependence) and does not account for the effect of landscape connectivity and barriers to movement among habitat patches.

The metapopulation approach assumes an environment consisting in discrete patches of suitable habitat (*i.e.* local populations) where local populations interact among each other via migration (Hanski 1998, Hanski and Gilpin 1997). Migration rate among local populations is determined by landscape factors such as the patch size, patch isolation and edge detection and thus account for landscape connectivity and barrier to movement (Bowman et al. 2002, Englund and Hambäck 2007, Hambäck and Englund 2005). The source-sink dynamics models (Dias 1996, Pulliam 1988) can be particularly relevant to exploring how immigration can affect the population dynamic between harvested and protected populations. Protected areas can act like sources and harvest areas can act as ‘mortality’ sinks (Delibes, Ferreras, et al. 2001, Delibes, Gaona, et al. 2001). Source-sink dynamics models include two transfer parameters, one parameter modeling the transfer of individuals from the source to the sink and one parameter modeling the transfer of individuals from the sink to the source. With the two transfer parameters, source-sink dynamics allow modeling population dynamics among harvest and protected areas where there is neither complete immobility (like sustainable harvesting model) nor complete mobility (Density-dependent habitat selection models) and can account for density-dependent movements (Amarasekare 2004, Howe et al. 1991, Pulliam 1988, Saether et al. 1999). Although considerable variability in mobility and behavior can be modeled with source-sink dynamics some important conditions cannot be adequately addressed. They cannot account for density-dependent changes in the direction (*i.e.* positive or negative) and magnitude of movements arising from simultaneous behavioral interactions in the harvest and protected areas (see *population size and density* subsection in the *Factors influencing home range relocation and immigration in a context of harvesting* for details about behavioral interactions). In addition, they cannot evaluate the relative effects of various limiting factors on immigration because migration between protected and harvest area is model with only one parameter.

These theories gave some good insights about population processes leading to migration between protected to harvest area but they have some strong limitations to predict immigration in a context of harvesting. A better theory, based on valid, tested assumptions about population dynamics and behavioral responses to density (Caro 1998, Gosling and Sutherland 2000), is needed to understand the effect of harvesting on immigration, to identify which factors can influence the magnitude of immigration in order to predict the effect of immigration on metapopulation dynamics.

WHAT IS MISSING TO DEVELOP A GENERAL THEORY ABOUT IMMIGRATION?

From this overview, we can conclude that very few studies have quantified the effect of limiting factors other than population density in the harvested area (Fig. I.2a) and even fewer have quantified the effect of multiple limiting factors on immigration (Fig. I.2b) and had enough replicates (Fig. I.3b) to draw conclusions about a relationship between limiting factors and immigration. In some studies, alternative hypotheses have been stated to explain the partial replacement of harvested individuals, but no strong empirical evidence has been provided to support these alternative hypotheses. Moreover, very few experiments have been designed to quantify density-dependent immigration (Fig. I.3c; massive initial removal), or have been carried out in controlled conditions (Fig. I.3a) and able to follow realized movement and get the fate of migrants.

In this thesis, we suggest using a small scale model system, with replication in a naturally variable environment to quantify the effect of five limiting factors to immigration (*i.e.* the density in the harvest area, the size of the population in the protected area, the density dependence, the relative habitat quality between the protected and the harvest areas and the functional connectivity). In order to be able to detect density dependence, we applied a constant and incremental reduction of the density over time.

FRINGING REEFS AND DAMSELFISH: A SMALL SCALE MODEL SYSTEM

To test questions related to immigration in a harvesting context, I used two small, closely related coral reefs fishes, the longfin damselfish (*Stegastes diencaeus*) and the dusky damselfish (*Stegastes adustus*) and their habitat as a small scale experimental model system. Sale (2002) suggests that coral reefs provide ideal natural laboratories for discovering density-dependent mechanisms because coral-reef fish are among the few vertebrates that are amenable to both *in situ* observations and experimental manipulations.

Damselfish of the genus Stegastes: an abundant and aggressive little gardener

Damselfish (family Pomacentridae) form a very diverse group of coral reef fish with more than 300 species and is mainly divided into aggregating planktivores (*e.g. Chromis*, *Dascyllus*) and omnivores (*e.g. Pomacentrus, Amphiprioninae*, including the famous cartoon Nemo) and territorial herbivores (*e.g. Stegastes, Microspathodon*). Most damselfish species are highly territorial, or at least are "home ranging" (Allen 1991, Sale 1991).

Stegastes damselfish have an extended distribution with strong representation in the eastern Pacific and the tropical Atlantic and are extensively studied, so we know much about their biology and ecology which is a major advantage. These energetic small fish spend their days taking care and patrolling a private algae patch that is vigorously defended against intruders. Because of their extreme territoriality and their effects on the algae-substratum composition and on the fish and invertebrate community, they are recognized as being keystone species (Williams 1980, Hixon and Brostoff 1983). In Barbados, there are four abundant *Stegastes* species and three that mainly inhabit fringing reefs (*Stegastes diencaeus, S. adustus and S. partitus*). In this thesis, I will focus on *S. dienaceus,* the longfin damselfish and *S. adustus*, the dusky damselfish, two species are very common in the Caribbean and inhabit the spur and groove zone of fringing reefs in Barbados (Fig. I.4; Cheney and Côté 2003, Robertson 1996, Solandt et al. 2003).

Longfin and dusky damselfish are a very suitable small scale model system because they have very small territories, are very site-specific and can be observed directly without being significantly disturbed. Territory acquisition appears to be vital for survival and reproductive success, and there is no evidence of "floaters" in longfin or other *Stegastes* damselfish populations (Bartels 1984, McDougall and Kramer 2007). Territories of both species are contiguous on reef (territory area; 1.38 ± 0.57 m^2 in longfin damselfish and 0.92 ± 0.29 m^2 in dusky damselfish). Adults longfin damselfish are slightly bigger (mean total length ± SD; 9.03 ± 1.90 cm), more aggressive and inhabit preferentially the deepest portion of the Spur and Groove zone. Dusky damselfish (7.15 ± 1.04 cm) inhabit the Crest zone and the upper portion of the Spur and Groove zone. Their respective distributions overlap in the Crest and in the Spur and Groove zone on fringing reefs. In both species, both sexes vigorously defend exclusive use territories against a variety of intruders (Robertson et al. 1976; Itzkowitz 1977; Robertson 1984). Territories are usually located over rock and eroded dead coral substrata, that provide food in the form of a cropped algal mat and holes used as refuges. Males grow to larger sizes than females in both species (Cheney and Côté 2003, Robertson 1984). Microhabitat distribution is size- and sex-structured in longfins (Cheney and Côté 2003), K. Turgeon, *unpublished data*). In Longfin damselfish, males often occupy the edges of the reef where the substratum provides more nest sites (Cheney and Côté 2003, Robertson 1984) and females tend to be found away from the edges. There is no clear habitat selection pattern in dusky damselfish. Territory locations are very stable in established populations of both species, but territories of experimentally removed individuals are visited by neighbors after as little as 3 min and can be reoccupied within 10 to 30 min (Cheney and Côté 2003, McDougall and Kramer 2007). This is a real advantage because they can be experimentally manipulated on a relatively small spatial and temporal scale.

Both species spawn every month (Thresher 1984). After a successful courtship, females lay eggs in a nest in male territories and male provide paternal care for eggs until hatching. After hatching, larvae disperse in the water column and spent between 19 to 24 days in the pelagic environment in longfin damselfish and between 20 to 23 days in the dusky damselfish (Wellington and Victor 1989). After the pelagic phase, larvae settle on reef. The peak in larvae settlement is just before and just after the new moon in dusky damselfish and longfin damselfish, respectively (Robertson 1992). Settlement refers to the first appearance of the smallest individuals and recruitment refers to the proportion of fish that survived to the end of the lunar cycle (Robertson et al. 1993). Juveniles are brightly colored (yellow and purple in longfin damselfish and orange and purple in dusky damselfish) and spend most of their time hidden in the substratum within adult territories. They undergo an ontogenetic color change at a size varying from 3 to 7 cm in longfin damselfish (S. Theleme, *unpublished data*) and defend suboptimal small territories at the margin of adult territories (K. Turgeon, *unpublished data*). Apparent adult mortality in longfin and dusky damselfish is very low as indicated by the few unexplained disappearances during relatively long-term monitoring in our study and by the low abundance of predatory fish on fringing reefs in Barbados (Rakitin and Kramer 1997).

Spur and Groove zone on fringing reefs in Barbados

I carried out my research on the west coast of the island of Barbados, West Indies (13°10'N, 59°30'W; Fig. I.4). I used 9 sites distributed among five fringing reefs along the west coast. Fringing reefs are found only on the west coast of the island growing like “hand-shape” structures on a gently sloping shelf extending about 300 m from the beach to a depth of 10 m (Lewis 1960, Stearn et al. 1977). Two reefs, North Bellairs and South Bellairs, are located within the Barbados Marine Reserve and at a central position along the west coast. Within the Barbados Marine Reserve, all types of fishing are prohibited, except for cast netting for clupeids which occurs only in the shallow water. The Barbados Marine Reserve seems to protect fish stock because there is evidence of greater size and abundance of fishes within the reserve (Chapman and Kramer 2000, Rakitin and Kramer 1996, Tupper and Juanes 1999). Longfin and dusky damselfish are not targeted by fisheries in Barbados, so we can assume that reefs outside the Barbados Marine Reserve can serve as unharvested areas. Two reefs, Heron Bay (four sites on Heron Bay at a distance of 75 m from each others) and Bachelor Hall (one site) are located to the north of the Barbados Marine Reserve and one reef to the south (Sandy Lane). The Bellairs Research Institute of McGill University is located in the center of the west coast, in front of North and South Bellairs and had the facilities, the equipment and a boat needed to carry out my research.

More specifically, I focused my research in the Spur and Groove zone. Fringing reefs in Barbados are divided into three ecological zones (Lewis 1960, Lewis and Oxenford 1996, Stearn et al. 1977). The Backreef is the zone adjacent to the shore and is composed of dead coral forming a nearly flat rock surface covered by sand and filamentous algae. The Crest is the zone extending approximately 50 m seaward of the Backreef and formed by mostly eroded dead reef with some live coral heads and characterized by high rugosity. The Spur and Groove zone is at the seaward edge of the reef and is characterized by "finger-shaped" seaward extensions of reef in the sea separated by sand channels (Lewis and Oxenford 1996); Fig. I.4). This zone is particularly suitable to explore the effect of functional connectivity on coral reef fish movement because it is naturally fragmented, where solid and often highly structured patches of reef are separated by low complexity substrata such as sand and rubble. In general, low complexity substratum are known to strongly impede movements of reef dwelling fishes (Barrett 1995, Chapman and Kramer 2000, Ogden and Buckman 1973) because they offer few refuges and are usually associated with high predation risk (Shulman 1985, Sweatman and Robertson 1994). In addition to its interest for functional connectivity, the Spur and Groove zone is particularly suitable for behavior observation by being shallow therefore allowing long underwater time in SCUBA diving.

THESIS STRUCTURE AND APPROACH

My thesis encompasses two main approaches to answer questions related to immigration via home range relocation into harvested populations. The first approach is theoretical. I developed a general theoretical model to predict immigration into harvested populations and to test the relative importance of some key limiting mobility factors that are susceptible to affect total catch and immigration rate. The development of this framework was not planned in the initial thesis proposal but the lack of a general theory, the use of inadequate assumptions to model immigration in a context of harvesting and the interesting insights and finding from my thesis motivated this development.

The second approach is experimental and is carried out on the field. To understand the underlying mechanisms leading to home range relocation at the scale of territory and to understand how immigration is affected by density at the landscape level, I reproduced the dynamics between a fished and a protected area by removing fish in a given area (called "harvest area") and observed immigration from the surrounding "protected area" in relation to decreasing density. To do so, I developed an experiment that reduces, incrementally, the density of two damselfish species in a natural setting. I replicated this design on seven sites, and I used two control sites where the density was not manipulated. The seven experimental sites were chosen to vary in three limiting mobility factors suspected to affect immigration: the relative habitat quality and the landscape functional connectivity between the fished and protected area and the availability of potential migrants in the protected area. However, we chose our sites to be similar in the initial damselfish density in the harvest area and in the size of the harvest area.

Over three field seasons (2005-2007) that lasted from 4 to 5 months each, I spent several hours per day, with an impressive team of research assistants, characterizing and mapping the sites (2 weeks per site), tagging damselfish (3-4 days per site), noting and observing damselfish behavior and movement before (2 weeks per site), during (4 to 7 weeks per site) and after (1 week per site) the incremental reduction of the density of damselfish. In 2005, I was able to apply the experimental setup on two sites (HB1 and HB2) with the help of two assistants, on three sites in 2006 (HB3, HB4 and NB1) with the help of 3 assistants and on four sites in 2007 (SB1, SL1, SL2 and BH1) with the help of 6 assistants. With the help of J. Grégoire (2006), A. Robillard and V. Duclos (2007), we also performed an independent translocation experiment (*i.e.* moving longfin damselfish from their territory to a pre-determined released site) and observation of homing path to define and quantify what constitute a barrier to movement from a reef fish perspective.

To predict immigration in response to harvest, it was necessary to determine how my model species perceived its environment and how structural and social habitat features may impede or facilitate its movement. In *Chapter 1*, I present a damselfish translocation experiment in its natural environment to quantify functional connectivity from a damselfish perspective. In this chapter, I also suggest a new methodological framework to compare the width and steepness of a barrier to movement among taxa. To predict immigration in response to harvest, it is also necessary to understand how its magnitude will be affected by the quality of the habitat and by the local density of potential neighbors. The relative importance of these effects is poorly known. In *Chapter 2*, I took the opportunity provided by the experimental, incremental reduction in density used in *Chapter 4* to evaluate how local density and the quality of individual territories affected the probability that they would be recolonized. Immigration in response to harvest has important implications for metapopulation dynamics, sustainable harvesting and conservation but we have limited empirical evidence of the mechanisms leading to immigration. In *Chapter 3*, I develop a general and simple theoretical framework to predict immigration in harvested populations and incorporate perspectives from *Chapters 1* and *2* about habitat quality and functional connectivity. My 'compensatory immigration model' is strongly inspired from the Beverton –Holt recruitment function (Beverton and. Holt 1957) and from the limitation approach developed by Schmitt et al. (1999). The compensatory immigration model suggests six alternative scenarios that increase in complexity by adding parameters that are related to different limiting factors to immigration (*i.e.* initial rate of replacement of removed individuals that could be influenced by habitat quality and functional connectivity and density dependence from behavioral interactions) and one variable (initial population size in the protected area). The quantification of immigration has been limited by the lack of replicated and controlled studies and by the small variation in density. In *Chapter 4*, I apply and test the model developed in *Chapter 3*, and I carry out an experimental, incremental and localized reduction of damselfish in their natural habitat in seven sites and monitored two control sites. I use findings from *Chapters 1* and *2* to develop independent habitat quality and functional connectivity indexes and compare the ability of these indexes to predict total proportional yield and the rate of replacement of harvested individuals among the seven sites. In addition to the studies described in the chapters of this thesis, I also worked on a multi-scale habitat selection model to predict damselfish distribution based on their species, size and sex as a function of micro-, meso-habitat characteristics and social environment (*i.e.* proximate neighbors). I am also working on a synthesis on compensatory immigration in vertebrate populations following localized mortality. These manuscripts are in preparation.

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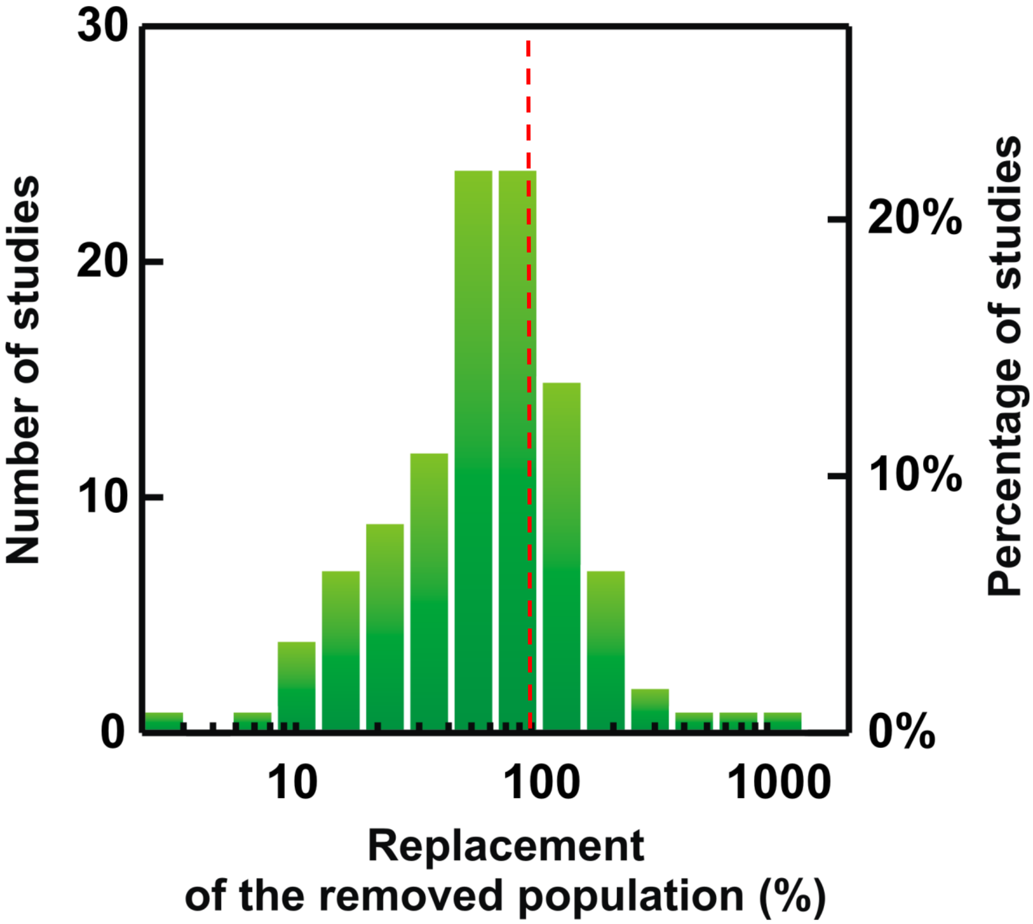
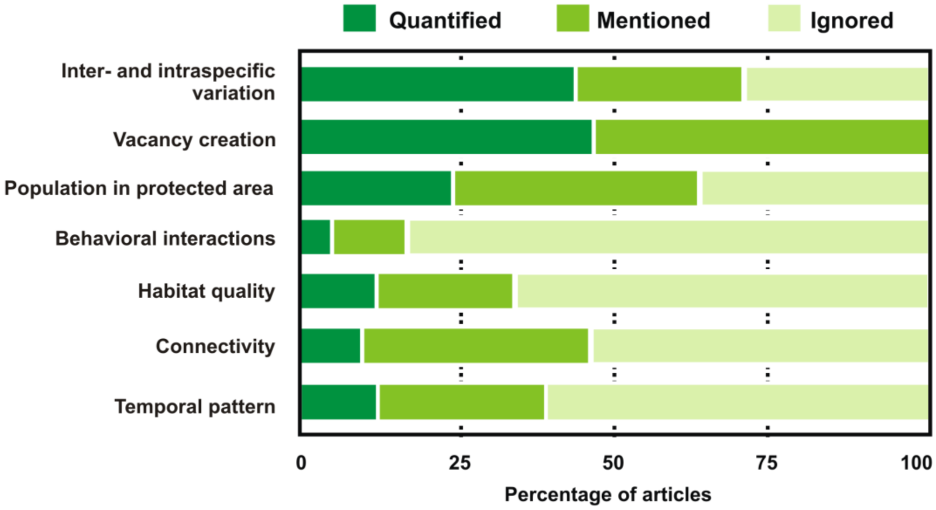


Figure I.1. The frequency and percentage of studies (from the 118 studies from the literature review on migration in vertebrate populations; *Appendix I.1*) that observed a variable replacement of removed individuals by migrants from adjacent areas. Replacement represents the proportion of removed individuals that were replaced by immigrants *100. The red dashed line represents a replacement of 100%. The x-axis is log transformed.

a) Limiting factors to immigration in response to harvest



b) Number of factors quantified simultaneously per study

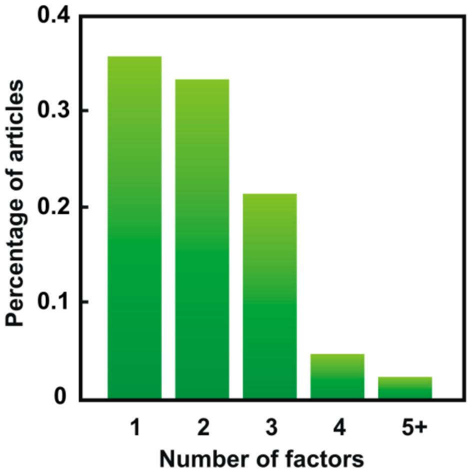


Figure I.2. a) percentage of the 44 articles from the literature review on migration in vertebrate populations that quantified (dark green), mentioned (lime green) or did not mentioned (light green) the effect of seven potential limiting factors to immigration, namely the inter- and intraspecific variation, creation of vacancies in the harvest area, population size in the protected area, density dependence, habitat quality, functional connectivity and temporal pattern, b) frequency distribution of the number of simultaneously quantified factors that could affect immigration

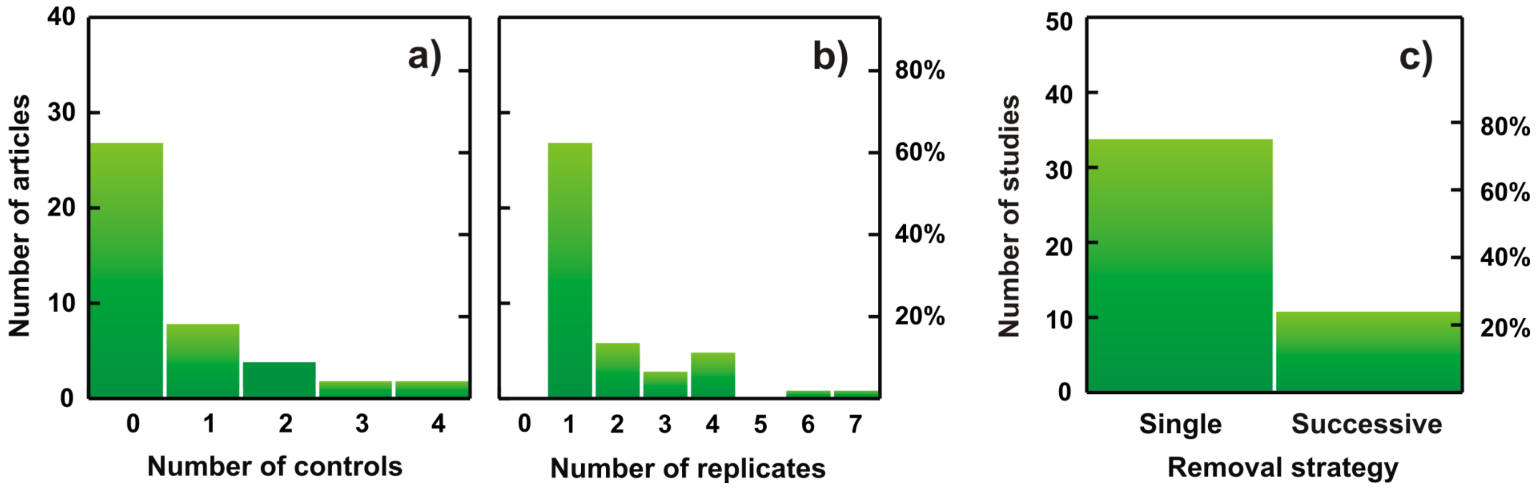


Figure I.3. The frequency and percentage of articles (from the 44 articles from the literature review on migration in vertebrate populations; *Appendix I.1*) in relation to a) the number of control sites (i.e. without reducing population size in the harvest area) and b) the number of replicates of experimental sites. c) the frequency of studies (from the 118 studies found in 44 articles) that performed either a single removal or a successive number of removal.

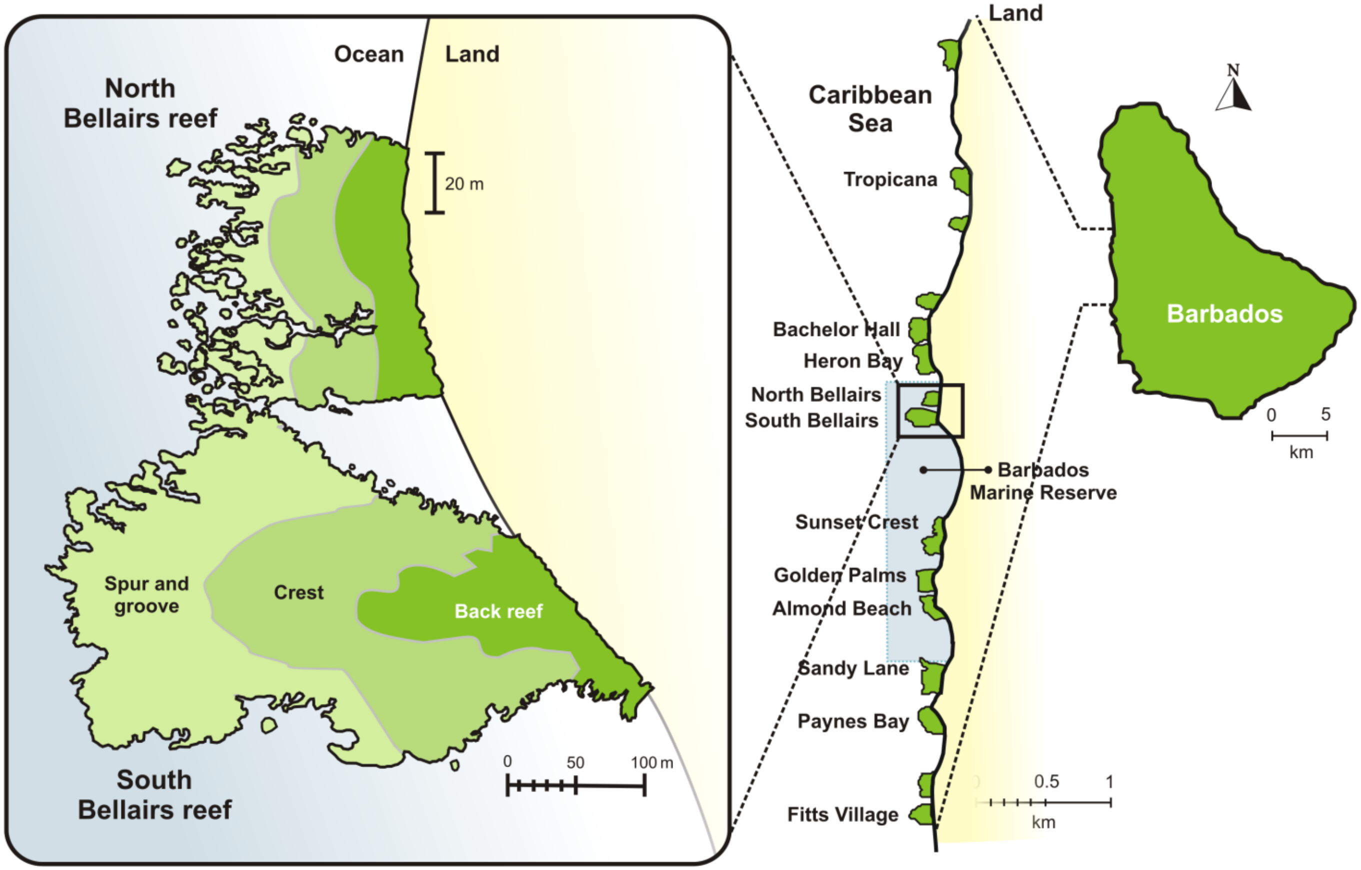


Figure I.4. Schematic representation of two fringing reefs on the west coast of Barbados, West Indies (13º15’ N, 59º30’ W). Reefs are in green and sand is in blue. The three reef zones are represented on both reefs with different shades of green (Back reef, Crest and Spur and Groove zones). The blue rectangle along the coast represents the area covered by the Barbados Marine Reserve. Modified from Lewis & Oxenford (1996).

CHAPTER 1:

FUNCTIONAL CONNECTIVITY FROM A REEF FISH PERSPECTIVE:

BEHAVIORAL TACTICS FOR MOVING IN A FRAGMENTED LANDSCAPE

LINKING STATEMENT 1

In fragmented landscapes, structural and social habitat features may impede or facilitate animal movement and may act as limiting factors to immigration. However, different species view the landscape very differently. Therefore, to predict immigration it was necessary to determine how the damselfish that were my experimental species perceived barriers to movement. In *Chapter 1*, I used a translocation experiment and visual tracking of homing paths in different landscape configurations to achieve this goal.

This chapter is published in *Ecology* (2010, 91(11): 3332-3342). The three appendices available online correspond to appendices 1.1, 1.2 and 1.3 of this thesis.

ABSTRACT

Functional connectivity, the degree to which the landscape facilitates or impedes movement, depends on how animals perceive costs and benefits associated with habitat features and integrate them into a movement path. There have been few studies on functional connectivity in marine organisms, despite its importance for the effectiveness of Marine Protected Areas. In this study, we asked how open sand and conspecific distribution affected functional connectivity of longfin damselfish (*Stegastes diencaeus*) on fringing reefs in Barbados. We translocated 102 individuals to sites varying in sand gap width and in configuration: Continuous (solid reef between release site and territory), Detour (sand along the direct path between release site and territory, but an alternative continuous solid “U-shaped” reef path) and Patch (sand between release site and territory, but an alternative stepping stone path). We visually tracked and mapped every homing path. We found no evidence of a barrier to movement in the Continuous configuration, but sand was a partial barrier in Detour and Patch configurations. The probability of crossing the sand gap dropped below 50% when its width was >1.85 m in Detour and > 3.90 m in Patch configuration. Damselfish avoiding large gaps took detours that approximated the route maximizing travel over reef, but crossed more short sand gaps and fewer conspecific territories, suggesting avoidance of agonistic interactions. This study quantifies for the first time the size and steepness of a barrier to movement in a marine organism and provides evidence for effects of both landscape configuration and conspecific distribution on functional connectivity.

INTRODUCTION

Functional connectivity (*i.e.* the degree to which the landscape facilitates or impedes movement among patches; Taylor et al. 1993) is an organism-based emergent property of the landscape, combining a description of its physical structure with the response of a species to that structure (Taylor et al. 2007, Tischendorf and Fahrig 2000). As a key determinant of metapopulation dynamics, landscape functional connectivity is essential to the persistence of extinction-prone populations (Hanski 1999, Pulliam 1988). Functional connectivity has strong implications for the site selection of protected areas because spatially clustered networks of protected areas increase the probabilities of species occurrence and persistence (Cabeza 2003, Lubchenco et al. 2003, Russ et al. 2008). In marine fish and invertebrate populations, demographic connectivity, achieved through long-distance dispersal of larvae by oceanographic currents, represents the primary opportunity for mixing among fragmented local marine populations (Cowen et al. 2006, Planes et al. 2009). Nevertheless, functional connectivity, which differs from demographic connectivity in being based more on individual behavior and a smaller scale, is also important because it influences the degree to which individuals that have settled in a reserve will be exposed to adjacent fisheries (Bartholomew et al. 2008, Kramer and Chapman 1999, Zeller and Russ 1998).

In heterogeneous landscapes, moving organisms encounter habitat patches differing in food quality and predation risk and may interact positively or negatively with resident conspecifics and congeners. Functional connectivity depends on how they perceive and respond behaviorally to habitat patches and ultimately select a movement path that minimizes costs (Bélisle 2005, Wiens 2002). Functional connectivity is influenced by intrinsic characteristics of the organism such as mobility and perceptual range (Lima and Zollner 1996, McDonald and St. Clair 2004), size (Bakker and Van Vuren 2004), sex (Pither and Taylor 1998) and state (*e.g.* competitive ability, nutritional and reproductive condition; Turcotte and Desrochers 2003). Extrinsic factors such as the total travel distance (Rothermel and Semlitsch 2002), landscape configuration (*i.e.* spatial distribution of habitat; Gillies and St. Clair 2008), and quality of the matrix (Baum et al. 2004, Bender and Fahrig 2005) are also likely to affect functional connectivity.

Translocations and gap-crossing experiments have contributed greatly to our understanding of functional connectivity in terrestrial animals by identifying the minimal width of a barrier to movement (the gap width at which the probability of crossing the barrier drops below some defined probability of crossing) and its steepness (the rate of decrease in the probability of crossing a barrier between the two inflection points). From these studies, we know that for many terrestrial taxa inhabiting highly structured habitats such as forest, open habitat represents a partial barrier (Awade and Metzger 2008, Bakker and Van Vuren 2004, Bélisle and Desrochers 2002, Bosschieter and Goedhart 2005) while structured habitats act as corridors that facilitate movement (Baum et al. 2004, Gillies and St. Clair 2008). Social habitat features, such as the distribution of conspecifics, may facilitate movement by indicating high habitat quality or safety (Sieving et al. 2004, Stamps 1988) or impede it through agonistic interactions, but there is little empirical evidence for social effects on functional connectivity. To our knowledge, no study has used an experimental gap-crossing approach comparable to those in terrestrial systems for a marine organism.

Coral reefs are naturally fragmented habitats, composed of solid, often highly structured patches of reef separated by low complexity substrata such as sand and rubble. Substrata with low structural complexity offer few refuges and are associated with high predation risk (Shulman 1985, Sweatman and Robertson 1994). Large sand gaps are known to impede fish movements between reefs (Barrett 1995, Chapman and Kramer 2000, Ogden and Buckman 1973) although relatively long-distance movements of newly settled juveniles have also been documented (Frederick 1997). However, there is little information about the minimal width or variation in response to width of such barriers. Moreover, on many coral reefs, the territories of the abundant, small, but very aggressive damselfishes might form a social barrier to movement because they can inhibit feeding activity of other species (Foster 1985) and limit access to refuges (Sweatman and Robertson 1994).

In this study, we used path choice by homing fish following experimental translocation for the first time in a marine system to quantify functional connectivity. Specifically, we asked whether sand formed a barrier to movement of homing longfin damselfish (*Stegastes diencaeus*) and, if so, what was the minimal width and steepness of this barrier. In addition, we asked whether the territories of conspecifics and congeners acted as a social barrier to movement. We used the natural variation in the width of sand gaps in two reef configurations (Detour and Patch) that differ in the extent to which sand formed a barrier to movement, and we used a Continuous configuration (no sand gap) as a control for hidden barriers. Our system offers a unique opportunity to study the effect of structural and social habitat features on movement paths because a highly mobile observer is able to continuously track each translocated individual on a small spatial and temporal scale.

METHODS

Study site and species

We carried out our study between June and August in 2006 and 2007 and in January 2008. We used the spur and groove zone of four fringing reefs along the west coast of Barbados (13°10’N, 59°38’W) at depths of 4 – 6 m. The spur and groove zone is characterized by finger-like, seaward extensions of the main reef with numerous small patches of reef separated by sand (Lewis 1960; Figure 1.1). Longfin damselfish are abundant in this habitat. Both sexes vigorously defend exclusive territories (area, mean ± SD; 1.38 ± 0.57 m^2), usually located over rock and eroded dead coral substrata, that provide food in the form of a cropped algal mat and holes used as refuges. Microhabitat distribution is size- and sex-structured (Cheney and Côté 2003, K. Turgeon, unpublished data). Males, which grow to larger sizes than females and are usually more aggressive, provide paternal care for eggs and often occupy the edges of the reef where the substratum provides more nest sites (Cheney and Côté 2003, Robertson 1984). Females tend to be found away from the edges. Territory acquisition appears to be vital for survival and reproductive success, and there is no evidence of “floaters” in longfin or other Stegastes damselfish populations (Bartels 1984, McDougall and Kramer 2007). Territory locations are very stable in established populations, but territories of experimentally removed individuals are visited by neighbors after as little as 3 min and can be reoccupied within 10 to 30 min (Cheney and Côté 2003, McDougall and Kramer 2007). Thus, absences from a territory may allow increased intrusions and require fighting to regain possession (Sikkel and Kramer 2006). We therefore assumed that this species would be highly motivated to home quickly although the quality of the territory and the competitive ability of individual might affect this motivation. We translocated 102 individuals (total length; TL, mean ± SD: 9.63 cm ± 1.92; range: 5.0-13.0 cm), each only once, all in the adult (dark) color pattern, including both males and females and individuals above and below the size of sexual maturity (9.3 cm TL, K. Turgeon, unpublished data).

Configurations and site description

We used 23 sites selected to conform to one of three distinct configurations (Figure 1.1), with some sites used for more than one translocation because of a limited number of suitable sites (mean ± SD: 3.38 ± 2.57 translocations per site; range: 1 to 11). In the Continuous configuration, the shortest path between the release site and the territory passed over solid substratum. In the Detour configuration, the shortest path crossed a sand gap but continuous reef was available along a roughly “U-shaped” alternative route. In the Patch configuration, the shortest path crossed a sand gap and all alternative routes also required movements across at least one sand gap. Detour sites were selected so that the shortest distance over reef was at least 1.5 times longer than the linear path, therefore incurring at least small energetic and time costs for individuals that chose the alternative. We chose a large range of sand gap widths (mean ± SD: 4.57 ± 2.31 m; range: 1.00 – 10.60 m), linear distances imposed between release site and territory (7.05 ± 2.93 m; 2.15 – 16.50 m) and distances along the shortest alternative route that maximized the use of reef (8.54 ± 2.91 m; 3.45 – 17.20 m). These distances are similar to spontaneous “forays” (Bartels 1984) beyond the territorial borders (3.20 ± 2.19 m; 0.44 – 23.3 m, N = 602, K. Turgeon, *unpublished data*). Prior to translocations, each site was drawn on a Plexiglas slate with a 1 x 1 m grid. We used the measured distance between distinctive reference points on the reef to export and georeference the raster map in a GIS program (MAPINFO Professional 6.5). On each site, we mapped all conspecific and congeneric (*S. adustus,* and *S. planifrons*) territories by observing each individual for 10 min and mapping territory boundaries in relation to fixed reference points. We estimated the size of conspecifics and congeners (nearest cm, TL) and, whenever possible, the sex based on courtship behavior or the presence of a nest.

Translocation

Using SCUBA, each focal individual was caught using a modified cast net, sexed by examination of the urogenital pore (Thresher 1984), measured to the nearest 0.5 cm (TL), and carried to the release site in the net. After release, one diver started a timer and followed the individual at a distance of 3 – 4 m, drawing its path on the slate. Damselfish are highly tolerant of divers and we were familiar with and careful not to elicit predator avoidance behavior; even a distance of 2 m has been indicated as large enough to not alter their behavior (Levin et al. 2000). A second diver noted the time of every attack or aggressive display by conspecifics and congeners as well as the size of the aggressor. Each translocation required 20 - 40 min. Fish were considered not to have homed if they remained in a shelter for more than 25 min or started to defend a new territory near the release site. We observed no predation attempts during our experiment. If homing was successful, we measured the linear distance between the center of the focal individual's territory and the release site, the width of the imposed sand gap and the length of the homing path with a measuring tape. All translocations were carried out between 9h00 to 17h00 because longfin damselfish are strictly diurnal, resting in holes on the reef at night.

Path mapping and description of predictors

We georeferenced each hand-drawn homing path onto the respective site map. From these paths, we extracted the following predictors using the GIS software: the linear distance from the release site to the territory, the width of the imposed sand gap along the line between the release point and territory, the distance of the shortest route that maximized the use of reef in Detour and Patch configurations, the damselfish density (number of individual territories per linear m) along the homing path, along the shortest detour that maximized the use of reef and along the linear distance. We used the field measurements to check these values. We also used the software to estimate the percent of sand along the homing path, the linear distance and the shortest detour that maximized the use of reef as well as the number of sand gaps along the homing path in the Patch configuration. For Detour and Patch configurations, we calculated the configuration ratio, which is the distance along the shortest detour that maximized the use of reef divided by the size of the imposed sand gap. This dimensionless value represents the relative increase in distance travelled for a translocated individual avoiding a sand gap (mean ± SD, 2.27 ± 1.34; range: 1.5 – 7.9).

Model construction and assessment

We used the information theoretic approach for model selection and assessment of performance. To select the best subset of models among the entire set of candidate models, we used the Akaike's Information Criterion modified for small sample sizes (AICc). For each candidate model, we compiled the normalized Akaike weights (w_i) to address model selection uncertainty (Burnham and Anderson 2002, Johnson and Omland 2004). The confidence set of candidate models includes all models for which w_i is within 10% of the maximum weight (Burnham and Anderson 2002). We used the conventional model averaging when more than one candidate model had substantial support as explanations of the response variables (Burnham and Anderson 2002). To determine the reliability of predictor estimates, we calculated the weighted unconditional standard error with its associated confidence intervals (95% CI).

We used Generalized Linear Mixed Models (GLMMs, lmer library in R with the restricted maximum likelihood method) to produce candidate models that examined the effects of predictor variables on response variables, to account for spatial and individual effects in the data and to infer statistical support. Non-normally distributed predictors and response variables were log-transformed and every predictor was z-standardized prior to analysis. For each candidate model, we examined the Tolerance value (1/Variance Inflation Factor) which is a measure of the amount of variation unique to each retained predictor and is used to detect multicollinearity problems.

We investigated three questions. First, we evaluated the percent deviation of homing paths from alternative paths (linear path or shortest path along the reef that maximized the use of reef) and compared the deviations of homing paths on Detour and Patch configurations from those on Continuous configuration. We calculated the deviation from the linear path for damselfish that crossed the sand gap and from the linear and shortest path for those that did not cross the sand gap. We used a treatment contrast (Continuous configuration as a priori contrast) and a Gaussian error structure with an identity link function in our GLMM. We controlled for spatial independence by using site, nested within reef as random factors. Our second question was whether the probability of crossing a sand gap was a function of structural (width of the sand gap, configuration ratio), social (damselfish density along the alternative path maximizing the use of reef), and intrinsic characteristics predictor (size and sex). We allowed an interaction between sand gap width and configuration ratio because we predicted that larger configuration ratios would increase the probability of gap crossing. We built separate models for Detour and Patch configurations because the variances of two predictors (damselfish density, configuration ratio) were very different among configurations. We built an a posteriori model to test whether configuration affected the probability of crossing a sand gap by using sand gap width, configuration and the interaction between these two predictors to test for a difference in barrier steepness among configurations. We used a binomial error structure with a Logit link function and controlled for spatial independence by using site, nested within reef. Our third question was whether microhabitat characteristics (i.e. proportion of sand and density of conspecifics and congeners) along the homing path differed from those along the shortest route maximizing the use of reef in Detour and Patch configurations for damselfish that did not cross the sand gap. We used a binomial error structure with a Logit link function and we controlled for individual effect and for spatial independence among sites and reefs by nesting individual within site, within reef.

RESULTS

When released, most individuals hid in a hole or under a ledge for a short period of time and then initiated the homing. Homing sometimes began following an attack by a nearby territory holder. Homing individuals usually adopted a paler color on their heads, erected their dorsal fins, and alternated between pauses and bouts of rapid swimming. Rather than immediately chasing or biting, conspecific and congeneric territory holders often performed a rapid charge without making contact. Of the 102 translocated damselfish among the three configurations, 18% did not home (6% on Continuous, 3% on Detour and 9% on Patch configurations). Fish that did not home were smaller and released farther from their territories (unpublished analyses). The following analyses include only fish that successfully homed.

Open sand area as a barrier

On Continuous sites, damselfish homed in a nearly linear path with a median deviation from the imposed linear distance of only 19% (Fig. 1.2 a). This deviation was independent of the total imposed distance and corresponded to an additional median distance of about 1.50 m. On Detour and Patch configurations, almost one third (Detour 28%, Patch 29%) of the damselfish crossed the imposed sand gap and also homed in a nearly linear path (median increase: Detour 4%, Patch 11%; Fig. 1.2 b). Their deviations were comparable to those observed on

Continuous configuration (Table 1.1, Fig. 1.2 a, b). On Detour and Patch configurations, the homing path of damselfish that did not cross the sand gap and used a detour was longer than the linear imposed distance (median increase: Detour 97%, Patch 71%; Fig. 1.2 c) and deviations from the linear imposed distance were larger than the deviations observed on Continuous configuration (Table 1.1, Fig. 1.2 a, c). Homing paths were similar to the shortest route maximizing reef in Patch (3% longer; Fig. 1d) but differed slightly in the Detour configuration (10% shorter; Fig. 1.2 d), because damselfish sometimes ‘cut corners’ to use a shorter path than the shortest route maximizing reef (Table 1.1, Fig. 1.2 a, d).

To explain the probability of crossing the sand gap, we retained three candidate models in the Detour and two in the Patch configuration (based on the AICc scores) and performed model averaging. The width of the sand gap was the most influential predictor, explaining 26% of the Percent of Deviance in Detour and 34% in Patch configurations (Appendix 1.1). Sand gaps greater than 1.85 m reduced the probability of crossing a sand gap below 50% in Detour configuration. This value was 3.90 m in Patch configuration (Fig. 1.3). The steepness of the barrier (i.e. the rate at which the probability of crossing a sand gap decreased) was sharp in both configurations. Each additional 0.5 m decreased the probability of crossing by 25% (Fig. 1.3). We found no support for an interaction between sand gap width and the configuration in the a posteriori model, but both predictors were supported (GLMM, N=55, Sand gap estimate ± SE = -2.41 ± 0.71, Configuration estimate ± SE = 3.02 ± 1.17, both predictors did not include zero in the 95% CI). Thus, the configuration affected the probability of crossing a sand gap at a given width but did not affect the steepness of the barrier. On Patch configurations, damselfish crossed one to six gaps (median width = 2.55 m, 1.13 – 3.28 m). Even though they crossed larger imposed sand gaps in Patch than in Detour configuration, most damselfish crossed the smallest sand gap available when there was a choice.

Other predictors had some support for effects on the probability of crossing a sand gap, but their estimates included zero within the 95% CI (Appendix 1.1). The configuration ratio had support in the Detour configuration model when interacting with sand gap width as predicted (Appendix 1.1). When the configuration ratio was large, the probability of crossing the sand gap increased slightly. Damselfish density along the alternative route that maximized the use of reef was suggested to affect the likelihood of crossing a sand gap in both configurations (Appendix 1.1). The probability of crossing a sand gap was higher when damselfish density was high along the alternative route. Damselfish body size and sex were not good predictors of the probability of crossing a sand gap.

Microhabitat used on detours

The paths used by damselfish had more sand than the alternative route that maximized the use of reef, independently of the configuration (Detour 50% more, Patch 10% more; Table 1.2, Fig. 1.4a). Trials in which the path were greater than the alternative route that maximized the use of reef were associated with more attacks on Continuous and Patch but not Detour configurations (Appendix 1.2). The number of attacks received was not related to damselfish density along the homing path in any configuration (Appendix 1.2).

The paths used by damselfish had a lower damselfish density than the alternative route on Detour and Patch configurations but this pattern has statistical support only on Detour configuration (Table 1.2). Damselfish used a path that had 37% fewer conspecifics $\cdot$ m^{-1} than the alternative route that maximized use of the reef on Detour and (Table 1.2, Fig. 1.4 b) 25% fewer damselfish $\cdot$ m^{-1} on Patch configuration. On Continuous configurations, the trend was in the opposite direction (6% more damselfish $\cdot$ m^{-1} along the used path, Table 1.2, Fig. 1.4 b).

DISCUSSION

By following the return of damselfish translocated to reef configurations of different patterns and sand gap widths, we have been able to quantify for the first time the size and the steepness of a barrier to movement in a marine organism. We have provided evidence that sand is a barrier, that the probability of crossing this barrier drops sharply as its width increases (steepness) and that the width but not the steepness of the drop depends on the configuration of reef around the barrier.

Nevertheless, the selected path crossed more sand than the path that offered maximal use of reef and, at the same time, in the Detour configuration, crossed fewer conspecific territories.

Sand gaps as a barrier to movement

When there was solid reef between the release site and the territory, the homing path of translocated damselfish was nearly linear over distances of 4.0 to 16.5 m. This suggests that there are no major barriers to movement on solid reef and that deviations observed in other configurations were a response to the sand gaps. When small sand gaps separated the release site and the territory, homing paths remained nearly linear. However, for larger sand gaps, damselfish consistently avoided the gap and took a longer detour. This shows that open sand is a powerful barrier to damselfish movement. Unfortunately, many studies of gap crossing failed to provide such controls, creating ambiguity regarding the influence of a specific barrier type (Bakker and Van Vuren 2004, Bosschieter and Goedhart 2005). Detour distances of 1.5 to 5.9 times longer than the direct path over sand suggest that damselfish perceive the cost per unit distance of crossing wide gaps as at least 5.9 times higher than that of moving over reef. The higher cost is likely to be due to increased risk of predation. Tethering experiments using small coral reef fishes have provided evidence that predation risk is higher over sand, particularly within 2 m of the reef edge, as a result of a low shelter availability coupled with a higher encounter rate with predatory fishes (Shulman 1985, Sweatman and Robertson 1994). Contrary to findings in birds and mammals (Bakker and Van Vuren 2004, Bélisle and Desrochers 2002), we did not find clear evidence for a tradeoff between the relative increase in the distance required for a detour and the probability of crossing a gap. In addition to the possible high cost of moving over wide sand gaps, damselfish may lack sufficient prior information about the landscape or a sufficient perceptual range ability (Lima and Zollner 1996) to make such decisions.

Although it is widely accepted that large sand gaps and other habitats with low structural complexity often impede movements of reef fishes and other marine organisms, the evidence is indirect and incomplete. The presence of 'grazing halos' (*i.e.*, zones of almost bare sand up to 10 m from reefs in seagrass beds; Hay 1984, Sweatman and Robertson 1994) suggests that herbivorous reef fishes forage mainly within this distance. Telemetric studies have observed avoidance of sandy substratum in some reef fish species (Afonso et al. 2008, Meyer and Holland 2005) but not others (Chateau and Wantiez 2009, Meyer et al. 2000). Mark-recapture studies indicated that coral reef fish rarely moved between reefs separated by more than 20 m, although translocated fish of several species returned home across these same gaps (Chapman and Kramer 2000). Studies on recolonization of depopulated patch reefs surrounded by sand suggest that gaps of 100 – 130 m provide a partial barrier (Brock et al. 1979, Ogden and Ebersole 1981). In a study of movements of newly settled juvenile reef fish from several families among units in experimental arrays of artificial reefs, there appeared to be a trend for movement to drop sharply at distances between 5 and 20 m (Frederick 1997, Fig. 2 in her contribution), but the distance effect was not examined, perhaps because it was confounded with species differences (which did affect movement) and because the author's primary interest was in the unexpected amount of movement. In a study of density-dependent predation on newly settled juvenile reef fishes, on the other hand, a gap of 5 m was enough to prevent nearly all movement by both juvenile and adult coral reef fish (Overholtzer-McLeod 2006). Invertebrates show similar patterns: the predation rate of blue crabs (*Callinectes sapidus*) on juvenile oysters is higher when there is a vegetated corridor linking marshes and reefs instead of a sandy bottom (Micheli and Petersen 1999). Defaunated drift algae located within seagrass beds had a greater abundance of amphipod compared to drift algae located on sand providing a corridor to amphipod movement (Brooks and Bell 2001). These previous studies have provided evidence that sand may impede movement and could represents a partial barrier for marine organisms. However, they did not examine a sufficient range of barrier widths to be able to quantify the size and steepness of the barrier. By testing a wide range of gap widths, our study shows that sand gaps are significant barriers to movement, even for homing individuals, at least when alternative paths are available. The size of gaps that inhibit movement under these conditions are much smaller than most of the upper limits to movement indicated by previous studies.

Our study is most comparable to previous studies of small, forest passerines crossing open gaps between forest patches. Data are available to compare 10 species from five studies to our results (Awade and Metzger 2008, Bosschieter and Goedhart 2005, Creegan and Osborne 2005, Desrochers and Hannon 1997, St. Clair et al. 1998; Appendix 1.3). These species range in mass from 6 – 21 g, similar to the mean mass of 19 g for damselfish in this study. However, the width at which the probability of crossing the gap drops below 50% are much larger (14 – 133 m; median = 49 m, Appendix 1.3). This may be related to higher mobility of the passerines which have average breeding territory diameters of 20 – 247 m, as compared to 1.3 m in the damselfish (Appendix 1.3). However, the barrier width is unrelated to territory size among the passerines (GLM; $R^2 = 0.13$).

In addition to the narrow width of barriers to damselfish movement, we also found that the barrier was very steep. The estimated probability of crossing dropped from 75% to 25% in only 0.3 m (Detour configuration) or 1.2 m (Patch configuration). Equivalent values for the data set from forest birds ranged from 18 – 126 m (Appendix 1.3). The steepness of the barrier appears to be related to its size among forest birds (GLM; $R^2 = 0.61$, p-value = 0.004) as well as in the data set including both birds and damselfish, although there is considerable variation (GLM; $R^2 = 0.72$, p-value < 0.001). Steepness of barriers is of interest as it influences the proportion of a population that moves over different distributions of gaps. If a gradual barrier is the result of intraspecific variation in the probability of crossing, intermediate barriers may generate selection in metapopulations.

Microhabitat selected when using a detour

Damselfish faced with large sand gaps in Patch and Detour configurations detoured along alternative routes that came close to the shortest distance that allowed them to maximize the use of reef. However, the microhabitat of their paths deviated from the expected alternative in crossing more sand but fewer conspecific territories. This suggests that detouring fish reduced the risk of attacks from conspecifics by 'cutting corners' as they skirted the larger gap. It seems less likely that moving across short sand gaps was simply a way of reducing the travel distance because there was not a significant difference between the actual distance travelled and the distance along the alternative route maximizing reef.

Although the presence of conspecifics has been suggested as a potential influence on movement paths (Bakker and Van Vuren 2004, Bélisle 2005), to our knowledge our study provides the first support for this proposal. While conspecifics or congeners may indicate resource quality (Stamps 1988) or safety (Schmidt et al. 2008, Sieving et al. 2004), crossing conspecific territories may also result in agonistic interactions that reduce vigilance and increase vulnerability to predation (Brick 1998). Minimizing the length of detours requires skirting the edge of the reef where encountered damselfish are more likely to be large aggressive males as compared to farther from the edge (Cheney and Côté 2003; K. Turgeon, unpublished data). The increased threat posed by large males along the edge in Detour and Patch and the potential higher familiarity with neighbors on Continuous configuration (Levin et al. 2000) may explain why damselfish avoided conspecific territories along the edge in Detour and Patch but not on Continuous configurations.

Implications for conservation

In coral reef fishes, identifying the size at which a sand gap (or any other habitat feature) acts as a barrier to movement and how steep the barrier is has strong implications for the design of effective Marine Protected Areas. Boundaries between fished areas and reserves that are located on sufficiently large sand gaps will increase the protective effect of reserves and therefore the size and reproductive output of fish within their boundaries. On the other hand, when reserves are intended to provide post-settlement individuals to a fishery, it is important that boundaries cross continuous reef (Bartholomew et al. 2008) or small gaps between adjacent patches so that fish can emigrate toward adjacent fished areas (Kramer and Chapman 1999).

The empirical evidence we provide for a negative impact of dominant and aggressive individuals on conspecific movement along the edge could have strong implications for landscape restoration, especially when establishing corridors. The distribution of dominant individuals on fragmented configurations could block dispersal even after structural connectivity has been restored (Hilty et al. 2006).

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Table 1.1. Generalized linear mixed models used to compare the deviation of the homing path from alternative paths (linear or shortest path that maximize the use of reef) on Detour and Patch configurations with those on Continuous configurations. Deviations from the linear path a) for damselfish that crossed the imposed sand gap and b) for those that used a detour along the reef instead of crossing the sand gap. Deviations from the shortest path on the reef that maximized the use of reef for damselfish that used a detour along the reef instead of crossing the sand gap. Parameter estimates associated standard errors (SE) and the 95% confidence intervals are presented. All models include a constant. For the configuration predictor, we used a treatment contrast with Continuous configuration as the contrast. Predictors in bold do not contain zero within the 95% confidence intervals.

Predictors	Estimate ± SE	95% CI
a) Deviation from the linear path for damselfish that crossed the sand gap (n = 47)		
(Constant)	0.05 ± 0.26	-0.45 to 0.55
Config.: Detour vs. Continuous	0.21 ± 0.48	-0.72 to 1.13
Config.: Patch vs. Continuous	-0.41 ± 0.35	-1.11 to 0.29
b) Deviation from the linear path for damselfish that used a detour (n = 70)		
(Constant)	**-0.47 ± 0.16**	**-0.78 to -0.16**
Config.: Detour vs. Continuous	**1.01 ± 0.26**	**0.51 to 1.51**
Config.: Patch vs. Continuous	**0.66 ± 0.26**	**0.15 to 1.17**
c) Deviation from the shortest path on the reef for damselfish that used a detour (n = 70)		
(Constant)	0.26 ± 0.17	-0.07 to 0.59
Config.: Detour vs. Continuous	**-0.78 ± 0.27**	**-1.31 to -0.26**
Config.: Patch vs. Continuous	-0.15 ± 0.27	-0.68 to 0.38

Table 1.2. Generalized Linear Mixed Models used to explain the difference between the homing path and the shortest alternative route that minimizes the use of sand in a) the percent sand along the paths for Detour and Patch configurations and b) damselfish density along paths for the three configurations. Parameter estimates, standard errors (SE) and the 95% confidence intervals (CI) of each parameter are presented. All models include a constant. For the configuration predictor, we used a treatment contrast and Detour configuration was the contrast with the percent of sand predictor and Continuous was the contrast for the damselfish density predictor. Predictors in bold do not contain zero within the 95% confidence intervals.

Predictors	Estimate ± SE	95% CI
a) Percent sand		
(Constant)	4.68 ± 2.91	-1.02 to 10.4
Percent sand	**5.42 ± 2.42**	**0.68 to 10.2**
Config.: Patch vs. Detour	-5.32 ± 2.95	-11.09 to 0.45
Percentage of sand*Config.: Patch vs. Detour	-3.96 ± 2.51	-8.89 to 0.97
b) Damselfish density		
(Constant)	-0.23 ± 0.94	-2.07 to 1.61
Damselfish density	0.67 ± 2.45	-4.13 to 5.47
Config.: Detour vs. Continuous	**5.10 ± 1.84**	**1.48 to 8.71**
Config.: Patch vs. Continuous	1.61 ± 1.26	-0.86 to 4.07
Density * Config.: Detour vs. Continuous	**-8.72 ± 3.52**	**-15.62 to -1.82**
Density * Config.: Patch vs. Continuous	-5.51 ± 3.67	-12.7 to 1.69

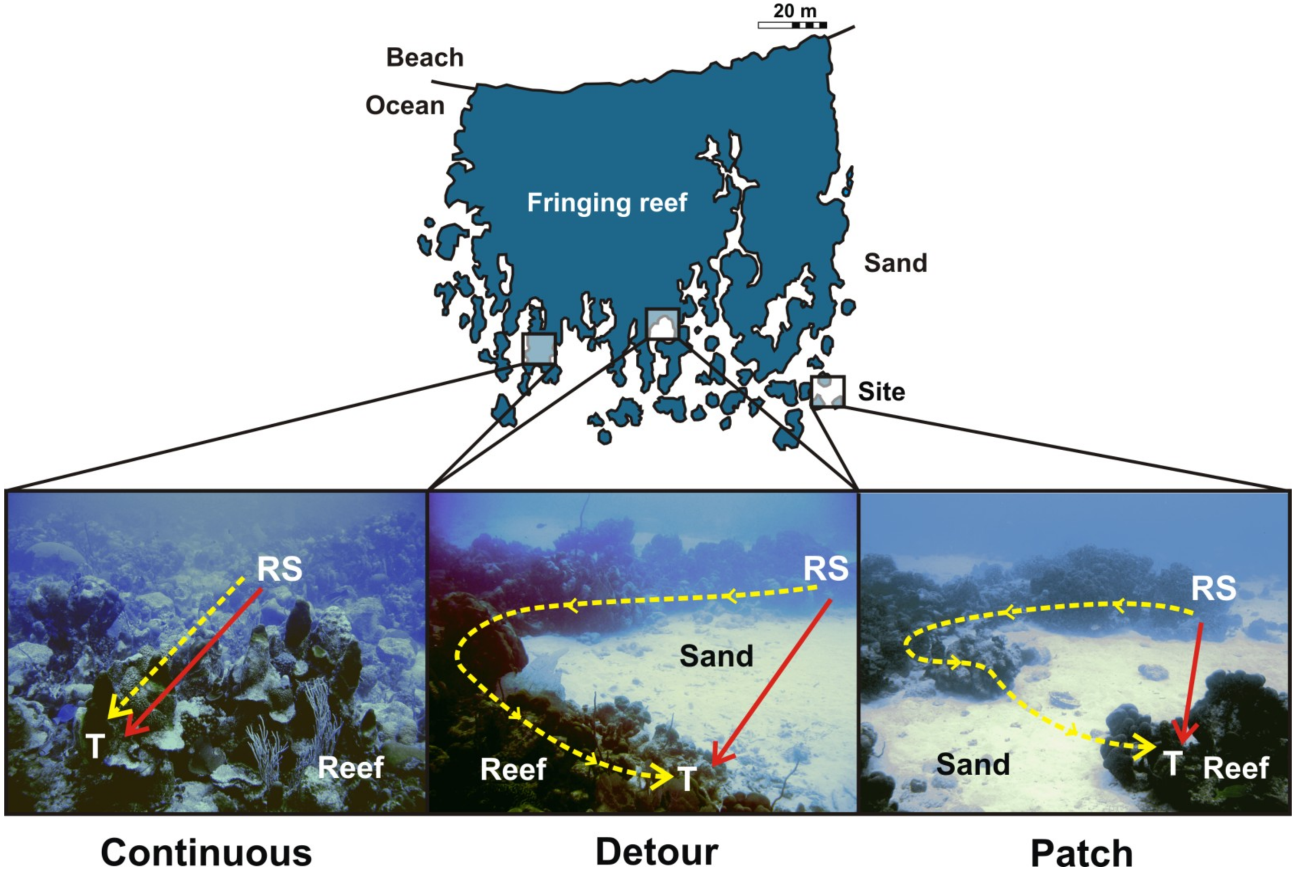

Figure 1.1. Illustration of the natural fragmentation of a fringing reef used to generate the three configurations used in this study: Continuous, Detour, and Patch. "T" indicates the territory location and "RS" indicates the release site location for translocations. The red lines represent the direct linear homing path that could be used to minimize energetic costs and agonistic interactions, and the dotted yellow lines represent the shortest detour that could be used to maximize the use of reef along the pathway.

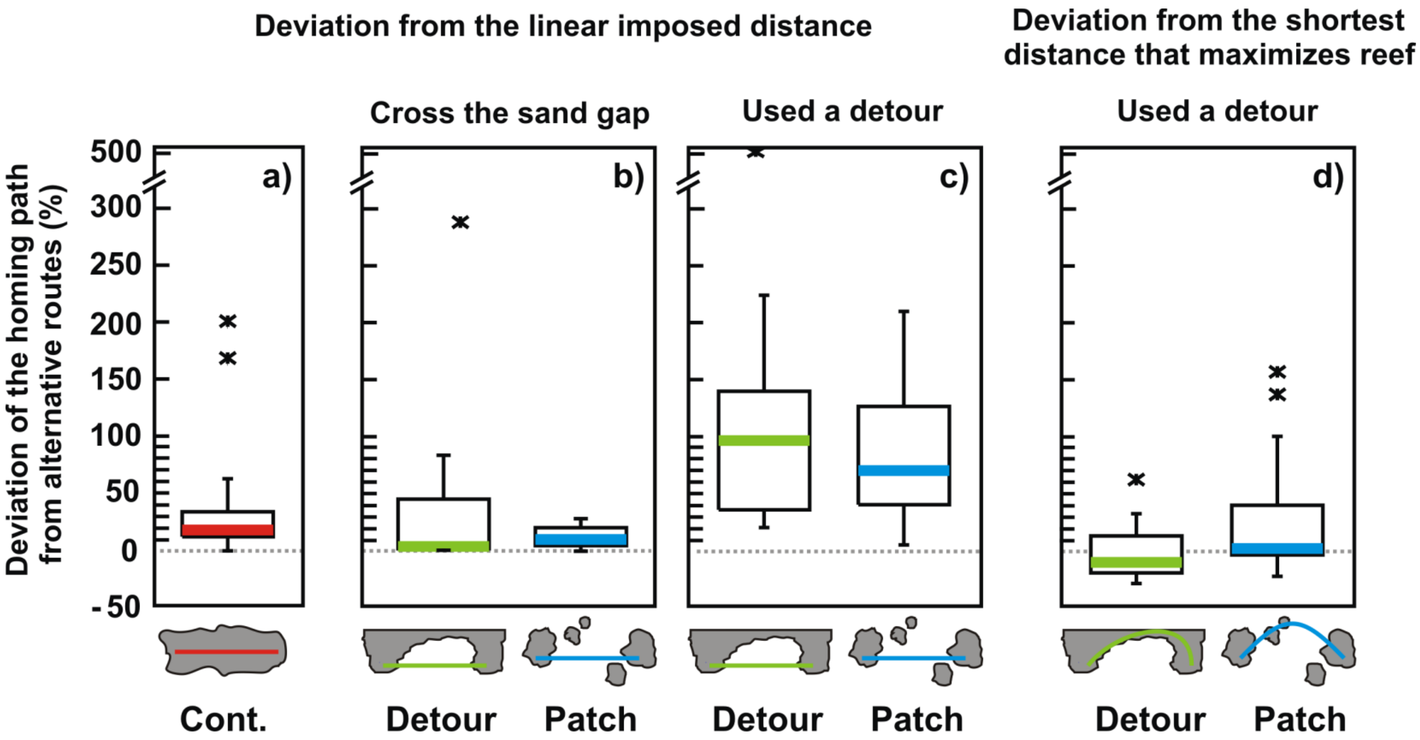

Figure 1.2. Deviation (%), calculated as the percent of deviation in distance of the homing paths used for returning to a territory from alternative routes. On Continuous configuration, deviations are calculated from the linear path from the release site to the territory. In Detour and Patch configurations, deviations are calculated separately for fish that crossed the sand gap and for those that used a detour along the reef. For fish that crossed the sand gap (a), we calculated the deviation from the linear path. For damselfish that did not cross the sand gap and used a detour, we calculated the deviation from the linear path (b) and from the route that maximized the use of reef (c). Horizontal line shows the median, the box represents the 25th and 75th percentiles, the top whisker ranges from the 75th to the 90th percentile and the bottom whisker ranges from the 25th to the 10th percentile. Asterisks indicate outliers.

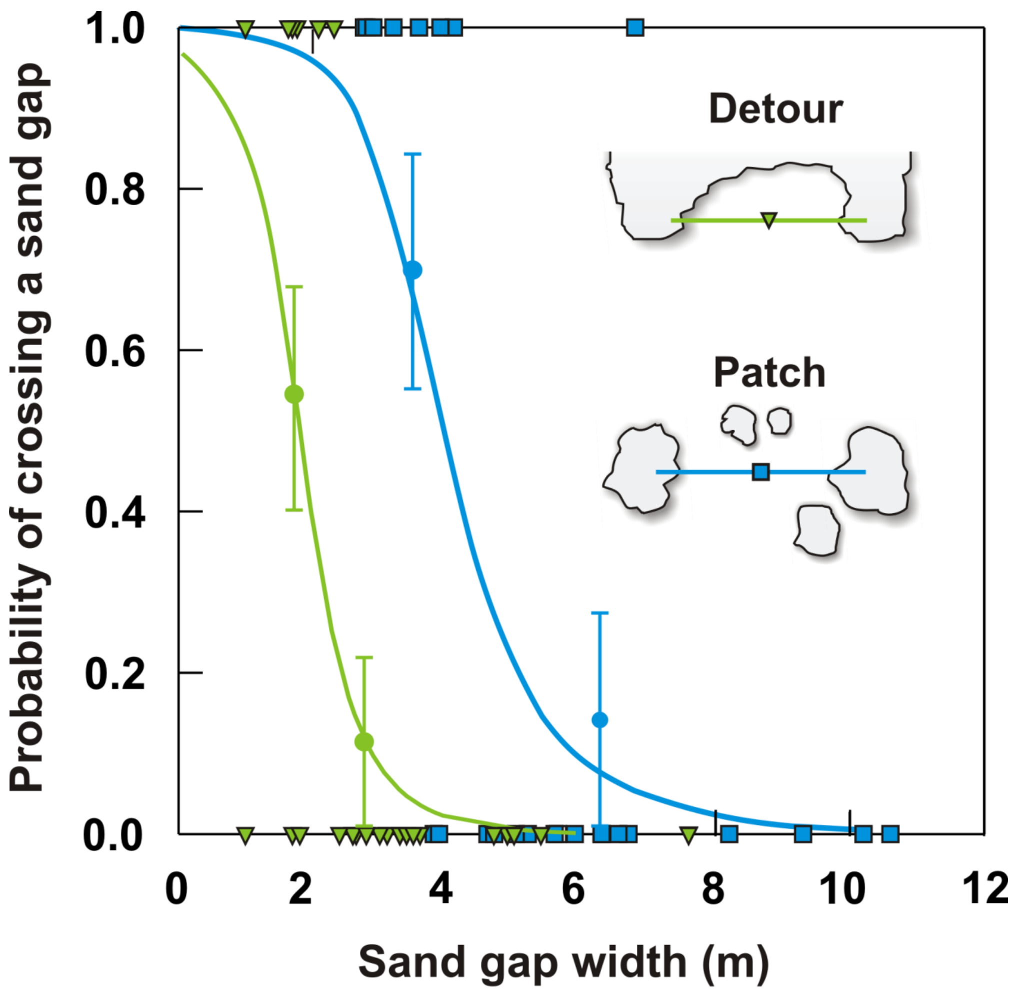

Figure 1.3. Probability of crossing an imposed sand gap in Detour and Patch configurations as a function of the width of the sand gap. The probability of crossing was evaluated with a Generalized Linear Model with Reef and Sites as random factors. The lines represent the best fitting Logit regressions for each configuration. The green triangles and blue squares represent the sand gap widths tested. We evaluated the fit and uncertainty of the Logit curve by using empirical probabilities (represented by large dots, calculated for two specified ranges of sand gaps, and corresponding to the proportion of sand gaps crossed over all sand gaps in the specified range.). The closer they are to the line, the better the fit. A measure of uncertainty (binomial standard error) is presented for each empirical probability.

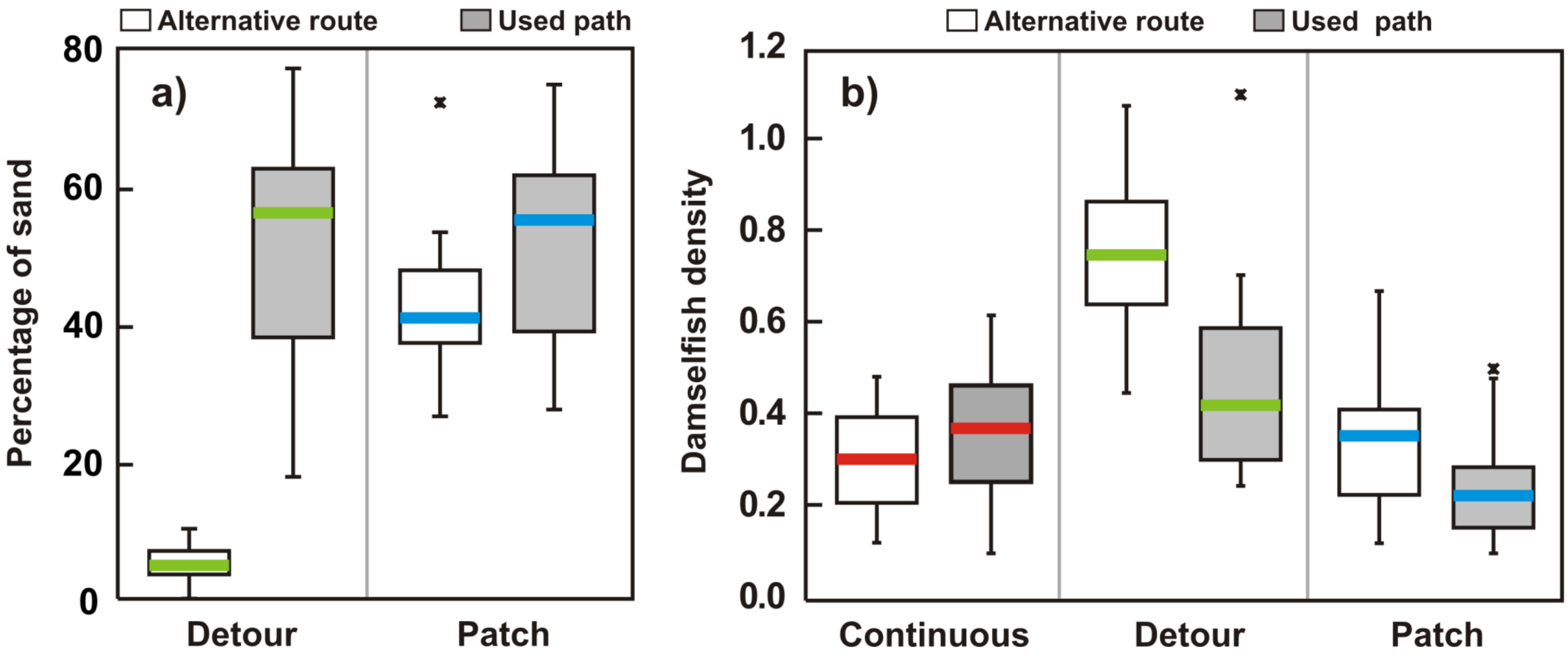

Figure 1.4. Differences between the path used by homing damselfish (grey box plots) and the alternative path that maximized the use of reef (white box plots) for a) percentage of sand along paths and b) damselfish density along paths in the three configurations. For Detour and Patch configurations, only fish that did not cross the imposed sand gap and used a detour are included. For Continuous configuration, there was no sand along either the linear or observed paths. See the caption of Figure 1 for interpretation of the box plots.

CHAPTER 2:

DENSITY AND HABITAT QUALITY INFLUENCE HOME RANGE RELOCATION IN A CORAL REEF FISH: IMPLICATIONS FOR SPILLOVER FROM MARINE PROTECTED AREAS

LINKING STATEMENT 2

Immigration following localized mortality may be affected by the quality of the habitat and the density of potential neighbors in a given area, but the magnitude and relative importance of these effects were poorly known. In *Chapter 2*, I took the opportunity provided by the experimental study of the effect of density on immigration at the metapopulation level (reported in *Chapter 4*) to examine how local density and the quality of individual territories affected the probability that they would be recolonized.

ABSTRACT

Marine protected areas (MPAs) have been suggested to benefit fisheries in adjacent waters by a net export of adults, called the ‘spillover effect’. Home range relocation (*i.e.* a permanent change in space use) by nearby individuals is an expected response to harvesting and would be a direct mechanism leading to spillover. There is accumulating evidence for home range relocation in reef fish, but, to date, no studies have documented the mechanisms and factors influencing home range relocation. In this study, we assessed the quantitative relationships between the probability that a vacant territory would be recolonized and the local density and habitat quality, as indicated by the characteristics of the previous occupant, in two small coral reef fish species (*Stegastes diencaeus*, *S. adustus*, Pomacentridae). We carried out an experimental, incremental, localized reduction of damselfish populations on seven sites and also monitored two control sites. We monitored vacant territories 30, 60, 360, 480, 840 and 1200 min after each removal event and mapped the territories at each site 1440 min after the removal. We observed a total of 385 territory shifts (*i.e.* recolonization by neighbors still using a portion of their original territory) and 217 territory relocations (*i.e.* recolonization by neighbors that completely abandoned their original territory or by damselfish from distant locations). Shifts preceded relocations with decreasing density. The probability of recolonization increased with territory quality and decreased with decreasing density in both species. The probability of recolonization via territory shifts decreased sharply with decreasing density in both species but increased slightly via relocation with decreasing density in longfin damselfish and increased and then decreased with decreasing density in dusky damselfish. As density decreased in the harvest area, individuals redistributed themselves to occupy territories previously occupied by larger individuals, assumed to be of higher quality. This study provides the first evidence that spillover in territorial species will be low at high densities likely due to some behavioral interactions (*e.g.* social fences, collective defense) to territory expansion and shifts of remaining survivors in the harvest area, will also be low at low densities due to the small benefits of

moving into very low density area for immigrants but will be higher at intermediate density. The higher probability of recolonization into high quality territories suggests that the magnitude of spillover into a harvest area will be higher if the harvest area is attractive compared to the adjacent protected area, independently from density.

INTRODUCTION

Marine protected areas (MPAs) have been recognized worldwide for their capacity to increase the abundance, biomass and diversity of fishes (Almany et al. 2007; Halpern and Warner 2002; Sanchez Lizaso et al. 2000). In the last two decades, MPAs have also been promoted for their benefits to fisheries in adjacent waters (DeMartini 1993; Hastings and Botsford 1999; Polacheck 1990; Roberts et al. 2001). Higher fish abundance and biomass in MPAs are suggested to sustain local fisheries by increased larval production (Almany et al. 2007; Botsford et al. 2009; Jones, Planes, and Thorrold 2005; Russ and Alcala 1996; Russ 2002) and by net emigration of adults into fished areas, a process called ‘spillover’ (Abesamis and Russ 2005; Gell and Roberts 2003; Halpern, Lester, and Kellner 2009; McClanahan and Mangi 2000).

Spillover can be the result of movements that are independent of reduced density in the fished area, for example daily movements within the home range, seasonal migrations and ontogenetic habitat shifts (Kramer and Chapman 1999; Russ 2002). Spillover can also result from home range relocations (Kramer and Chapman 1999; Pelletier and Mahevas 2005; Russ 2002) which are permanent changes in space use (Robertson 1988) and may be performed in response to a reduction in density therefore having a higher impact on adjacent fisheries. Home range relocation can be either density independent if they result from random movement analogous to molecular diffusion (Kramer and Chapman 1999; Russ 2002) or density-dependent if they result from optimal habitat selection, scramble competition, territoriality and other habitat-related behavioural interactions that are often density-dependent (Sanchez Lizaso et al. 2000; Sutherland, Gill, and Norris 2002).

To better predict the magnitude of spillover in response to harvest, we need to understand the mechanisms leading to home range relocation. Even though home-range relocation is considered rare in reef fishes (Sale 1971; 1978; McDougall and Kramer 2007), there is strong empirical evidence for its occurrence in density manipulation experiments. Home range relocations have been observed in several studies on damselfish performed to answer questions related to reef recolonization (Hourigan 1986; Syms and Jones 2000), territoriality and competition (Sale 1976; Williams 1978; Waldner and Robertson 1980; Itzkowitz 1991), short-term costs of relocation (McDougall and Kramer 2007) and habitat selection (Cheney and Côté 2003; Meadows 1995; 2001). They have also been documented in other reef fish species in studies on recolonization of depopulated reefs (Brock, Lewis, and Wass 1979; Lewis 1997), fish movements (Zeller and Russ 1998; Zeller, Stoute, and Russ 2003) and experiments testing the effect of intensive fishing on movement (Robertson 1988; Zeller, Stoute, and Russ 2003; Lowry and Suthers 2004). However, there is very little evidence for the mechanisms leading home range relocation. Many studies removed only large and dominant individuals from the population to create attractive vacancies (Cheney and Côté 2003; Itzkowitz 1991; McDougall and Kramer 2007), but knowing why relocation might not take place is equally important for understanding how spillover may develop and for controlling its magnitude. Other studies removed either only a very small proportion of the population (Cheney and Côté 2003; McDougall and Kramer 2007) or the entire population at once (Sale 1976; Waldner and Robertson 1980; Hourigan 1986; Robertson 1988; Sheldon and Meffe 1995), preventing clear conclusions about habitat selection and home range relocation in response to density. Observational radiotracking studies (Chateau and Wantiez 2009) can document relocation but cannot provide unambiguous evidence about the factors that influenced it.

Density and behavioral interactions have been suggested to influence home range relocation and spillover. For example, in an Ideal Free Distribution (Fretwell and Lucas 1969), fish would be expected to move from high density to low density locations following harvesting as a result of greater per capita resource availability in the low density area. This process would be even stronger in an Ideal Despotic Distribution (Fretwell and Lucas 1969) where dominant individuals obtain a disproportionate share of available resources and subordinates are subject to higher agonistic interactions as well as lower resource availability at high density (Abesamis and Russ 2005; Kramer and Chapman 1999; Sutherland, Gill, and Norris 2002). Furthermore, individuals may choose to immigrate only to areas of lower population density because high density areas result in higher levels of aggression than those experienced with neighbors at the source location as suggested by the social fence hypothesis of Hestbeck (1982). On the other hand, individuals may be less likely to immigrate to low density than to high density populations as suggested by the conspecific attraction hypothesis (Stamps 1991; Danielson and Gaines 1987). Finally, survivors in the fished area may prevent additional settlement by expanding their territories following localized mortality in high density population if they had been previously restricted to sub-optimal territory sizes (Hixon 1981; Schoener 1974). There is no direct empirical evidence of variation in home range relocation in response to a variation in density or behavioral interactions. Only two experiments manipulated fish density in a perspective to induce movement in response to a gradient of density, but their results were inconclusive (Lowry and Suthers 2004; Zeller, Stoute, and Russ 2003).

Costs and benefits related to habitat quality could represent key factors for understanding mechanisms leading to home range relocation. Individuals should only relocate their home range when the benefits of the new home range clearly outweigh those of the current location and the costs of moving (Kramer et al. 1997). Because prospecting and moving in a heterogeneous landscape can be costly due to energetic expenditures, higher risks of predation and agonistic interactions (Wiens 2002; Zollner and Lima 1999), animals may not relocate if the benefits are too low or if they cannot obtain information about the availability of alternative habitats.

Other factors are likely to affect home range relocation and the magnitude of spillover. Low functional connectivity of the landscape, the presence of total or partial barriers to movement and low mobility are likely to reduce spillover (Chapman and Kramer 2000; Kramer and Chapman 1999; Rakitin and Kramer 1996; Warner and Hoffman 1980), even if the density gradient between the fished and protected area is large and habitat quality is high in the fished area.

In a companion manuscript (*Chapter 4*), we examined the effect of experimental, incremental, localized reduction of damselfish populations on immigration from adjacent protected areas at the metapopulation scale, including information about landscape features in the protected area and in a fished area. Here, we took the opportunity to examine the effect of a reduction in local density on movement and habitat selection at the scale of the individual territory. Our main objective was to determine the probability that a territory would be reoccupied, following the removal of its occupant, in relation to local density and to habitat quality, as indicated by characteristics of the previous occupant (species, sex and body size). Damselfish are a good model system for our purpose because they are well studied, highly philopatric, easy to observe and respond quickly to creation of vacancies by relocating their territories (Bartels 1984; Cheney and Côté 2003; Hourigan 1986; Itzkowitz 1978; McDougall and Kramer 2007). We also examined whether a vacant territory would be reoccupied by a close neighbor shifting a portion of its territory to occupy the vacant territory (*i.e.* territory shift) or by a neighbor fish that completely left its original territory to occupy the vacant territory or by a fish from a more distant location (*i.e.* territory relocation). We then compared the occurrence and frequency of territory shifts and relocations with decreasing density.

MATERIALS AND METHODS

Study site and species

Our experiment was conducted during three consecutive years (2005-2007), from April/May to August/September on five fringing reefs along the west coast of Barbados (13°10’N, 59°38’W). Fringing reefs in Barbados extend to a maximum of 200 m offshore and are composed of three distinct zones (the back reef, the crest, and the spur and groove zone). We focused our study in the spur and groove zone which is characterized by finger-like, seaward extensions of the main reef with numerous small patches of reef separated by sand (Lewis 1960). Our nine sites, among which seven were chosen to be experimental (Sandy Lane; SL1, SL2, Heron

Bay; HB1, HB2, HB3 and HB4 and Bachelor Hall; BH1) and two control (South Bellairs; SB1, North Bellairs; NB1), were located at depths ranging from 4 to 7 m and varied slightly in area (mean ± SD; range: 147.8 ± 36.6 m^2; 93.1 – 217.83m^2; n= 9; Table 2.1) and in damselfish density (0.41 ± 0.13 damselfish·m^{-2}; 0.23 – 0.83 damselfish·m^{-2}).

Our study species were longfin damselfish, *Stegastes diencaeus,* and dusky damselfish *Stegastes adustus*, two abundant, intra- and interspecifically territorial pomacentrids that reach very high density in the spur and groove zone on fringing reefs in Barbados. Adult longfin damselfish are slightly larger (mean total length ± SD; 8.98 ± 1.95 cm, n = 443), more aggressive (K. Turgeon, *unpublished data*) and preferentially inhabit the deepest portion of the spur and groove zone. Dusky damselfish (7.16 ± 1.04 cm, n = 125) inhabit the crest zone and the upper portion of the spur and groove zone. Both sexes vigorously defend exclusive territories that provide food in the form of a cropped algal mat, refuges in the form of holes in the reef and, for males, nest sites in the form of vertical areas of coralline rock or small holes (Cheney and Côté, 2003). Both species are strictly diurnal, resting in holes on the reef at night. Territories of both species are small and contiguous on suitable hard substrate (territory area; 1.14 ± 0.50 m^2 in longfin damselfish, N = 345 and 0.79 ± 0.35 m^2 in dusky damselfish, n = 130). Their respective distributions overlap in the transition between the crest and the spur and groove zones. In both species, males grow to larger sizes than females, are usually more aggressive and provide paternal care for eggs. Male longfin damselfish often occupy the edges of the reef where the substratum provides more nest sites and females tend to be found away from the edges (Cheney and Côté 2003, Robertson 1984). Both species spawn every month and year-round (Robertson, Schober, and Braw, 1993; Thresher 1984) with a peak in larval settlement just after the new moon in longfin damselfish and just before the new moon in dusky damselfish (Robertson 1992). Juveniles of both species are brightly colored and distinctive (yellow in longfin damselfish, purple-orange in dusky damselfish) changing to a more similar, uniform dark brown to black color (Robertson and Allen 1981) before sexual maturity (K. Turgeon, *unpublished data*). In our system, longfin damselfish were sexually mature when they reached approximately 9.3 cm in total length (Logistic regression; t-ratio = -7.262, p-value < 0.001; n = 235) and 7.1 cm in dusky (Logistic regression; t-ratio = -6.64, p-value < 0.001; n = 157). In general, longfin damselfish were more abundant than dusky damselfish, comprising 50% (SL2) to 100% (NB1) of the total. The proportion of immature individuals in the adult-colored population of the combined species varied from 14% in NB1 to 75% in HB2.

Territory acquisition for both species appears to be vital for survival and reproductive success; there is no evidence of "floaters" in damselfish populations (Bartels 1984; McDougall and Kramer 2007). Territories are very stable in established populations, but territories of experimentally removed individuals are visited by neighbors after as little as 3 min, and high quality territories can be reoccupied within 10 to 30 min (Cheney and Côté 2003; McDougall and Kramer 2007). Damselfish are not targeted by fisheries in Barbados, so we assume that the areas adjacent to our manipulated sites act like "protected areas".

Experimental density manipulation and observations of movement

We applied a constant removal pressure on each of the seven manipulated sites by randomly removing 15% of the initial population of adult-colored individuals, including immatures with dark coloration, (initial population size: 48 - 74; Table 2.1) every 2-3 days until we created a local extinction on the site. Removal events started between 08h30 to 09h00 and required 20 – 45 min. Experienced divers removed the pre-selected individuals using modified cast nets and micro spears. Captured fish were placed individually in plastic bags (Ziploc© type) with an ID tag, immediately anesthetized using an overdose of CO_2 (Eno © in seawater), placed on ice and brought back in the lab. In the lab, we measured the weight (g) and total length (cm) of each removed individual, and validated the sex and sexual maturity by inspection of the gonads.

After the removal, we monitored all vacant territories during 5 min at 30 min and 60 min the same morning, at 360 and 480 min that afternoon and at 1440 and

1800 min the following day. Because damselfish are strictly diurnal, we removed 600 min (10 h) from the two territory monitoring periods in the following day to account for damselfish inactivity between 19:00 and 05:00. This resulted in 6 territory monitoring observation periods: 30, 60, 360, 480, 840 and 1200 min of potentially active time after removal. Territories of removed individuals were considered occupied if a new individual spent at least 80% of its time in the area and actively defended it with chases and displays. Vacant territories from previous removals were also monitored every two to three days during territory mapping (see below).

In this study, we made a distinction between territory relocations and territory shifts. We made this distinction clear because territory shifts are assumed to be less costly and risky than territory relocations because of higher familiarity with the neighborhood (McDougall and Kramer 2007). Territory relocation is a permanent change in space use (Robertson 1988) without any overlap between the new and the previous territory while in territory shifts there is still partial overlap between the former and new territory. In other studies, authors referred to relocation as being shift (Larsen and Boutin 1995; Crook 2004).

The day after removal, we mapped all occupied territories, including the new territories occupied by immigrants. From the map of damselfish territories, we extracted the percentage of territory overlap and the distance covered for territory relocations and territory shifts (cm) from one removal event to the other. A relocation was recorded if the occupying individual was either no longer using its previous territory within the site or was unmarked, indicating that it had immigrated from outside the site. A shift was recorded if the new defended territory comprised part of its original territory. Smaller changes in territory boundaries (change in area less than 5%) were not considered as a movement (*i.e.* shift or relocation). The distance covered for relocation and shift was evaluated from the center of the territory from one removal event to the next. Damselfish movement was categorized as being relocation or shift during a removal event, but the same individual can perform more than one movement over the course of the density manipulation experiment. Each movement was considered as an independent observation. In previous studies, territory relocations and shifts of damselfish following removals usually occur within 24 h (Cheney and Côté 2003; McDougall and Kramer 2007). In this study, the median time needed to relocation was 360 min (approximately 6h; 95% CI = 107 – 1750 min). Thus, we assume that the fish distribution was close to a new equilibrium within 2 days of each removal.

Two days after we removed the last residents and immigrants, sites were visited to ensure the absence of any new immigrants. If new immigrants were found, we removed them and visited the site until no new immigrants were observed on the site. After the removal of the last immigrants, sites were monitored during 5-6 days to ensure no new immigrants. All sites were observed for two weeks before starting the removal and for approximately five weeks during the experimental manipulation. The gradual, constant removal pressure resulted in 8 to 11 removal events, depending on the number of immigrants. The two control sites were observed for a comparable period of time (7-8 weeks).

Territory mapping

Prior to density manipulation and territory mapping, we tagged each resident damselfish > 5 cm total length in the nine sites to follow territory shifts and relocations and to recognize immigrants from the adjacent area. We caught individuals with a modified cast nest and tagged them underwater near their territories to reduce stress. We marked damselfish with VIE tags (Northwest Marine Technology) using 5 colors (yellow, green, red, orange and white) and 12 tag positions resulting in at least 60 different tags per site. We sexed them underwater by observing the genital papillae, measured them to the nearest mm, and released them on their territories after approximately 30 s. Sexual maturity was assessed by the examination of the gonads in the laboratory when the individual was removed from the population (see below). Tagging usually required two dives of 2 h (1 day) per site. Of 486 damselfishes tagged, we observed only 12 disappearances following tagging sessions (2% of the tagged damselfishes) due to post-tagging mortality or emigration. We monitored 486 damselfish territories on nine sites (seven density-manipulated and two control sites).

Before manipulating density, we mapped territories of all damselfish on the sites. We created a 1 x 1 m XY grid covering the entire site, took an underwater digital picture of each 1 x 1 m cell, and assembled the pictures using graphical software (Corel PhotoPaint 12) to produce a mosaic covering the entire site which was then georeferenced in GIS software (MapInfo Professional 6.5). Territory boundaries of each resident were evaluated during an observation period of at least 10 min after which we marked the territory boundary with 8-10 bleached coral pebbles. This short duration is appropriate because damselfish move rapidly and regularly over their entire small territories. Although other researchers such as Cheney and Côté (2003) used somewhat longer periods (15 min) to delimitate territory boundaries, we found that that 7 to 8 min was generally sufficient so that allowing 10 min made it unlikely that we missed parts of the territories. To ensure a precise territory position on the georeferenced site map we took a digital picture of each territory and noted useful landmarks surrounding the territory. Territory boundaries were drawn freehand on the mosaic layer of each site using the digital pictures and markers. For each site, we produced a georeferenced layer of all resident damselfish territories.

Analysis

All analyses were performed in R version 2.9.1, an open source language and environment for statistical computing and graphics.

The first question was whether the probability that a vacant territory would be recolonized after the removal of its original owner was affected by the density and the quality of the territory. For the probability of recolonization, we considered only recolonizations that occurred within two days (*i.e.* before the next removal event; between 7 to 9 vacant territories per removal event among seven sites) so that all territories would be considered with the same time availability and because most recolonizations took place within this interval. For the species pattern, we considered a recolonization successful if a territory was recolonized by either one or the other species but based on the species of the original occupant. We considered all recolonizations combined and also territory shifts and territory relocations separately. Because density varied somewhat among sites, in part as a result of the amount of suitable habitat, we used the percentage of the initial population removed within a site as the measure of density and this measure is for both species combined. As a surrogate for territory quality, we used the size of the original occupant. This assumes that body size is a correlate of territory quality in saturated populations such as those at our study sites. Body size is widely recognized to affect resource holding potential and dominance in fish (Candolin and Voigt 2001; Lindström 1992), which should influence their ability to obtain and hold more attractive territories. In addition to the single effect of predictors, we also looked for higher order terms and for the interaction among the two predictors (*i.e.* body size and percentage of the initial population removed). We used Generalized Linear Mixed Models (GLMMs, lmer library in R with the restricted maximum likelihood method) to examine the effects of population size and body size on and the probability of a territory to be recolonized and to infer statistical support. Statistical support was evaluated with 95% CI instead of p-values. A predictor had statistical support if its 95% CI did not include zero. We used a binomial error structure with a logit link function and controlled for spatial dependence among sites by using site as a random factor. We built separate models for longfin damselfish and dusky damselfish because the variances in body size were different enough to have inflated the error for the interaction term. Separate models also facilitated the interpretation of the results. We were also interested to determine whether territory recolonization was species and sex-maturity specific and tested this relationship with contingency tables using a χ^2 test.

If larger individuals occupied better territories and if individuals preferentially recolonized better territories, we expected that the average size of the original occupants of the occupied territories would increase as density declined. To examine this question, we averaged the body size values of original territory owners of all occupied territories at a removal event *t* (BS_t) and examined in the relationship between BS_t and the proportion of the initial population size removed. If damselfish redistributed themselves to occupy higher quality territories, we should observe a positive relationship between BS_t and the proportion of the initial population size removed. To model this relationship, we used Generalized Linear Mixed Models (GLMMs) with a Gaussian error structure and an identity link function and controlled for spatial independence by using site as a random factor.

The second question was to examine how the total frequency of territory shifts and relocations over the experiment varied among the nine sites (N=18, 9 sites and 2 types of movement), between experimental and control sites and between the two species (N=36, 9 sites, 2 types of movement and 2 species). For the species pattern, we counted the total number of territory shifts and relocations performed by the species over the experiment. To do so, we used GLMMs and GLMs (Generalized Linear Models). We used a Gaussian error structure and an identity link function. We controlled for spatial independence among sites by using site as a random factor. Statistical support was evaluated with 95% CI instead of p-values. A predictor has statistical support if its 95% CI does not include zero. In addition, we used Generalized Additive Mixed Models (GAMMs; package mgcv 1.3-19 in R 2.4.0; Wood and Augustin 2002) to describe the relationship between the number of territory shifts and relocations and the percentage of the initial population removed and the per capita number of territory shifts and relocations and the percentage of the initial population removed. Generalized Additive Models (GAMs) allow predictors to be fitted either as parametric terms or as non-parametric smoothing terms to explain response variables (Hastie and Tibshirani 1990). GAMMs extend this framework to allow some predictors to be modeled as random effects (Wood 2004) and, in our case, control for spatial independence among site (random factor). In addition, we compared the number of shifts and relocations and the per capita number of shifts and relocations per removal event in relation to the proportion of the initial population size removed. For this comparison, we used Generalized Linear Mixed Models (GLMMs) with a Gaussian error structure and an identity link function and controlled for spatial independence by using site as a random factor.

RESULTS

Probability of territory recolonization

Following the removal of the original occupant, 31% (152/486) of the vacant territories were never recolonized. For territories that were recolonized, the latency varied from less than 30 min to 3 days (mean ± SD; 928 ± 3693 min, median = 360 min; Poisson distribution). Following successive removals, territories were recolonized from 1 to 6 times (n = 263, 1 time: 143; 2 times: 73; 3 times: 32; > 3 times: 15).

The interaction between population size and body size had very low support to explain the probability that a vacant territory would be recolonized in both species indicating that the probability that a vacant territory would be recolonized did not change differently with varying population size if the original occupant was small or large. Higher order terms had also a low support but population size higher order term had support in dusky damselfish to explain the probability of recolonization of vacant territory via relocation (Fig. 2.1c, Table 2.2c).

Effect of local density

In longfin damselfish, the probability that a vacant territory would be recolonized within two days following the removal of the original occupant decreased slowly and gradually with decreasing population size (Fig. 2.1a, Table 2.2a). In dusky damselfish, the pattern was similar, but there appeared to be a sharper drop when more than 75% of the initial population size had been removed (Fig. 2.1a and Table 2.2a). This effect was the result of different trends for territory shifts and relocations. In both species, the probability that a vacant territory would be recolonized via a territory shift decreased sharply and approximately linearly from about 60% to about 10% as the removal proceeded from 0 to about 85% (Fig. 2.1b, Table 2.2b). In contrast, in longfin damselfish, the probability that a vacant territory would be recolonized via a territory relocation was much smaller (about 20%) when removal started and increased slowly as population size decreased (Fig. 2.1c, Table 2.2c). In dusky damselfish, the probability of recolonization by relocation was only about 10% when removal started, increased to about 20% and then decreased to about 10% with decreasing population size (Fig. 2.1c, Table 2.2c; support for the higher order term for the percentage of the initial population removed). Population size was not supported as an explanation for the probability that a vacant territory would be recolonized again after the removal of the first and second colonizers in either species (Appendix 2.1).

Effect of characteristics of the original occupant

The probability that a vacant territory would be recolonized following the removal of the original territory occupant increased strongly with increasing body size of the original occupant for both species (Fig 2.2 and Table 2.2a). For both species, an increase in length of less than 30% from 7 to 9 cm doubled the probability of recolonization from about 40% to 80%. In addition, body size of the first colonizer had support to explain the probability that a vacant territory would be recolonized after its removal in longfin damselfish, although this was not the case for dusky damselfish (Appendix 2.1). Body size of the second colonizer was supported as an explanation for the probability of territory recolonization in longfin damselfish but not for dusky damselfish (Appendix 2.1).

Territory shifts and relocations were species specific (Appendix 2.2a). Longfin damselfish mostly relocated into former longfin damselfish territories (89.7 %) and dusky damselfish relocated mainly into former dusky damselfish territories (73.1 %). In longfin damselfish, females recolonized territories originally held by females at a greater frequency than expected by chance (66.7%), and the same was true for males (63.2%) and immature individuals (55.5%; Appendix 2.2b). In dusky damselfish, females recolonized territories originally held by females at a greater frequency than expected by chance (63.6%); the same was true for males (60.0%) but not for immature individuals (Appendix 2.2c). In dusky damselfish, immature individuals also relocated to territories previously occupied by mature females and males.

Large individuals tended to recolonize territories previously occupied by large individuals in longfin (Appendix 2.3; GLMM; t-value = 8.638, estimate (95% CI) = 0.52 (0.41 to 0.65), n = 236) but not in dusky damselfish (Appendix 2.3; GLMM; t-value = 1.767, estimate (95% CI) = 0.25 (-0.03 to 0.54), n = 105). On average, colonizers were smaller than original occupants (Appendix 2.3).

Effect of density on average territory quality

As population size decreased in the harvest area, the remaining fish increasingly occupied territories originally held by larger individuals (Fig. 2.3). This was the case for both longfin (GLMM, t-value = -9.619, estimate (95% CI) = -1.06 (-0.844 to -1.276), n = 69) and dusky damselfish (GLMM; t-value = -9.082, estimate (95% CI) = -0.59 (-0.391 to -0.606), n = 68).

Frequency of territory shifts and relocations

We observed more territory shifts (n = 385) than territory relocations (n = 217) among the nine sites (GLMM; t-value = 3.406, estimate (95% CI) = 21.89 (9.29 to 34.48), n = 18). Shifts were nearly all (383/385) performed by individuals within the harvest area; two shifts were performed by untagged individuals that were on the boundary of the harvest area. In contrast, 75% of territory relocations (163/217) were performed by individuals from outside the harvest area. Although the number of territory shifts was 2.6 times greater in the seven density-manipulated sites than in the two controls, the experimental effect was not statistically supported likely due to the small sample size (GLM; t-value = 1.305, estimate (95% CI) = 32.26 (-16.23 to 80.95), n = 9; Table 2.1). The number of territory relocations was 30.2 times greater in density-manipulated sites than in controls (GLM; t-value = 2.57, estimate (95% CI) = 29.29 (6.97 to 51.61), n = 9; Table 2.1).

In density-manipulated sites, the total number of shifts and relocations that occurred after a removal event at the site scale varied non-linearly with population size in the harvest area (Fig. 2.4a). As we decreased population size, the total number of shifts (GAMM; F-value = 13.51, p-value < 0.001, Deviance explained = 54.8%, n = 70) and the total number of relocations per removal event (GAMM; F-value = 9.958, p-value < 0.001, Deviance explained = 28.3%, n = 75) increased and then decreased at intermediate and low population sizes (Fig. 2.4a). The rate of territory relocations is lower than the rate of territory shifts with declining population size (GLMM; t-value for the interaction between the proportion of the initial population size removed and type of movement = 3.951, estimate (95% CI) = 3.25 (1.64 to 4.85), n = 252; Fig 2.4a). The number of territory shifts per remaining individual per removal event (GAMM; F-value = 10.65, p-value < 0.001, Deviance explained = 37.6%, n = 70) and the number of relocations per remaining individual per removal event (GAMM; F-value = 12.32, p-value < 0.001, Deviance explained = 62.0%, n = 75) increased gradually with declining population size (Fig. 2.4b). The number of shifts reached a strong peak when the population size was reduced by 20%. The number of relocations increased slowly, peaked when the population size was reduced by 40% and then decreased slowly. The per capita number of relocations reached a strong peak when the population size was reduced by 75% of its original value. Shifts, on the other hand, were similar over most the population size range, with lower values at high and very low population size, the only part of the range at which shifts were less frequent than relocations. The proportion of relocations performed by immigrants coming from outside the harvest area increased with decreasing population size (GLMM; t-value = -4.911, estimate (95% CI) = -0.61 (-0.86 to -0.37), n = 58).

The distances moved for shifts were 0.33 ± 0.25 m (range: 0.05 to 1.56 m, n = 385) and 1.63 ± 0.96 m (range: 0.45 to 3.77 m) for relocations by individually tagged movers (n = 54). The mean distance for all territory relocations is likely to be greater because we did not know the exact distance travelled for immigrants from outside the harvest area who probably had traveled farther.

Species did not differ in their mean per capita number of territory relocations and shifts (GLMM; t-value for the interaction term between species and type of movement = -0.591, estimate (95% CI) = -0.07 (-0.31 to 0.17), n = 36).

DISCUSSION

Home range relocations observed in this study can be used to understand mechanisms behind spillover because 75% of the relocations were performed by individuals coming from the adjacent areas. We observed very few territory relocations, a lower number of territory shifts and only three unexplained disappearances in control sites and during the observation period prior to density reduction in the seven experimental sites. When we started to create vacancies in the harvest area of the seven sites, we observed an increasing number of territory shifts and relocations and a decreasing number at low local densities. We also observed a higher probability of recolonization of high quality vacant territories as indicated by the body size of original occupants. These results suggest that although damselfish are apparently very stable in their spatial distributions and that natural vacancies appear to occur only rarely, individuals in saturated populations are able to detect vacancies, evaluate the relative territory quality and benefits and move quickly to take advantage of them. These results also suggest that the cost of relocation is relatively low.

Home-range and territory relocations are often considered to be rare in reef fishes (Sale 1971; 1978; McDougall and Kramer 2007) and in terrestrial taxa (Stenseth and Lidicker 1992; Clobert et al. 2001). However, there is considerable empirical evidence of their existence in many taxa including coral reef fish (Sale 1976; Williams 1978; Waldner and Robertson 1980; Hourigan 1986; Itzkowitz 1991; Syms and Jones 2000; Zeller, Stoute, and Russ 2003; Cheney and Côté 2003; Lowry and Suthers 2004; McDougall and Kramer 2007), freshwater fish (Albanese, Angermeier, and Peterson 2009; Berra and Gunning 1970; Crook 2004; Sheldon and Meffe 1995) as well as amphibians, reptiles, birds, and mammals (see *Appendix*

I.1). What was missing is a better understanding of factors influencing home range relocation. This study is the first to provide direct empirical evidence of the combined effects of density and habitat quality on territory recolonization following localized mortality.

Mechanisms behind territory shifts and relocations

Local density affects relocation

When we started to create vacancies when the density was high, the density of remaining conspecifics negatively influenced the probability that a territory would be recolonized via territory relocation in (*i.e.* there was an increased probability of a territory being recolonized with declining density) and positively influenced the probability that a territory would be recolonized via territory shift in both species (*i.e.* there was a decreasing probability of a territory being recolonized with declining density). In addition, at the site level, we observed an increasing number of territory shifts and relocations per removal event and territory shifts preceded relocations and occurred more frequently. This pattern may be related to the aggression of remaining survivors in the harvest area. When density was high, there were many individuals near each new vacancy; being more familiar with the neighborhood, these neighboring individuals would have an advantage in acquiring the territories by a shift rather than a relocation. Individuals from farther away would be more likely to be attacked by remaining survivors in the harvest area (dear-enemy hypothesis; McDougall and Kramer 2007; Temeles 1994). As the density decreased, collective defense (Stamps, Buechner, and Krishnan 1987; Meadows 1995) by remaining survivors in the harvest area would become less effective and relocation would become more possible for individuals from farther away. In addition, aggression among potential emigrants in the protected area may play a role. The social fence hypothesis predicts inversely density-dependent emigration due to a high number of aggressive interactions among neighbors at high density (Hestbeck 1982; Hestbeck 1988). In the harvest area, we observed a higher rate of agonistic interactions among survivors at high density compared to lower density during the experiment (*unpublished data*; GLMM; t-value = 3.441, estimate (95% CI) = 0.12 (0.05 to 0.198), n = 396, using site (n = 3) and fish ID (n = 132) as random factors). If a similar pattern occurs in the protected area when individuals start to emigrate, an increased rate of agonistic interactions among individuals in the protected area can act as a social fence and decrease the motivation of individuals to explore vacancies in the harvest area resulting in a lower the probability of emigration at high density.

The expansion of resident damselfish' territories is another plausible hypothesis to explain an increasing rate of shifts and a higher probability of a territory to be recolonized via territory shifts with decreasing density when the harvest area was near saturation. Territory expansion following localized mortality is a well known process in coral reef fish (Ebersole 1980; Jones and Norman 1986; Norman and Jones 1984; Tricas 1989), birds (Hannon 1983) and mammals (Boutin and Schweiger 1988; Tuyttens and MacDonald 2000). Residents may expand temporarily or permanently their territory if they were constrained to a suboptimal territory by pressure from conspecifics. This limits the space available for territory establishment by potential immigrants. In our study, the area defended by damselfishes did not decrease linearly and proportionally with decreasing density (Appendix 2.4; a power function had higher support than a linear function using AICc scores; $w_i = 0.99$; $\Delta AIC_c = 40.6$; Burnham and Anderson 2002) which suggests that remaining survivors in the harvest area increased the size of their territories with decreasing density when they were at high density. However, territory expansion cannot go beyond a cost-benefit threshold where the cost of actively defending a large territory cancels its benefits (Hixon 1981; Schoener 1974). Home range relocations of damselfish in the adjacent area reached a peak when the original population was reduced by 45% (Fig. 2.4). At this population size, residents likely had already acquired a better quality territory and reached their optimal territory size. As a result, undefended territories of increasing quality become available for potential migrants increasing the benefits of moving over the costs.

From intermediate to low population densities, the density of remaining conspecifics positively affect the number of relocations and shifts per removal event with decreasing density (*i.e.* decreasing number of relocations and shifts with decreasing density; called depensatory mechanism in the fisheries literature; Rose et al. 2001) and also positively affect the probability of recolonization of vacant territories by territory shifts in both species (*i.e.* decreasing probability with decreasing density). However, the probability of a territory to be recolonized via territory relocation is still negatively affected by the density of remaining conspecifics in longfin damselfish but positively in dusky damselfish (*i.e.* decrease probability with declining density). Three alternative hypotheses can explain a decreasing rate of shifts and relocations with decreasing density. First, from the remaining survivors' perspective, there are likely small benefits of shifting or relocating if remaining individuals already occupy the higher quality territories in the site (Fig. 2.3). Second, from the potential immigrants' perspective, if the adjacent protected area density has declined sufficiently to remove negative effects of conspecifics (Kramer, Rangeley, and Chapman 1997; Rosenzweig 1981; Rosenzweig 1991), movement from the protected area to the fished area should decrease and then stop. Third, when density becomes very low, fitness can decrease if density becomes still lower. The Allee effect (after Allee 1938; Stephens and Sutherland 1999) occurs when fitness decreases at low to moderate densities. For example, for organisms with relatively low mobility like damselfish, low density sites could be unattractive because they reduce mate availability. Furthermore, before deciding to move into the fished area, potential migrants may use conspecifics to assess the relative quality of potential habitats (Danielson and Gaines 1987; Stamps 1991; 1987a; 2002) and might benefit from settling close to conspecifics if they are subject to high predation risk, despite the potential for competition after settlement (Stamps 2002). Finally, the decreasing rate of relocation at low density could be explained by limited availability of potential immigrants in the adjacent area. This hypothesis is unlikely in our system because the areas surrounding all but one of our manipulated sites were densely populated.

The increasing number of territory relocations in response to a decreasing density and an increasing probability of a territory to be recolonized via relocations suggest that spillover per fished individual in territorial species will be low at high densities due to some behavioral interactions (*e.g.* social fences, collective defense, and territory expansion of the survivors) and shifts of residents. Spillover per fished individual will also be low at low local densities due to the small benefits of moving into very low density area for immigrants but will be higher at intermediate levels. These results are based on saturated populations of a highly territorial species. It would be interesting and important to explore how the absence of strong behavioral interactions in nonterritorial species or in species that reached low density at equilibrium affects recolonization of vacant territories and the number of shifts and relocations in a harvest area.

Territory quality affects relocation

Habitat preferences influenced territory shifts and relocations in damselfish. Despite the very stable distribution of these species, larger individuals managed to occupy better territories. We showed that relocations and shifts were directed toward high habitat quality territory. We provided strong evidence that high quality territories were more likely to be recolonized than territories held by smaller individuals. In addition, we also showed that damselfish redistributed themselves in the harvest area to occupy territories held originally by larger individuals as density decreased.

Other empirical evidence and theoretical models on birds, monkey and fish suggested that movement behavioral responses (*e.g.* turnover rates and immigration) are strongly related to habitat quality (Winker, Rappole, and Ramos 1995; Isbell, Pruetz, and Young 1998; Bélanger and Rodríguez 2002). Winker et al. (1995) constructed a graphical model of habitat use in a territorial species and predicted that the turnover rate should be higher in optimal habitat (*i.e.* low stability of population distribution) than in suboptimal habitat. Our results demonstrate that this prediction is not true if individuals are constantly removed from the population.

When population density decreased in our system, we found a higher turnover and replacement rate in optimal habitats. Turnover models must integrate variation in density to be valid. To our knowledge, our study is the first to evaluate and test the combined effect of territory quality and density on movement at the individual level. This result suggests that differences in average habitat quality between harvest and adjacent protected areas will influence the magnitude of spillover.

The higher probability of recolonization of high quality territories, indicated by the body size of the original owner, suggests that the magnitude of spillover into a harvest area will be higher if the harvest area is attractive (*i.e.* higher relative habitat quality in the harvest area) compared to the adjacent protected area, independently from density.

Using body size as an index of habitat quality

We assumed that body size of the original occupant could be used as an index of territory quality in damselfish. Although resource holding potential (*i.e.* a measure of the absolute fighting ability of the individual; Parker 1974) is strongly related to body size in many taxa (Beletsky and Orians 1987; Eckert and Weatherhead 1987; Lindström 1992), this is a major assumption that needs to be discussed. Measures of individual reproduction rate, survival, and foraging success are generally viewed as being better indicators of habitat quality than the density of individuals in a particular habitat type because they are related to fitness (Van Horne 1983, Winker et al. 1995). However, body size, should be a better indicator than density or presence because it incorporates some information about individual success and, should be easier to assess in the field than reproduction rate and survival (Endler 1986).

An organism can acquire information about habitat quality during prospecting by assessing environmental cues such as resource abundance (Baker 1984, Oro et al. 2004, Lin et al. 2006) the presence and density of conspecifics (Stamps 1988a; Serrano and Tella 2003) or from personal previous experience and public information based on conspecific performance (Doligez, Danchin, and

Clobert 2002; Doligez et al. 2003). However, because prospecting may be energetically costly and risky in terms of predation and agonistic interactions, individuals may rely on indirect estimates of performance that can be acquired during a short period of observation, and body size is likely to be an honest estimate of territory quality.

Body size is likely to be a good index of habitat quality and individual success in damselfish. In many fish species with parental care, like the damselfish, male body size is correlated with egg survival and reproductive success (Bisazza and Marconato 1989; Côte and Hunte 1989; Hoelzer 1990; Magnhagen and Kvarnemo 1989; Oliveira et al. 2000; Schmale 1981) and in many species only larger mature males have active nest sites (Cheney and Côté 2003; Itzkowitz 1991; Knapp and Kovach 1991). Some studies did not find a direct relationship between body size and reproductive success in damselfish, but important variables related to individual success were related to body size (Itzkowitz and Makie 1986; Knapp and Warner 1991; Sikkel 1988). In many taxa, vacancies created in territories held by dominant and large individuals are recolonized faster and/or at a higher rate than those held by small and subordinate individuals. This pattern has been observed in lions (*Panthera leo*; Loveridge et al. 2007), cougars (*Puma concolor*; Robinson et al. 2008), small mammals (Lin and Batzli 2001; Jacquot and Solomon 2004), various bird species (reviews by Newton 1992; 1998; Studds and Marra 2005) as well as other reef fish species (Lowry and Suthers 2004; Waldner and Robertson 1980).

However, there are some conditions where the relationship between body size and habitat quality may not hold. For example, the prior residence effect, where the resident individual is usually successful in repelling conspecific intruders (Brown and Green 1976; Figler, Klein, and Peeke 1976; Stamps 1987b) can affect territory and home range acquisition independently of body size. Juvenile anoles *Anolis aeneus* that arrive first in an empty territory require only 6 h of residence to successfully defend it against arrivals of comparable size and in a few days can defend against larger individuals (Stamps 1988b; Stamps and Tollestrup 1984).

Furthermore, the relationship between body size and territory quality may not hold if juveniles and immature individuals have different habitat needs than mature individuals or if habitat needs differ among sexes. In our study, there was a tendency for fish to relocate to territories previously occupied by the same sex (Appendices 2.1a, b) suggesting that habitat needs of females and males may be different. Body size can still be a good index of habitat quality, but additional information could be used to reduce error in territory quality assessment. Finally, in some species with little variation in size at maturity, individuals may have to cue on other characteristics to evaluate quality such as color brightness in fish and birds (Endler 1983; Hill 1991; Kodric-Brown 1983; 1985) or song complexity in birds (Catchpole 1987). There are very few studies of the factors affecting relocations other than the creation of vacancies. Our results indicate that relocations are affected by both the density and the habitat quality of vacant territories and likely by social interactions among individuals.

Implications for density-dependent habitat selection theory, conservation and management

This study provides qualitative support for the prediction from the Ideal Free Distribution – Ideal Despotic Distribution (Fretwell and Lucas 1969; Fretwell 1972) that the range of habitat qualities occupied by a population will be larger and include more habitats of lower quality when the population is large than when it is small. We observed that the average size of the original occupants of occupied territories increased as population density decreased. This indicates that survivors and immigrants redistributed themselves to occupy territories originally held by larger damselfish which we assume were of higher quality. This is one of the first studies to show this pattern with a declining population density rather than increasing density as in Fretwell's model (but see Rutten, Oosterbeek, van der Meer, et al. 2010; Rutten, Oosterbeek, Verhulst, et al. 2010). Indeed, most experimental tests of these models have changed food distribution rather than population density (*e.g.* Milinski 1979; Harper 1982; Godin and Keenleyside 1984).

Our findings have implications for marine and terrestrial protected areas design and effectiveness. Behavioral interactions among residents and between residents and immigrants as well as habitat quality can strongly influence the magnitude of immigration from a protected area to a harvest area. If the goal is to completely protect populations, the magnitude of emigration to a harvest area can be greatly reduced if the highest quality habitats are inside the protected area and if there is not a patch of excellent habitat near the boundary of a protected area that would be accessible to fishers and/or hunters. If the highest quality habitats are located outside the protected area, the magnitude of emigration to a harvest area will be higher and could allow a more complete extraction of the resources from the protected area to benefit local fisheries or hunting success of targeted species. However, these high habitat quality harvest areas, called ’attractive sinks’ by Delibes, Ferreras, and Gaona (2001) and Delibes, Gaona, and Ferreras (2001) and could be problematic when managers try to control the spread or the impact of some pest species (Efford, Warburton, and Spencer 2000; Ji et al. 2001; Nakata and Satoh 1994; Rosatte et al. 2007) or try to protect small population of endangered species (Loveridge et al. 2007; Woodroffe and Ginsberg 1998; 2000). Knowing which factors facilitate or impede the rate and magnitude of immigration will help to reduce counterproductive efforts in pest population control and decrease the risk of local population extinction in endangered species.

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Table 2.1. Initial population size and area of the fished and protected areas, number of immigrants, number of removal events, number of territory shifts and territory relocations and per capita number of territory shifts (i.e. the number of territory shifts divided by the initial population size in the fished area (N_0) in each site) and per capita number of territory relocations in controls (NB1 and SB1) and in density-manipulated sites (HB1, HB2, HB3, HB4, SL1, SL2).

Variables	Controls		Density-manipulated						
	NB1	SB1	HB1	HB2	HB3	HB4	SL1	SL2	BH1
Initial population size in the fished area	41	52	51	51	48	61	70	59	53
Fished area (m^2)	112.2	154.8	140.3	217.8	153.4	143.9	141.7	93.1	144.4
Number of immigrants	1	1	5	13	27	22	44	31	14
Number of removal events	0	0	8	8	10	9	12	10	9
Number of territory shifts	28	14	23	42	33	37	124	51	33
Number of territory relocations	1	3	13	15	33	64	53	43	17
Per capita number of territory shifts	0.683	0.269	0.451	0.824	0.688	0.607	1.730	0.864	0.579
Per capita number of territory relocations	0.020	0.096	0.255	0.294	0.688	1.049	0.716	0.729	0.298

Table 2.2. Generalized Linear Mixed Models used to explain the probability that a territory would be recolonized within two days after the removal of the original owner in relation to population size and body size of the original occupants for a) territory shifts and relocations combined, b) territory shifts and c) territory relocations in longfin damselfish and dusky damselfish. Parameter estimates, standard errors (SE) , the 95% confidence intervals (CI) and the z-value of each parameter are presented. All models include a constant. Predictors in bold do not contain zero within the 95% confidence intervals.

	Longfin damselfish			Dusky damselfish		
Predictors	Estimate ± SE	95% CI	z-value	Estimate ± SE	95% CI	z-value
a) Territory shifts and relocations combined						
(Constant)	**-5.17 ± 0.80**	**-6.74 to -3.59**	**-6.427**	**-4.44 ± 1.43**	**-7.24 to -1.63**	**-3.107**
Population size	**1.59 ± 0.51**	**0.58 to 2.60**	**3.119**	**3.21 ± 0.71**	**1.82 to 4.60**	**4.517**
Body size	**0.57 ± 0.09**	**0.39 to 0.74**	**6.418**	**0.46 ± 0.19**	**0.08 to 0.83**	**2.383**
b) Territory shifts						
(Constant)	**-2.89 ± 0.73**	**-4.31 to -1.46**	**-3.974**	**-3.18 ± 1.43**	**-5.99 to -0.37**	**-2.218**
Population size	**2.55 ± 0.53**	**1.52 to 3.59**	**4.839**	**3.52 ± 0.75**	**2.06 to 4.99**	**4.718**
Body size	0.09 ± 0.07	-0.06 to 0.23	**1.146**	0.12 ± 0.18	-0.27 to 0.50	0.594
c) Territory relocations						
(Constant)	**-4.75 ± 0.80**	**-6.31 to -3.19**	**-5.959**	**-6.23 ± 1.92**	**-10.0 to -2.46.**	**-3.236**
Population size	**-1.07 ± 0.52**	**-2.08 to -0.06**	-2.077	**7.47 ± 3.50**	**0.60 to 14.3**	**2.133**
Population size ^{2}	**-**	**-**		**-8.26 ± 3.60**	**-15.3 to -1.20**	**-2.294**
Body size	**0.48 ± 0.08**	**0.32 to 0.65**	**5.767**	**0.51 ± 0.24**	**0.04 to 0.97**	**2.146**

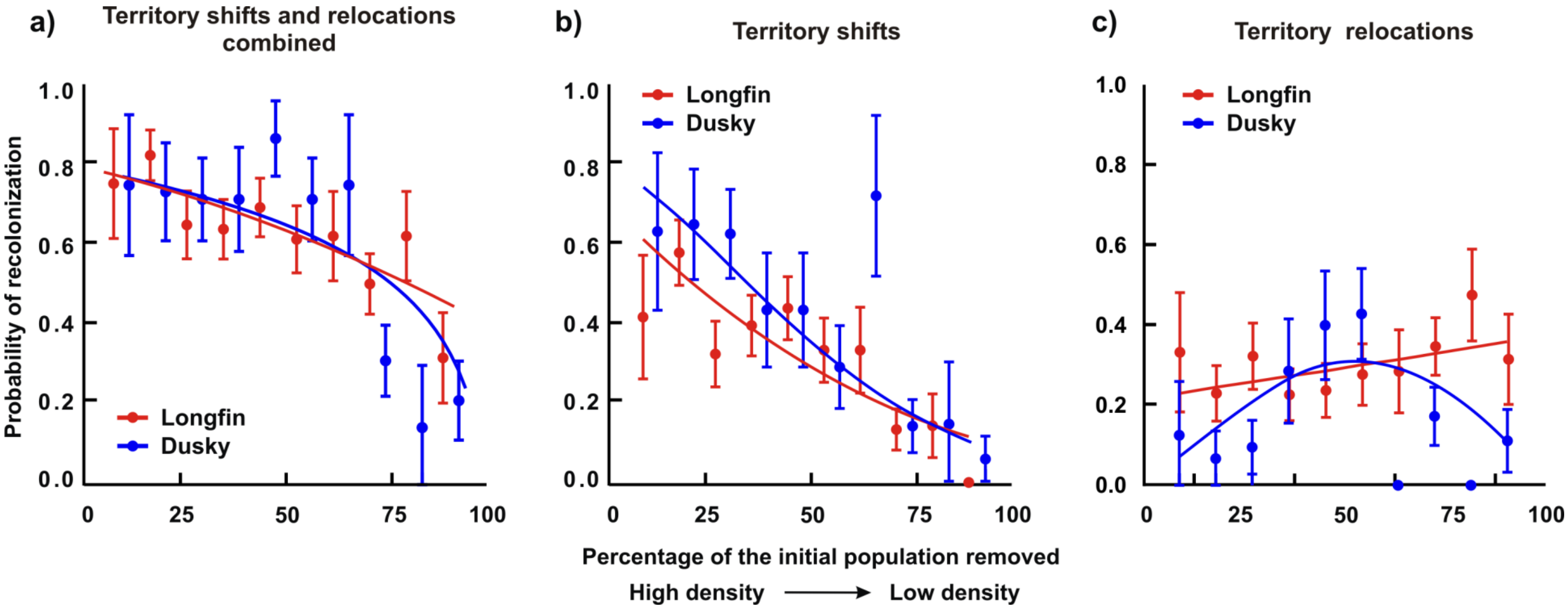

Figure 2.1. Probability that a territory will be recolonized within two days in relation to the percentage of the initial population size removed for longfin damselfish (red) and dusky damselfish (blue) for a) both shifts and relocations combined, b) territory shifts only and c) territory relocations only. The curve is the best fit from LOGIT function transformed into a probability function. For data presentation and to facilitate interpretation, each data point represents a bin of 10% reduction in percentage of the initial population (*e.g.* 0 - 10, 10 - 20, and so on) following partial replacement by immigration. The error bars on each data point represents ± 1 SE. Points within the bins perfectly overlap for the two species but we jittered dusky damselfish points for clarity.

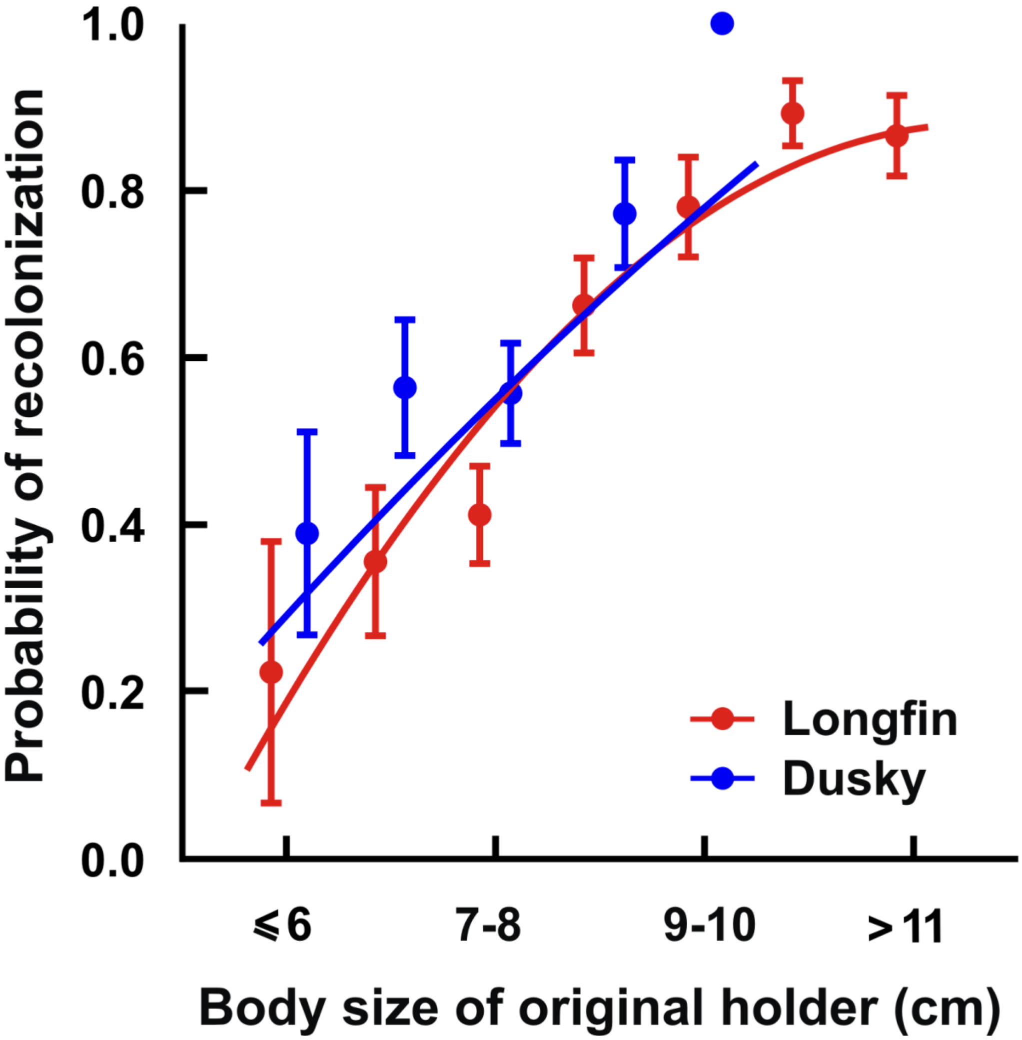

Figure 2.2. Probability that a territory will be recolonized within two days in relation to the body size of the original territory occupant for longfin damselfish (red) and dusky damselfish (blue). The curve is the best fit from LOGIT function transformed into a probability function. For data presentation and to facilitate interpretation, each data point represents a bin that covers the range of damselfish body size between the two values inclusively. The error bars on each data point represents ± 1 SE. Points within the bins perfectly overlap for the two species but we jittered dusky damselfish points for clarity.

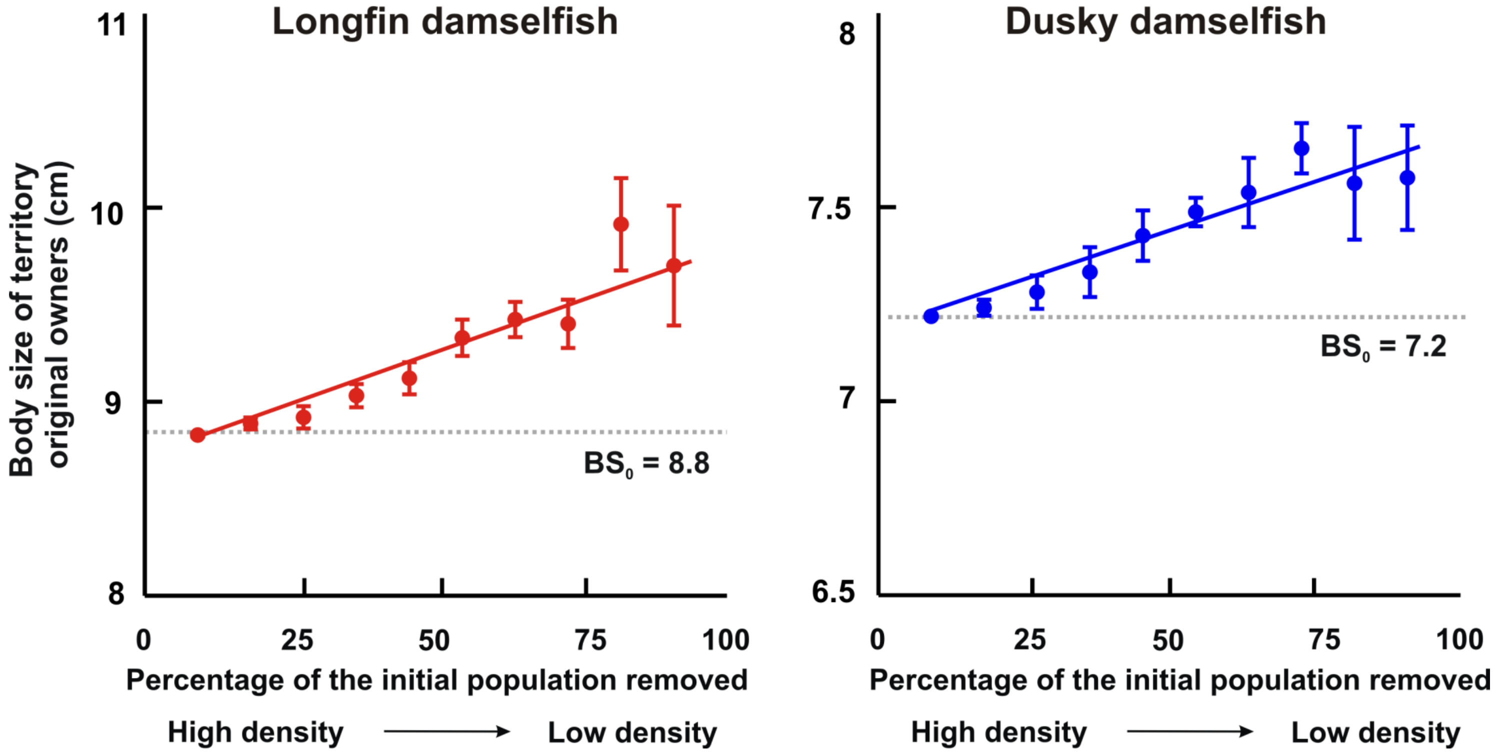

Figure 2.3. Average body size of the original territory occupants for all occupied territories in relation to the percentage of the initial population removed for longfin (red, left panel) and dusky damselfish (blue, right panel). The dotted grey line represents the average body size of territory owners before the population was manipulated (BS_0). For data presentation and to facilitate interpretation, each data point represents a bin of 10% reduction in percentage of the initial population removed (*e.g.* 0 - 10, 10 - 20 and so on). The error bars on each data point represent ± 1 SE.

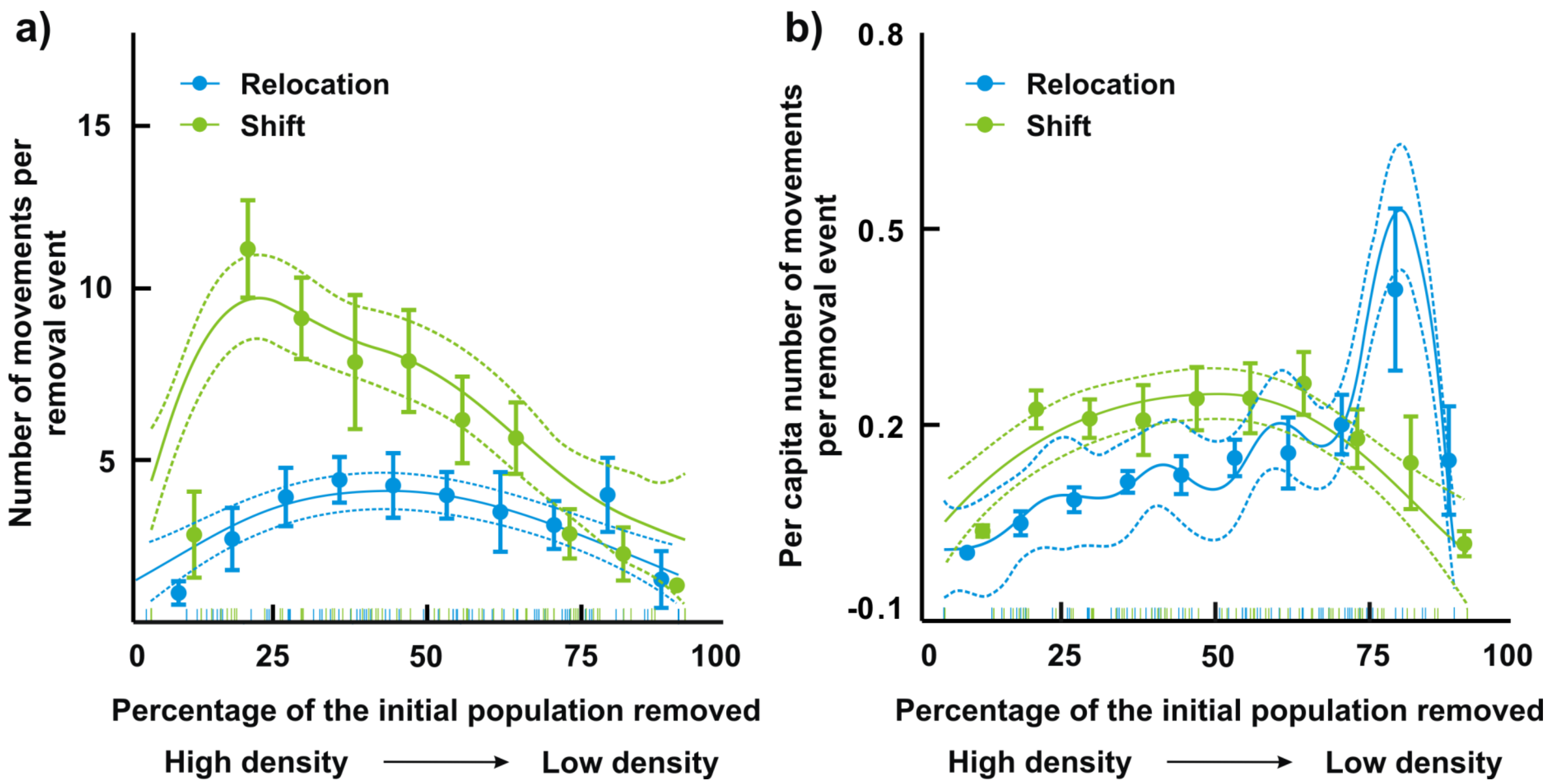

Figure 2.4. Number of territory relocations (blue) and shifts (green) for both species combined a) per removal event, and b) per remaining individual per removal event in relation to the percentage of the initial population size removed following sequential removal events on seven density-manipulated sites. Dots represent the average value among sites, and the error bars represent ± 1 SE. The solid lines are the GAMM function and dashed lines are ± 1 SE. There were between 7 to 9 territories made available per site at each removal event. The vertical small marks on the abscissa are the raw values of the percentage of the initial population size removed for relocations (blue) and shifts (green).

CHAPTER 3:

MODELING MIGRATION BETWEEN HARVESTED AND PROTECTED POPULATIONS

LINKING STATEMENT 3

Immigration in response to localized mortality has important implications for metapopulation dynamics, sustainable harvesting, and conservation. However, there is very limited empirical evidence for the mechanisms leading to immigration in response to harvest and on the factors that could increase or decrease immigration. For this reason, models use untested assumptions about migration. In *Chapter 1* and *Chapter 2*, I found that a fragmented landscape strongly limited movement and that the quality of vacant territories and the local density influenced the probability of recolonization. These factors were rarely considered in previous attempts to model the process of immigration. In *Chapter 3*, I used the perspective gained in these studies to propose a new theoretical framework to predict immigration in response to harvest in vertebrate populations.

ABSTRACT

Immigration to local populations experiencing high natural or anthropogenic mortality has important implications for metapopulation dynamics, sustainable harvesting, pest control, and the design of conservation reserves. Previous modeling of the population consequences of interactions between harvest and protected areas have often unrealistically assumed that migration between areas would be restricted to juveniles from subsequent reproduction or, conversely, that it would provide an unlimited adjustment of the population to variation in resource availability. Oriented migration in source-sink models allows for intermediate levels of mobility but cannot include density-dependent changes in direction (*e.g.* negative to positive) and magnitude of immigration in response to harvest, cannot model limits to immigration from physical properties of the landscape and cannot incorporate multiple mobility limitations to immigration. Furthermore, source-sink dynamics models require two equations, complicating their application to empirical data. Here, we propose a new theoretical framework, 'the compensatory immigration model', consisting of a single equation that includes effects of both harvested and protected populations and allows complex density-dependent changes in direction and magnitude of immigration. We modified the equation to reflect six alternative scenarios that varied in the roles of potential limiting factors such as the size of the protected population, properties of the landscape (relative habitat quality and functional connectivity) affecting the rate of replacement of harvested individuals and behavioral interactions that could lead to complex density dependence. These scenarios facilitate empirical testing of the relative effect sizes of different factors potentially limiting immigration. Together, the new and previous models predict that immigration from protected areas can contribute importantly to the total yield and to recovery of a harvest area and consequently can significantly affect population size and demography in protected areas. Immigration and total yield can show complex non-linear relationships in response to harvest as the size of the protected area, rate of replacement of harvested individuals, mobility and behavioral interactions vary. To predict the influence of protected areas, additional research is

needed to explore how species and landscape characteristics affect the spatial influence of harvesting on adjacent protected areas, how density-dependent processes affect the probability of emigration from protected areas and of immigration into harvest areas and how mobility factors limit immigration.

INTRODUCTION

In many populations targeted by hunters and fishers, harvest takes place in only part of the area occupied by the population as a result of legal protection (*e.g.* national parks or reserves) or natural features that limit access to harvesters (*e.g.* distance from roads for terrestrial animals (Novaro, Funes, and Walker 2005) and distance from boat launches for aquatic animals (Stuart-Smith et al. 2008). Harvested populations are suggested to recover in the short term by net immigration of surplus young produced in protected areas (Almany et al. 2007; Jonzén, Lundberg, and Gårdmark 2001; McCullough 1996; Novaro, Funes, and Walker 2005; Polacheck 1990) and in the longer term by higher recruitment through negatively density-dependent reproduction and/or survival of the remaining individuals in both harvest and protected areas (Sinclair and Pech 1996). Immigrants to harvest areas have been thought to be predominantly larvae in aquatic organisms (Gerber et al. 2003; Pelletier and Mahevas 2005; Roberts et al. 2001) and juveniles performing long distance natal dispersal in terrestrial organisms (McCullough 1996). However, there is accumulating empirical evidence for rapid, short distance home range relocation (*i.e.* a permanent change in space use; Robertson 1988) by sexually mature individuals from adjacent areas following localized mortality (see *General introduction* and *Appendix I.1*).

The use of protected areas or reserves as a spatial refuge strategy or spatial control (McCullough 1996), where a harvest area is adjacent to a protected area, is suggested to be a more sustainable and stable harvesting strategy in the presence of uncertainty than removing a fixed fraction or a fixed number of individuals from the available population each year (Hastings and Botsford 1999; Jonzén, Lundberg, and Gårdmark 2001; Joshi and Gadgil 1991; McCullough 1996; Neubert 2003; Nowlis and Roberts 1999). For this reason, protected areas have received a worldwide interest in fisheries, with the rapid development of marine protected areas (MPAs) for fish conservation and related benefits to fisheries (McClanahan and Mangi 2000; Nowlis and Roberts 1999; Roberts et al. 2001; Rowley 1994; Zeller, Stoute, and Russ 2003). Protected areas are similarly used for the management of bush meat hunting in the Neotropics (McCullough 1996; Naranjo and Bodmer 2007; Novaro, Redford, and Bodmer 2000).

Immigration from a protected area can benefit harvested populations if it allows the replacement of individuals in the short term, stabilizing population size. Immigration from a protected area can also benefit harvesters by increasing total yield (*i.e.* total yield will be a combination of residents from the harvest area and immigrants from the protected area). However, immigration can be detrimental to population persistence if it creates demographic changes in the protected area that adversely affect the metapopulation dynamics (Amarasekare 2004; Gundersen et al. 2001; Novaro, Redford, and Bodmer 2000). The population size in a protected area can be strongly reduced if a significant proportion of this population immigrates in response to harvest. Harvesters will have an impression of a growing or a stable population in the harvest area but the metapopulation (*i.e.* the harvest and protected areas combined) may be well into decline before harvesting pressure is reduced. The "ecological vacuum effect" (sometimes called the domino effect; Gaines, Vivas, and Baker 1979), in which individuals from surrounding areas attracted by reduced competition rapidly increase their home ranges or relocate them toward the harvest area , can expose individuals that were well within the core of a protected area to additional mortality from harvesting close to a protected area boundary. This may weaken the potential of even very large protected areas to prevent the decline of small populations at risk (*e.g.* large carnivores; Loveridge et al. 2007; Woodroffe and Ginsberg 1998).

Despite accumulating evidence for short term immigration to harvest areas, there is very limited empirical evidence for the mechanisms leading to immigration in response to harvest and on the factors that could increase or decrease immigration (Bowler and Benton 2005; Matthysen 2005) or the effect of immigration on the dynamics between the protected and harvest area (but see (Gundersen et al. 2001). For this reason, estimates of population flux between protected and harvest areas in theoretical models are based on some very simple assumptions. Some previous modeling efforts, mainly considering fishes and invertebrates, assume that adults do not move and restrict immigration to dispersing larvae from subsequent reproduction (reviews by Gerber et al. 2003; Guénette, Lauck, and Clark 1998; Pelletier and Mahevas 2005). The extreme opposite movement assumption is derived from the Ideal Free Distribution and related density-dependent habitat selection models (Fretwell and Lucas 1969; Rosenzweig 1981) which assume that movements occur freely between the protected and harvest area to equalize individual fitness among areas (Claessen, de Vos, and de Roos 2009; Doak 1995; MacCall 1990; Walters 2000; Watson, Alder, and Walters 2000). This is analogous to the commonly used diffusive model (Neubert 2003) where movement between the protected and harvest area is a function of the difference in density between the two areas. Other modeling efforts include oriented movements between the protected and harvest areas, where per capita transfer parameters are set independently for movements in each direction (Amarasekare 2004; Beverton and Holt 1993; DeMartini 1993; Polacheck 1990). This potentially facilitates the modeling of systems where there is neither complete immobility nor complete mobility of organisms.

Variation in mobility may result from species differences in locomotor abilities, body size, perceptual capacity, searching tactics and mortality risk associated with movement (Bowman, Cappuccino, and Fahrig 2002; Mech and Zollner 2002; Schooley and Wiens 2003; Zollner and Lima 1999). Variation in mobility may also originate from the degree to which the landscape facilitates or impedes movement among habitat patches (*i.e.* functional connectivity; Taylor et al. 1993), as well as the size, shape, quality and distance between habitat patches (Andreassen and Ims 2001; Bowman, Cappuccino, and Fahrig 2002; Doligez et al. 2004; Enfjäll and Leimar 2009). Density-dependent behavioral interactions among conspecifics may also affect mobility. For example, reduced effectiveness of territoriality in residents in a declining population can increase movement rate into the area as suggested by the social fence hypothesis of Hestbeck (1982). Also, individuals may be less likely to immigrate to low density than to high density populations as suggested by the conspecific attraction hypothesis (Stamps 1991; Danielson and Gaines 1987).

Because empirical evidence for mechanisms and factors affecting immigration in response to harvest is lacking and because immigration can have beneficial consequences for harvested populations and harvesters but also significant detrimental effects for population viability (Amarasekare 2004; Enfjäll and Leimar 2009; Gundersen et al. 2001), a strong body of theory with a set of robust testable predictions is needed to explore how different assumptions about immigration including variation in mobility factors, can affect immigration, total yield and metapopulation dynamics. For this purpose, source-sink models (Pulliam 1988) can be particularly relevant to exploring how immigration can affect the dynamics between harvested and protected populations. Source-sink models have one equation for the source, *i.e.* a patch with positive population growth where birth rate is greater than death and emigration is greater than immigration, and one equation for the sink, *i.e.* negative population growth where birth is smaller than death and emigration is smaller than immigration. Source-sink equations include transfer parameters that control population flux and can differ according to the direction of movement. Thus, protected areas can act like sources and harvest areas like sinks.

In this study, we first explore how source-sink models that use three common assumptions about immigration (*i.e.* complete immobility, complete mobility and oriented immigration between protected and harvest area) to predict immigration in response to harvest. More specifically, we examine how each immigration assumption affects: 1) total cumulative immigration, 2) total proportional yield (*i.e.* the number harvested individuals including residents and migrants from the protected area divided by the initial number of residents in the harvest area) and 3) population dynamics in harvest and protected areas in response to cumulative harvest. For each immigration assumption, we also evaluate the generality and limitations of its predictions regarding mobility factors. We then propose a novel alternative general theoretical framework, consisting of a single equation that is used to generate a variety of assumptions that account for the effect of three factors limiting to immigration (*i.e.* size of the protected population, rate of replacement of harvested individuals and behavioral interactions in both the harvest and protected areas), that could circumvent problems related with the use of source-sink models and their immigration assumptions. We examine how the successive inclusion of the three limiting factors to immigration in the model and the potential interactions among limiting factors affect total cumulative immigration, total proportional yield and population dynamics in harvest and protected areas in response to cumulative harvest. Finally, we present some suggestions on how to test the proposed framework.

HOW DO CURRENT ASSUMPTIONS ABOUT IMMIGRATION AFFECT PREDICTIONS OF TOTAL YIELD AND METAPOPULATION DYNAMICS IN RESPONSE TO HARVEST?

Overview of source-sink dynamics

Using source-sink dynamics, we examine how three current immigration assumptions affect population dynamics in the harvest and the protected areas. *Equations 1a* and *1b* are built to represent population size of a given cohort of adult and subadult individuals in a time frame t in a harvest area (H) and in an adjacent protected area (P). The time frame explored can represent a harvesting period and t can represent harvesting event over time. $N_{i,t}$ represents the number of individuals in the cohort in area$_i$ at time t. H_H represents the harvesting pressure in the harvest area (*i.e.* the proportion of the population in the harvest area that is removed at each time t). H_H can refer to a fixed number of individuals (*i.e.* constant harvest effort; fixed harvest strategy) if it is multiplied by the initial population size in the harvest area ($N_{H,0}$). It can refer to a per capita proportion of the remaining population at time t (*i.e.* per capita harvest strategy) if it is multiplied by $N_{H,t}$.(represented in *equations 1a* and *1b*). $M_{i:j}$ represents mobility and is a per capita proportion of the population that is transferred from area$_i$ to area$_j$ at a given time t. Analogous equations with minor differences have been used by Beverton and Holt (1957) and Polacheck

(1990) to model the temporal dynamics of a cohort with respect to spawning stock and yield following establishment of an area closed to fishing. In the present study, we ignore recruitment and reproduction of the cohort to focus on short term effects of movements on source-sink dynamics in a harvesting context. This model also assumes that natural mortality is negligible in the time frame examined. All symbols for model parameters in this study are summarized in Table 3.1.

Equation 1a: *Dynamics in the harvested area (H)*

$$N_{H,t+1} = N_{H,t} - \left(H_H N_{H,t} \right) - \left(M_{H:P} N_{H,t} \right) + \left(M_{P:H} N_{P,t} \right)$$

Equation 1b: *Dynamics in the protected area (P)*

$$N_{P,t+1} = N_{P,t} - \left(M_{P:H} N_{P,t} \right) + \left(M_{H:P} N_{H,t} \right)$$

A source-sink model is by definition a non-equilibrium model where there is always a net transfer of individuals from the source to the sink. Source-sink dynamics are at equilibrium when the transfer rate between area$_i$ and area$_j$, in each direction in absence of harvesting, is equal and results in no net transfer (*equation 2*). In this situation, the model is an approximation of random dispersion (see Beverton and Holt 1993 for a discussion about interchange of fish between adjacent sub-areas; p.136).

Equation 2: Net transfer rate between the protected and harvest areas at equilibrium in the absence of harvesting

$$M_{P:H} = \frac{M_{H:P} N_{H,t}}{N_{P,t}}$$

In the following simulations, we examine predictions from three immigration assumptions commonly used to model transfer rate in source-sink dynamics but apply them in a harvesting context to predict immigration into the harvesting area and its effect on the metapopulation. Note that population size decreases over time instead of increasing as in common population dynamics models. We start with a saturated population *(i.e.* at carrying capacity) and examine the effect of cumulative harvest on cumulative immigration. For each immigration assumption, we examine the effect of cumulative harvest on the rate and total cumulative net immigration (*i.e.* immigration from protected area minus emigration from the harvest area over time). We also examine the effect of cumulative harvest with the two harvest strategies, a per capita harvesting pressure ($H_H * N_{H,t}$) and a fixed harvesting pressure ($H_H * N_{H,0}$), on the rate of change in population sizes in the harvest and protected areas and on total potential yield (i.e. the number of harvested individuals, including residents of the harvest area and immigrants from the protected area). In the case of fixed harvesting pressure, when the population size in the harvest area drops below the number defined by the fixed harvesting pressure, we continue to remove remaining individuals in the harvest area until the harvest area is near extinction (*i.e.* $N_{H,t} < 1$). All simulations were run in Excel. We started with an initial total population size of 1000.

Assumption of no migration between protected and harvest areas

If migration of the adult and subadult cohort between the protected and the harvest areas is zero, we can ignore the terms related to the protected area in *equation 1a* and the transfer parameter related to harvest area, resulting in *equation 3*. Cumulative harvest proceeds until 100% of the local cohort in the harvest area is removed. Population size in the protected area does not change with cumulative harvest (*equation 3*, Fig. 3.1a). The potential total yield equals the original population size in the harvest area. Changing the harvesting strategy (*i.e.* per capita or fixed harvesting) affects neither total cumulative immigration nor the rate of population change in relation to cumulative harvest in both areas. Population size decrease faster over time with the fixed harvesting strategy compared to the per capita harvesting strategy, but in this study, we will focus on the rate of change of population size and cumulative immigration as a function of cumulative harvest.

Equation 3: Population dynamics in the harvest area assuming no movement

$$N_{H,t+1} = N_{H,t} - \left(H_H N_{H,t}\right)$$

Assuming no movement between the protected and harvest area can be adequate to model population dynamics for species where adults are sessile (*e.g.*

plants, mollusks, some crustaceans and other invertebrates) or for highly sedentary species (*e.g.* small coral reef fish, some insects). This movement assumption can also capture the immigration pattern in a mobile species where functional connectivity between the protected and harvest areas is very weak. However, predictions based on this assumption have very limited application on population dynamics for most mobile organisms in response to harvest.

Assumption of immigration from density-dependent habitat selection (DDHS)

Net immigration from the protected area to the harvest area in response to harvest is predicted by most density-dependent habitat selection (DDHS) models such as the ideal free distribution (Fretwell and Lucas 1969; Rosenzweig 1981). These models assume that individuals are highly mobile, able to assess the suitability of all habitat patches, make the best selection among them and move accordingly. Individuals are distributed uniformly within discrete areas that are characterized by their realized suitability, a measure of fitness (Fretwell and Lucas 1969). As population size decreases in a given area, its realized suitability increases. Therefore, realized suitability rises after harvest and immigration from the protected to the harvested area will proceed to equalize their realized suitabilities. There is no immigration from the harvest to the protected area. Applying the immigration assumption of DDHS to *equations 1a* and *1b* results in *equations 4a* and *4b*. The number of individuals in a given population (*i.e.* protected or harvested) could be affected by both the area and by the average habitat quality of this area. This is taken into account in the calculation of $M_{P:H}$. In $M_{P:H}$, we multiply the harvest pressure by the proportion of the combined harvested and protected population that is located in the protected area (*equation 4c*). That is, under the ideal free assumptions, the proportion of the population moving to the harvested area is equivalent to the fraction of the harvest pressure represented by the protected population. This controls for the area and/or habitat quality in the protected area relative to the harvest area.

Equation 4a: Dynamics in the harvest area assuming DDHS

$$N_{H,t+1} = N_{H,t} - \left(H_H * N_{H,t}\right) + M_{P:H}N_{H,t}$$

Equation 4b: Dynamics in the protected area assuming DDHS

$$N_{P,t+1} = N_{P,t} - M_{P:H}N_{H,t}$$

Equation 4c: Net transfer rate from protected to harvest area assuming immigration from DDHS

$$M_{P:H} = H_H\left(\frac{N_{P,t}}{N_{P,t} + N_{H,t}}\right)$$

Based on *equations 4a* and *4b*, cumulative immigration increases linearly with cumulative harvest and is a function of the proportion of the total population in the protected area. Because density dependence is defined as a non-constant functional relationship between the per capita rate of population change and population density, possibly involving lags (Murdoch 1994; Turchin 2003), immigration with DDHS is density independent. Immigration rate increases with the proportion of the total population that is in the protected area, whether due to a larger area or higher habitat quality (Fig. 3.1b). The percentage of the total yield due to immigration also varies with the proportion of the total population that is in the protected area. Population size in both the harvested and protected populations decreases linearly with cumulative harvesting (Fig. 3.1b; black and grey dotted lines; rates = $N_{P,t}/(N_{P,t}+N_{H,t})$ for protected area and 1 - ($N_{P,t}/(N_{P,t}+N_{H,t})$) for the harvest area), and both populations reach extinction under high cumulative harvest.

The assumption of free movements from optimal DDHS can be adequate to model population dynamics for highly mobile species. This movement assumption can account, indirectly, for differences in habitat quality between the harvest and protected areas by varying the proportion of the total population that is protected. A small proportion of the total population that is protected may represent low quality habitat in the protected area. However, in territorial or other despotic systems, high abundance can occur in low quality habitat if large and dominant individuals monopolize the best habitat (Van Horne 1983), violating the assumption that population size in a given area (harvest or protected) is related to habitat quality or area. This would results in strong deviations from DDHS predictions. In addition to deviation from DDHS predictions, this migration assumption cannot account variation in functional connectivity.

Assumption of oriented migration

Some source-sink models assume that between local populations oriented migration occurs that is not a consequence of density-dependent habitat selection (Amarasekare 2004; Beverton and Holt 1957; DeMartini 1993; Polacheck 1990). Oriented migration, where one parameter controls the transfer of individual from the protected area to the harvested area ($M_{P:H}$) and another parameter controls for the transfer of individuals from the harvest to the protected area ($M_{H:P}$; *equations 1a* and *1b*), allows the modeling of population dynamics where there is neither complete immobility nor complete mobility.

From the assumption of oriented immigration, net cumulative immigration in relation to cumulative harvest can be negatively density-dependent ($M_{P:H} = M_{H:P}$; Fig. 3.3a $M_{P:H} = 0.05$) for a given harvesting pressure and proportion of the total population that is protected. Net cumulative immigration can be density-independent which is analogous to predictions from density-dependent habitat selection when the number of transferred individuals from the protected area to the harvest area equalized the number of transferred individuals from the harvest to the protected area in addition to harvested individuals (*equation 5;* Fig. 3.3a $M_{P:H} = 0.10$). Net cumulative immigration can be positively density-dependent ($M_{P:H} >> M_{H:P}$; Fig. 3.2a $M_{P:H} = 0.15$). Under the condition of negative density dependence ($M_{P:H} = M_{H:P}$), population size in the harvest area declined at a higher rate than population size in the protected area (Fig. 3.2b, c). Under the conditions of density-independent immigration rate ($M_{P:H} > M_{H:P}$), population sizes in the harvest and protected area decrease linearly in relation to cumulative harvest (Fig 3.2; $M_{H:UH} = 0.10$). Under the condition of positive density dependence ($M_{P:H} >> M_{H:P}$), population size in the protected area decreases faster than population size in the harvest area.

Equation 5: Transfer rate from protected to harvest area to achieve equilibrium

$$M_{P:H} = \frac{\left(M_{H:P}N_{H,t}\right) + H_H N_{H,t}\left(\frac{N_{P,t}}{N_{P,t} + N_{H,t}}\right)}{N_{P,t}}$$

Predictions from source-sink models with oriented immigration assumptions differ, depending on the harvesting strategy. Cumulative immigration is higher with per capita harvesting than with a fixed harvesting strategy for low to intermediate cumulative harvesting (Fig 3.2a). With fixed harvesting, there is a point where it is not possible to remove the specified number of individuals (dotted red lines; Fig. 3.2a, b). From this point, all individuals in the harvest area are removed. The total yield is very high for any given initial population size and any transfer rate because we can remove virtually all individuals from the metapopulation (Fig. 3.2b, c). Varying the size of the protected population ($N_{P,0}$) will have an effect on the rate of cumulative immigration and on the percentage of the total yield that is due to immigration but not on total yield.

The assumption of oriented migration in source-sink models can be applied to moderate to highly mobile species and may include variation in habitat quality and/or landscape functional connectivity between the harvest and protected areas. For example, equal transfer rates between the two areas ($M_{P:H} = M_{H:P}$) may represent a symmetrical effect of functional connectivity (*e.g.* partial barrier such as an area without cover or a road) or comparable relative habitat quality between the harvest and protected area. Unequal transfer rates among areas ($M_{P:H} \neq M_{H:P}$) may represent an asymmetrical effect of functional connectivity (*e.g.* waterfalls and currents in a stream favoring movement in one direction more than the other) or difference in habitat quality between the protected and harvest area.

Source-sink models using oriented immigration can also model positive or negative density dependence because densities in both the harvest and protected areas are decreasing at a different rate. Positive and negative density-dependent immigration can result from behavioral interactions in both the harvest and protected areas. For example, in territorial species, tendency to emigrate could be positively density dependent (*i.e.* decreasing rate of emigration as density decreases) if some individuals are restricted to lower quality territories or receive high rates of aggression at high density but all individuals acquire high quality territories as the density in the protected area decreases (Kramer, Rangeley, and Chapman 1997; Sutherland, Gill, and Norris 2002). On the other hand, opportunities to immigrate to the harvest area might be limited at the highest densities by cooperative defence and obstacles to movement created by a high density of conspecifics (Chase 1980; Meadows 1995), and by territory expansion and redistribution of remaining individuals onto the best territories, resulting in negative density dependence (Hannon 1983; Hestbeck 1982; Hestbeck 1988; Norman and Jones 1984).

Some gaps in the migration assumptions of source-sink models

Although considerable variation in mobility and behavior can be modeled with source-sink dynamics by using assumptions of immobile adults, highly mobile adults or oriented migration from a per capita proportion of the population transferred between protected and harvest areas, some important conditions cannot be adequately addressed. None of these model assumptions can account for density-dependent changes in the direction (*i.e.* positive and negative density dependence) and magnitude of immigration arising from behavioral interactions in the harvest and protected areas. Because the negatively density dependent processes are likely to predominate at early stages of harvest while the positively density dependent processes should predominate when density is lower, there is likely to be a sigmoid relationship between cumulative harvesting and cumulative immigration. To our knowledge, only four studies have explored theoretically the effect of density-dependent as opposed to constant movement probabilities on metapopulation or source-sink dynamics (Amarasekare 2004; Howe, Davis, and Mosca 1991; Pulliam 1988; Saether, Engen, and Lande 1999), and none have considered the potential for a sigmoid relationship between population density and movement rate. The precise relationship between immigration and harvesting may be critical to predicting total yield and establishing harvesting strategies.

Another condition that source-sink dynamics model with existing immigration assumptions cannot realistically incorporate is the prediction of a limit to immigration and a limit to total yield in response to harvest. Immigration assumptions from source-sink model cannot deal with this issue because the number of immigrants that are transferred from one area to the other is a per capita rate controlled by the remaining population size in the respective areas (see *equation 5*). As the size of the protected and harvest areas decreases, the number of individuals moving also decreases but the immigration rate never reaches zero. Accumulating empirical evidence supports a limit to population replacement from immigration in many taxa (Fig. I.1 in the *General introduction*, *Appendix I.1*). Structural habitat features and a difference in habitat quality between the harvest and protected area can impede immigration and should result in a smaller total immigration and total yield than predictions from source-sink models.

Finally, parameters controlling immigration and movement in source-sink dynamics models cannot distinguish the relative effects of different limiting mobility factors on immigration in response to harvest. This is because the rate of transfer between the two areas is modeled with only one parameter (one parameter for transfer between the protected and harvest areas and one parameter for transfer between the harvest and protected area).

To adequately predict immigration in response to harvest, we need an immigration function that facilitates the modeling of these three limitations (*i.e.* complex density dependence, limit to immigration and testing the relative effect of limiting mobility factors) that source-sink dynamics model cannot address.

A NEW THEORETICAL FRAMEWORK TO PREDICT COMPENSATORY IMMIGRATION

In order to incorporate more realistic complexity of density-dependent processes and limits to immigration from protected to harvest areas, we propose a new theoretical framework which we refer to as the compensatory immigration framework. We develop an immigration function that consists of one equation relating cumulative harvest to cumulative immigration. This equation can be used to explore the effect of limiting factors using an analytical approach developed in the coral reef fish literature and successfully applied to egg mortality in frogs and seed recruitment in plants (Osenberg et al. 2002; Poulsen et al. 2007; Schmitt, Holbrook, and Osenberg 1999; Vonesh and De la Cruz 2002). To explore the relative effects of variation in limiting factors, we examine the relationship between cumulative immigration and cumulative harvest in six nested models representing alternative hypotheses to explain immigration in response to harvest. The alternative hypotheses increase in complexity by relaxing assumptions of "no effect" of mobility factors and limits on immigration. Alternative hypotheses will hereafter be called scenarios.

Our framework uses components of source-sink dynamics and the formulation of Beverton and Holt (1957) original stock-recruitment function (*equation 6*), yet contrasts from them in many aspects. Although the formulation is similar to the Beverton and Holt function, we predict net cumulative immigration (I_H) based on total yield (Y; the cumulative harvested individuals; *equation 7*) instead of predicting population recruitment (R_{t+1}) based on spawner density (S_t) in a closed population (*equation 6*). In the compensatory immigration model, density decreases and is time independent instead of an increasing density over time, because immigration is based on total yield and not population size is the respective areas. Immigration is modeled at the metapopulation level by using limits related to density in the harvest area (Y; number of harvested individuals) and the initial number of individuals in the protected population ($N_{P,0}$) in a single equation (*equation 7*). In the denominator of the equation, we use the initial population size in the protected area ($N_{P,0}$) to set the maximum number of immigrants. This plays a role analogous to carrying capacity in the Beverton-Holt model (k; *equation 6*). The parameter M_0 influences the initial rate of replacement of harvested individuals. In this model, we assume that the limiting effect of habitat quality and landscape connectivity can be controlled in the equation by varying M_0. Different forms of density dependence arising from interactions among individuals in both the harvest and the protected areas are modeled by θ and $N_{P,0}$ (*equation 7*). The parameter θ controls the direction of density dependence at high population size. Note that net I_H in the absence of harvesting could be modeled by inserting a constant before the right term of *equation 6*. All simulations were run in Excel. We started with an initial total population size of 1000.

For simplicity, we assume that net immigration in the absence of harvesting is zero. We also assume that harvest is randomly distributed within the harvest area. To keep the model independent of time, we assume temporary equilibrium after each harvesting event. Because the goal of the compensatory immigration model is to predict short-term immigration following harvesting, we assume that there is no recruitment from reproduction during the examined time frame. We also assume that individuals do not avoid the harvest area in response to any disturbance associated with harvest. Harvest ends when there are no individuals left in the harvest area or when the rate of immigration based on the number of harvested individuals reaches zero. In the following section, we will develop the model by adding some limiting factors to immigration.

Equation 6: Beverton and Holt recruitment function

$$R_{t+1} = \frac{\mathrm{\gamma_0 S_t}}{1 + \left[\frac{\mathrm{\gamma_0 S_t}}{\mathrm{k}}\right]}$$

Where R_{t+1} is the number or density or biomass of recruits in generation t+1 as a function of the number of spawners (*i.e.* reproduction individuals) in the previous generation (S_t). γ_0 is the population growth rate and k is the carrying capacity.

Equation 7: Cumulative immigration in response to cumulative harvesting predicted from the proposed compensatory immigration framework

$$I_H = \frac{M_0 * Y^{\theta}}{1 + \left[\frac{M_0}{N_{P,0}}\right] * Y^{\theta}}$$

Alternative scenarios

Scenario 1: The no mobility limitation

This scenario is the simplest and assumes that organisms are immobile which is analogous to the no immigration assumption in the source-sink models. Based on this limitation, the initial rate of replacement of harvested individuals (M_0) = 0, the parameter controlling for the direction of density dependence at high population size (θ) = 1 and the size of the protected area ($N_{P,0}$) → ∞. Thus, *equation 7* simplifies to *equation 8*.

Equation 8: Cumulative immigration predicted with the no mobility limitation

$$I_H = 0$$

Scenario 2: The only vacancy limitation

This scenario assumes that vacancies created in the harvest area (Y; number of harvested individuals) are the only limiting factor to immigration, with no effect of DDHS, habitat quality, landscape connectivity or behavioral interactions. Based on this limitation, the initial per capita immigration rate (M_0) = 1, the parameter controlling for the direction of density dependence at high population size (θ) =1 and the size of the protected area ($N_{P,0}$) → ∞. Thus, *equation 7* simplifies to *equation 9*. Mathematically, this scenario predicts that total yield should tend to infinity because each harvested individual results in a new immigrant (Fig. 3.3a, c; $M_0 = 1$, $N_{P,0} \rightarrow \infty$, black line). Realistically, however, population size in protected area is likely to be limited. Thus, $N_{P,0}$ will affect the maximum cumulative immigration and total yield but will not affect the rate of cumulative immigration ($N_{P,0} \rightarrow \infty$ in the denominator). Immigration stops when the protected area has been emptied, and harvesting can continue until the harvest area is also depleted (Fig. 3.3c, $M_0 = 1$ at $N_{P,0} = 500$ or 800; darker blue lines).

Equation 9: Cumulative immigration predicted with the only vacancy limitation

$$I_H = Y$$

This scenario predicts that the rate of cumulative immigration (*i.e.* the change in the number of immigrants in relation to cumulative harvest) is density-independent and not influenced by the size of the protected area (Fig. 3.3a, c; $M_0 = 1$ and $N_{P,0} = 500$ or 800). Maximum cumulative immigration increases with the size of the protected area (Fig. 3.3a; $M_0 = 1$ at $N_{P,0} = 500$ or 800 and Fig. 3.3a for $M_0 = 1$). Total yield is extremely high because the whole metapopulation (*i.e.* harvest and protected area) is harvested (Fig. 3.7a for $M_0 = 1$). The contribution of immigration to total yield (*i.e.* the proportion of harvested individuals that are immigrants) varies proportionally with the size of the protected area (Fig. 3.8a for $M_0 = 1$). Population size in the harvest area does not change in relation to cumulative harvest until all individuals have been extracted from the protected area because each harvested individual is replaced by a new migrant from the protected area. After this point (represented by E_P for extinction in the protected area, Fig. 3.3a; for $M_0 = 1$), population size in the harvest area decreases rapidly at a rate proportional to M_0 (Fig. 3.3b; $M_0 = 1$).

Biologically, this scenario implies that individuals have high mobility, large perceptual range and move freely in the landscape because each vacancy created by harvesting is detected and filled very rapidly by individuals from the protected area. The Only vacancy limitation scenario is likely to be the scenario that creates the highest risk of extinction for the metapopulation because all individuals can be extracted, rapidly and independently of the size of the protected area (Fig. 3.6a).

Scenario 3: The partial replacement limitation

This scenario assumes that a constant proportion of harvested individuals is replaced by immigration (Fig. 3.3a, c; $M_0 < 1$). Two rather different biological situations can lead to this scenario and may result in different predictions that could be explored within the framework. The first situation can arise from DDHS. Predictions from DDHS have been developed in detail in the section on source sink dynamics. In this situation, cumulative immigration can be modeled by setting M_0 equal to proportion of the total population that is protected (*i.e.* $N_{P,0}/(N_{P,0} + N_{H,0})$).

Under that condition, individuals should immigrate to equalize the realized suitability among the two areas. The second situation leading to this scenario occurs when the quality of the home range or territory affects individual fitness (Beletsky and Orians 1987; Both and Visser 2003) and/or when functional connectivity between the protected and the harvested area generates a constant and uniform resistance to immigration. The proportion of individuals that immigrate should be positively correlated with the relative habitat quality and the functional connectivity between harvested and protected area and should deviate from predictions of DDHS. In both biological situations, $N_{P,0}$ is limited but does not affect the rate of cumulative immigration so $N_{P,0}$ can be set to infinity in the denominator. E*quation 7* then simplifies to *equation 10*.

Equation 10: Cumulative immigration predicted with the partial replacement limitation

$$I_H = M_0 Y$$

The rate of immigration is density-independent in both situations, but predictions differ depending on whether immigration is influenced by DDHS or by the physical properties of the landscape. From DDHS, the rate of cumulative immigration in relation to cumulative harvest and the maximum cumulative immigration are functions of the size of the protected area (Fig. 3.3c). Total yield is very high because the whole metapopulation can be harvested (Fig. 3.3c and d). The contribution of immigration to total yield varies linearly with and is proportional to the size of the protected area (Fig. 3.3a). Population size declines at a rate -(1-M_0) in the harvest area and at a rate -M_0 in the protected area until extinction occurs simultaneously in both areas (Fig. 3.3d). From limitations by landscape properties, which is the second biological situation, the rate of cumulative immigration in relation to cumulative harvest is a function of M_0 (Fig. 3a; $M_0 < 1$ for $N_{P,0} = 500$). When M_0 is equal to or higher than the value predicted by DDHS, the maximum cumulative immigration is very high and proportional to the size of the protected area (Fig. 3.6a). Total yield is also very high because the whole metapopulation is harvested, independently of the size of the protected area (Fig. 3.3c; $M_0 < 0.5$ for $N_{P,0} = 500$ and Fig. 3.7a where the red line corresponds to predictions from DDHS). Because the rate of replacement is higher than the harvesting pressure, population size in the harvest area does not change in relation to cumulative harvest until all individuals have been extracted from the protected area. After the extinction of the protected area population, population size in the harvest area decreases at a rate proportional to M_0 (Fig. 3.3b; $M_0 = 1$). When M_0 is smaller than the M_0 value predicted by DDHS, the effect of the size of the protected area on maximum cumulative immigration, total yield and on the contribution of immigration to total yield varies non-linearly with M_0 (Figs. 3.6a, 3.7a and. 3.8a). One novel prediction from this biological situation is a limit to cumulative immigration when the replacement rate of harvested individuals is small. The maximum cumulative immigration is limited because the number of immigrants is controlled by a partial replacement of harvested individuals and immigration stops when we harvest all individuals in the harvest area (Fig. 3.6a). Maximum cumulative immigration decreases with decreasing M_0 and the effect is larger with increasing protected area size (Fig. 3.6a). Total yield also decreases with M_0 and this effect is exacerbated for very large protected areas (Fig. 3.3c and Fig. 3.7a). The contribution of immigration to total proportional yield, for M_0 smaller than the M_0 value predicted by DDHS, is proportional to M_0 (Fig. 3.8a). The contribution of immigration to total proportional yield is proportional to the size of the protected populations for M_0 larger than M_0 predicted by DDHS (Fig. 3.8a). Population size decreases at a rate 1- M_0 in the harvest area and at a rate equal to M_0 in the protected area.

Biologically, this scenario implies that even very large protected areas can put the metapopulation at risk if individuals have high mobility, large perceptual ranges and move freely in the landscape (Fig 3.6a; DDHS biological situation and landscape limitation where M_0 is higher than the one predicted by DDHS; *i.e.* above the grey line). However, resistance to immigration from a lower functional connectivity between the protected and harvest area or low habitat quality in the harvest area (Fig 3.6a; M_0 smaller than the value predicted by DDHS; below the red line) can successfully protect part of the population in the protected area and could reduce the risk of extinction of the metapopulation.

Scenario 4: The availability of immigrants limitation

This scenario assumes that the availability of migrants in the protected area can be a limiting factor to immigration in response to harvest. The availability of immigrants scenario will generate a decreasing rate of immigration with cumulative harvest, where the maximum cumulative immigration tends toward an asymptote corresponding to the number of available immigrants in the protected area ($N_{P,0}$;Fig. 3.4a). The behavior of a function approaching $N_{P,0}$ has been explored in the previous discussion of source-sink dynamics. Mathematically, the maximum cumulative immigration should reach $N_{P,0}$, but it may have a lower value when extinction occurs in the harvest area. When $N_{P,0} < \infty$ and $\theta = 1$, *equation 7* simplifies to *equation 11* with $M_0 = 1$.

Scenario 5: The availability of immigrants and partial replacement limitations

With the model, we can evaluate the independent effect of a limited number of available migrants on immigration (*i.e.* $M_0 = 1$ and $\theta = 1$; scenario 4) and the combined effect of the limitation from the availability of migrants and physical properties of the landscape (*i.e.* $M_0 < 1$ and $\theta = 1$). When $N_{P,0} < \infty$ and $\theta = 1$, *equation 7* simplifies to *equation 11*.

Equation 11: Cumulative immigration predicted with the availability of immigrants and partial replacement limitations

$$I_H = \frac{M_0 Y}{1 + \left[\frac{M_0 Y}{N_{P,0}}\right]}$$

The availability of immigrants limitation scenario predicts that the rate of immigration and the maximum cumulative immigration are strongly influenced by the size of the protected area and, to a lesser extent, by the initial rate of replacement of harvested individuals (M_0). Cumulative immigration rate decreases with cumulative harvesting and decreases faster for smaller protected areas (Fig. 3.4a; $M_0 = 1$ for $N_{P,0} = 100$, 500 and 800). If relative habitat quality and/or landscape functional connectivity affect immigration in addition to the size of the protected area, we observe a lower rate of cumulative immigration (Fig. 3.4a; for $M_0 < 1$ and $N_{P,0} = 500$). The maximum cumulative immigration is also limited by the size of protected area, mainly for small protected area size. At larger protected area sizes, the initial per capita rate of immigration (M_0) has the largest effect on maximum cumulative immigration (Fig. 3.6b). Total yield varies non-linearly with the size of the protected area for a given M_0, decreases with increasing protected area size and decreases faster for larger protected areas when M_0 increases (Fig 3.6b). The contribution of immigration to total yield is proportional to M_0 when M_0 is smaller than the value predicted by DDHS and is proportional to the size of the protected population when M_0 is larger than the value predicted by DDHS (Fig. 3.8b).

Biologically, this scenario implies that the number of immigrants in the protected population affect the rate of immigration and limit total cumulative immigration and total yield, independent of species mobility. Under this scenario, the risk of extinction of the metapopulation is greatly reduced even when species are highly mobile and protected populations small because the rate of immigration decreases with decreasing density (Fig. 3.7b).

Scenario 6: The complex density-dependent limitation

This scenario is the most complex and evaluates the consequences of behavioral interactions in both the harvest and protected areas at high (by adding θ) and low density ($N_{P,0} < \infty$) which results in *equation 7*. Behavioral interactions can change the direction of density dependence from negative to positive as density decreases and can affect the magnitude of immigration. Because the number of harvested individuals (Y) is raised to the power of θ, M_0 is not comparable to M_0

used in the previous scenarios. For example, using $M_0 = 1$ in *equation 6* for a $N_{P,0} = 500$ and $\theta = 2$ results in a replacement rate of 8.34 immigrants per harvested individual. The maximum M_0 in the complex density-dependent limitation scenario, allowing a comparison with $M_0 = 1$ in the others scenarios, corresponds to a M_0 where the maximum instantaneous rate of cumulative immigration in relation to cumulative harvest is equal to 1 (Fig 3.5a) from *equation 7*. This allows the examination of the independent effects of the consequences of behavioral interactions and properties of the landscape on immigration. When $\theta > 1$ and $N_{P,0} < \infty$, we obtain *equation 7*.

The complex density-dependent limitation scenario predicts that the rate of cumulative immigration can change direction and magnitude in relation to cumulative harvest (Fig. 3.5a). The rate of cumulative immigration increases at low to intermediate cumulative harvest and then decreases for higher cumulative harvest. The magnitude of density dependence increases with increasing θ (Fig. 3.5a) and can result in low immigration at low cumulative harvest but high immigration at moderate cumulative harvest. By including the effect of the relative habitat quality and/or landscape connectivity on immigration, we observe a decreasing rate of cumulative immigration with decreasing M_0 (Fig. 3.5a). The effect of θ (*i.e.* density dependence at high density) on total cumulative immigration increases with increasing size of protected populations and with increasing initial rate of replacement of harvested individuals (M_0; Fig. 3.6c). Total yield varies non-linearly with the size of the protected area for a given M_0 and increases with increasing θ (Fig. 3.6c). The contribution of immigration to total yield is proportional to M_0 for small protected areas but increases for large protected areas when M_0 is smaller than the value predicted by DDHS. It is proportional to the size of the protected populations when M_0 is larger than the value predicted by DDHS (Fig. 3.8c).

Biologically, this scenario implies that behavioral interactions at high and low density in both the harvest and protected area can affect the rate of immigration. Under this scenario, the risk of extinction of the metapopulation is lower than for the partial replacement limitation scenario but higher than the immigrants limitation scenario, mainly for higher θ (Fig. 3.7c) where the rate of immigration is very high for moderate cumulative harvest (Fig. 3.5a).

CONCLUSIONS

New predictions from our compensatory immigration framework

The compensatory immigration model, using one simple equation with only two parameters (M_0 and θ) and one variable ($N_{P,0}$) related to limiting factors, provides a framework to derive predictions concerning cumulative immigration in response to harvest from various alternative scenarios. Our model can simulate simple density-independent immigration in response to harvest, similar to predictions from DDHS, but also complex density-dependent immigration resulting from a limited availability of potential migrants and from behavioral interactions in the harvest and protected areas. A change in direction (*i.e.* from negative to positive density dependence) and magnitude of immigration over the harvest sequence has not been considered as a potential immigration assumption in current population models despite its plausibility, especially in territorial systems (see Amarasekare 2004; Howe, Davis, and Mosca 1991; Pulliam 1988; Saether, Engen, and Lande 1999 for other density-dependent movement assumptions in population dynamics models). Negative density dependence (*i.e.* lower immigration at higher density) in harvested populations can result in low cumulative immigration under light harvesting when populations are close to saturation but can produce unexpectedly high immigration at moderate harvest (Fig. 3.5). Similar to Allee effects recognized in reproductive dynamics, positive density dependence (*i.e.* lower immigration at lower density) may inhibit immigration, reducing the contribution of immigration to the restoration of severely depleted populations, and this effect will be magnified when the harvest area is unattractive or badly connected to the protected area.

The compensatory immigration model is also useful to predict the relative influence of limiting factors to immigration (*i.e.* M_0; initial rate of replacement of harvested individuals assumed to be influenced by habitat quality and connectivity, $N_{P,0}$; size of the protected populations and θ; behavioral interactions at high density) on different metrics related to immigration in response to harvest (*e.g.* maximum cumulative immigration, total yield and contribution of immigration to total yield). The only vacancy limitation, assuming very high mobility, habitat quality and connectivity between the harvest and protected area allowed the highest total immigration and had the highest negative impact on protected populations, leading the metapopulation to extinction, independent of the size of the protected population (Figs. 3.6 and 3.7). For the other limitation scenarios, the relationships between total cumulative immigration, total yield and the size of the protected populations varied non-linearly with the initial rate of replacement of harvested individuals (M_0). As a general pattern, the maximum cumulative immigration is proportional to the size of the protected population when M_0 is higher than the one predicted by DDHS (Fig. 3.6). When M_0 is smaller than the one predicted by DDHS, the maximum cumulative immigration is proportional to M_0 for small to large protected population sizes (*i.e.* when the proportion of the protected population represents less than 70% of the total population; Fig. 3.6). At very large protected population sizes, total immigration is affected positively by both M_0 and the size of protected populations (Fig. 3.6). The total yield is proportional to the size of the protected population at very low M_0 in all scenarios (Fig. 3.7). Increasing M_0 resulted in a higher total yield for a given protected population size. The rate of change in total yield with increasing M_0 for a given protected population size is higher in the partial replacement and complex density-dependent limitation scenario compared to the immigrants limitation scenario. The effect of a change in M_0 on total yield is small compared to the effect of changing the size of the protected area, mainly in the immigrant limitation scenario (Fig. 3.7).

Implications of predictions for population management and conservation

Immigration can result in important benefits for harvesters by increasing total yield and for the recovery of harvested population by compensating for local harvest. For example, immigration of post-settlement fish from marine protected areas into fished areas, a process called "spillover" is suggested to be a tangible short term benefit for local fishers from the establishment of marine protected areas (Russ and Alcala 1996; McClanahan and Mangi 2000; Roberts et al. 2001; Gell and Roberts 2003). Several forms of indirect evidence for spillover are available (Abesamis and Russ 2005; Goni et al. 2008; Russ and Alcala 1996; Zeller, Stoute, and Russ 2003; Chapman and Kramer 2000; Rakitin and Kramer 1996; Harmelin-Vivien et al. 2008), but direct empirical evidence is very limited, making this benefit controversial (but see *Chapter 4*). The compensatory immigration model could provide a new set of predictions concerning the magnitude of spillover if managers vary the size of the protected population and/or habitat quality and connectivity between the harvest and protected area.

Immigration in response to harvesting can detrimentally affect adjacent protected areas. The cost of a high rate of movement between the protected and harvest area for metapopulation persistence is an issue that has received much less attention than the persistence of sink populations via immigration (but see Amarasekare 2004; Gundersen et al. 2001). For example, immigration can be detrimental to protected populations when animals are harvested at the boundary of protected areas (Woodroffe and Ginsberg 2000) leading to maladaptive selection that will be exacerbated if the habitat quality in the harvest area is higher than in the protected area (Delibes, Gaona, and Ferreras 2001; Robinson et al. 2008). The compensatory immigration model could allow managers to develop predictions concerning the spatial extent of the impact of harvest on a reserve for a given a relative habitat quality and functional connectivity between a harvested and protected populations. This would affect design and size of protected area.

Harvesting can affect demography and population size at the metapopulation level if one component of the population has a higher probability of being harvested (*e.g.* trophy hunting; Festa-Bianchet and Apollonio 2003; Edeline et al. 2007). Protected areas have been suggested as a method for controlling the evolutionary impacts of harvesting cause by selective harvest (Baskett et al. 2005), but in many systems, smaller and younger individuals are more prone to emigrate in response to harvest (Harris 1970; Hourigan 1986; Krebs 1971; McDougall and Kramer 2007; Newton 1992; 1998; Robinson et al. 2008; Stickel 1946). Immigration of younger and smaller individuals from protected area may aggravate the effect of harvesting and may push temporary or permanently some local populations or the whole metapopulation away from their naturally selected evolutionally optima if they allow the selection for earlier age at maturation, smaller size at maturation and smaller size. More studies are needed to confirm if the effect of immigration is additive to the effect of selective harvest on demography.

Testing the compensatory immigration framework and future developments

Strong empirical evidence to support any immigration function in response to harvest is still lacking. The critical next step is to use a compensatory immigration model, like the one proposed in this study, and apply it on empirical data to assess whether protected areas can compensate local harvest for lost yields due to the establishment of the protected area (see *Chapter 4* for an empirical test of the compensatory immigration model). Answering these questions can be crucial to resolve debates about the usefulness of protected area as a management strategy. If compensatory immigration does occur, even if only partially, then protected area can play a key role in management, as well as in conservation. However, if compensatory immigration occurs in such a way that it makes the whole metapopulation at risk of extinction, harvesting quotas must be reduce to assure the persistence of the metapopulation.

To test the compensatory immigration model, the before-after-control-impact-pair design would be strongest experimental design (BACI or BACIP; Gell and Roberts 2003; Underwood 1994). This design consists of replicated protected areas and harvest areas that are paired with independent control locations (*i.e.* without protection). Data are collected at intervals before and after the start of protection or the start of harvest. However, because replication at the scale of a protected area may be difficult logistically, a BACIP design using small scale model systems (*e.g. Stegastes* damselfish in this thesis, small mammals, small birds and insects) may be particularly useful to study the mechanisms behind immigration in response to harvest.

The compensatory immigration model allows the modeling of complex density-dependent immigration in relation to harvest. However, to be able to detect density-dependent immigration, a wide range of population sizes in the harvest area is needed, and individuals in either the harvest or the protected area must be marked before the start of harvest to distinguish immigrants from residents in the harvest area. A review of migration in vertebrate populations (Fig. I.3c from the *General introduction* and *Appendix I.1*) revealed that more than 75% of the experimental removal studies used a single massive removal which prevents conclusions about density dependence.

The compensatory immigration model allows testing for the relative influence of the size of the protected population ($N_{P,0}$), behavioral interactions leading to density dependence (θ and $N_{P,0}$) and physical properties of the landscape (*i.e.* relative habitat quality and functional connectivity) that could affect the initial rate of replacement of harvested individuals (M_0) on immigration. Very few studies have provided empirical evidence for the effect of limiting factors other than density on immigration and even fewer have tested for the effects of multiple factors on immigration in response to harvest (Fig. I.2b from the *General introduction,* but see Haynes and Cronin 2003; Haynes and Cronin 2004). Studies evaluating the effect of independent empirical measurements of functional connectivity and relative habitat quality on immigration are needed to test immigration function and to improve the design of protected areas in order to improve management (see *Chapters 1, 2* and *4*). To quantify functional connectivity, translocations and gap-crossing experiments in terrestrial (Awade and Metzger 2008; Bakker and Van Vuren 2004; Bélisle and Desrochers 2002; Bosschieter and Goedhart 2005) and marine organisms (*Chapter 1*) can be particularly useful to identify the minimal width of a barrier to movement (*i.e.* the barrier width at which the probability of crossing the barrier drops below some defined probability of crossing) and could be used as starting point to design indexes of functional connectivity for a variety of taxa. To evaluate the relative habitat quality between the harvest and protected area, known variables influencing fitness for a given organism such as high cover and food availability, could be quantified and compared for their relative abundance in harvest and protected area. Also, individual characteristics, such as body size, may also be used as a surrogate for habitat quality (*Chapters 2* and *4*). In many density-manipulation studies, vacant territories held by dominant individuals are recolonized faster and/or at a higher rate than territory held by subordinate and smaller individuals in many taxa (Loveridge et al. 2007; Robinson et al. 2008; Lin and Batzli 2001; Jacquot and Solomon 2004; Newton 1992; 1998; Studds and Marra 2005; Hourigan 1986; Cheney and Côté 2003; Lowry and Suthers 2004; McDougall and Kramer 2007).

Another limiting factor that is not considered in this study, but could affect immigration independently from density and limiting mobility factors is the effect of season. The benefit of moving may be related to specific period of the year for some species, such as the breeding period in birds, where the value of defending a territory is not beneficial after that time (Newton 1998) or when the amount of temporal and spatial variation in food and its predictability is low in small mammals (Andreassen and Ims 2001).

In the future, the compensatory immigration model can be expanded in two ways. First, it would be interesting, as a more global management goal, to develop and test a multispecies compensatory immigration model by integrating competition for space, change in behavior and predation among species. As an example, this would be particularly useful for the management of the caribou (*Rangifer tarandus caribou*), wolves (*Canis lupus*), and moose (*Alces alces*) species assemblage in Canada. The caribou is a threatened species that suffer from habitat alteration and industrial development that has favored recent expansion of wolf (its main predator) and moose (competitor and wolf alternative prey) populations (James et al. 2004; Seip 1992). A multispecies compensatory immigration model would be particularly suitable for the management of coral reef fish community where intense fishing altered considerably complex interactions among species, mainly in large apex predators and large herbivores (McClanahan 1994; Brown-Saracino et al. 1994; Russ 2002). Second, the compensatory immigration model could be applied in a broader context and at a larger temporal scale by evaluating the effect of different short-term immigration functions, varying in the strength of their density dependence, on reproduction and survival of the population in the following year. Depending on the exact nature of density dependent immigration and its effect on reproduction and survival, the effects on metapopulation dynamics and persistence can be quite different (Amarasekare 2004; Saether, Engen, and Lande 1999).

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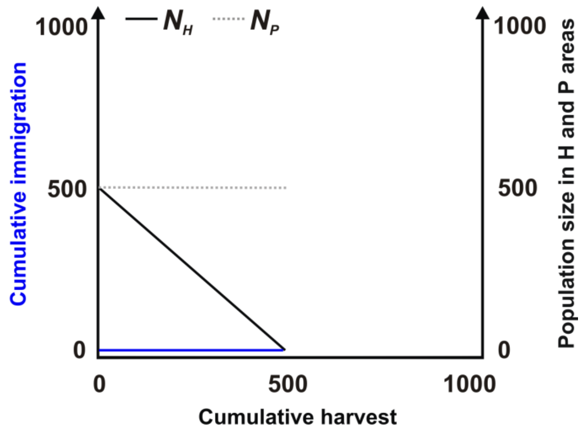
Table 3.1. Model parameters and variables in source-sink models using three assumptions about immigration (*i.e.* no immigration, free immigration and oriented immigration) and in the compensatory immigration model used to predict immigration in response to harvest.

Description of the parameters and variables	Symbol
Source-sink models	
Population size in the harvest area at time t	$N_{H,t}$
Population size in the protected area at time t	$N_{P,t}$
Harvesting pressure (proportion of harvested individuals from the harvest area at time t)	H_H
Mobility factor from the protected to the harvest area (proportion of individuals from the protected area moving from the protected area to the harvest area at time t)	$M_{P:H}$
Mobility factor from the harvest to the protected area (proportion of individuals from the harvest area moving from the harvest area to the protected area at time t)	$M_{H:P}$
Compensatory immigration model	
Cumulative net immigration in the harvest area (cumulative number of immigrants)	I_H
Initial rate of replacement of harvested individuals (proportion of the harvested individuals that are replaced by immigrants)	M_0
Cumulative total yield (cumulative number of harvested individuals)	Y
Initial population size in the protected area	$N_{P,0}$
Strength of density dependence at low cumulative harvest	θ

a) No immigration (immobile organisms)



b) Immigration from density-dependent habitat selection (complete mobility)

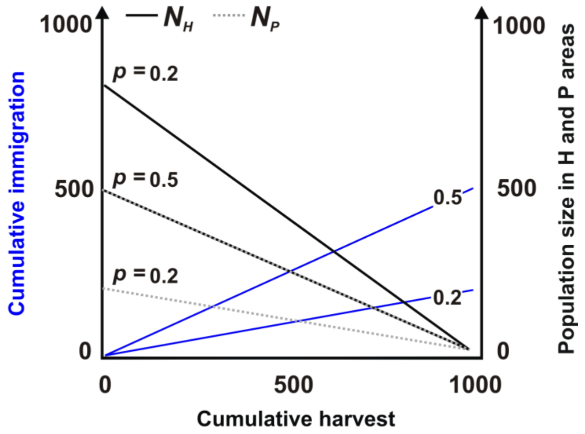


Figure 3.1. Predictions from source-sink dynamics model assuming a) no migration between harvest and protected areas (immobile organisms) and b) migration from density-dependent habitat selection (complete mobility). Blue lines represent cumulative net immigration from protected to harvest area in relation to cumulative harvest. Solid black lines represent population size in the harvest area (N_H) and dotted grey lines represent the population size in the protected area (N_P) in relation to cumulative harvest. For simulations in panel a, we used a fixed harvesting pressure (*i.e.* proportion of the population harvested) of 0.1 with $N_{H,0} = N_{P,0} = 500$. In panel b, the proportion of the total population that is located in the protected area is controlled by p ($N_{P,t}/ N_{P,t+} N_{H,t}$) and two p values are presented (p = 0.2 and 0.5). When p = 0.5, the line for population size in the harvest area overlap with the line for the population size in the protected area.

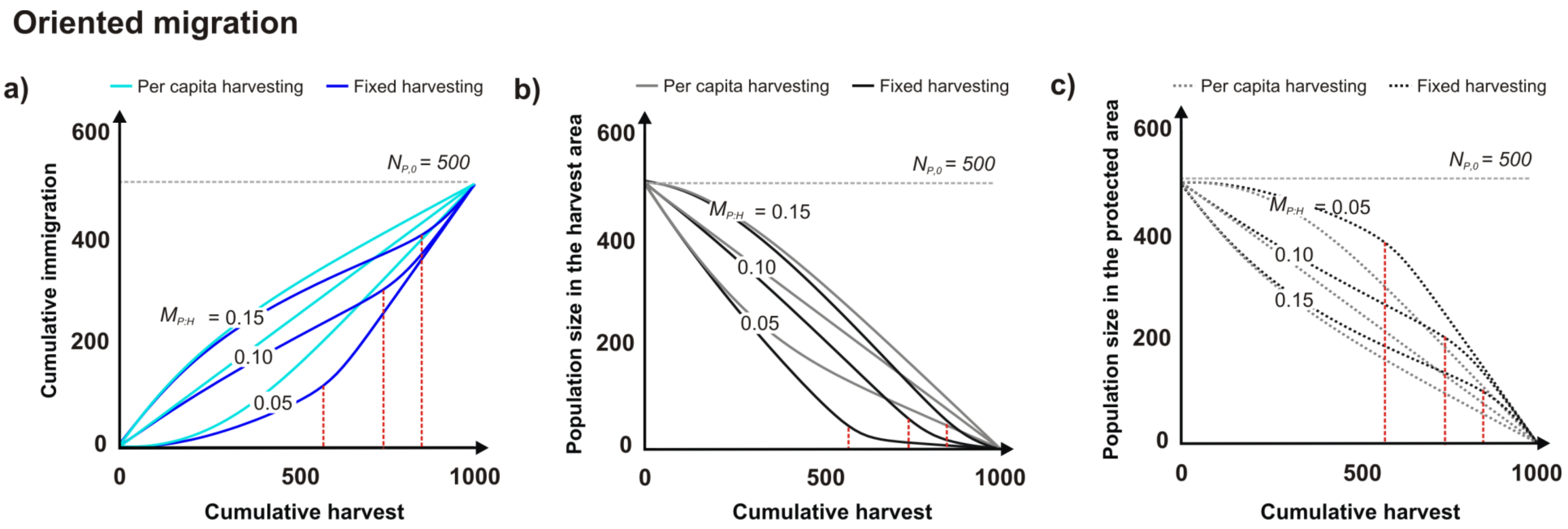


Figure 3.2. Predictions from source-sink models assuming oriented migration between harvest and protected areas. a) Blue lines represent cumulative net immigration from protected to harvest area in relation to cumulative harvest with three rates of transfer from the protected to the harvest area ($M_{P:H}$; 0.15, 0.10, and 0.05) and two harvesting strategies (per capita harvesting; light blue and fixed harvesting; dark blue). Solid black lines (b) represent population size in the harvest area (N_H) and dotted grey lines (c) represent the population size in the protected area (N_P) in relation to cumulative harvest with three rates of transfer from the protected to the harvest area and two harvest strategies. Vertical red dotted lines represent the cumulative harvest level at which each harvest removes fewer individuals than the number determined by the fixed harvesting strategy because of the small size of the remaining population in the harvest area. Harvesting pressure (*i.e.* proportion of the population harvested) was set at 0.1, and the rate of transfer from the harvest to the protected area ($M_{H:P}$) was kept constant at = 0.05. Initial total population size = 1000 and the proportion of the population in the protected area = 0.5.

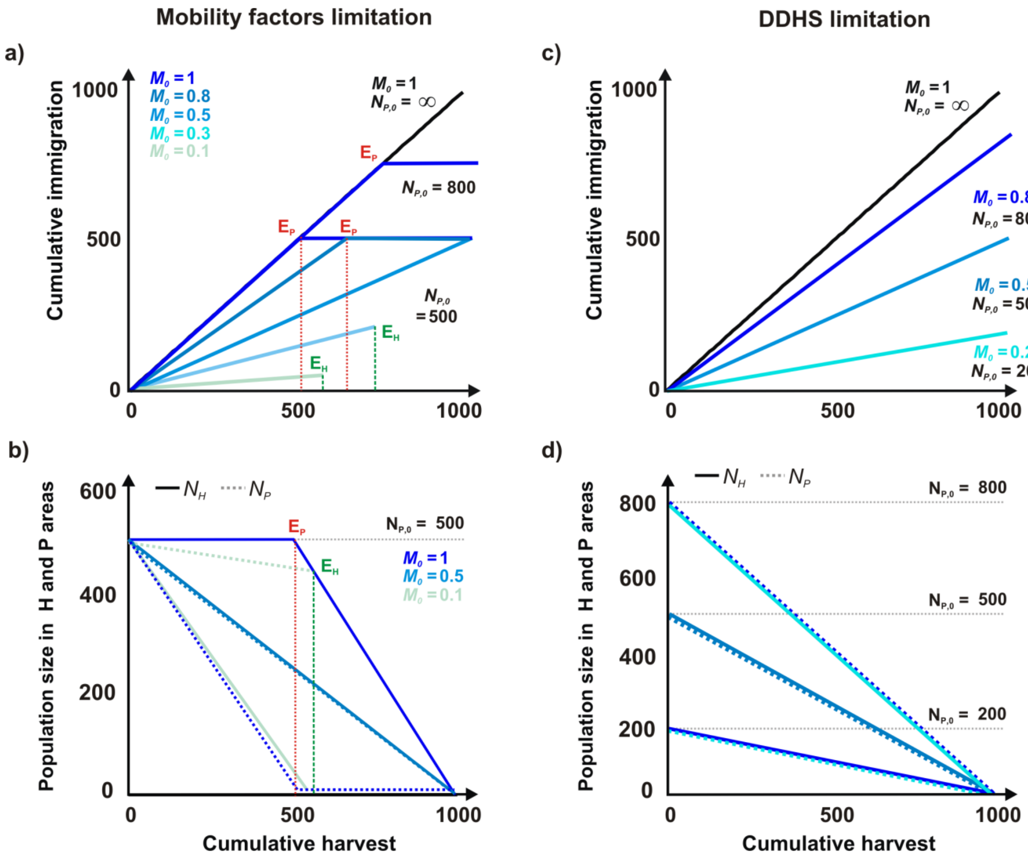


Figure 3.3. Predictions from the compensatory immigration model with two biological situations leading to the partial replacement limitation scenario: mobility factor limitation and density-dependent habitat selection limitation. For all simulations, harvesting pressure (*i.e.* proportion of the population harvested) was set at 0.1 and the initial total population size = 1000. Mobility factor limitation: a) cumulative immigration in relation to cumulative harvest with varying M_0 (M_0 = 0.1, 0.3, 0.5, 0.8, 1) for $N_{P,0}$ = 500 and 800 and ∞ and b) population size in the harvest (H) and protected (P) areas in relation to cumulative harvest with varying M_0 (M_0 = 0.1, 0.5, 1) for $N_{P,0}$ = 500. E_P represents extinction in the protected area and E_H represents extinction in the harvest area. Density-dependent habitat selection limitation: c) cumulative immigration in relation to cumulative harvest with varying M_0 (M_0 = 0.2, 0.5, 0.8, 1) and d) population size in the harvest and protected area in relation to cumulative harvest with varying M_0 (M_0 = 0.2, 0.5, 0.8). In density-dependent habitat selection limitation the initial rate of replacement of harvested individuals is dependent of the size of the protected population ($M_0 = N_{P,0}/(N_{P,0+} N_{H,0})$).

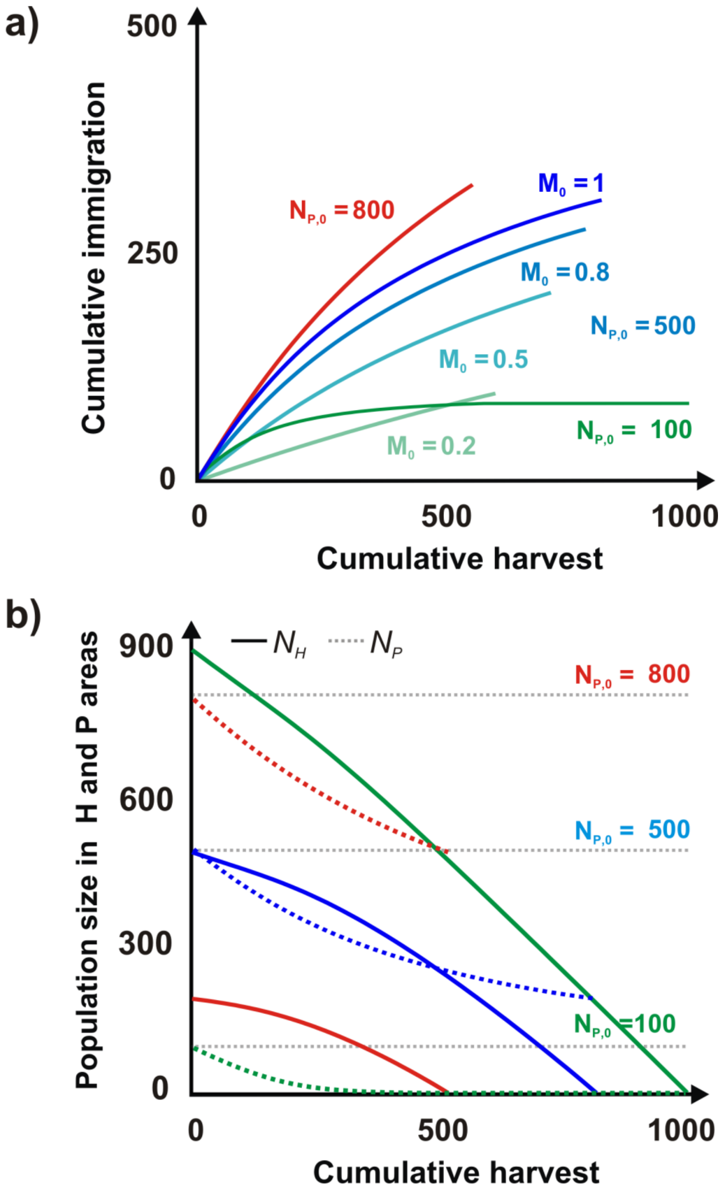


Figure 3.4. Predictions from the immigrant limited scenario. a) Cumulative immigration in relation to cumulative harvest with varying $N_{P,0}$ ($N_{P,0}$ = 100, 500 and 800) and varying M_0 (M_0 = 0.2, 0.5, 0.8, 1) when $N_{P,0}$ = 500. b) Population size in the harvest and protected area in relation to cumulative harvest with varying $N_{P,0}$ ($N_{P,0}$ = 100, 500 and 800) for M_0 = 1. For all simulations, harvesting pressure (*i.e.* proportion of the population harvested) was set at 0.1 and the total initial population size = 1000.

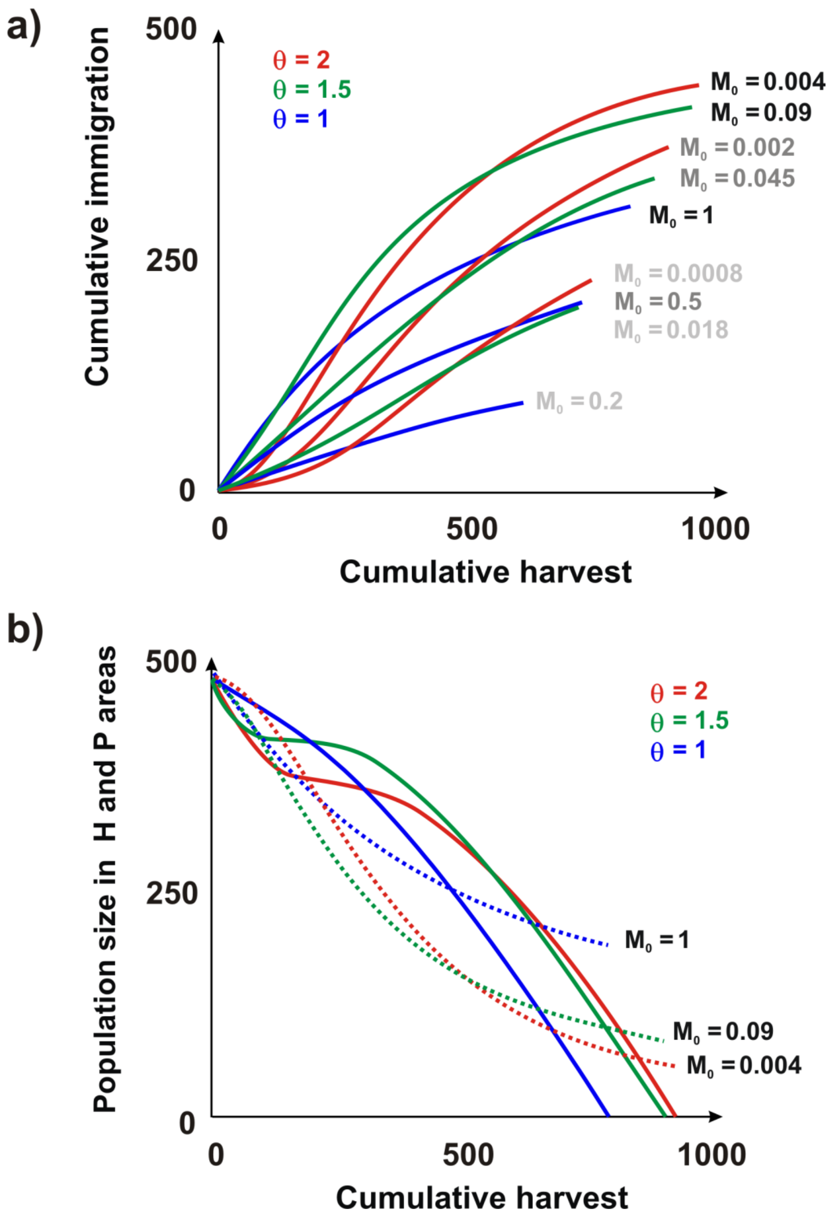
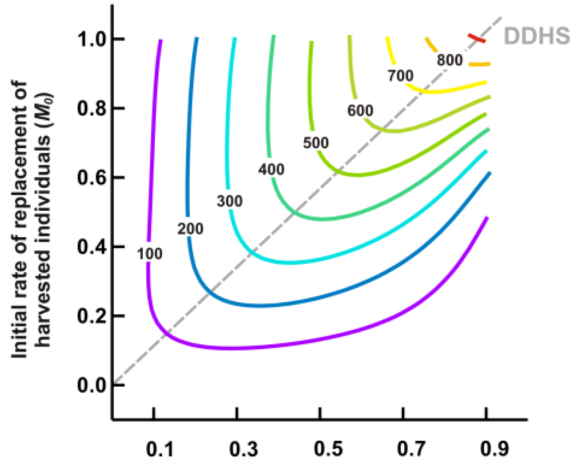


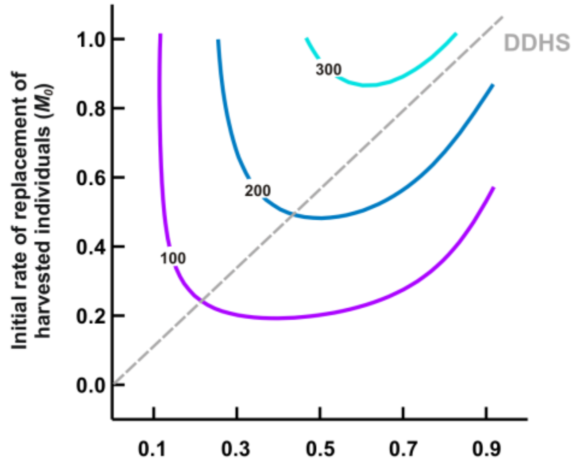
Figure 3.5. Predictions from the complex density-dependent limitation scenario. a) Cumulative immigration in relation to cumulative harvest with varying M_0 and varying θ (1, 1.5, 2) when $N_{P,0} = 500$. b) Population size in the harvest and protected area in relation to cumulative harvest with varying θ (1, 1.5, 2) when $N_{P,0} = 500$ and $M_0 = 1$. For all simulations, harvesting pressure (*i.e.* proportion of the population harvested) was set at 0.1 and the total population size = 1000.

Figure 3.6. Total cumulative immigration (indicated by the colored contour lines) predicted by a) the partial replacement limitation, b) the immigrant limitation and c) the complex density-dependent limitation scenario with varying the size of the protected population (*i.e.* the proportion of the total population in the protected area) and the initial rate of replacement of harvested individuals (M_0). In the lowest panel, predictions from the complex density-dependent limitation scenario with variable strength of density dependence ($\theta = 2$; left y-axis and bold contour lines) and ($\theta = 1.5$; right y-axis and dotted contour lines) are presented. The grey dashed lines in the three panels represent the prediction from the density-dependent habitat selection model (DDHS). For all simulations, harvesting pressure (*i.e.* proportion of the population harvested) was set at 0.1 and the total population size = 1000

a) Partial replacement limitation



b) Immigrants limitation



c) Complex density-dependent limitation

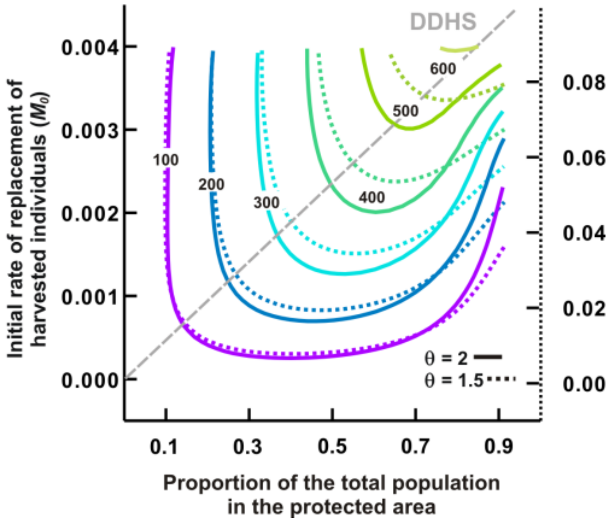
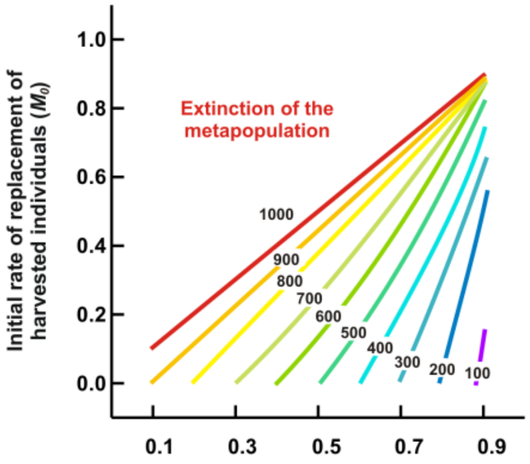
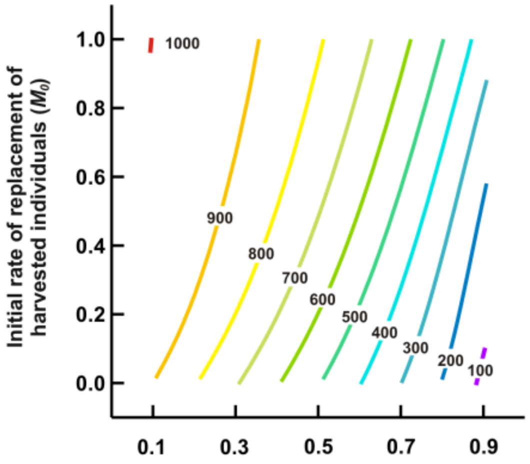


Figure 3.7. Total proportional yield (*i.e.* total number of harvested individuals and indicated by the colored contour lines) predicted by a) the partial replacement limitation, b) the immigrant limitation and c) the complex density-dependent limitation scenario with varying the size of the protected population (*i.e.* the proportion of the total population in the protected area) and the initial rate of replacement of harvested individuals (M_0). In the lowest panel, predictions from the complex density-dependent limitation scenario with variable strength of density dependence ($\theta = 2$; left y-axis and bold contour lines) and ($\theta = 1.5$; right y-axis and dotted contour lines) are presented. For all simulations, harvesting pressure (*i.e.* proportion of the population harvested) was set at 0.1 and the total population size = 1000.

a) Partial replacement limitation



b) Immigrants limitation



c) Complex density-dependent limitation

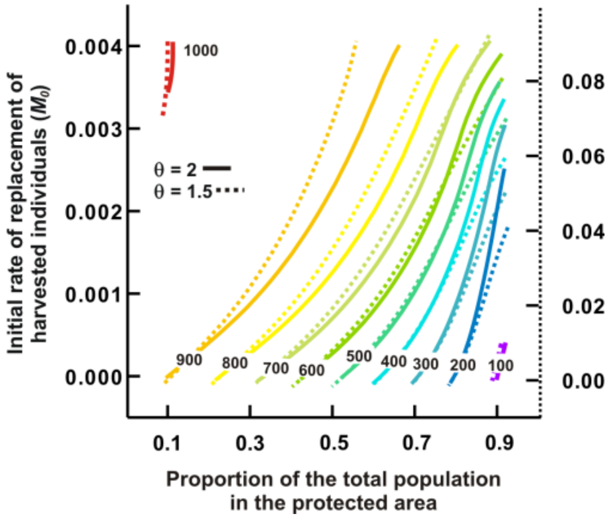
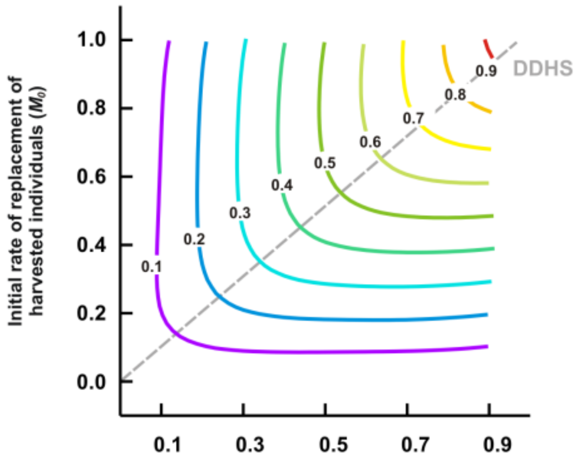
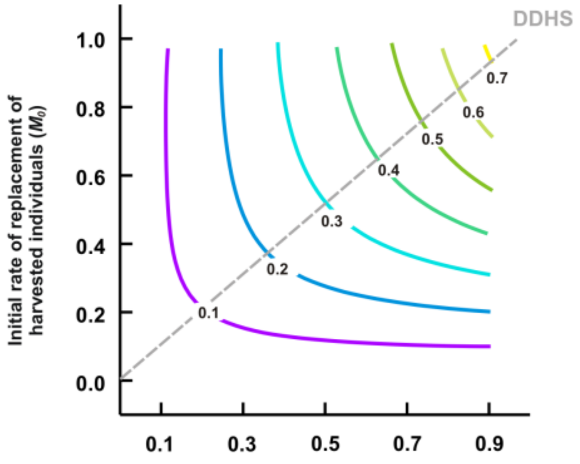


Figure 3.8. Contribution of immigration to total proportional yield (*i.e.* proportion of the total yield that is composed of immigrants and indicated by the colored contour lines) predicted by a) the partial replacement limitation, b) the immigrant limitation and c) the complex density-dependent limitation scenario with varying the size of the protected population (*i.e.* the proportion of the total population in the protected area) and the initial rate of replacement of harvested individuals (M_0). In the lowest panel, predictions from the complex density-dependent limitation scenario with variable strength of density dependence ($\theta = 2$; left y-axis and bold contour lines) and ($\theta = 1.5$; right y-axis and dotted contour lines) are presented. The grey dashed lines in the three panels represent the prediction from the density-dependent habitat selection model (DDHS). For all simulations, harvesting pressure (*i.e.* proportion of the population harvested) was set at 0.1 and the total population size = 1000.

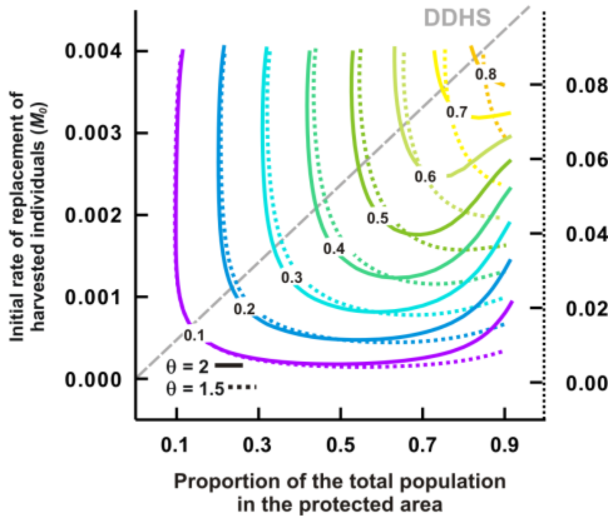
a) Partial replacement limitation



b) Immigrants limitation



c) Complex density-dependent limitation



CHAPTER 4:

SPILLOVER IN AN EXPERIMENTAL MODEL FISHERY:

INFLUENCE OF DENSITY, HABITAT QUALITY AND FUNCTIONAL CONNECTIVITY ON IMMIGRATION FROM PROTECTED TO HARVESTED AREAS

LINKING STATEMENT 4

Previous studies of immigration have been limited by both the theoretical framework and the lack of replicated, controlled studies in which immigration is measured while density varies. In *Chapter 4*, I addressed the second deficiency by carrying out an experimental, incremental, localized reduction of damselfish populations on seven sites in a naturally fragmented habitat and monitored two control populations. I tested the ability of the compensatory immigration model developed in *Chapter 3* to predict the patterns of immigration from a protected area in response to harvest. I used findings from *Chapters 1* and *2* to develop and calibrate empirical independent indices of functional connectivity and of habitat quality and to examine their roles as limiting factors to immigration.

ABSTRACT

Net immigration of fish from protected to harvest areas, called the ‘spillover’ effect, influences the effectiveness of marine protected areas as both management and conservation tools. However, little information is available about factors limiting immigration in vertebrate populations. To examine how local density, habitat quality, functional connectivity and size of adjacent protected populations affect immigration, we carried out an experimental, incremental, localized reduction of damselfish populations on seven sites in naturally fragmented coral reef habitat and monitored two control populations. Immigration occurred almost exclusively in response to harvest, occurred over the whole range of densities and eventually declined to zero. Using a compensatory immigration model (*Chapter 3*) to predict the outcome of alternative scenarios that differed in factors limiting immigration, we examined the relationship between cumulative immigration and cumulative harvest. Models that included partial replacement of fished individuals fit much better than models that included either no replacement or complete replacement. In three sites, the best model also included density dependence that changed in direction and magnitude over the harvesting sequence. A limitation analysis indicated that factors associated with partial replacement of fished individuals were more important than factors associated with density dependence and size of adjacent protected populations. The total yield and the proportion of immigrants replacing fished individuals on experimental sites were correlated more strongly with the combined effects of relative habitat quality and connectivity than with either variable alone or with the size of the protected population. Immigration to harvest areas in these damselfish populations is primarily influenced by the ability of individuals in adjacent areas to detect and move to vacated territories and by the potential improvement in territory quality that they could achieve by doing so. In addition, immigration can be modulated by social interactions between individuals in both the removal area and the adjacent populations. This study illustrates how concepts of density dependence and limiting factors used in studies of recruitment can be applied to immigration, suggests the

need for more complex transfer functions incorporating density dependence in metapopulation models, and provides one of the first analyses of multiple factors potentially limiting immigration in a natural population.

INTRODUCTION

Marine protected areas (MPAs) have been recognized worldwide for their capacity to increase the abundance, biomass and diversity of fishes (Gell and Roberts 2003, Halpern and Warner 2002). In the last two decades, MPAs have also been promoted for their benefits to fisheries in adjacent waters (Hastings and Botsford 1999, Polacheck 1990, Roberts et al. 2001) by being a more sustainable and stable strategy to manage fished populations in the presence of uncertainty compared to extracting fixed-quota or a fixed-effort each year (Hall 1998, Hastings and Botsford 1999). Higher fish abundance and biomass in MPAs are suggested to sustain local fisheries by increased larval production (Almany et al. 2007, Jones et al. 2005, Russ 2002) and by a net emigration of post-settlement adults and subadults from MPA into fished areas, a process called ‘spillover’ (Gell and Roberts 2003, Halpern et al. 2009, McClanahan and Mangi 2000, Zeller and Russ 1998).

There is increasing indirect evidence of spillover in response to fishing in the form of declining gradients in fish abundance (Aitor Forcada et al. 2009, Francini-Filho and Moura 2008, Harmelin-Vivien et al. 2008, Russ and Alcala 1996), fish catches and accumulations of fishers close to the MPAs (Galal et al. 2002, Goni et al. 2008, Murawski et al. 2005, Rakitin and Kramer 1996, Russ et al. 2004). Indirect evidence of spillover is also available from smaller scale studies that observed post-settlement fish movements across MPA boundaries (Chapman and Kramer 2000, Samoilys 1997, Zeller et al. 2003) and larger scale studies that observed recolonization of depopulated reefs (Brock et al. 1979, Lewis 1997, Syms and Jones 2000). Evidence is indirect because we cannot confirm that movements are in response to a change in density. Despite accumulating indirect evidence of spillover, fisheries benefits are controversial because clear direct empirical evidence of spillover is lacking (Gell and Roberts 2003, Roberts et al. 2001).

In addition to a lack of direct empirical evidence of spillover, very few experiments have been carried out to investigate the mechanisms involved in spillover (but see Abesamis and Russ 2005, Zeller et al. 2003) or to investigate which factors increase or decrease its magnitude. Spillover may result from daily movements within the home range, seasonal migration and ontogenetic habitat shifts. These movements are independent of the gradient of density between the fished and protected area. Spillover may also occur in response to density as a result of home range relocations (*Chapter 2*, Kramer and Chapman 1999, Pelletier and Mahevas 2005, Russ 2002). Home range relocations can be density-independent (*i.e.* constant rate of movement with decreasing density) if they result from random movement or density-dependent habitat selection which acts in a manner analogous to molecular diffusion (Kramer 1997, Kramer and Chapman 1999; Russ 2002). Home range relocations would be density-dependent (*i.e.* increasing and/or decreasing rate of movement with decreasing density) if they result from competitive interactions in both the harvest and protected area (Kramer and Chapman 1999, Sanchez Lizaso et al. 2000, Sutherland et al. 2002). Although density dependence is a major theme in sustainable harvesting theory and considerable theoretical interest has been devoted to population regulation via density-dependent movement (Saether et al. 1999, Travis and Dytham 1998), empirical evidence is scarce and few experiments have been designed to detect density dependent movement (Hixon and Webster 2002, Matthysen 2005).

Factors other than declining density in the fished area have been suggested to affect the magnitude of spillover. The size of the adjacent protected population can affect both the magnitude and rate of spillover. In removal studies on freshwater fish and small mammals (Beckley 1985, Grodzinski et al. 1966, Gundermann and Popper 1975) large population size in the protected area favored high magnitude of recolonization of depleted areas. Furthermore, in these studies the rate of immigration declined over time. A decreasing rate of immigration can result from lower benefits of immigrating into low density populations (Kuussaari et al. 1998, Stamps 1991). Potential immigrants might include all individuals in a protected area or just the ones near the boundary, depending on the mobility of the species and the size of the protected area (Rakitin and Kramer 1996). High relative habitat quality in the fished area than in the MPA should favour spillover. There should be strong selection for individuals that can recognize high habitat quality and move accordingly, but relocation should occur only when the benefits of the new home ranges outweigh the costs of energy expenditures, risk of predation and agonistic interactions incurred during prospecting behavior and the relocation itself (*Chapters 1 and 2*, Kramer and Chapman 1999, Kramer et al. 1997, Wiens 2002, Zollner and Lima 1999). Small reef fish species have been observed to relocate quickly into neighboring vacant territories that had been held by large, dominant individuals (Bartels 1984, Cheney and Côté 2003, Hourigan 1986, Itzkowitz 1978, McDougall and Kramer 2007). Finally, spillover in the fished area will be possible only if landscape functional connectivity (*i.e.* the degree to which the landscape facilitates or impedes movement; Taylor et al. 1993) allows the detection of alternative habitats and vacancies and movement between the fished and the MPA (Chapman and Kramer 2000, Forcada et al. 2009, Rakitin and Kramer 1996, Warner and Hoffman 1980). Weak connectivity is likely to limit spillover even if the harvest area is highly attractive and there is a strong density gradient between the fished and MPA.

In this study, we examined whether spillover, *i.e.* net immigration of fish, occurred as we gradually fished two small coral reef fishes from seven sites. Sites consisted of a 'fished area' surrounded by adjacent undisturbed populations ('protected areas'). We also monitored fish populations in two control sites. We chose our sites to be of similar size, area of reef and initial population size in the fished area but to vary in relative habitat quality and in functional connectivity between the fished area and the nearby protected area and in population size in the protected area. We also examined how these three factors affected immigration rate in the context of harvesting. To do so, we applied the compensatory immigration model developed in *Chapter 3* and compared the observed relationship between cumulative immigration and cumulative harvest for each site with that predicted by six model scenarios that varied in the inclusion of potential limiting factors. To assess the relative effect size of the limiting factors to spillover in the set of seven sites, we carried out a limitation analysis (Schmitt et al. 1999). The limitation approach evaluates absolute and relative deviations between observed and predicted values as a function of cumulative harvest for all sites for each scenario. Finally, we examined how among-site variation in total yield (*i.e.* number of harvest individuals divided by the initial population size in the harvest area) and the replacement rate of fished individuals can be explained by measured values of a relative habitat quality and functional connectivity between the harvest and protected area and by the size of the protected population.

METHODS

Study sites

Our experiment was conducted over three consecutive years (2005-2007), from April/May to August/September on five fringing reefs along the west coast of Barbados (13°10'N, 59°38'W). Fringing reefs in Barbados extend to a maximum of 200 m offshore and are composed of three distinct zones (the back reef, the crest, and the spur and groove zone). We focused our study in the spur and groove zone which is characterized by finger-like, seaward extensions of the main reef with numerous small patches of reef separated by sand (Fig. 4.1; Lewis 1960). As a naturally fragmented landscape, the spur and groove zone is particularly suitable for testing the effect of functional connectivity on damselfish movement (see *Chapter 1*). Seven sites were chosen to be experimental (removal experiment) and two sites were used as controls. Our nine sites (Sandy Lane; SL1, SL2, South Bellairs; SB1, North Bellairs; NB1, Heron Bay; HB1, HB2, HB3 and HB4 and Bachelor Hall; BH1) were located at depths ranging from 4 to 7 m. Each consisted of a rectangular fished area surrounded by a 10-m wide protected area (Fig. 4.1). The two control sites (SB1 and NB1) were located in the Barbados Marine Reserve where fish collection is forbidden except for cast netting for clupeids in shallow water. Five sites (BH1, HB1, HB2, HB3 and HB4) were located to the north of the Reserve and SL1 and SL2 were to the south.

Experimental sites were selected so that fished area (mean ± SD; range: 147.8 ± 36.6 m^2; 93.1 – 217.83 m^2; coefficient of variation (C_v) = 21%; Table 4.1), number of damselfish in the fished area (57.3 ± 8.8 damselfish; 52 – 74 damselfish, C_v = 20%; Table 4.1), area covered with reef in the fished area (91.8 ± 18.9 m^2; 91.5 – 121.0 m^2, C_v = 21%) were relatively similar among sites. In contrast, to examine effects of limiting factors on immigration, the seven sites varied in number of damselfish in the protected area (151.7 ± 128.8 damselfish; 9 - 420 damselfish, C_v = 85%; Table 4.1), in habitat quality between the fished and protected area with the *RHQ* index (explained below; -0.05 ± 0.67 cm; -1.096 – 0.632 cm, C_v = 64%, Table 4.1) and in functional connectivity between the fished and protected area. As surrogates for landscape functional connectivity, we used two indexes: the area covered with reef in the protected area (313.0 ± 147. 1 m^2, 52.7 – 451.8 m^2, C_v = 46%, Table 4.1) and the WPI_B (Weighted proportion index explained below; 0.246 ± 0.149, 0.003 - 0.437; C_v = 61%; Table 4.1). Limiting factors were not strongly correlated with each other. The number of damselfish in the protected area is correlated with the area covered with reef (Spearman correlation coefficient; r^2 = 0.643) and with WPI_B (r^2 = 0.588) and not correlated with *RHQ* (r^2 = 0.106). Area covered with reef is mildly correlated with *RHQ* (r^2 = 0.418) and highly correlated with WPI_B (r^2 = 0.895).

Study species

Longfin (*Stegastes diencaeus*) and dusky damselfish (*S. adustus*) are abundant, intra- and interspecifically territorial damselfish that reach saturation in the spur and groove zone on fringing reefs in Barbados. They provide an excellent opportunity to quantify the relative effect of limiting factors to immigration following harvesting in a natural setting and on a small spatial and temporal scale. They are highly philopatric with very small territories and low mobility and despite their apparent very stable distribution, they respond quickly to vacancies in higher habitat quality by relocating their territories (*Chapter 2*, Bartels 1984, Cheney and Côté 2003, Hourigan 1986, Itzkowitz 1978, McDougall and Kramer 2007). They are also easy to observe and tolerate close proximity with divers without changing their behavior. Both species are strictly diurnal, resting in holes on the reef at night.

Adult longfin damselfish are slightly larger (mean total length ± SD; 8.98 ± 1.95 cm, N = 443), more aggressive (K. Turgeon, unpublished data) and preferentially inhabit the deeper spur and groove zone. Dusky damselfish (7.16 ± 1.04 cm, N = 125) inhabit the crest zone and the upper portion of the spur and groove zone, partially overlapping with longfin damselfish. In both species, males grow to larger sizes than females, are usually more aggressive and provide paternal care for eggs. Male longfin damselfish often occupy the edges of the reef where the substratum provides more nest sites; females tend to be found away from the edges (Cheney and Côté 2003, Robertson 1984). Both species spawn every month, year-round (Robertson et al. 1993, Thresher 1984). Larvae disperse in the plankton and then settled as juveniles in or near adult habitat. The peak in larval settlement is just after the new moon in longfin damselfish and just before the new moon in dusky damselfish (Robertson 1992). Juveniles of both species are brightly colored and distinctive (yellow in longfin damselfish, purple-orange in dusky damselfish) changing to a more similar, uniform dark brown to black color (Robertson and Allen 1981) before sexual maturity (K. Turgeon, *unpublished data*). In our system, longfin damselfish sexually mature at approximately 9.3 cm, while dusky damselfish mature at about 7.1 cm total length (Logistic regressions; t-ratio =-7.262 for longfin and -6.64 for dusky damselfish, p-values < 0.001 for both species; N = 235 for longfin and N = 157 for dusky damselfish). Both sexes vigorously defend exclusive territories that provide food in the form of a cropped algal mat, refuges in the form of holes in the reef and, for males, nest sites in the form of a vertical area of coralline rock or a small hole (Cheney and Côté, 2003). Territories of both species are small (territory area; 1.14 ± 0.50 m^2 in longfin damselfish, N = 345 and 0.79 ± 0.35 m^2 in dusky damselfish, N = 130) and contiguous on suitable hard substrate. Territory acquisition for both species appears to be vital for survival and reproductive success; there is no evidence of “floaters” (Bartels 1984, McDougall and Kramer 2007). Territories are very stable in established populations, but territories of experimentally fished individuals are visited by neighbors after as little as 3 min, and high quality territories can be reoccupied within 10 to 30 min (Cheney and Côté 2003, McDougall and Kramer 2007). Damselfish are not targeted by fisheries in Barbados, so we assume that habitat adjacent to our treatment area (fished area) can be considered as "protected areas".

Damselfish mapping

The site-attachment and very small territory size of damselfish permit us to obtain very complete information about their distribution in the fished and protected areas. We tagged all residents, defined as individuals in the fished area > 5 cm total length that were actively defending a territory, prior to density manipulation and territory mapping. This allowed us to recognize immigrants, defined as individuals with territories outside the fished area at the start of manipulation that established territories in the fished area during the manipulation. We caught individuals with a modified cast nest and tagged them underwater close to their territory to reduce stress. We marked damselfish with VIE tags (Northwest Marine Technology) using 5 colors (yellow, green, red, orange and white) and 12 tag positions resulting in at least 60 different tags per site. We sexed fish underwater by observing the genital papillae, measured them to the nearest mm, and released them on their territories after approximately 30 s. Sexual maturity was assessed by laboratory examination of the gonads of individuals fished from the population. Tagging usually required two dives of 2 h (1 day) per site. Of 649 damselfishes tagged, we observed only 12 disappearances following tagging sessions (2%) due to post-tagging mortality or emigration.

Before reducing the density, we mapped territories of all damselfish in the fished area. This was done at high resolution to allow us to quantify territory relocations in relation to density and habitat quality for the companion manuscript (*Chapter 2*). We created a 1 x 1 m XY grid covering the entire site, took an underwater digital picture of each 1 x 1 m cell, and assembled the pictures using graphical software (Corel PhotoPaint 12) to produce a mosaic covering the entire site which was then georeferenced in GIS software (MapInfo Professional 6.5). Territory boundaries of each resident were evaluated during an observation period of at least 10 min after which we marked the edges of the space used with 8-10 bleached coral pebbles. This short duration was sufficient because damselfish move rapidly and regularly over their entire small territories. Although other researchers such as Cheney and Côté (2003) used somewhat longer periods (15 min) to delimitate territory boundaries, we found that that 7 to 8 min was generally sufficient so that allowing 10 min made it unlikely that we missed parts of the territories. To ensure a precise territory position on the georeferenced site map we took a digital picture of each territory and noted useful landmarks surrounding the territory. Territory boundaries were drawn freehand on the mosaic layer of each site using the digital pictures and markers. For each site, we produced a georeferenced layer of all resident damselfish territories.

The adjacent protected area was defined as habitat within 10 m of the edges of the fished area (Fig. 4.1). Potential migrants in the protected area were not tagged because we only needed to estimate the population size and body size distribution We mapped the distribution of all potential migrants by creating a 2 x 2 m grid using an underwater compass and measuring tape, marking corners with flagging tape attached to weights. Within each 2 x 2 m cell we drew the distribution of substratum types (sand, rubble, rock, eroded dead coral, live coral identified to the species) on a PVC slate. We observed all damselfish territories for 2-3 min to ensure that the observed focal individual was actively defending, then drew the territory distribution over the substratum layer on the PVC slate. For each damselfish, we noted the species, size (nearest 0.5 cm) and sex whenever possible by observing courtship forays and displays or by locating a nest site for males. The PVC slates were subsequently scanned and georeferenced.

Experimental density manipulation and observation of immigration

All sites were observed for two weeks before starting the removal and for approximately five weeks during the experimental manipulation. We applied a constant removal pressure to each of the seven fished areas by means of a series of removal events at 2-3 day intervals. In each event we randomly removed a number of residents and immigrants equal to 15% of the initial population of damselfish > 5 cm total length, continuing until we created a local extinction on the site. Removal events started between 08h30 and 09h00 and required 20 – 45 min. Experienced divers fished the pre-selected individuals using modified cast nets and micro spears. Captured fish were placed individually in plastic bags (Ziploc© type) with an ID tag, immediately anesthetised using an overdose of CO_2 (Eno © in seawater), placed on ice and brought back in the lab. In the lab, we recorded the weight (g), total length (cm), sex and maturity of each fished individual. After the removal, six territory monitoring observation periods were completed (*i.e.* 30, 60, 360 and 480 min after removal in the same day and 840 and 1200 min after removal in the day following the removal, excluding the inactive nocturnal period (about 10 h from 19:00 to 05:00) to document territory shifts and relocations (see *Chapter 2* for detailed methods). The day after removal, we mapped all occupied territories and noted which territories were occupied by immigrants. Territory recolonisation in longfin damselfish occurred within one day in previous studies (Cheney and Côté 2003, McDougall and Kramer 2007) and within 6 h in this study (median 360 min; 95% CI = 107 – 1750 min) excluding the inactive nocturnal period (about 10 h from 19:00 to 05:00). We thus assumed that the fish distribution was close to a new equilibrium the day after removal. Six to seven days after we fished the last residents and immigrants, sites were visited to ensure the absence of any new immigrants. If new immigrants were found, they were fished and the site was visited two days after until no new immigrants were observed on the site. The gradual, constant removal pressure resulted in 8 to 14 removal events per site, depending on the number of immigrants. The two control sites were observed for a comparable period.

Empirical measurement of limiting factors

Number of potential immigrants in the protected area

We assumed that the number of potential immigrants under the influence of harvesting includes all individuals within 10 m of the boundary of the fished area.

This was based on the 95th percentile of 630 observations of distances that we observed damselfish to move during spontaneous exploratory movements outside their territories (K. Turgeon, *unpublished data*).

Relative habitat quality between the fished and protected area (RHQ)

As an index of relative habitat quality (*RHQ*), we used the difference in mean damselfish body size between the fished and protected areas (*equation 1*). This assumes that body size is a correlate of territory quality in saturated populations such as those at our study sites. Body size is widely recognized to affect resource holding potential and dominance in fish (Candolin and Voigt 2001, Lindström 1992), which should influence their ability to obtain and hold more attractive territories. Territories occupied by larger damselfish are more likely to be reoccupied and are occupied more quickly after a removal than territories occupied by smaller damselfish (*Chapter 2*). For each site, we calculated the *RHQ* index for each species separately and then calculated a weighted mean based on relative abundance. Positive values represent a relatively attractive fished area whereas negative values indicate a relatively attractive protected area.

Equation 1: Relative habitat quality index (RHQ)

$$RHQ = \left(\frac{\sum_{i=0}^{N} BS_{i,F}}{N_{F,0}} - \frac{\sum_{i=0}^{N} BS_{i,P}}{N_{P,0}}\right)$$

where the sum of body size ($BS_{i,P}$) of damselfish i in the protected area divided by the initial population size in the protected area ($N_{P,0}$) is subtracted from the sum of body size ($BS_{i,F}$) of damselfish i in the fished area divided by the initial population size in the fished area ($N_{F,0}$).

Landscape functional connectivity indexes

We used two different measurements as indices of landscape connectivity. The first and simpler index is the percentage of the protected area covered with solid reef. This index assumes that damselfish movement is limited by sand and low complexity substratum, independent of their distance from the fished area (*see Chapter 1*).

The second measurement for landscape functional connectivity used components of a proximity index called weighted proportion index (Winfree et al. 2005) and findings from *Chapter 1* about the width and steepness of a barrier to movement in damselfish. In *Chapter 1*, we found that relatively small sand gaps represent significant partial barriers to movement in longfin damselfish (1.85 m in a detour configuration that takes the form of a "U-shaped" reef and 3.90 m in a patchy configuration). The weighted proportion index is adapted to use grid cells instead of habitat patches to measure landscape connectivity from a focal point (Gu et al. 2001, Luoto et al. 2001) and is more suitable for landscapes where discrete habitat patches are not readily defined. The weighted proportion - barrier index (WPI_B where B is for barrier; *equation 2*) used in this study took into account the connectivity of each cell to the fished area as measured by the fraction of the cell covered with suitable habitat (F_j), in this case reef. F_j is multiplied by B_j where B_j represents the probability of an individual moving toward the fished area as determined in *Chapter 1*. If cell j is connected by continuous reef to the fished area, B_j takes a value of one (fully connected and high landscape connectivity). If cell j is separated from reef in the fished area by sand gaps smaller than 1.85 m, B_j takes a value of 0.75. If cell j is separated by a sand gap smaller than 3 m but larger than 1.85 m, B_j takes a value of 0.50. If cell j is separated by a sand gap smaller than 5 m but larger than 3 m, B_j take a value of 0.25. Finally, if the smallest sand gap between cell j and reef is larger than 5 m B_j takes a value of 0.This index assumes that the importance of surrounding habitat declines gradually with distance from the focal point (d). In this study, we use the fished area boundary as the focal point for each quadrat in the protected area (see Fig. 4.1). We also used a species-specific mobility constant (D) set at 6 m, based on a conservative (75% quartile) measure of the distances of damselfish exploratory forays (N = 630; K. Turgeon, *unpublished data*). D is the species-specific mobility constant (fixed at 6 m in this study) and A_j is the area of a grid cell, which is constant in our study (2

m^2). Different D values (2, 4, 6, 8 and 10 m) resulted in very similar and highly correlated indices. We assumed that dusky damselfish will be affected in a similar way to longfin damselfish.

Equation 2: Weighted proportion index (WPI_B)

$$WPI_B = \frac{\sum_{j \notin x} B_j F_j e^{-d_j / D} A_j}{\sum_{j \notin x} e^{-d_j / D} A_j}$$

Compensatory immigration framework

We developed a compensatory immigration model that derived from source-sink dynamics theory and the original stock-recruitment function (Beverton and Holt 1957) to predict net cumulative immigration into the fished area (I_F) as a function of cumulative fish catch (C; *equation 3,*see *Chapter 3* for details). Cumulative net immigration is modeled at the metapopulation level by incorporating variables related to both the fished area and the protected area into a single equation. The initial population size in the protected area ($N_{P,0}$) in the denominator sets the maximum possible number of immigrants and can affect the rate of immigration. The parameter M_0 influences the initial rate of replacement of per fished individual. The combination of the exponent θ for cumulative harvest and $N_{P,0}$ allows modeling complex forms of density-dependent immigration, accounting for social interactions among individuals in the fished and in the protected area.

Equation 3: Compensatory immigration model to predict cumulative net immigration following cumulative fish catch

$$I_F = \frac{M_0 * C^\theta}{1 + \left[\frac{M_0}{(N_{P,0})}\right] * C^\theta}$$

By changing the assumptions as to which parameters correspond to limiting factors to immigration in *equation 3*, we derived six nested scenarios as alternative hypotheses for observed cumulative immigration in relation to cumulative fish catch. The first and simplest scenario assumes that immigration is limited by a failure to respond to vacancies created by harvesting ($M_0 = 0$). This could occur if the species is sessile in the adult stage, if there are strong barriers to movement (*i.e.* low functional connectivity), or if very poor habitat quality in the fished area makes movement unprofitable. When $M_0 = 0$, *equation 3* simplifies to *equation 4*.

Equation 4: Cumulative immigration predicted by mobility limitation

$$I_F = 0$$

The second scenario assumes that the only factor limiting immigration is the availability of vacancies in the fished area ($M_0 = 1$; $N_{P,0} \to \infty$; $\theta = 1$). This could occur for highly mobile species, where there are no barriers to movement and where there is a large population in the protected area. Thus, *equation 3* simplifies to *equation 5*.

Equation 5: Cumulative immigration predicted by vacancy limitation

$$I_F = C$$

The third scenario assumes that immigration is limited by a partial replacement of fished individuals ($M_0 < 1$; $N_{P,0} \to \infty$; $\theta = 1$). This scenario could arise from redistribution following density-dependent habitat selection (the Ideal Free Distribution; Fretwell and Lucas 1969, Morris 1989, Rosenzweig 1981) or from limited mobility, partial barriers to movement, and low habitat quality in the fished area that can result in deviations from the predictions of density-dependent habitat selection. *Equation 3* simplifies to *equation 6.*

Equation 6: Cumulative immigration predicted by partial replacement limitation

$$I_F = M_0 C$$

The fourth and fifth scenarios both assume that immigration can be limited by the number of potential migrants in the protected area ($N_{P,0} < \infty$; $\theta = 1$). This allows the modeling of positive density-dependent immigration in which the rate of immigration decreases as density is reduced. This could arise from limitation in the number of potential immigrants that could improve their situation by moving (see *Chapter 2*) or from decreasing attractiveness of the fished area due to low density (Stamps 1991, 1988). In the fourth scenario, mobility, barriers to movement and habitat quality in the fished area do not limit immigration, resulting in an initial replacement rate of fished individuals (M_0) = 1. In the fifth scenario, mobility, barriers and habitat quality can limit immigration, so the replacement rate of fished individuals is partial ($M_0 < 1$). *Equation 3* simplifies to *equation 7* with $M_0 = 1$ for scenario four or $M_0 < 1$ for scenario five.

Equation 7: Cumulative immigration predicted by immigrant limitation and partial replacement

$$I_F = \frac{M_0 * C}{1 + \left[\frac{M_0}{(N_{P,0})}\right] * C}$$

Finally, the sixth scenario, referred to as *complex density-dependent limitation*, assumes that density-dependent immigration can vary from negative to positive density dependence with cumulative harvesting, in addition to limitations from vacancies, partial replacement and potential immigrants ($\theta > 1$). This scenario could arise as a result of social interactions in both the fished and protected areas. For example, while populations are still at high density, remaining individuals in the fished area may resist immigration by expanding their territories into vacated areas or by group defense (Chase 1980, Meadows 1995). As density falls, immigration becomes easier, increasing the rate, but eventually declines as the low density habitat becomes less attractive or there are fewer individuals in the protected area that can benefit by moving. This scenario uses the complete model expressed by *equation 3*.

Data analysis

To examine the relationship between observed cumulative immigration (i.e. the cumulative number of immigrants in the harvest area) and cumulative harvest (i.e. cumulative number of fish fished over time), we compared the fit between predictions from the six limitation scenarios described above and the observed data. We estimated parameter values (M_0 and θ) for each limitation scenario using a maximum likelihood approach with the mle2 function available on the bbmle package version 0.9.5.1 (Bolker 2010). We chose a normal distribution to model our data, but Gamma and log-normal distributions resulted in similar estimates. The value for $N_{P,0}$ variable in the scenarios was determined by the number of potential migrants in the protected area (Table 4.1).

Model fitting and model selection

To compare the ability of each scenario to predict cumulative immigration on each site, we used the Information Theoretic Approach. We used Akaike's Information Criterion modified for small sample sizes (AICc; Burnham and Anderson 2002) to assess the fit of the model i corresponding to each scenario with observed data. Lower AICc values indicated a better fit. We also calculated the difference between AICc for each model i and the lowest observed AICc (ΔAICc) and compiled normalized Akaike weights (w_i) to address model selection uncertainty (Burnham and Anderson 2002). To select the best scenario among the six, we calculated the mean Akaike weights among sites (mean w_i).

To increase our statistical power, we combined both species to evaluate the effect of cumulative harvest on cumulative immigration for having a general pattern. An a posteriori test for the effect of species on the number of immigrants as a function of cumulative harvesting showed that the interaction between species and cumulative harvest was not significant to explain cumulative immigration (GLMM; t-value = -1.026, estimate and 95% CI = -0.681 and -1.983 to 0.620; N = 154).

Limitation approach

We used the limitation approach (Schmitt et al. 1999, Poulsen et al. 2007, Osenberg et al. 2002) to estimate how much each factor limits immigration. To estimate the effect of each limiting factor or combination of limiting factors on immigration, we added the limitation (s) imposed by one scenario and compared the predicted number of cumulative immigrants with the observed number of cumulative immigrants. Using parameter estimates for M_0 and θ and the number of potential migrants in the protected area ($N_{P,0}$), we explored how cumulative immigration in damselfish is limited by mobility limitation (scenario 1; $M_0 = 0$, $N_{P,0} \to \infty$, $\theta = 1$), by vacancy only limitation (scenario 2; $M_0 = 1$, $N_{P,0} \to \infty$, $\theta = 1$), by a partial replacement limitation (scenario 3; $M_0 < 1$, $N_{P,0} \to \infty$, $\theta = 1$), by the number of immigrants in the protected area (scenario 4; $M_0 = 1$, $N_{P,0} < \infty$, $\theta = 1$), by a combined effect of immigrant and partial replacement limitation (scenario 5; $M_0 < 1$, $N_{P,0} < \infty$, $\theta = 1$), or by complex density-dependent limitation (scenario 6; $M_0 < 1$, $N_{P,0} < \infty$, $\theta > 1$). Limitation was expressed either as an absolute change in the number of cumulative immigrants for a scenario i from equations 3 to 7 ($I_{PRED_i} - I_{OBS}$) or as a relative change (($I_{PRED_i} - I_{OBS} / I_{OBS}$) * 100). A value of zero for the absolute change in limitation indicates a perfect fit between the predicted and the observed values. A value above zero indicates that the scenario overestimated immigration and value below zero indicates that the scenario underestimated immigration.

Correlates of total yield and the partial replacement of fished damselfish (M_0)

To examine the role of limiting factors on immigration, we examined how total yield was predicted by the empirically measured limiting factors such as the number of potential migrants in the protected area, the relative habitat quality and the functional connectivity between the harvest and protected area. Total yield was the total number of fished damselfish divided by the initial number of damselfish in the harvest area. We allowed all possible two-way interactions in the modeling process which resulted in 13 candidate models. We used Generalized Linear Models (glm library in R) to produce candidate models that examined the effects of the candidate models on total yield. To select the best subset of models among the entire set of candidate models, we used the Akaike's Information Criterion modified for small sample sizes (AICc; N = 7). For each candidate model, we compiled the normalized Akaike weights (w_i; Burnham and Anderson 2002). The confidence set of candidate models includes all models for which w_i is within 10% of the maximum weight (Burnham and Anderson 2002). Non-normally distributed predictors were log-transformed, and all predictors were z-standardized prior to analysis. For each candidate model, we examined the Tolerance value (1/Variance Inflation Factor) which is a measure of the amount of variation unique to each retained predictor and used to detect multicollinearity problems. Tolerance values among predictors were all below 0.3 which represents mild multicollinearity.

To test our assumption that the partial replacement of fished individuals (M_0) can be influenced by habitat quality and functional connectivity, we also examined how the M_0 estimated for each site by maximum likelihood can be predicted by the empirically measured limiting factors for the relative habitat quality and the functional connectivity between the harvest and protected area. We used the same procedure as above on the four candidate models.

RESULTS

We first evaluated which scenarios from the compensatory immigration model were best supported by the data to predict spillover following cumulative harvest on each fished site. Next, we evaluated which factors limiting immigration had the highest relative influence on spillover among sites using the limitation approach (Schmitt et al. 1999). Finally, we assessed the predictive ability of quantitative measurements of limiting factors to predict observed total yield and parameter estimates from the compensatory immigration model among sites.

General results

On the seven fished sites, we did not observe any immigration during the two week observation period before we started to remove fish (Fig. 4.2, cumulative harvest = 0). On each of the two control sites, we observed only a single immigrant over a monitoring period of five weeks. Both were very large male longfin damselfish that migrated in the fourth week in NB1 and in the third of the five week monitoring period in SB1. There were also two unexplained disappearances in control site NB1 during the second and third week and three disappearances in control site SB1, one in the second week and two in the third week. These vacant territories were rapidly filled by neighbouring damselfish that temporarily increased the size of their territories and were not followed by immigration during our observations.

Immigration into the harvest area started after the first removal in three sites (BH1, SL1 and SL2) and after the second to seventh removal events in the others (Fig. 4.2). In general, immigration rate per removal started at a low level, increased and then declined. Immigration rate peaked when 83% of the initial population in the harvest area had been removed in HB2, at 77% in BH1, 79% in HB3, 21% in HB4, 19% in SL1, 42% in SL2 and at more than 90% in HB1. After 8 (HB1 and HB2) to 14 (SL1) removal events, there was no more immigration within the 6-day 'after removal' monitoring period (Table 4.1). The total number of immigrants varied from 5 (HB1) to 44 damselfish (SL1; Table 4.1). The total yield varied from 1.1 to 1.64 times the original population (Fig. 4.2).

Predicting cumulative immigration following cumulative harvest

We fit the six scenarios (*eqs 3 to 7*) to all sites. Three scenarios provided the best fit at one or more sites, and three fit poorly at all sites (Table 4.2, Fig. 4.2). The complex density-dependent limitation model (scenario 6; *equation 3*) provided the best fit in sites BH1, HB2 and HB3 (Fig. 4.2a), even though it was penalized in the calculation of AICc scores for including the largest number of parameters. This model also had the highest mean Akaike weight (mean w_i; Table 4.2). The rate of immigration in this scenario increased and then decreased with decreasing density in the fished area. Estimates for M_0 in the complex density-dependent limitation varied among sites from 0.007 in HB3 to 0.1 immigrants per fished individual in SL1, and estimates for θ varied from 1.2 in SL1 to 2 in HB3 (Table 4.1). The partial replacement limitation model (scenario 3, *equation 6*), predicting cumulative immigration as a simple linear fraction of cumulative harvest, provided the best fit at another three sites, HB1, SL1 and SL2 (Fig. 4.2b) and had the second highest mean w_i (Table 4.2). Estimates for M_0 in the partial replacement limitation model varied among sites from 0.06 in HB1 to 0.39 immigrants per fished individual in SL1 (Table 4.1). The immigrant and partial replacement limitation model (scenario 5, *equation 7*) provided the best fit at one site, HB4 (Fig. 4.2c). Because this model also provided a moderate fit at two other sites, its mean w_i was also quite high (Table 4.2). The rate of immigration in this scenario decreased with decreasing density in the fished area. Estimates for M_0 in the immigrant and partial replacement limitation model varied among sites from 0.07 in HB1 to 0.51 in SL1 (Table 4.1). The three remaining models based on scenarios of mobility limitation (scenario 1, *equation 4*), vacancy limitation (complete replacement, scenario 2, *equation 5*, and immigration limitation with complete replacement (scenario 4, *equation 7*) had a very little support as explanations of cumulative immigration in relation to cumulative harvest (Table 4.2 and Fig. 4.2). Based on the mean w_i of the scenarios (Table 4.2), the complex density-dependent limitation was 1.2 times more likely than the partial replacement limitation model and 1.9 times more likely than the immigrant and partial replacement limitation model and over 47 times more likely than the other three scenarios as an explanation of cumulative immigration.

Quantifying the relative importance of limiting factors to immigration

Using parameters estimates for M_0 and θ and the number of potential migrants in the protected area ($N_{P,0}$), we explored how predictions from the six scenarios deviated from observed cumulative immigration in damselfish. Absolute deviations are minimal when cumulative harvest is 0 in all sites and for each limitation or combination of limitations because scenarios predicted no net immigration in the absence of harvesting, and we did not observe immigration before harvesting (Fig. 4.3). Relative deviations decreased with increasing cumulative harvest (Fig. 4.4; Appendix 4.1).

The complex density-dependent limitation, where parameters varied ($M_0 < 1; \theta > 1$) and immigrants were limited ($N_{P,0} < \infty$), had the smallest absolute (Fig. 4.3f) and relative deviations from observed data (Fig. 4.4). Predictions deviated by only 6% at low cumulative harvest and fitted almost perfectly at high cumulative harvest

(Fig. 4.4). Absolute deviations increased then decreased with cumulative harvest in HB3 and HB1, decreased then increased with cumulative harvest in HB4 and SL2 and were close to 0 in BH1, HB2 and SL1 (Fig. 4.3f). Removing the complex density dependence limitation (*i.e.* θ =1) resulted in the partial replacement and immigrant limitation scenario. Relative deviations increased to 94% at low cumulative harvest but did not change for high cumulative harvest (Fig. 4.4). Absolute deviations increased then decreased with cumulative harvest in all sites excepted HB4 where deviations decreased then increased with cumulative harvest (Fig. 4.3e). Removing the immigrant limitation ($N_{P,0} \rightarrow \infty$) resulted in the partial replacement limitation scenario. Predictions deviated by 76% at low cumulative harvest and by 32% at high cumulative harvest (Fig. 4.4). Absolute deviations increased and decreased with cumulative harvest in BH1, HB2, HB1and HB3, decreased and increased in HB4 and mainly increased with cumulative harvest in SL1 and SL2 (Fig. 4.3c). Removing the partial replacement limitation ($M_0 = 1$) but keeping the immigrant limitation ($N_{P,0} < \infty$) resulted in the immigrant limitation scenario. Relative deviations significantly increased to 654% at low cumulative harvest and to 87% at high cumulative harvest (Fig. 4.4). Absolute deviations increased with cumulative harvest in BH1, HB2, HB4, SL1 and SL2 but increased then decreased with cumulative harvest in HB3 and HB1 (Fig. 4.3d). Removing the immigrant limitation ($N_{P,0} \rightarrow \infty$) resulted in the vacancy only limitation scenario. Relative deviations increased to 737% at low cumulative harvest to 213% at high cumulative harvest (Fig. 4.4). The vacancy only limitation had the highest absolute and relative deviations from observed data and absolute deviations increased (Fig. 4.3b), and relative deviations decreased with cumulative harvest in all sites. By fixing M_0 at 0, we obtained the no mobility scenario. The no mobility limitation had high absolute (Fig. 4.3a) and relative deviations (Fig. 4.4), and was the only scenario to strongly underestimate immigration (Fig. 4.3a). Deviations increased with cumulative harvest for almost all sites excepted in HB1 (Fig. 4.3a). Relative deviations were constant over cumulative harvest (Fig. 4.4).

Absolute and relative deviations were smaller in the partial replacement, the immigrant and partial replacement and the complex density-dependent limitation scenarios, *i.e.* when M_0 varied (Fig. 4.3 c,e,f and Fig. 4.4). Even though the complex density-dependent limitation had the smallest deviations, the relationship between relative deviation and cumulative harvest in this scenario did not differ from the partial replacement, the partial replacement and immigrant relationships (Appendix 4.1). Deviations strongly increased when we removed the partial replacement limitation (Fig. 4.3 a,b,d and Fig. 4.4). Relationships between relative deviations and cumulative harvest in the immigrant, the only vacancy and the no mobility limitation scenarios all differed from the relationship between relative deviations and cumulative harvest in the complex density-dependent limitation (Appendix 4.1).

Correlates of total yield and M_0 among sites

Based on their AICc scores, only two of the 13 candidate models had significant support to explain total yield. The number of available immigrants in the protected area had the highest support to explain among site variation in total yield. A larger number of potential immigrants was correlated with a greater total yield (Table 4.3 and Appendix 4.2a). This predictor explained 52.6% of the Deviance and its 95% CI did not include zero. The second model with support was the model including RHQ, WPI_B and their interaction (Table 4.3; Appendix 4.2d). This model explained 91.8% of the Deviance and the 95% CI for the WPI_B estimate and for the interaction term estimate did not include zero (Table 4.3). By itself, the RHQ index explained only 16.2% of the Deviance, its 95% CI estimate included zero and was 7.3 times less likely to explain immigration than the number of potential migrants in the protected area (Table 4.3, Appendix 4.2c). WPI_B had also very low support to explain total yield. This predictor explained 28.1% of the Deviance, its 95% CI estimate included zero (Table 4.3, Appendix 4.2b), and it was 3.87 times less likely to explain total yield than the number of potential migrants in the protected area (Table 4.3, Appendix 4.2d).

Based on their AICc scores, only one model has some support to explain M_0. Again, the model including *RHQ*, $WPCI_B$ and the interaction between the two predictor had the highest support to explain M_0 ($w_i = 0.83$). This model explained 92.5% of the Deviance and its 95% CI did not include zero. Alone, the RHQ and WPI_B indexes explained respectively 16.2% and 33.9% of the Deviance and their 95% CI included zero.

DISCUSSION

Spillover occurs in response to density reduction

We observed almost no spillover in control sites and none during the observation period prior to harvest in the fished sites, indicating that spillover depends almost completely on vacancies in damselfish. Spillover occurred over the full range of harvest densities. We observed spillover even when the harvest fish population was at high density, excepted in HB1 site. Spillover occurred via territory relocation of untagged damselfish coming from the adjacent protected area, resulting in a total yield varying from 110 to 164% (mean 132%). This result supports the argument that the protected area stabilizes declining populations and increases total yield in the very short term and strongly disagrees with theoretical models on the effectiveness of MPAs (DeMartini 1993, Polacheck 1990) suggesting that harvest has to be high to initiate net immigration. In our experiment, a reduction of as little as 10-15% of the population resulted in spillover in 3 sites over 7 with a mean replacement rate of .0.3 immigrants per fished damselfish. This study provides one of the first direct empirical evidence for an increase in spillover in response to local harvest in a coral reef fish.

Previous studies examining the responses of coral reef fish to a reduction of density, half of which were performed on damselfish species, observed net immigration of adult and subadult fish (Brock et al. 1979, Hixon 1980, Hourigan 1986, Lewis 1997, Lowry and Suthers 2004, Ogden and Ebersole 1981, Sale 1976, Syms and Jones 2000). However, most of these studies performed a single massive removal and did not monitor immigration in control sites. This impedes clear conclusions about the effect of a range of harvest densities on the magnitude of spillover. In five studies, where the initial population size in the fished area and the number of immigrants were provided, the total yield varied from 140 to 286% (mean 193%; (Hixon 1980, Hourigan 1986, Lowry and Suthers 2004, Sale 1976, Syms and Jones 2000) which is slightly higher than the total yield observed in our study. Although these studies did not directly monitor control sites for immigrants, some monitored the stability of the population in independent controls and suggest that vacancies are needed to observe net immigration (Hixon 1980, Sale 1976, Syms and Jones 2000) . A review of compensatory immigration in vertebrate populations (Turgeon and Kramer, *in prep*. see *Appendix I.1*) found that immigration of adults and subadults has been observed in many terrestrial and aquatic taxa and has been suggested as a processes resulting in short term stabilization of declining populations. In these studies, total yield varied from 142 to 473% (mean 205%) in birds and varied from 102 to 1185% (mean 253%) in mammals, values which are considerably higher than total yield observed in our study and other coral reef fish studies. All these studies were performed on systems showing territoriality and dominance behavior with high density populations before the manipulation. A reduction in density may affect non-territorial species or populations that occur naturally at low densities differently, and this should be investigated to have a more general pattern of immigration in a context of harvesting.

In three of seven sites, we observed a change in magnitude and direction (*i.e.* from negative to positive density dependence) in immigration rate with cumulative harvest. In one site we observed positive density dependence and in the three other sites a nearly linear replacement rate (*i.e.* density-independent) with cumulative harvest. Immigration rate decreased in four of seven sites, and we successfully created a local extinction in all sites suggesting that spillover has a definite end in damselfish. The only previous attempt to document density-dependent movement in response to density reduction in coral-reef fishes was made by Zeller et al. (2003), but they did not detect a significant change in the frequency and direction of fish movement with decreasing density. Most studies of compensatory immigration in vertebrate populations (see *Appendix I.1*) used a massive first removal, impeding any conclusion about the rate of replacement with different harvest densities. Only three studies on birds continuously removed residents and immigrants in the harvest area over time and provided partial information about the rate of immigration (Hannon 1983, Knapton and Krebs 1974, Manuwal 1974). (Knapton and Krebs 1974) found an almost perfect replacement of fished individuals in the song sparrow (*Melospiza melodia*), corresponding to our only vacancy limitation scenario, but they never reduced the population to very low density, preventing conclusions for small population sizes. Hannon (1983) and Manuwal (1974) observed very high immigration (replacement rates of fished individuals of > 0.9 and 0.77, respectively) that decreased and then stopped when females started to lay eggs in the willow ptarmigan (*Lagopus lagopus*) and in the Cassin's auklet (*Ptychoramphus aleuticus*), respectively. This is similar to the immigrant limitation scenario. Both studies performed a massive first removal at the beginning of the treatment, so we cannot extract clear patterns of density dependence and compensatory processes at high population density. In damselfish, the decreasing rate of immigration is unlikely to be related to a seasonal pattern because both species spawn every month during the whole year (Thresher 1984), and the territory provides multiple benefits (*i.e.* feeding and refuge and breeding) and not just for reproduction. By having a wide range of harvest densities, this study provides the first evidence of density-dependent movement in coral reef fish and one of the first and clearest empirical evidence of compensatory immigration in vertebrates.

Factors limiting spillover

Spillover depends almost completely on removal, but the rate of replacement of fished individuals by immigrants is smaller than the rate of creation of vacancies as shown by the very low support for the vacancy only limitation model (Table 4.2) and by the high deviations from observed data in the limitation approach (Fig. 4.3b and Fig. 4.4). These results suggest that factors other than vacancy availability are likely to limit immigration in damselfish in response to harvest. Based on the limitation approach, the effect size of θ (i.e. behavioral interactions at high density) on cumulative immigration in damselfish was smaller than that of M_0 (i.e. rate of replacement of fished fish) but larger than that of $N_{P,0}$ (immigrant limitation). Even though the complex density-dependent limitation scenario was the best predictor of cumulative immigration in relation to cumulative harvest (Table 4.2), adding θ in the model only slightly reduced deviations between predicted and observed data as compared to adding M_0 in the model (Fig. 4.4). $N_{P,0}$ is likely not a strong limiting factor to immigration in damselfish because adding $N_{P,0}$ in the model did not strongly reduce deviations from observed data (Fig. 4.4). However, immigrant limitation deserves some attention because it was included in two scenarios that had high support (complex density-dependent limitation and immigrant and partial replacement limitation scenarios).

M_0: Habitat quality, functional connectivity or both?

The parameter M_0 had the highest effect size in the limitation approach (Fig. 4.4), and the partial replacement limitation scenario, which only includes one parameter ($M_0 < 1$), had the second highest support to explain immigration pattern and was the best scenario in three of seven sites (Table 4.2). The partial replacement limitation scenario can be derived from density-dependent habitat selection and related hypothesis such as the Ideal Free Distribution (*Chapter 3*). Predictions from a density-dependent habitat selection model, where the rate of replacement equalizes the realized suitability between the protected and harvest area in relation to respective densities, produced strong deviations from observed values (Appendix 4.3). This hypothesis therefore is not well supported as an explanation of partial replacement.

Partial replacement limitation can also result from properties of the landscape such as variation in habitat quality and functional connectivity. Our multi-site analysis revealed a high correlation between the parameter estimates for M_0 and predictions from the model that included the interaction between empirically measured indexes of relative habitat quality (*RHQ*) and functional connectivity (WPI_B, Table 4.3 and Fig. 4.5d). We had strong support for a synergistic effect of landscape connectivity and relative habitat quality on spillover in damselfish. However, because our sample size was small (N = 7 sites), this conclusion is tentative and requires additional experiments to strengthen this evidence and to disentangle the relative effect of habitat quality and landscape connectivity on immigration.

As a measure of relative habitat quality between the protected and fished area, we used the *RHQ*, which is an index using the difference in the mean damselfish body size between the protected and harvest area. This index is suitable as an indicator of local habitat quality in damselfish because in a previous studies, we found that territories that were originally held by larger individuals had a higher probability of recolonization (*Chapter 2*), indicating a stronger preference. Other studies have found evidence that body size of male damselfish was related to quality territory, where only larger males have active nest sites (Cheney and Côté 2003, Itzkowitz 1991, Knapp and Kovach 1991) or where important variables related to individual success, such as access to higher cover and food quality, were related to body size (Itzkowitz and Makie 1986, Knapp and Warner 1991, Sikkel 1988). In many other taxa, from large and small mammals, to birds and reef fish, territories held by larger and dominant individuals are recolonized faster and/or at a higher probability than those held by smaller and subordinate individuals (Jacquot and Solomon 2004, Lin and Batzli 2001, Loveridge et al. 2007, Lowry and Suthers 2004, Marra et al. 1993, Newton 1992, 1998, Robinson et al. 2008, Waldner and Robertson 1980). However, body size can be poorly correlated with habitat quality if prior residence, where the resident individual is usually successful in repelling conspecific intruders, is a strong determinant of conflict over territories (Brown and Green 1976, Figler et al. 1976, Stamps 1987) or if there is very little variation in size at maturity between individuals (*e.g.* some fish, birds and small mammals; Endler 1983, Hill 1991, Kodric-Brown 1983, 1985).

Measuring landscape connectivity is difficult, so numerous studies have considered indexes of connectivity to predict immigration and colonization (Calabrese and Fagan 2004, Prugh 2009, Schumaker 1996, Winfree et al. 2005). However, none of the proposed indices have been particularly effective in predicting movements when tested in a variety of systems. Our use of WPI_B as a surrogate for functional connectivity between the protected and fished area combined suitability of habitat within grid cells (*i.e.* reef = suitable; sand = unsuitable) and a probability of moving among grid cells based on the empirically measured probability of crossing sand gaps of various sizes (*Chapter 1*). In damselfish and reef fish in general, sand strongly influences movement because many fishes are unwilling to move far from the protection of structured reef habitat (*Chapter 1*, Barrett 1995, Chapman and Kramer 2000, Ogden and Buckman 1973). Barriers to movement and unsuitable habitat matrix are known to limit movement in many taxa and to slow the rate of population recovery following a disturbance (Arvidsson and Klaesson 1984, Berra and Gunning 1970, Kozakiewicz and Jurasińska 1989, M'Closkey et al. 1997, Rosatte et al. 2007). However, barriers to movement are likely to vary strongly among taxa. Translocations and gap-crossing experiments could be particularly useful to identify barriers to movement (Awade and Metzger 2008, Bakker and Van Vuren 2004, Bélisle and Desrochers 2002, Bosschieter and Goedhart 2005) and habitats that can act as corridors (Baum et al. 2004, Gillies and St. Clair 2008).

Density ($N_{P,0}$ and θ)

The complex density-dependent limitation scenario included density dependent immigration that changed in direction (*i.e.* negative and then positive density dependence) and magnitude in response to harvest. This study provided the first direct empirical evidence for density-dependent spillover in coral reef fish. Other evidence for density-dependent movements in fishes comes mainly from salmonid populations showing positive density-dependent movement to avoid overcrowding (*i.e.* emigration from high density populations), but clear empirical evidence for negative density-dependent movement is lacking (Rose et al. 2001).

The density dependence appearing during our experiment is likely to be a response to the change in density rather than an apparent or a 'pseudo-density-dependent' process created by mathematical artifacts. Pseudo-density dependence has been observed in some coral reef larvae recruitment studies where each recruit represents a decreasing proportion of the total population as local population size increases but this per capita density dependence could occur in the absence of biotic feedbacks if per-area recruitment was constant through time and new recruits simply accumulated within an area (Hixon and Webster 2002, Sale and Tolimieri 2000). To avoid pseudo-density dependence, we used cumulative immigration instead of per capita immigration in relation to cumulative harvest to avoid an inflated non-linear pattern caused by a constant flux of immigrants through time in the area with decreasing density (Hixon and Webster 2002). In addition, after each removal event, we allowed the system to reach a new equilibrium. Territory recolonisation in longfin damselfish occurred within one day (Cheney and Côté 2003, McDougall and Kramer 2007) and within 6 h in this study (median 360 min; 95% CI = 107 – 1750 min) if we exclude the inactive nocturnal period (about 10 h from 19:00 to 05:00). Allowing equilibrium reduced the error of attributing immigration due to event t to event $t+1$. Furthermore, because there is no strong seasonal pattern affecting damselfish abundance, we are confident that immigration patterns do not change over the course of the study. Finally, in a companion study using the same density reduction experiment (*Chapter 2*), we documented behavioral interactions and a chronology in the movement sequence that could explain a change in magnitude and direction of immigration in response to harvest.

Behavioral interactions in both the fished and protected area can explain a change in magnitude and direction in the rate of immigration (*i.e.* negative and then positive density dependence) with in response to harvest. The absence of immigration in saturated populations and the increasing rate of immigration in three sites when we started to harvest when the populations were at high density can be explained by hypotheses such as the social fence (*i.e.* negative density-dependent immigration when agonistic interactions among neighbors limit movement at high density; Clobert et al. 2001, Hestbeck 1982, 1988), territory expansion of neighbors (Hixon 1981, Schoener 1974) and the cost of prospecting for vacancies at high density (Sikkel and Kramer 2006). In *Chapter 2*, we found a higher rate of agonistic interactions among residents, an expansion of the territories in the fished area and a high occurrence of territory shifts of residents (*i.e.* a change in space use that overlaps with the previous territory) at high density. In *Chapter 1*, we observed an avoidance of conspecific territories when moving in a fragmented landscape, likely as a way to avoid agonistic interactions. Territory expansion of the survivors in the fished area may limit the space available for migrants at high density. This is a well known phenomenon in coral reef fish and has been also observed in small mammals (Arvidsson and Klaesson 1984, Ebersole 1980, Norman and Jones 1984). For damselfish that have already acquired a good quality territory, prospecting for vacancies may be costly at high density because fish would likely have to fight intruders to regain the possession of a territory (Sikkel and Kramer 2006). A vacant territory is explored within minutes by neighbors, patrolled after as little as 15 min and fully defended within less than 24 h in longfin damselfish and threespot damselfish (*Stegastes planifrons*) (*unpublished data*; Cheney and Côté 2003, McDougall and Kramer 2007, Meadows 2001).

At least two hypotheses can explain the positive density-dependent immigration at low density. First, because damselfish have low mobility and short distance exploratory forays (10 m based on the 95th percentile of 630 observations of spontaneous exploratory movements outside their territories; K. Turgeon, *unpublished data*) they are perhaps attracted to areas with many conspecifics and avoided heavily fished area (Stamps 1991, Danielson and Gaines 1987). In severely depleted areas, the cost and risk associated with low population density (e.g. the risk of reproduction failure; Kuussaari et al. 1998) may be higher than the benefits of moving into a higher quality territory. The second hypothesis is a limited availability of potential migrants in the adjacent area (Beckley 1985, Hansson 1992). This hypothesis is, however, less plausible in our system because the available number of potential immigrants after the fished areas were depleted was still very high in six sites over seven (HB2 = 69, HB3 = 87, HB4 = 105, SL1, = 99, SL2 = 389, BH1 = 153). In HB1 there were only four potential immigrants left after the fished area was depleted.

Although our compensatory immigration framework allows the detection of density-dependent immigration, it may be problematic to detect a decreasing rate of immigration with cumulative harvest (*i.e.* the saturating part of the function) in some situations. It will be hard to detect a saturating relationship if harvesting pressure is high and constant over time (i.e. fixed proportion of the initial population) in small populations. The asymptote will be reached quickly and not gradually thus harder to detect mathematically. In our system, immigration stopped on each site but three sites were described by the partial replacement limitation scenario. This description of the pattern is likely to be best described by a "hockey stick shape" relationship with cumulative harvest (see Fig. 4.2).

Developing and applying the compensatory immigration framework

Validating and testing a proposed model is as important as developing it. To test the compensatory immigration model proposed in *Chapter 3*, we provided one of the most extensive experiments performed on a natural setting. We had seven manipulated sites that varied in three limiting factors (habitat quality, functional connectivity and the number of potential migrants in the protected area), two control sites and at least 8 densities per site, ranging from saturated populations to extinction. Very few density-manipulation experiments have quantified the effect of factors limiting immigration other than local population density, and even fewer quantified the effect of multiple limiting factors on immigration (Turgeon and Kramer; *in prep. Appendix I.1*; see Fig I.2 in the *General Introduction*). In addition to replication, having independent controls is another crucial component of the quantification of intrinsic population processes, such as immigration in the absence of harvesting. Surprisingly, more than 60% of the studies from the review did not have independent control sites (*i.e.* far enough to not be affected by the density manipulation; Fig. I.3a in the *General Introduction*), limiting the interpretation of the effect of the treatment.

Implications for management, theory and future work

Depending if the management goal of a protected area is to limit spillover and immigration in the case of endangered species or to optimally control the amount of spillover and immigration as a harvesting strategy, we must known which factors facilitate or impede immigration and how the rate change with density. Harvesting in high quality habitats that are well connected to a source of potential migrants can produce "attractive sinks" if individuals perform home range relocation from protected to fished area (Delibes, Ferreras, et al. 2001, Delibes, Gaona, et al. 2001). This can be problematic when we try to protect endangered species or stocks if harvesting affects the demography in the protected area (Loveridge et al. 2007, Woodroffe and Ginsberg 1998, 2000). Having a thorough knowledge of the limiting factors affecting immigration and managing the landscape in consequence will reduce our uncertainty concerning population dynamics and regulatory processes in managed populations.

By using a small model system, we have explored an interesting alternative to develop and test theories about the benefits of MPAs. In this study, we shed some light on the factors that could affect immigration in a context of harvesting. We strongly suggest revising some simplistic assumptions made by some theoretical models predicting the effectiveness of protected area as a management tool. For example, McCullough (1996) assumed that the only requirement to predict immigration in harvest area is an estimate of harvest, Hastings and Botsford (1999) assumed stationary adult fish, and Polacheck's (1990) model did not explicitly account for density-dependent movement of adults. In this study, we provided evidence that spillover occurs and can result in significant population recovery and that immigration rate can vary with cumulative harvest in response to behavioral interactions. Although our study evaluated the impact of starting the local exploitation of saturated populations, it is also interesting and important to understand the impact of establishing a protected area within a heavily fished area through a similar combination of theory and field experiment.

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Table 4.1. Variables characterizing harvest and protected areas, parameters estimates from the six scenarios used to predict cumulative immigration in relation to cumulative harvest and number of removal events for seven sites located on five fringing reefs along the West coast of Barbados. The coefficient of variation (C_v) is presented for each variable and parameter.

Variables and parameters	**Sites**							C_v
	HB1	**HB2**	**HB3**	**HB4**	**SL1**	**SL2**	**BH1**	
Variables								
Number of residents in the harvest area	51	51	48	61	74	59	57	0.197
Number of potential immigrants in the protected area	9	82	114	127	143	420	167	0.849
Number of immigrants	5	13	27	22	44	31	14	0.485
Area covered with reef in the harvest area (m^2)	91.5	121.0	70.4	86.8	80.7	78.2	114.5	0.206
Area covered with reef in the protected area (m^2)	51.7	457.3	403.7	328.3	200.5	451.8	297.8	0.462
WPI_B	0.003	0.437	0.244	0.230	0.153	0.414	0.239	0.605
RHQ (cm)	-0.693	0.516	0.632	-0.341	0.500	0.107	-1.096	0.644
Parameters								
M_0; partial replacement limitation	0.06	0.16	0.33	0.25	0.39	0.32	0.16	0.491
M_0; immigrant and partial replacement limitation	0.07	0.17	0.38	0.28	0.51	0.35	0.18	0.539
M_0; complex density-dependent limitation	0.01	0.02	0.007	0.03	0.21	0.1	0.02	1.316
θ; complex density-dependent limitation	1.5	1.5	2.0	1.5	1.2	1.3	1.5	0.168
Number of removal events	8	8	10	10	14	11	9	0.208

Table 4.2. AICc scores (AICc) and Akaike weights (w_i) for each of the six scenarios used to predict cumulative immigration following cumulative harvest on seven harvested sites. The mean Akaike weight (Mean w_i) for each scenario is given at the bottom of each column. For each site, the scenario having the highest support has its AICc score and w_i in bold. The three scenarios having the highest support among sites have their Mean w_i values in bold.

	Scenarios											
Sites	**No mobility**		**Only vacancy**		**Partial replacement**		**Immigrants**		**Partial replacement and immigrants**		**Complex density dependence**	
	AICc	w_i	AICc	w_i	AICc	w_i	AICc	w_i	AICc	w_i	AICc	w_i
HB1	47.66	0.064	151.08	< 0.001	**43.20**	**0.597**	61.22	< 0.001	44.48	0.315	49.66	0.024
HB2	70.78	< 0.001	151.52	< 0.001	36.68	0.045	129.08	< 0.001	39.18	0.013	**30.60**	**0.942**
HB3	153.46	< 0.001	184.50	< 0.001	69.57	0.001	156.32	< 0.001	72.93	< 0.001	**55.97**	**0.999**
HB4	145.76	< 0.001	195.40	< 0.001	48.41	0.285	168.90	< 0.001	**46.57**	**0.715**	63.31	< 0.001
SL1	250.78	< 0.001	278.14	< 0.001	**67.50**	**0.649**	222.14	< 0.001	76.30	0.008	68.78	0.343
SL2	181.13	< 0.001	215.61	< 0.001	**52.28**	**0.649**	202.95	< 0.001	53.20	0.383	60.65	0.010
BH1	107.13	< 0.001	175.29	< 0.001	40.00	0.237	57.81	0.105	41.62	< 0.001	**37.96**	**0.657**
Mean w_i		0.009		< 0.001		**0.352**		< 0.001		**0.220**		**0.425**

Table 4.3. Generalized Linear Models (GLM) used to explain total yield (number of harvested fish divided by the initial population size in the harvest area) in relation to the number of potential immigrants in the protected area, relative habitat quality index (*RHQ*) and functional connectivity index (WPI_B). The AICc score, the Akaike weight (w_i), the percent of the deviance explained, parameter estimates and the 95% confidence interval (CI) of each predictor are presented. Predictors in bold do not contain zero within the 95% CI.

Predictors	**AICc**	**w_i**	**% Dev.**	**Estimate**	**95% CI**
Number of potential migrants	**27.562**	**0.451**	**52.6%**	**0.725**	**0.122 to 1.329**
Relative habitat quality (*RHQ*)	31.547	0.048	16.2%	1.021	-0.400 to 1.205
Functional connectivity (WPI_B)	30.689	0.073	25.9%	0.509	-0.246 to 1.263
$WPI_B + RHQ + WPI_B * RHQ$	**29.269**	**0.149**	**91.8%**		
WPI_B				**-0.236**	**0.354 to 2.530**
RHQ				1.442	-0.806 to 0.334
$WPI_B * RHQ$				**-3.828**	**-5.956 to -1.700**

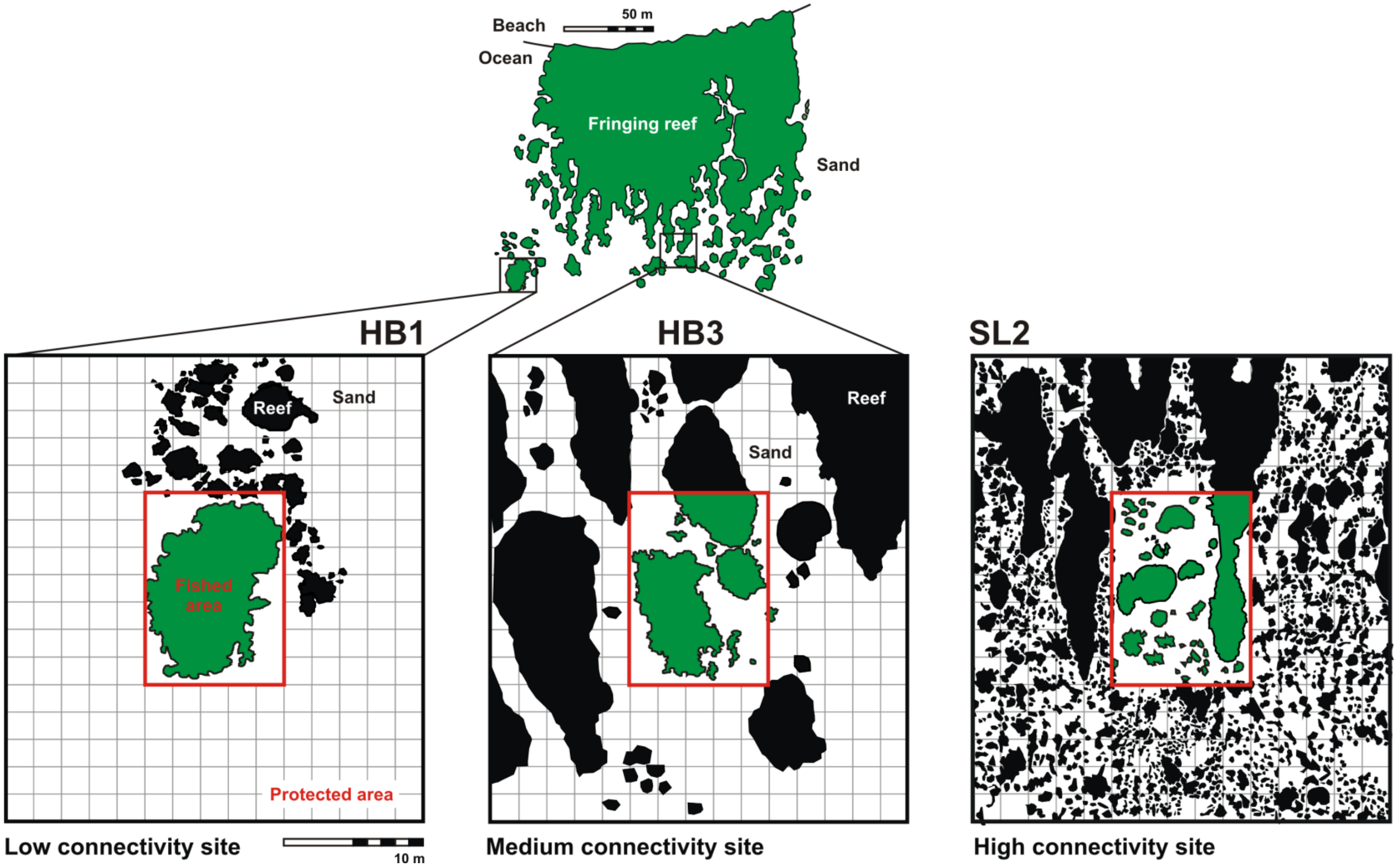
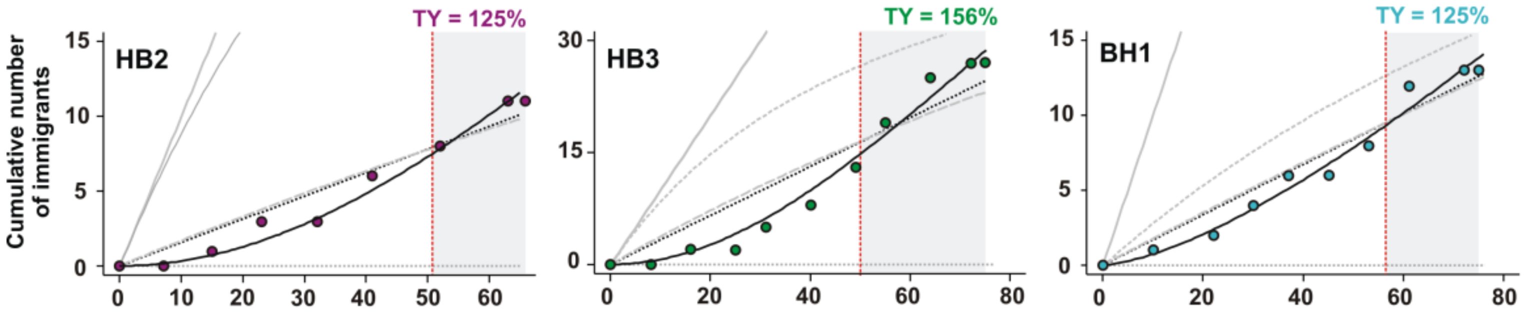


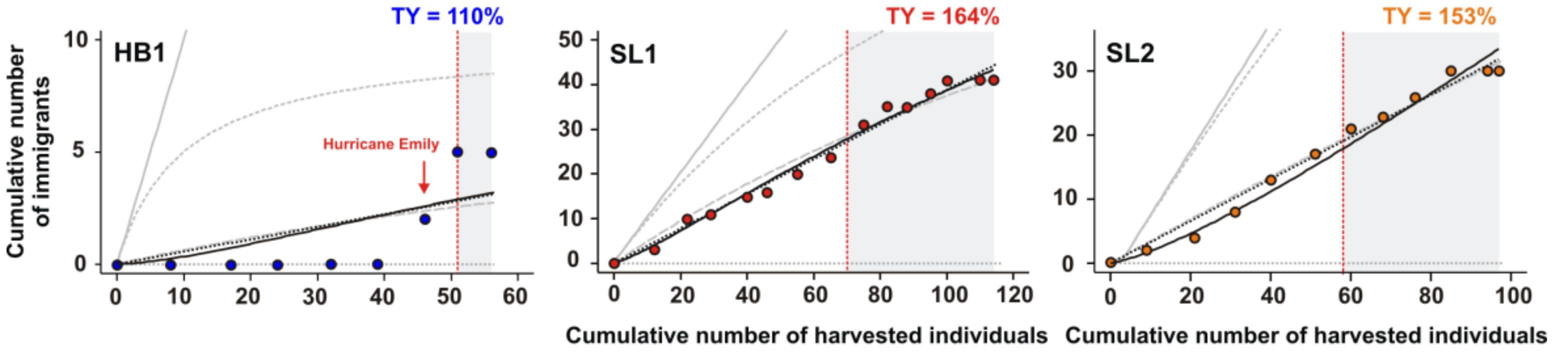
Figure 4.1. Study site design illustrated with three study sites showing examples of the natural fragmentation and functional connectivity observed in the spur and groove zone of fringing reefs in Barbados (HB1, HB3 and SL2, respectively). The fished area is framed with a red rectangle and the adjacent protected area is framed with a black rectangle. Reef substratum is represented by green in the fished area and by black in the protected area; sand is represented by white.

Figure 4.2. Observed cumulative number immigration in relation to cumulative harvest on each of seven sites. Sites (Bachelor Hall reef site: BH1, Heron Bay reef sites: HB1, HB2, HB3, HB4 and Sandy Lane reef sites: SL1, SL2) are grouped by their respective best fitting scenarios that are a) the complex density-dependent scenario, b) the partial replacement of fished individuals scenario and c) the immigrants and partial replacement scenario. Predictions from the six limitation scenarios (curves from Equations 3 to 7) are fitted to the observed data (colored dots) by using maximum likelihood estimates of parameter values. The vertical red dotted line indicates the initial population size in the fished area. The shaded area indicates harvest that exceeded the original resident population and participate to the total yield (TY; number of harvested fish divided by the initial number of fish in the fished area * 100). Note that the ordinate and abscissa scales vary among sites.

a) Cumulative immigration best predicted by the complex density-dependent limitation scenario



b) Cumulative immigration best predicted by the partial replacement limitation scenario



c) Cumulative immigration best predicted by the immigrants and partial replacement limitation scenario

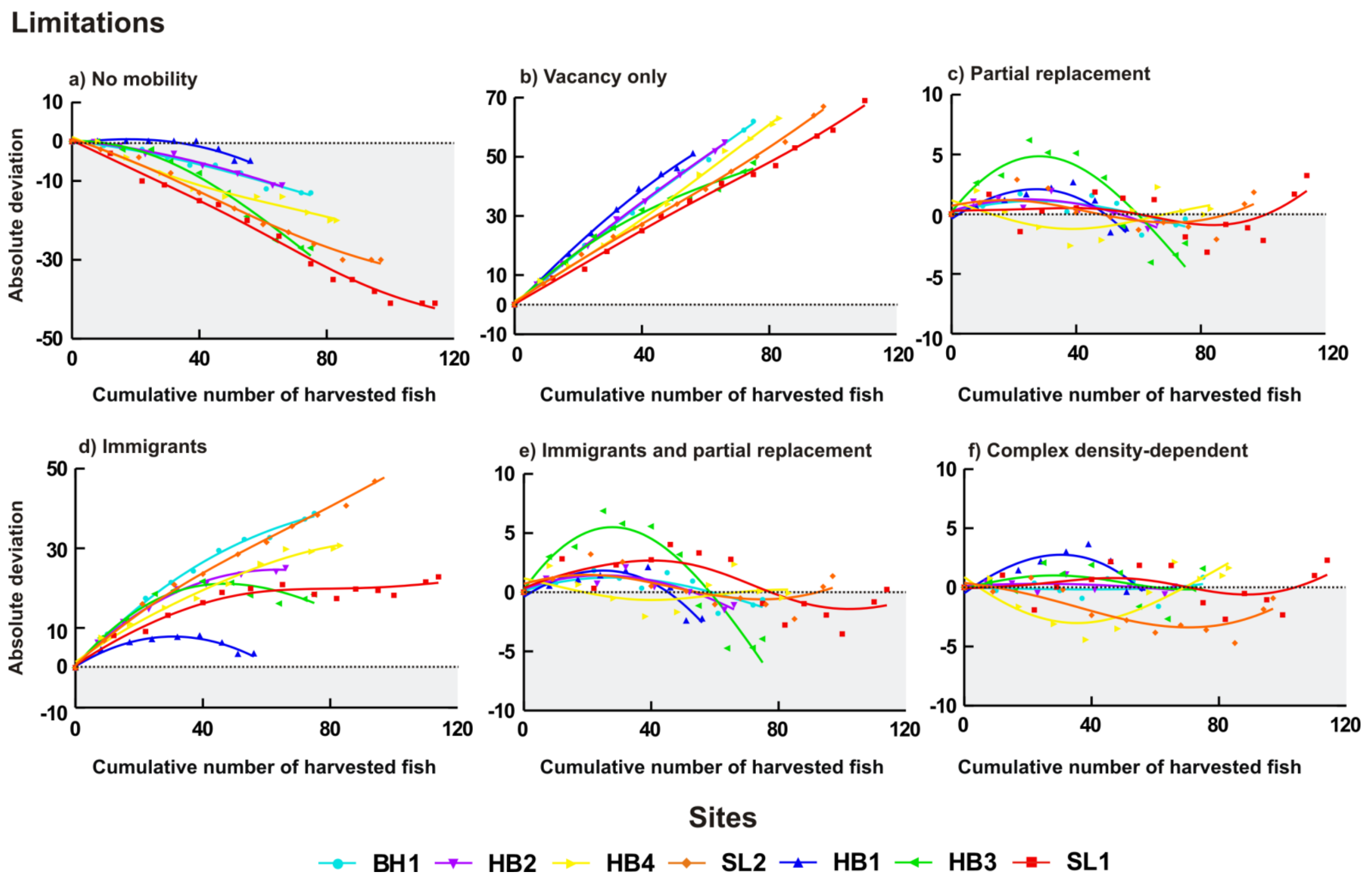


Figure 4.3. Absolute change in limitation (*i.e.* predicted values – observed values) in relation to the cumulative number of harvested fish for each of the six alternative scenarios (*Equations* 3 to 7). Each color represents a site (Bachelor Hall reef site: BH1, Heron Bay reef sites: HB1, HB2, HB3, HB4 and Sandy Lane reef sites: SL1, SL2). When the predicted line is closer to zero, the fit between observed and predicted values is better. When the scenario overestimates immigration the dots are in the white area, above the zero line. When the scenario underestimates immigration, the dots are in the grey area.

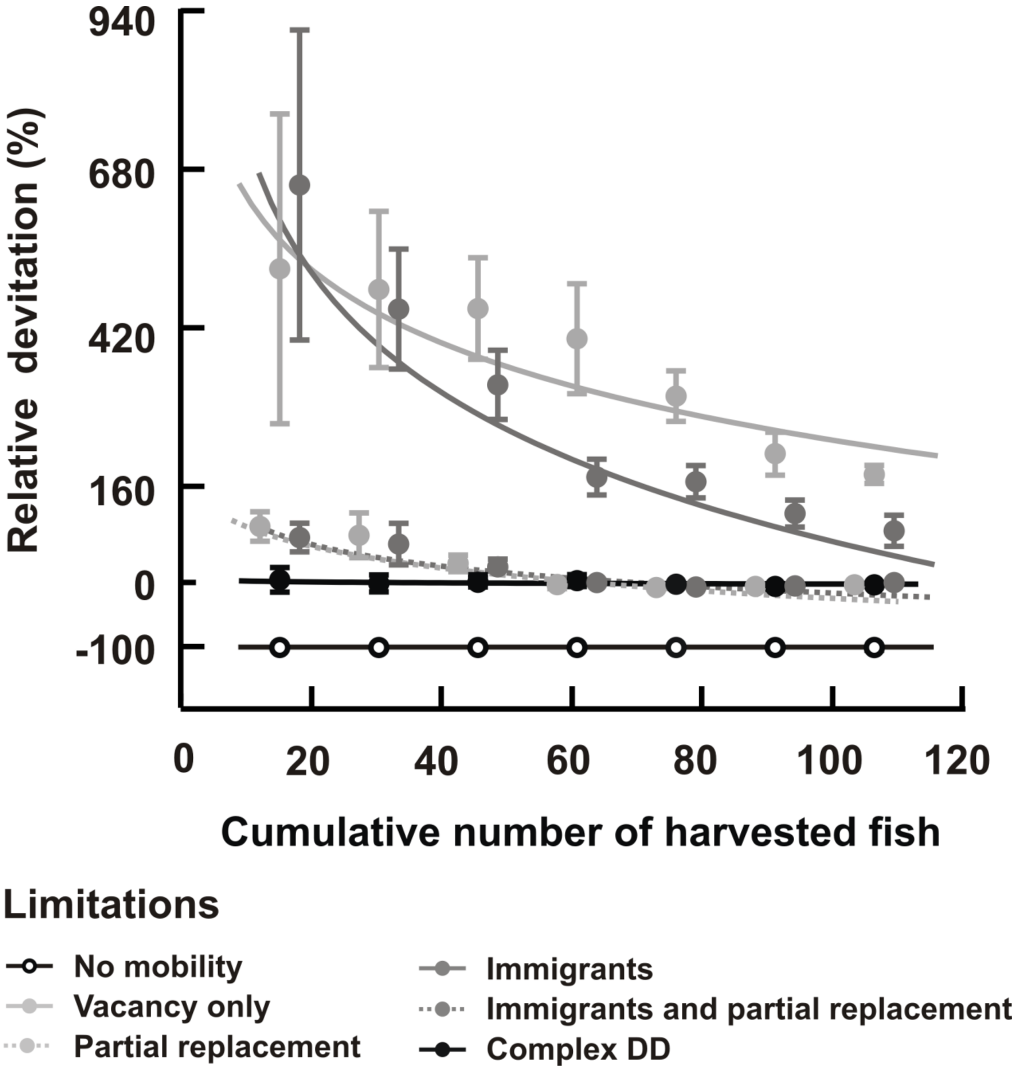


Figure 4.4. Relative change in limitation (*i.e.* (predicted values – observed values)/predicted values) in relation to the cumulative number of harvested fish for each of the six alternative scenarios (*Equations* 3 to 7). Symbols represent the mean relative change in limitation among the seven sites ± SE for the seven sites.

FINAL CONCLUSIONS

SYNTHESIS AND FUTURE DIRECTIONS

Synthesis

Short-term immigration following localized mortality has implications for metapopulation dynamics, sustainable harvest and pest control strategies, and the design of protected areas and reserves (Gell and Roberts 2003, McCullough 1996, Woodroffe and Ginsberg 1998). Although accumulating evidence is available to support the argument that immigration can successfully compensate for harvest in the short term (see *Appendix I.1*), very little evidence is available on the effect of immigration on the population dynamics in both the harvest and protected area (Amarasekare 2004, Enfjäll and Leimar 2009, Gundersen et al. 2001) and on the factors that could increase or decrease the magnitude of immigration. Because of this dearth in knowledge, previous modeling efforts to explore population flux between protected and harvest areas assumed either no movement (Hastings and Botsford 1999), free movement (*i.e.* diffusion-like movement; Claessen et al. 2009, Doak 1995, MacCall 1990, Walters 2000, Watson et al. 2000) or oriented movement (*i.e.* per capita transfer parameters set independently for the protected and harvest area; Amarasekare 2004, Beverton and Holt 1993, DeMartini 1993, Polacheck 1990). Using oriented movements facilitate the modeling of systems with intermediate mobility and allows the modeling of negative or positive density dependence. However, no, free and oriented movements assumptions cannot account for a change in direction in density dependence in immigration that can arise from behavioral interactions in the harvest and protected area. Moreover, population flux between protected and harvest areas in these model assumptions is controlled by one parameter, preventing the evaluation of the relative effect of multiple limiting factors on immigration.

In my thesis, I examine how short term immigration, through home range relocation, can affect the population dynamics in both a protected and a harvest area. I also investigate in more detail the effect of some limiting factors on immigration, namely the number of potential immigrants in the adjacent protected area, the habitat quality, landscape functional connectivity and behavioral interactions in both the harvest and protected area. I develop a new compensatory immigration framework predicting immigration in a context of harvesting and exploring the relative effect of limiting factors to immigration. I develop a set of robust predictions to evaluate how total yield, total cumulative immigration, cumulative immigration rate and population size in both the harvest and protected area vary with factors such as species mobility, size of the protected area, habitat quality, landscape connectivity and the strength of behavioral interactions (*Chapter 3*). I also use a combination of experiments to understand the effect of two limiting factors, namely functional connectivity (*Chapter 1*) and habitat quality (*Chapter 2*), on damselfish movement at the individual level. These two small scale experiments allow me to develop and calibrate empirical measurements of landscape connectivity and habitat quality as limiting factors to immigration at the landscape scale. I use a large scale experimental incremental reduction of fish populations and the empirical measurements from *Chapters 1* and *2*, to test the proposed compensatory immigration model and to evaluate the relative importance of limiting factors to immigration at the landscape scale (*Chapter 4*). I found that movement and home range relocation in damselfish are strongly limited by the landscape functional connectivity (*Chapters 1* and *4*) and habitat preference (*Chapters 2* and *4*). More specifically, relatively small sand gaps represent partial barrier to movement in damselfish which could limit immigration if vacancies following localized mortality cannot be detected and filled (*Chapter 1*). I also found that damselfish are able to detect vacancies, are able to evaluate the quality of the vacant territory and are able to move quickly to take advantage of them. In addition, I observed that behavioral interactions among neighbors in the harvest area can modulate the rate of movement and the distance travelled, mainly at high and low population density (*Chapter 2*). These habitat preferences and behavioral interactions could strongly influence the rate of immigration into a harvest area and thus explain the complex density-dependent immigration function (*i.e.* negative and then positive density dependence) observed in three of the seven replicates (*Chapter 4*).

Future directions

My thesis may generate a series of interesting avenues for future work. In Chapter 1, we developed and proposed a conceptual framework to compare the width and steepness of barrier to movement among taxa. We compared our results with other birds studies (Awade and Metzger 2008, Bélisle and Desrochers 2002, Bosschieter and Goedhart 2005, Creegan and Osborne 2005, St. Clair et al. 1998) and a preliminary analysis suggested that mobility, as indicated by the size of the territory, would be an interesting surrogate to evaluate functional connectivity for a given species. More translocation and gap-crossing studies, on a variety of taxa, are needed to strengthen this pattern.

A critical next step will be to test our compensatory immigration model on other natural systems. We tested our compensatory immigration model on two extremely territorial species that reached saturation on our study sites. The relationship between immigration and harvesting may be quite different in non-territorial species or for species that are not reaching saturation. The strongest experimental design to test our framework is likely the before-after-control-impact-pair design (BACI or BACIP; Gell and Roberts 2003, Underwood 1994). This design consists of replicated protected areas and harvest areas that are paired with control locations (without protection). Data are collected at intervals before and after the start of protection. However, replication at the scale of a protected area is difficult because control and treatment sites have to be far enough to be independent but not so far to change the environmental conditions. In addition, demands for manpower can be very high making it nearly impossible to do multiple replicates in the same time period. Tracking movement of species targeted by protected area at the scale of a protected area can be also quite challenging because they are often highly mobile and have large home ranges. Small scale model systems (*e.g.*

Stegastes damselfish in this thesis, small mammals and insects with classic experiments on *Tribolium* sp.) may circumvent some of these complexities. Instead of establishing a protected area in a harvested region, we established harvest area in an unharvested region. However, we should not assume that observed immigration pattern when establishing a harvest area will necessary be a mirror pattern of establishing a protected area. This has to be tested experimentally.

In our study, we tested the effect of harvesting on immigration from one protected area. In the future, it may be relevant to test the effects of multiple smaller harvest areas and protected areas on immigration and stability of the metapopulation as suggested by McCullough (1996). This is strongly related to the debate of using a single large or several small protected areas (*i.e.* SLOSS; McNeill and Fairweather 1993, Simberloff 1976, Wilcox and Murphy 1985). Using several small protected areas adjacent to harvest areas will likely increase the edge effect near the protected area boundary (Woodroffe and Ginsberg 1998), and a higher proportion of the population in the protected area will be affected by harvesting. This can have beneficial effect for harvesters if the target species has low mobility and a small perceptual range but can increase the risk of metapopulation extinction for highly mobile species. This could have strong implications for population management and conservation with the design of protected areas.

In the future, I see two major ways in which the compensatory immigration model can be expanded. First, it would be interesting as more global management goal to develop and test a multispecies or a community compensatory immigration model by integrating competition for space. During the data collection, we observed that the removal of damselfish strongly affected the behavior and space use of large herbivores such as parrotfishes and surgeonfishes (K. Turgeon; *unpublished data*). A change in behavior and space use of heterospecifics following the removal of a species can affect the population dynamics of both the removed species and heterospecifics. In addition, to apply the multispecies model, we should calibrate functional connectivity and habitat quality indexes for each species of interest. Second, the compensatory immigration model could be applied in a broader context and at a larger temporal scale by evaluating the effect of different short-term immigration functions, that vary in their magnitude and strength of density dependence, on reproduction and survival of the population in the following year. Immigration can have both positive and negative effects on metapopulation dynamics by causing the per capita growth rate to be higher at lower abundances compared to an isolated population or by accelerating population decline by phenomena related to Allee effect (Stenseth and Lidicker 1992, Saether et al. 1996, Travis et al. 1999). Depending on the exact nature of immigration (*i.e.* magnitude and density dependence) and its effect on reproduction and survival, the effects on metapopulation dynamics and persistence can be quite different. I am confident that we can improve our predictions concerning the metapopulation dynamics in a context of harvesting by using the compensatory immigration model as migration function between the harvest and protected area.

BEHAVIORAL INTERACTIONS AND HETEROGENEOUS LANDSCAPES AFFECT IMMIGRATION. IMPLICATIONS FOR POPULATION MANAGEMENT

This thesis and other studies (Amarasekare 2004, Enfjäll and Leimar 2009, Gundersen et al. 2001, Woodroffe and Ginsberg 2000) have suggested that immigration can have beneficial consequences for harvested populations and harvesters but can also have significant detrimental effects for the metapopulation viability, depending on species mobility, landscape characteristics, behavioral interactions, and the population size in the protected area. Heterogeneous landscapes, variable population sizes, demographic changes and behavioral interactions in both the harvest and protected area considerably complicate the management of animal populations. In this thesis, we provide some direct and indirect empirical evidence for a strong effect of all these factors on immigration. Thus, there is an urgent need to develop realistic but general immigration models that account for the inherent complexity of natural system in a context of harvesting and to test their predictions. This is needed to reduce uncertainty in management strategies and to avoid overharvesting that could lead to local population extinctions. I believe that my compensatory immigration model is easy to understand, applicable and sufficiently general to be used in sustainable harvesting and conservation on a variety of systems.

Having strong support for specific immigration function in a harvesting context is crucial for resolving debates about the usefulness of protected areas as a management strategy. If compensation from immigration does occur, even if only partially, then protected areas can play a key role in management, as well as in conservation. Although the use of protected area and related compensatory immigration sounds promising, additional studies are needed to strengthen our confidence in the usefulness of protected areas as a management strategy. To do so, we have to bring some tangible proof to hunters and fishers that a protected area will increase the yield in the short term via immigration and in the long term by enhancing reproduction and survival. In addition, we have to understand which factors can increase or decrease the magnitude of immigration. In this thesis, I provide evidence that immigration from protected area to harvest area occurred, and occurred over the whole range of density and is modulated by difference in habitat quality and landscape functional connectivity.

Together, the four chapters of my thesis bring some insight about population processes and individual behavior affecting immigration in response to harvest. I hope this thesis will generate discussions to improve the theory of sustainable harvesting. The theory could be improved by actively including the use of protected areas and density-dependent immigration as a sustainable and stable harvesting strategy. Hopefully, this thesis will help to decrease uncertainty in management by a better understanding of the factors that can increase or decrease the rate of immigration and its potential effects at the metapopulation level and will participate to reduce overharvesting of exploited populations.

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APPENDICES

APPENDIX I.1: METHODOLOGY USED FOR THE LITERATURE SEARCH IN THE SYNTHESIS ABOUT MIGRATION IN VERTEBRATE POPULATIONS WITH THE LIST OF REFERENCES

Methodology for the literature search and database construction for the synthesis on compensatory immigration in vertebrate populations (Turgeon and Kramer, In prep.)

To survey the literature and identify studies reporting compensatory immigration following a decrease in population size in vertebrates, we searched with ISI Web of Science (1968-2010) and Google scholar (1900-2010) using the keywords “immigra*”, “compensat*” “density reduction”, “recovery”, “removal and experiment”, “density and experiment” “density and manipulation”, “density-dependent movement” in the title and in the abstract. Google scholar allows searching for keywords in the core text of recent articles as well. The latest access was on June 22nd 2010. We also considered studies cited in or citing these references.

We used certain criteria to include studies in the database. First, the study had to contain initial population size (or density) before the density manipulation. Second, information about the removal pressure (e.g. number of individual removed for the whole removal experiment) and strategy (one removal event or successive removals) should be available. Third, the study has to be clear and unequivocal about the number of immigrants observed over a given period of time. Fourth, the period of time examined should not include recruitment from reproduction because we are interested to quantify the magnitude of short term compensatory immigration for a given cohort. Finally, we excluded data on invertebrates and focus on vertebrates.

From the 44 articles found and respecting the above mentioned criteria, 118 data points (hereafter called studies) were extracted and used as independent replicates. Individual article frequently yielded multiple studies (range: 1 to 14 studies per article) because compensatory immigration can vary among spatial replicates, temporal replicates and/or species in multi-species articles.

For each study, we extracted the initial density or population size, the number of removed individuals, the removal strategy (i.e. one single removal or successive removals) and the number of immigrants. With this information, we calculated the percentage of replacement (i.e. proportion of removed individuals replaced by immigrants * 100). For each article, we obtained information about the number of replicates and independent controls and we extracted information about identified factors susceptible to affect compensatory immigration and if they were explicitly quantified (Q), only mentioned (M) or not mentioned at all (NM).

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APPENDIX 1.1: MODELS EXPLAINING THE PROBABILITY OF CROSSING AN IMPOSED SAND GAP IN TWO REEF CONFIGURATIONS

Generalized Linear Mixed Models used to explain the probability of crossing an imposed sand gap in Detour and Patch configurations in relation to width of the sand gap, configuration ratio, linear density of damselfish along the alternative route that maximized the use of reef and the interaction between sand gap width and the configuration ratio. Model-averaged standardized estimates of predictors, unconditional standard errors (SE), 95% Confidence intervals and the Akaike weight (w_i), which is interpreted as the proportional weight of evidence for a particular model, are presented for each predictor. All models include a constant. Predictors in bold do not contain zero within the 95% confidence intervals.

Predictors	Detour configuration (n = 28)			Patch configuration (n = 27)		
	Estimate ± SE	95% CI	w_i	Estimate ± SE	95% CI	w_i
(Constant)	**-4.11 ± 2.24**	**-8.48 to 0.26**	**1.0**	**-1.65 ± 0.78**	**-3.17 to -0.13**	**1.0**
Sand gap width	**-6.10 ± 3.04**	**-11.9 to 0.12**	**1.0**	**-2.23 ± 0.90**	**-3.98 to -0.49**	**1.0**
Configuration ratio	-1.45 ± 1.38	-4.14 to 1.22	0.83	-	-	-
Density·	-0.33 ± 0.71	-1.71 to 1.05	0.36	-0.09 ± 0.16	-0.40 to 0.23	0.23
Sand gap * Conf. ratio	-6.39 ± 3.36	-12.9 to 0.17	0.83	-	-	-

APPENDIX 1.2: MODELS EXPLAINING THE DEVIATION OF THE HOMING PATH IN RELATION TO THE NUMBER OF AGONISTIC INTERACTIONS AND EXPLAINING THE NUMBER OF AGONISTIC INTERACTIONS RECEIVED IN RELATION TO CONSPECIFIC DENSITY

Generalized Linear Mixed Models used to explain a) the number of agonistic interactions received during homing in relationship to the deviation of the homing path from the alternative route maximizing the use of reef and b) the relationship between the number of agonistic interactions received and the density of damselfish along the homing path. Parameter estimates, standard errors (SE) and the 95% confidence intervals of each parameter are presented. All models include a constant. For the configuration predictor, we used a treatment contrast and Continuous configuration was the contrast. Predictors in bold do not contain zero within the 95% confidence intervals.

Predictors	Estimate ± SE	95% CI
a) Deviation from the alternative path in relation to agonistic interactions		
(Constant)	**0.10 ± 0.05**	**0.01 to 0.20**
Number of attacks received	**0.02 ± 0.01**	**0.01 to 0.04**
Configuration: Detour	**-0.17 ± 0.07**	**-0.31 to -0.03**
Configuration :Patch	-0.02 ± 0.07	-0.17 to 0.12
Attacks received* Config.: Detour	**-0.02 ± 0.01**	**-0.05 to -0.01**
Attacks received* Config.: Patch	-0.01 ± 0.02	-0.05 to 0.03
b) Relationship between the agonistic interactions and conspecific density		
(Constant)	2.73 ± 1.793	-0.78 to 6.25
Damselfish density along the route	-2.85 ± 3.64	-9.98 to 4.27
Configuration: Detour	3.11 ± 1.62	-0.07 to 6.29
Configuration: Patch	0.18 ± 1.63	-3.00 to 3.37

APPENDIX 1.3: VARIATION IN BARRIER SIZE AND STEEPNESS AMONG TAXA IN RELATION TO BODY MASS AND TERRITORY DIAMETER

Species mass (g) and territory diameter (m) in relationship to the size of the barrier (defined as the minimal barrier width at a 50% probability of crossing the gap), the Delta (difference in the size of the gap at probabilities of crossing between 25 and 75%), the steepness (% drop in the probability of crossing a gap per m) and the relative steepness (% drop in the probability of crossing a gap per m scaled to the barrier size) for 11 species distributed among 6 studies. The barrier size at 50% probability of crossing and the Delta values were extracted by using the Logit equation (if provided in the article) or by using figures (if the equation was not available).

Species	Taxon	Mass (g)	Territory diameter (m)	Barrier size (m)	Delta (25 - 75%)	Steepness % drop · m^{-1}	Relative steepness
[1]*Stegastes diencaeus* (detour)	Fish	19.0	1.2	1.85	0.3	166.7	3.08
[1]*Stegastes diencaeus* (patch)	Fish	19.0	1.2	3.9	1.2	41.7	1.63
[3]*Acrocephalus scirpaceus*	Bird	9.5	-	14.0	18	0.40	0.19
[2]*Basileuterus culicivorus*	Bird	10.0	20.0	49.0	126	2.78	1.06
[5]*Dendroica coronata*	Bird	11.0	247.0	133.0	73	0.78	0.31
[4]*Fringilla coelebs*	Bird	12.5	101.0	40.0	55	0.68	0.41
[4]*Parus ater*	Bird	10.5	205.0	60.0	36	0.91	0.13
[5]*Poecile atricapillus*	Bird	6.0	147.0	20.0	54	1.39	0.57
[6]*Poecile atricapillus*	Bird	10.0	20.0	49.0	0.3	0.50	0.67
[5]*Regulus satrapa*	Bird	20.6	113.0	35.0	1.2	2.27	0.45
[5]*Sitta canadensis*	Bird	19.0	1.2	1.85	18	0.93	0.56
[2]*Thamnophilus caerulescens*	Bird	10.5	160.0	38.0	73	1.61	0.57
[5]*Vireo olivaceus*	Bird	19.0	1.2	3.9	55	0.96	0.62

Literature cited in Appendix 1.3

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APPENDIX 2.1: MODELS EXPLAINING THE PROBABILITY THAT A TERRITORY WOULD BE RECOLONIZED AFTER THE REMOVAL OF THE FIRST COLONIZER AND THE SECOND COLONIZER

Generalized Linear Mixed Models used to explain a) the probability that a territory would be recolonized after the removal of the first colonizer and b) the removal of the second colonizer for longfin damselfish and dusky damselfish. Parameter estimates, standard errors (SE) and the 95% confidence intervals (CI) of each parameter are presented. All models include a constant. Predictors in bold do not contain zero within the 95% confidence intervals. The partial deviance explained by each predictor is presented.

	Longfin damselfish		Dusky damselfish	
Predictors	Estimate ± SE	95% CI	Estimate ± SE	95% CI
a) Probability that a territory would be recolonized after the removal of the first colonizer (Longfin, n = 133; Dusky, n = 64)				
(Constant)	**-4.43 ± 1.39**	**-7.16 to -1.70**	-3.73 ± 2.46	-8.54 to 1.09
Population size	1.04 ± 0.83	-0.60 to 2.67	2.21 ± 1.21	-0.17 to 4.59
Body size	**0.33 ± 0.13**	**0.08 to 0.58**	0.25 ± 0.30	-0.36 to 0.85
b) Probability that a territory would be recolonized after the removal of the second colonizer (Longfin, n = 82; Dusky, n = 33)				
(Constant)	**-3.38 ± 1.61**	**-6.53 to -0.23**	-4.61 ± 4.60	-13.7 to 4.41
Population size	1.21 ± 1.08	-0.91 to 3.33	2.66 ± 2.42	-2.08 to 7.41
Body size	*0.24 ± 0.14*	*-0.04 to 0.53*	0.23 ± 0.58	-0.90 to 1.36

APPENDIX 2.2: CONTINGENCY TABLE AND PEARSON χ^2 TO TEST WHETHER RECOLONIZATION IS SPECIES AND SEX SPECIFIC IN LONGFIN AND DUSKY DAMSELFISH

Appendix 2.2a: Contingency table and Pearson χ^2 to test whether recolonization is species specific

Species of the colonizers, i.e. individual that performed territory relocations and shifts and of former territory occupants among the 9 sites (7 density-manipulated sites and two controls)

Former occupant Colonizer	Dusky damselfish	Longfin damselfish	Total
Dusky damselfish	76 (73.1%)	28 (26.9%)	104
Longfin damselfish	24 (10.0%)	209 (89.7%)	233
Total	100	237	337

Pearson χ^2 value = 135.789, p-value < 0.001

Appendix 2.2b: Contingency table and Pearson χ^2 to test whether recolonization is a function of sex and maturity level in longfin damselfish

Sex and maturity level of colonizers, *i.e.* individual that performed territory relocations and shifts and of former territory occupants among the 9 sites for longfin damselfish. Classes are exclusive (*e.g.* males with nest are not included in the mature males class)

Former occupant Colonizer	Immatures	Mature females	Mature males	Males with nest	*Total*
Immatures	55 (55.5%)	21 (21.2%)	17 (17.1%)	6 (6.1%)	99
Mature females	6 (13.3%)	30 (66.7%)	5 (11.1%)	6 (8.9%)	45
Mature males	8 (16.3%)	10 (20.4%)	15 (30.6%)	16 (32.6%)	49
Males with a nest	0 (0.0%)	5 (71.4%)	0 (0.0%)	2 (28.6%)	7
Total	69	66	37	28	200

Pearson χ^2 value = 75.923, p-value < 0.001

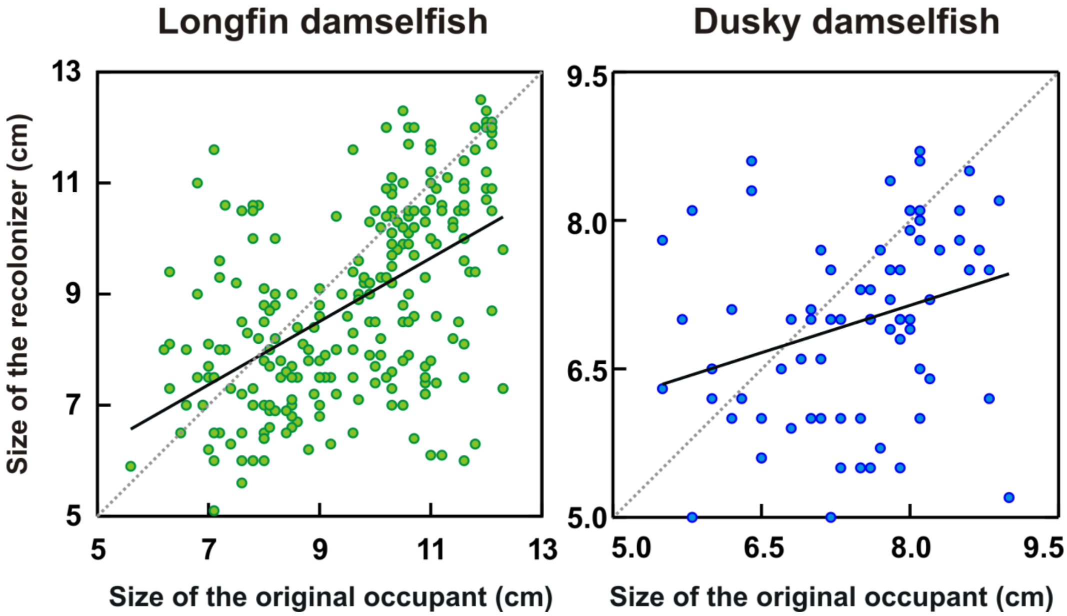
Appendix 2.2c: Contingency table and Pearson χ^2 to test if recolonization is function of sex and maturity level in dusky damselfish

Sex and maturity level of colonizers, *i.e.* individual that performed territory relocations and shifts and of former territory occupants among the 9 sites for dusky damselfish. Classes are exclusive (*e.g.* males with nest are not included in the mature males class).

Former occupant Colonizer	Immatures	Mature females	Mature males	Males with nest	*Total*
Immatures	12 (34.3%)	9 (25.7%)	12 (34.3%)	2 (5.7%)	22
Mature females	4 (18.2%)	14 (63.6%)	4 (18.2%)	0 (0.0%)	35
Mature males	2 (20.0%)	2 (20.0%)	4 (40.0%)	2 (20.0%)	10
Total	18	25	20	4	67

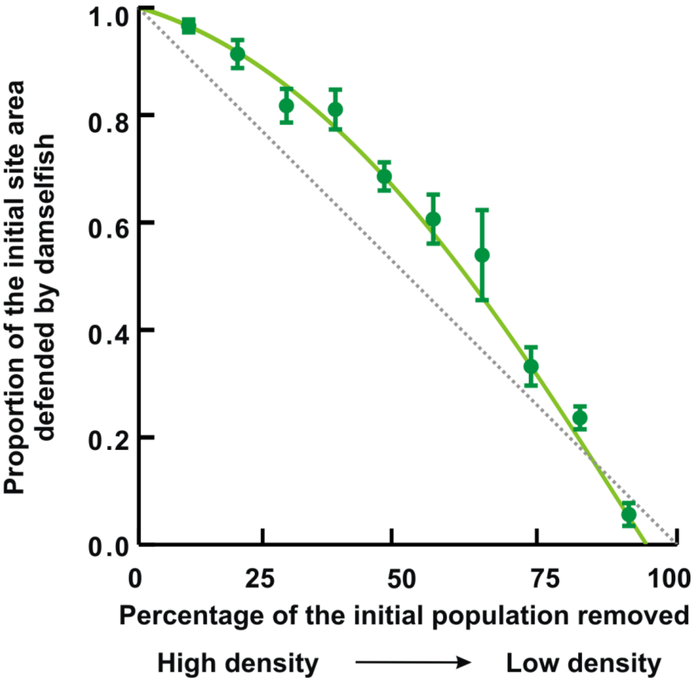
Pearson χ^2 value = 13.854, p-value = 0.031

APPENDIX 2.3: RELATIONSHIP BETWEEN BODY SIZE OF THE DAMSELFISH THAT RECOLONIZED A VACANT TERRITORY AND BODY SIZE OF THE ORIGINAL OCCUPANT



Body size of the damselfish that recolonized vacant territories in relation to the body size of the original occupant for longfin damselfish and dusky damselfish. The black line represents the best fit from a regression model. The dotted grey lines represent the 1:1 relationship.

APPENDIX 2.4: RELATIONSHIP BETWEEN THE AREA DEFENDED BY DAMSELFISH AND THE PERCENTAGE OF THE INITIAL POPULATION SIZE REMOVED



Proportion of the site area defended by damselfish (*i.e.* occupied by territories) after a removal event t compared to the initial area defended when the site was at saturation in relation to the percentage of the initial population size removed. The dashed grey line represents a linear proportional ($f(x) = ax + b$) reduction of the area defended by damselfish in relation to the percentage of the initial population size removed and the grey curve represents the best fitting curve using a power function ($f(x) =ax^b$). To fit the two functions we used (100- percentage of the initial population size removed for x values), Symbols represent the mean proportion of the initial site area defended by damselfish among the seven sites ± SE for the seven sites.

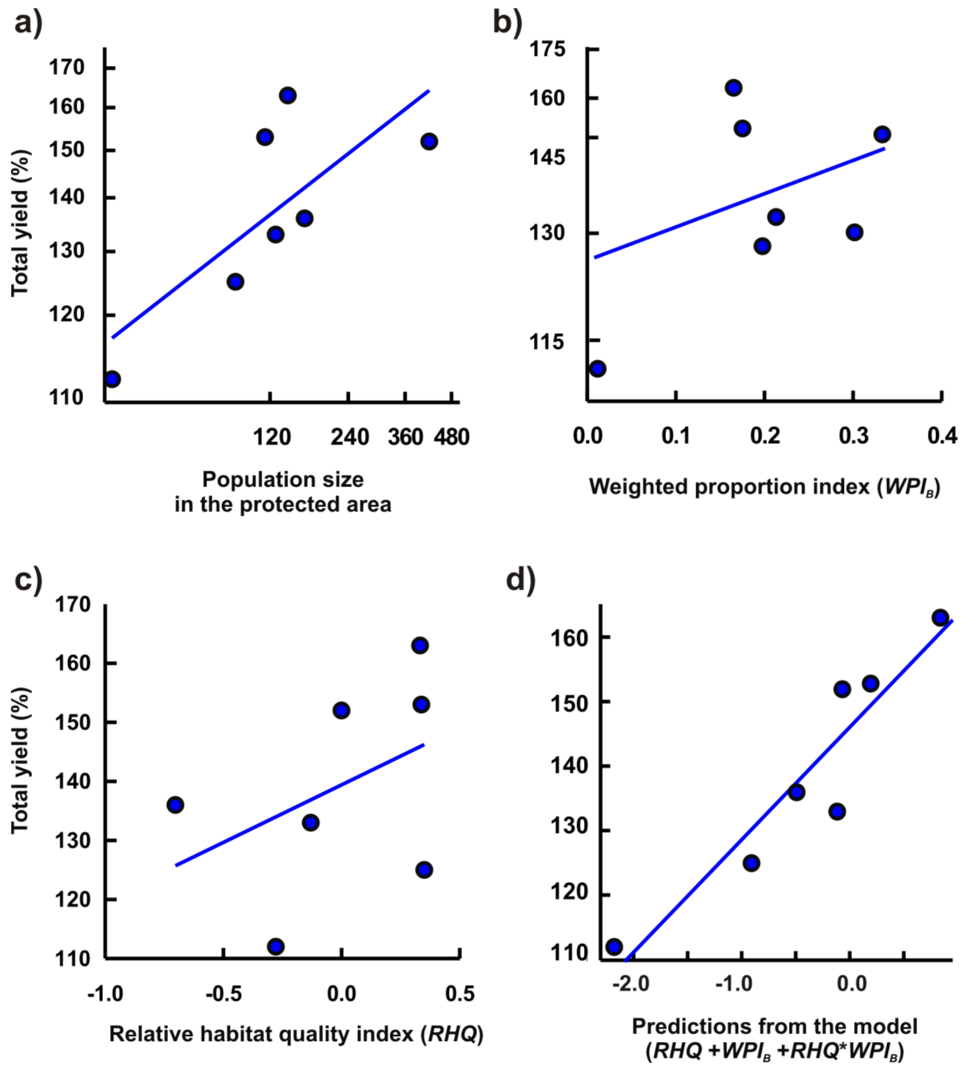
The power function ($f(x) =ax^b$) had a higher support than a linear function ($f(x) = ax + b$) to explain the proportion of the site area defended by damselfish in relation to the percentage of the initial population size removed using AICc scores ($w_i = 0.99$; $\Delta AIC_c = 40.6$). See Methods in *Chapter 1* (*Model construction and assessment;* Burnham and Anderson 2002) for details about AICc calculation and interpretation.

APPENDIX 4.1: MODEL SHOWING WHICH ALTERNATIVE SCENARIOS DIFFER FROM THE COMPLEX DENSITY-DEPENDENT LIMITATION SCENARIO WHEN CONTROLLING FOR CUMULATIVE HARVEST

Generalized Linear Model (GLM) used to explain the difference between the six alternative limitation scenarios (*Equations* 3 to 7 from *Chapter 4*) predicting cumulative immigration in relation to cumulative harvest when controlling for cumulative harvest in the model. The scenario 6, the complex density-dependent scenario is used as the contrast. Predictors in bold do not contain zero within the 95% CI.

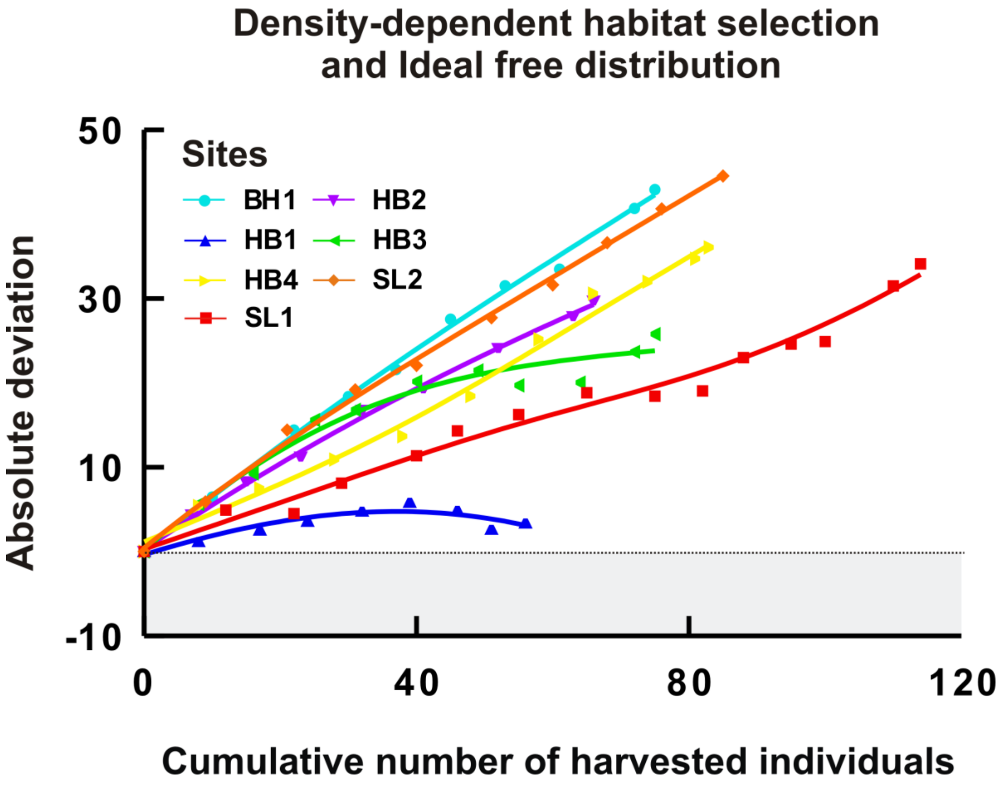
Predictors	**Estimate**	**SE**	**t-value**	**95% CI**
Constant	**118.14**	**28.72**	**4.113**	**61.84 to 174.44**
Cumulative harvest	-2.17	0.34	-6.311	-2.84 to -1.50
Difference between limitations				
Complex density-dependent (CDD) vs. partial replacement	17.73	31.08	0.570	-43.18 to 78.64
CDD vs. immigrants	**257.58**	**31.08**	**8.288**	**196.67 to 318.50**
CDD vs. immigrants and partial replacement	20.86	31.08	0.671	-40.05 to 81.77
CDD vs. no mobility	**-101.41**	**31.08**	**-3.263**	**-162.32 to -40.50**
CDD vs. vacancy only	**412.76**	**31.08**	**13.281**	**351.85 to 473.67**

APPENDIX 4.2: RELATIONSHIP BETWEEN TOTAL YIELD AND INDEPENDENT MEASUREMENTS OF PROTECTED POPULATION SIZE, HABITAT QUALITY AND FUNCTIONAL CONNECTIVITY



Relation between total yield (number of harvested fish divided by the initial number of fish in the fished area * 100) at the end of the removal experiment and a) the population size in the adjacent protected area, b) the Weighted Proportional Index ($\mathrm{WPI_B}$) used as a surrogate for landscape functional connectivity, c) an index of relative habitat quality (*RHQ*) and d) predictions from the model including *RHQ*, WPI_B and their interaction. Each dot represents a site.

APPENDIX 4.3: ABSOLUTE CHANGE IN LIMITATION FROM THE DENSITY-DEPENDENT HABITAT SELECTION MODEL (PARTIAL REPLACEMENT SCENARIO)



Absolute change in limitation (*i.e.* predicted values – observed values) in relation to the cumulative number of harvested fish for each of the partial replacement scenarios, assuming density-dependent habitat selection (*Equation 5*). Each color represents a site (Bachelor Hall reef site: BH1, Heron Bay reef sites: HB1, HB2, HB3, HB4 and Sandy Lane reef sites: SL1, SL2). See Figure 4.3 for interpretation.