Seascape Genetics and Conservation Management of the Olive Ridley Turtle (*Lepidochelys olivacea*) in the Eastern Pacific

Clara Jimena Rodríguez Zárate

MSc in Marine Ecology

Thesis submitted in fulfilment of the requirements for the

Degree of Doctor of Philosophy

School of Biological Sciences
Faculty of Science and Engineering
Flinders University of South Australia

December 2014

This study was supported by the Australian Research Council (DP110101275 to Beheregaray, Möller & Waters).

This dissertation should be cited as:

Rodríguez-Zárate (2014) *Seascape Genetics and Conservation Management of the Olive Ridley Turtle (Lepidochelys olivacea) in the Eastern Pacific.* PhD Thesis, Flinders University of South Australia, Australia.

to the divine energy that creates and sustains all within us

to my mum that accompanied every moment of this journey

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Clara Jimena Rodríguez Zárate

December 2014

I consent to this thesis being made available for photocopying and loan under the appropriate Australian copyright laws.

ACKNOWLEDGMENTS

This work would not be possible without the multiple and wonderful coincidences of life that gradually arranged situations, collaborations, and guidelines for encouraging this work. I thank each of the people who directly or indirectly allowed this learning process and who accompanied me. I would like to thank in particular:

To Professor Luciano Beheregaray my supervisor, to open this opportunity to work together, without him this would not have been possible. Thanks for your support and guidance during this work. For the valuable experience and constructive criticism of my work. I did learn a lot and not only as a scientist but as a human being. Especially I am grateful for your understanding and support in the personal situations of recent years.

To Associate Professor Luciana Moller my co-supervisor for supporting this work and collaborating with valuable ideas. I also appreciate your understanding and support in the personal situations of recent years.

To Axayacatl Dr. Rocha Olivares for the opportunity to continue working together, and his contributions to this work.

To Dr. Pitta Verweij for your interest and important contributions to this work.

To Ms. Emelina Corrales and Dr. Thomas Legrand for their interest, ideas and

contributions to this work. Thank you for offering me a great environment to work during my stay in Paris, and for the interesting conversations while enjoying a wonderful *mousse au chocolat!*.

To Dr. Rob Keane and his group for their contribution and collaboration with oceanographic data processing. Especially thank you for your patience with the turtle project "Madness". Thanks for the laughs, and the stories that made those evenings the most relaxing and enjoyable of my PhD work, besides my fieldwork offcourse!!.

To Dr. Erick Van Seville for his interest and contribution. For his valuable help with the analysis of oceanographic modelling.

To Dr. Jeffrey Seminoff for his support and donation of tags.

To all who contributed to the collection of samples. I am especially grateful to: CONANP camp sites in Mexico, ASUPMATOMA, ProPenínsula, Grupo Tortuguero - Pescadero, City of Los Cabos, Cabo Pulmo- AC, Technological Institute of Banderas Bay, Puerto Vallarta Tortugas Marinas, GAPEA, Mexican Turtle Center and State Government Program Chiapas, Fundacion ARCAS, AKAZUL, Fauna & Flora International, Nicaragua, Ministry of environment and Natural resources of El Salvador, FUNZEL, ASVO, and Authority Panama aquatic resources for assistance in the field.

To all my colleagues at the Molecular Ecology Laboratory at Flinders University:

Kerstin Bilgmann, Rita Amaral, Jo Wiszniewski, Catherine Attard, Minami Sasaki, Peter Teske, Shannon Loughnan, Fabricius Domingos, Chris Brauer, Jonathan Sandoval-Castillo for their friendship and help when needed.

To My office friends Kerstin Bilgmann, Rita Amaral, Katharina Peters, Fabricius Domingos, Chris Brauer, Nikki Sanardo for their friendship, and the good coffee times shared. Especially, thank you Fabricius for the rescue kit with amazing Brazilian coffee and traditional sorted biscuits. Thank you all for your support and fun.

All members of the School of Biological Sciences at Flinders University especially Sandra Marshall for all their help with administrative processes during my manager position at the Laboratory of Molecular Ecology and the stories made me laugh.

To my soul friends Chini, Kerstin Bilgmann, Rita Amaral, Katharina Peters, Dafne Sandoval, Nahid Shokri, for their unconditional support, their affection through all these years, and the moments of joy that always got me emotional balance. Without them I would not have been able to go through the many difficult moments in these years but neither could laugh out loud on this crazy but wonderful life.

To Chini, for her invaluable friendship, commitment to nature, time and also adventurous ideas. For having always a good joke to cheer me up, and the long conversations even at dawn.

To Guido Parra my compatriot in Adelaide for your friendship, support, advice and fun. Specially, thanks for the jokes at the best *consteño* style.

To my dear friend Mario Jolon-Morales for his support, contributions and excellent long conversations about turtles.

To David Rudd for his advice and encouragement during the final stage of my PhD.

To my beautiful family for their support and affection. Especially my sister and my dad, who have been a key support for my existence, a divine gift in my life. To my brother Rodolfo who created the most beautiful illustrations for this work.

To the Conte family, for being my family in Adelaide. For welcoming me, loving me, taking care and supporting me. Especially Maria Conte whom unconditionally extended her love as mother to me. Thank you Conte Family for sharing your magnificent vineyards and beautiful wine, this was a precious gift, which gave me happiness, and wonderful and unforgettable moments.

To Danial for being by my side, supporting me, for making hard times something lighter. Thank you for your natural way to make me smile; for being the place where to rest in peace every day. Without you this adventure would have been more difficult.

To the *TURTLES,* for their magnificent nature that represent wisdom, endurance and strength.

STATEMENT OF AUTHORSHIP

Chapter I

C.J.R.Z.

Chapter II

Data collection : C.J.R.Z.

Laboratory methods : C.J.R.Z.

Statistical analysis : C.J.R.Z.

Manuscript writing : C.J.R.Z., A.R.O, L.B.

Chapter III

Data collection : C.J.R.Z., R.K.

Laboratory methods : C.J.R.Z.

Statistical analysis : C.J.R.Z., E.V.S.

Manuscript writing : C.J.R.Z., L.B.

Chapter IV

Data collection : C.J.R.Z.

Analysis : C.J.R.Z.

Manuscript writing : C.J.R.Z., E.C., T.L., P.V.

Chapter V

C.J.R.Z.

SUMMARY

The assessment of the conservation status of olive ridley turtles (*Lepidochelys olivacea*) in the eastern Pacific remains poorly known due to a lack of information about solitary nesting sites and due to inadequate definition of population boundaries. This dissertation contributes to the evaluation of the status of olive ridley nesting colonies in the eastern Pacific, including those that experienced substantial demographic declines. The main aims of the thesis are to use nuclear DNA datasets from a large sample (n = 634 individuals collected at 28 nesting sites) and a combination of population and seascape genetics approaches to (i) clarify population structure and recent demographic history in olive ridley turtles at various spatial scales and (ii) assess environmental factors influencing population connectivity in this species. In addition, the genetic findings of this work are combined with information from the literature and from data of interviews with relevant stakeholders to review current conservation practices and propose ways to tackle challenges associated with large-scale conservation management. The analysis of the genetic consequences of demographic declines revealed signatures of a recent bottleneck along Mexico's eastern Pacific coast. The bottleneck signal was strong across the highly connected metapopulation and also apparent in six nesting sites in a pattern consistent with the history of demographic disequilibria produced by their overexploitation. This likely represents the first report of recent signatures of anthropogenic-driven population declines in sea turtles based on genetics. On a much larger geographic extent, olive ridley turtles were used as a model system to investigate the role of space in assessing and understanding processes shaping population divergence in highly mobile marine species. The prevailing hypothesis of panmixia for this species in the eastern Pacific was rejected. A seascape genetics approach showed that meso-scale features and associated oceanographic variability likely promote and maintain population divergence in olive ridley turtles, allowing us to propose a new paradigm of isolation-by–ecology for sea turtles. The combined results highlight the importance of reframing management policies and actions to pursue large-scale conservation actions for this taxon. They also provide a framework that enables reconciliation between biological phenomena and conservation management. The Mesoamerican region has the opportunity to assume the challenges of large-scale conservation management based on the multiple capacities developed in recent decades. To achieve this target, a list of perceived limitations that must be sufficiently addressed is presented and a series of management recommendations are made.

Keywords: conservation genetics, isolation-by-ecology, seascape genetics, anthropogenic harvest, sea turtles, eastern Pacific.

List of Publications and Collaborations Developed During this Thesis

Chapter II has been published in Biological Conservation (2013) 168, 10-18.

Chapter III will be submitted to Ecology Letters.

Chapter IV will be submitted to PLoS ONE.

During the period of her PhD thesis candidature, the candidate also contributed to other research collaborations that resulted in the following publications:

- Proietti, M.C., Reisser, J., Marins, L.F., **Rodríguez-Zárate, C.**, Marcovaldi, M.A., Monteiro, D.S., Pattiaratchi, C., Secchi, E.R., 2014. Genetic Structure and Natal Origins of Immature Hawksbill Turtles (*Eretmochelys imbricata*) in Brazilian Waters. PLoS ONE 9, e88746.

- **Rodríguez-Zárate, C**., Carvalho, D., Hammer, M., Beheregaray, L., 2014. A set of microsatellite markers for the threatened Murray hardyhead, *Craterocephalus fluviatilis* (Pisces: Atherinidae) from the southern Murray–Darling Basin. Conservation Genetics Resources, 1-3.

- Carvalho, D., **Rodríguez-Zárate, C.**, Hammer, M., Beheregaray, L., 2011. Development of 21 microsatellite markers for the threatened Yarra pygmy perch (*Nannoperca obscura*) through 454 shot-gun pyrosequencing. Conservation Genetics Resources 3, 601-604.

- Gongora, J., Cuddahee, R.E., Nascimento, F.F.d., Palgrave, C.J., Lowden, S., Ho, S.Y.W., Simond, D., Damayanti, C.S., White, D.J., Tay, W.T., Randi, E., Klingel, H., **Rodríguez-Zárate, C.J.**, Allen, K., Moran, C., Larson, G., 2011. Rethinking the evolution of extant sub-Saharan African suids (Suidae, Artiodactyla). Zoologica Scripta 40, 327-335.

Chapter I:

General Introduction

For centuries, sea turtles have captured the attention of human societies and been seen as the sailors of the sea. Their ancient characteristics have made them part of early cosmogonies around the world, which have conceived them as spiritual beings of wisdom, longevity, and great fertility (Garfield, 1986; Stookey, 2004). Sea turtles have provided nutritional and economic sustenance to remote communities around the world for millennia (Barragán, 2012; Frazier, 2003). In the last century the intensification of sea turtle exploitation brought some populations to exhaustion (Bjorndal, 1981; Frazier, 1980; Márquez-M *et al.*, 1982; Witzell, 1994), and today global efforts are carried out to recover them, due to sea turtles' ecological value and their role to sustain entire ecosystems (Bjorndal and Jackson, 2003; Bouchard and Bjorndal, 2000). Moreover, the evolutionary success of this ancient lineage – which includes strong resilience to past environmental changes in the face of substantial morphological stasis (Hendrickson, 1980) makes sea turtles a group of great biodiversity value.

However, sea turtle conservation management practices have been challenged by increasingly wide-scale anthropogenic activities (Campbell, 2003). The latter, combined with their slow growth rate and sensitivity to selective pressures, may place their recovery in jeopardy. Understanding the role that anthropogenic actions play in sea turtles populations relies on improving our knowledge about sea turtle population dynamics, distribution of genetic variability, as well as identification of key ecological processes that influence their adaptive potential. This knowledge becomes crucial for the successful implementation of actions to bring sea turtles back from the brink, while trying to maintain interactions between human societies and sea turtles. Thanks to recent advances in the field of molecular ecology, researchers are now able to provide fine-scale resolution assessments about sea turtle population connectivity and knowledge about species biology to better assist conservation management programs (Avise, 1989; Bowen and Avise, 1995; Bowen and Karl, 2007; Lee, 2008).

This work represents a contribution to advance our knowledge about one of the most enigmatic sea turtles worldwide, the olive ridley. This species displays massive synchronized nesting (10,000-500,000 females) in just a few places around the world; an unparalleled behaviour known as *arribada* (the Spanish word for 'arrival'). The eastern Pacific is the area that comprises most of these unique places and where fine-scale resolution of functional population segments known as Management Units (MUs, Moritz, 1994) for conservation is required, informing decision making around sensitive issues, like sustainable use.

1.1. Cheloniids

1.1.1. Sea Turtles Life History and Biological Traits

There are seven living species of sea turtles grouped in two taxonomic families. Dermocheliidae with a single species, the leatherback turtle (*Dermochelys coriacea*) and the Cheloniidae (Ernst and Barbour, 1989) compromising the hawksbill turtle (*Eretmochelys olivacea*), loggerhead turtle (*Caretta caretta*), green turtle (*Chelonia mydas*), olive ridley (*Lepidochelys olivacea*), kemp's ridley (*Lepidochelys Kempii*) restricted to the gulf of Mexico, and flatback turtle (*Natator depressus*) restricted to Australia, New Guinea and adjacent areas (Meylan and

Meylan, 1999).

Sea turtles spend most of their lives in the sea among coastal and oceanic habitats, making use of sandy beaches only for nesting. The life cycle (Figure 1.1) is usually characterized by a pelagic stage, except for *N. depressus,* and ontogenic shifts in habitat use (Musick and Limpus, 1997). Adults perform long distance migrations from oceanic feeding grounds to breeding areas near the coast, where they concentrate in front of beaches to mate (Meylan, 1982). However, there is evidence that males remain in oceanic waters where they breed with females along migration routes (Plotkin *et al.*, 1996). Females remain faithful to their natal areas to where they come back in inter-annual intervals of 1-3 years – such intervals can differ between species (Hirth, 1980; Owens, 1980). Females return in successive attempts, usually 2-3 times along the nesting season (inter-nesting interval ~14 days), and remain near the coast occupying neritic areas (interesting habitats) (Carr and Ogren, 1960; Limpus *et al.*, 1984). It is believed that adults congregate in breeding areas around one month before the female's first nesting emergence, and that after the nesting season has commenced, males start their migration back to feeding grounds (Limpus *et al.*, 1992; Miller, 1997).

Females deposit 50 to 130 eggs per nest, depending on the species. Incubation of eggs usually takes ~ 60 days after which hatchlings emerge and enter the water, where they are drifted by ocean currents to pelagic and oceanic areas of high productivity. What happens next is unknown and has been denominated "the lost year" (Carr, 1987; Musick and Limpus, 1997). During the juvenile stage sea turtles migrate to shallow coastal waters where they recruit to mixed-stock foraging grounds (Bowen and Karl, 2007) and remain (Kopitsky *et al.*, 2000; Musick and Limpus, 1997) until sexual maturity is reached (around 13-35 years depending on the species; Zug *et al.*, 2006; Chaloupka and Musick, 1996). Juveniles often go through ontogenic shifts in habitat preference that encompass transitions from protected bays or lagoons to high-energy coastal areas (green turtles, López-Mendilaharsu *et al.*, 2005; Seminoff *et al.*, 2002), and trans-oceanic migrations (loggerhead turtles, Boyle *et al.*, 2009). In the case of leatherbacks and olive ridley turtles shifts are less evident with individuals remaining in offshore waters (Plotkin, 2003; Shillinger *et al.*, 2008). As described, sea turtle life history is complex, involving long distance migrations thus comprising multiple habitats. Identification of migration routes have been made possible using satellite tracking and also inferred from genetic analysis, and mark-recapture observations. The use of satellite tracking has been particularly important to describe horizontal and vertical movements of sea turtles (Godley *et al.*, 2008), to identify physical features such as fronts, gyres and eddies that provide habitat for the foraging of several species (Polovina *et al.*, 2001), and to characterize migration routes (e.g. leatherbacks in the eastern Pacific; Shillinger *et al.*, 2008). In addition, the use of this technology has supported the influence of ocean currents on sea turtle migrations (Luschi *et al.*, 2003a; Hays *et al.*, 2010; Monzon-Arguello *et al.*, 2012; Putman *et al.*, 2010).

In turtles, natal philopatry is a biological trait in which females have the propensity to return to their natal nesting area to deposit eggs (natal homing behavior) (Carr, 2002). It has also been shown that females can exhibit a high level of nest fidelity (nest site fidelity), returning subsequently year after year to the same beach for nesting (Bass *et al.*, 1996; Bowen *et al.*, 1992; Dethmers *et al.*, 2006; Encalada *et* *al.*, 1998). A strong degree of fidelity (~10 km) has been reported on hawksbill turtles (Bass *et al.*, 1996) and green turtles (Limpus *et al.*, 1992) but that can vary widely between the other sea turtle species. Tagging studies in olive ridley turtles have suggested a lower degree of fidelity based on evidence of movements between nesting beaches in a range of 50 km to 320 km (Cornelius and Robinson-Clark, 1986; Meylan, 1982; Tripathy and Pandav, 2007; Schulz, 1971).

Importantly, natal philopatry makes it possible to expect some degree of independence between different nesting colonies, since each colony tends to be composed of a group of females that belongs to the same lineage. Genetic studies have supported the independence between nesting colonies based on mitochondrial (mtDNA) analysis (Bass *et al.*, 1996; Broderick and Moritz, 1996; Encalada *et al.*, 1998; Dutton *et al.*, 1999; Hatase *et al.*, 2002; Shanker *et al.*, 2004; Dethmers *et al.*, 2006). However, the relationship between the degree of population structure expected by female philopatry and geographic distance is not entirely clear, with differences reported on ranges of tens to hundreds of kilometers (Bowen *et al.*, 2005; Dethmers *et al.*, 2006) to thousands of kilometers (Broderick *et al.*, 1994; Dutton *et al.*, 2007; López-Castro and Rocha-Olivares, 2005).

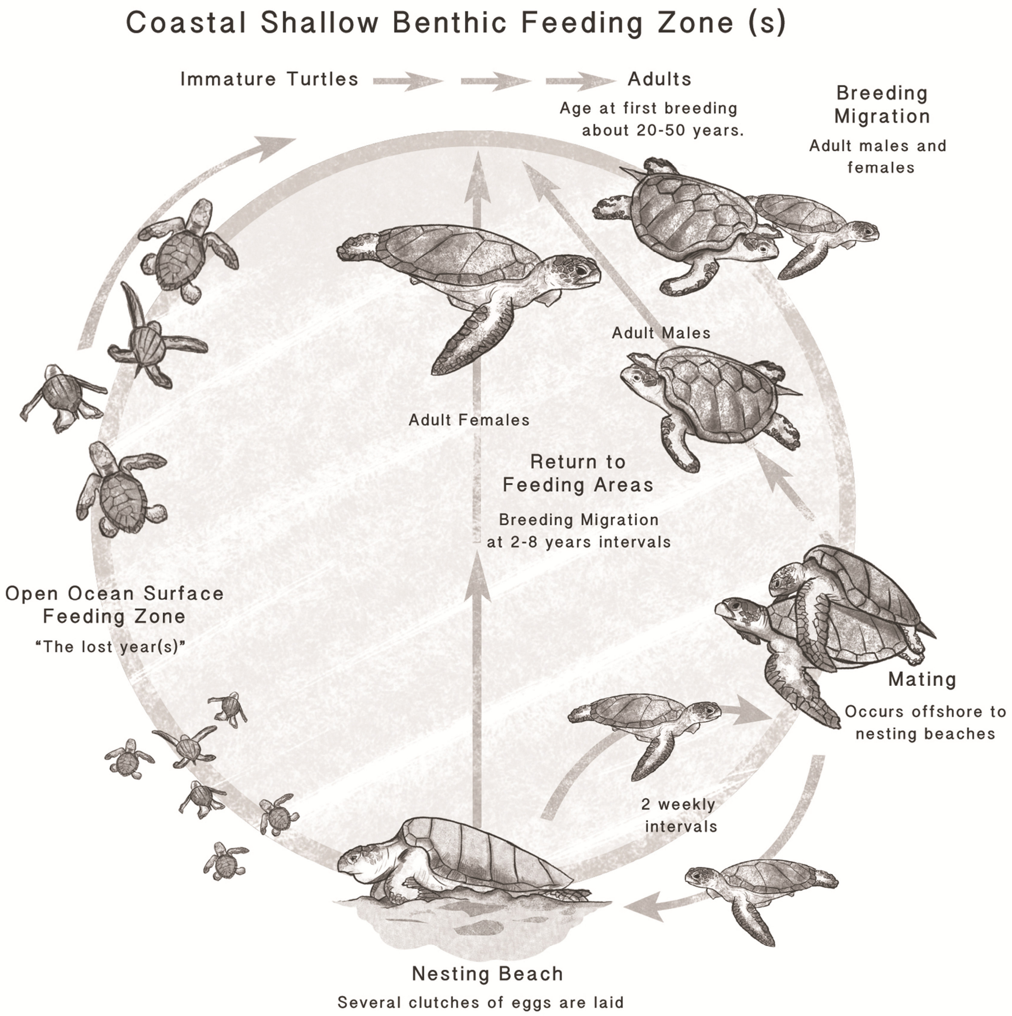


Figure 1. 1 Generalized life cycle for sea turtles. Adapted from Lanyon *et al.*, (1989). Illustration designed by Rodolfo Rodriguez Blandon 2013.

1.1.2. The Olive Ridley Turtle

1.1.2.1. Distribution and reproduction modes

Olive ridley turtle (*Lepidochelys olivacea*, Eschscholtz, 1829) Figure 1.2 are distributed across tropical and subtropical areas in the Pacific, Indian and Atlantic Oceans between the surface and isotherms of 20°C (Márquez-M, 1990). The main nesting areas are concentrated in the northeast coast of India (Shanker *et al.*, 2004) and in the eastern Pacific (Fritts *et al.*, 1982; Márquez-M, 1996 ; Pritchard and Mortimer, 1999).

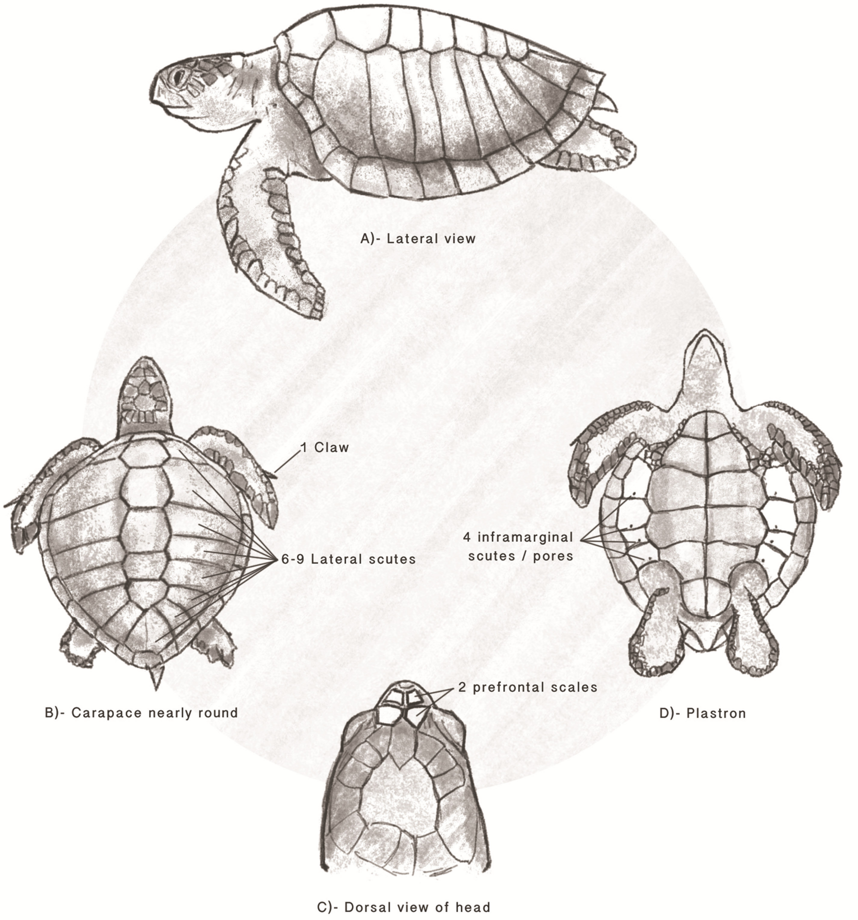


Figure 1. 2 The olive ridley turtle (*Lepidochelys olivacea*, Eschscholtz, 1829) guide to morphometric characteristics. Adapted from Pritchard and Mortimer, 1999. Illustration designed by Rodolfo Rodriguez Blandon 2013.

The eastern Pacific is recognized as the second most important area for the species worldwide, extending from South of Baja California Peninsula to Ecuador (Fritts et al., 1982) and providing food and important nesting habitats for populations

(Cliffton *et al.*, 1995; Márquez-M, 1996). The species exhibit three modes of reproduction, namely: synchronized massive nesting or *arribada*, dispersed or solitary nesting and mixed strategy (Bernardo and Plotkin, 2007). Solitary nesting, the most common mode, takes place when individual females emerge to lay eggs at low densities with no apparent synchronicity between events. On the other hand, the less common *arribada* mode consists of large numbers of females emerging synchronously (Figure 1.3) over relatively short intervals (2-7days) to nest at very high densities. This reproductive strategy is unique to the genus *Lepidochelys* and occurs annually in a few places worldwide, with seasonal variability between regions.

Figure 1. 3 Olive ridley turtles *arribada* (mass nesting). Illustration designed by Rodolfo Rodriguez Blandon 2013.

However, the *arribada* behavior remains poorly studied (Bernardo and Plotkin, 2007). A combination of the two previous modes has been reported to occur in some localities. In the eastern Pacific the breeding season extends from July to December, and olive ridley females are known to nest almost annually laying ~105 eggs per nest, in up to 3 inter-nesting interval spaced by periods of 14 days for solitary nesters and around 28 days for *arribada* nesters (Márquez-M, 1990). In the Eastern Pacific, the main nesting activity is concentrated in *arribada* beaches located in Escobilla (Mexico), La Flor and Chacocente beach (Nicaragua), Ostional and Nancite beach (Costa Rica) and Isla Cañas beach (Panama). In the last decade, two new *arribada* nesting beaches have emerged: Ixtapilla beach and La Marinera beach. The former is located in the estate of Michoacan, in Mexico and the latter is north of Isla Caña beach, in Panama (Figure 1.4).

Figure 1. 4 Location of current (circle) and former (star) arribada nesting sites of olive ridley turtles in the eastern Pacific. Showed from north to south they are: Mismaloya, Ixtapilla, Piedra de Tlacoyunque, San Juan de Chacagua, Escobilla and Morro Ayuta (Mexico), Chacocente and La Flor (Nicaragua), Nancite and Ostional (Costa Rica), La Marinera and Isla Caña (Panama).

1.1.2.2. Long distance migrations and habitat utilization

Studies of long distance migrations in sea turtles have described two main types of movements that comprise the dispersal of females from breeding sites to feeding grounds (inter and post-nesting movements) and to oceanic areas wandering over long distances (Luschi *et al.*, 2003a; Luschi *et al.*, 2003b; Plotkin, 2003). In olive ridley turtles studies have showed that individuals spent much of their time in pelagic habitats exhibiting the first type of post-nesting movements (Beavers and Cassano, 1996; Pandav and Choudhury, 1998; Plotkin *et al.*, 1995). However, new evidence suggest they can display mixed patterns remaining in feeding areas within the continental shelf to forage on the benthos (McMahon *et al.*, 2007; Whiting *et al.*, 2007). In general, post-breeding movements of olive ridley males and females from the same area have shown to be similar and overlap, with individuals mainly moving out into open areas of the Pacific after breeding (Plotkin, 2010; Plotkin *et al.*, 1996; Plotkin *et al.*, 1995). However, migrations to nesting beaches are poorly describe since most tagging efforts initiate on nesting beaches; and it has been presumed that these migrations may emulate the observed migrations back to foraging areas as has been observed for other sea turtles (i.e green turtles, Limpus *et al.*, 1992). Although near shore breeding is a common strategy for olive ridleys, it has been proposed that males probably exhibit alternate strategies with breeding taking place sometimes far from shore (i.e along migration routes) in response to a variety of selective pressures (see Morreale *et al.*, 2007).

Information about feeding areas of the species is scarce due to their pelagic behavior and generalized diet, but it is known that the area includes coastal and offshore zones across the Eastern Tropical Pacific (ETP) (Eguchi *et al.*, 2007; Márquez-M, 1996). The diet includes benthic invertebrates (gastropods, crabs) and other items such as jellyfish and tunicates (Swimmer *et al.*, 2006). No evidence of migration patterns have been detected for olive ridley turtles, in contrast with other pelagic sea turtles (Bailey *et al.*, 2012; Benson *et al.*, 2011; Shillinger *et al.*, 2008), and it is believed they are nomadic and explore vast areas across the eastern Pacific in search of prey (Plotkin, 2010).

1.1.2.3. Phylogeography and population structure

Early studies suggested that the contemporary distribution of the species is explained by the isolation that occurred after the formation of the Central American land bridge and the closure of the Isthmus of Panama (3-4 Million years ago) (Hughes, 1972). The proposed biogeographic model for the species suggest the Indo West Pacific region as the centre of radiation for olive ridley lineages followed by colonization of the Atlantic and then the eastern Pacific around 0.3 million years ago (Bowen *et al.*, 1998). More recent studies confirmed this hypothesis but also suggested a source-sink scenario where the Pacific and Atlantic Oceans represent evolutionary marginal habitats, in which populations were extirpated after the closure of the Isthmus of Panama and re-colonized by ancestral olive ridley turtles from the Indo-Pacific region (Shanker *et al.*, 2004). Particularly for the eastern Pacific, phylogeographic analyses also suggested a constraint of species range to tropical waters during glacial periods with subsequent expansions from southern (nesting colonies in Costa Rica) to northern areas (López-Castro and Rocha-Olivares, 2005).

For this species, the apparent lack of population structuring within regional scales goes against predictions based on natal philopatry. The olive ridley turtle has been recognized as a panmictic species (random mating of individuals within a population) at regional levels (i.e. within ocean basins, Bowen *et al.*, 1998), only showing high levels of differentiation among ocean basins (Bowen *et al.*, 1998; Bowen and Karl, 2007; Shanker *et al.*, 2004). In the eastern Pacific, evidence originated from small solitary nesting areas in the northern limit of the species' distribution (Baja California Peninsula, Mexico) have suggested that Baja

California compromises a divergent and less diverse population compared to continental areas in Mexico and Costa Rica (mtDNA Φ_{ST}=0.048, P=0.006) (López-Castro and Rocha-Olivares, 2005). These results suggest that the contribution of small solitary nesting beaches to overall population structure and diversity in olive ridley turtles has been largely underestimated. Since the analysis of mtDNA does not account for biparental gene flow, information from nuclear DNA (nDNA), together with sampling at finer spatial scales, could make a substantial contribution to clarify patterns of genetic structure in this species.

1.1.2.4. Human induced impacts on olive ridley turtles

In the eastern Pacific, coastal communities traditionally consume and use the derived product of sea turtles. In general this includes the consumption of meat, eggs, and derived products such as skin, oil and shells (Campbell, 2007b; Cornelius *et al.*, 2007). Since olive ridley turtles are the most abundant sea turtle species along the region (Seminoff *et al.*, 2012), and high concentration of individuals were originally found on *arribada* sites and surrounding marine areas, this species was severely overexploited in the 1960s in Mexico, resulting in a rapid decline of *arribada* nesting beaches (Cliffton *et al.*, 1982; Márquez-M *et al.*, 2007). Motivated by the increasing international demand of skin for luxury goods, a small fishery began operating in Ecuador, capturing thousands of turtles (Green and Ortiz-Crespo, 1982). Although several laws and regulations for protection were implemented after the closure of these fisheries (Cornelius, 2007), illegal harvest of eggs still occurs, and their effect on olive ridley populations is unknown (Plotkin, 2012).

On the other hand, increasing large-scale threats present in the region potentially compromise the recovery of this species. The incidental capture of olive ridley turtles has been correlated with the decline of the species in many areas across the world due to interaction with trawl, longline, gill nets and line fisheries (Frazier, 2007). Global assessments of bycatch indicate an estimated incidental capture of ~85,000 turtles in gillnet, long lines and trawling fisheries between 1990 and 2008 (Wallace *et al.*, 2010b). Areas such as the Mediterranean Sea and the eastern Pacific have been emphasized as key to conservation action due to the capture of large turtles and the existence of regions where artisanal fisheries interact with high densities of marine turtles (Peckham *et al.*, 2007).

Records of bycatch in the eastern Pacific reveal a great impact by trawling, long line gear and small-scale fisheries on olive ridley turtles considered as one single Regional Management Unit (RMU) (Wallace *et al.*, 2010a; Wallace *et al.*, 2013a). In recent years this issue has increasingly captured the attention of the general public, when in several cases national media in Costa Rica, Guatemala and Panama documented hundreds of dead turtles that came to shore. Shrimp trawl fishery is common along Central America, having a distinct impact on the population of olive ridleys. Early studies reported annual captures for Guatemala of 10,000 turtles, El Salvador of 21,280, Nicaragua of 8,000 and Costa Rica of 20,762, representing over 60,000 turtles/year (Arauz *et al.*, 1996). However, recent evidence from longline fishery bycatch for Costa Rica indicated an estimated capture of 699,600 olive ridleys, including 92,300 adult females from 1999 to 2010 (Dapp *et al.*, 2013). These data are an indication to the magnitude of this threat in the region, however, little is known about its implications. The integration of information on fine-scale population structuring, patterns of movement and seascape analysis would likely contribute to resolving the extent of impact on different population segments or MUs (functional population segments; Moritz, 1994), and to properly assess recovery trends of the species in this region. Moreover, the benefit could be extensive to new global frameworks aimed to organize sea turtles into units of protection that integrate different source of information (biological and ecological information, including available data from genetic stocks) to facilitate management of sea turtles under the level of species, but above the level of nesting colonies. This approach emerged in 2010, proposing Regional Management Units (RMUs) for conservation of sea turtles (Wallace *et al.*, 2010a). Although the framework represents a valuable contribution, fine-scale data is still required. Under this recent global framework, the eastern Pacific olive ridley turtle only comprises a single RMU (Wallace *et al.*, 2010a).

1.1.2.5. Conservation status in the eastern Pacific

Although a relatively recent global population assessment of olive ridleys (Abreu-Grobois and Plotkin, 2008) resulted in a change of its IUCN Red List classification from ‘Endangered’ to ‘Vulnerable’, the breeding eastern Pacific population is still classified as ‘Endangered’ by the U.S. Endangered Species Act (ESA). It has been recognized that global assessments for the species require conservation priority definitions at finer resolution (i.e. within regions), to properly reflect the disparate population trends for the species at this level (Seminoff and Shanker, 2008). So far, population trends vary among geographic regions and show differences that may indicate independent demographic histories. For instance, *arribadas* in Mexico historically occurred in Mismaloya, Piedra de Tlacoyunque, San Juan de Chacagua, La Escobilla and Morro Ayuta (Figure 1.4). However, since legal protection started in 1990 (DOF-1990), some remain at levels of solitary nesting sites (<5,000 indv/year) (Abreu-Grobois and Plotkin, 2008). Although significant olive ridley population decline was observed along the eastern Pacific, the species is still the most abundant sea turtle in this region, nesting in an order of magnitude between hundreds and a few thousand females/year, with populations appearing to be stable. This is particularly the case when considering trends on *arribada* beaches such as Escobilla, Mexico (50,000 nests to over 1 million; Briseño-Dueñas, 1998; Márquez-M *et al.*, 2007). Of important note is that long-term data to assess recovery on solitary beaches have been more difficult to obtain due to limitations related with management of more widespread and low nest density areas; in addition to financial constrains to perform long-term monitoring. Moreover, illegal egg harvest and bycatch in shrimp trawls are still significant threats (Wallace *et al.*, 2010b).

1.2. The Eastern Pacific

The eastern tropical Pacific is defined as the area confined between the coast of Central and South America to 140°W and within the Tropics of Cancer and Capricorn at 23.5 °N and S, respectively. It is centred on the eastern Pacific warm pool off southwest Mexico and Central America. The region includes the eastern and equatorial branches of the north and south Pacific subtropical gyres, the south and north equatorial currents, and two coastal Counter currents (California current and Peru current) (Pennington *et al.*, 2006) (Figure 1.5). Although the region is considered of great oceanographic variability, macro and meso-scale features are relatively permanent and predictable (Fiedler and Talley, 2006; Kessler, 2006). Wind is a major force shaping its circulation, characterized by permanent eddies and significant off-equatorial upwelling.

Important meso-scale phenomena include anti-cyclonic and cyclonic eddies that originate off the coast of Central America and southern Mexico (Willett *et al.*, 2006). These take place due to the influence of inter-isthmic wind jets that blow across the continental gaps located at the isthmus of Tehuantepec in Mexico, the lake district in Nicaragua and Costa Rica and Panama canal (Amador *et al.*, 2006; Willett *et al.*, 2006). Their influence is highly seasonal contributing to the formation of major features of thermocline depth variation (Costa Rican Dome and Tehuantepec Bowl) and biological-enriching effect (Fernandez-Ålamo and Farber-Lorda, 2006). Particularly, the Gulfs of Tehuantepec, Papagayo, and Panama are fertile zones as a result of the nutrient supply by wind-driven upwelling and near-surface mixing that extends up to 1000 km offshore due to the influence of coastal eddies (Willett *et al.*, 2006). The meso-scale features in the region have been recognized for their particular biological relevance to seabirds and cetaceans (Ballance *et al.*, 2006).

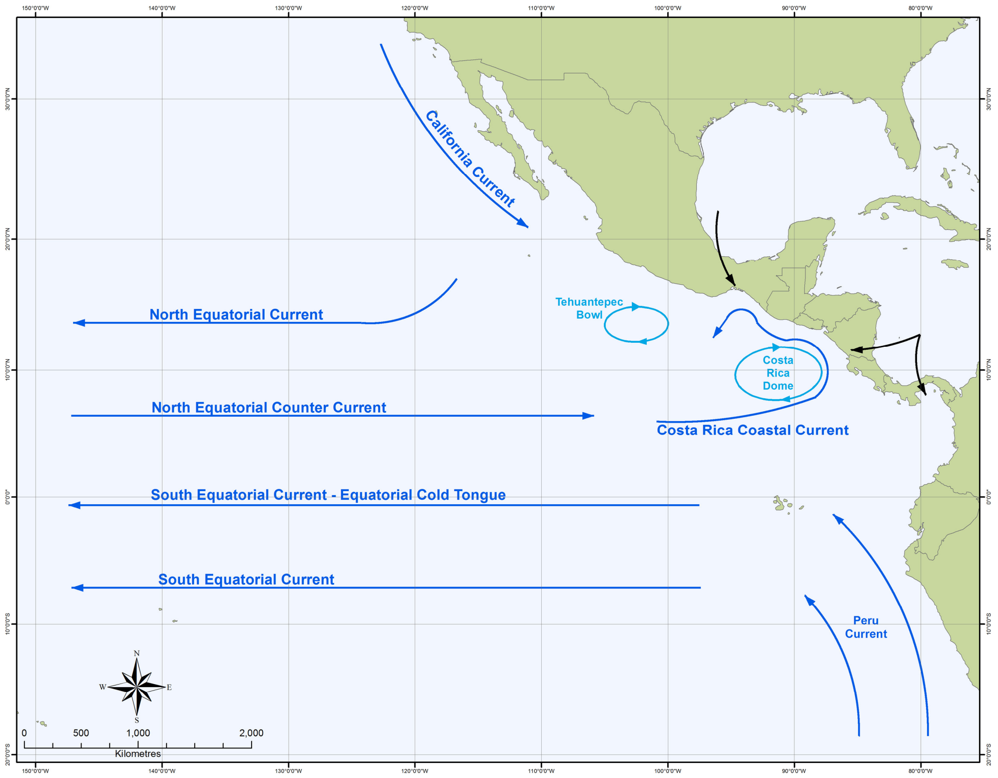


Figure 1. 5 Surface schematic ocean circulation of the eastern Pacific. Oceanographic features: Tehuantepec Bowl (TB), Costa Rica Dome (CRD), Costa Rica Coastal Current (CRCC). Inter-isthmic wind jets are represented with black arrows.

1.2.1. Olive ridley turtle nesting sites of study in the eastern Pacific

The nesting areas of olive ridley turtles selected on this study comprise both solitary and arribada nesting sites along the eastern Pacific, representing the dispersed and synchronized reproduction modes for the species, respectively. The 28 nesting sites studied (Figure 1.6) are distributed across five nations, that from north to south include: (i) Mexico, where nesting colonies that are located in Baja California Peninsula represent one extreme of the nesting distribution for olive ridleys in the region. All peninsular localities are solitary nesting sites that include the nesting beaches of: Todos Santos (23°26'43.34"N, 109°56'43.94"W), Pescadero

(23°21'1.68"N, 110° 6'15.55"W), San Cristobal (22°57'58.18"N, 110° 4'3.38"W), San José del Cabo (23° 4'20.93"N, 109°37'35.41"W), Cabo Pulmo (23°25'58.27"N, 109°25'39.54"W), and Punta Colorada/Punta Arenas (23°32'54.96"N, 109°14'23.03"W). Continental nesting areas covered the northern, central and southern pacific coast of Mexico. Nesting sites selected in the northern region are located in the states of Sinaloa (El Verde, 23°26'10.18"N, 106°34'30.10"W), and Nayarit (Platanitos, 21°21'8.19"N, 105°14'23.90"W; Nuevo Vallarta, 20°48'13.03"N, 105°28'59.81"W). Nesting sites selected in the central coast are located in the states of Jalisco (Puerto Vallarta-La Gloria, 20°37'12.98"N, 105°13'56.04"W; Mismaloya, 19°59'46.66"N, 105°29'41.80"W), Colima (Boca de Apiza, 18°44'29.79"N, 103°47'38.49"W), Michoacan (Playa Ticuiz, 18°39'14.33"N, 103°42'6.51"W), and Guerrero (Tierra Colorada, 16°29'47.71"N, 98°43'27.93"W). Finally, nesting sites selected in the southern coast are located in the states of Oaxaca (San Juan de Chacahua, 15°58'38.62"N, 97°46'17.59"W; Escobilla -*arribada* site-, 15°43'37.99"N, 96°45'23.76"W; Barra de la Cruz, 15°50'17.94"N, 95°55'13.13"W), and Chiapas (Puerto Arista, 15°55'59.79"N, 93°48'35.77"W). Nesting areas selected further south from Mexico that are located in central American countries include: (ii) Guatemala (Hawaii, 13°51'50.10"N, 90°24'35.45"W); (iii) El Salvador (Playa Dorada, 13°30'39.97"N, 89°35'54.71"W; San Diego, 13°27'58.72"N, 89°15'13.96"W; Bocanitas, 13°25'17.83"N, 89° 9'45.20"W; San Juan del Gozo, 13°13'28.65"N, 88°43'5.72"W); (iv) Nicaragua (Salamina, 11°58'45.58"N, 86°39'17.53"W; Veracruz, 11°33'55.23"N, 86°14'1.60"W; Chacocente -*arribada* site- 11°32'8.42"N, 86°11'23.75"W; La Flor -*arribada* site- 11° 8'28.96"N, 85°47'38.62"W); and (v) Panama (La Marinera -*arribada* site- 7°16'20.96"N, 80°25'13.40"W).

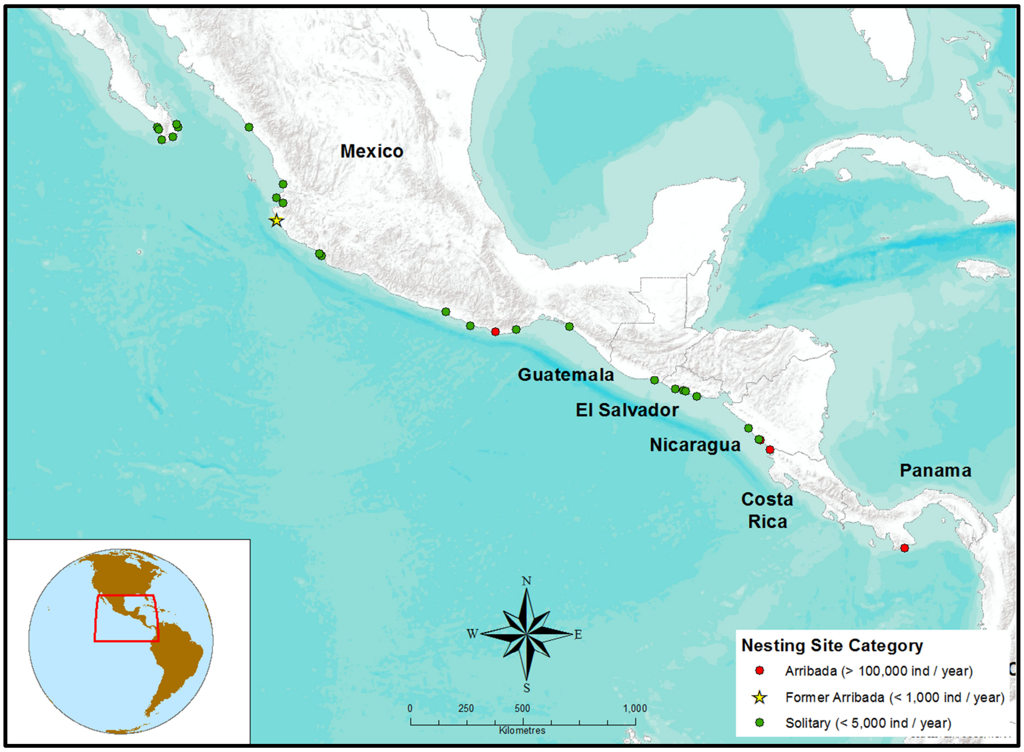


Figure 1. 6 Study area showing sampling sites of olive ridley turtles in the eastern Pacific. Sampling sites from north to south along Baja California Peninsula are: Todos Santos, Pescadero, San Cristobal, San José del Cabo, Cabo Pulmo, Punta Colorada and Punta Arenas. Continental sampling sites are: El Verde, Platanitos, Nuevo Vallarta, Puerto Vallarta-La Gloria, Mismaloya, Boca de Apiza, Playa Ticuiz, Tierra Colorada, San Juan de Chacahua, Escobilla, Barra de la Cruz, Puerto Arista, Hawaii, Playa Dorada, San Diego, Bocanitas, San Juan del Gozo, Salamina, Veracruz, Chacocente, La Flor, La Marinera.

1.3. Conservation Genetics

1.3.1. Genetic markers in sea turtles

Genetic studies of sea turtles have mostly used mtDNA as a molecular marker of preference due to its effectiveness in detecting phylogenetic relationships and population structure (Avise, 1995; Bowen and Witzel, 1996). Given the matrilineal inheritance of mtDNA, its evolutionary dynamics is sensitive to female natal fidelity (Bowen, 1995; FitzSimmons *et al.*, 2000). For example, using information from this molecular marker, population genetic structure was described on green turtles in the western Atlantic (Encalada *et al.*, 1996), hawksbill turtles in the Caribbean (Bass *et al.*, 1996), leatherbacks (Dutton *et al.*, 1999) and olive ridley turtles globally (Bowen *et al.*, 1998). Analysis using mtDNA have also been useful to disclose the existence of stocks of different origins (i.e. from different nesting areas) in sea turtle feeding grounds (Bass *et al.*, 1998; Blumenthal *et al.*, 2006; Broderick *et al.*, 2007; Naro-Maciel *et al.*, 2012; Proietti *et al.*, 2014)

However, because mtDNA primarily reflects matrilineal population dynamics it does not inform on male gene flow, leading to partial conclusions about population structure. Thus, conservation genetic assessments would benefit from using molecular markers suitable to reflect biparental gene flow, such as nDNA microsatellites. Such markers also offer better resolution to infer connectivity in ecological time frames relevant to conservation management (Sunnucks, 2000). Microsatellites have provided insights about male-mediated gene flow in sea turtles (Karl *et al.*, 1992), suggesting that males may exhibit comparable fidelity to breeding areas to that of females, even when sporadic mating can take place where adult populations overlap in migratory corridors (FitzSimmons *et al.*, 1997). Thus, the implementation of genetic assessments in sea turtles using microsatellite markers can contribute to clarify patterns of population structure and provide valuable information for management. For instance, its use has recently allowed the recognition of additional genetic variation in Atlantic leatherbacks and the clarification of population connectivity in the Caribbean (Dutton *et al.*, 2013). In addition, microsatellites were very effective for recent mixed stock analysis in Mediterranean loggerhead turtles, where a higher percentage of individuals (87%)

from feeding grounds were successfully assigned to nesting areas when both nuclear and mtDNA data were used compared to mtDNA only (52%) (Carreras *et al.*, 2011). Finally, microsatellite markers have also been useful for investigating multiple paternity in marine turtles (FitzSimmons, 1998; FitzSimmons *et al.*, 1996; Jensen *et al.*, 2006; Kichler *et al.*, 1999; Moore and Ball, 2002).

1.3.2. Population connectivity in the sea and definition of units for conservation

Phylogeographic studies allow the recognition of historical processes (biogeographic and demographic) that may be responsible for the contemporary geographic distributions of individuals and the prioritization of areas of high value for conservation. Based on unique geographic distribution and patterns of genetic divergence, Evolutionarily Significant Units (ESUs) (Moritz, 1994) can be defined to conserve genetic uniqueness and long-term evolutionary potential. However, of major interest for conservation at ecological time frames are the functional population segments or MUs, which can exhibit independent demographic dynamics even in scenarios of relatively low genetic differentiation.

A major challenge when identifying MUs is the definition of population boundaries, particularly on widely distributed and highly mobile marine species such as sea turtles. In the marine environment, dispersal of individuals can significantly impact on population dynamics, population differentiation and individual fitness (Bowler and Benton, 2005; Hellberg, 2009; Palumbi, 2003). Thus, patterns of genetic structure generally correspond to the natural histories of the species and their dispersal potential (Slatkin, 1993). Since the habitat characteristics in space and time can facilitate or impede movement of organisms, their influence on species dispersal is a relevant factor to be considered. Physical oceanography has an important influence on the biology of marine organisms, distribution of species, species-habitat relationships and dispersal patterns. Evidence of such influences have been reported for sea turtles (Bailey *et al.*, 2012; Etnoyer *et al.*, 2006a; Hays *et al.*, 2001; Luschi *et al.*, 2003a; Morreale *et al.*, 1996; Polovina *et al.*, 2001; Quiñones *et al.*, 2010).

1.3.3. The seascape genetics approach

The multidisciplinary approach known as *landscape genetics* (i.e. *seascape genetics* for marine studies) is a relatively novel area within the broad field of molecular ecology that allows the integration of ecological variables with spatial statistics and population genetics (Manel *et al.*, 2003) Through this approach, analysis of oceanographic data can be statistically combined with inferences about connectivity generated by high-resolution population genetic datasets to assess environmental variables shaping population structure (Amaral *et al.*, 2012; Banks *et al.*, 2010; Liggins *et al.*, 2013; Riginos and Liggins, 2013).

The analysis involves the integration of multiloci genetic data with information from seascape features. The features can be grouped in quantitative and qualitative factors such as surface temperature, salinity, and ocean currents, eddies and other oceanographic processes. Studies of marine organisms have documented the usefulness of this approach to understand larval migration (Galindo *et al.*, 2006), identification of barriers to dispersal (Jorgensen *et al.*, 2005) and the influence of fine-scale oceanography on large-scale gene flow (Banks *et al.*, 2007). Information can also be integrated to evaluate specific hypotheses on how the ecology of the species can influence patterns of genetic variation (Schultz *et al.*, 2008), allowing the identification of bioregions, responses to ecological variables and climate change events (Banks *et al.*, 2010). Analytical methods have included matrix correlations and dispersal route analysis (Jorgensen *et al.*, 2005; Michels *et al.*, 2001). Other methods include autocorrelations to quantify genetic variation over distance (Banks *et al.*, 2007), and spatial interpolations useful for both the analysis of continuously distributed species and for representing allele frequency data across the seascape (Jorgensen *et al.*, 2005).

In particular, recent advances in oceanographic modelling have promoted the application of biophysical models as tools by which dispersal probabilities can be estimated. These models accurately emulate integrated information from ocean circulation variability and biological parameters of the species to allow direct comparisons with the observed distribution of genetic variation (e.g. Galindo *et al.*, 2006; Kool *et al.*, 2010; Kool *et al.*, 2011). Studies that performed seascape genetic analysis have shown their value for conservation, contributing to management decisions for fisheries (Pujolar *et al.*, 2006; Selkoe *et al.*, 2007; Stenseth *et al.*, 2006) and for networks of marine reserves (Selkoe *et al.*, 2008). Seascape genetics is yet to be applied for sea turtle research. Such studies would greatly assist with the definition of MUs to guide conservation actions, and more importantly, to fit biological processes relevant for the conservation of sea turtles to the scale of management.

1.4. Aims

The general aim of this thesis is to contribute to the conservation management of olive ridley turtles in the eastern Pacific by characterizing genetic diversity and population connectivity and clarifying unresolved issues about species dynamics by implementing an integrative seascape genetics approach. Specific aims of this work are:

1. To clarify recent demographic history in olive ridley turtles after intensive commercial exploitation in Mexico;

2. To clarify population structure and connectivity in olive ridley turtles by (i) implementing a seascape genetic approach at a large regional scale and (ii) testing the influence of oceanographic variables on the distribution of genetic variability;

3. To review current conservation management procedures of sea turtles in the Mesoamerican region and evaluate their agreement to sea turtle population dynamics.

1.5. Thesis Structure

The thesis encompasses five chapters. Chapter I corresponds to the general introduction. Chapter II, III and IV correspond to the research conducted to address each specific aim. Chapter V corresponds to the conclusion and final remarks.

Chapter II: (Article 1)

Genetic Signature of a Recent Metapopulation Bottleneck in the Olive Ridley Turtle (*Lepidochelys Olivacea*) After Intensive Commercial Exploitation in Mexico

---

Clara J. Rodríguez-Zárate[a *], A. Rocha-Olivares[b] and Luciano B. Beheregaray[a]

[a]Molecular Ecology Laboratory, School of Biological Sciences, Flinders University, Adelaide, SA 5001, Australia.

[b]Laboratorio de Ecología Molecular, Departamento de Oceanografía Biológica, Centro de Investigación Científica y de Educación Superior de Ensenada, , Ensenada Baja California 22860, Mexico.

Biological Conservation (2013) 168, 10-18

Genetic Signature of a Recent Metapopulation Bottleneck in the Olive Ridley Turtle (*Lepidochelys olivacea*) After Intensive Commercial Exploitation in Mexico

2.1. Abstract

Information on the demographic and genetic consequences of overexploitation of large marine vertebrates is often difficult to demonstrate on ecological time frames. We investigate the genetic impacts of recent commercial activities along Mexico's Pacific coast on the nesting colonies of a long-lived vertebrate of conservation concern, the olive ridley turtle (*Lepidochelys olivacea*). This species was severely impacted by a commercial fishery between 1960 and 1990 (e.g. >350 000 individuals were caught in a single year), depleting important nesting areas within few decades. Microsatellite DNA variation of 365 samples representing 18 nesting sites revealed a clear signature of recent bottlenecks associated with changes in allelic diversity. Consistent with theoretical expectations and other empirical studies, we found no evidence for bottlenecks based on measures of heterozygosity. The bottleneck signal was strong across the highly connected metapopulation and also apparent in six nesting sites in a pattern consistent with the history of demographic disequilibria produced by their overexploitation. In addition, we clarify population structure across Mexico and show that Mismaloya, a key colony where human harvest led to a dramatic change in the species' reproduction mode, has not been supplemented by gene flow after the bottleneck and has diverged genetically from other demes, as a result of the recent overexploitation. This is perhaps the first study to detect recent signatures of anthropogenic-driven population declines in sea turtles using genetics. This enables managers to consider information about genetic signatures of contemporary demographic changes during the development of conservation management plans and during population monitoring.

Keywords: conservation genetics, anthropogenic harvest, marine connectivity, genetic bottleneck, sea turtles.

2.2. Introduction

Pressures imposed by overharvesting of wildlife have accounted for the decline of several populations over the last century and have placed many others at high risk of extinction (Hutchings, 2000; Larson *et al.*, 2002). Such changes in effective population size (*Ne*), known as population bottlenecks, are usually accompanied by reductions in genetic diversity. The identification of recent genetic bottlenecks (i.e. during ecological timeframes) in species of conservation concern can provide a framework for enhancing management practices directed to restoring metapopulation connectivity and minimizing further loss of genetic variability and fitness (e.g. Taylor *et al.*, 1997; Reed and Frankham, 2003; Shama *et al.*, 2011). In marine ecosystems, the lack of systematic broad-scale inventories and baseline data makes it particularly difficult to assess the impacts of humans on the decline of marine populations (Edgar *et al.*, 2005). Furthermore, genetic signatures of recent demographic collapses are hard to demonstrate in marine vertebrates targeted by commercial activities because these species usually have long generation times, relatively large pre-exploitation *Ne* and moderate to high connectivity – features that should buffer processes driving the loss of genetic variability (e.g. Busch *et al.*, 2007; Hailer *et al.*, 2006). Therefore, information is generally not available for resource managers and thus hardly incorporated into management plans, a problem particularly germane in developing countries (Harris *et al.*, 2002; Allendorf *et al.*, 2008).

Here we investigate the genetic consequences of a recent, large-scale commercial exploitation in a long-lived marine vertebrate, the olive ridley turtle (*Lepidochelys olivacea*). These turtles exhibit two modes of reproduction that define nesting areas as either solitary or *arribada* sites. Solitary nesting, the most common mode, takes place when individual females emerge to lay eggs at low densities with no apparent synchronicity between individual events. On the other hand, the less common *arribada* mode, consists of large numbers of females emerging synchronously over relatively short intervals (2-7days) to nest at very high densities. This reproductive strategy is unique to the genus *Lepidochelys* and occurs annually in a few places worldwide, with seasonal variability between regions (Bernardo and Plotkin, 2007). During the 1960s, nesting females and eggs of olive ridleys were severely harvested by humans along the Pacific coast of Mexico. The extensive industrial harvest depleted important nesting colonies of olive ridleys within a few decades (Márquez-M, 1996). For instance, 14 000 tons (~350 000 individuals) were caught in a single year (1968), but it has been suggested that statistics were underestimated by an order of magnitude (Márquez-M *et al.*, 1982). Commercial exploitation continued thorough the 80s and depleted several massive nesting colonies in Mexico where *arribadas* no longer occur (e.g. Mismaloya Beach) and almost collapsed other *arribada* colonies such as Escobilla Beach (in Oaxaca). Eventually, the industrial harvest was officially banned in 1990 (Diario Oficial de la Federacion, DOF-1990) and since then demographic recoveries were observed for a few nesting sites, especially in Escobilla (Márquez-M *et al.*, 2007). Although a recent global population assessment of olive ridleys (Abreu-Grobois and Plotkin, 2008) resulted in a change of its IUCN Red List classification from 'Endangered' to 'Vulnerable', the breeding population in the Mexican Pacific is still classified as 'Endangered' by the U.S. Endangered Species Act (ESA). Moreover, long-term data for other areas remain limited, and illegal egg harvest and bycatch in shrimp trawls are still significant threats (Wallace *et al.*, 2010b). In addition, genetic findings suggest the existence of a genetically divergent and less diverse population in the Baja California Peninsula, Mexico (mtDNA Φ_{ST}=0.048, P=0.006) (López-Castro and Rocha-Olivares, 2005). These results imply that the contribution of small solitary nesting beaches to overall population structure and diversity in olive ridleys might have been underestimated by previous studies (Briseño-Dueñas, 1998; López-Chávez, 2000, Bowen and Karl, 2007).

The recorded history of massive harvesting of olive ridleys across several colonies in Mexico (Márquez-M *et al.*, 1982) provides an unique opportunity to test for genetic signatures of recent anthropogenic-driven demographic collapses in a marine vertebrate and to identify nesting colonies that might have declined but for which little ecological information exist. In sea turtles, genetic bottlenecks have been linked to historic human activities and environmental changes that took place over the last 2000 years (Plot *et al.*, 2012). However studies that explored demographic reductions over recent time frames failed to detect genetic evidence for bottlenecks (Carreras *et al.*, 2007). Assessment of bottlenecks in olive ridleys at the levels of both the deme and the regional nesting area enables the identification of links between nesting colony exploitation and metapopulation dynamics and the evaluation of recovery trends associated with conservation policies and practices in sea turtles. In addition, Mexico holds one of the world's largest nesting colonies of the species (Escobilla Beach), considered by some as a reservoir of genetic variability and by others as a valuable resource for humans (Campbell, 1998).

In this study we generated what is arguably the largest microsatellite DNA dataset for a nesting geographic area of a sea turtle species (i.e. 334 individuals from 18 nesting sites) to (i) clarify fine-scale population structure of olive ridleys along Mexico's Pacific coast and (ii) test for bottlenecks potentially linked to the recent history of commercial exploitation. During the process of achieving these aims we explore two popular statistical approaches of bottleneck detection: heterozygosity excess (Cornuet and Luikart, 1996) and the M-ratio (Garza and Williamson, 2001). These approaches are expected to show differential sensitivity to detect signal associated with transient population reductions, such as the one recorded for our system. Our study has broader implications to genetic surveys of demographic variation in marine vertebrates targeted by commercial activities. It is perhaps the first study to detect recent genetic signatures of anthropogenic-driven declines in sea turtles and to show that localized exploitation (i.e. at the nesting site) can have genetic consequences across the entire regional metapopulation (i.e. along Mexico's Pacific coast).

2.3. Materials and Methods

2.3.1. Sample collection

We sampled solitary and *arribada* nesting beaches of olive ridley in Mexico (18 sites) during 2006 (Figure 2.1). Categories of nesting beaches are detailed in Table 2.1. Skin biopsies were collected from tagged nesting females to avoid replication of samples (FitzSimmons *et al.*, 2000) and tissue was preserved using 20% DMSO/saturated NaCl solution. In areas where sampling of females was difficult, tissue from one dead hatchling per nest was taken within the 15-day inter-nesting period. Genetic analyses are based on 13 nesting areas as beaches with less than 15 samples were assigned to major nesting areas using the criterion of the geographically closest neighbour. This criterion is based on the assumption that closest points on the geographic space would be more similar than those located far apart. Then the closest neighbour search consists on determining the shorter linear distance from a given point on the geographic space to others around.

2.3.2. DNA purification, amplification and genotyping

We extracted DNA using a modified salting-out protocol (Sunnucks and Hales, 1996) by increasing volumes on digestion (600µl of TNES) and precipitation (170µl NaCl) steps. A total of 365 samples were genotyped at 10 microsatellite loci (OR1, OR2, OR4, OR7, OR9, OR11, OR14, OR16, OR20 and OR22) (Aggarwal *et al.*, 2008; Aggarwal *et al.*, 2004). Touchdown PCR profile consisted of 3 min at

94°C followed by 35 cycles (94°C/20 s; 61°C down to 53°C until fifth cycle/45 s; 72°C/1 min), and 10 min at 72°C. Touchdown for locus OR20 was modified to 57°C - 53°C. Amplification reactions contained: ~5-10 ng DNA, 1xMango taq reaction buffer (Bioline), 1.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.4 mM each primer, 0.5 U MangoTaq DNA Polymerase (Bioline), 0.1 mM fluorescently labelled M13 primer. Allele separation was performed on an ABI 3730 (Applied Biosystems Inc, CA) and genotypes scored on GENEMAPPER™ 4.0 (Applied Biosystems). Null alleles and large allele dropout were assessed in MICRO-CHECKER (Oosterhout *et al.*, 2003).

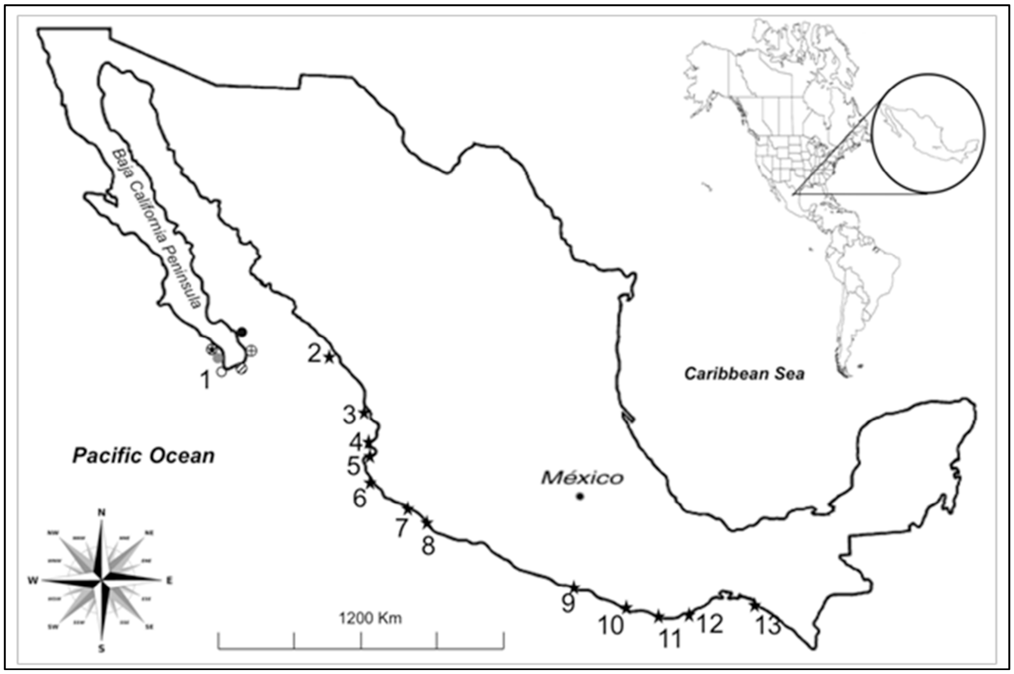


Figure 2. 1 Sampling sites of olive ridleys in Mexico. (1) Baja California Peninsula: (star) Todos Santos, (grey dot) Pescadero, (white dot) San Cristobal, (striped dot), San José del Cabo, (crossed dot) Cabo Pulmo, (black dot) Punta Colorada and Punta Arenas. In the continent: (2) El Verde, (3) Platanitos, (4) Nuevo Vallarta, (5) Puerto Vallarta-La Gloria, (6) Mismaloya, (7) Boca de Apiza, (8) Playa Ticuiz, (9) Tierra Colorada, (10) San Juan de Chacahua, (11) Escobilla, (12) Barra de la Cruz and (13) Puerto Arista.

Table 2. 1 Categories of olive ridley nesting areas in Mexico.

State	Locality	Category	Number of nests*	Source
Baja California Sur ⊗(5, 6)	Todos Santos Δ	S	NR	-
	Pescadero Δ	S	NR	-
	San Cristóbal Δ	S	NR	-
	El Suspiro Δ	S	101-500	1
	San Jose del cabo Δ	S	NR	-
	Cabo Pulmo Δ	S	55	3
	Punta Arenas Δ	S	NR	-
	Punta Colorada Δ	S	NR	-
Sinaloa	El Verde ⊗(7)	S	1607	1
			523	2
			1160	4
Nayarit	Platanitos ⊗(7)	S	1001-5000	1
			424 / 439	2
			1301	4
	Nuevo Vallarta Δ	S	1001-5000	1
Jalisco	Puerto Vallarta/Las Glorias Δ	S	NR	-
	Mismaloya ⊗(5, 6, 7)	S	232 / 251	2
			2328	4
Colima	Boca de Apiza Δ	S	1001-5000	1
			458	2
Michoacan	Playa Ticuiz Δ	S	NR	-
Guerrero	Tierra Colorada Δ	S	868	1
Oaxaca	Escobilla ⊗(5, 6, 7)	A	1 502 393	1
			248 063 / 956 108	2
	Barra de la Cruz ⊗(5, 6)	S	662	1
			67	2
	San Juan de Chacahua ⊗(5, 6)	S	501-1000	1
			717 / 3944	2
			2042	4
Chiapas	Punta Arista ⊗(7)	S	3924	1
			137	2
			707	4

*Annual number of nests. (⊗) Commercially exploited sites, (Δ) Non-commercially exploited sites, (S) Solitary sites, (A) *arribada* sites, (NR) not reported. Sources: (1) Convención Interamericana de Tortugas Marinas (2012), (2) Programa nacional de protección, conservación, investigación y manejo de tortugas marinas (2000), (3) Lopéz-Castro et al., 2004, (4) SEMARNAT report 2001-2005 In: Abreu-Grobois and Plotkin, 2008, (5) Marquez et al., 1982, (6) Marquez et al., 2007, (7) Abreu-Grobois and Plotkin, 2008.

2.3.3. Genetic diversity and detection of bottlenecks

Departures from Hardy-Weinberg expectations (HWE) and linkage disequilibrium (LD) among loci were tested in GENEPOP v 4.0 (Rousset, 2008), and significance adjusted with sequential Bonferroni correction. Expected (*He*) and observed (*Ho*) heterozygosity, allelic richness (AR) and F_{IS} were estimated using FSTAT 2.9.3 (Goudet, 2001).

Recent genetic bottlenecks were assessed using two distinct analytical approaches: heterozygosity excess (Cornuet and Luikart, 1996) and the ratio (M) of the total number of alleles (*k*) to the range in allele sizes (*r*), or M-ratio (Garza and Williamson, 2001). Both tests compare observed results to theoretical expectations based on a population at equilibrium. The two approaches were used to explore our data using the same sets of parameter conditions and mutational models. Genetic bottleneck tests generally make assumptions about microsatellite evolution, and are usually simulated as evolving according to a two-phase mutation model where mutations result in the addition or loss of multiple number of repeats. Two parameters are considered, P_g (the proportion of multi-step mutations) and δ_g (the mean size of multi-step mutations). However, these parameters are usually unknown for the species of interest, and therefore parameters are estimated indirectly from allele frequency distributions observed in stable populations (i.e values proposed by Piry *et al.*1999, and Garza and Williamson, 2001). Variation encompassed the values for P_g and δ_g according to estimates for olive ridley turtles (P_g = 0.27, δ_g = 3.3; Hoekert *et al.*, 2002), green turtles (P_g = 0.57, δ_g = 4.0; FitzSimmons, 1998), widely used parameters (P_g = 0.10, δ_g = 3.1; Piry *et al.*1999, and P_g = 0.10, δ_g = 3.5; Garza and Williamson, 2001) and values recently proposed as suitable for assessing population bottlenecks (P_g = 0.22, δ_g = 3.1; Peery *et al.*, 2012). Additionally, we explored conservative scenarios by gradually increasing the proportion of multi-step mutations by 0.05 units up to P_g=0.57, using a constant value of δ_g =3.1. Data were explored at two levels: (1) whole population and (2) deme (nesting colony), since the latter is of management interest. Mainland nesting colonies were also tested independently from peninsular nesting sites.

To assess the significance of heterozygosity excess we used a Wilcoxon sign-rank test based on a two-phase mutation model and a qualitative descriptor of allele frequency distribution (mode-shift indicator), both implemented in BOTTLENECK v 1.2.02 (Cornuet and Luikart, 1996). The variance of the size of multi-step mutations was estimated following the equations proposed by Williamson-Natesan, 2005). For the M-ratio, we estimated empirical M-value and M critical. The value of M decreases after a population is reduced in size with magnitude correlated with the severity and duration of the bottleneck (Garza and Williamson, 2001). The empirical M-value was compared to a simulated distribution of values (M critical) to assess significance based on 10 000 simulations. The M critical is set to the lower 5% tail of the distribution, below which it is assumed that observed ratios are from a population that has experienced a significant reduction in size. We obtained values using the parameters of theta (4*(historical) N_e *mutation rate μ), δ_g and p_s (as described above), a mutation rate of 5.7×10^{-4} for microsatellites (FitzSimmons, 1998) and a wide range of pre-bottlenecked N_e of 1000, 2000, 4000 and 6000 and 50 000. Additionally, historical values of N_e were used using two long-term estimators proposed by Hartl and Clark (1989) and Ohta and Kimuraa (1973) based on the infinite allele (IAM) and step-wise (SMM) mutation models, respectively: $N_e = H_E / 4\mu(1-H_E)$ and $N_e=(1/(1-H_E))^2-1/8\mu$. Our estimates of N_e varied from 1112.9 to 2038.1 (IAM) and from 2351.5 to 6191.8 (SMM). To assess statistical power for inferring bottlenecks under our study conditions (i.e. number of samples and loci), we simulated scenarios incorporating liberal and conservative pre-bottleneck N_e for both *arribada* and solitary nesting sites. In addition, we simulated power of inference for the metapopulation using information from large documented population reductions, such as the one that took place in the *arribada* site of Mismaloya (Márquez-M *et al.*, 1982; Abreu-Grobois and Plotkin, 2008). Power analysis simulations use information from evolutionary history parameters according to the recovery or non-recovery model chosen. Parameters include size of pre-bottleneck population, time of start of bottleneck, size of bottleneck population at its lowest point, and size of current population. The non-recovery model was used since it assumes a severe reduction on population size and a slight rise in numbers but not substantial after bottleneck, and in this particular case most of the sampled nesting colonies had their historic population size reduced to low numbers and have not shown substantial recovery. We set additional parameters to $P_g = 0.22$, mutation rate = 5.7×10^{-4}, and generation time to 20 years. We implemented 1000 replicates to estimate the statistical power of the data set using SPOTG (Hoban *et al.*, 2013).

2.3.4. Analysis of spatial population structure

Population subdivision considering both global and pairwise Wright's F_{ST} was tested for significance using ARLEQUIN 3.11 (Excoffier *et al.*, 2005), and adjusted with Bonferroni sequential correction. We also calculated Jost' D_{EST} estimate (10 000 permutations) in GENALEX 6.5 (Peakall and Smouse, 2012) for comparison, as F_{ST} may not accurately measure the magnitude of genetic differentiation under low divergence and high heterozygosity (Heller and Siegismund, 2009). A hierarchical analysis of molecular variance (AMOVA) among colonies at Baja California Peninsula (4; n=80) and those in mainland (12; n=285) was carried out in ARLEQUIN.

We examined relationships between genetic differentiation and geographic distance at various spatial extents, calculating autocorrelation coefficients of multilocus genotypes (r) among individuals sampled in the same locality (distance class 0) and among individuals separated by 100 km up to 1800 km in GENALEX. A broader test of isolation by distance in IBDWS 3.16 (Jensen *et al.*, 2005) using both F_{ST} and D_{EST} was also carried out. Geographic distances corresponded to the shortest possible sea distance between nesting sites estimated in GOOGLE EARTH.

We further tested population subdivision using a Bayesian model-based clustering analysis in STRUCTURE 2.1 (Pritchard *et al.*, 2000). Two admixture models were tested: standard and LocPrior models, with the latter designed to detect weak population structure. The identification of populations or K-clusters followed the method of Evanno *et al.*, 2005), with ten independent runs for each of K=1-13 using $1\text{x}10^5$ MCMC iterations after a burn-in of $1\text{x}10^4$, as results did not change with longer runs.

2.4. Results

2.4.1. Genetic variation and bottlenecks

No deviations from HWE or evidence of LD were detected in our data. Null alleles were identified for one locus (OR2) at only six out of 18 nesting areas. This locus was included in subsequent analyses since results remained unchanged if removed from the data set. All microsatellite loci were variable, with an average of 10.5 alleles per locus, mean observed heterozygosity of 0.76 and allelic richness of 6.18 (Table 2.2, Appendix Table A 2.1).

A strong signal associated with population bottlenecks was detected for olive ridley turtles in Mexico based on the M-ratio test, a result observed across a wide range of mutational models and theta values (Table 2.3). Observed M-values suggestive of bottlenecks (i.e. lower than the estimated M critical values and the M of 0.70 associated with populations known to have undergone recent bottlenecks (Garza and Williamson, 2001) varied between 0.59 and 0.77. These statistically significant results were consistently observed in six nesting areas: Baja California Peninsula, Mismaloya, Playa Ticuiz, Boca de Apiza, Barra de la Cruz and Puerto Arista. Remarkably, the signal of genetic bottleneck also remained strong when M-ratio was estimated across all Mexican nesting colonies pooled as a single population (n=334) or when pooling all mainland colonies (n=258; after excluding peninsular Baja California). When testing more conservative scenarios (i.e. $P_g \geq 0.32$) at the deme level, the signal of bottlenecks remained significant for the nesting colonies of Baja California Peninsula and Playa Ticuiz (Table 2.3, Appendix Table A 2.2).

Table 2. 2 Summary statistics of genetic diversity based on ten microsatellite markers for 13 nesting areas of olive ridleys in Mexico.

Region	Collection Site		Sample Size	N_A	Ho	He	AR	F_{IS}
Baja California Sur	Todos Santos, Pescadero, San Cristobal, San José del Cabo, Cabo Pulmo, Punta Colorada, Punta Arenas.	(BCP)	80	15.3	0.738	0.803	6.436	0.087
Sinaloa	El Verde	(EVE)	18	9.4	0.658	0.732	5.957	0.13
Nayarit	Platanitos	(PLA)	21	11.1	0.770	0.789	6.519	0.049
	Nuevo Vallarta	(NVA)	20	9.7	0.598	0.757	5.928	0.237
Jalisco	PuertoVallarta / La Gloria	(PVG)	25	11.3	0.703	0.690	6.098	0.103
	Mismaloya	(MIS)	25	9.2	0.626	0.690	5.610	0.118
Michoacan	Ticuiz	(PTI)	15	10	0.781	0.781	6.491	0.04
Colima	Boca de Apiza	(BAP)	21	10.7	0.743	0.779	6.426	0.074
Guerrero	Tierra Colorada	(TCO)	18	10.2	0.712	0.776	6.390	0.114
Oaxaca	San Juan de Chacahua	(SJC)	30	11.5	0.738	0.777	6.194	0.068
	Barra de la Cruz	(BCR)	24	9.8	0.697	0.795	6.116	0.151
	Escobilla	(ESC)	40	12.7	0.737	0.801	6.434	0.094
Chiapas	Puerto Arista	(PAR)	28	10.7	0.650	0.743	5.856	0.148

(NA) number of alleles, (Ho) observed heterozygosity, (He) expected heterozygosity, (AR) allelic richness, (F_{IS}) coefficient of inbreeding.

Table 2. 3 Results of significant tests of genetic bottlenecks based on the M-ratio for olive ridley turtles in Mexico. Values are shown across a range of parameter conditions and mutational models for both the entire population and subpopulation (nesting colonies) levels.

Nesting Area	N_e	Θ	*M-ratio*	M_C Pg=0.10 δg=3.5	M_C Pg=0.10 δg=3.1	M_C Pg=0.22 δg=3.1	M_C Pg=0.27 δg=3.3	M_C Pg=0.32 δg=3.*1*	M_C Pg=0.37 δg=3.1
Entire population (n=334)	1000	2	0.632	**0.759**	**0.798**	**0.722**	**0.679**	**0.689**	**0.673**
	2000	4	0.632	**0.749**	**0.789**	**0.732**	**0.690**	**0.706**	**0.696**
	4000	8	0.632	**0.750**	**0.793**	**0.745**	**0.711**	**0.729**	**0.718**
	6000	12	0.632	**0.756**	**0.795**	**0.754**	**0.723**	**0.737**	**0.729**
	50 000	100	0.632	**0.785**	**0.798**	**0.766**	**0.745**	**0.750**	**0.744**
	IAM	4.0	0.632	**0.749**	**0.793**	**0.732**	**0.690**	**0.706**	**0.696**
	SMM	11.8	0.632	**0.757**	**0.796**	**0.756**	**0.722**	**0.737**	**0.730**
Mainland population (n=258)	1000	2	0.684	**0.758**	**0.796**	**0.722**	0.675	**0.685**	0.668
	2000	4	0.684	**0.746**	**0.788**	**0.727**	**0.687**	**0.701**	**0.689**
	4000	8	0.684	**0.747**	**0.789**	**0.741**	**0.702**	**0.720**	**0.713**
	6000	12	0.684	**0.751**	**0.791**	**0.746**	**0.715**	**0.727**	**0.722**
	50 000	100	0.684	**0.762**	**0.787**	**0.755**	**0.729**	**0.736**	**0.796**
	IAM	3.9	0.684	**0.746**	**0.790**	**0.728**	**0.685**	**0.698**	**0.772**
	SMM	11.4	0.684	**0.789**	**0.791**	**0.749**	**0.714**	**0.725**	**0.719**
Baja California Peninsula (n=80)	1000	2	0.658	**0.751**	**0.784**	**0.702**	0.655	**0.660**	0.641
	2000	4	0.658	**0.731**	**0.770**	**0.700**	0.654	**0.666**	0.650
	4000	8	0.658	**0.720**	**0.759**	**0.700**	**0.660**	**0.671**	**0.660**
	6000	12	0.658	**0.716**	**0.755**	**0.700**	**0.664**	**0.675**	**0.663**
	50 000	100	0.658	**0.675**	**0.703**	0.653	0.623	0.627	0.615
	IAM	4.1	0.658	**0.731**	**0.769**	**0.698**	0.656	**0.666**	0.651
	SMM	12.4	0.658	**0.717**	**0.755**	**0.702**	**0.664**	**0.676**	**0.664**
Mismaloya (*n*=25)	1000	2	0.667	**0.737**	**0.764**	**0.676**	0.624	0.626	0.604
	2000	4	0.667	**0.697**	**0.735**	0.653	0.604	0.607	0.591
	4000	8	0.667	**0.668**	**0.703**	0.632	0.584	0.593	0.577
	6000	12	0.667	0.649	**0.683**	0.613	0.571	0.577	0.563
	50 000	100	0.667	0.502	0.531	0.465	0.429	0.430	0.415
	IAM	2.2	0.667	**0.731**	**0.758**	**0.675**	0.624	0.623	0.603
	SMM	4.7	0.667	**0.691**	**0.725**	0.649	0.600	0.603	0.587
Playa Ticuiz (*n*=15)	1000	2	0.591	**0.724**	**0.751**	**0.660**	**0.610**	**0.607**	0.584
	2000	4	0.591	**0.785**	**0.705**	**0.620**	0.570	**0.610**	0.553
	4000	8	0.591	**0.626**	**0.662**	0.581	0.532	0.537	0.520
	6000	12	0.591	**0.596**	**0.629**	0.555	0.509	0.513	0.496
	50 000	100	0.591	0.394	0.419	0.357	0.324	0.323	0.311
	IAM	3.6	0.591	**0.682**	**0.711**	**0.624**	0.576	0.577	0.557
	SMM	9.9	0.591	**0.608**	**0.642**	0.564	0.520	0.525	0.508
Boca de Apiza (*n*=21)	1000	2	0.637	**0.734**	**0.761**	**0.674**	0.623	0.622	0.599
	2000	4	0.637	**0.694**	**0.729**	**0.646**	0.596	0.599	0.582
	4000	8	0.637	**0.657**	**0.695**	0.618	0.577	0.578	0.563
	6000	12	0.637	0.637	**0.675**	0.599	0.577	0.562	0.546
	50 000	100	0.637	0.476	0.582	0.440	0.403	0.404	0.457
	IAM	3.5	0.637	**0.700**	**0.734**	**0.651**	0.600	0.604	0.584
	SMM	9.7	0.637	0.646	**0.683**	0.608	0.566	0.573	0.557
Barra de la Cruz (*n*=24)	1000	2	0.631	**0.731**	**0.760**	**0.760**	0.622	0.619	0.598
	2000	4	0.631	**0.695**	**0.726**	**0.640**	0.594	0.596	0.580
	4000	8	0.631	**0.655**	**0.691**	0.615	0.569	0.575	0.558
	6000	12	0.631	**0.634**	**0.668**	0.595	0.553	0.557	0.543
	50 000	100	0.631	0.466	0.495	0.498	0.394	0.394	0.381
	IAM	3.9	0.631	**0.693**	**0.726**	**0.643**	0.594	0.596	0.578
	SMM	11.4	0.631	**0.637**	**0.672**	0.597	0.554	0.559	0.545
Puerto Arista (*n*=28)	1000	2	0.651	**0.739**	**0.766**	**0.679**	0.628	0.629	0.610
	2000	4	0.651	**0.704**	**0.741**	**0.659**	0.610	0.615	0.601
	4000	8	0.651	**0.673**	**0.712**	0.642	0.595	0.599	0.588
	6000	12	0.651	**0.659**	**0.695**	0.625	0.584	0.592	0.575
	50 000	100	0.651	0.524	0.552	0.489	0.450	0.453	0.440
	IAM	2.9	0.651	**0.721**	**0.751**	**0.667**	0.619	0.621	0.605
	SMM	7.1	0.651	**0.679**	**0.716**	0.644	0.596	0.606	0.589

(*Ne*) effective population size, Θ=4 N_eμ, (IAM) infinite alleles mutation model, (SMM) step-wise mutation model, *Pg*= proportion of multi-step mutations, *δg*= mean size of multi-step mutations. M_C (M critical) values higher than observed M-ratios are in bold.

In marked contrast, results from the test based on excess of heterozygotes did not provide evidence for genetic bottlenecks (P=0.99; P=0.98 and normal L-shift distribution; Appendix Table A 2.3), regardless if nesting colonies were analyzed separately or pooled.

Simulation analyses indicated a fairly good power (79.7%) to correctly reject the null hypothesis of no bottlenecks for the entire metapopulation. In general, simulations indicated probabilities decreasing with smaller sample sizes and they resulted generally in reduced power either for *arribada* or solitary sites regarding of the scenarios tested (up to 17.5% and 12.9%; Appendix Figure A 2.1).

2.4.2. Population differentiation

Olive ridleys in Mexico showed very low levels of differentiation and no clear geographic pattern of population structure. The hypothesis of random mating across the vast sampled area in the Pacific coast could not be rejected when all colonies were pooled together ($P=1.000$). Overall, most pairwise nesting comparisons were non-significant for both F_{ST} and D_{EST}, except for nesting colonies of Mismaloya, San Juan de Chacahua and Puerto Arista which showed low but statistically significant differentiation (Table 2.4). Hierarchical AMOVA indicated no significant structure between colonies on Baja California Peninsula and those from mainland (F_{ST}=-0.0004, P=0.595). No signal of isolation by geographic distance was detected (r=0.027, P=0.351). However, as expected due to the natal homing behaviour of the species, positive spatial clustering of genotypically similar individuals was observed at a nesting colony level (distance

Table 2. 4 Pairwise comparisons of F_{ST} (below the diagonal) and D_{EST} (above the diagonal) for 13 nesting areas of olive ridley turtles in Mexico. Bold indicate significant values ($P<0.05$).

	BCP	EVE	PLA	NVA	PVG	MIS	PTI	BAP	TCO	SJC	BCR	ESC	PAR
BCP		0.05	0.02	0.05	0.05	**0.14**	0.06	0.02	0.03	**0.08**	0.04	0.03	**0.14**
EVE	0.01		0.04	0.10	0.07	0.04	**0.15**	**0.09**	0.08	**0.12**	0.09	0.05	**0.18**
PLA	0.009	0.005		0.07	0.04	**0.12**	0.06	0.05	0.06	**0.11**	0.07	0.05	**0.15**
NVA	0.007	0.02	0.01		0.09	**0.19**	0.04	0.05	0.04	**0.14**	0.07	0.02	**0.19**
PVG	0.01	0.02	0.004	0.01		**0.16**	0.04	-0.003	-0.03	0.07	0.02	0.04	0.06
MIS	**0.02**	0.01	0.02	**0.04**	**0.04**		**0.22**	**0.17**	**0.18**	**0.22**	**0.18**	**0.15**	**0.26**
PTI	0.002	0.02	0.0005	0.009	-0.0005	**0.04**		0.05	0.02	0.06	0.02	0.06	0.06
BAP	0.001	**0.02**	0.006	0.01	0.006	**0.03**	0.004		-0.03	**0.12**	0.01	0.04	0.08
TCO	0.005	0.01	0.01	0.008	-0.01	**0.04**	-0.0007	-0.01		**0.10**	0.002	0.02	0.06
SJC	**0.02**	**0.03**	**0.02**	**0.03**	**0.01**	**0.05**	0.008	**0.03**	**0.02**		0.009	**0.07**	**0.08**
BCR	-0.02	-0.007	-0.01	-0.004	-0.02	0.004	-0.01	-0.01	-0.03	-0.01		0.004	0.06
ESC	0.006	0.01	0.01	0.003	0.009	**0.03**	0.008	0.01	0.008	**0.01**	-0.02		**0.15**
PAR	**0.02**	**0.03**	**0.02**	**0.03**	0.01	**0.06**	0.008	0.01	0.0008	**0.02**	-0.02	**0.03**	

class=0 km; *r*=0.008, *P*=0.001, Figure 2.2), but not over larger distance intervals. Although the Bayesian analysis of structure suggested K=2 as the most likely number of populations, the vast majority of individuals across all nesting colonies show mixed coancestry. Nonetheless, some of the nesting sites such as Mismaloya show a greater membership to one population only (black bars in Appendix Figure A 2.2).

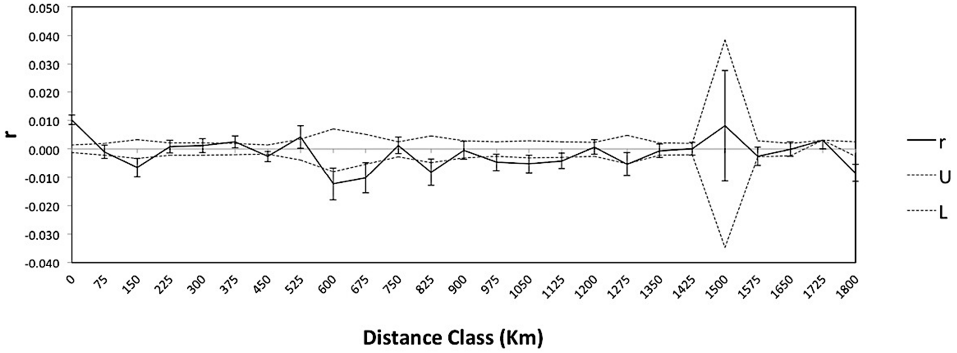


Figure 2. 2 Spatial autocorrelation coefficient (r) for nesting colonies of olive ridleys in Mexico over a range of distance classes. The permuted 95% confidence interval (dashed lines; upper (U) and lower (L) confidence limits) and the bootstrapped 95% confidence error bars are also shown.

2.5. Discussion

We disclose genetic signal associated with recent and brief (around 1.5 generations) human-driven population bottlenecks in olive ridleys from the Mexican Pacific coast. The results indicate that the intensive harvesting of sea turtles between 1960 and late 1980s at the deme level (i.e. nesting beaches) has caused genetic erosion of the metapopulation found along the Mexico's Pacific coast - a conclusion supported with good statistical power. In addition, genetic bottlenecks were in some cases also identified (albeit with low statistical power) for colonies where historical records were not available. We demonstrate the importance of genotyping a large sample collected across a vast nesting geographic region that includes both commercially exploited and non-exploited demes (Table 2.1) and the exploration of statistical tests that encompass a range of population parameters for genetic assessments of bottlenecks in a marine vertebrate. Our study showed that recent and localized anthropogenic harvest has an effect in the genetic diversity of a sea turtle metapopulation. This enables managers to consider information about genetic signatures of contemporary demographic changes during both the development of conservation management plans and during population monitoring.

2.5.1. Genetic diversity and the effect of commercial fishery

Pre-exploitation levels of genetic diversity in olive ridleys from Mexico are unknown. Our estimates indicated high levels of genetic diversity for the species in Mexico's Pacific coast (mean H_e varied between 0.69 and 0.80 across the 13 nesting sites; Table 2.2). Diversity levels were similar to olive ridleys from nesting areas in the broader region, such as Costa Rica (mean H_e varied from 0.78 to 0.94 across three nesting sites) (Jensen *et al.*, 2006), and generally higher than in a depleted population from the Atlantic Ocean (mean H_e was 0.61 based on two sites) (Plot *et al.*, 2012). Reductions of genetic diversity associated with population bottlenecks are typically slow and normally detected after prolonged and intensive demographic collapses (e.g. Beheregaray *et al.*, 2003). During early stages of bottlenecks, populations may still contain substantial heterozygosity showing only distortions in the distribution of allele frequencies, with distortions being transient and likely detectable for only a few dozen generations (Luikart *et al.*, 1998). Our analyses detected loss of allelic diversity but not heterozygosity in olive ridleys (Table 2.3, Appendix Table A 2.3) suggestive of a recent bottleneck after three decades of over-exploitation. This represents only 1.5 discrete generation (20 years average age of parents; Abreu-Grobois and Plotkin, 2008), but is consistent with the severity of the large-scale commercial exploitation of olive ridleys in Mexico (e.g. ~ 350 000 individuals caught in a single year; Márquez-M *et al.*, 1982).

The detected bottlenecks are indicative of changes in the genetic composition of olive ridleys in Mexico due to intense anthropogenic harvest. Stock collapses in populations under intensive fishing pressure, such as the North Sea cod (*Gadus morhua*), resulted in marked reductions of genetic diversity and changes in population structure with implications for subsequent recovery and adaptive potential (Hutchinson *et al.*, 2003). In our study, the genetic results are consistent with available historic records of colonies heavily impacted by the commercial fishery in Mexico. This was particularly true for the genetically bottlenecked colony in Mismaloya (Table 2.3), where a higher concentration of individuals led to major harvesting efforts. In this beach, estimated changes of population size over time revealed a 99% reduction of the number of nesting females (Abreu-Grobois and Plotkin, 2008). The severe decline may have compromised the recovery of this important nesting colony, even under a scenario of moderate to high connectivity (details below) and currently increasing levels of beach protection. In fact, recent nesting activity on Mismaloya – a nesting site formerly characterized by an *arribada* mode of reproduction, remains to levels of solitary sites (Abreu-Grobois and Plotkin, 2008; Table 2.1).

It is also known that the fishery in Mexico relied on the contribution of solitary nesting areas to supply the market (Márquez-M *et al.*, 1982). Our results reflect this fishing effort by identifying bottlenecks in the solitary nesting areas of Baja California Peninsula, Playa Ticuiz, Boca de Apiza, Barra de la Cruz and Puerto Arista. Importantly, demographic reductions were also suggested for colonies such as Playa Ticuiz and Baja California Peninsula, areas with very limited ecological data. However, some over-exploited nesting colonies did not show signs of population bottlenecks. This might be related to a combination of factors, such as the short span of the fishery, the success of corrective actions, and the N_e pre and after decline (N_e would be higher in *arribada* nesting sites). For instance, the *arribada* colonies of Mismaloya and San Juan de Chacahua are thought to have similar pre exploitation *Ne* to Escobilla (Abreu-Grobois and Plotkin, 2008), but so far have not responded to increased protection. It is also plausible that the modest size of our deme samples and the number of loci used influenced the probability of bottleneck detection in some nesting colonies. Theoretical simulations have shown that this probability decreases with less markers and individuals sampled (Peery *et al.*, 2012). The power analysis explored here followed a similar trend, showing reduced power when inferring population bottlenecks at deme level. However, some nesting colonies with comparable bottleneck detection probability (i.e. Mismaloya and Puerto Vallarta/La Gloria) derived different conclusions about evidence of bottlenecks that seems to agree with the expectations from demographic data of exploitation in Mexico. Overall, our study provides a good indication of the genetic effects of recent exploitation on the entire olive ridley metapopulation in Mexico. Finally, other biological factors such as reproductive variance (unequal reproductive output from females to a cohort) can also affect N_e, and therefore impact the estimation of M-ratios.

In Mediterranean loggerhead turtles, nDNA analyses revealed no evidence of population bottlenecks, even when fisheries, egg harvest and tourism development had considerable effect on their populations in the last decades (Carreras *et al.*, 2007). Carreras *et al.* (2007), suggested that other variables such as male-mediated gene flow and the existence of stepping stone colonies in the region might have contributed to the maintenance of allelic and genetic variability in this species. On the other hand, uncertainty regarding variation of mutation process, particularly for microsatellite markers, number of molecular markers used, and small sample sizes could have influenced the detection of bottlenecks. In our case, using a large sample (n=334) and exploring models that encompass a reasonable range of variation for both P_g (0.10-0.57) and δ_g (3.1-4.0) and various values of theta, allowed us to confidently assess reductions of N_e. Given that specific parameters available for olive ridleys were derived from only two microsatellite markers, we favor the model proposed by Peery *et al.*(2012) as a more robust choice of parameters. Finally, M-ratio can be less sensitive to the reintroduction of rare alleles by high levels of gene flow in contrast to the heterozygosity excess method implemented in BOTTLENECK (Williamson-Natesan, 2005), which also has a reduced power of detection compared to M-ratio test (Garza & Williamson, 2001).

2.5.2. High connectivity along the Mexican coast

Our analyses disclosed high levels of connectivity among most nesting colonies and very low population substructure for olive ridleys in Mexico. Shallow genetic structure was expected considering the scenario of recent colonization of the eastern Pacific by olive ridleys around 0.3 million years ago (Shanker *et al.* 2004), and the possible recent divergence of populations with large effective population sizes. Previous studies also suggested a lack of nuclear differentiation in olive ridleys (Bowen *et al.*, 1998; Shanker *et al.*, 2004). Our results did not support previous mitochondrial-based findings of a divergent population in Baja California (López-Castro and Rocha-Olivares, 2005). Genetic discordances between mtDNA and nDNA have been reported for other sea turtles due to strong matrilineal population structure and substantial male-mediated gene flow among nesting colonies (Bowen *et al.*, 2005; Roberts *et al.*, 2004). In addition, mark-recapture data for the species shows high levels of exchange indicating some degree of flexibility in nesting site fidelity, potentially associated with opportunistic behaviour to explore new areas (Morreale *et al.*, 2007). Finally, the lack of correlation observed between genetic differentiation and geographic distance (Figure 2.2) is consistent with the long-distance dispersal pattern reported for olive ridleys in other regions (see Shanker *et al.*, 2004).

Despite the overall finding of reduced population structure, our spatial autocorrelation analysis shows that individuals sampled in the same nesting beach have greater-than-random genetic similarity (Figure 2.2), suggesting that females exhibit some degree of fidelity to nesting sites. In addition, the nesting colonies of Mismaloya, San Juan de Chacahua and Puerto Arista accounted for most of the low but statistically significant genetic differentiation (Table 2.4). It is possible that the demes at Mismaloya and Puerto Arista, which show a signal of bottlenecks, were also impacted at the level of allele frequency. Alternatively, one can speculate on environmental and topographic features impacting on these subpopulations. For instance, the oceanographic system of the Tehuantepec Gulf (Fiedler, 2002) may influence dispersal of individuals reaching the nesting colony of Puerto Arista during the breeding season. This and other competing hypotheses should be investigated by seascape genetics studies designed to statistically assess the interactions between environmental features and evolutionary processes, such as gene flow, in olive ridley nesting colonies.

2.5.3. Conservation implications for olive ridleys in Mexico

The olive ridley sea turtle was listed as 'endangered' in the IUCN Red List until 1996. Recent global population assessments have placed this taxon under the 'vulnerable' category, in which species are considered to have declined by 30% and 50% (Abreu-Grobois and Plotkin, 2008). This general recovery may reflect conservation policies and practices in recent decades. However, the limited and unevenly distributed data across oceanic regions and possible bias from well monitored (and therefore better protected) nesting colonies is recognized as the main limitation of the current olive ridley population assessment.

Our results indicated low but biologically relevant population genetic structure in Mexico suggesting that a few colonies might behave as independent demographic units with differing population dynamics over time. In this context, barriers to dispersal (i.e. oceanographic currents) can reduce the probability of colonization on depleted areas and contribute to differences observed on trends of recovery among nesting sites (Briseño-Dueñas, 2007; Márquez-M *et al.*, 2007). On the other hand, most of the colonies included in this study appear well connected over a vast spatial range. Although, our analysis indicated genetic erosion at metapopulation level as result of the recent intensive harvesting of olive ridley turtles, key factors such as the high levels of genetic variation retained, could importantly contribute to population persistence over time. In addition, under the increasing levels of nesting sites protection, it would not be expected that heterozygosity will decrease in the near future. However, important life-stage threats such as bycatch should be urgently attended. The recovery of severely depleted colonies of sea turtles in Mexico (e.g. Escobilla) and elsewhere (e.g. Hawaiian green turtle; Balazs and Chaloupka, 2004; reviewed by Hays, 2004), give us an indication of the positive effects of long-term conservation efforts and expected timeframes for recovery.

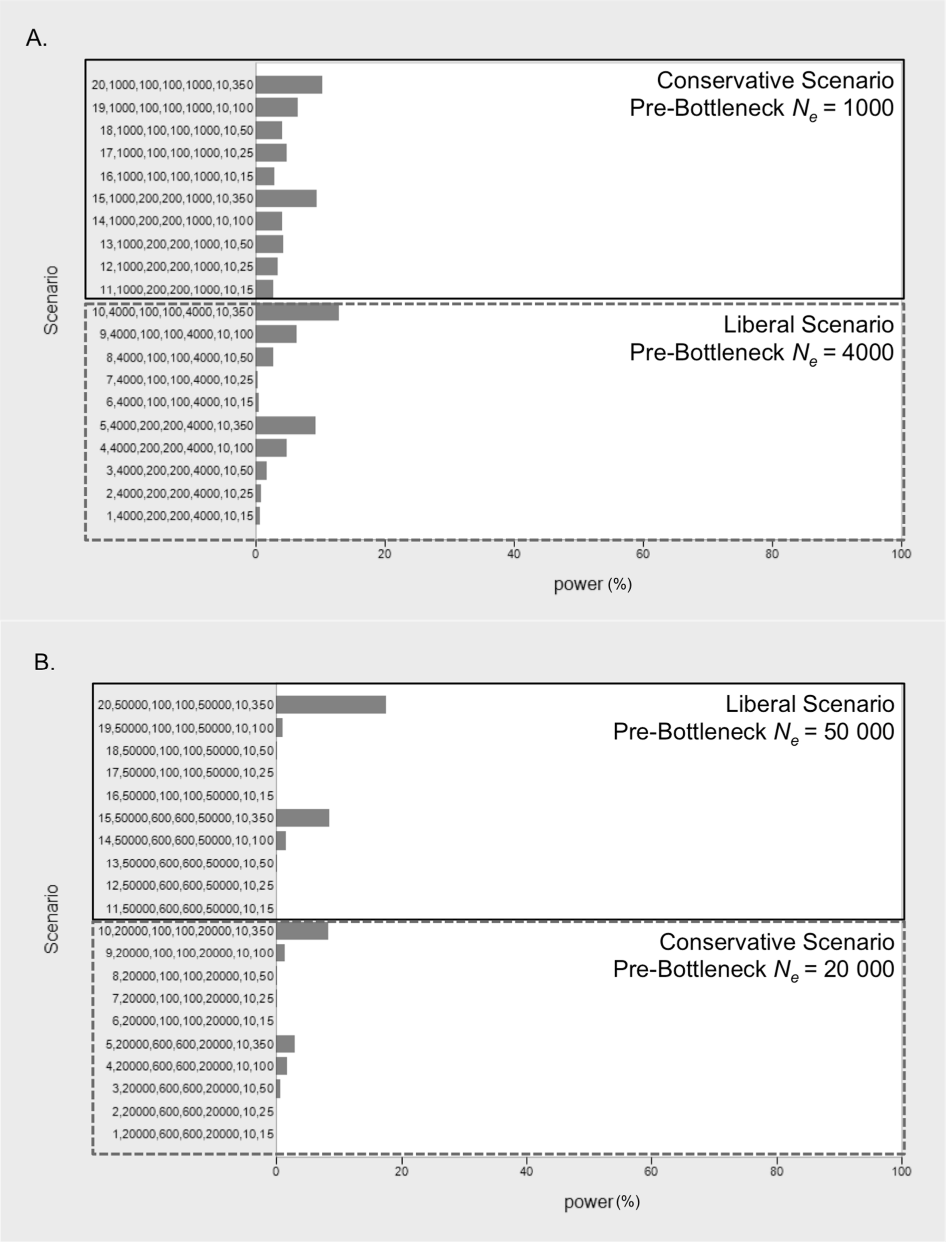
The population dynamics and connectivity patterns described for olive ridley turtles are important information for conservation managers and may contribute on decisions related to allocation of resources and conservation efforts, considering the wide nesting distribution of the species along the pacific coast of Mexico. For instance, our results suggested key sites that are highly genetically differentiated, and that may be relevant on maintaining contemporary levels of genetic diversity and population persistence. In addition, areas that showed evidence of genetic bottlenecks may be of interest to managers particularly to avoid further loss of heterozygosity that could compromise the potential of recovery of already depleted nesting sites.

The clear link described between recent human overexploitation of sea turtles and the resulting genetic erosion illustrates the potential risk of similar effects on other sea turtle populations worldwide, which have shown accelerated declines due to either direct or indirect anthropogenic activities of great magnitude. Despite that conservation efforts on nesting beaches in Mexico have notably expanded in the last decade, the protection of olive ridleys in the sea continue to be challenging and important threats such as bycatch are still present. Moreover, changing environmental conditions could also be of particular relevance since sea turtles are particularly vulnerable to global issues such as climate change (Hays *et al.*, 2003). A better understanding of the multiple interacting forces in driving recovery is needed to improve conservation actions and polices, especially when applied to marine ecosystems. To achieve recovery, marine species have almost entirely depended on the reduction of human impacts, particularly exploitation, habitat loss and pollution. However, the understanding of demographic changes at a deme level is highly relevant to accurately address the cumulative impact of human activities; such as magnitude of depletion, allele effects, genetic diversity, population and metapopulation structure (Lotze *et al.*, 2011). Thus, an enhanced understanding of each of these factors and their interaction with major drivers is needed to allow for improved conservation of sea turtles.

2.6. Acknowledgments

We thank CONANP camp sites, ASUPMATOMA, PROPENINSULA, Grupo Tortuguero-Pescadero, Ayuntamiento de los Cabos, AC-Cabo Pulmo, Instituto Tecnológico de Bahía Banderas, Programa Tortugas Marinas-Puerto Vallarta, GAPEA, Centro Mexicano de la Tortuga and Gobierno del estado de Chiapas for assistance in the field. Tags were donated by Laura Sarti (CONANP) and Jeffrey Seminoff (South West Fishery Service-NOAA). Funding was provided by the Australian Research Council (DP110101275 to Beheregaray, Möller & Waters) and by grants from Texas A&M-CONACYT (2006-10) and CICESE to Rocha-Olivares. Part of this research was carried out under a fellowship from CONACYT to CJR-Z. Samples were collected under permit 04687-SGPA/DGVS/06 Dirección General de Vida Silvestre de Mexico. This is MEGMAR article contribution #48.

2.7. Appendix


A.
Conservative Scenario
Pre-Bottleneck N_e = 1000
Liberal Scenario
Pre-Bottleneck N_e = 4000
Scenario
20,1000,100,100,1000,10,350
19,1000,100,100,1000,10,100
18,1000,100,100,1000,10,50
17,1000,100,100,1000,10,25
16,1000,100,100,1000,10,15
15,1000,200,200,1000,10,350
14,1000,200,200,1000,10,100
13,1000,200,200,1000,10,50
12,1000,200,200,1000,10,25
11,1000,200,200,1000,10,15
10,4000,100,100,4000,10,350
9,4000,100,100,4000,10,100
8,4000,100,100,4000,10,50
7,4000,100,100,4000,10,25
6,4000,100,100,4000,10,15
5,4000,200,200,4000,10,350
4,4000,200,200,4000,10,100
3,4000,200,200,4000,10,50
2,4000,200,200,4000,10,25
1,4000,200,200,4000,10,15
0
20
40
60
80
100
power (%)
B.
Liberal Scenario
Pre-Bottleneck N_e = 50 000
Conservative Scenario
Pre-Bottleneck N_e = 20 000
Scenario
20,50000,100,100,50000,10,350
19,50000,100,100,50000,10,100
18,50000,100,100,50000,10,50
17,50000,100,100,50000,10,25
16,50000,100,100,50000,10,15
15,50000,600,600,50000,10,350
14,50000,600,600,50000,10,100
13,50000,600,600,50000,10,50
12,50000,600,600,50000,10,25
11,50000,600,600,50000,10,15
10,20000,100,100,20000,10,350
9,20000,100,100,20000,10,100
8,20000,100,100,20000,10,50
7,20000,100,100,20000,10,25
6,20000,100,100,20000,10,15
5,20000,600,600,20000,10,350
4,20000,600,600,20000,10,100
3,20000,600,600,20000,10,50
2,20000,600,600,20000,10,25
1,20000,600,600,20000,10,15
0
20
40
60
80
100
power (%)

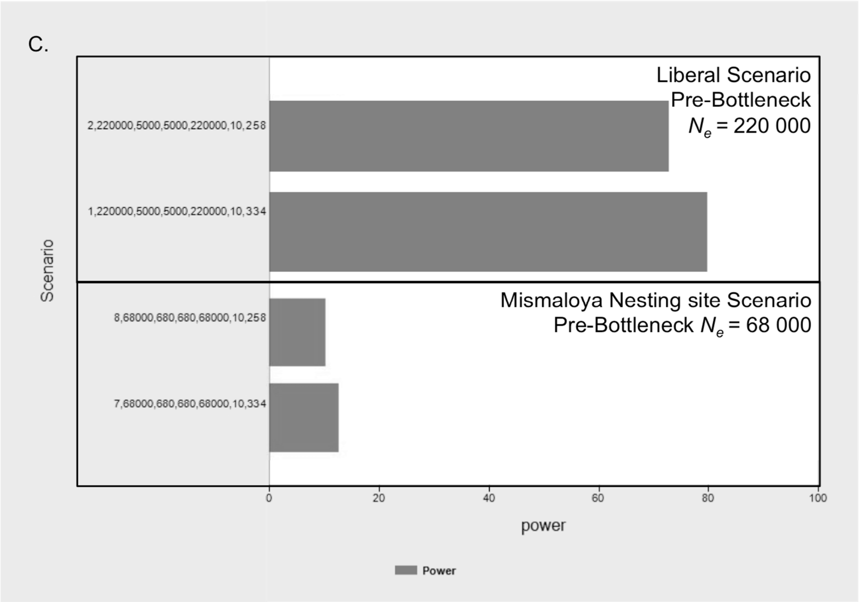


Figure A 2. 1 Estimated probabilities of detection of bottlenecks for solitary sites (A), *arribada* sites (B) and the entire metapopulation plus Mismaloya Beach (C) of olive ridley turtles in Mexico based on 10 microsatellite markers and sampling sizes (15, 25, 50,100, 350). Scenario on metapopulation level is based on total sample size (n=334) and total sample size for mainland nesting colonies (n=258). Scenarios can be read from left to right as follows: scenario number, Pre-Bottleneck Ne, Ne during Bottleneck, Pre-Bottleneck Ne, constant population size for the null hypothesis, number of loci, number of sampled individuals.

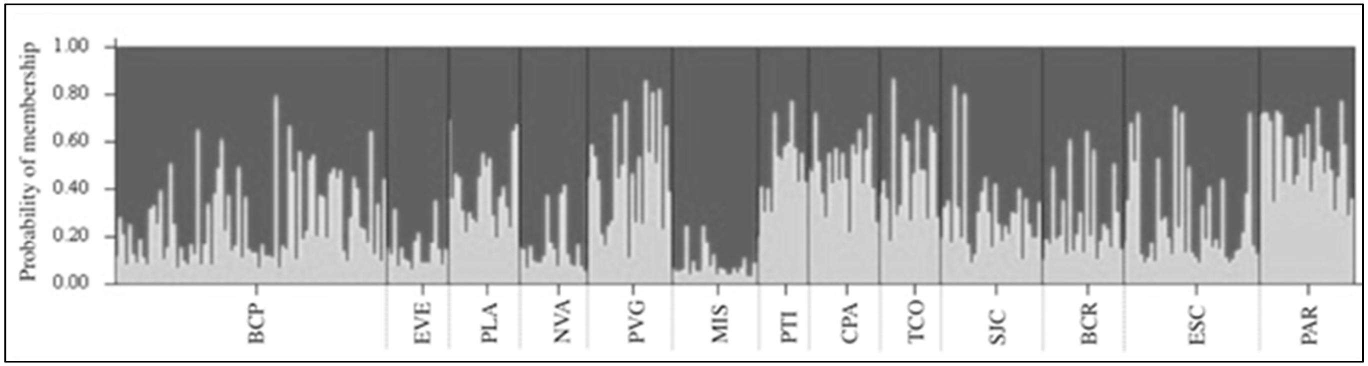


Figure A 2. 2 Estimated probabilities of membership coefficients for each individual turtle in the inferred clusters based on STRUCTURE. Each bar represents an individual with the proportion of color representing assignment to cluster 1 or 2.

Table A 2. 1 Detailed summary statistics of genetic diversity based on ten microsatellite markers for 13 nesting areas of olive ridley in Mexico.

Locus	Location												
	BCP N=80	EVE N=18	PLA N=21	NVA N=20	PVG N=25	MIS N=25	PTI N=15	BAP N=21	TCO N=18	SJC N=30	BCR N=24	ESC N=40	PAR N=28	Mean N_A
OR2														
N_A	11	6	9	7	8	4	7	6	6	6	7	9	8	7.2
Ho	0.48	0.17	0.60	0.36	0.50	0.14	0.417	0.471	0.38	0.51	0.250	0.38	0.294	
He	0.80	0.76	0.80	0.76	0.78	0.33	0.768	0.766	0.79	0.66	0.810	0.78	0.643	
AR	5.61	4.72	5.81	4.77	5.12	2.46	5.15	4.81	5.08	4.16	5.20	5.24	4.90	
F_{IS}	0.40	0.77	0.26	0.52	0.36	0.57	0.469	0.393	0.52	0.21	0.697	0.51	0.551	
OR4														
N_A	18	14	15	12	15	14	12	14	14	14	16	20	13	14.
Ho	0.80	0.80	0.95	0.82	1.00	0.72	0.923	0.933	0.88	0.78	0.833	0.94	0.833	
He	0.92	0.90	0.92	0.90	0.91	0.93	0.929	0.929	0.94	0.90	0.932	0.93	0.913	
AR	8.35	8.07	8.35	7.54	8.20	8.26	8.19	8.45	8.71	7.62	8.44	8.67	7.80	
F_{IS}	0.12	0.12	-0.02	0.08	-0.09	0.22	0.007	-0.005	0.05	0.13	0.108	-0.01	0.089	
OR7														
N_A	13	6	11	7	8	3	6	5	9	9	8	8	7	7.7
Ho	0.75	0.68	0.81	0.33	0.65	0.33	0.857	0.833	0.82	0.78	0.792	0.81	0.600	
He	0.82	0.59	0.85	0.72	0.68	0.31	0.765	0.736	0.77	0.77	0.754	0.74	0.811	
AR	5.80	4.16	6.59	4.43	4.37	3.00	4.51	4.36	5.27	5.42	5.10	5.07	5.32	
F_{IS}	0.08	-0.16	0.05	0.54	0.04	-0.05	-0.12	-0.14	-0.06	-0.01	-0.05	-0.09	0.267	
OR11														
N_A	22	12	15	13	15	13	12	16	12	18	11	18	15	14.
Ho	0.90	0.72	0.80	0.80	0.92	0.95	1.000	0.857	0.77	0.90	0.833	0.79	0.821	
He	0.92	0.90	0.92	0.90	0.93	0.90	0.913	0.923	0.90	0.93	0.894	0.93	0.883	
AR	8.36	7.64	8.24	7.57	8.44	7.66	7.71	8.41	7.43	8.69	7.11	8.45	7.44	
F_{IS}	0.02	0.20	0.13	0.12	0.01	-0.05	-0.09	0.073	0.13	0.03	0.069	0.14	0.000	
OR16														
N_A	12	8	10	8	9	7	13	11	10	10	8	10	8	9.5
Ho	0.80	0.64	0.80	0.29	0.68	0.62	0.933	0.688	0.72	0.57	1.000	0.83	0.630	
He	0.80	0.70	0.81	0.78	0.75	0.72	0.883	0.849	0.84	0.67	0.844	0.77	0.655	
AR	5.56	5.21	6.11	5.14	5.07	4.74	7.35	6.76	6.26	4.95	6.16	5.45	3.93	
F_{IS}	-0.01	0.08	0.01	0.63	0.09	0.13	-0.05	0.195	0.14	0.15	-0.19	-0.08	0.039	
OR20														
N_A	8	6	7	8	8	6	6	9	8	6	6	8	7	7.2
Ho	0.69	0.77	0.90	0.90	0.44	0.68	0.636	0.750	0.70	0.63	0.643	0.64	0.679	
He	0.75	0.82	0.82	0.75	0.81	0.74	0.823	0.783	0.80	0.72	0.741	0.74	0.771	
AR	5.60	5.68	5.85	5.75	5.68	5.55	5.78	6.42	6.00	5.23	5.16	5.00	5.57	
F_{IS}	0.13	0.08	-0.06	-0.09	0.47	0.17	0.259	0.077	0.16	0.19	0.217	0.18	0.181	
OR1														
N_A	12	10	9	9	9	12	10	9	9	10	8	9	10	9.7
Ho	0.91	0.77	0.81	0.94	0.84	0.92	0.846	0.950	0.88	0.92	0.737	0.89	0.889	
He	0.87	0.89	0.85	0.87	0.86	0.89	0.883	0.877	0.89	0.89	0.859	0.88	0.860	
AR	7.70	6.99	6.67	7.53	7.25	7.60	7.56	7.37	8.03	7.57	6.65	7.57	6.98	
F_{IS}	-0.01	0.13	0.08	-0.03	0.06	-0.02	0.06	-0.04	0.03	-0.02	0.168	0.02	-0.007	
OR9														
N_A	8	4	5	4	5	4	4	5	4	5	5	7	5	5.0
Ho	0.30	0.27	0.28	0.26	0.36	0.20	0.267	0.286	0.22	0.60	0.231	0.30	0.250	
He	0.32	0.25	0.30	0.24	0.32	0.44	0.303	0.265	0.25	0.56	0.600	0.51	0.263	
AR	2.63	2.38	2.77	2.32	2.67	2.92	2.60	2.50	2.46	3.69	3.98	3.68	2.45	
F_{IS}	0.08	-0.08	0.06	-0.07	-0.12	0.53	0.125	-0.08	0.14	-0.05	0.625	0.40	0.05	
OR14														
N_A	28	17	18	17	23	18	18	20	17	20	20	22	21	19.
Ho	0.89	0.88	0.95	0.88	0.96	0.91	0.933	0.905	0.87	0.93	0.875	0.92	0.857	
He	0.94	0.95	0.94	0.94	0.94	0.94	0.968	0.954	0.95	0.94	0.934	0.95	0.933	
AR	9.17	9.67	9.33	9.03	9.18	9.08	9.98	9.40	9.27	9.24	8.90	9.70	8.67	
F_{IS}	0.05	0.07	-0.00	0.06	-0.01	0.03	0.037	0.052	0.08	0.01	0.064	0.04	0.083	
OR22														
N_A	13	9	8	9	9	7	9	9	9	11	7	10	9	9.2
Ho	0.78	0.83	0.80	0.36	0.68	0.75	1.000	0.714	0.83	0.69	0.783	0.82	0.654	
He	0.79	0.71	0.78	0.78	0.76	0.76	0.841	0.825	0.77	0.72	0.716	0.77	0.793	
AR	5.59	5.05	5.48	5.21	5.00	4.84	6.08	5.77	5.39	5.39	4.48	5.53	5.50	
F_{IS}	0.00	-0.17	-0.01	0.53	0.10	0.01	-0.19	0.137	-0.07	0.04	-0.09	-0.05	0.179	
Multilocus														
N_A	15.3	9.4	11.1	9.7	11.3	9.2	10.0	10.7	10.2	11.5	9.8	12.7	10.7	
He	0.80	0.73	0.78	0.75	0.69	0.69	0.781	0.779	0.77	0.77	0.795	0.80	0.743	
AR	6.43	5.95	6.51	5.92	6.09	5.61	6.491	6.426	6.39	6.19	6.116	6.43	5.856	
F_{IS}	0.08	0.13	0.04	0.23	0.10	0.11	0.040	0.074	0.11	0.06	0.151	0.09	0.148	
Multilocus excluding locus OR2														
N_A	15.7	9.7	11.3	10	11.6	9.7	10.3	11.2	10.6	12.1	10.1	13.1	11	
He	0.80	0.73	0.78	0.75	0.76	0.73	0.786	0.783	0.77	0.79	0.796	0.80	0.756	
AR	6.52	6.09	6.59	6.05	6.20	5.96	6.641	6.606	6.53	6.42	6.218	6.56	5.962	
F_{IS}	0.05	0.03	0.02	0.19	0.06	0.10	0.001	0.029	0.07	0.05	0.101	0.06	0.106	

(*N*) sample size, (N_A) number of alleles, (*Ho*) observed heterozygosity, (*He*) expected heterozygosity, (*AR*) allelic richness, (F_{IS}) coefficient of inbreeding.

Table A 2. 2 Genetic bottleneck tests based on the M-ratio for olive ridley turtles in Mexico. Values are shown across a range of parameter conditions and mutational models for the entire population and the subpopulation (nesting colonies) levels.

Nesting Area	N_e	Θ	*M-ratio*	M_C *Pg= 0.10 δg= 3.5*	M_C *Pg= 0.10 δg= 3.1*	M_C *Pg= 0.22 δg= 3.1*	M_C *Pg= 0.27 δg= 3.3*	M_C *Pg= 0.32 δg= 3.1*	M_C *Pg= 0.37 δg= 3.1*	M_C *Pg= 0.42 δg= 3.1*	M_C *Pg= 0.47 δg= 3.1*	M_C *Pg= 0.52 δg= 3.1*	M_C *Pg= 0.57 δg= 4.0*
Entire population (n=334)	1000	2	0.632	**0.759**	**0.798**	**0.722**	**0.679**	**0.689**	**0.673**	**0.662**	**0.651**	**0.641**	0.516
	2000	4	0.632	**0.749**	**0.789**	**0.732**	**0.690**	**0.706**	**0.696**	**0.689**	**0.681**	**0.672**	0.555
	4000	8	0.632	**0.750**	**0.793**	**0.745**	**0.711**	**0.729**	**0.718**	**0.711**	**0.704**	**0.700**	0.593
	6000	12	0.632	**0.756**	**0.795**	**0.754**	**0.723**	**0.737**	**0.729**	**0.725**	**0.717**	**0.709**	0.610
	50 000	100	0.632	**0.785**	**0.798**	**0.766**	**0.745**	**0.750**	**0.744**	**0.737**	**0.729**	**0.724**	**0.656**
	IAM	4.0	0.632	**0.749**	**0.793**	**0.732**	**0.690**	**0.706**	**0.696**	**0.689**	**0.681**	**0.672**	0.555
	SMM	11.8	0.632	**0.757**	**0.796**	**0.756**	**0.722**	**0.737**	**0.730**	**0.722**	**0.715**	**0.709**	0.608
Mainland population (n=258)	1000	2	0.684	**0.758**	**0.796**	**0.722**	0.675	**0.685**	0.668	0.657	0.645	0.634	0.511
	2000	4	0.684	**0.746**	**0.788**	**0.727**	**0.687**	**0.701**	**0.689**	0.680	0.673	0.663	0.545
	4000	8	0.684	**0.747**	**0.789**	**0.741**	**0.702**	**0.720**	**0.713**	**0.703**	**0.697**	**0.690**	0.582
	6000	12	0.684	**0.751**	**0.791**	**0.746**	**0.715**	**0.727**	**0.722**	**0.712**	**0.707**	**0.699**	0.599
	50 000	100	0.684	**0.762**	**0.787**	**0.755**	**0.729**	**0.736**	**0.796**	**0.722**	**0.713**	**0.707**	0.636
	IAM	3.9	0.684	**0.746**	**0.790**	**0.728**	**0.685**	**0.698**	**0.772**	0.681	0.672	0.661	0.546
	SMM	11.4	0.684	**0.789**	**0.791**	**0.749**	**0.714**	**0.725**	**0.719**	**0.711**	**0.705**	**0.698**	0.596
Baja California Peninsula (n=80)	1000	2	0.658	**0.751**	**0.784**	**0.702**	0.655	**0.660**	0.641	0.628	0.612	0.600	0.479
	2000	4	0.658	**0.731**	**0.770**	**0.700**	0.654	**0.666**	0.650	0.640	0.629	0.615	0.497
	4000	8	0.658	**0.720**	**0.759**	**0.700**	**0.660**	**0.671**	**0.660**	0.651	0.641	0.629	0.518
	6000	12	0.658	**0.716**	**0.755**	**0.700**	**0.664**	**0.675**	**0.663**	0.653	0.644	0.635	0.530
	50 000	100	0.658	**0.675**	**0.703**	0.653	0.623	0.627	0.615	0.605	0.595	0.588	0.498
	IAM	4.1	0.658	**0.731**	**0.769**	**0.698**	0.656	**0.666**	0.651	0.639	0.628	0.619	0.582
	SMM	12.4	0.658	**0.717**	**0.755**	**0.702**	**0.664**	**0.676**	**0.664**	0.652	0.644	0.634	0.528
El Verde (*n*=18)	1000	2	0.658	**0.732**	**0.757**	**0.668**	0.619	0.616	0.594	0.575	0.560	0.544	0.432
	2000	4	0.658	**0.689**	**0.723**	0.640	0.591	0.593	0.577	0.559	0.542	0.531	0.419
	4000	8	0.658	0.650	**0.686**	0.608	0.563	0.569	0.552	0.540	0.525	0.513	0.406
	6000	12	0.658	0.627	**0.664**	0.589	0.546	0.551	0.535	0.520	0.507	0.498	0.396
	50 000	100	0.658	0.457	0.484	0.419	0.384	0.385	0.372	0.359	0.348	0.338	0.263
	IAM	2.7	0.658	**0.712**	**0.745**	0.656	0.609	0.606	0.588	0.570	0.554	0.538	0.428
	SMM	6.5	0.658	**0.662**	**0.697**	0.619	0.572	0.576	0.559	0.545	0.531	0.519	0.413
Platanitos (*n*=21)	1000	2	0.778	0.732	0.762	0.672	0.624	0.622	0.604	0.583	0.566	0.550	0.438
	2000	4	0.778	0.699	0.730	0.646	0.599	0.604	0.585	0.570	0.554	0.542	0.429
	4000	8	0.778	0.661	0.695	0.717	0.576	0.584	0.567	0.554	0.542	0.529	0.495
	6000	12	0.778	0.640	0.680	0.606	0.562	0.568	0.552	0.540	0.527	0.516	0.483
	50 000	100	0.778	0.485	0.513	0.450	0.412	0.414	0.399	0.388	0.376	0.366	0.340
	IAMS	3.7	0.778	0.700	0.734	0.648	0.602	0.608	0.586	0.571	0.557	0.542	0.501
	MM	10.7	0.778	0.64	0.684	0.612	0.567	0.572	0.557	0.544	0.530	0.520	0.486
Nuevo Vallarta (*n*=20)	1000	2	0.659	**0.734**	**0.761**	**0.674**	0.623	0.621	0.600	0.582	0.564	0.547	0.438
	2000	4	0.659	**0.694**	**0.729**	0.646	0.596	0.600	0.580	0.565	0.553	0.537	0.427
	4000	8	0.659	0.657	**0.695**	0.618	0.577	0.579	0.563	0.549	0.536	0.524	0.417
	6000	12	0.659	0.636	**0.675**	0.599	0.577	0.562	0.548	0.533	0.528	0.509	0.407
	50 000	100	0.659	0.476	0.582	0.440	0.403	0.404	0.392	0.377	0.367	0.357	0.279
	IAM	3.1	0.659	**0.709**	**0.741**	0.655	0.607	0.607	0.587	0.573	0.559	0.543	0.430
	SMM	8.0	0.659	0.657	**0.695**	0.618	0.577	0.579	0.563	0.549	0.536	0.524	0.417
Puerto Vallarta/ La Gloria (*n*=25)	1000	2	0.762	0.737	**0.764**	0.676	0.624	0.626	0.604	0.587	0.571	0.556	0.442
	2000	4	0.762	0.697	0.735	0.653	0.604	0.607	0.591	0.576	0.562	0.549	0.435
	4000	8	0.762	0.668	0.703	0.632	0.584	0.593	0.577	0.561	0.550	0.535	0.428
	6000	12	0.762	0.649	0.683	0.613	0.571	0.577	0.563	0.549	0.538	0.526	0.422
	50 000	100	0.762	0.502	0.531	0.465	0.429	0.430	0.415	0.404	0.393	0.383	0.302
	IAM	2.2	0.762	0.728	0.760	0.673	0.621	0.623	0.603	0.584	0.570	0.554	0.441
	SMM	4.7	0.762	0.692	0.725	0.647	0.598	0.603	0.587	0.573	0.557	0.546	0.434
Mismaloya (*n*=25)	1000	2	0.667	**0.737**	**0.764**	**0.676**	0.624	0.626	0.604	0.587	0.571	0.556	0.442
	2000	4	0.667	**0.697**	**0.735**	0.653	0.604	0.607	0.591	0.576	0.562	0.549	0.435
	4000	8	0.667	**0.668**	**0.703**	0.632	0.584	0.593	0.577	0.561	0.550	0.535	0.428
	6000	12	0.667	0.649	**0.683**	0.613	0.571	0.577	0.563	0.549	0.538	0.526	0.422
	50 000	100	0.667	0.502	0.531	0.465	0.429	0.430	0.415	0.404	0.393	0.383	0.302
	IAM	2.2	0.667	**0.731**	**0.758**	**0.675**	0.624	0.623	0.603	0.584	0.570	0.554	0.442
	SMM	4.7	0.667	**0.691**	**0.725**	0.649	0.600	0.603	0.587	0.573	0.557	0.546	0.436
Playa Ticuiz (*n*=15)	1000	2	0.591	**0.724**	**0.751**	**0.660**	**0.610**	**0.607**	0.584	0.563	0.547	0.528	0.421
	2000	4	0.591	**0.785**	**0.705**	**0.620**	0.570	**0.610**	0.553	0.535	0.518	0.507	0.398
	4000	8	0.591	**0.626**	**0.662**	0.581	0.532	0.537	0.520	0.503	0.492	0.478	0.375
	6000	12	0.591	**0.596**	**0.629**	0.555	0.509	0.513	0.496	0.481	0.467	0.453	0.359
	50 000	100	0.591	0.394	0.419	0.357	0.324	0.323	0.311	0.300	0.290	0.280	0.214
	IAM	3.6	0.591	**0.682**	**0.711**	**0.624**	0.576	0.577	0.557	0.540	0.528	0.512	0.405
	SMM	9.9	0.591	**0.608**	**0.642**	0.564	0.520	0.525	0.508	0.492	0.479	0.467	0.367
Boca de Apiza (*n*=21)	1000	2	0.637	**0.734**	**0.761**	**0.674**	0.623	0.622	0.599	0.582	0.564	0.549	0.438
	2000	4	0.637	**0.694**	**0.729**	**0.646**	0.596	0.599	0.582	0.566	0.553	0.538	0.427
	4000	8	0.637	**0.657**	**0.695**	0.618	0.577	0.578	0.563	0.549	0.537	0.523	0.417
	6000	12	0.637	0.637	**0.675**	0.599	0.577	0.562	0.546	0.535	0.519	0.510	0.407
	50 000	100	0.637	0.476	0.582	0.440	0.403	0.404	0.457	0.378	0.367	0.357	0.279
	IAM	3.5	0.637	**0.700**	**0.734**	**0.651**	0.600	0.604	0.584	0.570	0.553	0.541	0.429
	SMM	9.7	0.637	0.646	**0.683**	0.608	0.566	0.573	0.557	0.544	0.531	0.519	0.412

Table A 2. 3 cont. Genetic bottleneck tests based on the M-ratio for olive ridley turtles in Mexico. Values are shown across a range of parameter conditions and mutational models for the entire population and the subpopulation (nesting colonies) levels.

Nesting Area	N_e	Θ	*M-ratio*	M_C *Pg*= *0.10* *δg*= *3.5*	M_C *Pg*= *0.10* *δg*= *3.1*	M_C *Pg*= *0.22* *δg*= *3.1*	M_C *Pg*= *0.27* *δg*= *3.3*	M_C *Pg*= *0.32* *δg*= *3.1*	M_C *Pg*= *0.37* *δg*= *3.1*	M_C *Pg*= *0.42* *δg*= *3.1*	M_C *Pg*= *0.47* *δg*= *3.1*	M_C *Pg*= *0.52* *δg*= *3.1*	M_C *Pg*= *0.57* *δg*= *4.0*
Tierra Colorada (*n*=18)	1000	2	0.770	0.731	0.760	0.760	0.622	0.619	0.598	0.579	0.563	0.549	0.435
	2000	4	0.770	0.695	0.726	0.640	0.594	0.596	0.580	0.562	0.550	0.535	0.423
	4000	8	0.770	0.655	0.691	0.615	0.569	0.575	0.558	0.544	0.533	0.519	0.413
	6000	12	0.770	0.634	0.668	0.595	0.553	0.557	0.543	0.528	0.517	0.504	0.403
	50 000	100	0.770	0.466	0.495	0.498	0.394	0.394	0.381	0.369	0.358	0.347	0.272
	IAM	3.5	0.770	0.702	0.735	0.732	0.597	0.603	0.583	0.566	0.552	0.539	0.425
	SMM	9.5	0.770	0.645	0.681	0.606	0.563	0.567	0.551	0.538	0.523	0.513	0.407
San Juan de Chacahua (*n*=30)	1000	2	0.762	0.737	**0.768**	0.681	0.630	0.635	0.615	0.597	0.581	0.566	0.449
	2000	4	0.762	0.708	0.744	0.665	0.616	0.624	0.603	0.590	0.575	0.563	0.449
	4000	8	0.762	0.681	0.718	0.648	0.604	0.607	0.594	0.582	0.571	0.558	0.448
	6000	12	0.762	0.666	0.703	0.633	0.595	0.601	0.586	0.575	0.561	0.551	0.446
	50 000	100	0.762	0.542	0.571	0.509	0.471	0.475	0.460	0.447	0.434	0.426	0.340
	IAM	3.5	0.762	0.715	0.747	0.667	0.616	0.623	0.606	0.592	0.578	0.566	0.449
	SMM	9.6	0.762	0.676	0.709	0.642	0.601	0.606	0.592	0.578	0.565	0.554	0.449
Barra de la Cruz (*n*=24)	1000	2	0.631	**0.731**	**0.760**	**0.760**	0.622	0.619	0.598	0.579	0.563	0.549	0.435
	2000	4	0.631	**0.695**	**0.726**	**0.640**	0.594	0.596	0.580	0.562	0.550	0.535	0.423
	4000	8	0.631	**0.655**	**0.691**	0.615	0.569	0.575	0.558	0.544	0.533	0.519	0.413
	6000	12	0.631	**0.634**	**0.668**	0.595	0.553	0.557	0.543	0.528	0.517	0.504	0.403
	50 000	100	0.631	0.466	0.495	0.498	0.394	0.394	0.381	0.369	0.358	0.347	0.272
	IAM	3.9	0.631	**0.693**	**0.726**	**0.643**	0.594	0.596	0.578	0.564	0.548	0.537	0.426
	SMM	11.4	0.631	**0.637**	**0.672**	0.597	0.554	0.559	0.545	0.529	0.518	0.507	0.402
Escobilla (*n*=40)	1000	2	0.696	**0.744**	**0.775**	0.689	0.640	0.645	0.623	0.604	0.589	0.575	0.459
	2000	4	0.696	**0.716**	**0.751**	0.675	0.630	0.636	0.620	0.607	0.596	0.580	0.464
	4000	8	0.696	**0.697**	**0.734**	0.667	0.622	0.631	0.619	0.608	0.593	0.585	0.475
	6000	12	0.696	0.687	**0.723**	0.661	0.619	0.627	0.611	0.600	0.590	0.579	0.473
	50 000	100	0.696	0.591	0.621	0.558	0.522	0.527	0.512	0.501	0.489	0.479	0.391
	IAM	4.0	0.696	**0.716**	**0.751**	0.675	0.630	0.636	0.620	0.607	0.596	0.580	0.464
	SMM	12.1	0.696	0.684	**0.722**	0.658	0.611	0.624	0.615	0.600	0.589	0.581	0.473
Puerto Arista (*n*=28)	1000	2	0.651	**0.739**	**0.766**	**0.679**	0.628	0.629	0.610	0.589	0.575	0.560	0.446
	2000	4	0.651	**0.704**	**0.741**	**0.659**	0.610	0.615	0.601	0.583	0.569	0.557	0.445
	4000	8	0.651	**0.673**	**0.712**	0.642	0.595	0.599	0.588	0.572	0.560	0.550	0.441
	6000	12	0.651	**0.659**	**0.695**	0.625	0.584	0.592	0.575	0.563	0.549	0.541	0.434
	50 000	100	0.651	0.524	0.552	0.489	0.450	0.453	0.440	0.427	0.417	0.405	0.322
	IAM	2.9	0.651	**0.721**	**0.751**	**0.667**	0.619	0.621	0.605	0.586	0.572	0.561	0.446
	SMM	7.1	0.651	**0.679**	**0.716**	0.644	0.596	0.606	0.589	0.575	0.564	0.551	0.441

(*Ne*) Effective population size, Θ=4 $N_e\mu$, (IAM) infinite alleles mutation model, (SMM) step-wise mutation model, *Pg*= the proportion of multi-step mutations, *δg*= the mean size of multi-step mutations. M_C values higher than observed M-ratios are denoted on bold numbers.

Table A 2. 3 Genetic bottleneck tests based on heterozygosity excess for olive ridley turtles in Mexico. Values are shown for the Two-Phase Mutational model (TPM) across a range of parameter conditions and for the entire population and the subpopulation (nesting colonies) levels.

Nesting Area		Entire population	Mainland population	Baja California Peninsula	El Verde	Platanitos	Nuevo Vallarta	Puerto Vallarta/ La Gloria	Mismaloya	Playa Ticuiz	Boca de Apiza	Tierra Colorada	San Juan de Chacahua	Barra de la Cruz	Escobilla	Puerto Arista
	n	(334)	(258)	(80)	(18)	(21)	(20)	(25)	(25)	(15)	(21)	(18)	(30)	(24)	(40)	(28)
Model	*TPM Variance*															
TPM 90%, Pg=0.10	2.09	1.000	0.999	0.996	0.903	0.903	0.995	0.993	0.812	0.753	0.947	0.934	0.947	0.934	0.987	0.997
TPM 90%, Pg=0.10	2.5	1.000	0.999	0.997	0.903	0.883	0.995	0.993	0.784	0.721	0.919	0.947	0.947	0.919	0.934	0.997
TPM 78%, Pg=0.22	3.4	1.000	0.998	0.997	0.997	0.903	0.753	0.993	0.983	0.615	0.615	0.919	0.903	0.883	0.903	0.919
TPM 73%, Pg=0.27	4.4	0.999	0.993	0.983	0.903	0.687	0.990	0.947	0.615	0.539	0.883	0.883	0.862	0.812	0.862	0.995
TPM 68%, Pg=0.32	4.5	0.998	0.990	0.947	0.903	0.687	0.990	0.958	0.577	0.577	0.862	0.883	0.862	0.812	0.812	0.995
TPM 63%, Pg=0.37	5.04	0.993	0.987	0.919	0.903	0.615	0.983	0.934	0.500	0.539	0.812	0.838	0.812	0.721	0.784	0.995
TPM 58%, Pg=0.42	5.6	0.990	0.983	0.903	0.903	0.577	0.919	0.919	0.500	0.460	0.784	0.753	0.753	0.721	0.687	0.987
TPM 53%, Pg=0.47	6.13	0.983	0.987	0.862	0.903	0.577	0.919	0.919	0.500	0.347	0.784	0.784	0.721	0.652	0.687	0.958
TPM 48%, Pg=0.52	6.7	0.919	0.883	0.687	0.903	0.500	0.883	0.903	0.460	0.384	0.721	0.652	0.652	0.615	0.577	0.947
TPM 43%, Pg=0.57	12.9	0.784	0.838	0.384	0.903	0.347	0.753	0.862	0.312	0.312	0.652	0.539	0.539	0.460	0.460	0.862
L-shaped distribution		N	N	N	N	N	N	N	N	N	N	N	N	N	N	N

Wilcoxon-test probabilities at 97% confidence level. (*n*) sample size, *Pg*= the proportion of multi-step mutations, (N) normal L-shaped distribution.

Chapter III: (Article 2)

Population Divergence in the Sea: A New Paradigm of Isolation by Ecological Distance for the Highly Mobile Olive Ridley Turtle (*Lepidochelys olivacea*) in the Eastern Pacific

---

Clara J. Rodríguez-Zárate[a] *, Erik Van Sebille[b], Robert G. Keane[c], Axayácatl Rocha-Olivares[d] , Jose Urteaga[e], and Luciano B. Beheregaray[a]

[a]Molecular Ecology Laboratory, School of Biological Sciences, Flinders University, Adelaide, SA 5001, Australia.

[b]ARC Centre of Excellence for Climate System Science & School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.

[c] Geographic Information Systems, School of the Environment, Flinders University, Adelaide, SA 5001, Australia.

[d]Laboratorio de Ecología Molecular, Departamento de Oceanografía Biológica, Centro de Investigación Científica y de Educación Superior de Ensenada, , Ensenada Baja California 22860, Mexico.

[e]Flora y Fauna International, Managua, Nicaragua.

Population Divergence in the Sea: A New Paradigm of Isolation by Ecological Distance for the Highly Mobile Olive Ridley Turtle (*Lepidochelys olivacea*) in the Eastern Pacific

3.1. Abstract

Spatial and temporal scales at which processes modulate genetic variation over the landscape can be usually overlooked; an issue that can significantly impact the design of conservation management practices for widely distributed species. Here, we use the case of panmixia of the olive ridley turtles in the eastern Pacific as a model system to investigate the role of scale in assessing and understanding processes shaping population divergence in highly mobile species. We re-assessed panmixia by implementing a seascape genetic analysis based on nuclear DNA variation of 634 samples collected across the eastern Pacific. The results revealed two genetically distinct populations (F_{ST} =0.015, P <0.001) and showcase the influence of oceanic variability of meso-scale features as main drivers of the population divergence observed. We rejected panmixia and proposed a new paradigm of isolation-by-ecology for the eastern Pacific olive ridley turtles, demonstrating the relevance of spatial scale and the use of integrative approaches for genetic assessments of marine organisms. Our findings are of relevance for conservation management of sea turtles and may also extend to other marine species with highly mobile behaviours.

Keywords: Isolation-by-ecology, panmixia, marine connectivity, landscape genetics, sea turtles, conservation genetics, eastern Pacific.

3.2. Introduction

Panmixia (i.e. the random mating within a breeding population) is an unusual pattern in widely distributed marine species that challenges expectations of population structure over large spatial ranges. Patterns of population genetic structure are expected to emerge over time as a result of different dispersal schemes, life history traits and geographic features (Waples, 1998; Palumbi, 2003). In relation to the spatial arrangement of populations, genetic structure has been generally related to patterns of 'isolation by distance' (IBD), a model that proposes the correlation between genetic distance and geographic separation based on the principle of limited dispersal between populations separated by greater spatial distances (Wright, 1943). However, in the last decade evidence has accumulated demonstrating the agreement between environmental and genetic discontinuities, denoting the emergence of different patterns of gene flow respect to environmental variation (Alberto *et al.*, 2011; Gaggiotti *et al.*, 2009; Mendez *et al.*, 2010). Under models of IBD, distance predicts differentiation among populations. However, when patterns of gene flow are the result of adaptation to environmental heterogeneity, then the environmental distance predicts differentiation among populations. This model is known as Isolation by Ecology or Isolation by Environment (IBE) (Cooke *et al.*, 2012; Wang and Summers, 2010), which arises as a result of diverse mechanisms, including: (i) nonrandom mating due to adaptation to different environments (i.e. mismatch on reproductive timing); or (ii) nonrandom mating due to environmentally mediated phenotypic plasticity (i.e. selection of particular feeding environments based on learned experiences) (Sexton *et al.*, 2014). In recent years, important lessons have been learned about the influence of ecological landscapes on the spatial variation of gene flow and resulting patterns of genetic divergence (Galindo *et al.*, 2006; Selkoe *et al.*, 2008). This is particularly true regarding the relevance of geographic scales at which ecological landscapes must be studied to accurately reveal patterns and processes influencing population connectivity and divergence (Als *et al.*, 2011; Côté *et al.*, 2013).

Our capacity to understand the extent to which the structure of natural populations is influenced by the landscape can be challenged in the ocean. In the marine realm processes are highly dynamic in space and time, and the lack of obvious physical boundaries is generally the norm. Therefore, issues with spatial ecology of marine populations require implementing new approaches that combine genetic data with environmental information to account for the effects of seascape features on gene flow (Liggins *et al.*, 2013; Riginos and Liggins, 2013). This multidisciplinary approach, known as seascape genetics, has been successfully applied to address ecological questions in marine organisms (Amaral *et al.*, 2012; Banks *et al.*, 2010; Banks *et al.*, 2007; Jorgensen *et al.*, 2005; Kool *et al.*, 2011; Liggins *et al.*, 2013; Riginos and Liggins, 2013; Schultz *et al.*, 2008; Selkoe *et al.*, 2010; Wilkins *et al.*, 2013). In particular, recent advances in oceanographic modelling have promoted the application of biophysical models as tools by which dispersal probabilities can be estimated. These models integrate data from ocean circulation variability and biological parameters of the species and allow direct comparisons with information about the distribution of observed genetic variability (i.e. Galindo *et al.*, 2006; Kool *et al.*, 2010). Such improved assessment of connectivity in marine populations could contribute to our understanding about biodiversity persistence under scenarios of human-driven pressures and environmental challenges such as climate change.

Sea turtles are highly mobile species known for performing long distance migrations between feeding and nesting grounds and for using a great variety of habitats during their lifetime (Luschi *et al.*, 2003a). Population structure in sea turtles is fundamentally promoted by natal homing behaviour and fine-scale site fidelity, reducing gene flow among groups of individuals that breed in geographically distant locations. This biological trait common to several aquatic and terrestrial species (Greenwood, 1980) is mainly exhibited by female turtles to nesting areas (Lee, 2008) and in a few cases also described for males (i.e. green turtles, FitzSimmons *et al.*, 1997). However, for some species the observed lack of population structuring disagrees with expectations for natal homing. This is the case of the olive ridley turtle recognized as a panmictic species at regional level (within ocean basins, Bowen *et al.*, 1998) and for which the lack of population structure has been associated to low site fidelity and high nomadic behaviour. Particular attempts on understanding the factors influencing dispersal on this specie have been related to the study of the *arribada* phenomenon (massive synchronous nesting of females), and the factors triggering this behaviour (reviewed by Bernardo and Plotkin, 2007). However, uncertainty still remains. In addition, the relationship of the reproductive behavioural polymorphism of olive ridley turtles (massive and solitary nesting behaviour) to population structure has also remained an opened question. The olive ridley turtle is widely distributed in the eastern Pacific, the second main area for the reproduction of the species worldwide, occupying nesting areas from Mexico to Ecuador (Fritts *et al.*, 1982). The region is considered of great oceanographic variability (Fiedler and Lavin, 2006) with circulation influenced by wind forces and permanent meso-scale features known for affecting the distribution of several marine vertebrates (Ballance *et al.*, 2006; Fiedler, 2002).

We conducted a fine-scale seascape genetic analysis aimed to (i) assess the role of spatial scale (i.e. local to regional) on population structure in the olive ridley turtle, and (ii) assess the influence of ecological landscapes on population divergence in sea turtles. To achieve these aims we analysed nuclear genetic variation of 634 samples across a vast geographic area and implemented a biophysical model based on a hydrodynamic numerical ocean model in combination with a Lagrangian trajectory toolset. Here, we provide evidence of two distinct genetic populations and clarify the role of oceanic variability associated with meso-scale features as main driver of population divergence in olive ridleys. By doing so, we reject panmixia and propose a new paradigm of isolation-by-ecology for the species. The results have great relevance for conservation management that may also extent to other marine species. The re-assessment of panmixia in this endangered species (U.S. Endangered Species Act, ESA) contributes to the need to clarify management units for conservation within regional scales by which large-scale threats can be properly addressed.

3.3. Materials and Methods

3.3.1. Study area - The eastern tropical Pacific

The eastern tropical Pacific is defined as the area confined between the coast of Central and South America to 140°W and within the Tropics of Cancer and Capricorn at 23.5°N and S, respectively. The region includes the eastern and equatorial branches of the north and south Pacific subtropical gyres, the south and north equatorial currents, and two coastal Counter currents (California current and Peru current) (Pennington *et al.*, 2006) (Figure 1). The oceanographic dynamics is influenced by wind forcing that generates coastal eddies, imprinting sea surface temperature as well as circulation. Although the region is considered to have large amounts of oceanographic variability, macro and meso-scale features are relatively permanent and predictable (Fiedler and Talley, 2006; Kessler, 2006). The main meso-scale features are the cyclonic and anticyclonic eddies of the Costa Rica Dome and Tehuantepec Bowl that originate off the coast of Costa Rica and southern Mexico respectively. These domes result from highly seasonal trans-isthmic wind jets (Figure 1), making associated marine areas fertile zones that extent up to 1000 km offshore (Pennington *et al.*, 2006). These features have been recognized as an integral part of the seasonal hydrography, circulation and biology of the eastern tropical Pacific, influencing the distribution of several species, such as blue whales, short-beaked common dolphins, spinner and spotted dolphins, and planktivorous seabirds (Ballance *et al.*, 2006; Fiedler, 2002). In addition to these systems, coastal and equatorial upwelling are biological hotspots offering a wide range of foraging habitat to green turtles, leatherbacks and olive ridleys in the region (Saba, 2012). Our study area was defined by the location of nesting sites and it also comprises the marine areas of high use by eastern Pacific olive ridley turtles (Eguchi *et al.*, 2007; Plotkin, 2010).

3.3.1.1. Variability of the main meso-scale features in the eastern tropical Pacific

The Costa Rica Dome & Tehuantepec Bowl

The Costa Rica Dome (CRD) is centred at 9°N 90°W, corresponding to the lifting on the thermocline due to Ekman pumping. It extends 300-900 km^2 on the surface and more than 300 m deep below the thermocline, and is characterized by upwelling and a shallow thermocline (at 25 m) (Fiedler, 2002; Kessler, 2006). Its annual cycle is well known and can be generalized as follows: (1) coastal shoaling of the thermocline off the Gulf of Papagayo (February–April); (2) separation from the coast (May–June) when the wind jet stops; (3) expansion of the dome to the west (July–November); and (4) dome deepening (December–January) when strong trade winds blow over the dome (Fiedler, 2002). The Tehuantepec Bowl (TB) is a shallower feature (up to 200 m deep and 300 km^2) that corresponds to a thermocline depression (90m) located at 14°N, 105°W. Its annual cycle is less known than the CRD. When the eddy is mature the thermocline deepens and coastal circulation is driven on its northern edge. The circulation changes during summer with the cessation of wind forcing and is dominated by the influence of the Costa Rica Counter Current (CCCR) (McCreary *et al.*, 1989). In general, both the CRD and TB features develop and intensify during the boreal winter-spring exhibiting strong currents speeds around their edges of about 20-50 cm s^{-1}, and weaken during summer, coinciding with the strengthening of the North Equatorial Counter Current (Kessler, 2006).

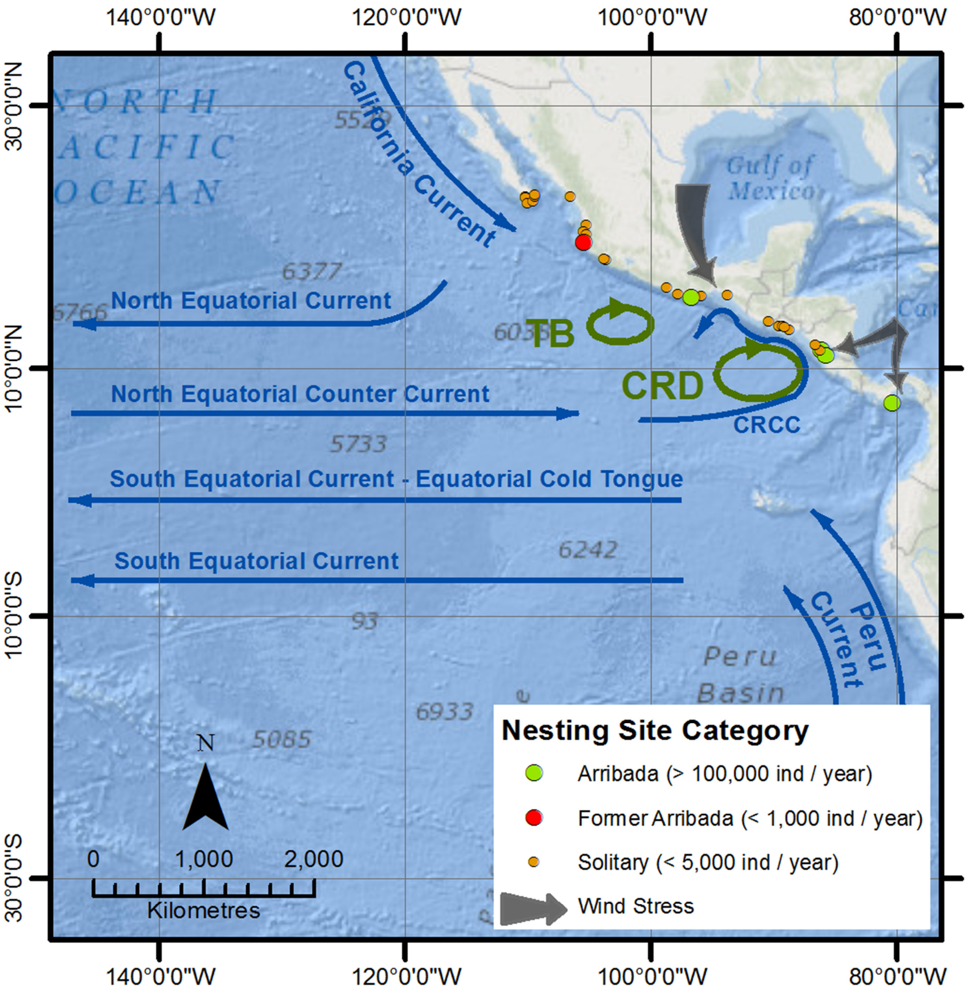


Figure 3. 1 Study area showing sampling sites of olive ridley turtles in the eastern Pacific and schematic ocean surface circulation. Sampling sites from north to south along Baja California Peninsula are: Todos Santos, Pescadero, San Cristobal, San José del Cabo, Cabo Pulmo, Punta Colorada and Punta Arenas. Continental sampling sites are: El Verde, Platanitos, Nuevo Vallarta, Puerto Vallarta-La Gloria, Mismaloya, Boca de Apiza, Playa Ticuiz, Tierra Colorada, San Juan de Chacahua, Escobilla, Barra de la Cruz, Puerto Arista, Hawaii, Playa Dorada, San Diego, Bocanitas, San Juan del Gozo, Salamina, Veracruz, Chacocente, La Flor, La Marinera. Oceanographic features: Tehuantepec Bowl (TB), Costa Rica Dome (CRD), Costa Rica Coastal Current (CRCC).

3.3.2. Sample collection and microsatellite genotyping

We sampled nesting beaches of olive ridley turtles across 28 sites in five countries in the eastern Pacific region during the 2006 and 2010 nesting seasons (Figure 3.1). Skin biopsies were collected from tagged nesting females to avoid replication of samples (FitzSimmons *et al.*, 2000) and tissues were preserved in a 20% DMSO/saturated NaCl solution. In areas where sampling of females was difficult, tissue from one dead hatchling per nest was taken within the 15-day inter-nesting period. Analyses are based on a maximum of 27 nesting areas and beaches with less than 15 samples were assigned to major nesting areas using the criterion of the geographically closest neighbour. Procedures used for DNA extractions and collection of data from ten olive ridley turtle microsatellite DNA loci are described in Chapter II. Null alleles and large allele dropout were assessed in MICRO-CHECKER (Oosterhout *et al.*, 2003).

3.3.3. Genetic diversity and analysis of spatial population structure

Departures from Hardy-Weinberg expectations (HWE) and linkage disequilibrium (LD) among loci were tested in GENEPOP v 4.0 (Rousset, 2008) and significance adjusted with sequential Bonferroni correction. Genetic diversity was estimated as expected (He) and observed (Ho) heterozygosity, allelic richness (AR) and FIS using FSTAT 2.9.3 (Goudet, 2001). Population subdivision considering both global and pairwise Wright's F_{ST} was tested for significance using ARLEQUIN 3.11 (Excoffier *et al.*, 2005), and adjusted with Bonferroni sequential correction. We also calculated Jost' D_{EST} estimate (10,000 permutations) in GENALEX 6.5 (Peakall and Smouse, 2012) for comparison, as F_{ST} may not accurately measure the magnitude of genetic differentiation under low divergence and high heterozygosity (Heller & Siegismund, 2009). A hierarchical analysis of molecular variance (AMOVA) was carried out in ARLEQUIN in order to test the influence of local and regional spatial scales on population subdivision. Different hierarchical levels were tested considering differences between and within populations.

We further tested population subdivision using a Bayesian model-based clustering analysis in STRUCTURE 2.1 (Pritchard *et al.*, 2000). Two admixture models were tested: standard and LocPrior models, with the latter model designed to detect weak population structure. The identification of populations or K-clusters followed the method of Evanno *et al.* (2005), with 20 independent runs for each of K=1-22 using 1x105 MCMC iterations after a burn-in of $1x10^4$, as results did not change with longer runs. Relationships among populations based on the similarity of their allelic states were visualized using a factorial correspondence analysis (FCA) performed in GENETIX 4.05 (Belkhir, 2004).

In order to identify geographic scales of genetic exchange we calculated autocorrelation coefficients of multilocus genotypes (*r*) among individuals sampled in the same locality (distance class 0) and among individuals separated by 100 km up to 3000 km in GENALEX. We used IBDWS 3.16 (Jensen *et al.*, 2005) to test for the influence of geographic distance on population genetic structure (using both F_{ST} and D_{EST} genetic distances). Geographic distances were calculated as the shortest sea distance between nesting sites estimated in GOOGLE EARTH. We also used partial mantel tests implemented in GENODIVE 2.0b25 (Meirmans and Van Tienderen, 2004) to test for correlation between genetic and geographic matrices while controlling for the effect of spatial genetic structure.

First generation migrants among nesting areas were assessed using a Bayesian approach implemented in GENECLASS 2.0 (Piry *et al.*, 2004). We computed a likelihood ratio test comparing the population where the individual was sampled over the highest likelihood value among all available populations (L = L_home⁄ L_max). We selected the Bayesian criterion of Rannala and Mountain(1997) with the resampling method of Paetkau *et al.*(2004) to determine the critical value of Lh/Lmax using 10,000 simulated individuals and an alfa of 0.01.

3.3.4. Environmental heterogeneity profiles

We used four oceanographic variables to assess whether genetic connectivity could be influenced by environmental heterogeneity. These variables were night-time sea surface temperature (SST), chlorophyll a concentration (Chl_a, mg/m3), sea surface height (SSH, cm) relative to a 450 m reference level, and thermocline depth (Therm, 20°C isotherm depth, m).

The selected variables are known to influence migration patterns, habitat preference and distribution in many marine species (Bost *et al.*, 2009; Etnoyer *et al.*, 2006b; Palacios *et al.*, 2006; Ream *et al.*, 2005), including sea turtles (Fossette *et al.*, 2010; Shillinger *et al.*, 2008). For instance, dynamic processes such as those conformed by SST and Chlorophyll fronts can influence the spatio-temporal distribution of preys, and consequently migration patterns and habitat utilization of predators (Polovina *et al.*, 2001). Habitat utilization by sea turtles hatchlings has been also linked to geostrophic currents, and other oceanographic features such as dynamic eddies and convergent zones of high productivity (Polovina *et al.*, 2004). Data for these variables were obtained from remote sensing, with exception of the latter variable for which float data were used. Data sources included: AVHRR Pathfinder SST data Version 5.2 from US National Oceanographic Data Center and GHRSST (http://pathfinder.nodc.noaa.gov); Chl_a data from the Ocean Color Data NASA/MODIS-Aqua Sensor (http://oceancolor.gsfc.nasa.gov/); SSH data from AVISO (http://www.aviso.oceanobs.com/duacs/); and thermocline data used MBT, XBT, and CTD profiles from World Ocean Database (WOD) 2009 (http://www.nodc.noaa.gov/OC5/WOD09/pr_wod09.html).

We defined areas of 1000km from each geographic point (nesting colony). Data were extracted and monthly averages of the four variables were obtained to reconstruct climatology maps for five seasonal periods. Each pixel in the maps corresponded to the ten-year (2001 to 2011) average value for a 37 km grid (see Appendix, Figure A 3.1, A 3.2, A 3.3, A 3.4). Data were processed using ArcGIS software v.10.1 (http://www.esri.com). Maps were coupled with data of geostrophic currents (gathered from AVISO), and visually inspected to identify areas of oceanographic heterogeneity. We focus on the analysis of seasonal periods defined on general knowledge about olive ridley turtles migration in this region (Morreale *et al.*, 2007; Márquez-M, 1996) and included: MIG-migration to breeding areas (April); MATE-mating season (May-June); NES1-beginning of nesting season (July, August, September); NES2-ending of nesting season (October, November, December); and FEED-migration and residence on feeding areas (January, February, March).

3.3.5. Analysis of environmental heterogeneity

Environmental variability over the 10year period was used to examine associations with genetic data. We implemented an exploratory Mantel test using environmental Euclidean distances calculated as pairwise differences in mean SST, Chl_a, SSH, and Therm between regions, and pairwise F_{ST} and D_{EST} as genetic distances. Tests were performed at different scales: among nesting colonies (subpopulation level), and between putative populations (population level). Environmental heterogeneity between putative populations was qualitative investigated by comparing averaged monthly time series for each environmental variable, and assessing differences between means using a paired t-test. Since the geographical distance between localities may influence isolation by ecological distance (IBED) patterns, we also used partial Mantel tests to control for this effect. The tests were performed using the package VEGAN in R (Oksanen *et al.*, 2013). Correlation between genetic similarity of the olive ridley turtle populations and environmental heterogeneity was also tested by means of a stepwise multiple regression analysis of standardized distance matrices, following the methods outlined in Legendre *et al.* (1994), and implemented in R. The stepwise procedure adds one variable at a time with each step resulting in a model modified in every successive step. Each model is then tested for statistical significance. In addition, we performed a hierarchical Bayesian analysis in GESTE (Foll and Gaggiotti, 2006) to assess the relative importance of environmental factors on the genetic structure of olive ridley turtles. This method estimates F_{ST} values for each local population and relates them to environmental factors via a generalized linear model. We used 10 pilot runs of 7000 iterations, and an additional burn-in of $5x10^5$ iterations with a thinning interval of 20. Here, the simulation with the highest posterior probability is the one that best explains the data. Additionally, we used the BIOENV procedure as implemented in BIOENV package in R. This procedure calculates the Spearman's rank correlation coefficient (*r*) between predictor variables and response variables (F_{ST} and D_{EST} genetic distances), selecting all possible subsets of environmental variables until it finds the 'best fit' or combination of predictor variables with the highest value of *r*.

3.3.6. Seascape genetics

To investigate the potential effect of ocean currents on the dispersal of olive ridley turtles and population connectivity we implemented a biophysical model that simulates movement of individuals by incorporating ocean dynamics from a hydrodynamic numerical ocean model in combination with a Lagrangian trajectory toolset. Three-dimensional velocity data were used to generate a connectivity distance matrix between nesting sites. The ocean model used was the Ocean Model for Earth Simulator (OFES, Masumoto *et al.*, 2004). The Connectivity Modeling System43 v1.1 (Paris *et al.*, 2013) was used to integrate virtual Lagrangian particles within the velocity fields saved every three days for the period January 1980 to December 2010. For each site, one particle was released every day (with a total of 1891 particles per site). The particles were released at the location of each nesting site at 10 m of depth, and two-dimensional locations of the particles were saved every day. Particles were released in May and June (mating season) and their trajectories were tracked back 150 days. The results were combined into single matrices describing the proportion of particles (individuals) from a given source-nesting colony (rows) reaching a specific destination (columns) at a given time. A connectivity matrix was generated for the maximum of sampled sites possible with available genetic data (27 sites). A more simplified connectivity matrix based on 22 sites (total of pooled sites used on general analysis due to low number of samples), was also generated for comparative purposes.

Connectivity matrices generated by the biophysical model provide the possibility of statistically comparing both sources of information to determine the correspondence between the genetic data and those generated by model simulations. The test of the ocean circulation effect on sea turtle dispersal was performed using a Mantel test, testing connectivity distance matrices against D_{EST} genetic distances. To test the hypothesis that ocean circulation influences populations structure independent of distance and genetic clustering, a partial Mantel test was performed correlating connectivity distance matrix with genetic distances while both geographic distance matrix and genetic clustering were held constant. The latter was also conducted using the package VEGAN in R.

3.4. Results

3.4.1. Regional assessment of population structure and genetic diversity

No deviations from HWE or evidence of LD were detected in our data. Null alleles were identified for one locus (OR2) at only 4 out of 22 nesting areas. The locus OR2 was included in subsequent analyses since results remained unchanged if this was removed from the data set. All microsatellite loci were variable, with an average of 10.9 alleles per locus, mean observed heterozygosity of 0.72 and allelic richness of 5.85 (Table 3.1 and Table A 3.1).

Olive ridley turtles showed relatively weak but highly significant genetic structure (F_{ST} =0.015, P<0.001) in the eastern Pacific. The hypothesis of random mating across the vast sampled area in the Pacific coast was rejected (P<0.0001). Pairwise comparisons were significant and also supported by values of D_{EST} genetic distances in a pattern where Mexican nesting colonies were differentiated from those in Central America (Table 3.2). Results were confirmed by hierarchical AMOVA between these groups (F_{ST} = 0.027, P<0.001) (Table 3.3).

The Bayesian analysis of structure corroborated previous results by indicating two spatial clusters (K=2) as the most likely number of populations. These are referred herein as northern population (i.e. all Mexican nesting colonies) and southern population (i.e. all Central American nesting colonies). Populations were well defined regardless of the admixture model used, with the majority of individuals across nesting sites showing lower mixed coancestry when LocPrior model was used (Figure 3.2). The multidimensional analysis of FCA also confirmed the existence of two populations and some level of mixing (Figure 3.3). GENECLASS analysis revealed a total of nine first generation migrants. The majority of them (8), coming from nesting colonies belonging to the southern population, and only one migrant from the northern population (Table A 3.2).

Positive correlations of genetic variation with geographic distance were found at population levels, suggesting a pattern of isolation-by-distance (IBD) (F_{ST}: r=0.439, P<0.0001; D_{EST}: r=0.361 P<0.0003) (Figure A 3.5). However, this pattern disappeared when analysis were performed at subpopulation level (northern population: F_{ST}: *r*=0.027 *P*=0.351; D_{EST}: *r*=0.025 *P*=0.4003; southern population: F_{ST}: *r*=0.0078 *P*=0.446; D_{EST}: *r*= -0.0615 *P*=0.558). Positive spatial clustering of genotypically similar individuals across the entire region was observed up to 400 Km scale (*r*=0.008, *P*=0.001, Figure A 3.6).

Table 3. 1 Summary statistics of genetic diversity based on ten microsatellite markers for 22 nesting areas of olive ridley turtles in the eastern Pacific.

Country	Collection Site		Sample Size	N_A	Ho	He	AR	F_{IS}
Mexico	Todos Santos, Pescadero (PES), San Cristobal (SAC), San José del Cabo (SJC), Cabo Pulmo (CP), Punta Colorada-Punta Arenas (PCA).	(BCP)	80	15.3	0.738	0.803	6.436	0.087
	El Verde	(EVE)	18	9.4	0.658	0.732	5.957	0.130
	Platanitos	(PLA)	21	11.1	0.770	0.789	6.519	0.049
	Nuevo Vallarta	(NVA)	20	9.7	0.598	0.757	5.928	0.237
	PuertoVallarta / La Gloria	(PVG)	25	11.3	0.703	0.690	6.098	0.103
	Mismaloya	(MIS)	25	9.2	0.626	0.690	5.610	0.118
	Ticuiz	(PTI)	15	10	0.781	0.781	6.491	0.040
	Boca de Apiza	(BAP)	21	10.7	0.743	0.779	6.426	0.074
	Tierra Colorada	(TCO)	18	10.2	0.712	0.776	6.390	0.114
	San Juan de Chacahua	(SJC)	30	11.5	0.738	0.777	6.194	0.068
	Barra de la Cruz	(BCR)	24	9.8	0.697	0.795	6.116	0.151
	Escobilla	(ESC)	40	12.7	0.737	0.801	6.434	0.094
	Puerto Arista	(PAR)	28	10.7	0.650	0.743	5.856	0.148
Guatemala	Parque el Hawaii	(GH)	40	12.3	0.775	0.775	5.476	0.013
El Salvador	Playa Dorada	(SPD)	38	12.0	0.759	0.769	5.430	0.027
	San Juan del Gozo	(SJG)	15	7.7	0.652	0.720	5.155	0.139
	Las Bocanitas-SanDiego (SD)	(SB)	38	11.4	0.767	0.772	5.495	0.021
Nicaragua	Chacocente	(NC)	50	13.1	0.792	0.781	5.459	-0.003
	La Flor	(NF)	52	9.2	0.672	0.746	5.306	0.127
	Playa Veracruz	(NV)	30	11.0	0.725	0.738	5.331	0.035
	Playa Salamina	(NS)	20	10.3	0.758	0.768	5.630	0.039
Panama	La Marinera	(PMA)	60	12.9	0.751	0.781	5.521	0.047

(N_A) number of alleles, (Ho) observed heterozygosity, (He) expected heterozygosity, (AR) allelic richness, (F_{IS}) coefficient of inbreed.

.

Table 3. 2 Pairwise comparisons of F_{ST} (below the diagonal) and D_{EST} (above the diagonal) for 22 nesting areas of olive ridley turtles in the eastern Pacific. Bold indicate significant values (P<0.05).

	BCP	*EVE*	*PLA*	*NVA*	*PVG*	*MIS*	*PTI*	*BAP*	*TCO*	*SJC*	*BCR*	*ESC*	*PAR*	*GH*	*SPD*	*SJG*	*SB*	*NC*	*NF*	*NV*	*NS*	*PMA*
BCP	-	**0.08**	**0.04**	**0.06**	**0.08**	**0.19**	**0.19**	**0.09**	**0.10**	0.02	**0.10**	**0.03**	**0.26**	**0.17**	**0.15**	**0.16**	**0.12**	**0.14**	**0.19**	**0.16**	**0.12**	**0.16**
EVE	0.01	-	**0.06**	**0.11**	**0.06**	**0.07**	**0.22**	**0.18**	**0.07**	**0.08**	**0.05**	**0.04**	**0.23**	**0.14**	**0.16**	**0.12**	**0.10**	**0.15**	**0.12**	**0.10**	**0.09**	**0.16**
PLA	0.004	0.01	-	**0.07**	0.04	**0.17**	**0.19**	**0.15**	0.05	**0.07**	**0.09**	**0.05**	**0.29**	**0.15**	**0.16**	**0.15**	**0.10**	**0.13**	**0.18**	**0.12**	**0.11**	**0.15**
NVA	0.01	0.03	0.01	-	**0.12**	**0.23**	**0.11**	**0.13**	**0.13**	**0.07**	**0.12**	**0.05**	**0.21**	**0.18**	**0.16**	**0.19**	**0.14**	**0.16**	**0.19**	**0.16**	**0.15**	**0.17**
PVG	0.01	0.01	0.001	0.02	-	**0.11**	**0.17**	**0.08**	0.01	**0.11**	**0.08**	**0.08**	**0.18**	**0.18**	**0.19**	**0.19**	**0.13**	**0.18**	**0.19**	**0.17**	**0.15**	**0.19**
MIS	-0.00	-0.00	-0.01	0.02	0.01	-	**0.33**	**0.25**	**0.11**	**0.20**	**0.14**	**0.16**	**0.30**	**0.22**	**0.22**	**0.19**	**0.21**	**0.25**	**0.21**	**0.19**	**0.20**	**0.25**
PTI	-0.01	-0.00	-0.01	-0.02	-0.01	-0.01	-	**0.20**	**0.19**	**0.25**	**0.13**	**0.18**	**0.08**	**0.28**	**0.28**	**0.30**	**0.24**	**0.25**	**0.29**	**0.28**	**0.25**	**0.26**
BAP	-0.00	0.02	-0.00	0.004	0.006	**0.03**	-0.02	-	**0.13**	**0.12**	**0.20**	**0.13**	**0.18**	**0.28**	**0.26**	**0.28**	**0.24**	**0.26**	**0.27**	**0.27**	**0.25**	**0.29**
TCO	0.01	0.009	0.006	0.01	-0.01	-0.00	-0.005	-0.01	-	**0.15**	**0.08**	**0.09**	**0.21**	**0.20**	**0.20**	**0.19**	**0.15**	**0.19**	**0.20**	**0.18**	**0.17**	**0.17**
SJC	0.003	0.01	0.009	0.01	0.01	0.000	0.006	0.009	0.02	-	**0.11**	0.01	**0.29**	**0.19**	**0.20**	**0.20**	**0.16**	**0.19**	**0.20**	**0.18**	**0.15**	**0.22**
BCR	-0.02	-0.01	-0.01	-0.00	-0.02	-0.05	-0.02	-0.02	-0.03	-0.01	-	**0.07**	**0.21**	**0.18**	**0.21**	**0.20**	**0.16**	**0.19**	**0.21**	**0.18**	**0.17**	**0.21**
ESC	0.004	0.007	0.004	0.01	0.005	-0.01	-0.00	0.003	0.009	0.002	-0.02	-	**0.26**	**0.15**	**0.15**	**0.18**	**0.12**	**0.15**	**0.15**	**0.15**	**0.11**	**0.15**
PAR	**0.01**	**0.03**	0.01	0.01	0.009	**0.05**	0.004	0.01	-0.00	**0.03**	-0.03	0.01	-	**0.30**	**0.30**	**0.28**	**0.28**	**0.30**	**0.31**	**0.28**	**0.26**	**0.30**
GH	**0.03**	**0.03**	**0.03**	**0.04**	**0.03**	0.007	0.003	**0.03**	**0.03**	**0.03**	-0.00	**0.02**	**0.02**	-	0.01	0.05	0.006	-0.00	0.02	-0.00	-0.02	-0.00
SPD	**0.03**	**0.04**	**0.03**	**0.04**	**0.04**	0.01	0.004	**0.03**	**0.03**	**0.04**	0.009	**0.03**	**0.03**	0.002	-	0.01	0.02	0.02	**0.05**	0.02	-0.00	0.005
SJG	**0.04**	0.03	**0.04**	**0.06**	**0.04**	0.02	0.01	0.04	**0.04**	**0.04**	0.02	**0.04**	0.04	0.01	0.004	-	0.02	0.04	0.06	0.01	-0.01	0.03
SB	**0.02**	0.02	**0.02**	**0.03**	**0.02**	0.009	-0.01	0.02	**0.02**	**0.03**	0.001	**0.02**	0.01	0.001	0.003	0.007	-	-0.00	**0.05**	0.004	-0.02	0.006
NC	**0.03**	**0.03**	**0.02**	**0.03**	**0.03**	0.01	-0.00	**0.02**	0.03	**0.03**	0.001	**0.02**	**0.01**	-0.00	0.003	0.01	-0.00	-	0.03	0.002	-0.00	-0.00
NF	**0.02**	0.03	**0.02**	**0.04**	**0.03**	0.01	-0.00	**0.03**	0.02	**0.03**	0.01	0.02	**0.03**	-0.01	-0.00	0.009	-0.00	-0.01	-	0.01	0.01	0.03
NV	**0.04**	**0.02**	**0.03**	**0.04**	**0.03**	0.01	0.007	**0.03**	**0.03**	**0.04**	0.01	**0.03**	**0.03**	-0.00	0.006	0.006	0.002	0.000	-0.01	-	-0.02	0.008
NS	**0.02**	0.02	**0.02**	**0.03**	0.02	0.004	-0.00	**0.02**	**0.02**	**0.03**	0.003	**0.02**	0.01	-0.00	-0.00	-0.00	-0.00	-0.00	-0.01	-0.00	-	-0.01
PMA	**0.03**	**0.03**	**0.03**	**0.03**	**0.03**	0.008	-0.00	**0.02**	**0.02**	**0.04**	0.007	**0.02**	0.01	0.000	-0.00	0.008	0.001	-0.00	-0.01	0.002	-0.00	-

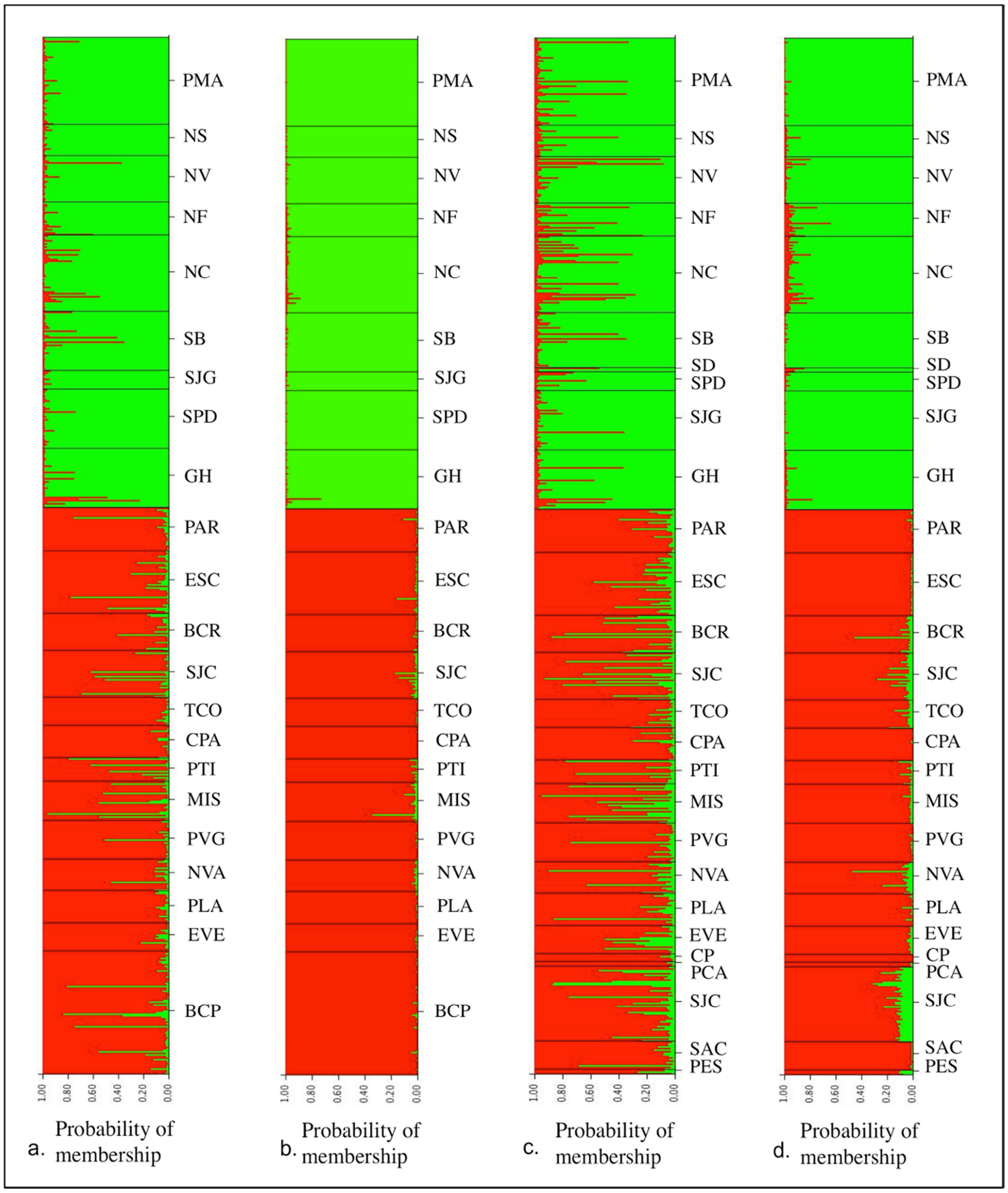


Figure 3. 2 Estimated probabilities of membership coefficients for each individual turtle in the inferred clusters estimated by STRUCTURE based on two STRUCTURE admixture models: (a, c) standard; and (b, d) LocPrior. Each bar represents an individual from a total of 22 (a,b) and 27 (d,c) sampling sites with the proportion of colour representing assignment to cluster 1 or 2.

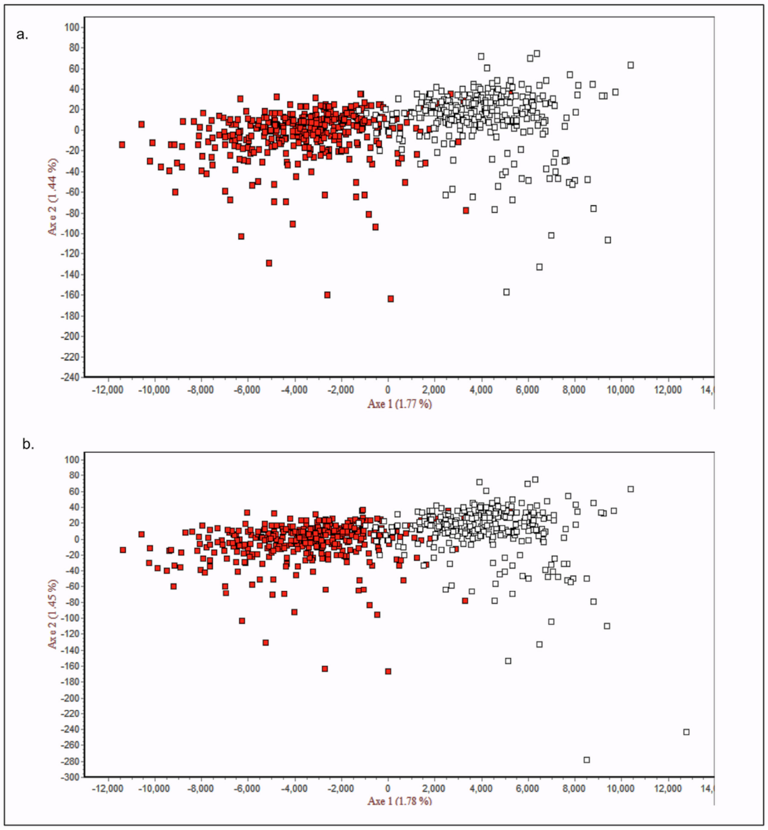


Figure 3. 3 Genetic clusters summarizing population structure. Factorial component analysis (FCA) for 22 (a) and 27 (b) sampling sites, dots of different colours identify individuals from different genetic clusters.

Table 3. 3 Analysis of hierarchical variance (AMOVA) results obtained for olive ridley turtle populations in the eastern Pacific.

Source of variation	**Percentage of variation**	***F*-statistics**	***P***
Among groups	2.80	F_{CT}=0.0279	0.0000
Among populations within groups	0.04	F_{SC}=0.0043	0.2880
Among individuals within population	2.61	F_{IS}=0.0268	0.0000
Within individuals	94.55	F_{IT}=0.0545	0.0000

3.4.2. Influences of environmental heterogeneity on genetic structure

Environmental heterogeneity between putative populations was confirmed for the variables of Chla and Therm (Mean=0.067, paired t=3.8, p=0.018; Mean=12.297, paired t=3.9, p=0.016; respectively). Exploratory analysis using Mantel test indicated that only Chl_a and Therm for the seasons of MATE and MIG, respectively, remained positively correlated after controlling for the effects of both geographic distance and genetic clustering in the two groups (Table 3.4). Analysis based on multiple regression analysis indicated low but still significant regression coefficient correlations for both estimators of genetic differentiation (D_{ST} and F_{ST}) (Table 3.5). Specifically correlations were higher between environmental variables and genetic variability based on D_{ST} values. The predicted model included only Therm and Chl_a as common explanatory variables to the MATE, MIG and FEED seasons. A significant model for the remaining seasons (NES1 and NES2) only suggested SSH as predictor variable. Analysis based on general linear models indicated that genetic variability was best explained by the variation of SSH and Chl_a in the seasons of MATE and MIG, respectively (Table 3.6). The constant model (excluding all variables) was chosen for the remaining seasons. In general, model probabilities were low, and sigma square values indicated that the program might have failed to determine the variables that best explain the distribution of genetic variability observed. When we used the BIOENV procedure, the "best fit" models were those that applied D_{EST} genetic distances. The model including three variables (Chl_a, SSH and Therm) was significant (r=0.23, P= 0.029) for the MATE season, and only the model with two variables (Chl_a and SSH; r= 0.318, P= 0.003; r=0.21, P= 0.014, respectively) was selected for the MIG and NES1 seasons (Table 3.4). No model proved to be significant for the remaining seasons. Variability of Chl_a, SSH and Therm for the MIG and MATE seasons are shown in Figure 3.4.

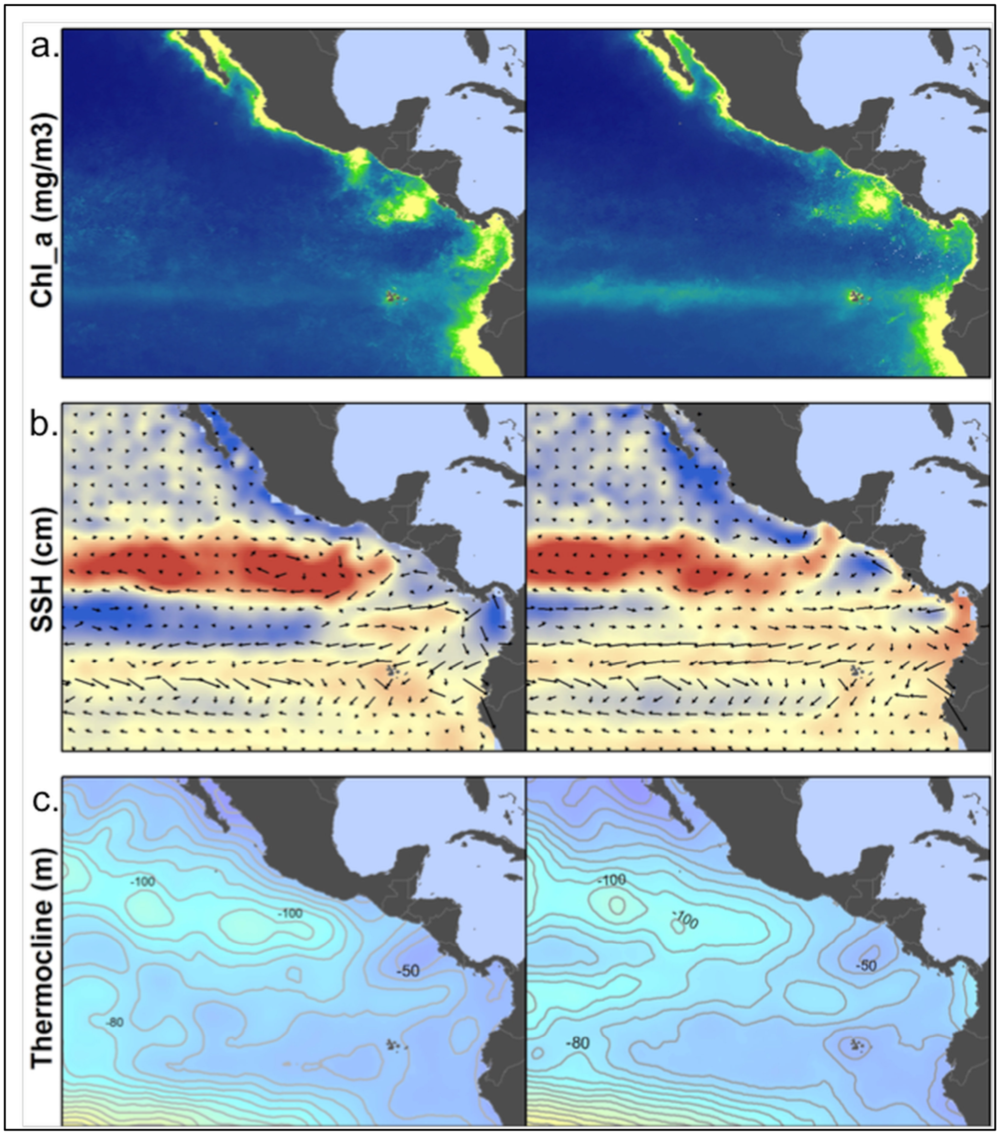


Figure 3. 4 Oceanographic predictors for the eastern Pacific showing 11-years average values for the MIG (left) and MATE (right) seasons for: (a) chlorophyll concentration (Chl_a); (b) sea surface height dynamic (SSH) and geostrophic currents (relative to 450 m); and (c) thermocline depth variation.

Table 3. 4 Results of Mantel tests and partial Mantel tests between genetic differentiation of olive ridley turtle nesting colonies in the eastern Pacific and pairwise differences in sea surface temperature (SST), chlorophyll concentration (Chl_a), sea surface high anomaly (SSH) and thermocline depth (Therm) at different seasons. The controlled variable in the partial Mantel tests is indicated in parentheses. Significant tests are denoted in bold.

Season	Response		Exploratory variable											
			SST	SST Geodist	SST Scluster	Chl_a	Chl_a Geodist	Chl_a Scluster	SSH	SSH Geodist	SSH Scluster	Therm	Therm Geodist	Therm Scluster
MIG	F_{ST}	*P*	0.635	0.813	0.398	0.568	0.783	0.623	0.585	0.923	0.747	**0.029**	0.880	0.519
(April)		*r*	-0.03	-0.11	0.055	-0.01	-0.08	-0.02	-0.01	-0.15	-0.07	0.158	-0.12	0.001
		P	0.423	0.753	0.387	0.082	0.095	0.070	**0.027**	0.065	**0.028**	**0.001**	**0.046**	**0.023**
		r	0.011	-0.11	0.000	0.149	0.189	0.254	0.198	0.174	0.259	0.326	0.197	0.269
MATE	F_{ST}	*P*	0.233	0.853	0.578	0.563	0.924	0.825	0.105	0.635	0.329	0.156	0.944	0.616
(MJ)		*r*	0.082	-0.15	-0.00	-0.00	-0.19	-0.13	0.100	-0.03	0.052	0.092	-0.18	-0.00
	D_{EST}	*P*	0.197	0.791	0.481	**0.011**	**0.046**	**0.023**	0.197	0.457	0.299	**0.003**	0.072	0.019
		r	0.094	-0.12	-0.03	0.276	0.243	0.323	0.068	0.001	0.055	0.312	0.177	0.282
NES1	F_{ST}	*P*	**0.036**	0.890	0.602	0.173	0.959	0.852	0.388	0.906	0.879	**0.019**	0.977	0.236
(JAS)		*r*	0.146	-0.14	-0.17	0.079	-0.20	-0.12	0.022	-0.13	-0.13	0.175	-0.19	0.081
	D_{EST}	*P*	0.245	0.972	0.840	0.061	0.278	0.167	**0.009**	**0.050**	0.056	**0.017**	0.446	0.076
		r	0.057	-0.18	-0.12	0.156	0.051	0.119	0.248	0.185	0.201	0.212	0.005	0.166
NES2	F_{ST}	*P*	**0.026**	0.946	0.252	0.972	0.873	0.901	0.128	0.608	0.753	**0.021**	0.766	0.198
(OND)		*r*	0.178	-0.19	0.094	-0.21	-0.16	-0.22	0.092	-0.02	-0.07	0.171	-0.07	0.090
	D_{EST}	*P*	0.263	0.989	0.614	0.292	0.613	0.687	0.176	0.635	0.810	**0.016**	0.194	0.044
		r	0.058	-0.23	-0.05	0.052	-0.06	-0.09	0.077	-0.04	-0.10	0.197	0.089	0.204
FEED	F_{ST}	*P*	0.434	0.689	0.269	0.699	0.728	0.691	0.716	0.901	0.675	0.100	0.987	0.419
(JFM)		*r*	0.022	-0.04	0.103	-0.04	-0.06	-0.04	-0.04	-0.13	-0.04	0.113	-0.24	0.030
	D_{EST}	*P*	0.349	0.662	0.350	0.324	0.398	0.365	0.093	0.219	0.097	**0.029**	0.456	0.123
		r	0.031	-0.08	0.010	0.031	0.010	0.025	0.120	0.082	0.163	0.198	0.004	0.151

Migration to breeding areas, April (MIG, A); mating period, May-June (MATE, MJ); beginning of nesting season July to August (NES1, JAS); ending of nesting season, October to December (NES2, OND); and migration and residence on feeding areas, January to March (FEED, JFM).

Table 3. 5 Results of stepwise multiple regression analysis indicating associations between environmental heterogeneity and genetic structure for olive ridley turtles in the eastern Pacific in different seasons. Results are shown for two different estimators of genetic differentiation D_{EST} and F_{ST} as response variables.

	D_{EST}					F_{ST}				
Season	Model	Factors included	β	R^2	P	Model	Factors included	β	R^2	P
MIG	1	Constant,				1	Constant,			
		Therm	0.304	0.093	<0.001		Therm	0.19	0.036	0.004
	2	Constant,								
		Therm	0.264	0.115	<0.001					
		Chl_a	0.155		0.017					
MATE	1	Constant,				1	Constant,			
		Chl_a	0.278	0.073	<0.001		SSH	0.176	0.031	0.007
						2	Constant,			
							SSH,	0.304	0.070	<0.001
							Therm	0.235		0.002
NES1	1	Constant,				1	Constant,			
		SSH	0.349	0.122	<0.001		SST	0.165	0.027	0.012
						2	Constant,			
							SST	0.136	0.044	0.042
							SSH	0.132		0.047
NES2	1	Constant,	0.361	0.126	<0.001	1	Constant,			
		SSH					SSH	0.289	0.084	<0.001
						2	Constant,			
							SSH	0.268	0.103	<0.001
							SST	0.141		0.027
FEED	1	Constant,	0.215	0.046	0.001	1	Constant,			
		Therm					Therm	0.147	0.022	0.025
						2	Constant,			
							Therm	0.197	0.047	0.004
							SSH	-0.16		0.015

Sea surface temperature (SST), chlorophyll concentration (Chl_a), sea surface high anomaly (SSH) and thermocline depth (Therm). Migration to breeding areas (MIG); mating period (MATE); beginning of nesting season (NES1); ending of nesting season (NES2); and migration and residence on feeding areas (FEED). Standardized regression coefficient (β) measured in standard deviation units that provide insights of the importance of a predictor in the model; multiple regression coefficient (R^2); level of marginal significance of the model or P-value (P).

Table 3. 6 Results of associations between environmental heterogeneity and genetic structure showing posterior probabilities of the most probable model for the GESTE analysis and the best fit obtained with the BIOENV procedure for olive ridley turtles in the eastern Pacific in different seasons. Population structure for GESTE analysis is based on population specific's F_{ST} only.

	GESTE analysis							BIOENV procedure							
									D_{EST}				F_{ST}		
Season	Model	Factors included	Probability	Coefficient	Mean	Mode	95% HPDI	Variable	***Spearman rho***	***r* (slope)**	***P***	Variable	***Spearman rho***	***r* (slope)**	***P***
MIG	1	Constant, Chl_a	0.070	α_0	-5.60	-5.93	-12.9; 0.07	Chl_a, **SSH, Therm**	0.318	0.287	**0.003**	Therm	0.157	0.091	0.159
				α_2	0.013	-0.19	-5.61; 5.54								
				σ	1.9e03	1.7e03	808; 3.1e03								
MATE	1	Constant, Therm	0.072	α_0	-5.53	-6.46	-11.5; 1.09	Chl_a, **SSH, Therm**	0.318	0.237	**0.029**	SSH, Therm	0.154	0.085	0.209
				α_3	0.095	-0.16	-6.37; 5.49								
				σ	1.9e03	1.7e03	918; 3.2e03								
NES1	1	Constant	0.073	α_0	-5.48	-6.06	-11.7; 1.29	Chl_a, **SSH**	0.300	0.210	**0.014**	Therm	0.175	0.079	0.176
				σ	1.9e03	1.8e03	854; 3.2e03								
NES2	1	Constant	0.072	α_0	-5.65	-5.60	-12.4; 1.10	Chl_a, SSH	0.132	0.012	0.451	SST, SSH, Therm	0.216	0.139	0.062
				σ	1.9e03	1.6e03	845; 3.1e03								
FEED	1	Constant	0.074	α_0	-5.39	-5.74	-11.3; 1.47	Therm	0.198	0.116	0.133	SST, Therm	0.178	0.080	0.195
				σ	1.9e03	1.7e03	838; 3.2e03								

Sea surface temperature (SST), chlorophyll concentration (Chl_a), sea surface high anomaly (SSH) and thermocline depth (Therm). Migration to breeding areas (MIG); mating period (MATE); beginning of nesting season (NES1); ending of nesting season (NES2); and migration and residence on feeding areas (FEED). Regression coefficient (α); estimate of the variation that remains unexplained by the regression model (σ); highest probability density interval (HPDI). Significant correlations for BIOEV procedure are shown in bold.

3.4.3. A biophysical model for sea turtles: environmental barriers to dispersal over the seascape

The connectivity matrix based on 27 sites for particles sampled back 150 days during the migration period showed zones of moderate to high retention of particles, suggesting restricted connectivity among all nesting sites (Figure 3.5). A similar pattern was observed when simulations included only 22 nesting sites (Figure A 3.7). Statistical analysis supported the hypothesis that environmental heterogeneity contributes to spatial genetic divergence by influencing dispersal of turtles during this period. This pattern remained significant when connectivity matrices and genetic distances were compared and correlation controlled by geographic distance and genetic clustering (r= 0.1972; P=0.482; r= 0.2697; P=0.0241, respectively).

For comparative purposes, we explored connectivity among nesting sites during nesting season by sampling particles back to 185 days (July). Connectivity among sites increased (Figure A 3.7), and ocean connectivity was negatively correlated with genetic information when controlling for geographic distance and genetic clustering (r=0.005; P=0.4559; r=0.1668; P=0.0768), respectively. Plots of particle distribution (sampled back 150 days) supported two spatially distinct groups in the eastern Pacific, with a mixing zone located in southern Mexico (Figure 3.6).

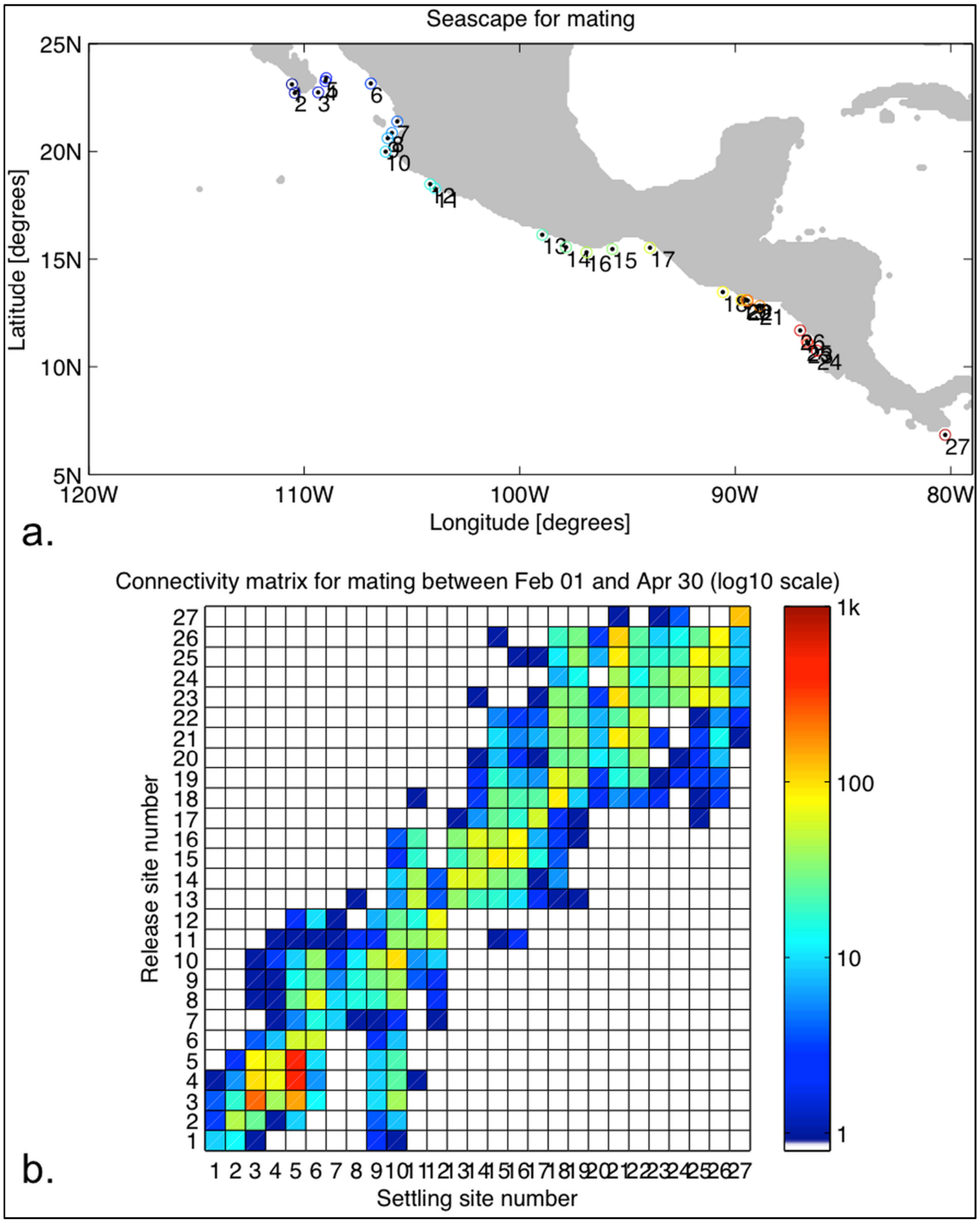


Figure 3. 5 Connectivity matrix for olive ridley turtles in the eastern Pacific based on Lagrangian particles simulations. (a) nesting sites for particles release; (b) connectivity matrix linking nesting sites. Here, the connectivity matrix quantifies the degree of inter-site connectivity by tracking particles released on 27 nesting sites during the mating season and tracked back in time 150 days. The scale indicates number of particles settled per site up to 1000 particles (1 to 1K).

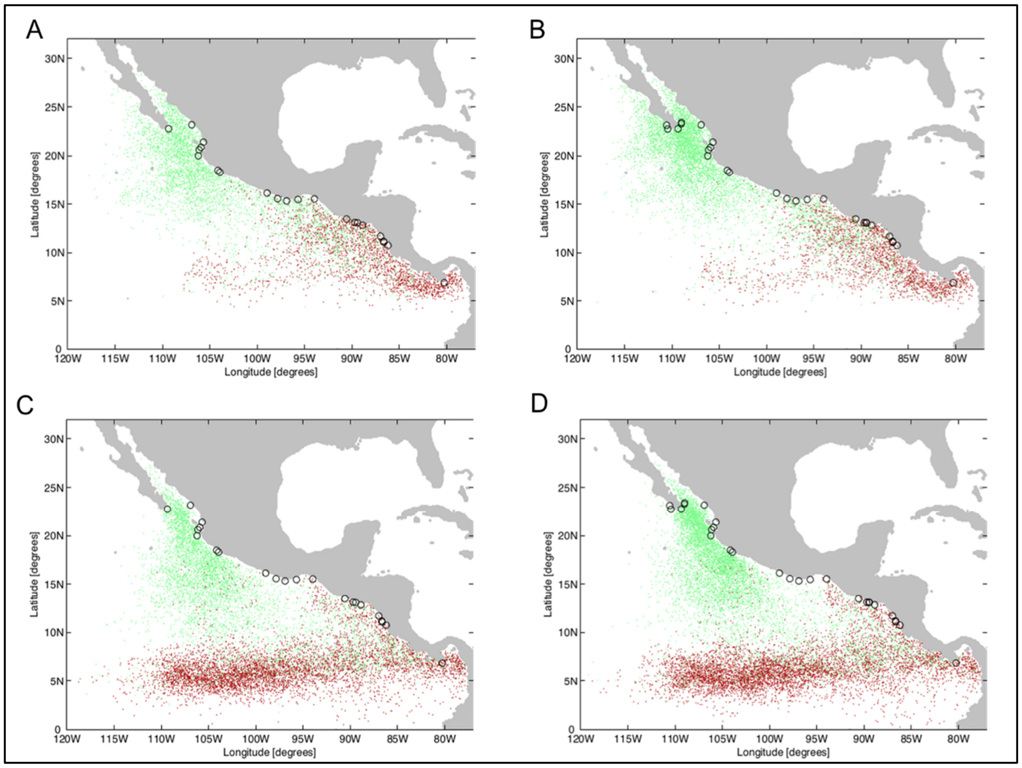


Figure 3. 6 Lagrangian particles distribution for olive ridley turtles in the eastern Pacific (a) particles released on 22 nesting sites during the mating season and tracked back in time 150 days; (b) particles released on 27 nesting sites during the mating season and tracked back in time 150 days; (c) particles released on 22 nesting sites during nesting season and tracked back in time 185 days; and (d) particles released on 27 nesting sites during nesting season and tracked back in time 185 days.

3.5. Discussion

We rejected the hypothesis of panmixia for olive ridley turtles in the eastern Pacific and demonstrated that patterns of population divergence in the species are correlated with environmental variability and with the dynamics of specific meso-scale features in the region. Results confirmed the risk of overlooking spatial scales when assessing population structure in highly mobile marine organisms. They also demonstrated the synergistic influence of environmental factors and life history traits in observed genetic patterns. A new paradigm of isolation-by-ecology for sea turtles is proposed as the main process driving population structuring in the eastern Pacific olive ridley turtles, in which spatial variation in gene flow is influenced by the heterogeneity of the landscape and population differentiation increases as ecological distance increase. These findings have important implications for conservation management at regional level.

3.5.1. Dispersal, connectivity and population configuration over the seascape

Our study disclosed weak yet highly significant population structure in olive ridley turtles in the eastern Pacific and challenged the paradigm of panmixia proposed for the species. The reduced level of population structure may be the result of the recent colonization of the eastern Pacific by olive ridleys (~0.3 million years ago; Shanker *et al.* 2004), and associated recent divergence in two populations with large effective sizes. Previous genetic assessments reported a general lack of differentiation in olive ridley turtles (Bowen and Karl, 2007; Bowen *et al.*, 1998; Briseño-Dueñas, 1998; López-Chávez, 2000). Marine turtles are known for exhibiting complex population structures that can be defined by female nesting site fidelity, male-mediated gene flow, opportunistic gene flow during migrations and progressing differentiation in developmental life stages (reviewed by Bowen and Karl, 2007). Importantly, the genetic structure based on bi-parentally inherited microsatellites is suggestive of male fidelity to regional breeding areas. Moreover, the results suggest that previously associated male fidelity to arribada-breeding sites, may not be exclusive to this reproductive behaviour, and that males may exhibit high fidelity to breeding areas regardless of whether they congregate on coastal waters of solitary or massive nesting areas. The clustering of genotypically similar individuals is reported as up to 400km, a geographic scale at which population structure has been observed in other regions (Shanker *et al.*, 2004). However, the pattern of population structure observed was not either explained by the scale of site fidelity inferred or by the geographic distance among sites (Table 3.7). In addition, the results do not indicated that population structure could be associated to the type of reproductive behaviour exhibited by the species.

Table 3. 7 Summary of isolation by distance tests conducted on nesting colonies of olive ridley turtles at different geographic scales. Results of partial Mantel tests corrected by regional population clustering are also shown. Significant tests are denoted in bold.

	P	*r* (slope)	R^2
All eastern Pacific			
F_{ST}	**<0.0001**	0.4399	0.1935
D_{EST}	**0.0003**	0.3618	0.1309
Partial Mantel			
F_{ST}	0.7600	-0.0030	-
D_{EST}	0.3533	0.0189	-
Within Cluster 1			
F_{ST}	0.3510	0.0270	0.0092
D_{EST}	0.4003	0.0255	0.0006
Within Cluster 2			
F_{ST}	0.4460	0.0078	0.0012
D_{EST}	0.5580	-0.0615	0.0040

3.5.2. Genetic population divergence and environmental heterogeneity

A notable discovery was the positive correlation between environmental variables and the distribution of genetic variability of olive ridley turtles in the eastern Pacific, supporting our hypothesis of isolation by ecological distance. It is well known that ocean currents play an important role in the dispersal of many marine organisms, including sea turtles (Galli *et al.*, 2012; Luschi *et al.*, 2003a; Luschi *et al.*, 2003b; Seminoff *et al.*, 2008) and that particular cues (e.g. sea surface temperature, chlorophyll concentration) can influence habitat preference and therefore the distribution of individuals (Fossette *et al.*, 2010; Polovina *et al.*, 2004; Shillinger *et al.*, 2008). Ocean currents may reduce the associated cost of dispersal, something particularly advantageous for reproductive females during the breeding season. In addition habitat preference may also play an important role, influencing patterns of horizontal and vertical migration of sea turtles. For instance olive ridley turtles prefer to swim in warm water temperatures (between 22°C and 28°C), and perform depth dives (~60m) in search for prey (Swimmer *et al.*, 2006).

Our initial analysis based on Mantel tests suggested Chl_a, SSH, and Therm as possible explanatory variables for the seasons of MIG, MATE and NES1 only. The correlation found could indicate that dispersal of individuals is influenced by oceanographic conditions during these key seasons, representing ecological benefits to sea turtles. For instance, turtles may benefit from staying close to oceanographic systems of high productivity, while migrating towards coastal areas for reproduction. Advantages could specifically relate to reducing energy cost for feeding, since areas with high chlorophyll concentration would translate in higher abundance of preys. In addition, diving time and energy spend when searching for preys could potentially be reduced by availability of preys, which can be concentrated in upper layers of the water column by physical variations on thermocline depth; which is generally associated with zones of upwelling (Pennington *et al.*, 2006). In addition, increased feeding opportunities could help to the storage of energy by reproductive females before mating but also through the breeding season, considering their high reproductive output in a single nesting season (~1 up to 3 clutches per season, Márquez-M, 1990). Finally, the use of highly productive oceanographic systems near nesting areas would not only enhance feeding by adult turtles but also the energetic cost associated to migration. This could be particularly true for reproductive females, which are known, to return to same natal areas every season for reproduction; thus contributing to the pattern of isolation by ecological distance observed.

Debate on the limitation of inferences based on Mantel tests has been discussed in literature. However, its use is generally well received for exploratory analysis (as implemented here) and when distance matrices are used (Legendre and Fortin, 2010). The previous results were further confirmed by the multiple stepwise regression analyses, showing a significant overall association between genetic distance and both Therm and SSH variation despite marginal significant associations. Posterior analysis using general linear models also agree on pointing out the role of environmental factors (Therm and Chl_a) during two critical seasons (MATE and MIG), contributing evidence in favour of a pattern of isolation by ecological distance. The low estimated probabilities may have been limited by the use of F_{ST} as a measure of genetic distance, an estimator that can show reduced power when applied to species with high levels of genetic diversity (Meirmans and

Hedrick, 2011). It is important to note that even though the low probabilities and correlation indices obtained in the models considered in these analyses, their general agreement in identifying a positive correlation between environmental predictors and genetic variability, constitutes a clear evidence supporting the pattern of Isolation-by-Ecology for this species. Here, we focused on determining the processes behind the structuring of populations in olive ridley turtles rather than identifying the relative contribution of each factor. None of the analyses were conclusive on specific variables that in particular could drive population differentiation in olive ridley turtles. Therefore, we consider that further tests may offer better proxies of key variables. We do not ignore the possibility that multiple variables may interact synergistically and that our analysis may not distinguish between independent effects.

3.5.3. Application of a biophysical model to infer connectivity in Sea turtles

Our implementation of a biophysical model to predict the degree of connectivity among nesting colonies of olive ridley turtles provides key insights about the role of oceanography in shaping population divergence and connectivity in the eastern Pacific. The results are consistent with the scenario of two populations in the region with reduced connectivity during the mating season. They also support the proposition of multiple nesting sites linked by high levels of connectivity within each putative population – as reported for Mexican samples in Chapter II.

The distribution of simulated particles also reflected the spatial segregation of the two putative populations identified in STRUCTURE; indicating the existence of a physical barrier in the area where genetic partition occurs. The break is actually located between the boundaries of two active permanent meso-scale features: the CRD and TG. We uphold the suggestion that the characteristics and seasonal dynamics of these two systems generate a physical barrier to dispersal and gene flow. These features develop during boreal winter and become particularly active during spring (time where olive ridley turtles may migrate to breeding areas). Since meso-scale eddies are also known to concentrate biological productivity, we propose that not only the mechanical influence of eddies' circulation (strength and directionality), but also the reduced cost of dispersing to areas further away in search for prey, will influence dispersal and, consequently, regional patterns of gene flow.

The results in this chapter demonstrate that despite the turtles' ability to migrate and actively disperse against currents, population structure may emerge as a result of environmental heterogeneity. In addition, selective pressures related with cost-benefit of dispersal may play an important role on ruling patterns of genetic variability in the species. The active barrier may also be strengthened by vertical variation in thermocline depth, influencing vertical movement when searching for prey. Shallow thermoclines, such as the one in the CRD, are known to aggregate marine life, preventing prey from dispersing and providing abundant feeding opportunities for marine top predators (Bailleul *et al.*, 2010; Pelletier *et al.*, 2012). In Atlantic leatherback turtles, temporary residency areas have been found associated to mesoscale surface oceanographic features as depicted in altimetry features and chlorophyll a concentration (see Fossette *et al.*, 2010).

Model simulations also suggest that there are areas of moderate to high particle retention in the southern portion of Mexico (Tehuantepec Gulf). Ocean circulation may trap individuals reaching this area, restricting dispersal to breeding areas in the north. This could potentially explain patterns of population structure within Mexico and provides insights about subpopulation dynamics. On the other hand, largely regional connectivity was observed during the nesting season, a finding that is perhaps associated with changes in ocean circulation during summer. During this time, the system of the CRD relaxes and starts to separate from the coast giving space to the CRCC to flow northwards along Central America extending its influence up to the Tehuantepec gulf in southern Mexico. This change in circulation patterns could explain levels of admixture between putative populations as well as the patterns of migration based on our assignment tests. This possibility is consistent with observations of post-nesting movements for the species, particularly females tagged in Costa Rica (Plotkin *et al.*, 1995; Plotkin, 2010). In summary, the model implemented in this study has proved to be effective for simulating connectivity among nesting colonies and for inferring the directionality of dispersal.

Processes of isolation-by-ecology have been revealed in other taxa, even between oceanographic regions (Kool *et al.*, 2010; Kool *et al.*, 2011). Whether specific seascape features or locations contribute to common spatial genetic patterns among other sea turtles species in the region is a question that could be explored in future studies. Most seascape genetic studies have focused on species with larval stages in which the influence of environmental variables such as ocean currents and sea temperature are highly expected (Banks *et al.*, 2007; Selkoe *et al.*, 2010; Teacher *et* *al.*, 2013). Only a few studies have focused on top predators; these are situations in which the quantification of biological parameters can be more difficult across different environments (but see Amaral *et al.*, 2012; Fontaine *et al.*, 2007; Mendez *et al.*, 2010; Mendez *et al.*, 2011). We highlight the need for a simplistic model as a descriptive basis for studying regional scale connectivity that can guide other models including reproductive variation and habitat quality (i.e. a reasonable base is required for model design to test further influencing factors in gene flow). Nonetheless, we provide support for isolation-by-ecology in olive ridley turtles in the eastern Pacific and emphasise the synergistic interaction that natal homing behaviour, cost/benefit of dispersal and environmental barriers could have on driving population structure in this species. We demonstrate the importance of the spatial scale on the assessment of population structure and connectivity in highly mobile marine organisms, and the relevance of integrative approaches to provide insights on the development of population structure in the marine environment. These approaches allow us to reject the well-accepted panmixia in olive ridley turtles, and provide conclusive evidence to propose a new paradigm for the species in the eastern Pacific.

3.5.4. Conservation implications and future directions

The results presented here provide a remarkable regional perspective of connectivity and population divergence for a highly mobile marine species across the eastern Pacific. These findings can contribute to the definition of management units (MUs) for the olive ridley turtle at regional scale, assisting planning and development of large-scale strategies for the conservation of olive ridley turtles across the eastern Pacific. In addition, recovery trend and extinction risk assessments could benefit from considering the key role of solitary nesting sites to the regional connectivity, and the maintenance of genetic variability in the species. This is particularly important since *arribada* sites have generally driven the species' population trends, due to the abundance of turtles. It is important to note that populations at *arribada* sites may not be necessarily genetically independent from those at solitary sites. The protection of nesting sites that represent the polymorphic reproductive behaviour evolved by olive ridley turtles is important, as these reproductive strategies may result on long-term fitness benefits for this pelagic species (see, Bernardo and Plotkin, 2007). However, it is clear that even when *arribada* sites concentrate a great abundance of individuals, the majority of nesting areas along the eastern Pacific are used by solitary nesters; making them significant for the recovery of olive ridleys. Olive ridley turtles are still listed as endangered by the U.S. Endangered Species Act (ESA) due to increasing mortality associated with bycatch (Wallace *et al.*, 2010a; Dapp *et al.*, 2013). Challenges when resolving threats in widely distributed marine species have been specifically related to geographic scale whereby threats can affect different segments of a population (Wallace *et al.*, 2010a). In this sense, ongoing efforts to quantify the effect of widely distributed threats on sea turtles populations can benefit from the information provided here; guiding the implementation of effective conservation actions.

Our results recall the need for regional cooperation among nations that share the proposed units for conservation, advocating also more efforts on water protection. The described connectivity dynamics at local and regional scales also draws attention to the potential consequences of ongoing threats on the recovery of the species. In this sense, recent evidence has shown that despite high levels of metapopulation connectivity, the recovery of genetically eroded nesting colonies may be compromised (Chapter II).

As shown here, seascape features play a key role on the preservation of genetic variability in olive ridley turtles. Consequently, environmental changes associated with climate warming are of great concern. As increasing temperatures and thermocline circulations patterns are expected to change (Stocker and Schmittner, 1997), affecting global ocean circulation and therefore the dynamic of meso-scale feature structures (i.e. strength and position) with potential consequences for the dispersal of adults and hatchling survival. For instance, Shillinger *et al.*(2012) proposed an evolutionary adaptation to ocean circulation in leatherback turtles, where hatchlings' fitness may be increased by the location of nesting sites, allowing them to drift to areas of high productivity along the eastern Pacific.

Our work used information from neutral genetic variation and structure that is presumably influenced by meso-scale oceanographic features. However, our understanding about drivers of population divergence in sea turtles would benefit from work based on next-generation sequencing (NGS) approaches that explore genomic signatures of selection in individuals and populations. Such approaches can be used to identify gene regions targeted by divergent natural selection and to link them to underlying landscape or seascape features (Schoville *et al.*, 2012). An even greater contribution would probably be made by using NGS data in studies that combine landscape genomics, transcriptomics and candidate gene approaches to identify genomic signatures associated with putatively adaptive traits in sea turtles. Such studies would be in a stronger position to clarify crucial aspects of the biology of sea turtles and to build a framework for conservation management that takes into account the functional role that heterogeneous landscapes play maintaining biodiversity structure and dynamics.

3.6. Acknowledgments

We thank CONANP camp sites in Mexico, ASUPMATOMA, PROPENINSULA, Grupo Tortuguero-Pescadero, Ayuntamiento de los Cabos, AC-Cabo Pulmo, Instituto Tecnológico de Bahía Banderas, Programa Tortugas Marinas-Puerto Vallarta, GAPEA, Centro Mexicano de la Tortuga and Gobierno del estado de Chiapas, Fundacion ARCAS, AKAZUL, Fauna & Flora International-Nicaragua, Ministerio de medio ambiente y recursos naturales de El Salvador, FUNZEL, and Autoridad de recursos acuaticos de Panama for assistance in the field. Tags were donated by Laura Sarti (CONANP) and Jeffrey Seminoff (South West Fishery Service-NOAA). Funding was provided by the Australian Research Council (DP110101275 to Beheregaray, Möller & Waters) and by grants from Texas A&M-CONACYT (2006-10) and CICESE to Rocha-Olivares. Part of this research was carried out under a fellowship from CONACYT to CJR-Z. This is a MEGMAR (Molecular Ecology Group for Marine Research) article contribution #54.

3.7. Appendix

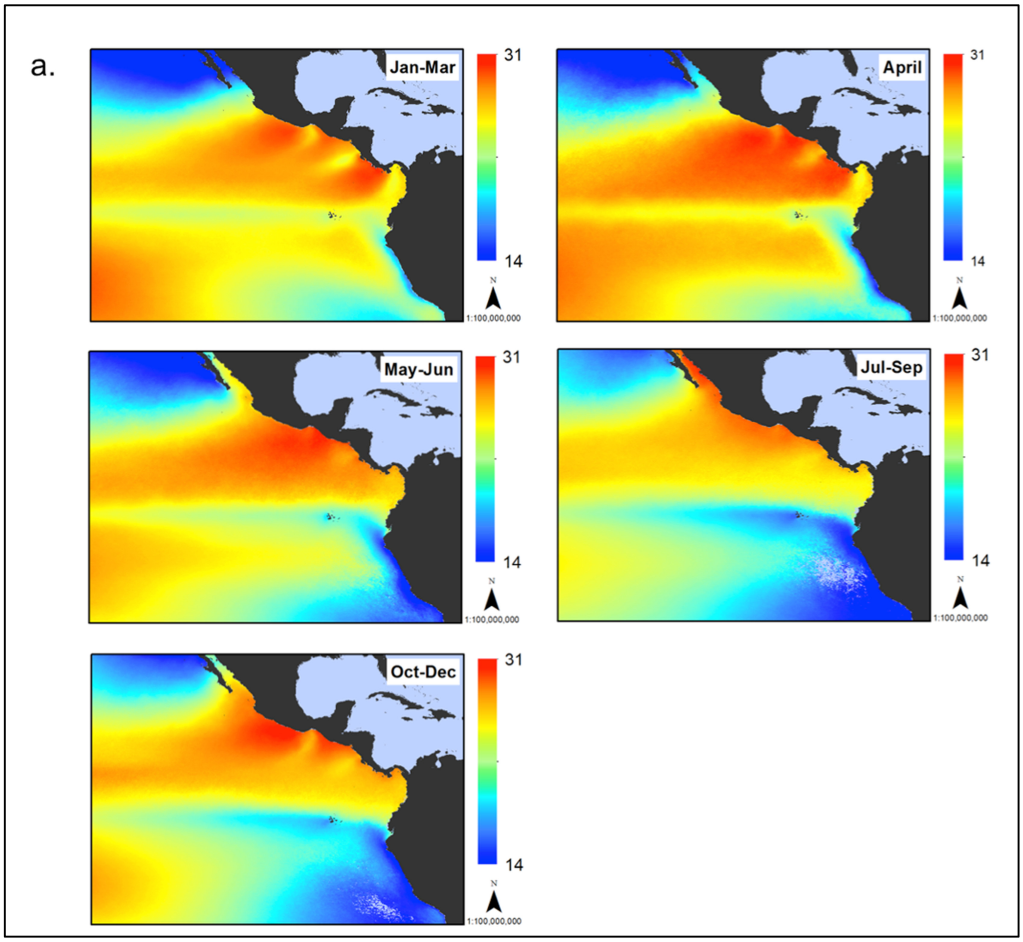


Figure A 3. 1 Annual variability of sea surface temperature in the eastern Pacific for different seasons: migration to feeding grounds (Jan-Mar, FEED); migration to breeding areas (April, MIG); mating (May-Jun, MATE); start of nesting season (Jul-Sep, NES1); ending of nesting season (Oct-Dec, NES2).

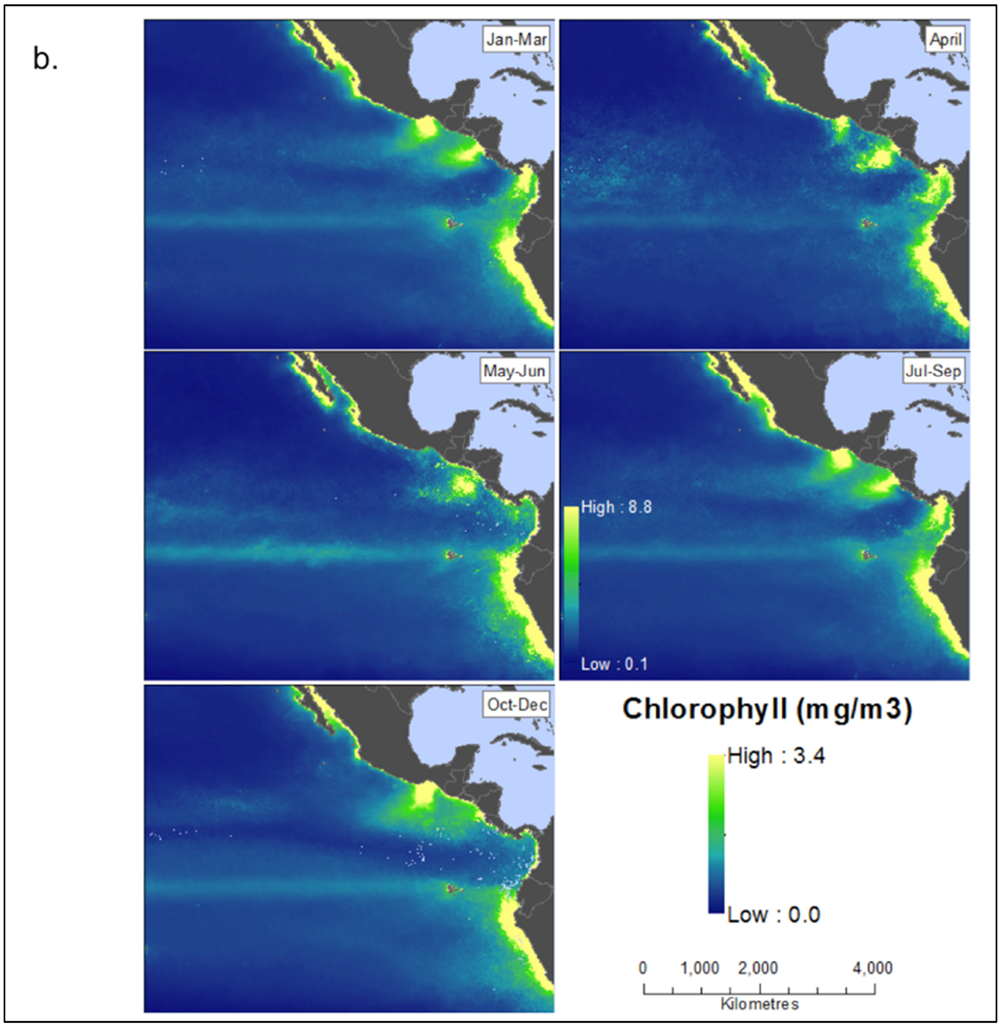


Figure A 3. 2 Annual variability of chlorophyll_a in the eastern Pacific for different seasons: migration to feeding grounds (Jan-Mar, FEED); migration to breeding areas (April, MIG); mating (May-Jun, MATE); start of nesting season (Jul-Sep, NES1); ending of nesting season (Oct-Dec, NES2).

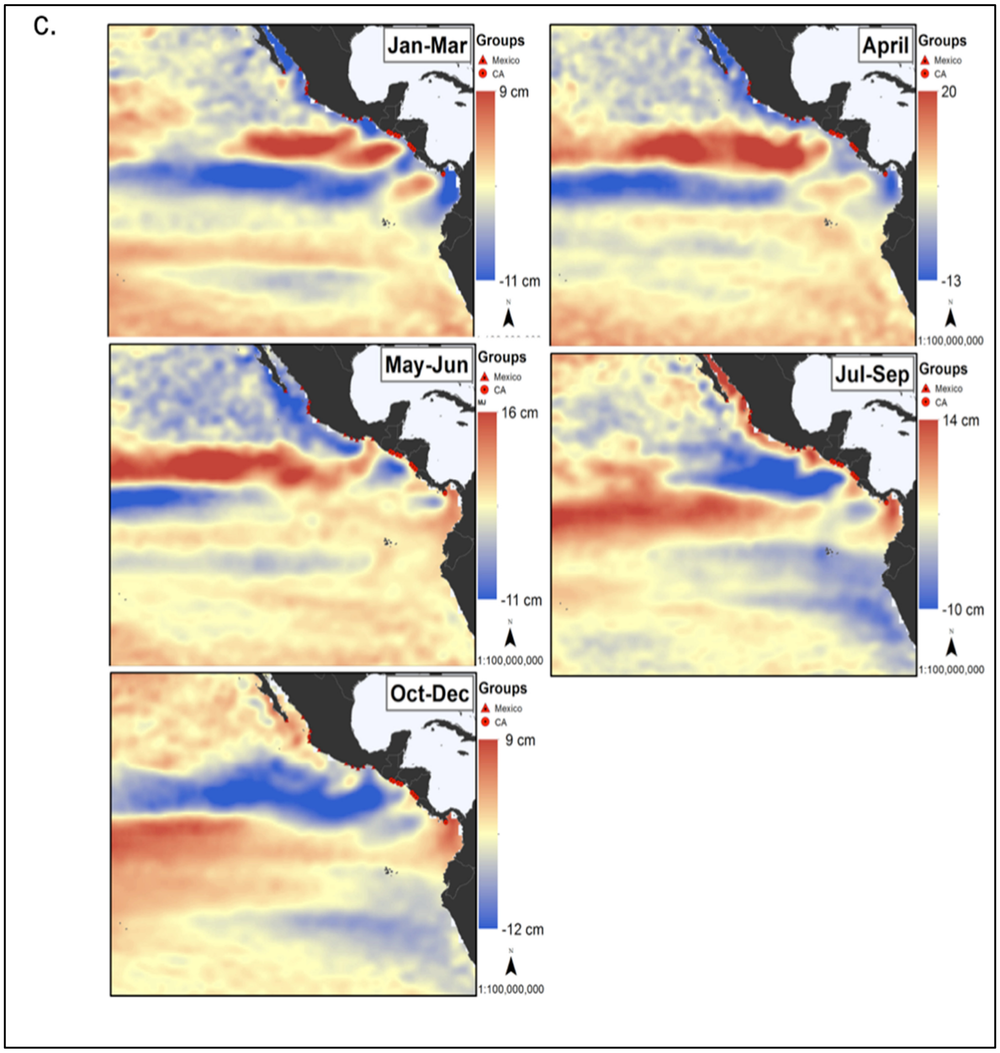


Figure A 3. 3 Annual variability of sea surface height dynamic in the eastern Pacific for different seasons: migration to feeding grounds (Jan-Mar, FEED); migration to breeding areas (April, MIG); mating (May-Jun, MATE); start of nesting season (Jul-Sep, NES1); ending of nesting season (Oct-Dec, NES2).

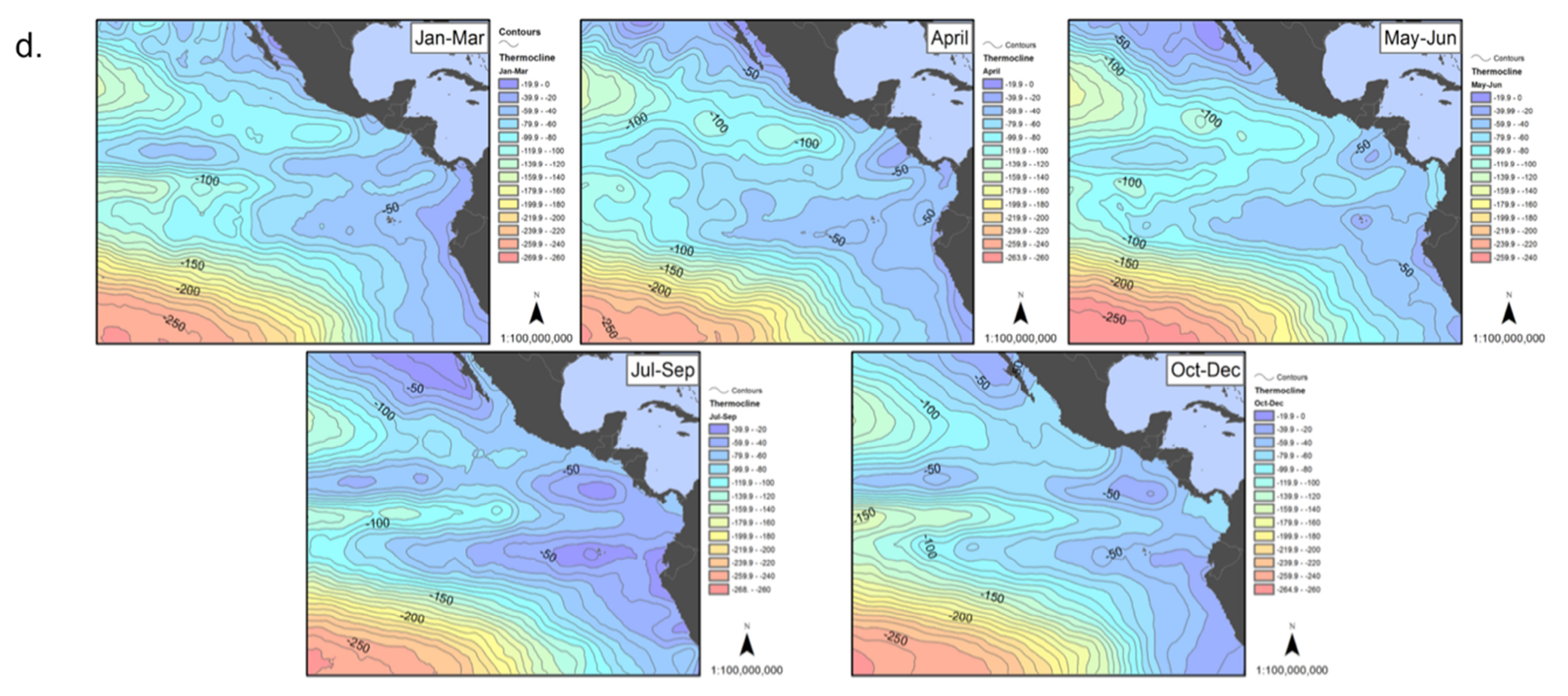


Figure A 3. 4 Annual variability of Thermocline depth in the eastern Pacific for different seasons: migration to feeding grounds (Jan-Mar, FEED); migration to breeding areas (April, MIG); mating (May-Jun, MATE); start of nesting season (Jul-Sep, NES1); ending of nesting season (Oct-Dec, NES2).

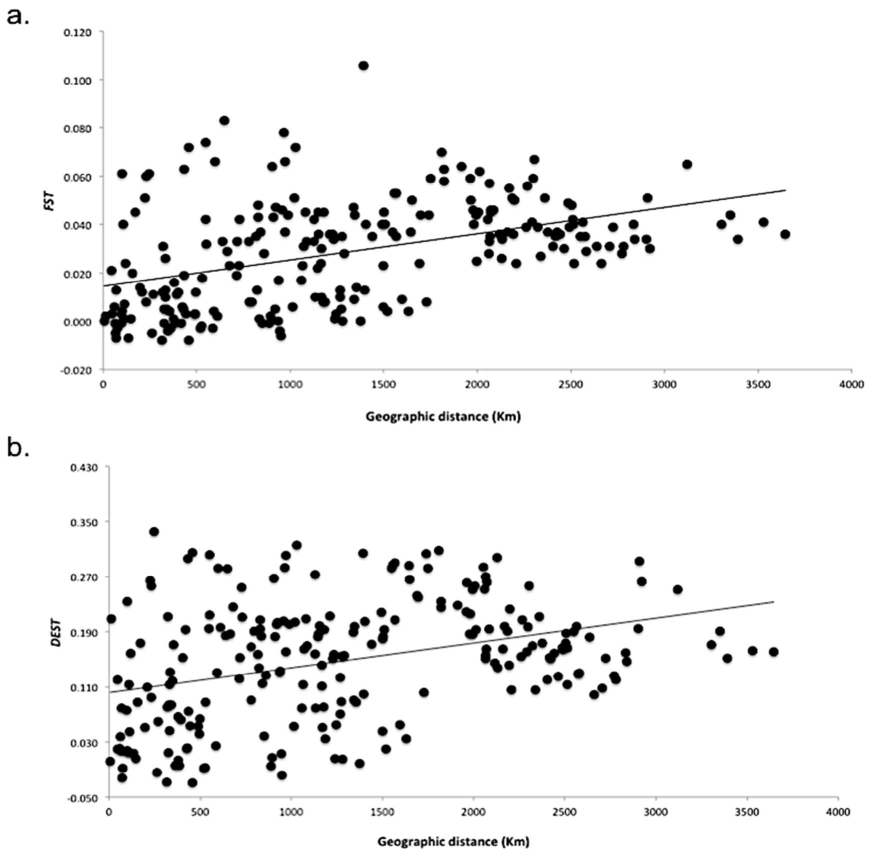


Figure A 3. 5 Scatter plot of isolation by distance (IBD) correlation for olive ridley turtles in the eastern Pacific based on F_{ST} and D_{EST} genetic distances.

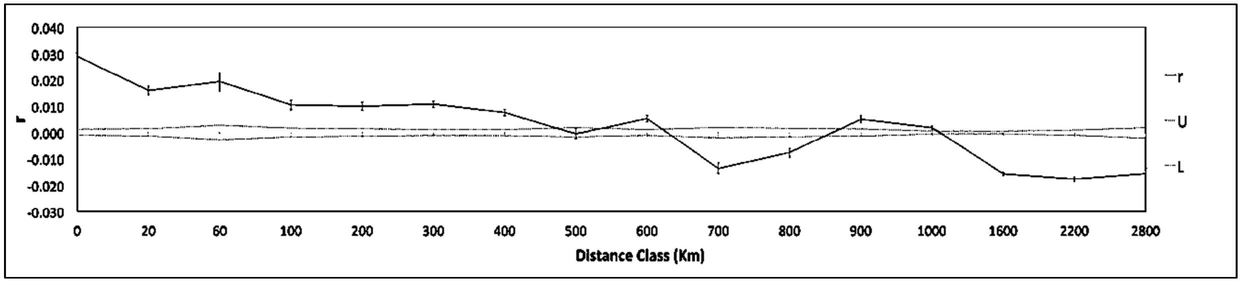


Figure A 3. 6 Spatial autocorrelation coefficient (*r*) for nesting colonies of olive ridley turtles in the eastern Pacific over a range of distance classes with 95% confidence level (upper (U) and lower (L) confidence limits).

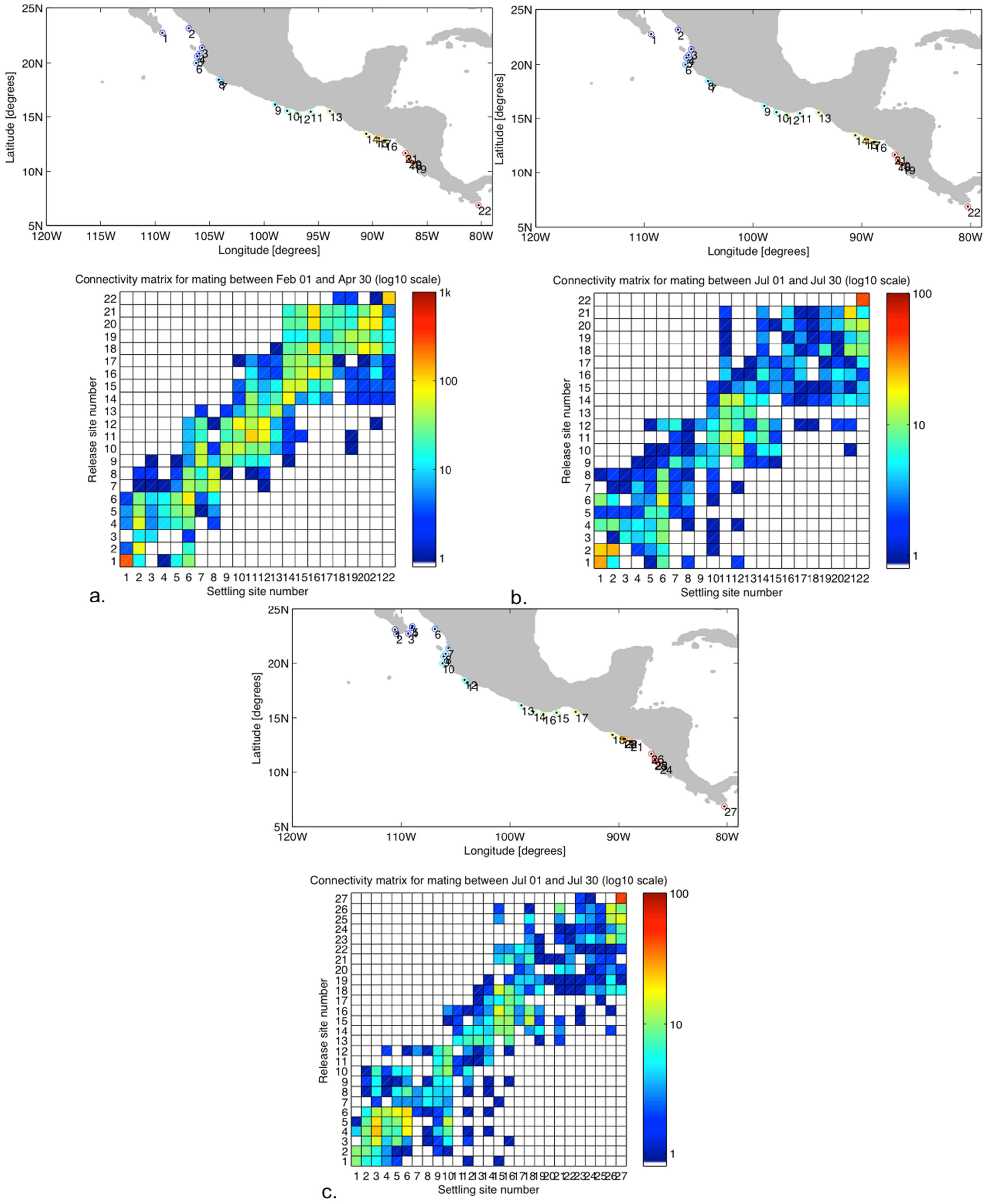


Figure A 3. 7 Connectivity matrix for olive ridley turtles in the eastern Pacific based on Lagrangian particle simulations. (a) particles released on 22 nesting sites during the mating season and tracked back 150 days; (b) particles released on 22 nesting sites during nesting season and tracked back in time 120 days; and (c) particles released on 27 nesting sites during nesting season and tracked back in time 120 days.

Table A 3. 1 Detailed summary statistics of genetic diversity based on ten microsatellite markers for 22 nesting areas of olive ridley turtles in the eastern Pacific.

Locus	**Location**																						
	BCP N=80	EVE N=18	PLA N=21	NVA N=20	PVG N=25	MIS N=25	PTI N=15	BAP N=21	TCO N=18	SJC N=30	BCR N=24	ESC N=40	PAR N=28	GH N=40	SPD N=38	SJG N=15	SB N=38	NC N=50	NF N=52	NV N=30	NS N=20	PMA N=60	Mean N_A
OR2																							
N_A	12	6	8	7	6	2	6	5	6	9	7	7	5	13	10	6	9	9	6	7	7	9	7.2
Ho	0.479	0.177	0.556	0.368	0.526	0.150	0.400	0.500	0.333	0.792	0.200	0.364	0.214	0.649	0.790	0.83	0.842	0.796	0.550	0.733	0.70	0.804	
He	0.748	0.762	0.831	0.765	0.779	0.224	0.888	0.747	0.775	0.691	0.787	0.765	0.484	0.739	0.787	0.79	0.835	0.792	0.776	0.705	0.78	0.729	
AR	4.581	4.431	5.335	4.442	4.401	1.783	6	4.11	4.68	4.228	4.614	4.464	3.299	4.756	4.953	4.76	5.372	5.02	4.438	4.15	4.90	4.406	
F_{IS}	0.362	0.774	0.339	0.525	0.331	0.337	0.579	0.339	0.581	-0.14	0.751	0.529	0.567	0.124	-0.002	-0.04	-0.008	-0.00	0.297	-0.04	0.11	-0.102	
OR4																							
N_A	18	14	15	12	15	14	13	14	14	14	16	20	13	15	15	9	16	16	13	15	13	17	14.7
Ho	0.809	0.800	0.950	0.824	1.000	0.727	0.857	0.933	0.889	0.786	0.833	0.946	0.833	0.921	0.849	0.66	0.973	0.898	0.800	0.900	0.95	0.893	
He	0.927	0.905	0.929	0.900	0.918	0.930	0.936	0.928	0.941	0.900	0.931	0.933	0.912	0.918	0.915	0.88	0.930	0.912	0.919	0.920	0.92	0.926	
AR	7.389	7.107	7.393	6.738	7.246	7.343	7.525	7.449	7.686	6.8	7.462	7.612	6.966	7.1	6.977	6.26	7.411	6.997	7.184	7.176	7.10	7.31	
F_{IS}	0.129	0.12	-0.02	0.088	-0.09	0.222	0.088	-0.00	0.057	0.13	0.108	-0.01	0.089	-0.003	0.074	0.25	-0.047	0.016	0.134	0.022	-0.03	0.037	
OR7																							
N_A	13	6	11	7	8	3	6	5	9	9	8	8	7	9	10	7	10	13	7	9	9	12	7.7
Ho	0.753	0.688	0.810	0.333	0.650	0.333	0.857	0.833	0.824	0.786	0.792	0.816	0.600	0.737	0.686	0.50	0.730	0.796	0.579	0.700	0.80	0.786	
He	0.821	0.592	0.855	0.722	0.680	0.318	0.764	0.735	0.771	0.772	0.753	0.745	0.811	0.744	0.770	0.67	0.763	0.774	0.692	0.773	0.81	0.73	
AR	5.325	3.801	5.958	4.098	4.008	2.667	4.243	4.134	4.813	4.96	4.679	4.656	4.952	4.636	4.884	4.29	4.884	4.883	4.385	4.61	5.25	5.349	
F_{IS}	0.08	-0.16	0.056	0.546	0.046	-0.05	-0.12	-0.14	-0.06	-0.01	-0.05	-0.09	0.267	0.011	0.112	0.27	0.045	-0.02	0.168	0.007	-0.03	0.032	
OR11																							
N_A	22	12	15	13	15	13	12	16	12	18	11	18	15	19	19	12	17	17	16	16	15	17	14.8
Ho	0.908	0.722	0.800	0.800	0.920	0.957	1.000	0.857	0.778	0.900	0.833	0.795	0.821	0.892	0.947	1.00	0.974	0.857	0.810	0.933	0.90	0.893	
He	0.929	0.905	0.923	0.906	0.934	0.909	0.913	0.923	0.900	0.936	0.894	0.931	0.883	0.920	0.920	0.90	0.918	0.892	0.913	0.914	0.92	0.917	
AR	7.421	6.824	7.295	6.788	7.473	6.857	6.905	7.402	6.668	7.639	6.437	7.466	6.617	7.256	7.232	6.98	7.188	6.611	7.193	7.099	7.33	7.107	
F_{IS}	0.023	0.206	0.136	0.12	0.015	-0.05	-0.09	0.073	0.139	0.039	0.069	0.148	0.071	0.031	-0.031	-0.10	-0.062	0.04	0.116	-0.02	0.03	0.026	
OR16																							
N_A	12	8	10	8	9	7	13	11	10	10	8	10	8	10	10	7	9	13	8	9	9	11	9.5
Ho	0.805	0.647	0.800	0.294	0.682	0.625	0.933	0.688	0.722	0.571	1.000	0.838	0.630	0.763	0.737	0.58	0.658	0.796	0.611	0.700	0.80	0.714	
He	0.802	0.702	0.814	0.781	0.755	0.720	0.883	0.849	0.843	0.671	0.844	0.773	0.655	0.760	0.765	0.70	0.729	0.772	0.808	0.706	0.77	0.806	
AR	5.126	4.699	5.514	4.726	4.617	4.373	6.53	6.047	5.683	4.461	5.615	4.97	3.636	4.871	4.818	4.31	4.554	4.82	5.35	4.632	5.25	5.195	
F_{IS}	-0.00	0.081	0.081	0.018	0.63	0.099	0.134	-0.05	0.195	0.147	0.151	-0.19	-0.08	0.039	-0.005	0.03	0.176	0.098	-0.03	0.249	0.00	0.115	
OR20																							
N_A	9	7	8	9	9	7	7	10	9	7	7	9	8	8	8	6	7	9	7	9	5	7	7.2
Ho	0.718	0.778	0.900	0.900	0.440	0.680	0.636	0.800	0.706	0.667	0.643	0.649	0.679	0.790	0.790	0.75	0.790	0.755	0.600	0.633	0.50	0.673	
He	0.835	0.849	0.844	0.824	0.826	0.816	0.848	0.865	0.845	0.821	0.815	0.791	0.826	0.803	0.776	0.82	0.816	0.804	0.776	0.811	0.80	0.771	
AR	5.215	5.32	5.407	5.286	5.236	5.145	5.37	5.866	5.504	4.915	4.832	4.667	5.17	4.865	4.594	5.01	4.788	4.859	4.546	4.895	4.47	4.291	
F_{IS}	0.141	0.086	-0.06	-0.09	0.473	0.17	0.259	0.077	0.169	0.191	0.217	0.182	0.181	0.017	-0.017	0.09	0.033	0.062	0.231	0.222	0.38	0.129	
OR1																							
N_A	18	10	11	11	12	14	12	11	12	14	9	12	13	11	10	8	9	11	10	11	11	13	9.7
Ho	0.923	0.777	0.809	0.944	0.84	0.92	0.846	0.95	0.888	0.928	0.736	0.891	0.888	0.868	0.789	0.833	0.789	0.938	0.937	0.866	0.95	0.857	
He	0.907	0.890	0.878	0.911	0.900	0.900	0.898	0.906	0.924	0.906	0.882	0.911	0.883	0.872	0.886	0.855	0.882	0.884	0.903	0.902	0.873	0.884	

Table A 3. 1 cont. Detailed summary statistics of genetic diversity based on ten microsatellite markers for 22 nesting areas of olive ridley turtles in the eastern Pacific.

Locus	Location																						
	BCP N=80	EVE N=18	PLA N=21	NVA N=20	PVG N=25	MIS N=25	PTI N=15	BAP N=21	TCO N=18	SJC N=30	BCR N=24	ESC N=40	PAR N=28	GH N=40	SPD N=38	SJG N=15	SB N=38	NC N=50	NF N=52	NV N=30	NS N=20	PMA N=60	Mean N_A
AR	6.882	6.349	6.078	6.79	6.556	6.785	6.731	6.666	7.17	6.787	6.088	6.813	6.303	6.075	6.187	5.884	6.094	6.208	6.592	6.542	6.191	6.263	
F_{IS}	-0.01	0.13	0.08	-0.03	0.068	-0.02	0.06	-0.04	0.039	-0.02	0.168	0.021	-0.00	0.004	0.11	0.02	0.106	-0.06	-0.03	0.039	-0.09	0.031	
OR9																							
N_A	8	4	5	4	5	4	4	5	4	5	5	7	5	6	5	3	5	4	3	4	7	5	5.0
Ho	0.304	0.278	0.286	0.263	0.360	0.208	0.267	0.286	0.222	0.600	0.231	0.308	0.250	0.500	0.342	0.16	0.316	0.367	0.286	0.300	0.35	0.286	
He	0.332	0.257	0.305	0.245	0.322	0.445	0.303	0.265	0.259	0.567	0.600	0.518	0.263	0.480	0.306	0.30	0.285	0.369	0.261	0.273	0.36	0.302	
AR	2.44	2.191	2.51	2.138	2.453	2.744	2.386	2.282	2.246	3.426	3.678	3.367	2.241	3.22	2.386	2.23	2.286	2.573	2.136	2.222	2.88	2.339	
F_{IS}	0.085	-0.08	0.066	-0.07	-0.12	0.537	0.125	-0.08	0.145	-0.05	0.625	0.409	0.05	-0.04	-0.11	0.45	-0.10	0.005	-0.09	-0.10	0.03	0.056	
OR14																							
N_A																							19.9
Ho	0.896	0.889	0.952	0.889	0.960	0.917	0.933	0.905	0.875	0.933	0.875	0.921	0.857	0.947	0.974	0.72	0.895	0.918	0.947	0.900	0.89	0.891	
He	0.946	0.962	0.951	0.946	0.944	0.947	0.968	0.954	0.952	0.949	0.934	0.960	0.933	0.942	0.940	0.95	0.935	0.950	0.882	0.943	0.95	0.942	
AR	7.986	8.387	8.114	7.9	7.983	7.938	8.611	8.172	8.077	8.047	7.752	8.389	7.607	7.916	7.798	8.01	7.737	8.091	6.474	7.915	8.19	7.835	
F_{IS}	0.053	0.078	-0.00	0.062	-0.01	0.033	0.037	0.052	0.083	0.017	0.064	0.041	0.083	-0.00	-0.03	0.24	0.043	0.034	-0.07	0.046	0.06	0.055	
OR22																							
N_A	13	9	8	9	9	7	9	9	9	11	7	10	9	8	9	6	9	12	8	8	8	13	9.2
Ho	0.785	0.833	0.800	0.368	0.680	0.750	1.000	0.714	0.833	0.690	0.783	0.825	0.654	0.684	0.684	0.45	0.703	0.796	0.600	0.586	0.73	0.714	
He	0.792	0.716	0.787	0.787	0.760	0.761	0.841	0.825	0.775	0.723	0.716	0.779	0.793	0.672	0.731	0.61	0.733	0.742	0.738	0.632	0.70	0.789	
AR	5.104	4.58	5.018	4.796	4.599	4.515	5.547	5.309	4.898	4.849	4.15	5.045	5.035	4.065	4.47	3.78	4.635	4.531	4.757	4.073	4.69	5.117	
F_{IS}	0.009	-0.17	-0.01	0.538	0.107	0.014	-0.19	0.137	-0.07	0.047	-0.09	-0.05	0.179	-0.01	0.065	0.27	0.041	-0.07	0.191	0.073	-0.04	0.096	
Multilocus																							
N_A	15.4	9.4	11	9.7	11.1	9	10	10.6	10.2	11.8	9.8	12.5	10.4	12.3	12	7.7	11.4	13.1	9.2	11	10.3	12.9	
He	0.798	0.732	0.791	0.757	0.764	0.680	0.789	0.777	0.774	0.78	0.793	0.800	0.727	0.775	0.769	0.72	0.772	0.781	0.746	0.738	0.76	0.781	
AR	5.747	5.369	5.862	5.370	5.457	5.015	5.985	5.744	5.743	5.611	5.531	5.745	5.183	5.476	5.430	5.15	5.495	5.459	5.306	5.331	5.63	5.521	
F_{IS}	0.037	0.095	0.015	0.168	0.030	0.049	-0.07	-0.04	0.056	-0.00	0.016	0.029	0.017	0.007	0.004	0.12	0.013	-0.00	0.027	0.032	0.02	0.044	
Multilocus excluding locus OR2																							
N_A	15.8	9.8	11.3	10.0	11.7	9.8	10.4	11.2	10.7	12.1	10.1	13.1	11.0	12.2	12.2	7.9	11.7	13.6	9.6	11.4	10.7	13.3	
He	0.811	0.755	0.810	0.785	0.784	0.751	0.818	0.806	0.803	0.806	0.821	0.816	0.775	0.790	0.779	0.75	0.777	0.789	0.768	0.757	0.78	0.795	
AR	6.537	6.094	6.599	6.057	6.207	5.961	6.675	6.606	6.536	6.421	6.218	6.567	5.962	6.167	6.072	5.75	6.101	6.098	5.983	6.077	6.36	6.257	
F_{IS}	0.054	0.056	0.025	0.205	0.074	0.095	0.004	0.040	0.067	0.054	0.090	0.049	0.110	0.001	0.031	0.16	0.024	-0.00	0.108	0.043	0.03	0.063	

(*N*) sample size, (N_A) number of alleles, (*Ho*) observed heterozygosity, (*He*) expected heterozygosity, (*AR*) allelic richness, (F_{IS}) coefficient of inbreeding.

Table A 3. 2 First generation migrants of olive ridley turtle based on likelihood probabilities among nesting areas in the eastern Pacific.

				M29	**V60**
Assigned Sample	**Home**	**-log(L_home / L_max)**	**Probability**	**-log(L)**	**-log(L)**
A32	**M29**	**1.395**	**0.0016**	**23.361**	**21.966**
A59	**M29**	**0.635**	**0.0069**	**17.881**	**17.246**
F3	**M29**	**0.063**	**0.0085**	**14.926**	**14.863**
F5	**M29**	**3.536**	**0.0000**	**18.552**	**15.016**
J3	**M29**	**0.356**	**0.0067**	**16.065**	**15.708**
J17	**M29**	**0.812**	**0.0040**	**21.216**	**20.404**
L4	**M29**	**0.336**	**0.0084**	**18.181**	**17.844**
L11	**M29**	**0.640**	**0.0061**	**22.246**	**21.605**

Home = northern population (M29); southern population (V60). Potential first generation migrants (red); most likely population (green).

Chapter IV: (Article 3)

New Insights on Sea Turtle Conservation: State of Progress and Reframing of Management Approaches Based on Latest Genetic Findings in the Eastern Pacific Region

Clara J Rodríguez-Zárate[a], *Emelina Corrales-Cordero*[b], *Thomas Legrand*[b], *Luciano Beheregaray*[a] *and Pita Verweij*[c]

[a]Molecular Ecology Laboratory, School of Biological Sciences, Flinders University, Adelaide, SA 5001, Australia.

[b] Greensynergie Consultants, Paris, 75012, France.

[c] Copernicus Institute of Sustainable development, Utrecht University, Utrecht, The Netherlands.

New insights on sea turtle conservation: state of progress and reframing of management approaches based on latest genetic findings in the Mesoamerican region

4.1. Abstract

During their lifetime, sea turtles occupy multiple habitats, thus experiencing a wide range of anthropogenic threats. Joint conservation actions suited to their biological scale are vital. To illustrate this, we examined recent scientific findings for the eastern Pacific olive ridley turtles and analyzed their relevance towards sea turtles management in the Mesoamerican region. Through a vast bibliographical research of relevant genetic data, archival documents and key stakeholders surveys, we assessed the progress of conservation management actions in the last decade after the creation of an international treaty promoting regional cooperation. The study case indicated that for the eastern Pacific, olive ridleys' Regional Management Units (RMUs) should be reassessed and integrated into management plans. Based on the reaffirmed need for regional large-scale conservation management, a shift to adjust vision planning and action must take place in the region. Our results indicated that despite being a long way from having improved management strategies, the region has the opportunity to assume large-scale conservation management challenges based on capacities developed. To achieve this target, communication channels must be strengthened and perceived limitations specific to enforcement and surveillance must be addressed.

Key words

Scale; collaborative conservation; management units; sea turtles; Mesoamerica.

4.2. Introduction

It is well known that jurisdictional boundaries rarely follow bio-geophysical systems, allowing for a scales mismatch and impinging successful conservation practices (Boyd *et al.*, 2008; Cash and Moser, 2000). Mismatches relating not only to spatial scales but also to the scale of management response and change, depend on interactive dynamics within and across levels of governance (Cash *et al.*, 2006). To overcome this limitation, interdisciplinary communication is essential and can be supported by facilitating structures and proactive feedback loops across management levels (Cook *et al.*, 2013). Communication mechanisms ensure that policies and action plans adjust to achieve successful regulation and protection of biological systems (Cash *et al.*, 2006).

Sea turtles are widely distributed and highly mobile species that occupy multiple habitats during their lifetime (Musick and Limpus, 1997; Luschi *et al.*, 2003a), experiencing a wide range of anthropogenic threats. This taxon calls upon international cooperation to attain long-term conservation (Blumenthal *et al.*, 2006; Frazier, 2000; Hamann *et al.*, 2010). Additionally sea turtles are shared by multiple human communities which confer a multiple dimensions to sea turtle management (Campbell and Cornwell, 2008). Recently, genetics contributed in defining population genetic stocks, and informed about the spatial extent at which they are shared. Population genetic information has been increasingly incorporated into global assessments to guide management. Global population assessments for sea turtles are usually performed by recognized organizations (i.e the World Conservation Union's (IUCN) Marine Turtle Specialist Group (MTSG) that contributes to sea turtles assessments for the IUCN Red List). The Red listing process has been criticized for the lack of fine-scale resolution to guide management, thus failing to reflect the disparate population trends for the species at regional levels (Seminoff and Shanker, 2008).

A new approach, responding to this limitation and the need to organize sea turtles into units of protection emerged in 2010. The Regional Management Units (RMUs) framework (Wallace *et al.*, 2010a) integrated biological and ecological information, including data from genetic stocks, to facilitate sea turtles management at species level, but above nesting colonies level. This represents a valuable contribution but fine-scale data is still required. Precise guidelines at regional levels will guide decisions on sensitive issues such as sustainable use and help to address regional scale threats (Hamann *et al.*, 2010), such as bycatch (Dapp *et al.*, 2013; Wallace *et al.*, 2010b). In other words, having a fine resolution of population boundaries will allow threat impact assessments on population segments including recovery trends and extinction risk.

In this chapter, we focus in the Mesoamerican region comprising eight nations: Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica and Panama (Figure 4.1). We used new scientific findings of genetic analysis for the olive ridley turtles in the eastern Pacific obtained in this thesis, to illustrate the relevance of the agreement between biological processes and management to achieve long-term conservation in sea turtles, and implications for the species management.

Substantial efforts oriented at protecting this species in the American continent have occurred since the last century. These efforts made possible the ratification of the Inter-American Convention (IAC) for the Protection and Conservation of sea Turtles in 2001; the only legally binding international treaty specific for the sea turtles. The Convention origins date back to 1994-1996 (for history, see Frazier, 1997; Naro-Maciel, 1998), but it came into force in 2001. The objective of the Convention as mentioned in the Article II is: "to promote the protection, conservation and recovery of sea turtle populations and of the habitats on which they depend, based on the best available scientific evidence, taking into account the environmental, socio-economic and cultural characteristics of the Parties". Six Mesoamerican countries have ratified the Convention: Belize, Costa Rica, Guatemala, Honduras, Panama and Mexico. In Nicaragua and El Salvador ratification is pending. However, how do these advances fit the need of large-scale sea turtle conservation? Of importance to note is that participation, coordination and cooperation are key elements for large-scale conservation processes; ensuring that decision-making is focussed on broadening the vision of current local actions (Clark *et al.*, 2010). These premises arise important questions: what are the predominant characteristics of sea turtle conservation management in the region? What is the current action performance? Are there efficient regional mechanisms to support large-scale conservation?

We review sea turtles conservation management in Mesoamerica using the eastern

Pacific olive ridley turtles case in order to (i) explore the implications of recent findings about sea turtles population dynamics; and (ii) evaluate the sea turtles conservation management progress in Mesoamerica after the IAC ratification, and (iii) to identify opportunities and limitations according to actor's perceptions in order to achieve regional sea turtle large-scale management.

4.3. Methodology

For this study, we employed comparative qualitative research methods that provide flexibility to analyse what can be a complex phenomenon (Ritchie, 2003). We used literature reviews and interviews to understand the findings about sea turtles Management Units (MUs) and their importance in large-scale conservation management actions (design process, objectives and philosophy), including strengths and limitations. We compiled sea turtles genetic stock information in the region from mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) studies. We searched Wiley and ScienceDirect online database using the following key words: "sea turtle" and "genetic population structure". To increase results, we also jointly search the terms "management unit", "genetic stock" and "natal homing".

We performed an extensive review of scientific literature and archival documents such as internal and external reports as well as official documents that include procedure manuals, national decrees, legislation and other executive documents. To complement these datasets, semi-structured interviews were conducted aimed to (1) gain a better understanding of current sea turtle management strategies and polices in Mesoamerica; (2) conduct a qualitative assessment of its implementation; and (3) collect complementary qualitative data necessary for management performance assessment.

Data collection took place in 2010 and 2013. In 2010 we visited projects in five countries and collected personal *in situ* observations. In 2013 surveys (Appendix A1) were mostly distributed using a limited access IT platform and some were directly handed to stakeholders during the International Symposium of Sea Turtle Biology and Conservation. The surveys involved stakeholders that participate in conservation management of sea turtles in Mesoamerica (Appendix Table A 4.1). Thirty-one responses were compiled, representing six Mesoamerican countries (Table 4.1). In one case only, the respondent represented two countries. A wide range of stakeholders were represented as listed in their primary responsibilities: public officers, management directors, program monitoring coordinators, marine protected areas coordinators, project managers, independent consultants, scientific directors, fisheries coordinators, independent researchers, academics, field technicians, environmental lawyers, teachers and eco-tourist guides. Most respondents had a background in natural sciences (94%). Other training fields included legal sciences and environmentalists.

Table 4. 1 Summary of characteristics of respondents.

Affiliation	N	Area	Country
Government	8	police/management	Costa Rica, Guatemala, Mexico, Nicaragua
Academic	5	research	Belize, Costa Rica, Mexico, Panama
NGO	16	both	Costa Rica, El Salvador, Guatemala, Mexico, Nicaragua, Panama
Independent	1	practice	Costa Rica
Total	30		

Two sets of questions where used: (i) what are the supporting institutional and legislative structures behind the sea turtles management strategies implementation and it's performance? (ii) what have been the management strategies and conservation actions applied to support the marine turtle conservation and what is their performance? The first set of questions enables us to capture the progress of capacity and adequacy to support management processes. The second set was used to understand the sea turtles conservation management strategies and their performance, especially their long-term impacts, as well as their main weaknesses and strengths.

The qualitative data collected through the surveys were critically assessed. First, the surveys were analyzed to measure accordance of views expressed amongst stakeholders, paying special attention to conflicting perspectives. In those cases, we distinguished stakeholders' perceptions that were subjective and whose differences should be a recognised contributor of information for management strategies, and resulting performance. Thus, thus allowing the process to be more objective and subject to verification. Only then can there be a systematic verification looking at other qualitative and quantitative data backing or contradicting the information and positions expressed by the respondents.

4.4. Results and Discussion

4.4.1. Reframing Managements Units according to recent findings for the eastern Pacific

Information on genetic population and proposed MUs for sea turtles species inhabiting the Mesoamerica is summarized in Table 4.2. Results compiled information from proposed RMUs (Wallace *et al.*, 2010a), and their estimated resilience index (RI) (most resilient 0.76 ≤ RI ≤ 1.26; least resilient 1.77 ≤ RI ≤ 2.28; Fuentes *et al.*, 2013). The Resilience Index is based on qualitative information of each RMU using two sets of traits: the first set assesses population characteristics that influence risk of decline or genetic diversity loss (relative population size, rookery vulnerability, and genetic diversity). The second set assesses the relative population-level impacts from non-climatic threats (fisheries, individuals take, coastal development, and pollution/pathogens). The RI of each RMU is then calculated by weighting the relative influence of each of these criteria to the each RMU resilience (see Fuentes *et al.*, 2013). Population genetic assessments delineating genetic stocks were based on information from both mtDNA and nDNA. A total of 28 mtDNA stocks, 12 nDNA stocks and eight sea turtles RMUs were found.

Due to the information relevance for the assessment of population conservation, we also reviewed the integration of findings into global assessments by the World Conservation Union’s (IUCN) Marine turtle Specialist Group (MTSG), IUCN Red List. The search resulted in only one case (leatherback turtles assessment) where information from RMUs has been incorporated (Wallace *et al.*, 2013b). In that assessment, seven subpopulations are listed reflecting proposed RMUs, considered functionally equivalent to IUCN subpopulation definitions. For the other species population assessments are based on worldwide key sites: green turtle (32 sites), hawksbill turtle (25 sites), loggerhead (none-described as consulted on January 2014), olive ridley turtle (28 sites), and Kemp's turtle (none-described; considered to be represented by a single population).

Previously to this thesis findings, it was believed that solely one olive ridley turtles population, characterized by high connectivity, was present in the eastern Pacific (Bowen and Karl, 2007; Bowen *et al.*, 1998; Briseño-Dueñas, 1998; López-Chávez, 2000). Under this panmixia paradigm nesting sites are highly connected facilitating population recovery, a population dynamics that allows flexibility when selecting sites for protection. In contrast, when isolation among populations emerges due to restricted connectivity, possibilities for population recovery decrease (Chapter II) and specific-site protection becomes critical. Protecting sites with unique genetic variation will secure the preservation of a species adaptive potential, contributing to their long-term conservation (Moritz, 1994; Moritz, 1999).

The first evidence suggesting the possibility of regional genetic structure within this species appeared in 2005 with the recognition of a less diverse and genetically independent population in Baja California Peninsula, Mexico (López-Castro and Rocha-Olivares, 2005); opening the possibility to reconsider the well-accepted panmixia paradigm for the species. The fine-scale genetic assessment conducted in this thesis (Chapter III) confirmed the existence of two distinct genetic stocks with important management implications at regional scale.

Management actions in the region should consider the two new proposed MUs and therefore current RMUs must be reassessed for this species. Generally, agreement lack between genetic stocks indicated by either mtDNA and nDNA analysis have limited the use of this information by managers. However, bi-parental nuclear genetic variability characterization can provide better insights on present population connectivity (Selkoe and Toonen, 2006; Sunnucks, 2000). Stocks defined using such type of genetic marker will be of particular interest for managers. The findings may also be used to change the current olive ridley turtles regional assessment approach based on key sites, which usually is biased to main nesting sites (Plotkin, 2012).

Therefore, the genetic survey conducted in this thesis offers comprehensive definition of MUs for the assessment of recovery trends, responding to a globally recognized need to achieve effective conservation (Hamann *et al.*, 2010). Improved fine-scale assessments have also revealed the importance for management decisions in other species (see, Dutton *et al.*, 2013). Secondly, due to the large-scale boundaries of these MUs, the conservation actions require a coordinated approach from nations that share these units. The MUs proposed so far comprise the northern portion of the eastern Pacific (nesting colonies located in Mexico), and the southern part of the eastern Pacific (Central American nesting colonies from Guatemala to Panama) (Figure 4.1). Although this research covered a vast geographic area, it is desirable to determine whether other nesting colonies in the

Table 4. 2 Summary of information on genetic stocks and resilience index of proposed Regional Managements Units (RMUs) for species of sea turtles present in the Mesoamerican region.

Species	Geographic Area	RMU s	Resilience Index[1]	mtDNA stocks	nDNA Stocks	Reference
Caretta caretta	Northwest Atlantic	1	0.96	6	1	Bowen *et al.*, 1993; Bowen *et al.*, 1994; Bowen *et al.*, 2004; Bowen *et al.*, 2005; Encalada *et al.*, 1996; Encalada *et al.*, 1998
Chelonia mydas	Northwest Atlantic	1	0.99	8	1	Bowen *et al.*, 1992; Bjorndal *et al.*, 2005; Encalada *et al.*, 1996; Lahanas *et al.*, 1994; Lahanas *et al.*, 1998; Shamblin *et al.*, 2012; Roberts *et al.*, 2004
	East Pacific	1	-	3	3	Chassin-Noria *et al.*, 2004; Roden *et al.*, 2013
Dermochelys coriacea	Northwest Atlantic	1	0.89	1	3	Dutton *et al.*, 1999; Dutton *et al.*, 2013
	East Pacific	1	-	1	1	Dutton *et al.*, 1999
Eretmochelys imbricata	Western Atlantic Caribbean USA	1	1.23	9	ND	Bass *et al.*, 1996; Bowen *et al.*, 2007; Leroux *et al.*, 2012
	East Pacific	1	1.91	ND	ND	
Lepidochelys olivacea	East Pacific	1	1.07 (*arribadas*)	2	1	Bowen *et al.*, 1998; López-Castro and Rocha-Olivares, 2005; López-Chávez, 2000
					2	This thesis
Lepidochelys kempii	Northwest Atlantic	1[3]	1.84	*	*	

[1] Resilance index=RI (most resilient 0.76 ≤ RI ≤ 1.26; least resilient 1.77 ≤ RI ≤ 2.28; Fuentes et al., 2013). RI is calculated based on information of relative population size, rookery vulnerability, genetic diversity, fisheries, take, coastal development, and pollution/pathogens for each RMU. [2] No genetic studies have been performed on this species. [3] *L. kempii* is proposed as a single RMU by Wallace et al., (2010).

southern part of the species distribution (Colombia and Ecuador) belong to any of these MUs or compose a unit on their own.

Finally, the new findings are the result of a comprehensive approach suggesting the ocean circulation influence and main meso-scale features on sea turtle dispersal and genetic connectivity, results that also may indicate the need for more holistic management. Ocean currents play an important role in sea turtle migrations (Galli *et al.*, 2012; Luschi *et al.*, 2003a; Luschi *et al.*, 2003b; Seminoff *et al.*, 2008), and survival of hatchlings and juveniles (see Table A 4.2). Consequently, we could ask how climate change will impact biological processes and population segments.

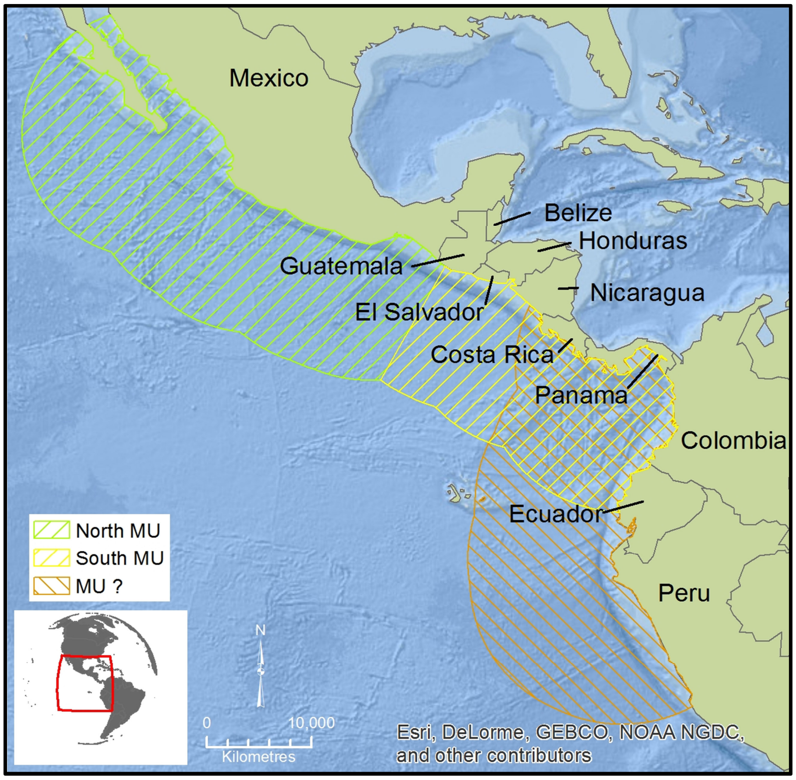


Figure 4. 1 Management Units for olive ridley turtles in the eastern Pacific based on seascape genetic analysis of 27 nesting sites along the region. The map shows MUs proposed in Chapter III: northern population (green lines), and southern population (yellow lines). The geographic area delimited with yellow lines corresponds to nesting sites (located in Colombia and Ecuador) not included in this study.

Little is known on climate change effects on migration patterns and connectivity on sea turtles, in contrast to nesting beaches (Hawkes *et al.*, 2009; Janzen, 1994; McMahon and Hays, 2006). However, changes in global ocean circulation, and particularly alteration in atmospheric and thermocline circulation for the Eastern Pacific are expected (Collins *et al.*, 2010); impacting hydrological cycles, upwelling processes, food web dynamics, and dispersal and distribution of marine organisms (Clark *et al.*, 2002; Doney *et al.*, 2012; Stocker and Schmittner, 1997). These changes could influence hatchling survival by changing location of developmental and foraging grounds (McMahon and Hays, 2006) and potentially the connectivity among populations. Population resilience assessments will then rely greatly on the accurate definition of population boundaries at regional scales to assess risk. Proposed resilience index for olive ridley turtles in the eastern Pacific based on one single RMU (Table 4.2), might then be re-evaluated.

The implications derived from these findings represent practical issues for sea turtles managers. Specifically, a large-scale conservation vision for this taxon should be embraced, and practical changes made at different levels to successfully incorporate scientific findings and adapt practices to the scale of need for the species. This vision will also be required to perform effective conservation of different life stages and critical habitats within a multilateral context. Similar approaches have been proposed for western Pacific sea turtles, explicitly to rehabilitate the leatherback turtles population (see, Dutton *et al.*, 2011; Dutton and Squires, 2008).

4.4.2. Regional capacity to perform large-scale conservation

4.4.2.1. Legal and institutional capacity

The region has a long history of concern on sea turtles protection that started in 1927 –in Guatemala (*personal communication* Jolon-Morales). With this particular experience, capacities have been developed, and conservation has evolved to be multidisciplinary (Marcovaldi *et al.*, 2003). Some of the benefits from this long-term experience are the comprehensive legislation frameworks at national levels. However, dissimilar progress stages are the result of various socio-political realities (Q26), impacting legal frameworks development. This limitation has been partly overcome since the IAC establishment.

Although, countries such as Guatemala, Mexico and Costa Rica created specific sea turtle protection laws prior the Convention (Chacón and Arauz, 2001) during and after the IAC ratification, a homogenization of national's legal framework process took place, providing a base line for cooperation across the region (). In Panama and Honduras, laws, management strategies and monitoring programs are in progress (Table 4.3). Nowadays all the Mesoamerican countries have a legal structure that regulates actions towards sea turtles (Table A 4.3). In the countries where the convention has not yet been ratified there is still an assumed responsibility towards sea turtle conservation, and their laws or management programs reflect the main aspects of the Convention.

Sea turtles are also protected under environmental organic laws, fishery legislations (i.e. regulating the Turtle Excluder Devices (TEDs) implementation) and biodiversity laws. In some countries (i.e El Salvador and Nicaragua) legal protection is provided by executive agreements or ministerial regulations in contrast to national laws as is seen for countries such as Mexico, Panama and others. Under this legal instrumentation, sea turtles protection would remain susceptible to government life spams, compromising long-term protection. Despite this limitation, we recognize the intrinsic value of these instruments in supporting the taxon conservation.

A key advance with the IAC validation was the inclusion of crucial aspects (i.e protection of individuals in marine habitats, Article IV of the Convention), into national laws. In addition, possibilities were opened for conservation on different levels including discussions on scientific and management issues under a legally binding structure. Since its creation, the IAC scientific committee has produced important resolutions related to conservation issues on bycatch mitigation and sea turtles habitat adaptation to climate change (Resolution COP3/2006/R-1 and R2). Therefore, due to the action level and the possibility to discuss integrated scientific findings this legal instrument constitutes a clear capacity for large-scale conservation in the region. However, fundamental issues deserve attention to fully develop its potential, which has been largely questioned (Campbell *et al.*, 2002). Finally, the reality that two countries have not yet ratified this agreement could represent a limitation to secure a large-scale conservation commitment.

Table 4. 3 State of progress of key element considered for the Inter-American Convention (IAC) for the Protection and Conservation of sea Turtles for the Mesoamerican countries.

Country	IAC status	Last annual report	Is there a management strategy?	Are there laws at local and national wide[1] level?	Are there monitoring Programs?	Comments
Mexico	R, 2000	2013	yes	yes	yes	The management program is nested at central government level. Implementation is done through the program called Programas de Accion para Proteccion de Especies (PACE). Each species of turtle has its own. These programs have evaluation mechanisms for monitoring at short medium and long terms. There is a nationwide program to preserve marine ecosystems and consists of surveillance and preservation of marine biodiversity, particularly sea turtles.
Belize	R, 2003	2011	yes	yes	yes	No comments.
Guatemala	R, 2003	2013	yes	yes	yes	The national program is called Estrategia Nacional de Conservacion y Manejo de Tortugas Marinas (2002). During 2013 this strategy was under evaluation.
El Salvador	NF	-	-	-	-	No information available in the IAC webpage
Honduras	R, 2001	2013	In progress	In progress	In progress	Recently a diagnostic of sea turtles in the country was performed and it is planned to develop a management strategy in collaboration with the program of international cooperation MAREA-USAID. At regional (national wide) level they have been working in the Gulf of Fonseca. Monitoring has been done by governmental entities and NGOs that are located in nesting sites, but is not done in a consistent way.
Nicaragua	F, 1997	-	-	-	-	No information available in the IAC webpage
Costa Rica	R, 2000	2010	yes	yes	yes	In 2007 the plan for use of olive ridley turtle eggs was signed and approved for the RNVS Ostional for a period of 5 years.
Panama	R, 2008	2013	In progress	In progress	In progress	There is a draft initiative of the management plan that will be submitted for national consultation and evaluation to establish an action plan in the short-term. This national action plan is financed by Conservation International together with the national authority of aquatic resources of Panama. This will include a technical legal and socioeconomic diagnosis of the areas where there are sea turtles. The central government of Panama (Minister of Environment) are in the process of including international legislation and actions for the different species in the different regions of the country. It is intended that the management strategy contain an evaluation and follow up program.

*status: Not signatory (NS); Signatory (S, year of signature); Ratified (R, year of ratification). [1]National wide=in the documents of the convention this is understood as regions within a country. Source: Annual reports of the IAC for each country (http://www.iacseaturtle.org/informes.htm).

Other instruments at supra-national level that may also contribute to broaden the action scope are multilateral legal frameworks such as the “Tri-Partite Agreement” (created in 1998), as these instruments are much easier to negotiate compared to larger treaties (Hykle, 2002). However it is recognized that its efficacy depends on its integration at national level and different scales coordination (Frazier, 2012). Although the “Tri-Partite Agreement” has assured partnership and sea turtle protection among three nations (Costa Rica, Nicaragua and Panama), its coverage is limited (i.e. Caribbean coasts). Further agreements of this type should aim to enhance legal protection among nations that share the resource of sea turtles along the Pacific coast of the Mesoamerican region.

Potential perceived constraints identified to large-scale conservation are poor performance of law compliance and enforcement. Some reasons expressed were the generalized ignorance of the law by those performing functions of surveillance and control. This issue common to other conservation processes worldwide (Eyebe *et al.*, 2012; Keane *et al.*, 2008) is generally related to limitation of financial resources and lack of adequate communication mechanisms; and has been previously recognized for the region (Chacón and Arauz, 2001). Nevertheless among stakeholders, there is a general perception of sufficient adequacy of current legal frameworks indicating that they are comprehensive enough to allow sea turtles conservation.

4.4.2.2. Stakeholders for sea turtles management and implementation of actions

We were able to identify stakeholders according to their level of action and stages within the management process (planning, implementation, control and communication). They varied depending on the internal political organization and governance system in each country and resulted in different arrangements as well as stakeholders' functions (Table 4.4).

- Inter-governmental stakeholders

The only stakeholder identified at hemispherical level was the IAC. The IAC acts as information compiler due to the annual reports generated by each party and also function as observer assessing the progress of actions and compliance of the treaty. The IAC scientific committee role is also to compile information and distribute it within the parties. The structure of the Convention as a legal body includes the secretariat, the consulted committee, the scientific committee and the monitoring programs.

-Governmental stakeholders (environmental dependencies, species-specific offices, environmental police and other guards)

The government functions were related to two main activities: legal framework development and law enforcement. The Mexico Government (federal and state) is highly involved in monitoring programs, in contrast with government actions in other countries.

Table 4. 4 Description of stakeholders present at different scales of action in the Mesoamerican region.

Scale level	Actor	Category	Commentary
Hemispherical	IAC	Inter-governmental	This is a convention that at regional level creates the legal framework.
Regional	CCAD-SICA	Inter-governmental	This entity is the office in charge of the environmental issues in the Central American system of integration but there is no specific office for biodiversity. The SICA has a dedicated fishery office (OESPESCA) that deals with fisheries in the region and with bycatch for sea turtles.
Regional	WWF	NGO	This NGO has been working in the region for over 25 years and has worked at regional and local level in the conservation of sea turtles.
Regional	WIDECAST	network/NGO	This is a network of sea turtle managers, experts and conservationist in the Caribbean region. Its activity began in 1994.
Regional	Central American Sea Turtle Network	network	This network was active from 1998 to 2001. There is not reported activity at present time.
Multi-National	STC, FFI, TNC etc	multi-national NGOs	They work at different levels of protection and action (nesting beaches, fisheries and environmental education).
National Governmental	Environmental ministries, administrative offices. fisheries dependencies, and law enforcement agents (police, army, coast guard etc)	governmental	These institutions vary within countries' structure. In the specific case of Mexico there is a national government network that is in charged of nesting beaches camps across the national territory.
Non-governmental	Grupo Tortuguero de las Californias, Akazul, Arcas, ICAPO, Paso Pacifico, ASVO, PRETOMA, Fundacion Agua y Tierra etc	local NGOs and networks	The NGOs mentioned here, are just an example of this type of organizations in each of the countries.
Local	(i.e Ojochal beach, Costa Rica)	Local community	It relates to groups of citizens or private business that decide to participate and protect specific nesting beaches.
Local	Asociacion de Desarrollo Integral de Ostional Community –based conservation program of Bahia Jiquilisco, El Salvador Community –based conservation program of Estero Padre Ramos Nature Reserve, Nicaragua etc	Community-based Conservation	Organize community groups that actively participate on the management and execution of conservation programs. Projects of similar kind are emerging in recent years.

Inter-American Convention (IAC) for the Protection and Conservation of Sea Turtles, Central American Commission for Environment and Development (CCAD, spanish acronym), Central American Integration System (SICA, spanish acronym), World Wide Fund for Nature (WWF), Wider Caribbean sea Turtle Conservation Network (WIDECAST), Sea Turtle Conservancy (STC), Fauna & Flora International (FFI), The Nature Conservancy (TNC), eastern Pacific Hawksbill Initiative (ICAPO spanish acronym), Asociacion de Voluntarios para las Areas Protegidas de Costa Rica (ASVO), Programa Restauracion de Tiburones y Tortugas Marinas (PRETOMA).

-Non-governmental stakeholders (local and regional)

According to our findings NGOs play different roles across the conservation management levels. At regional level they function as networks, mobilizing agents and financial resources, and achieving certain regional cohesion. They also are involved as governmental advisors on the regulations and management plans design (i.e. Sea Turtle Conservancy; the Word Wildlife Fund, WWF; The Nature Conservancy, TNC; Conservation International, Flora and Fauna International). At the base level community-based conservation has been greatly promoted by grass root organizations, with groups conducting nesting beaches monitoring, implementing conservation programs and raising awareness among the general public. Management strategies observed in the region comprise an approach mosaic going from exclusive protection to legal-sustainable-use (Table A 4.3). This mosaic does not necessarily constitute a limitation to large-scale conservation, since there is an intrinsic value on recognizing and adapting management systems to specific countries realities. However, difficulties may arise in threats reduction. For instance, respondents suggested that illegal sea turtle eggs commercialization is promoted if different management approaches coexist between neighbours' countries, a problem that is exacerbated by the difficulty for control and surveillance due to limited financial resources.

Management strategies in the region are regulated through national management action plans. Only one strategy exists at regional scale. The Central American strategy for the conservation of sea turtles (Chacón and Arauz, 2001), was focused on Central American countries only, excluding Mexico. No actualization to this management strategy was found. In general, management actions have been focused on nesting beaches protection throughout hatcheries establishment and eggs translocation; while actions in marine habitats have remained challenging and have focused on the TEDs implementation in trawling fishing ships, and circle hooks conversion for longline fisheries. Data collection and monitoring is usually performed by NGOs in collaboration with other stakeholders (Table 4.4).

Our search showed two regional networks and some species oriented initiatives that facilitate communication at regional level: Wider Caribbean Sea Turtle Conservation Network (WIDECAST) – created in 1981 includes over 40 nations and territories through the wider Caribbean region, representing only seven of the eight Mesoamerican nations. Results indicate that the Mesoamerican Pacific region lacks a network analogous to WIDECAST in the Caribbean. The Central American Regional Network for the conservation of sea turtles created in 1996 does not have registered activity since 2001. However, in the past decades species oriented networks such as the leatherback conservation network (see, Barragán, 2012), and the Eastern Pacific hawksbill Initiative (Iniciativa Carey del Pacifico Oriental, or ICAPO, in Spanish) (see, Gaos *et al.*, 2010; Gaos and Yanéz, 2012) have played a crucial role , contributing to cooperation among different stakeholders.

4.4.2.3. Perceptions on sea turtle conservation

- On legal instruments and enforcement

All participants expressed knowledge of the taxon legislation and polices, and 78% were aware of recent updates. The overall perception on compliance performance was poor (50%), and average (38%) with only one respondent (#Q31) rating a very good performance in Belize. To measure performance we inquired about eggs harvesting or hunting prosecution cases. 31% of the respondents reported to know a couple of cases where legal penalty was imposed. In most cases illegal actions are not prosecuted (84%), and only illegal eggs confiscation takes place (Appendix, Figure A 4.1).

- On the performance of management strategies on the ground

We explored management strategies strengths, weaknesses and limitations. For every topic more than ten factors were listed that vary among countries (Figure A 4.2, A 4.3 and A 4.4). Here we summarize the most common factors. Strengths listed were related with communities' interest and involvement (22%); and increasing awareness (16%). The mentioned weakness were law-penalties enforcement and communication and action coordination (25%, 19% respectively), respondents agreed that financial resources (control, management, conservation, research) is the main limitation (66%) for current conservation actions, followed by the lack of human resources (control, research, specialists) (22%).

When asked about possible alternatives considered to the current system the answers varied as follows: Mexico=*in situ* protection (25%); Guatemala=absolute or area-specific total protection (43% each); Belize=networking (100%); El

Salvador=sustainable economic alternatives, ecotourism, and none (50% each); Nicaragua=involvement of communities, private-beach protection and sustainable economic alternatives (50% each); Costa Rica=none (29%); Panama=none (40%).

Stakeholders were questioned about the effectiveness of actions as a whole as well as regarding the level of coverage, and benefits to local communities. General performance were equally rated between average and poor levels (34% each) as follows: Mexico=average (63%); Guatemala=poor (71%); Belize=excellent (100%); El Salvador=average and poor (50% each); Nicaragua=poor (100%); Costa Rica=average (43%); Panama=average and poor (40% each).

Regarding action coverage (geographical area covered and sea turtles species protected), the majority rated their countries as very good (31%). Countries were rated as follow: Mexico= very good (63%); Guatemala=average (43%); Belize=very good (100%); El Salvador=very good (100%); Nicaragua=average and poor (50% each); Costa Rica=average (43%); Panama=poor (80%).

In general, it was expressed that several threats are being neglected (44%) or partially attended (41%), and attention lack to threats in marine habitats (i.e. bycatch, fisheries regulation and direct hunting) (47%). Other threats mentioned were actions outside protected areas to address illegal eggs harvesting (22%), and habitat degradation by urban/tourism development (19%). Interestingly, respondent Q26 mentioned drug trafficking as an indirect threat that is not being attended (Figure A 4.5).

Regarding local communities benefits, countries were rated average (34%) and very good (31%); and only Nicaragua had a poor qualification. 91% of the respondents indicated that their countries encourage citizen participation promoting multi-sectorial involvement, government-economic alternatives (i.e ecotourism), NGOs community programs (i.e. education-awareness), community-based management and participation in monitoring and a combination of both.

- On the performance of actions within the region

The individual country performance when compared to others in the region was commonly rated as very good (50%) and average (25%). Specifically, Belize=very good (100%); El Salvador=very good (100%); Mexico=very good (75%); Costa Rica=very good (71%); Nicaragua=average and poor (50% each); Panama=poor (60%). In Guatemala performance was equally rated as very good, average and bad (29% each). Interestingly, 38% selected Costa Rica as a model to follow. However, 19% expressed the difficulty in selecting one single system/country; other mentioned Mexico (13%) and Brazil (9%). Reasons included: resource investment, work quality, action effectiveness, higher awareness, and better community benefits (particularly for Brazil).

4.4.2.4. Identifying implementation capacity

Advances have been made towards strengthening networks promoting collaboration. However coordination is still perceived as a major limitation for successful threat reduction, minimizing the possibility to capitalize on the developed opportunities and capacities.

In management processes planning is essential and it is challenged by system complexity as well as the failure to adopt ecological knowledge (Lindenmayer *et al.*, 2008). It is known that interactions between scientist-managers and policy makers represent a challenge for environmental sciences; due to different discipline interactions (Cash *et al.*, 2006). Therefore, to achieve effective regional management, this issue should be explored. NGOs have played a crucial role on closing this gap (Agarwal, 2008), resulting in valuable contributions. For instance, a plan focused on critical endangered sea turtles species and priority habitats was generated for Latin America and the Caribbean by WWF (2008), using available relevant scientific data. This case demonstrates that planning at suitable scales is possible by adequately integrating scientific information. It is still desirable that such plans can be generated including all six species, with revisions as part of an adaptive planning-action process.

Although the area has generated valuable information on sea turtle ecology, it is perceived as underused. This indicates that communication mechanisms or practical means by which information is integrated are to some extent missing. Therefore, scientific and ground information transfer mechanisms should be strengthened to improve adaptive conservation dynamics (top-bottom and bottom-up processes, see Sodhi *et al.*, 2011). Even for species that have shown signs of recovery, scientific findings at smaller scales have potential to aid management (e.g. Chapter II).

No less important is the benefit that multiple stakeholders participation by means of diverse views, needs, experiences, and expertise can contribute to planning processes (Reed, 2008). As mentioned by interviews planning processes have been increasingly opened to participation, and reaffirmed by IAC Secretariat Pro-Tempore (2011). This constitutes an opportunity to facilitate the discussion process needed in the construction of a new regional management vision.

Relevant to note is that institutional capacity (lack of human and financial resources) can be a limitation to achieve supra-national planning; constraining government's ability for cross-planning and consequently, efforts at national level are usually prioritized. In comparison with nesting habitats, action coordination at sea proposes more difficulties; specifically for fisheries regulation (bycatch) (Campbell *et al.*, 2009; Hall *et al.*, 2012). In addition, financial constrains can also impact enforcement and monitoring capacity, representing a hurdle for countries to engage in systematic collection of long-term quality information (i.e. Q4, Q6, Q9) to assess populations recovery trends.

The long-term experiences built in Mexico and Costa Rica is a capacity perceived as strength and opportunity to undertake regional conservation. Additionally, experience on collaborative actions has increased through the development of some regional initiatives (i.e ICAPO)[1], and those from trans-national NGOs in

---

[1] The eastern Pacific Hawksbill Initiative (ICAPO) since 2008 promotes hawksbill turtle's protection along the eastern Pacific and advocates collaboration of nations from US to Peru.

collaboration with local partners[2] [3]. Nevertheless, its potential also relies on effective mechanisms for experience transfer among nations and the communication dynamics among different levels of the conservation management process.

Finally, it is important to understand that real collaboration at supra-national level is a reflection of the achievements at national level. In this sense, networks are essential to stimulate information and experiences exchange. Therefore, networking scale up should be improved and oriented to all species. In addition, network actions could be supported by supra-national structures, which could offer a space for discussion and institutional support for long-term initiatives. Our review indicated potential structures (umbrella inter-governmental bodies) to fulfil this role: the Central American Commission for Environment and Development (CCAD, Spanish acronym), and Central American Integration System (SICA, Spanish acronym), by which also inspection and verification of systems can be sought.

Looking back since the IAC came into force it is evident that the region has generated a positive capacity and institutional maturity, enabling the region to move towards a new large-scale conservation management. This step forward will require an analytical process at each national level to observe the decision-making processes and the long-term vision in relation to the taxon. This analysis is also needed to understand the responsibilities associated to the resource ownership,

---

[2] WWF-CIAT Bycatch fishery program-2004-2008; MAREA-USAID project of international cooperation-2010-2014.

[3] The Eastern Pacific Marine Corridor (CMAR), The Eastern Tropical Pacific Seascape Program, Inter-American Tropical Tuna Commission (IATTC).

clarifying the vision in a regional context. In addition, it is vital to tackle underlying assumptions, expectations and norms that will be used in short, medium and long-term processes. Achieving a real consensus across nations will enable the needed conservation management shift. At this point it is clear that due to the functional role that sea turtles play at an ecosystem level (Bouchard and Bjorndal, 2000), decisions to perform large-scale conservation for the species will likely have positive effects in the broader marine ecosystem.

4.5. Conclusion and Final Remarks

This study highlights that using scientific information is key to better understand the scale at which management actions should be undertaken, and to conciliate scale mismatch between biological systems and management. The current conservation practices analysis at different levels provided a clear picture in the stage of progress in sea turtles conservation management in Mesoamerica, contributing to identify areas to be improved and those that contribute to scaling up current actions. The results highlight opportunities for strengthening legal frameworks that encompasses all nations, based on a hemispherical legal umbrella (IAC), structures for implementation of actions, as well as, increased experience, participation of stakeholders, protection coverage and interest towards sea turtles protection. However, key limitations (financial resources, communication and coordination of actions) may threaten large-scale conservation management. Finally, the proposed shift will greatly depend on the political will, government awareness and their commitment to the contribution of a regional consenting vision for sea turtles management.

4.6. Acknowledgments

We thank anonymous participants that voluntarily contributed with their perceptions to this study. Funding was provided by the Australian Research Council (DP110101275 to Beheregaray, Möller & Waters). This research was conducted under research permit #6164 from Flinders University Social and Behavioural Research Ethics Committee. This is MEGMAR (Molecular Ecology Group for Marine Research) article contribution #55.

4.7. Appendix

A 1 Survey distributed among stakeholders on their perception on conservation management of sea turtles in Mesoamerica.

Questionnaire- Perceptions on Sea Turtle Conservation in Mexico and Central America

Dear,

The analysis is part of the doctoral research conducted by my student Ms. Clara Jimena Rodriguez-Zarate entitled: "Seascape genetics and conservation management of olive ridley turtle (Lepidochelys olivacea) in the Eastern Pacific" at Flinders University, Australia. This study focuses on the analysis of current issues related to the conservation of sea turtles, particularly looking at activities, polices and management strategies across six countries (Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica and Panama). The aim is to contribute with management guidelines to improve sea turtle conservation in the region.

Your collaboration is entirely voluntary and will consist in filling out the online questionnaire, which appears following the electronic link included with this message. The questionnaire consists of 22 questions about your views of the effectiveness and limitations of conservation practices and polices for the protection of sea turtles. It should take no more than 45 minutes to respond. Responses will be saved automatically and can be submitted by clicking on the link at the end of the questionnaire.

Please note that both your answers and your personal information will remain confidential. If you are willing to participate, please complete the questionnaire and submit your responses before 15 days after receiving this email. Detailed information is included in the Introduction letter and information letter files that you will find attached to this message.

We thank you in advance for your collaboration as this is of great value for the conservation of sea turtles.

Any enquiries you may have concerning this project should be directed to me at the following email address jimena.rodriguez@flinders.edu.au

Thank you for your attention and assistance.
Yours sincerely,

Professor Luciano B. Beheregaray
School of Biological Sciences, Flinders University
Adelaide SA 5001, Australia
Tel: 08 8201 5243; Fax: 08 8201 3015
E-mail: luciano.beheregaray@flinders.edu.au
Website: http://www.molecularecology.flinders.edu.au

This research project has been approved by the Flinders University Social and Behavioural Research Ethics Committee (Project Number 6164). For more information regarding ethical approval of the project the Secretary of the Committee can be contacted by telephone on 8201 5962, by fax on 8201 2035 or by email human.researchethics@flinders.edu.au

* Required

Personal Information

Note: Please remember that all your personal information will remain confidential. Only fields noted with (*) are mandatory.

1. **Name**

2. **Email** *

3. **Organization**

4. **Position**

5. **Professional degree**

6. **Country** *

This research project has been approved by the Flinders University Social and Behavioural Research Ethics Committee (Project Number 6164). For more information regarding ethical approval of the project the Secretary of the Committee can be contacted by telephone on 8201 5962, by fax on 8201 2035 or by email human.researchethics@flinders.edu.au

School of Biological Sciences Faculty of Science and Engineering, Biological Sciences Building GPO Box 2100 Adelaide SA 5001 Tel: +61 8 82012180 Fax:+61 8 8201 3015 jimena.rodriguez@flinders.edu.au

Section of Questions

Below you will find questions organized in consecutive order. You can enter your answers in the space provided electronically and provide a detailed explanation when needed.

Part 1

7. **1. Which entities are involved in the management of ST in your country?**

8. **2. Which are the entities responsible for the compliance of existing regulations?**

9. **3. Who are those responsible for managing and implementing conservation actions in your country?**

10. **4. Do you know when was the last update to regulation for ST conservation made in your country?**
    If possible explain what the change was about

11. **5. Apart from the specific legislation which other laws do you consider relevant for ST in your country?**

12. **6. Does your country prohibit the use of ST?**
    Note: you can provide details in following sections
    Mark only one oval.

    ○ Yes, totally
    ○ Yes, partially
    ○ No

13. **7. How many cases do you know of people who have broken any law of protection of ST has been penalized? What was the sentence?**

14. **8. How many cases do you know where no penalty was applied? Explain the reason if you know.**

This research project has been approved by the Flinders University Social and Behavioural Research Ethics Committee (Project Number 6164). For more information regarding ethical approval of the project the Secretary of the Committee can be contacted by telephone on 8201 5962, by fax on 8201 2035 or by email human.researchethics@flinders.edu.au

Part 2

For the next section of questions please provide information to both coasts of the country (Pacific and Caribbean), if applicable.

15. **9. How many ST species occur in your country?**

16. **10. Are there cultural uses of ST species in your country?.**
    For your answer consider whether they differ by species and ethnic or community group.

17. **11. What are the management systems that are currently applied for different species of ST in your country?**

18. **12. From your experience, what do you think are the strengths of conservation actions in your country?** *

19. **13. What are the weaknesses?** *

20. **14. What are the limitations?** *

21. **15. Have any other viable alternatives been considered to improve the management of ST? Which are they?** *

22. **16. Do you consider ecotourism as an activity that promotes the protection of ST in your country?**

23. **17. What is the role of ecotourism in the country?**

24. **18. Does your country encourage citizen participation on conservation of ST? Could you mention any region or project in particular?**

25. **19. In your opinion the actions of protection that exist now help to mitigate every threats that has been identified for ST in your country? Which are not being addressed?**

This research project has been approved by the Flinders University Social and Behavioural Research Ethics Committee (Project Number 6164). For more information regarding ethical approval of the project the Secretary of the Committee can be contacted by telephone on 8201 5962, by fax on 8201 2035 or by email human.researchethics@flinders.edu.au

Part 3

26. **20. Using a scale from 1 to 5 Could you describe the actions of conservation in your country, if we talk about: a. Legal compliance:** *
Mark only one oval.

	1	2	3	4	5	
bad (no action is	○	○	○	○	○	excellent (all that is done is well

taken)	○	○	○	○	○	executed)

27. **b. Effectiveness of actions:** *

Mark only one oval.

	1	2	3	4	5	
bad (no action is taken)	○	○	○	○	○	excellent (all that is done is well executed)

28. **c. Coverage by species geographically:** *

Mark only one oval.

	1	2	3	4	5	
bad (no action is taken)	○	○	○	○	○	excellent (all that is done is well executed)

29. **d. Benefits to local communities:** *

Mark only one oval.

	1	2	3	4	5	
bad (no action is taken)	○	○	○	○	○	excellent (all that is done is well executed)

30. **21. How do you rate the performance of ST conservation actions in your country compared to other countries in the region?** *

Mark only one oval.

	1	2	3	4	5	
bad (no action is taken)	○	○	○	○	○	excellent (all that is done is well executed)

31. **22. What other country do you consider a model to follow? and why?**

Table A 4. 1 Characteristics of respondents.

Code	Affiliation	Country
Q1	NGO	Guatemala
Q2	NGO	Guatemala
Q3	NGO	Nicaragua
Q4	NGO	Panama
Q5	Government	Nicaragua
Q6	Government	Costa Rica
Q7	Academic	Panama
Q8	Government	Mexico
Q9	University	Mexico
Q10	Independent	Costa Rica
Q11	NGO	Panama
Q12	NGO	Costa Rica
Q13	Government	Mexico
Q14	Government	Guatemala
Q15	Academic	Costa Rica
Q16	NGO	Panama
Q17	NGO	El Salvador
Q18	NGO	Guatemala
Q19	NGO	Costa Rica
Q20	Government	Costa Rica
Q21	Government	Mexico
Q22	Academic	Mexico
Q23	NGO	Mexico
Q24	Government	Mexico
Q25	NGO	Guatemala
Q26	NGO	Guatemala
Q27	NGO	El Salvador
Q28	NGO	Guatemala
Q29_a	NGO	Costa Rica
Q29_b	NGO	Panama
Q30	Academic	Mexico
Q31	Academic	Belize

Table A 4. 2 Summary of studies showing the influence of ocean currents on dispersal of sea turtles.

Stage life	Species	Activity	Reference
hatchlings	*Caretta caretta*	trans-Pacific dispersal	Okuyama *et al.*, 2011
hatchlings	*Caretta caretta*	off-shore dispersal from natal to foraging grounds	Putman *et al.*, 2012
hatchlings	*Dermochelys coreacea*	dispersal from nesting sites	Shillinger *et al.*, 2012
juveniles	*Caretta caretta*	feeding / use of eddies	Polovina *et al.*, 2006 Revelles *et al.*, 2007
juveniles	*Chelonia mydas*	trans-Atlantic migration dispersal from natal to foraging grounds	Monzón-Argüello *et al.*, 2010 Putman and Naro-Maciel, 2013
juveniles	*Eretmochelys imbricata*	dispersal from natal to foraging grounds	Putman *et al.*, 2014
adults	*Caretta caretta*	post-nesting migrations	Hays *et al.*, 2010
	Lepidochelys olivacea	influence on dispersal towards nesting beaches	This thesis

Table A 4. 3 Management systems for conservation of sea turtles identified for the Mesoamerican region.

Strategy	**General Description**	**Country**	**Law that confer protection and/or regulate use**
Total protection	Under this system extractive use is completely banned. This includes the capture of individuals or derived products.	Mexico[1]	Law DOF-1990. Article 60 Bis1-Ley General De Vida Silvestre DOF 16-11-2011. In Mexico due to the habits and customs of the group Seri o Conca'ac, the indian Act (Ley indigena de usos y costumbres), protects and authorize the extraction of 2-3 sea turtles (*chelonian mydas*) every year for the celebration of their new year.
		Belize	Legal instrument 66, 2002 section 13 of fishery law, chapter 210.
		El Salvador	Executive Decision No.343 of Agriculture and Livestock branch. Executive Decision No.74 Branch of Environment and Natural Resources 12-11-2008.
		Honduras	Legalization process of the national committee of sea turtles.
		Nicaragua[1]	Ministerial Resolution (MARENA) No. 043-2005. Exception of use: Article 96 Law 489-2004 (Fishery Act).
		Costa Rica[2,4]	Protection Act 8325, conservation recovery of sea turtle populations 28-11-2002.
		Panama[1]	Law 8 January 2008 (Ley 8 de Enero 2008 that approved the IAC).
Mixed system	Under this system total protection coexist with a usage policy	Guatemala[3]	Government Agreement 17/02/1981 unnumbered (continuous validation processes). Exception to legal use regulated by hierarchical level administrative resolutions through CONAP Executive Secretary resolutions.

[1] traditional use permitted for certain indigenous communities. [2] exception of use in Ostional nesting beach, Article 6 Law 8325. [3] total protection applies to four sea turtles species, and partial use of olive ridley turtle eggs is permitted. [4] non-extractive use (ecotourism).

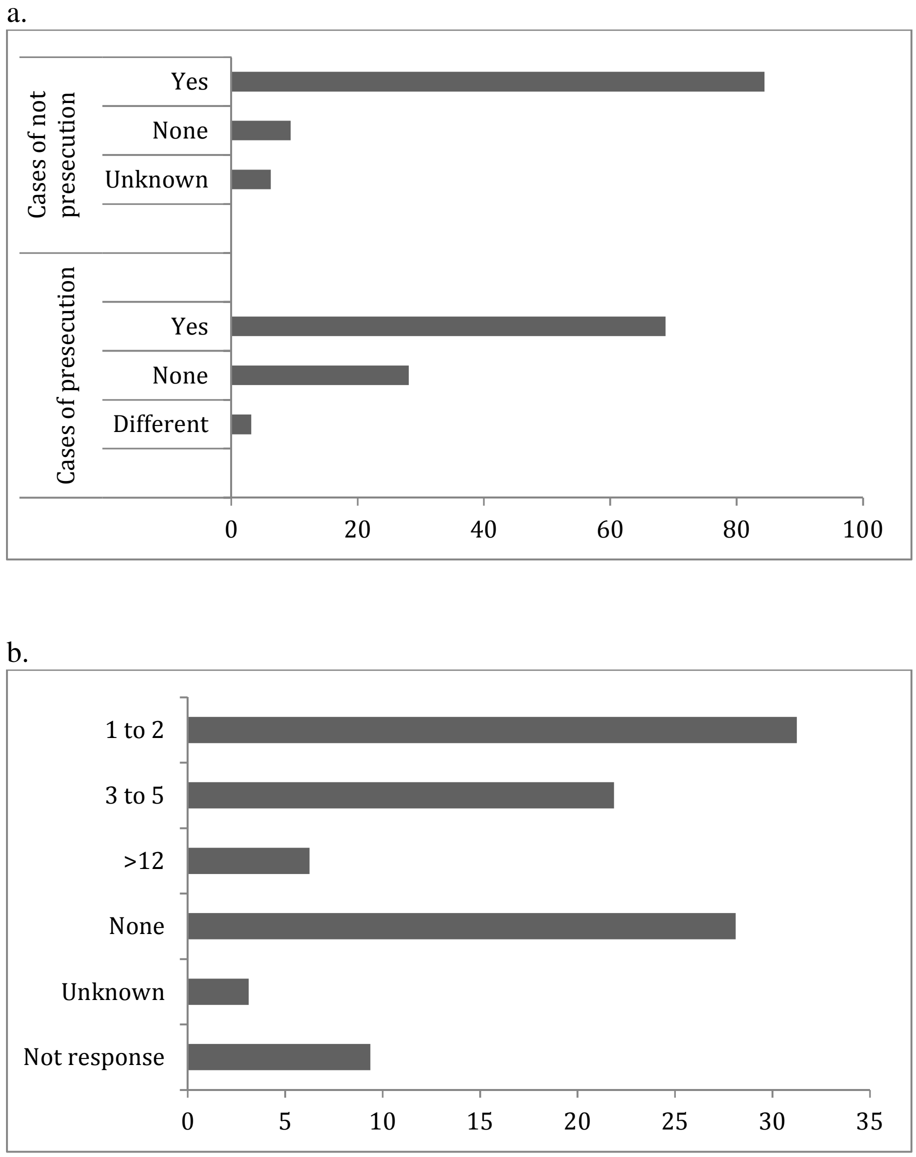


Figure A 4. 1 Summary of responses indicating stakeholders perceptions in regards to Penalties (a) and law enforcement and prosecution (b) in Mesoamerican countries.

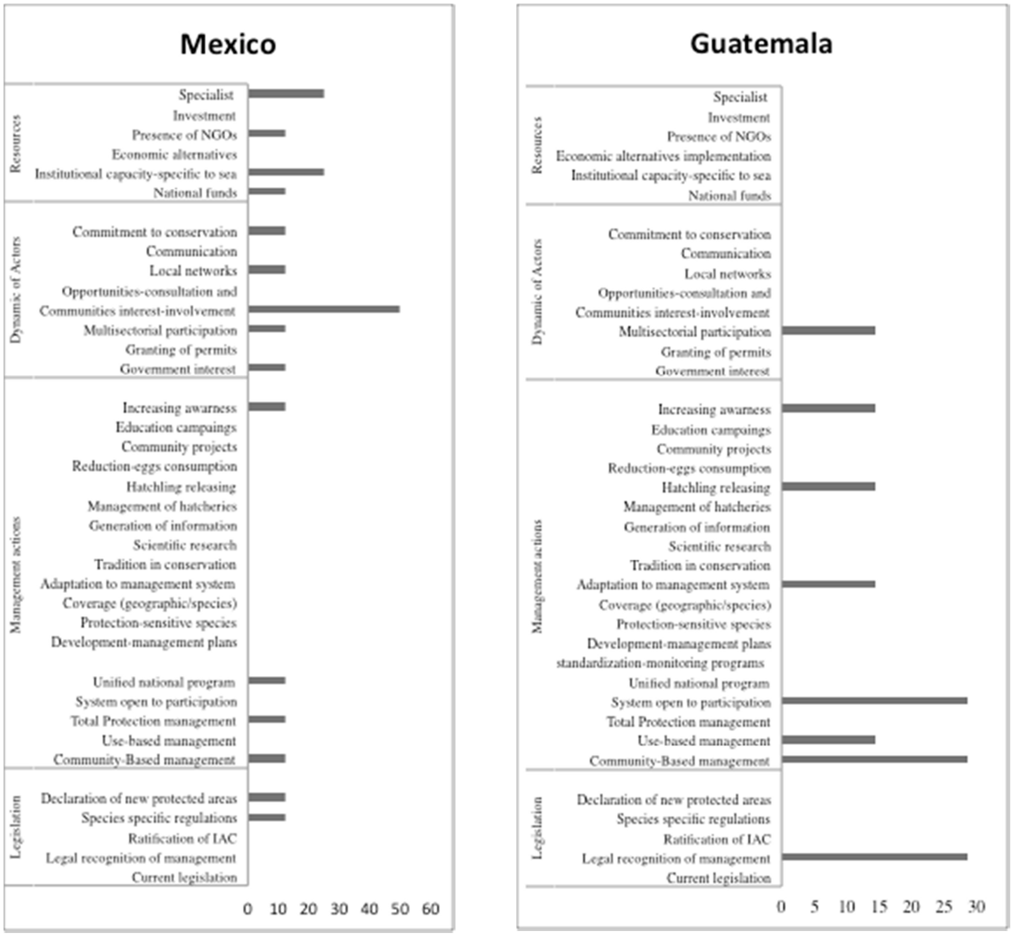


Figure A 4. 2 Summary of responses indicating stakeholders perceptions in regards to strengths in each Mesoamerican country and a summary across countries.

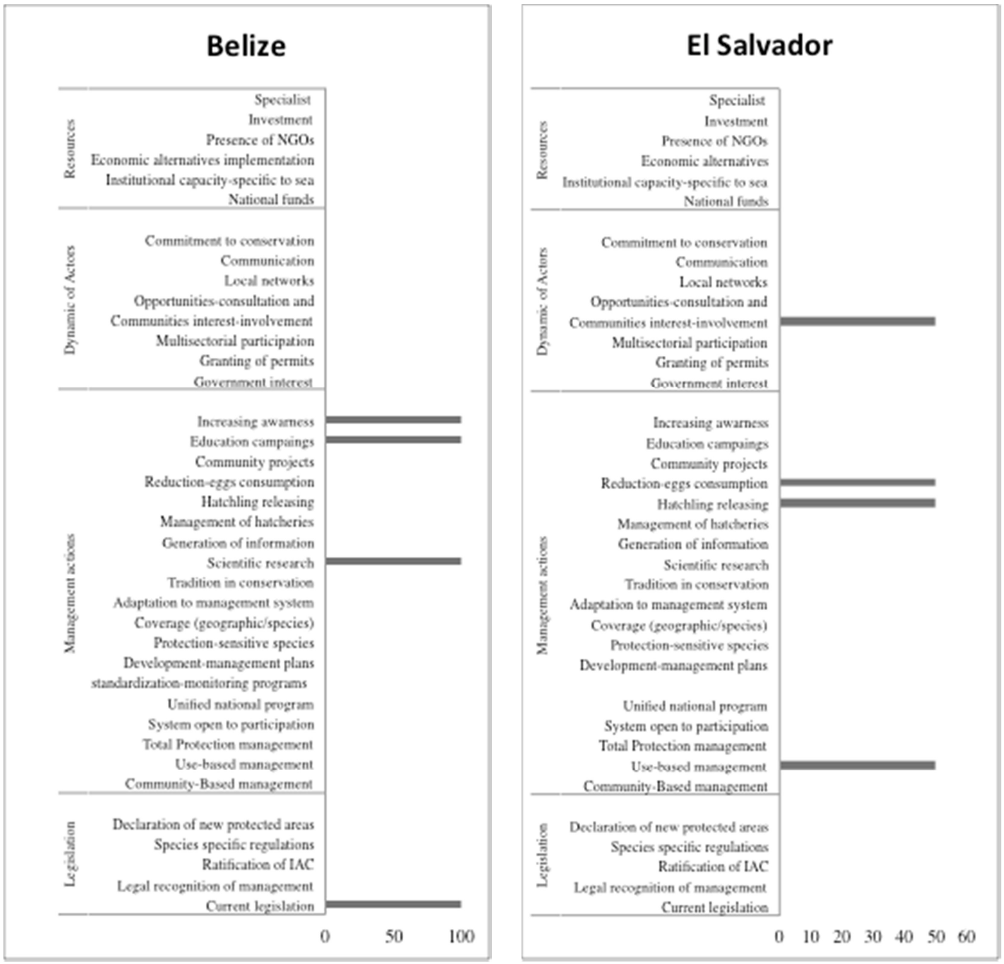


Figure A 4. 2 cont. Summary of responses indicating stakeholders perceptions in regards to strengths in each Mesoamerican country and a summary across countries.

\

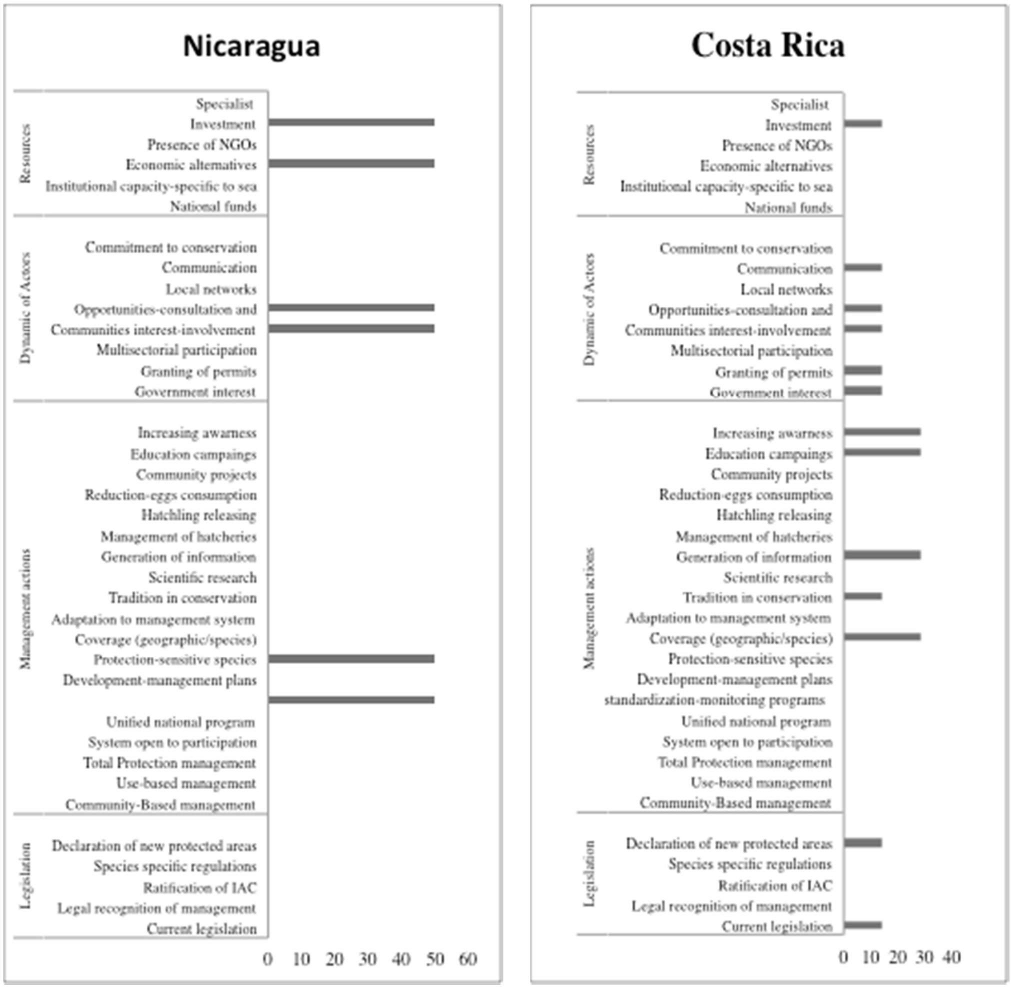


Figure A 4. 2 cont. Summary of responses indicating stakeholders perceptions in regards to strengths in each Mesoamerican country and a summary across countries.

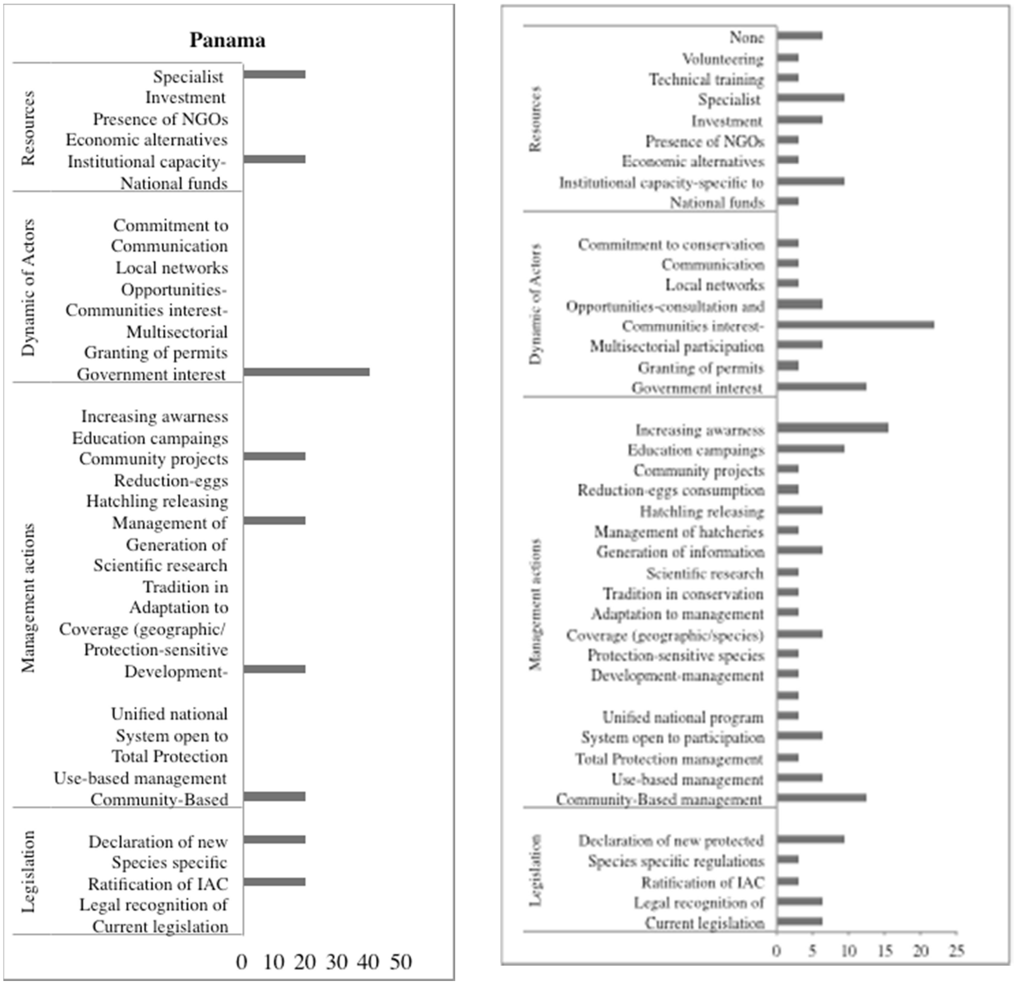


Figure A 4. 2 cont. Summary of responses indicating stakeholders perceptions in regards to strengths in each Mesoamerican country and a summary across countries.

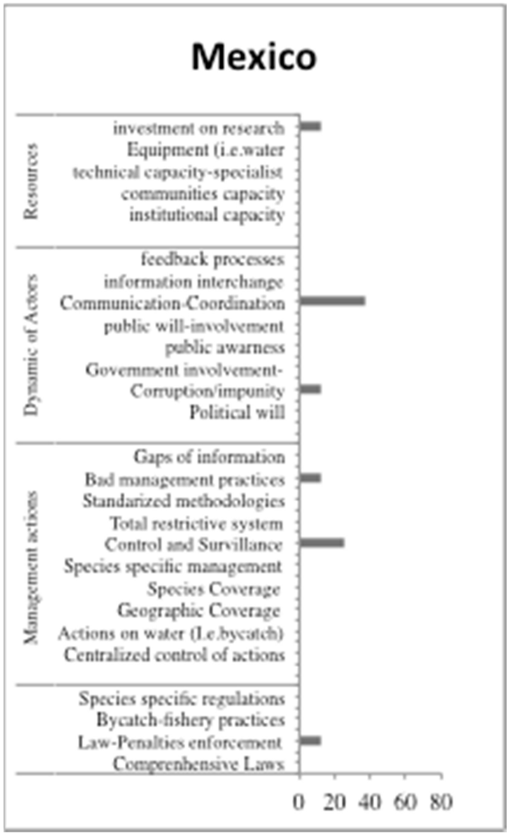


Figure A 4. 3 Summary of responses indicating stakeholders perceptions in regards to weaknesses in each Mesoamerican country and a summary across countries.

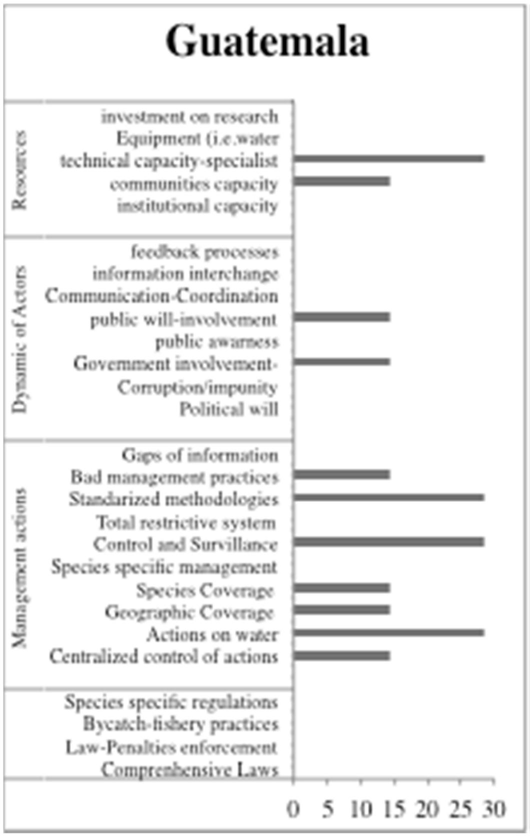


Figure A 4. 3 cont. Summary of responses indicating stakeholders perceptions in regards to weaknesses in each Mesoamerican country and a summary across countries.

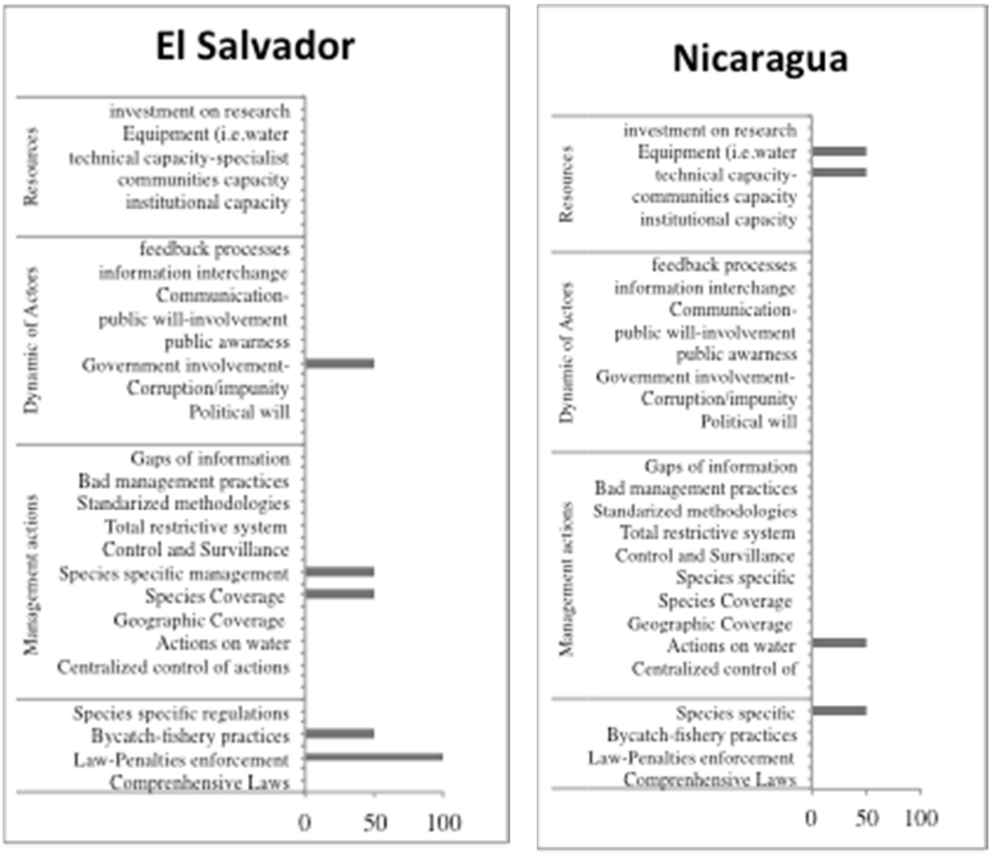


Figure A 4. 3 cont. Summary of responses indicating stakeholders perceptions in regards to weaknesses in each Mesoamerican country and a summary across countries.

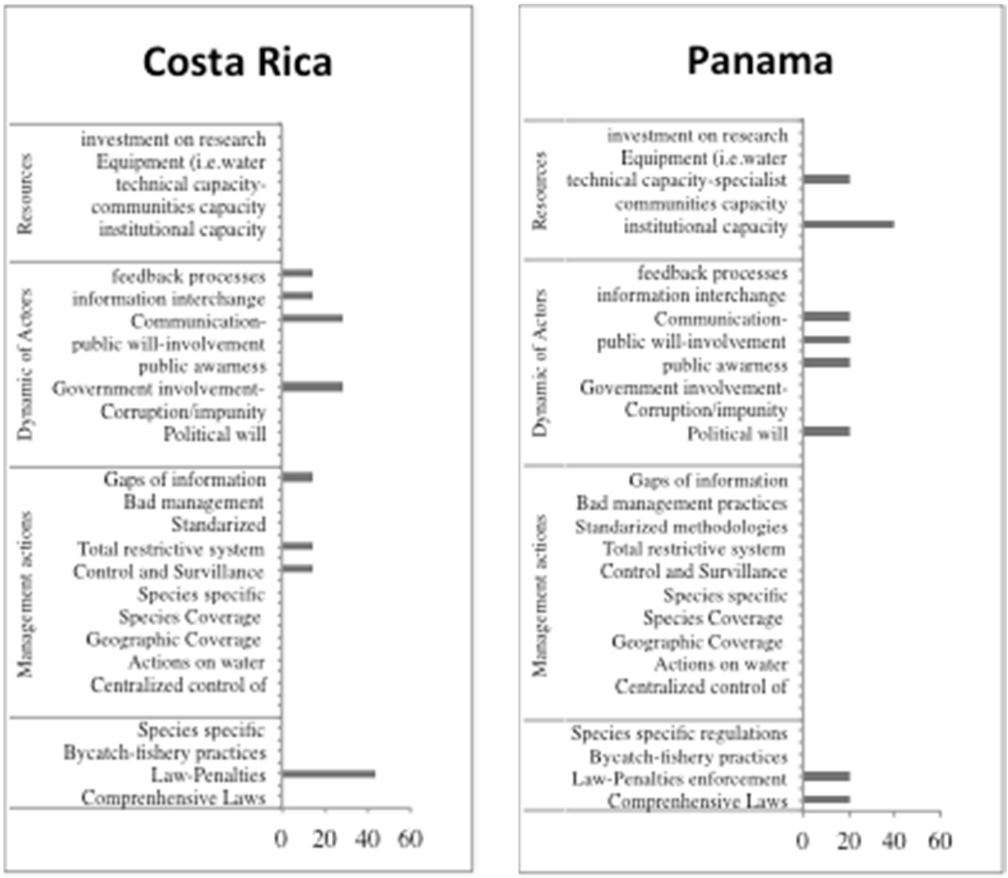


Figure A 4. 3 cont. Summary of responses indicating stakeholders perceptions in regards to weaknesses in each Mesoamerican country and a summary across countries.

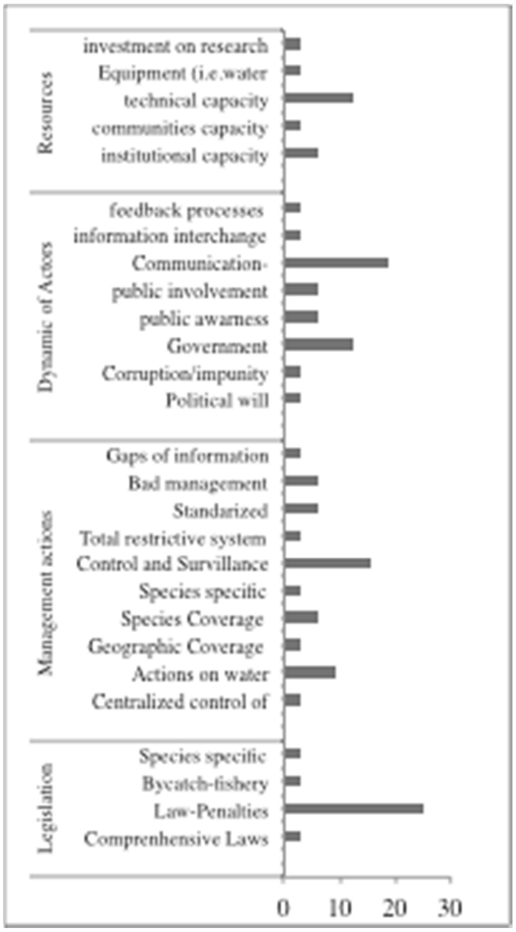


Figure A 4. 3 cont. Summary of responses indicating stakeholders perceptions in regards to weaknesses in each Mesoamerican country and a summary across countries.

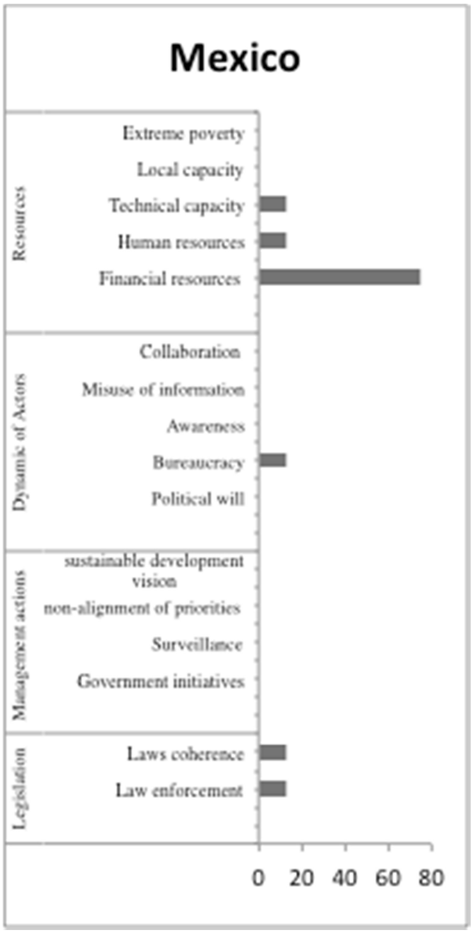


Figure A 4. 4 Summary of responses indicating stakeholders perceptions in regards to limitations in each Mesoamerican country and a summary across countries.

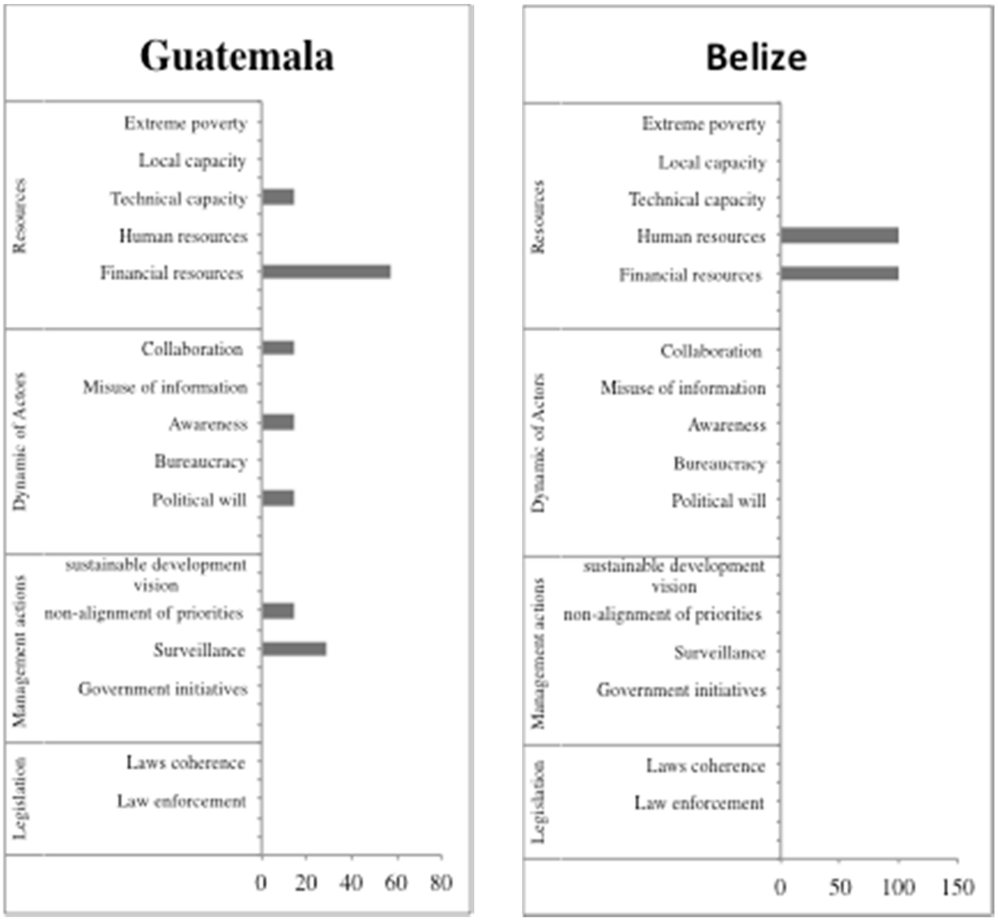
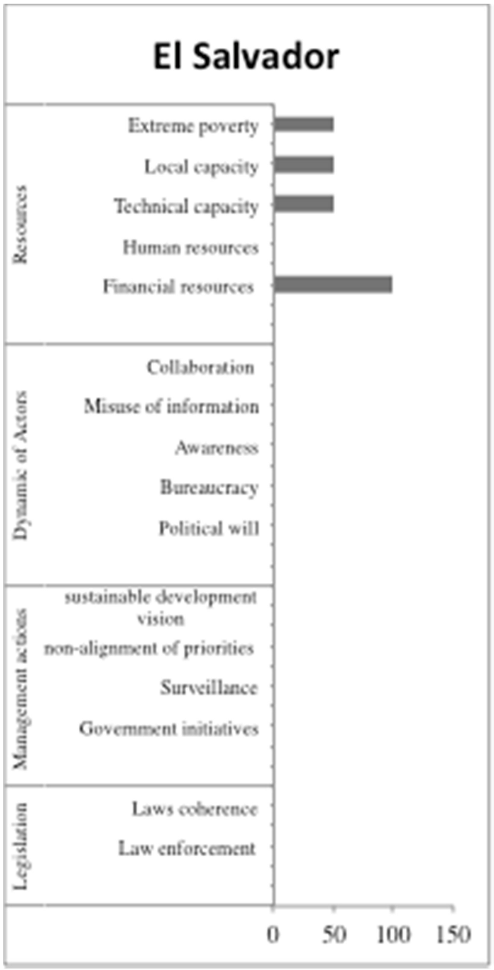


Figure A 4. 4 cont. Summary of responses indicating stakeholders perceptions in regards to limitations in each Mesoamerican country and a summary across countries.



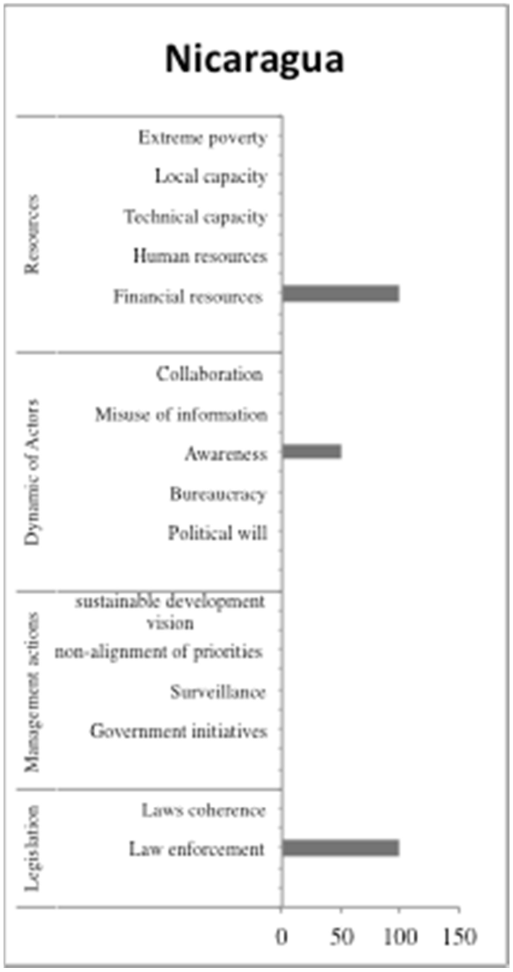


Figure A 4. 4 cont. Summary of responses indicating stakeholders perceptions in regards to limitations in each Mesoamerican country and a summary across countries.

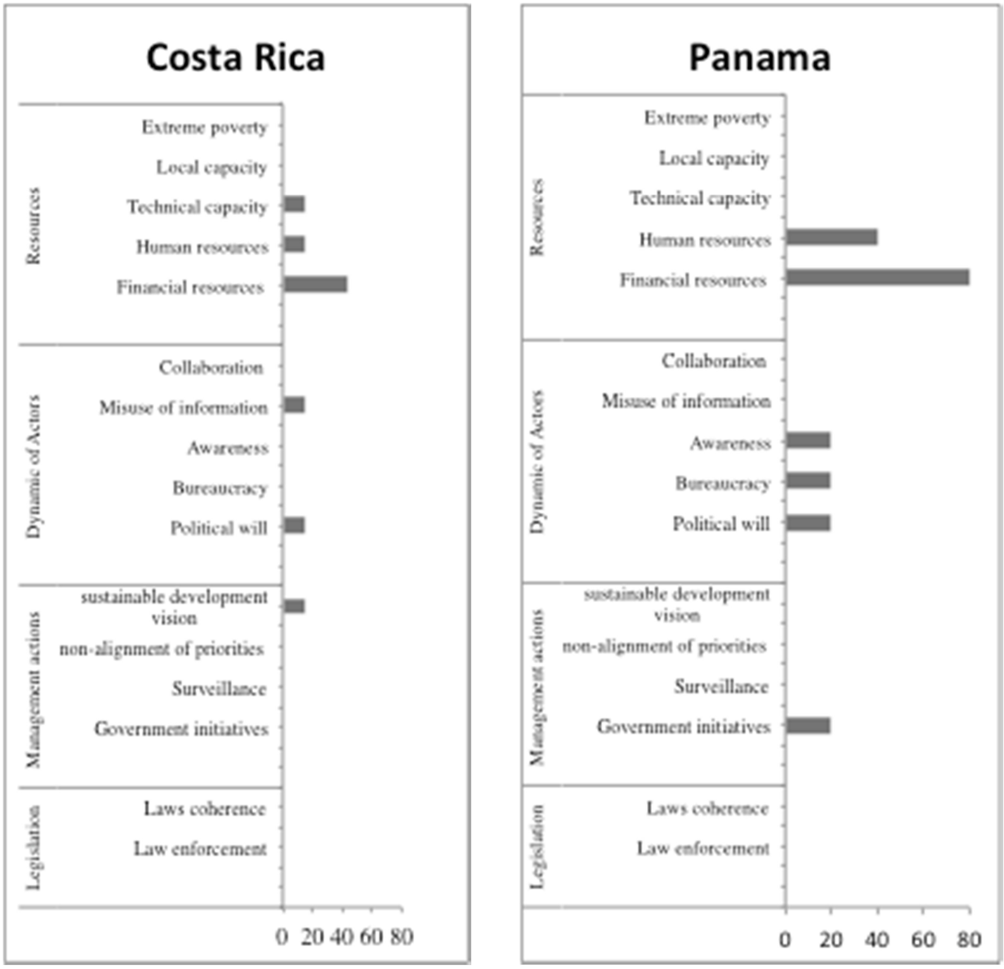


Figure A 4. 4 cont. Summary of responses indicating stakeholders perceptions in regards to limitations in each Mesoamerican country and a summary across countries.

Figure A 4. 4 cont. Summary of responses indicating stakeholders perceptions in regards to limitations in each Mesoamerican country and a summary across countries.

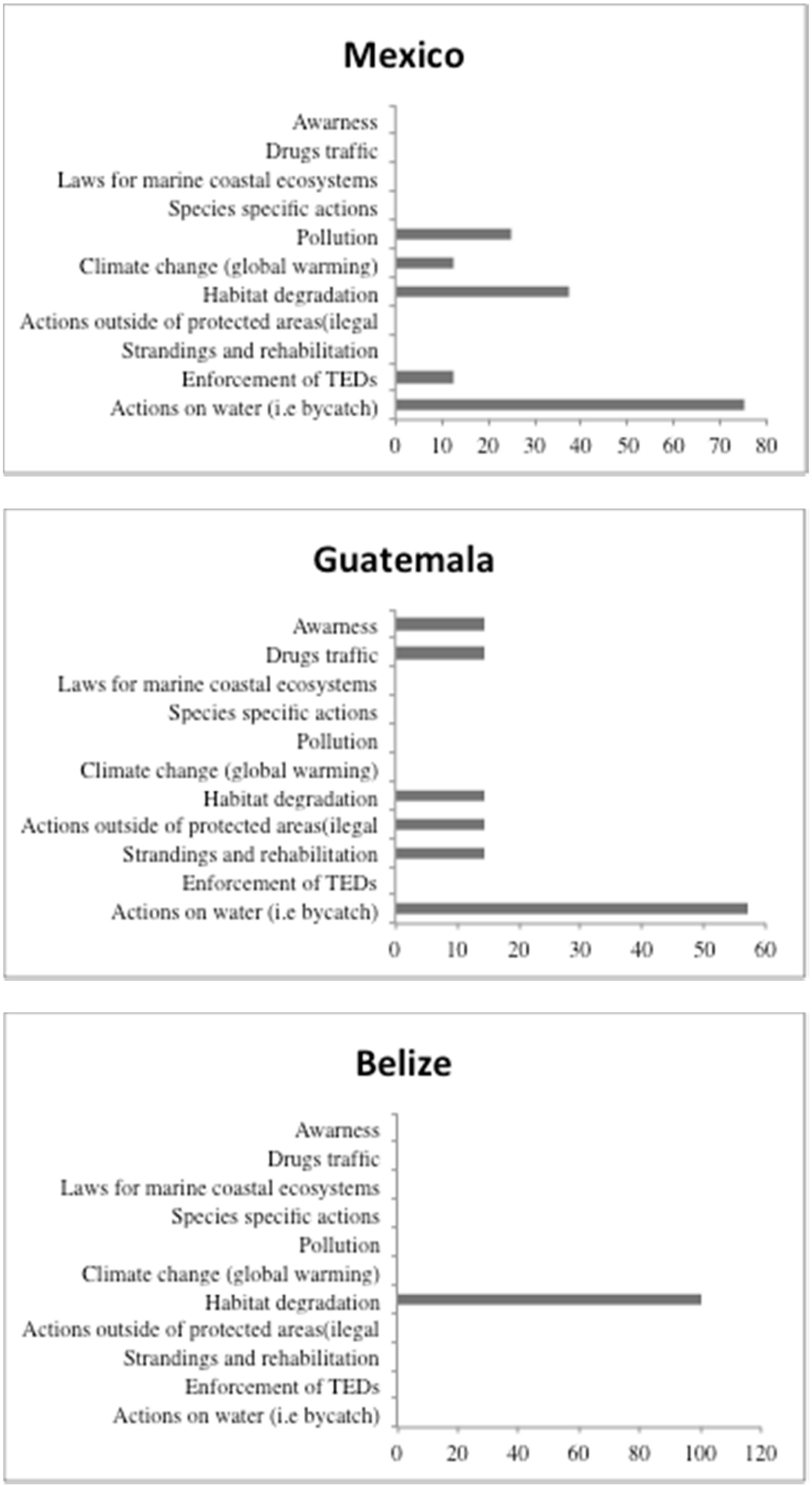
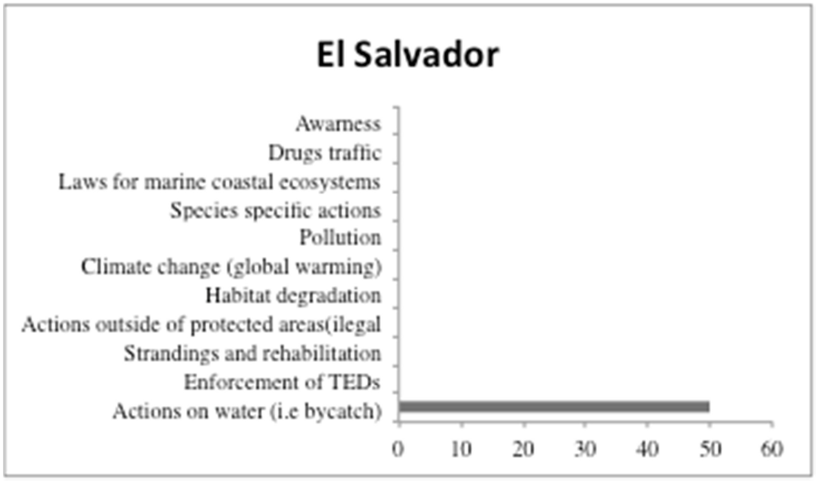
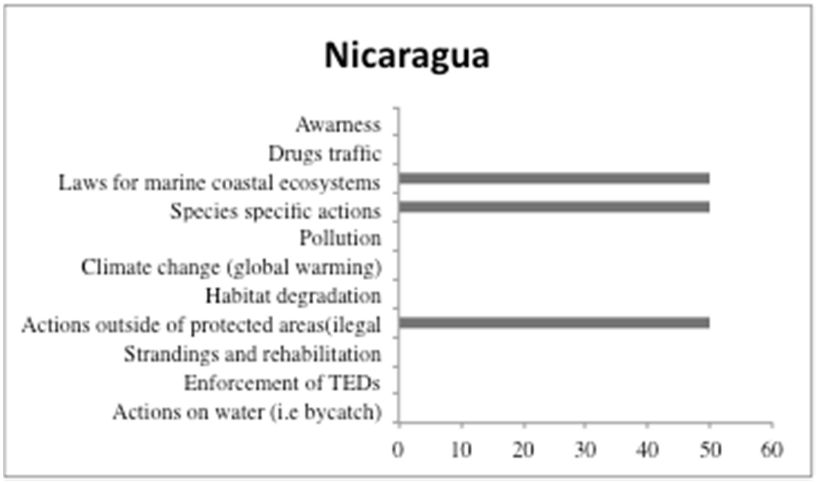


Figure A 4. 5 Summary of responses indicating stakeholders perceptions in regards to non-attended threats for sea turtles in each Mesoamerican country and a summary across countries.





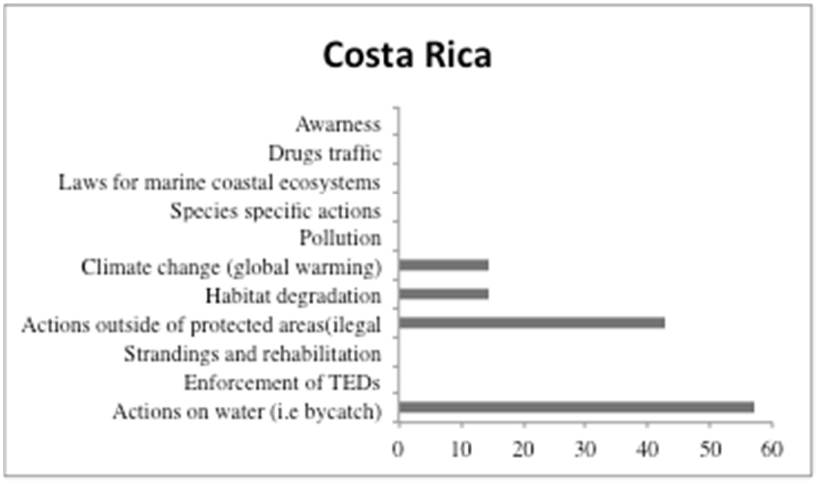
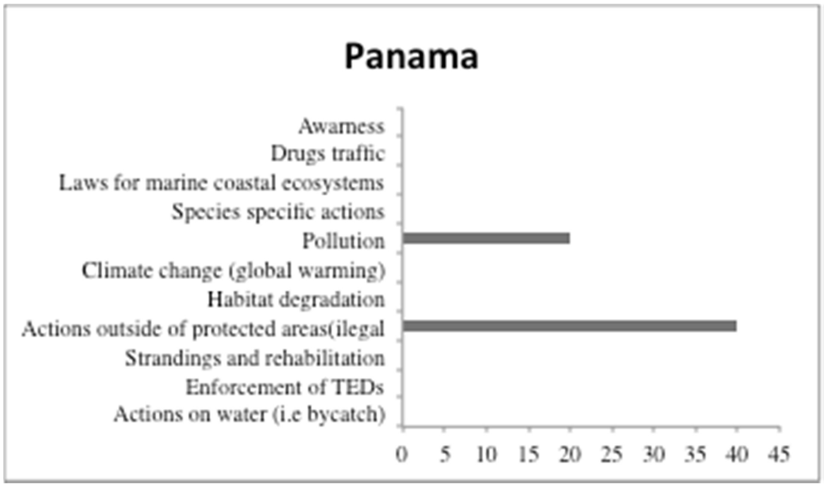


Figure A 4. 5 cont. Summary of responses indicating stakeholders perceptions in regards to non-attended threats for sea turtles in each Mesoamerican country and a summary across countries.



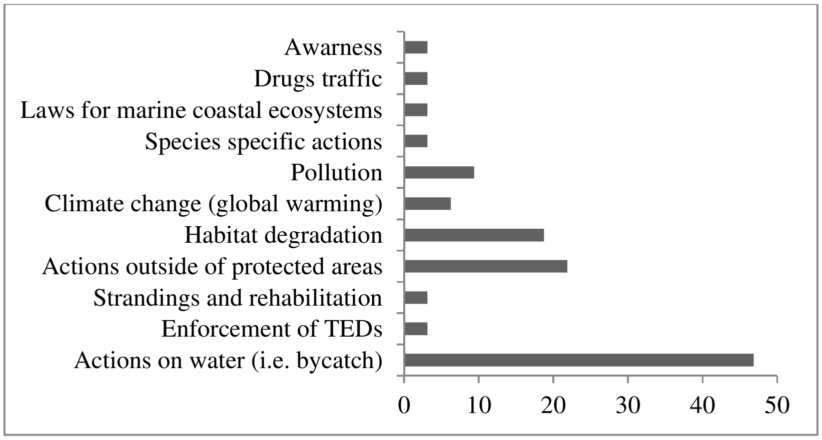


Figure A 4. 5 cont. Summary of responses indicating stakeholders perceptions in regards to non-attended threats for sea turtles in each Mesoamerican country and a summary across countries.

Chapter V:

Conclusions

5.1. Conclusions

This dissertation combines innovative analytical approaches to contribute to a better understanding of olive ridley turtles population in the eastern Pacific within the context of their demographic history and current conservation approaches in the region.

The eastern Pacific is the second most important area for the reproduction of olive ridley turtles worldwide (Fritts *et al.*, 1982). The olive ridley is considered as the most abundant species of sea turtle in the region and the only species that has a regulated use in some countries along the eastern Pacific (Chapter IV). However, important gaps in our understanding of the status of the eastern Pacific population (Plotkin, 2007) impose limitations for management decisions regarding sustainable use. In addition, recent studies indicate that bycatch is an ongoing threat in this region (Dapp *et al.*, 2013; Wallace *et al.*, 2010b). Therefore, data collection at various scales is needed to inform upon the relevant scale for status assessments, and improve conservation efforts while assisting the design and implementation of conservation polices. This need has been generally identified as a priority to enhance sea turtle conservation worldwide (Hamann *et al.*, 2010).

In a comprehensive evaluation of conservation status of sea turtle populations, the study of the consequences of demographic reductions becomes critical. Particularly the quantification of populations' genetic variability, an attribute that allows adaptive responses to environmental changes, and long-term persistence of the species (Crandall *et al.*, 2000). In addition, information from genetic assessments can greatly assist management decisions to achieve recovery of diminished populations. Despite the well documented history of overexploitation and demographic decline of olive ridley turtles during the 60s (Márquez-M *et al.*, 1982), its impact on the genetic variability of the species remained unknown.

Genetic signatures of recent demographic collapses (i.e. during ecological time frames) are generally hard to demonstrate in marine vertebrates (i.e. Busch *et al.*, 2007; Hailer *et al.*, 2006). In sea turtles, studies that explored demographic reductions over recent time frames have failed to detect genetic evidence for bottlenecks (Carreras *et al.*, 2007). Such limitations could be related to uncertainty in variations of mutational processes (particularly for microsatellite markers), low number of molecular markers used, and small sample sizes. This thesis addressed this issue in Chapter II by implementing approaches with different sensitivities and an exhaustive exploration of mutational models. Through the fine-scale characterization of microsatellite DNA variation that chapter revealed clear signatures of recent genetic bottlenecks in a pattern consistent with the history of demographic disequilibria produced by their overexploitation. Chapter II provided important insights on recent genetic erosion and the link between local overexploitation at the nesting site level and its effects across the entire regional metapopulation (i.e. along Mexico's Pacific coast). This was perhaps the first study to detect recent genetic signatures of anthropogenic-driven declines in sea turtles, demonstrating its potential application to other marine species.

Conservation of nesting habitat across the region has expanded during the last decade, and nowadays most of olive ridley nesting sites have some level of protection. However, recovery in certain areas has been slow and historical nesting levels have not been recovered. Chapter II provided important insights in this sense by indicating that recovery of nesting sites might be compromised if declines occur under certain levels. Moreover, it shows that patterns of connectivity at different scales may also limit the potential for recovery of nesting sites.

The genetic connectivity among nesting sites as well as patterns of population structure were investigated at different scales in Chapters II and III. In the past, patterns of population genetic divergence in sea turtles have usually been characterized using mtDNA markers, with most cases indicating clear patterns of structure strongly associated with female natal philopatry to nesting areas (Allard *et al.*, 1994; Bass *et al.*, 1996; Encalada *et al.*, 1996; Dutton *et al.*, 1999). Nonetheless, fine-scale population structure in eastern Pacific olive ridley turtles remained unclear. Patterns of connectivity were assessed using both mitochondrial and nuclear genetic markers from scattered nesting colonies across the region (Bowen and Karl, 2007; Bowen *et al.*, 1998; Briseño-Dueñas, 1998; López-Chávez, 2000), with no evidence of differentiation (except in Baja California Peninsula but that was based on mtDNA genetic variation only; López-Castro and Rocha-Olivares, 2005).

Nevertheless, the scenario of panmixia has prevailed for the species and a lack of further studies has prevented a better understanding of regional connectivity. This thesis addressed this issue with particular attention to unique characteristics of the ecology of the species. It considered the relevance of solitary reproductive sites (most common reproductive mode of the species) to the general genetic diversity of this widely distributed species, widening the scope of attention from massive nesting sites (i.e. *arribada* sites).

Chapter II, and III provided a comprehensive fine-scale analysis of nuclear genetic variation in a vast geographic area in the eastern Pacific and included sampling to more solitary nesting sites. Information from microsatellite markers revealed patterns of genetic connectivity at a scale that is informative for sea turtle management. Results at the broader scale (Chapter III) provided evidence of a clear pattern of population divergence and supported the existence of two previously undetected olive ridley populations in the eastern Pacific. These results confirmed the relevance of the scale in assessments of population connectivity in sea turtles, and suggested that previous studies were limited by a combination of reduced spatial sampling and the lack of characterization of integral genetic variation contained in solitary nesting sites. In addition, the results can contribute to the critical debate on sustainability of consumptive use in the region (Campbell, 2002) by providing information on population structure and contemporary connectivity at different scales, which could also facilitate the assignment of threats to populations.

Another notable discovery was the detection of population structure based on bi-parentally inherited markers, revealing the possible existence of male philopatry to specific mating grounds at regional level. Male philopatry to breeding areas has been suggested for sea turtles (e.g. green turtles in Australia FitzSimmons *et al.*, 1997); this study is the first to indicate this possibility for olive ridley turtles. At smaller scales, male-mediated gene flow showed to be substantial and could be associated to opportunistic behaviour, as in other sea turtle species (Bowen *et al.*, 2005; Karl *et al.*, 1992; Roberts *et al.*, 2004).

Natal philopatry is believed to be the main biological process promoting population structure in sea turtles (Bowen, 1995; FitzSimmons *et al.*, 2000). Such process could not account for the observed patterns seen for olive ridley turtles in Chapters II and III. Findings reported in Chapter III can promote a discussion on the ecological forces driving the evolution of population divergence in sea turtles and on the alternative processes that may be dictating the emergence of reproductive isolation in sea turtles. Evidence of environmental isolation in marine species has increased (Banks *et al.*, 2007; Galindo *et al.*, 2006; Selkoe *et al.*, 2010; Selkoe et al., 2008), and it has been observed that widely distributed species do not necessary exhibit isolation by distance (Wright, 1943), the most common eco-evolutionary pattern in nature (Jenkins *et al.*, 2010). Here, the influence of environmental variability on population structuring of sea turtles is clarified (Chapter III), a result that may also be promoted by selective pressures related with the cost-benefit of dispersal.

Although the influence of oceanography (ocean currents, associated fronts and eddies) on movements and dispersal of hatchlings, juveniles and adults has been previously reported (Chapter IV, Table A 4.3), this thesis demonstrates that population structure may emerge as a result of environmental heterogeneity. To the best of our knowledge this is the first time that such an approach was undertaken and that such a result was obtained. It is then concluded that the environmental spatial variability in the eastern Pacific reduced gene flow in olive ridley turtles. Rather than geographic distance, it is ecological distance that correlates with the neutral genetic differentiation observed. This launches a new paradigm of isolation by ecology (IBE; Cooke *et al.*, 2012; Wang *et al.*, 2013) for the eastern Pacific olive ridley turtles (Chapter III), and confirms the relevance of geographic scales at which ecological landscapes must be studied (Als *et al.*, 2011; Côté *et al.*, 2013) to accurately reveal patterns and processes influencing population connectivity and divergence.

These findings represent a key piece of the puzzle on population structuring in sea turtles and also offer insights into the role of oceanography in the ecology and evolutionary history of sea turtles. Increasing evidence has pointed out that evolutionary adaptations to oceanographic variability by sea turtles may take place by adjusting nesting timing and the selection of strategic nesting sites to increase hatchlings survival (Shillinger *et al.*, 2012). Thus, the inferred influence of oceanographic features in adult dispersal (Chapter III), together with evidence of conserved migration patterns by hatchlings and adult turtles (Hays *et al.*, 2010) suggest that turtles could remain faithful to key oceanographic systems of a certain scale (meso to large-scale) in order to increase fitness. Fidelity to these systems may balance the cost-benefit for mating, long distance, reproductive-feeding migrations and hatchlings dispersal. These findings advance our understanding of how environmental heterogeneity influences key biological processes at different life stages on sea turtles. Consequently, environmental changes associated with climatic warming are of great concern, and may take a new dimension for sea turtles management, as explained in Chapter IV.

In the face of increasing wide-scale threats and bycatch statistics in the region

(Dapp *et al.*, 2013), the southern population of eastern Pacific olive ridleys described in Chapter III could potentially be more vulnerable to wider-scale threats; and current regional connectivity may not facilitate colonization from northern population nesting sites. It is important to note that several eastern Pacific *arribada* nesting beaches are located within the southern population. In the scope of conservation biology, two new MUs are suggested. Recent global frameworks of Regional Management Units (RMUs) for sea turtles proposed that the eastern Pacific olive ridley turtles are comprised of a single RMU (Wallace et al., 2010). In Chapter IV, the re-definition of RMUs and their resilience index for the species in this region is recommended.

On the other hand, results from Chapter III indicated the need to reframe conservation management plans in the region to appropriately reflect the characteristics of the biological system to be protected. Chapter III reinforced large-scale conservation management for sea turtles, confirming the need for collaborative and joint action across the region (Boyd *et al.*, 2008; Lindenmayer *et al.*, 2008). Therefore, a shift to adjust management vision, planning and action must take place in the region. This issue was evaluated in Chapter IV focusing on the analysis of progress in conservation management actions and their performance in order to assess opportunities, capacities and limitations towards regional scale conservation of sea turtles.

Historically conservation management in the Mesoamerican region consisted of localized efforts from unilateral government decisions. The development of a regional legal framework exclusively for sea turtles, The Inter-American

Convention (IAC) for the Protection of Sea Turtles, resulted in significant impacts on sea turtle conservation in the Americas (Campbell *et al.*, 2002; Campbell, 2007a; Namnum, 2002; Tiwari, 2002). However, the IAC by itself could have not ensured the progress of actions in the last 13 years towards a regional action plan. Through the analysis performed in Chapter IV it was possible to assemble a general vision of sea turtle management characteristics in Mesoamerica, and its progress after the IAC was created.

Chapter IV summarized important steps of progress towards a more holistic protection of sea turtles and their habitats through initiatives created to attend increasing threats to sea turtles (e.g. bycatch) based on collaboration of key factors such as governmental agencies, trans-national and local NGOs. This demonstrates that the experience needed for a large-scale management exists, and has the potential to be transferred horizontally and vertically across different scales and levels of the conservation processes. In addition, the region has developed comprehensive legislative frameworks at national levels, and valuable scientific information through research and long-term monitoring programs. This progress, together with the human capacity built through the recent decades, represents opportunities for large-scale management.

Although conservation of sea turtles in the region has increasingly become a multidisciplinary field, communication between scientist and managers is still challenging and requires of proactive feedback loops across the different management levels to ensure that polices and action plans adjust to achieve successful regulation and protection of sea turtles. Through the extensive bibliographic revision, fieldwork observations, and analysis of stakeholders' perceptions in Chapter IV, discernible limitations were identified at different levels of the management cycle (planning, implementation, communication). In particular, communication channels must be strengthened and specific perceived limitations regarding enforcement and surveillance must be efficiently addressed. Even when there is still a long way to go to achieve ameliorated management strategies in the region, results of Chapter IV indicate that the region is prepared to assume the challenge of a large-scale conservation management based on the multiple capacities developed in the last decades. The practical and conceptual reframing of the management vision will have to permeate every level of the conservation management process and will greatly depend on the awareness and commitment of the governments involved.

5.2. Future Research Directions

The findings outlined in this thesis have opened opportunities for further research, including:

- Investigating whether specific seascape features described here contribute to spatial genetic patterns in other sea turtles species in the region and also in other geographic areas.
- Extending sampling of olive ridley nesting colonies to the southern edge of their geographic distribution in the eastern Pacific to identify whether they belong to any of the proposed MUs.
- Using NGS data in studies combining landscape genomics, transcriptomics and candidate gene approaches to identify genomic

signatures associated with putatively adaptive traits in sea turtles.

- Exploring mechanisms by which communication, coordination and cooperation can be improved to enable decision at local level while working towards a large-scale conservation vision. This may require interdisciplinary studies focused on conservation connectivity and the analysis of relationships of governance for the management of sea turtles in the region.

References

ABREU-GROBOIS, A. & PLOTKIN, P. 2008. (IUCN SSC Marine Turtle Specialist Group). *Lepidochelys olivacea. IUCN 2012.* IUCN Red List of Threatened Species. version 2012. 2. <http://www.iucnredlist.org> downloaded 5 May 2012.

AGARWAL, A. 2008. Role of ngos in the protection of environment. *Journal of Environmental Research and Development,* 2.

AGGARWAL, R. K., LALREMRUATA, A., VELAVAN, T. P., SOWJANYA, A. P. & SINGH, L. 2008. Development and characterization of ten novel microsatellite markers from olive ridley sea turtle (*Lepidochelys olivacea*). *Conservation Genetics,* 9**,** 981-984.

AGGARWAL, R. K., VELAVAN, T. P., UDAYKUMAR, D., HENDRE, P. S., SHANKER, K., CHOUDHURY, B. C. & SINGH, L. 2004. Development and characterization of novel microsatellite markers from the olive ridley sea turtle (*Lepidochelys olivacea*). *Marine Ecology Notes,* 4**,** 77-79.

ALBERTO, F., RAIMONDI, P. T., REED, D. C., WATSON, J. R., SIEGEL, D. A., MITARAI, S., COELHO, N. & SERRAO, E. A. 2011. Isolation by oceanographic distance explains genetic structure for Macrocystis pyrifera in the Santa Barbara Channel. *Molecular Ecology,* 20**,** 2543-2554.

ALLARD, M., W., MIYAMOTO, M., M., BJORNDAL, K., A., BOLTEN, A., B. & BOWEN, B., W. 1994. Support for natal homing in green turtles from mitochondrial DNA sequences. Lawrence, KS, ETATS-UNIS: American Society of Ichthyologists and Herpetologists.

ALLENDORF, F. W., ENGLAND, P. R., LUIKART, G., RITCHIE, P. A. & RYMAN, N. 2008. Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution,* 23**,** 327-337.

ALS, T. D., HANSEN, M. M., MAES, G. E., CASTONGUAY, M., RIEMANN, L., AARESTRUP, K. I. M., MUNK, P., SPARHOLT, H., HANEL, R. & BERNATCHEZ, L. 2011. All roads lead to home: panmixia of European eel in the Sargasso Sea. *Molecular Ecology* 20**,** 1346.

AMADOR, J. A., ALFARO, E. J., LIZANO, O. G. & MAGANA, V. O. 2006. Atmospheric forcing of the eastern tropical Pacific: A review. *Progress In Oceanography,* 69**,** 101-142.

AMARAL, A. R., BEHEREGARAY, L. B., BILGMANN, K., BOUTOV, D., FREITAS, L., ROBERTSON, K. M., SEQUEIRA, M., STOCKIN, K. A., COELHO, M. M. & M∂LLER, L. M. 2012. Seascape genetics of a globally distributed, highly mobile marine mammal: The short-beaked Common Dolphin (Genus Delphinus). *PLoS ONE,* 7**,** e31482.

ARAUZ, R. M., VARGAS, R., NARANJO, I. & GAMBOA, C. Analysis of the incidental capture and mortality of sea turtles in the shrimp fleet of pacific Costa Rica. *In:* EPPERLY, S. P. & BRAUN, J., eds. Proceedings of the Seventeenth annual Sea turtle Symposium, 1996. NOAA Technical Memorandum. .

AVISE, J. C. 1989. A role for molecular genetics in the recognition and conservation of endangered species. *Trends in Ecology & Evolution,* 4**,** 279-281.

AVISE, J. C. 1995. Mitochondrial DNA polymorphism and a connection between genetics and demography of relevance to Ccnservation. *Conservation Biology,* 9**,** 686-690.

BAILEY, H., BENSON, S. R., SHILLINGER, G. L., BOGRAD, S. J., DUTTON, P. H., ECKERT, S. A., MORREALE, S. J., PALADINO, F. V., EGUCHI,

T., FOLEY, D. G., BLOCK, B. A., PIEDRA, R., HITIPEUW, C., TAPILATU, R. F. & SPOTILA, J. R. 2012. Identification of distinct movement patterns in Pacific leatherback turtle populations influenced by ocean conditions. *Ecological Applications,* 22**,** 735-747.

BAILLEUL, F., COTTE, C. & GUINET, C. 2010. Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Marine Ecology Progress Series,* 408**,** 251-264.

BALAZS, G. H. & CHALOUPKA, M. 2004. Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock. *Biological Conservation,* 117**,** 491-498.

BALLANCE, L. T., PITMAN, R. L. & FIEDLER, P. C. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: A review. *Progress In Oceanography,* 69**,** 360-390.

BANKS, S. C., LING, S. D., JOHNSON, C. R., PIGGOTT, M. P., WILLIAMSON, J. E. & BEHEREGARAY, L. B. 2010. Genetic structure of a recent climate change-driven range extension. *Molecular Ecology,* 19**,** 2011-2024.

BANKS, S. C., PIGGOTT, M. P., WILLIAMSON, J. E., BOVE, U., HOLBROOK, N. J. & BEHEREGARAY, L. B. 2007. Oceanic variability and coastal topography shape genetic structure in a long-dispersing sea urchin. *Ecology,* 88**,** 3055-3064.

BARRAGÁN, A. R. 2012. Nesting beach conservation in the Mexican Pacific: the bridge between sea turtles and people. *In:* SEMINOFF, J. A. & WALLACE, B. P. (eds.) *Sea turtles of the eastern Pacific: Advances in* *research and conservation.* Tucson: Arizona-Sonora Desert Museum Studies in Natural History. University of Arizona Press.

BASS, A., LAGUEUX, C. & BOWEN, B. 1998. Origin of green turtles *Chelonia mydas* at "sleeping rocks" of the northeast coast of Nicaragua. *Copeia***,** 1064-1069.

BASS, A. L., GOOD, D. A., BJORNDAL, K. A., RICHARDSON, J. I., HILLIS, Z. M., J.A., H. & BOWEN, B. W. 1996. Testing models of female reproductive migratory behaviour and population structure in the Caribbean hawksbill turtle, *Eretmochelys imbricata*, with mtDNA sequences. *Molecular Ecology,* 5**,** 321-328.

BEAVERS, S. C. & CASSANO, E. R. 1996. Movements and dive behavior of a male sea turtle (*Lepidochelys olivacea*) in the Eastern Tropical Pacific. *Journal of Herpetology,* 30**,** 97-104.

BEHEREGARAY, L. B., CIOFI, C., GEIST, D., GIBBS, J. P., CACCONE, A. & POWELL, J. R. 2003. Genes record a prehistoric volcano eruption in the Galapagos. *Science,* 302**,** 75.

BELKHIR, K., BORSA, P, CHIKHI, L, RAUFASTE, N, BONHOMME, F 2004. GENETIX 4.05, logiciel sous Windows pour la genetique des populations. Laboratoire Genome, Populations, Interactions, CNRSUMR5171, Universite de Montpellier II, Montpellier, France.

BENSON, S. R., EGUCHI, T., FOLEY, D. G., FORNEY, K. A., BAILEY, H., HITIPEUW, C., SAMBER, B. P., TAPILATU, R. F., REI, V., RAMOHIA, P., PITA, J. & DUTTON, P. H. 2011. Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. *Ecosphere,* 2**,** art84.

BERNARDO, J. & PLOTKIN, P. T. 2007. An evolutionary perspective on the arribada phenomenon and reproductive behavioural polymorphism of olive ridley sea turtles (*Lepidochelys olivacea*). *In:* PLOTKIN, P. T. (ed.) *Biology and conservation of ridley sea turtles.* Baltimore, MD: Johns Hopkins University Press.

BJORNDAL, K., BOLTEN, A. & TROËNG, S. 2005. Population structure and genetic diversity in green turtles nesting at Tortuguero, Costa Rica, based on mitochondrial DNA control region sequences. *Marine Biology,* 147**,** 1449-1457.

BJORNDAL, K. A. 1981. *Biology and conservation of sea turtles. Proceedings of the World Conference on Sea Turtle Conservation,* Washington, Smithsonian Institute.

BJORNDAL, K. A. & JACKSON, B. C. 2003. IU Roles of sea turtles in marine ecosystems: reconstructing the past. *In:* LUTZ, P. L. & MUSICK, J. A. (eds.) *The Biology of Sea Turtles.* CRC Marine Science Series. CRC press.

BLUMENTHAL, J., M. , JONI, L. S., CATHERINE, D. B., TIMOTHY, J. A., GINA, E.-P., MICHAEL, S. C., ANNETTE, C. B. & BRENDAN, J. G. 2006. Satellite tracking highlights the need for international cooperation in marine turtle management. *Endangered Species Research,* 2**,** 51-61.

BOST, C. A., COTTÉ, C., BAILLEUL, F., CHEREL, Y., CHARRASSIN, J. B., GUINET, C., AINLEY, D. G. & WEIMERSKIRCH, H. 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems,* 78**,** 363-376.

BOUCHARD, S. S. & BJORNDAL, K. A. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology,* 81**,** 2305-2313.

BOWEN, B., AVISE, J. C., RICHARDSON, J. I., MEYLAN, A. B., MARGARITOULIS, D. & HOPKINS-MURPHY, S. R. 1993. Population structure of loggerhead turtles (*Caretta caretta*) in the northwestern Atlantic Ocean and Mediterranean sea. *Conservation Biology,* 7**,** 834-844.

BOWEN, B. W. 1995. Tracking marine turtles with genetic markers voyages of the ancient mariners. *BioScience,* 45**,** 528-534.

BOWEN, B. W. & AVISE, J. C. 1995. Conservation genetics of marine turtles. *In:* HAMRICK, J. C. A. Y. J. L. (ed.) *Conservation Genetics: case histories from nature.* U. S. A. : Chapman and Hall.

BOWEN, B. W., BASS, A. L., CHOW, S.-M., BOSTROM, M., BJORNDAL, K. A., BOLTEN, A. B., OKUYAMA, T., BOLKER, B. M., EPPERLY, S., LACASELLA, E., SHAVER, D., DODD, M., HOPKINS- MURPHY, S. R., MUSICK, J. A., SWINGLE, M., RANKIN-BARANSKY, K., TEAS, W., WITZELL, W. N. & DUTTON, P. H. 2004. Natal homing in juvenile loggerhead turtles (*Caretta caretta*). *Molecular Ecology,* 13**,** 3797-3808.

BOWEN, B. W., BASS, A. L., SOARES, L. & TOONEN, J. 2005. Conservation implications of complex population structure: lessons from the loggerhead turtle (*Caretta caretta*). *Molecular Ecology,* 34**,** 2389-2402.

BOWEN, B. W., CLARK, A. M., ABREU-GROBOIS, F. A., CHAVES, A., REICHART, H. A. & FERL, R. J. 1998. Global phylogeography of the ridley sea turtles (*Lepidochelys* spp.) as inferred from mitochondrial DNA sequences. *Genetica,* 101**,** 179-189.

BOWEN, B. W., GRANT, W. S., HILLIS-STARR, Z., SHAVER, D. J., BJORNDAL, K. A., BOLTEN, A. B. & BASS, A. L. 2007. Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. 16**,** 49-60.

BOWEN, B. W., KAMEZAKI, N., LIMPUS, C. J., HUGHES, G. R., MEYLAN, A. B. & AVISE, J. C. 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution,* 48**,** 1820-1828.

BOWEN, B. W. & KARL, S. A. 2007. Population genetics and phylogeography of sea turtles. *Molecular Ecology,* 16**,** 4886-4907.

BOWEN, B. W., MEYLAN, A. B., ROSS, J. P., LIMPUS, C. J., BALAZ, G. H. & AVISE, J. C. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. *Evolution,* 46**,** 865-881.

BOWEN, B. W. & WITZEL, W. N. Sea Turtle conservation genetics. *In:* BOWEN, B. W. & WITZELL, W. N., eds. Proceedings of the international Symposium on Sea Turtle Conservation Genetics, 1996 Miami, Florida. Septiembre 12-14. NOAA Technical Memorandum NMFS-SEFSC, 1-7.

BOWLER, D. E. & BENTON, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews,* 80**,** 205-225.

BOYD, C., BROOKS, T. M., BUTCHART, S. H. M., EDGAR, G. J., DA FONSECA, G. A. B., HAWKINS, F., HOFFMANN, M., SECHREST, W., STUART, S. N. & VAN DIJK, P. P. 2008. Spatial scale and the conservation of threatened species. *Conservation Letters,* 1**,** 37-43.

BOYLE, M. C., FITZSIMMONS, N. N., LIMPUS, C. J., KELEZ, S., VELEZ-ZUAZO, X. & WAYCOTT, M. 2009. Evidence for transoceanic migrations by loggerhead sea turtles in the southern Pacific Ocean. *Proceedings of the Royal Society B-Biological Sciences,* 276**,** 1993-1999.

BRISEÑO-DUEÑAS, R. 1998. *Variación genética en la región control del ADN mitocondrial de poblaciones de la tortuga golfina, Lepidochelys olivacea, en el Pacífico oriental y las implicaciones para su conservación.* Master Thesis, Universidad Autonoma de Sinaloa.

BRISEÑO-DUEÑAS, R. Situacion actual de la tortuga golfina en playas de anidacion solitaria en el pacifico. Reunion nacional sobre conservacion de tortugas marinas, 25-28 Noviembre 2007 Veracruz, Mexico.

BRODERICK, A. C., COYNE, M. S., FULLER, W. J., GLEN, F. & GODLEY, B. J. 2007. Fidelity and over-wintering of sea turtles. *Proceedings of the Royal Society B-Biological Sciences,* 274**,** 1533-1538.

BRODERICK, D. & MORITZ, C. Hawksbill breeding and foraging populations in the Indo-Pacific region. *In:* BOWEN, B. W. & WITZELL, W. N., eds. Proceedings of the International Symposium on Sea Turtle Conservation Genetics, Septiembre 12-14 1996 Miami, Florida. NOAA Technical Memomorandum. NMFSSEFSC, 119-128.

BRODERICK, D., MORITZ, C., MILLER, J. D., GUINEA, M., PRINCE, R. I. T. & LIMPUS, C. J. 1994. Genetic studies of the Hawksbill turtle *Eretmochelys imbricata*: evidence for multiple stocks in Australian waters. *Pacific Conservation Biology,* 1**,** 123-131.

BUSCH, J. D., WASER, P. M. & DEWOODY, J. A. 2007. Recent demographic bottlenecks are not accompanied by a genetic signature in banner-tailed kangaroo rats (*Dipodomys spectabilis*). *Molecular Ecology,* 16**,** 2450-2462.

CAMPBELL, L. & CORNWELL, M. 2008. Human dimensions of bycatch reduction technology: current assumptions and directions for future research. *Endangered Species Research,* 5**,** 325-334.

CAMPBELL, L. M. 1998. Use them or lose them? Conservation and the consumptive use of marine turtle eggs at Ostional, Costa Rica. *Environmental Conservation,* 25**,** 305-319.

CAMPBELL, L. M. 2002. Science and sustainable use: views of marine turtle conservation experts. *Ecological Applications,* 12**,** 1229-1246.

CAMPBELL, L. M. 2003. Contemporary culture, use, and conservation of sea turtles. *In:* LUTZ, P. A., MUSICK, J. A. & WYNEKEN, J. (eds.) *The Biology of Sea Turtles Vol. 2.* Boca Raton, Florida: crc Press.

CAMPBELL, L. M. 2007a. Local conservation practice and global discourse: A political ecology of sea turtle conservation. *Annals of the Association of American Geographers,* 97**,** 313-334.

CAMPBELL, L. M. 2007b. Understanding human use of olive ridleys: implications for conservation. *In:* PLOTKIN, P. T. (ed.) *Biology and Conservation of Ridley Sea Turtles.* Baltimore: The Jonhs Hopkins University Press.

CAMPBELL, L. M., GODFREY, M. H. & DRIF, O. 2002. Community‐based conservation via global legislation? Limitations of the inter‐American convention for the protection and conservation of sea turtles. *Journal of International Wildlife Law & Policy,* 5**,** 121-143.

CAMPBELL, L. M., SILVER, J. J., GRAY, N. J., RANGER, S., BRODERICK, A., FISHER, T., GODFREY, M. H., GORE, S., JEFFERS, J., MARTIN, C., MCGOWAN, A., RICHARDSON, P., SASSO, C., SLADE, L. & GODLEY, B. 2009. Co-management of sea turtle fisheries: Biogeography versus geopolitics. *Marine Policy,* 33**,** 137-145.

CARR, A. 1987. New perspectives on the pelagic stage of sea turtle development. *Conservation Biology,* 1**,** 103-121.

CARR, A. 2002. Notes on the zoogeography of the Atlantic sea turtles of the genus Lepidochelys (Reprinted from Rev. Biol. Trop. vol 5, pg 45-61, 1957). *Revista De Biologia Tropical,* 50**,** 717-733.

CARR, A. F. & OGREN, L. 1960. The ecology and migrations of sea turtles. 4. The green turtle in the Caribbean Sea. . *Bulletin of the American Museum of Natural History* 1–48.

CARRERAS, C., PASCUAL, M., CARDONA, L., AGUILAR, A., MARGARITOULIS, D., REES, A., TURKOZAN, O., LEVY, Y., GASITH, A., AUREGGI, M. & KHALIL, M. 2007. The genetic structure of the loggerhead sea turtle (*Caretta caretta*) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. *Conservation Genetics,* 8**,** 761-775.

CARRERAS, C., PASCUAL, M., CARDONA, L., MARCO, A., BELLIDO, J. J., CASTILLO, J. J., TOMAS, J., ANTONIO RAGA, J., SANFELIX, M., FERNANDEZ, G. & AGUILAR, A. 2011. Living together but remaining apart: Atlantic and Mediterranean loggerhead sea turtles (*Caretta caretta*) in shared feeding grounds. *Journal of Heredity,* 102**,** 666-677.

CASH, D. W., ADGER, W., BERKES, F., GARDEN, P., LEBEL, L., OLSSON, P., PRITCHARD, L. & YOUNG, O. 2006. Scale and cross-scale dynamics: governance and information in a multilevel world. *Ecology and Society,* 11**,** 8.

CASH, D. W. & MOSER, S. C. 2000. Linking global and local scales: Designing dynamic assessment and management processes. *Global Environmental Change,* 10**,** 109-120.

CHACÓN, D. & ARAUZ, R. 2001. Diagnóstico regional y planificación estratégica para la conservación de las tortugas marinas en centroamérica. *Red Regional para la Conservación de las Tortugas Marinas en Centroamérica. Fundación Acceso y el Programa Regional Ambiental para Centroamérica USAID / G-CAP*.

CHALOUPKA, M. & MUSICK, J. A. 1996. Age, growth, and population dynamics. *In:* LUTZ, P. L. & MUSICK, J. A. (eds.) *The Biology of Sea Turtles.* Boca Raton, Florida: CRC press.

CHASSIN-NORIA, O., ABREU-GROBOIS, A., DUTTON, P. H. & OYAMA, K. 2004. Conservation genetics of the east Pacific green turtle (*Chelonia mydas*) in Michoacan, Mexico. *Genetica,* 121**,** 195-206.

CLARK, P. U., PISIAS, N. G., STOCKER, T. F. & WEAVER, A. J. 2002. The role of the thermohaline circulation in abrupt climate change. *Nature,* 415**,** 863.

CLARK, S. G., PICARD, C. & HOHL, A. 2010. Large scale conservation in the common interest: an overview. *In:* SUSAN G. CLARK, A. H., CATHERINE PICARD, AND DARCY NEWSOME (ed.) *Large Scale*

Conservation: Integrating science, Management, and Policy in the Common Interest. Yale School of Foresty & Environmental Studies.

CLIFFTON, K., CORNEJO, D. O. & FELGER, R. S. 1982. Sea turtles of the pacific coast of Mexico. *In:* BJORNDAL, K. A. (ed.) *Biology and Conservation of sea turtles.* Washington DC: Smithsonian Institution Press.

CLIFFTON, K., CORNEJO, D. O. & FELGER, R. S. 1995. Sea turtles of the pacific coast of Mexico. *In:* BJORNDAL, K. A. (ed.) *Biology and conservation of sea turtle.* Revise edition ed. Washington D.C.: Smithsonian Institution Press.

COLLINS, M., AN, S.-I., CAI, W., GANACHAUD, A., GUILYARDI, E., JIN, F.-F., JOCHUM, M., LENGAIGNE, M., POWER, S., TIMMERMANN, A., VECCHI, G. & WITTENBERG, A. 2010. The impact of global warming on the tropical Pacific Ocean and El Nino. *Nature Geoscience,* 3**,** 391-397.

COOK, C. N., MASCIA, M. B., SCHWARTZ, M. W., POSSINGHAM, H. P. & FULLER, R. A. 2013. Achieving conservation science that bridges the knowledge–action boundary. *Conservation Biology,* 27**,** 669-678.

COOKE, G. M., CHAO, N. L. & BEHEREGARAY, L. B. 2012. Divergent natural selection with gene flow along major environmental gradients in Amazonia: insights from genome scans, population genetics and phylogeography of the characin fish Triportheus albus. *Molecular Ecology,* 21**,** 2410-2427.

CORNELIUS, S. E., ARAUZ, R., FRETEY, J., GODFREY, M. H., MARQUEZ-M, R. & SHANKER, K. 2007. Effect of land-based harvest of Lepidochelys. *In:* PLOTKIN, P. T. (ed.) *Biology and Conservation of Ridley Sea Turtles.* Baltimore Johns Hopkins University Press.

CORNELIUS, S. E. & ROBINSON-CLARK, D. C. 1986. Post-nesting movements of female olive ridley turtles tagged in Costa Rica. Movimientos post-anidamiento de la hembra de las tortugas lora marcadas en Costa Rica. *Vida Silvestre Neotropical,* 1**,** 12-23.

CORNELIUS, S. E. A., R., FRETEY, J., GODFREY, M.H., MÁRQUEZ-M., R. AND SHANKER, K. 2007. Effect of land-based harvest of Lepidochelys. *In:* P.T., P. (ed.) *Biology and Conservation of Ridley Sea Turtles.* Baltimore, MD: Johns Hopkins University Press.

CORNUET, J. M. & LUIKART, G. 1996. Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics,* 144**,** 2001-2014.

CÔTÉ, C. L., GAGNAIRE, P.-A., BOURRET, V., VERREAULT, G., CASTONGUAY, M. & BERNATCHEZ, L. 2013. Population genetics of the American eel (*Anguilla rostrata*): FST = 0 and North Atlantic Oscillation effects on demographic fluctuations of a panmictic species. *Molecular Ecology,* 22**,** 1763-1776.

CRANDALL, K. A., BININDA-EMONDS, O. R. P., MACE, G. M. & WAYNE, R. K. 2000. Considering evolutionary processes in conservation biology. *Trends in Ecology & Evolution,* 15**,** 290-295.

DAPP, D., ARAUZ, R., SPOTILA, J. R. & O'CONNOR, M. P. 2013. Impact of Costa Rican longline fishery on its bycatch of sharks, stingrays, bony fish and olive ridley turtles (*Lepidochelys olivacea*). *Journal of Experimental Marine Biology and Ecology,* 448**,** 228-239.

DETHMERS, K. M., BRODERICK, D., MORITZ, C., FITZSIMMONS, N. N., LIMPUS, C. J., LAVERY, S., WHITING, S., GUINEA, M., PRINCE, R. J.

T. & KENNETT, R. 2006. The genetic structure of Australasian green turtles (*Chelonia mydas*): exploring the geographical scale of genetic exchange. *Molecular Ecology,* 15**,** 3931-3946.

DONEY, S. C., RUCKELSHAUS, M., EMMETT DUFFY, J., BARRY, J. P., CHAN, F., ENGLISH, C. A., GALINDO, H. M., GREBMEIER, J. M., HOLLOWED, A. B., KNOWLTON, N., POLOVINA, J., RABALAIS, N. N., SYDEMAN, W. J. & TALLEY, L. D. 2012. Climate change impacts on marine ecosystems. *Annual Review of Marine Science,* 4**,** 11-37.

DUTTON, P., RODEN, S., STEWART, K., LACASELLA, E., TIWARI, M., FORMIA, A., THOMÉ, J., LIVINGSTONE, S., ECKERT, S., CHACON-CHAVERRI, D., RIVALAN, P. & ALLMAN, P. 2013. Population stock structure of leatherback turtles (*Dermochelys coriacea*) in the Atlantic revealed using mtDNA and microsatellite markers. *Conservation Genetics,* 14**,** 625-636.

DUTTON, P. H., BOWEN, B. W., OWEN, D. W., BARRAGAN, A. & DAVIS, S. K. 1999. Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). *Journal of Zoology***,** 397-409.

DUTTON, P. H., HITIPEUW, C., ZEIN, M., BENSON, S. R., PETRO, G., PITA, J., REI, V., AMBIO, L. & BAKARBESSY, J. 2007. Status and genetic structure of nesting populations of leatherback turtles (*Dermochelys coriacea*) in the western Pacific. *Chelonian Conservation and Biology,* 6**,** 47-53.

DUTTON, P. H. & SQUIRES, D. 2008. Reconciling biodiversity with fishing: a holistic strategy for Pacific sea turtle recovery. *Ocean Development & International Law,* 39**,** 200-222.

DUTTON, P. H., SQUIRES, D. & MAHFUZUDDIN, A. 2011. *A holistic strategy for Pacific sea turtle conservation,* Honolulu, Hawaii, USA, University of Hawaii Press.

EDGAR, G. J., SAMSON, C. R. & BARRETT, N. S. 2005. Species extinction in the marine environment: Tasmania as a regional example of overlooked losses in biodiversity. *Conservation Biology,* 19**,** 1294 -1300.

EGUCHI, T., GERRODETE, T., PITMAN, R. L., SEMINOFF, J. A. & DUTTON, P. H. 2007. At-sea density and abundance estimates of the olive ridley turtle *Lepidochelys olivacea* in the eastern tropical Pacific. *Endangered Species Research,* 3**,** 191-203.

ENCALADA, S. E., BJORNDAL, A., BOLTEN, A. B., ZURITA, J. C., SCHROEDER, B., POSSARDT, E., SEARSC.J. & BOWEN, B. W. 1998. Population structure of loggerhead turtle (*Caretta caretta*) nesting colonies in the Atlantic and Mediterranean as inferred from mitochondrial DNA control region sequences. *Marine Biology,* 130**,** 567-575.

ENCALADA, S. E., LAHANAS, P. N., BJORNDAL, A., BOLTEN, A. B., MIYAMOTO, M. M. & BOWEN, B. W. 1996. Phylogeography and population structure of the Atlantic and Mediterranean green turtle *Chelonia mydas:* a mitochondrial DNA control region sequence assessment *Molecular Ecology,* 5**,** 473-483.

ERNST, C. H. & BARBOUR, R. W. 1989. *Turtles of the World,* Washington, DC., Smithsonian Institution Press.

ETNOYER, P., CANNY, D., MATE, B. R., MORGAN, L. E., ORTEGA-ORTIZ, J. G. & NICHOLS, W. J. 2006a. Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California

Peninsula, Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography,* 53, 340-358.

ETNOYER, P., CANNY, D., MATE, B. R., MORGAN, L. E., ORTEGA-ORTIZ, J. G. & NICHOLS, W. J. 2006b. Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. *Deep Sea Research Part II: Topical Studies in Oceanography,* 53, 340-358.

EVANNO, G., REGNAUT, S. & GOUDET, J. 2005. Detecting the number of clusters of individuals using the software structure: a simulation study. *Molecular Ecology,* 14, 2611–2620.

EXCOFFIER, L., LAVAL, G. & SCHNEIDER, S. 2005. Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* 1, 47-50.

EYEBE, A. J., SIMEON, A. E., ANGU, K. A. & ENDAMANA, D. 2012. Integrating biodiversity conservation into Development Policy: A case study of Cameroon. *Poverty and Conservation Learning Group (PCLG) Discussion Paper No 09.*

FERNANDEZ-ÅLAMO, M. A. & FARBER-LORDA, J. 2006. Zooplankton and the oceanography of the eastern tropical Pacific: A review. *Progress In Oceanography,* 69, 318-359.

FIEDLER, P. C. 2002. The annual cycle and biological effects of the Costa Rica Dome. *Deep Sea Research Part I: Oceanographic Research Papers,* 49, 321-338.

FIEDLER, P. C. & LAVIN, M. F. 2006. Introduction: A review of eastern tropical Pacific oceanography. *Progress In Oceanography,* 69, 94-100.

FIEDLER, P. C. & TALLEY, L. D. 2006. Hydrography of the eastern tropical Pacific: A review. *Progress In Oceanography,* 69**,** 143-180.

FITZSIMMONS, N. N. 1998. Single paternity of clutches and sperm storage in the promiscuous green turtle (*Chelonia mydas*) *Molecular Ecology,* 7**,** 575-584.

FITZSIMMONS, N. N., LIMPUS, C. J., NORMAN, J. A., GOLDIZEN, A. R., MILLER, J. D. & MORITZ, C. 1997. Phylopatry of male marine turtles inferred from mitochondrial DNA markers. *Proceeding of Natural Academy of Science,* 94**,** 8912-8917.

FITZSIMMONS, N. N., MORITZ, C. & BOWEN, B. W. 2000. Population identification. *In:* ECKERT, K. L., BJORNDAL, K. A., ABREU-GROBOIS, F. A. & DONNELLY, M. (eds.) *Research and management techniques for the conservation of sea turtles.* IUCN/SSC Marine turtle specialist group.

FITZSIMMONS, N. N., MORITZ, C., LIMPUS, C. J., MILLER, J. D., PARMENTER, C. J. & PRINCE, R. Comparative genetic structre of green, loggerhead, and flatback populations in Australia based on variable mtDNA and DNA regions. *In:* BOWEN, B. W. & WITZELL, W. N., eds. Proceedings of the international Symposium on Sea Turtle Conservation Genetics, 1996 Miami, Florida. September 12-14. NOAA Technical Memorandum NMFS-SEFSC 25-32.

FOLL, M. & GAGGIOTTI, O. 2006. Identifying the environmental factors that determine the genetic structure of populations. *Genetics,* 174**,** 875-891.

FONTAINE, M. C., BAIRD, S. J. E., PIRY, S., RAY, N., TOLLEY, K. A., DUKE, S., BIRKUN, A., FERREIRA, M., JAUNIAUX, T., LLAVONA, A., OZTURK, B., OZTURK, A. A., RIDOUX, V., ROGAN, E., SEQUEIRA,

M., SIEBERT, U., VIKINGSSON, G. A., BOUQUEGNEAU, J. M. & MICHAUX, J. R. 2007. Rise of oceanographic barriers in continuous populations of a cetacean: the genetic structure of harbour porpoises in Old World waters. *Bmc Biology,* 5**,** 16.

FOSSETTE, S., HOBSON, V. J., GIRARD, C., CALMETTES, B., GASPAR, P., GEORGES, J.-Y. & HAYS, G. C. 2010. Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *Journal of Marine Systems,* 81**,** 225-234.

FRAZIER, J. 1980. Exploitation of marine turtles in the Indian Ocean. *Human Ecology* 329–370.

FRAZIER, J. 1997. Guest editorial: Inter-American Convention for the Protection and Conservation of sea turtles. *Marine Turtle Newsletter,* 7**,** 7-13.

FRAZIER, J. 2003. Prehistoric and ancient historic interactions between humans and marine turtles. *In:* P.A. LUTZ, J.A. MUSICK & WYNEKEN, A. J. (eds.) *The biology of sea turtles.* Boca Raton, Florida: CRC Press.

FRAZIER, J. 2012. International instruments: critical tools for conserving marine turtles in the eastern Pacific Ocean. *Sea turtles of the eastern Pacific: Advances in research and conservation.* Tucson: Arizona-Sonora Desert Museum Studies in Natural History. University of Arizona Press.

FRAZIER, J., R. ARAUZ, J. CHEVALIER, A. FORMIA, J. FRETEY, M.H. GODFREY, R. MÁRQUEZ-M., B. PANDAV & K. SHANKER 2007. Human-turtle interactions at sea. *In:* PLOTKIN, P. T. (ed.) *Biology and Conservation of Ridley Sea Turtles.* Baltimore, MD: Johns Hopkins University Press.

FRAZIER, J. G. 2000. Building support for regional sea turtle conservation in ASEAN and the Asian region: leaning from the Inter-American Convention for the Protection and Conservation of Sea Turtles. *In:* PILCHER, N. & ISMAIL, G. (eds.) *Sea Turtles of the Indo-Pacific.* Sarawak, Malaysia: Institute of Biodiversity and Environmental Conservation, University of Malaysia.

FRITTS, T. H., STINSON, M. L. & MÁRQUEZ, R. 1982. Status of sea turtle nesting in southern Baja California, México. *Bulletin of Southern California Academy of Science* 81**,** 51-60.

FUENTES, M. M. P. B., PIKE, D. A., DIMATTEO, A. & WALLACE, B. P. 2013. Resilience of marine turtle regional management units to climate change. *Global Change Biology,* 19**,** 1399-1406.

GAGGIOTTI, O. E., BEKKEVOLD, D., JØRGENSEN, H. B. H., FOLL, M., CARVALHO, G. R., ANDRE, C. & RUZZANTE, D. E. 2009. Disentangling the Effects of Evolutionary, Demographic, and Environmental Factors Influencing Genetic Structure of Natural Populations: Atlantic Herring as a Case Study. *Evolution,* 63**,** 2939-2951.

GALINDO, H. M., OLSON, D. B. & PALUMBI, S. R. 2006. Seascape genetics: A coupled oceanographic-genetic model predicts population structure of Caribbean corals. *Current Biology,* 16**,** 1622-1626.

GALLI, S., GASPAR, P., FOSSETTE, S., CALMETTES, B., HAYS, G. C., LUTJEHARMS, J. R. E. & LUSCHI, P. 2012. Orientation of migrating leatherback turtles in relation to ocean currents. *Animal Behaviour,* 84**,** 1491-1500.

GAOS, A. R., ABREU-GROBOIS, F., ALFARO-SHIGUETO, J., AMOROCHO, D., ARAUZ, R., BAQUERO, A., BRISEÑO, R., CHACÓN, D., DUEÑAS, C. & HASBÚN, C. 2010. Signs of hope in the eastern Pacific: international collaboration reveals encouraging status for a severely depleted population of hawksbill turtles *Eretmochelys imbricata*. *Oryx,* 44**,** 595-601.

GAOS, A. R. & YANÉZ, I. L. 2012. Saving the eastern Pacific hawksbill from extinction: last chance or chance lost? *In:* SEMINOFF, J. A. & WALLACE, B. P. (eds.) *Sea turtles of the eastern Pacific: Advances in research and conservation.* Tucson: Arizona-Sonora Desert Museum Studies in Natural History.

GARFIELD, E. 1986. The Turtle: A Most Ancient Mystery. 1. Its Role in Art, Literature, and Mythology. *Current Contents* 39**,** 3-7.

GARZA, J. C. & WILLIAMSON, E. G. 2001. Detection of reduction in population size using data from microsatellite loci. *Molecular Ecology,* 10**,** 305-318.

GODLEY, B. J., BLUMENTHAL, J. M., BRODERICK, A. C., COYNE, M. S., GODFREY, M. H., HAWKES, L. A. & WITT, M. J. 2008. Satellite tracking of sea turtles: Where have we been and where do we go next? *Endangered Species Research,* 4**,** 3-22.

GOUDET, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available. at http://www. unil.ch/izea/softwares/fstat.html.

GREEN, D. & ORTIZ-CRESPO, F. 1982. Status of sea turtle populations in the Central Eastern Pacific. *In:* BJORNDAL, K. A. (ed.) *Biology and Conservation of Sea Turtles* Washington, D.C. : Smithsonian Institution Press.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour,* 28**,** 1140-1162.

HAILER, F., HELANDER, B. R., FOLKESTAD, A. O., GANUSEVICH, S. A., GARSTAD, S., HAUFF, P., KOREN, C., NYGARD, T., VOLKE, V., VILJO, C. & ELLEGREN, H. 2006. Bottlenecked but long-lived: high genetic diversity retained in white-tailed eagles upon recovery from population decline. *Biology Letters,* 2**,** 316-319.

HALL, M., SWIMMER, Y. & PARGA, M. 2012 No "Silver Bullets" but plenty of options: working with artisanal fishers in the eastern Pacific to reduce incidental sea turtle mortality in longline fisheries. *In:* SEMINOFF, J. A. & WALLACE, B. P. (eds.) *Sea turtles of the eastern Pacific: Advances in research and conservation.* Tucson: Arizona-Sonora Desert Museum Studies in Natural History.

HAMANN, M., GODFREY, M., SEMINOFF, J., ARTHUR, K., BARATA, P., BJORNDAL, K., BOLTEN, A., BRODERICK, A., CAMPBELL, L., CARRERAS, C., CASALE, P., CHALOUPKA, M., CHAN, S., COYNE, M., CROWDER, L., DIEZ, C., DUTTON, P., EPPERLY, S., FITZSIMMONS, N., FORMIA, A., GIRONDOT, M., HAYS, G., CHENG, I., KASKA, Y., LEWISON, R., MORTIMER, J., NICHOLS, W., REINA, R., SHANKER, K., SPOTILA, J., TOM, J., WALLACE, B., WORK, T., ZBINDEN, J. & GODLEY, B. 2010. Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endangered Species Research,* 11**,** 245-269.

HARRIS, R. B., WALL, W. A. & ALLENDORF, F. W. 2002. Genetic consequences of hunting: what do we know and what should we do? *Wildlife Society bulletin,* 30**,** 634-643.

HARTL, D. L. & CLARK, A. G. 1989. *Principles of population genetics,* Sunderland, USA, Sinauer Associates

HATASE, H., KINOSHITA, M., BANDO, T., KAMEZAKI, N., SATO, K., MATSUZAWA, Y., GOTO, K., OMUTA, K., NAKASHIMA, Y., TAKESHITA, H. & SAKAMOTO, W. 2002. Population structure of loggerhead turtles, *Caretta caretta*, nesting in Japan: bottlenecks on the Pacific population. *Marine Biology,* 141**,** 299-305.

HAWKES, L., BRODERICK, A., GODFREY, M. & GODLEY, B. 2009. Climate change and marine turtles. *Endangered Species Research,* 7**,** 137-154.

HAYS, G. C. 2004. Good news for sea turtles. *Trends in Ecology & Evolution,* 19**,** 349-351.

HAYS, G. C., BRODERICK, A. C., GLEN, F. & GODLEY, B. J. 2003. Climate change and sea turtles: a 150-year reconstruction of incubation temperatures at a major marine turtle rookery. *Global Change Biology,* 9**,** 642-646.

HAYS, G. C., DRAY, M., QUAIFE, T., SMYTH, T. J., MIRONNET, N. C., LUSCHI, P., PAPI, F. & BARNSLEY, M. J. 2001. Movements of migrating green turtles in relation to AVHRR derived sea surface temperature. *International Journal of Remote Sensing,* 22**,** 1403-1411.

HAYS, G. C., FOSSETTE, S., KATSELIDIS, K. A., MARIANI, P. & SCHOFIELD, G. 2010. Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. *Journal of the Royal Society Interface,* 7**,** 1319-1327.

HELLBERG, M. E. 2009. Gene flow and isolation among populations of marine animals. *Annual Review of Ecology Evolution and Systematics,* 40**,** 291-310.

HELLER, R. & SIEGISMUND, H. R. 2009. Relationship between three measures of genetic differentiation GST, DEST and G'ST: how wrong have we been? *Molecular Ecology,* 18**,** 2080-2083.

HENDRICKSON, J. R. 1980. The ecological strategies of sea turtles. *American Zoologist,* 20**,** 597-608.

HIRTH, H. F. 1980. Some aspects of the nesting behavior and reproductive biology of sea turtles. *American Zoologist* 507–523.

HOBAN, S., GAGGIOTTI, O., CON, G. C. & BERTORELLE, G. 2013. Sample Planning Optimization Tool for conservation and population Genetics (SPOTG): a software for choosing the appropriate number of markers and samples. *Methods in Ecology and Evolution,* 4**,** 299-303.

HOEKERT, W. E. J., NEUFÉGLISE, H., SCHOUTEN, A. D. & MENKEN, S. B. J. 2002. Multiple paternity and female-biased mutation at a microsatellite locus in the olive ridley sea turtle (*Lepidochelys olivacea*). *Heredity,* 89**,** 107-113.

HUGHES, G. R. 1972. The olive ridley sea-turtle (*Lepidochelys olivacea*) in South-east Africa. *Biological Conservation,* 4**,** 128-134.

HUTCHINGS, J. A. 2000. Collapse and recovery of marine fishes. *Nature,* 406**,** 882-885.

HUTCHINSON, W. F., OOSTERHOUT, C. V., ROGERS, S. I. & CARVALHO, G. R. 2003. Temporal analysis of archived samples indicates marked genetic changes in declining North Sea cod (*Gadus morhua*). *Proceedings* *of the Royal Society of London. Series B: Biological Sciences,* 270**,** 2125-2132.

HYKLE, D. 2002. The convention on migratory species and other international instruments relevant to marine turtle conservation: Pros and cons. *Journal of International Wildlife Law & Policy,* 5**,** 105-119.

IAC SECRETARIAT PRO-TEMPORE. *2011. Cooperating to Conserve Sea Turtles - The InterAmerican Convention for the Protection and Conservation of Sea Turtles Celebrates its 10 Year Anniversary, May 2011* [Online].

JANZEN, F. J. 1994. Climate change and temperature-dependent sex determination in reptiles. *Proceedings of the National Academy of Sciences of the United States of America,* 91**,** 7487-7490.

JENKINS, D. G., CAREY, M., CZERNIEWSKA, J., FLETCHER, J., HETHER, T., JONES, A., KNIGHT, S., KNOX, J., LONG, T., MANNINO, M., MCGUIRE, M., RIFFLE, A., SEGELSKY, S., SHAPPELL, L., STERNER, A., STRICKLER, T. & TURSI, R. 2010. A meta-analysis of isolation by distance: relic or reference standard for landscape genetics? *Ecography,* 33**,** 315-320.

JENSEN, J., BOHONAK, A. & KELLEY, S. 2005 Isolation by distance, web service. *BMC Genetics* 6**,** 13.

JENSEN, M. P., ABREAU-GROBOIS, F. A., FRYDENBERG, J. & LOESCHCKE, V. 2006. Microsatellites provide insight into contrasting mating patterns in arribada vs. non-arribada olive ridley sea turtle rookeries. *Molecular Ecology,* 15**,** 2567-2575.

JOLON-MORALES, M. January of 2013. *RE: personal communication. On the history of sea turtles conservation in Guatemala.*

JORGENSEN, H. B. H., HANSEN, M. M., BEKKEVOLD, D., RUZZANTE, D. E. & LOESCHCKE, V. 2005. Marine landscapes and population genetic structure of herring (*Clupea harengus L.)* in the Baltic Sea. *Molecular Ecology,* 14**,** 3219-3234.

KARL, S. A., BOWEN, B. W. & AVISE, J. C. 1992. Global population genetic structure and male-mediated gene flow in the Green turtle (*Chelonia mydas*): RFLP Analyses of Anonymous Nuclear Loci. *Genetics,* 131**,** 163-173.

KEANE, A., JONES, J. P. G., EDWARDS-JONES, G. & MILNER-GULLAND, E. J. 2008. The sleeping policeman: understanding issues of enforcement and compliance in conservation. *Animal Conservation,* 11**,** 75-82.

KESSLER, W. S. 2006. The circulation of the eastern tropical Pacific: A review. *Progress In Oceanography,* 69**,** 181-217.

KICHLER, K., HOLDER, M. T., DAVIS, S. K., MÁRQUEZ, R. & OWENS, D. W. 1999. Detection of multiple paternity in the Kemp´s ridley sea turtle with limited sampling. *Molecular Ecology,* 8**,** 819-830.

KOOL, J. T., PARIS, C. B., ANDRÉFOUËT, S. & COWEN, R. K. 2010. Complex migration and the development of genetic structure in subdivided populations: an example from Caribbean coral reef ecosystems. *Ecography,* 33**,** 597-606.

KOOL, J. T., PARIS, C. B., BARBER, P. H. & COWEN, R. K. 2011. Connectivity and the development of population genetic structure in Indo-West Pacific coral reef communities. *Global Ecology and Biogeography,* 20**,** 695-706.

KOPITSKY, K., PITMAN, R. L. & PLOTKIN, P. T. 2000. Investigations on at-sea mating and reproductive status of olive ridleys, *Lepidochelys olivacea,* captured in the eastern tropical Pacific *In:* KALB, H. J. & WIBBELS, T. (eds.) *Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation.* NOAA Technical Memorandum

LAHANAS, P., MIYAMOTO, M., BJORNDAL, K. & BOLTEN, A. 1994. Molecular evolution and population genetics of Greater Caribbean green turtles (*Chelonia mydas*) as inferred from mitochondrial DNA control region sequences. *Genetica,* 94**,** 57-66.

LAHANAS, P. N., BJORNDAL, K. A., BOLTEN, A. B., ENCALADA, S. E., MIYAMOTO, M. M., VALVERDE, R. A. & BOWEN, B. W. 1998. Genetic composition of a green turtle (*Chelonia mydas*) feeding ground population: evidence for multiple origins. *Marine Biology* 130**,** 345-352.

LANYON, J. M., LIMPUS, C. J. & MARSH, H. 1989. *Dugongs and turtles - grazers in the seagrass system,* New York, Elsevier.

LARSON, S., JAMESON, R., ETNIER, M., FLEMING, M. & BENTZEN, P. 2002. Loss of genetic diversity in sea otters (*Enhydra lutris*) associated with the fur trade of the 18th and 19th centuries. *Molecular Ecology,* 11**,** 1899-1903.

LEE, P. L. M. 2008. Molecular ecology of marine turtles: New approaches and future directions. *Journal of Experimental Marine Biology and Ecology,* 356**,** 25-42.

LEGENDRE, P. & FORTIN, M.-J. 2010. Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. *Molecular Ecology Resources,* 10**,** 831-844.

LEGENDRE, P., LAPOINTE, F.-J. & CASGRAIN, P. 1994. Modeling brain evolution from behavior: a permutational regression approach. *Evolution***,** 1487-1499.

LEROUX, R. A., DUTTON, P. H., ABREU-GROBOIS, F. A., LAGUEUX, C. J., CAMPBELL, C. L., DELCROIX, E., CHEVALIER, J., HORROCKS, J. A., HILLIS-STARR, Z., TROËNG, S., HARRISON, E. & STAPLETON, S. 2012. Re-examination of population structure and phylogeography of hawksbill turtles in the Wider Caribbean using longer mtDNA sequences. *Journal of Heredity,* 103**,** 806-820.

LIGGINS, L., TREML, E. A. & RIGINOS, C. 2013. Taking the plunge: an introduction to undertaking seascape genetic studies and using biophysical models. *Geography Compass,* 7**,** 173-196.

LIMPUS, C. J., FLEAY, A. & V., B. 1984. The flatback turtle, *Chelonia depressa*, in Queensland: Reproductive periodicity, philopatry, and recruitment. *Australian Wildlife Research* 579–587.

LIMPUS, C. J., MILLER, J. D., PARMENTER, C. J., REIMER, D., MCLACHLAN, N. & WEBB, R. 1992. Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries *Wildlife Research,* 19**,** 347-358.

LINDENMAYER, D., HOBBS, R. J., MONTAGUE-DRAKE, R., ALEXANDRA, J., BENNETT, A., BURGMAN, M., CALE, P., CALHOUN, A., CRAMER, V., CULLEN, P., DRISCOLL, D., FAHRIG, L., FISCHER, J., FRANKLIN, J., HAILA, Y., HUNTER, M., GIBBONS, P., LAKE, S.,

LUCK, G., MACGREGOR, C., MCINTYRE, S., NALLY, R. M., MANNING, A., MILLER, J., MOONEY, H., NOSS, R., POSSINGHAM, H., SAUNDERS, D., SCHMIEGELOW, F., SCOTT, M., SIMBERLOFF, D., SISK, T., TABOR, G., WALKER, B., WIENS, J., WOINARSKI, J. & ZAVALETA, E. 2008. A checklist for ecological management of landscapes for conservation. *Ecology Letters,* 11**,** 78-91.

LÓPEZ-CASTRO, M. C. & ROCHA-OLIVARES, A. 2005. The panmixia paradigm of Eastern Pacific olive ridley turtles revised: consequences for their conservation and evolutionary biology. *Molecular Ecology,* 14**,** 3325-3334.

LÓPEZ-CHÁVEZ, F. J. 2000. *Determinación de la estructura genética de colonias de tortuga golfina en el Pacífico central mexicano con microsatelites del DNA nuclear.* Master thesis, Thesis. Universidad de Colima.

LÓPEZ-MENDILAHARSU, M., GARDNER, S. C., SEMINOFF, J. A. & RIOSMENA-RODRIGUEZ, R. 2005. Identifying critical foraging habitats of the green turtle (*Chelonia mydas*) along the Pacific coast of the Baja California peninsula, Mexico. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 15**,** 259-269.

LOTZE, H. K., COLL, M., MAGERA, A. M., WARD-PAIGE, C. & AIROLDI, L. 2011. Recovery of marine animal populations and ecosystems. *Trends in Ecology & Evolution,* 26**,** 595-605.

LUIKART, G., ALLENDORF, F. W., CORNUET, J. M. & SHERWIN, W. B. 1998. Distortion of allele frequency distributions provides a test for recent population bottlenecks. *Journal of Heredity,* 89**,** 238-247.

LUSCHI, P., GRAEME, C. & FLORIANO, P. 2003a. A review of long-distance movements by marine turtles, and the possible role of ocean currents. *Oikos,* 103**,** 293-302.

LUSCHI, P., SALE, A., MENCACCI, R., HUGHES, G. R., LUTJEHARMS, J. R. E. & PAPI, F. 2003b. Current transport of leatherback sea turtles (*Dermochelys coriacea*) in the ocean. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 270**,** S129-S132.

MANEL, S., SCHWARTZ, M. K., LUIKART, G. & TABERLET, P. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution,* 18**,** 189-197.

MARCOVALDI, M. Â., THOMÉ, J & FRAZIER, J. G. 2003. Marine Turtles in Latin America and the Caribbean: A Regional Perspective of Successes, Failures and Priorities for the Future. *Marine Turtle Newsletter,* 100**,** 38-42.

MÁRQUEZ-M, R. 1990. *FAO species catalogue: Sea turtles of the world. An annotated and illustrated catalogue of sea turtle species known to date,* Rome, FAO fisheries Synopsis.

MÁRQUEZ-M, R. 1996 *Las tortugas marinas y nuestro tiempo,* México, Fondo de Cultura Económica.

MÁRQUEZ-M, R., PEÑAFLORES, C. S. & JIMENEZ, M. C. Q. 2007. Protección de la tortuga marina en la costa de Oaxaca por el Instituto Nacional de la Pesca. *In:* FUENTES-MASCORRO, G., MARTÍNEZ, B. S. & LÓPEZ ROJAS, F. A. (eds.) *Tomo II Santuario "La Escobilla" Un compromiso de conservación con la humanidad.* Oaxaca, México: Universidad Autónoma "Benito Juárez" de Oaxaca.

MÁRQUEZ-M, R., VILLANUEVA-O, A., PEÑAFLORES-S, C. & RIOS-O, D. 1982. Situacion actual y recomendaciones para el manejo de las tortugas marinas de la costa occidental mexicana, en especial la tortuga golfina (*Lepidochelys olivacea). Ciencia Pesquera***,** 83-91.

MASUMOTO, Y., SASAKI, H., KAGIMOTO, T., KOMORI, N., ISHIDA, A., SASAI, Y., MIYAMA, T., MOTOI, T., MITSUDERA, H. & TAKAHASHI, K. 2004. A fifty-year eddy-resolving simulation of the world ocean: Preliminary outcomes of OFES (OGCM for the Earth Simulator). *J. Earth Simulator,* 1**,** 35-56.

MCCREARY, J. P., LEE, H. S. & ENFIELD, D. B. 1989. The response of the coastal ocean to strong offshore winds: With application to circulations in the Gulfs of Tehuantepec and Papagayo. *Journal of Marine Research,* 47**,** 81-109.

MCMAHON, C., R., COREY, J. A. B. & GRAEME, C. H. 2007. Satellite tracking reveals unusual diving characteristics for a marine reptile, the olive ridley turtle *Lepidochelys olivacea. Marine Ecology Progress Series,* 329**,** 239-252.

MCMAHON, C. R. & HAYS, G. C. 2006. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Global Change Biology,* 12**,** 1338.

MEIRMANS, P. G. & HEDRICK, P. W. 2011. Assessing population structure: FST and related measures. *Molecular Ecology Resources,* 11**,** 5-18.

MEIRMANS, P. G. & VAN TIENDEREN, P. H. 2004. genotype and genodive: two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Notes,* 4**,** 792-794.

MENDEZ, M., ROSENBAUM, H. C., SUBRAMANIAM, A., YACKULIC, C. & BORDINO, P. 2010. Isolation by environmental distance in mobile marine species: molecular ecology of franciscana dolphins at their southern range. *Molecular Ecology,* 19**,** 2212-2228.

MENDEZ, M., SUBRAMANIAM, A., COLLINS, T., MINTON, G., BALDWIN, R., BERGGREN, P., SARNBLAD, A., AMIR, O. A., PEDDEMORS, V. M., KARCZMARSKI, L., GUISSAMULO, A. & ROSENBAUM, H. C. 2011. Molecular ecology meets remote sensing: environmental drivers to population structure of humpback dolphins in the Western Indian Ocean. *Heredity,* 107**,** 349-361.

MEYLAN, A. B. 1982. Sea turtle migration: evidence from tag returns. *In:* BJORNDAL, K. A. (ed.) *Biology and conservation of sea turtles.* Washington, D.C.: Smithsonian Institution Press.

MEYLAN, A. B. & MEYLAN, P. A. 1999. Introduction to the evolution, life history, and biology of sea turtles. *In:* ECKERT, K. L., BJORNDAL, K. A., ABREU-GROBOIS, F. A. & DONNELLY, M. E. (eds.) *Research and management techniques for the conservation of sea turtles.* IUCN/SSC Marine turtle specialist group.

MICHELS, E., COTTENIE, K., NEYS, L., DE GELAS, K., COPPIN, P. & DE MEESTER, L. 2001. Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. *Molecular Ecology,* 10**,** 1929-1938.

MILLER, J. D. 1997. Reproduction in sea turtles. *In:* LUTZ, P. L. & MUSICK, J. (eds.) *Biology of Sea Turtles.* Boca Raton, Florida: CRC Press.

MONZON-ARGUELLO, C., DELL'AMICO, F., MORINIERE, P., MARCO, A., LOPEZ-JURADO, L. F., HAYS, G. C., SCOTT, R., MARSH, R. & LEE, P. L. M. 2012. Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal. *Journal of the Royal Society Interface,* 9**,** 1725-1732.

MONZÓN-ARGÜELLO, C., LÓPEZ-JURADO, L. F., RICO, C., MARCO, A., LÓPEZ, P., HAYS, G. C. & LEE, P. L. M. 2010. Evidence from genetic and Lagrangian drifter data for transatlantic transport of small juvenile green turtles. *Journal of Biogeography,* 37**,** 1752-1766.

MOORE, M. K. & BALL, R. 2002. Multiple paternity in loggerhead turtle (*Caretta caretta*) nest on Melbourne beach, Florida: a microsatellite analysis. *Molecular Ecology,* 11**,** 281-288.

MORITZ, C. 1994. Defining "Evolutionary Significants Units" for conservation. . *Trends Ecology & Evolution,* 9**,** 373-375.

MORITZ, C. 1999. Conservation units and translocations: strategies for conserving evolutionary processes. *Hereditas,* 130**,** 217-228.

MORREALE, S. J., PLOTKIN, P. T., SHAVER, D. J. & KALB, H. J. 2007. Adult migration and habitat utilization. *In:* PLOTKIN, P. T. (ed.) *Biology and Conservation of Ridley Sea Turtles.* Baltimore: The Johns Hopkins University Press.

MORREALE, S. J., STANDORA, E. A., SPOTILA, J. R. & PALADINO, F. V. 1996. Migration corridor for sea turtles. *Nature,* 384**,** 319-320.

MUSICK, J. A. & LIMPUS, C. 1997. Habitat utilization and migration in juvenile sea turtles. *In:* LUTZ, P. L. & MUSICK, J. A. E. (eds.) *The biology of sea turtles.* CRC Press.

NAMNUM, S. 2002. The Inter-American Convention for the Protection and Conservation of Sea Turtles and Its Implementation in Mexican Law. *Journal of International Wildlife Law & Policy,* 5**,** 87-103.

NARO-MACIEL, E., BONDIOLI, A. C. V., MARTIN, M., DE PÁDUA ALMEIDA, A., BAPTISTOTTE, C., BELLINI, C., MARCOVALDI, M. Â., SANTOS, A. J. B. & AMATO, G. 2012. The interplay of homing and dispersal in green turtles: a focus on the southwestern Atlantic. *Journal of Heredity,* 103**,** 792-805.

NARO‐MACIEL, E. 1998. The Inter‐American convention for the protection and conservation of sea turtles: An historical overview. *Journal of International Wildlife Law & Policy,* 1**,** 169-178.

OHTA, T. & KIMURAA, M. 1973. *A model of mutation appropriate to estimate the number of electrophoretically detectable alleles in a finite population*, Cambridge.

OKSANEN, J. F., BLANCHET, G., KINDT, R., LEGENDRE, P., MINCHIN, P. R., O'HARA, R. B., SIMPSON, G. L., SOLYMOS, P., HENRY, M., STEVENS, H. & WAGNER, H. 2013. vegan: Community Ecology Package. R package version 2.0-7. http://CRAN.R-project.org/package=vegan.

OKUYAMA, J., KITAGAWA, T., ZENIMOTO, K., KIMURA, S., ARAI, N., SASAI, Y. & SASAKI, H. 2011. Trans-Pacific dispersal of loggerhead turtle hatchlings inferred from numerical simulation modeling. *Marine Biology,* 158**,** 2055-2063.

OOSTERHOUT, C. V., HUTCHINSON, W. F., WILLS, D. P. M. & SHIPLEY, P. F. 2003. Micro-Checker software. Molecular Ecology & Fisheries Genetics Laboratory. The University of Hull.

OWENS, D. W. 1980. The comparative reproductive physiology of sea turtles. *American Zoologist***,** 549–563.

PAETKAU, D., SLADE, R., BURDEN, M. & ESTOUP, A. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Molecular Ecology,* 13**,** 55-65.

PALACIOS, D. M., BOGRAD, S. J., FOLEY, D. G. & SCHWING, F. B. 2006. Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective. *Deep Sea Research Part II: Topical Studies in Oceanography,* 53**,** 250-269.

PALUMBI, S. R. 2003. Population Genetics, Demographic Connectivity, and the Design of Marine Reserves. *Ecological Applications,* 13**,** S146-S158.

PANDAV, B. & CHOUDHURY, B. C. 1998. Olive ridley tegged in Orissa recovered in coastal waters of Eastern Sri Lanka. *Marine Turtle Newsletter,* 82**,** Pp 9-10.

PARIS, C. B., HELGERS, J., VAN SEBILLE, E. & SRINIVASAN, A. 2013. Connectivity Modeling System: A probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environmental Modelling & Software,* 42**,** 47-54.

PEAKALL, R. & SMOUSE, P. E. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research, an update. *Bioinformatics,* 28**,** 2537-2539.

PECKHAM, S. H., DIAZ, D. M., WALLI, A., RUIZ, G., CROWDER, L. B. & NICHOLS, W. J. 2007. Small-scale fisheries bycatch jeopardizes endangered pacific loggerhead turtles. *PLoS ONE,* 2**,** e1041.

PEERY, M. Z., KIRBY, R., REID, B. N., STOELTING, R., DOUCET-BEER, E., ROBINSON, S., VASQUEZ-CARRILLO, C., PAULI, J. N. & PALSBØLL, P. J. 2012. Reliability of genetic bottleneck tests for detecting recent population declines. *Molecular Ecology,* 21**,** 3403-3418.

PELLETIER, L., KATO, A., CHIARADIA, A. & ROPERT-COUDERT, Y. 2012. Can Thermoclines Be a Cue to Prey Distribution for Marine Top Predators? A Case Study with Little Penguins. *PLoS ONE,* 7**,** e31768.

PENNINGTON, J. T., MAHONEY, K. L., KUWAHARA, V. S., KOLBER, D. D., CALIENES, R. & CHAVEZ, F. P. 2006. Primary production in the eastern tropical Pacific: A review. *Progress In Oceanography,* 69**,** 285-317.

PIRY, S., ALAPETITE, A., CORNUET, J.-M., PAETKAU, D., BAUDOUIN, L. & ESTOUP, A. 2004. GENECLASS2: A software for genetic assignment and first-generation migrant detection. *Journal of Heredity,* 95**,** 536-539.

PIRY, S., LUIKART, G. & CORNUET, J.-M. 1999. Computer note. BOTTLENECK: a computer program for detecting recent reductions in the effective size using allele frequency data. *Journal of Heredity,* 90**,** 502-503.

PLOT, V., DE THOISY, B., BLANC, S., KELLE, L., LAVERGNE, A., ROGER-BÉRUBET, H., TREMBLAY, Y., FOSSETTE, S. & GEORGES, J.-Y. 2012. Reproductive synchrony in a recovering bottlenecked sea turtle population. *Journal of Animal Ecology,* 81**,** 341-351.

PLOTKIN, P. 2010. Nomadic behaviour of the highly migratory olive ridley sea turtle *Lepidochelys olivacea* in the eastern tropical Pacific Ocean. *Endangered Species Research,* 13**,** 33-40.

PLOTKIN, P. T. 2003. Adult migrations and habitat use. *In:* LUTZ, P. L., MUSICK, J. A. & WYNEKEN, J. (eds.) *The Biology of Sea Turtles II.* Boca Raton, FL.: CRC Press.

PLOTKIN, P. T. 2007. Near exctintion and recovery. *In:* PLOTKIN, P. T. (ed.) *Biology and Conservation of Ridley Sea Turtles.* Baltimore: The Johns Hopkins University Press.

PLOTKIN, P. T., BYLES, R. A., ROSTAL, D. C. & OWENS, D. W. 1995. Independent versus socially facilitated oceanic migrations of the olive ridley, *Lepidochelys olivacea. Marine Biology,* 122**,** 137-143.

PLOTKIN, P. T., OWENS, D. W., BYLES, R. A. & PATTERSON, R. 1996. Departure of male olive ridley turtles (*Lepidochelys olivacea*) from a nearshore breeding ground. *Herpetological Conservation and Biology,* 52**,** 1-7.

PLOTKIN, P. T. B.-D., R.; ABREU-GROBOIS, F.A. 2012. Interpreting signs of Olive Ridley recovery in the eastern Pacific *In:* J.A, S. & WALLACE, B. P. (eds.) *Sea turtles of the eastern Pacific: Advances in research and conservation.* Tucson University of Arizona Press. Arizona-Sonora Desert Museum Studies in Natural History

POLOVINA, J., UCHIDA, I., BALAZS, G., HOWELL, E. A., PARKER, D. & DUTTON, P. 2006. The Kuroshio extension bifurcation region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep Sea Research Part II: Topical Studies in Oceanography,* 53**,** 326-339.

POLOVINA, J. J., BALAZS, G. H., HOWELL, E. A., PARKER, D. M., SEKI, M. P. & DUTTON, P. H. 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fisheries Oceanography,* 1**,** Pp 35-51.

POLOVINA, J. J., HOWELL, E., KOBAYASHI, D. R. & SEKI, M. P. 2001. The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress In Oceanography,* 49**,** 469-483.

PRITCHARD, J. K., STEPHENS, M. & DONNELLY, P. 2000. Inference of population structure using multilocus genotype data. *Genetics,* 155**,** 945-959.

PRITCHARD, P. C. H. & MORTIMER, J. A. 1999. Taxonomy, External Morphology, and species Identification. *In:* ECKERT, K. L., BJORNDAL, K. A., ABREU-GROBOIS, F. A. & DONNELLY, M. (eds.) *Research and Management Techniques for the Conservation of Sea Turtles* IUCN/SSC Marine Turtle Specialist Group.

PROIETTI, M. C., REISSER, J., MARINS, L. F., RODRIGUEZ-ZARATE, C., MARCOVALDI, M. A., MONTEIRO, D. S., PATTIARATCHI, C. & SECCHI, E. R. 2014. Genetic structure and natal origins of immature hawksbill turtles (*Eretmochelys imbricata*) in brazilian waters. *PLoS ONE,* 9**,** e88746.

PUJOLAR, J. M., MAES, G. E. & VOLCKAERT, F. A. M. 2006. Genetic patchiness among recruits in the European eel *Anguilla anguilla*. *Marine Ecology-Progress Series,* 307**,** 209-217.

PUTMAN, N. F., ABREU-GROBOIS, F. A., BRODERICK, A. C., CIOFI, C., FORMIA, A., GODLEY, B. J., STROUD, S., PELEMBE, T., VERLEY, P. & WILLIAMS, N. 2014. Numerical dispersal simulations and genetics help explain the origin of hawksbill sea turtles in Ascension Island. *Journal of Experimental Marine Biology and Ecology,* 450**,** 98-108.

PUTMAN, N. F., BANE, J. M. & LOHMANN, K. J. 2010. Sea turtle nesting distributions and oceanographic constraints on hatchling migration. *Proceedings of the Royal Society B-Biological Sciences,* 277**,** 3631-3637.

PUTMAN, N. F. & NARO-MACIEL, E. 2013. Finding the 'lost years' in green turtles: insights from ocean circulation models and genetic analysis. *Proceedings of the Royal Society B: Biological Sciences,* 280.

PUTMAN, N. F., VERLEY, P., SHAY, T. J. & LOHMANN, K. J. 2012. Simulating transoceanic migrations of young loggerhead sea turtles: merging magnetic navigation behavior with an ocean circulation model. *The Journal of Experimental Biology,* 215**,** 1863-1870.

QUIÑONES, J., GONZALEZ CARMAN, V., ZEBALLOS, J., PURCA, S. & MIANZAN, H. 2010. Effects of El Niño-driven environmental variability on black turtle migration to peruvian foraging grounds. *Hydrobiologia,* 645**,** 69-79.

RANNALA, B. & MOUNTAIN, J. L. 1997. Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences,* 94**,** 9197-9201.

REAM, R. R., STERLING, J. T. & LOUGHLIN, T. R. 2005. Oceanographic features related to northern fur seal migratory movements. *Deep Sea Research Part II: Topical Studies in Oceanography,* 52**,** 823-843.

REED, D. H. & FRANKHAM, R. 2003. Correlation between Fitness and Genetic Diversity. *Conservation Biology,* 17**,** 230-237.

REED, M. S. 2008. Stakeholder participation for environmental management: A literature review. *Biological Conservation,* 141**,** 2417-2431.

REVELLES, M., ISERN-FONTANET, J., CARDONA, L., SAN FÉLIX, M., CARRERAS, C. & AGUILAR, A. 2007. Mesoscale eddies, surface circulation and the scale of habitat selection by immature loggerhead sea turtles. *Journal of experimental marine biology and ecology,* 347**,** 41-57.

RIGINOS, C. & LIGGINS, L. 2013. Seascape genetics: populations, individuals, and genes marooned and adrift. *Geography Compass,* 7**,** 197-216.

RITCHIE, J. 2003. The application of qualitative methods to social research. *In:* RITCHIE, J., LEWIS, J. (ed.) *Qualitative Research Practice: a Guide for Social Science Students and Researchers.* London, UK: Sage Publications.

ROBERTS, M. A., SCHWARTZ, T. S. & STEPHEN, A. K. 2004. Global population genetic structure and male-mediated gene flow in the green sea turtle (*Chelonia mydas*): analysis of microsatellite loci. *Genetics,* 166**,** 1857-1870.

RODEN, S., PA, M., A, F., GH, B., P, Z., IJ, C. & PH, D. 2013. Green turtle population structure in the Pacific: new insights from single nucleotide polymorphisms and microsatellites. *Endangered Species Research,* 20**,** 227-234.

ROUSSET, F. 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Molecular Ecology Resources* 8**,** 103-106.

SABA, V. S. 2012. Sea turtles in the tropical high seas: climate variability, oceanography, and ecosystem responses. *In:* SEMINOFF, J. A. & WALLACE, B. P. (eds.) *Sea turtles of the eastern Pacific: Advances in research and conservation* Tucson: Arizona-Sonora Desert Museum Studies in Natural History. University of Arizona Press.

SCHOVILLE, S. D., BONIN, A., FRANÇOIS, O., LOBREAUX, S., MELODELIMA, C. & MANEL, S. 2012. Adaptive genetic variation on the landscape: methods and cases. *Annual Review of Ecology, Evolution, and Systematics,* 43**,** 23-43.

SCHULTZ, J. K., FELDHEIM, K. A., GRUBER, S. H., ASHLEY, M. V., MCGOVERN, T. M. & BOWEN, B. W. 2008. Global phylogeography and seascape genetics of the lemon sharks (genus Negaprion). *Molecular Ecology,* 17**,** 5336-5348.

SCHULZ, J. P. 1971. Nesting beaches of sea turtles in west French Guiana. *Proc. Koninkl. Nederl. Akad. Wetensch. C,* 74**,** 398-404.

SELKOE, K. A., HENZLER, C. M. & GAINES, S. D. 2008. Seascape genetics and the spatial ecology of marine populations. *Fish and Fisheries,* 9**,** 363-377.

SELKOE, K. A. & TOONEN, R. J. 2006. Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. *Ecology Letters,* 9**,** 615-629.

SELKOE, K. A., VOGEL, A. & GAINES, S. D. 2007. Effects of ephemeral circulation on recruitment and connectivity of nearshore fish populations spanning Southern and Baja California. *Marine Ecology Progress Series,* 351**,** 209-220.

SELKOE, K. A., WATSON, J. R., WHITE, C., BEN HORIN, T., IACCHEI, M., MITARAI, S., SIEGEL, D. A., GAINES, S. D. & TOONEN, R. J. 2010. Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Molecular Ecology,* 19**,** 3708-3726.

SEMINOFF, J., ZARATE, P., COYNE, M., FOLEY, D., PARKER, D., LYON, B. & DUTTON, P. 2008. Post-nesting migrations of Galapagos green turtles *Chelonia mydas* in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data. *Endangered Species Research,* 4**,** 57-72.

SEMINOFF, J. A., ALFARO-SHIGUETO, J., AMOROCHO, D., R., A., BAQUERO GALLEGOS, A., CHACÓN CHAVERRI, D., GAOS, A. R., S., K., MANGEL, J. C., URTEAGA, J. & WALLACE, B. P. 2012. Biology and Conservation of Sea Turtles in the eastern Pacific Ocean: A General Overview. *In:* SEMINOFF, J. A. & WALLACE, B. P. (eds.) *Sea turtles of the eastern Pacific: Advances in research and conservation.* Tucson: Arizona-Sonora Desert Museum Studies in Natural History. University of Arizona Press.

SEMINOFF, J. A., RESENDIZ, A. & NICHOLS, W. J. 2002. Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. *Marine Ecology Progress Series,* 242**,** 253-265.

SEMINOFF, J. A. & SHANKER, K. 2008. Marine turtles and IUCN Red Listing: A review of the process, the pitfalls, and novel assessment approaches. *Journal of Experimental Marine Biology and Ecology,* 356**,** 52-68.

SEXTON, J. P., HANGARTNER, S. B. & HOFFMANN, A. A. 2014. Genetic Isolation by Environment or Distance: which pattern of gene flow is most common? *Evolution,* 68, 1-15.

SHAMA, N. S., KUBOW, K. B., JOKELA, J. & ROBINSON, C. T. 2011. Bottlenecks drive temporal and spatial genetic changes in alpine caddisfly metapopulations. *BMC Evolutionary Biology,* 11, 278.

SHAMBLIN, B. M., BJORNDAL, K. A., BOLTEN, A. B., HILLIS-STARR, Z. M., LUNDGREN, I. A. N., NARO-MACIEL, E. & NAIRN, C. J. 2012. Mitogenomic sequences better resolve stock structure of southern Greater Caribbean green turtle rookeries. *Molecular Ecology,* 21, 2330-2340.

SHANKER, K., RAMADEVI, J., CHOUDHURY, B. C., SINGH, L. & AGGARWAL, R. K. 2004. Phylogeography of olive ridley turtles (*Lepidochelys olivacea*) on the east coast of India: implications for conservation theory. *Molecular Ecology,* 13, 1899-1909.

SHILLINGER, G. L., DI LORENZO, E., LUO, H., BOGRAD, S. J., HAZEN, E. L., BAILEY, H. & SPOTILA, J. R. 2012. On the dispersal of leatherback turtle hatchlings from Mesoamerican nesting beaches. *Proceedings of the Royal Society B: Biological Sciences,* 279, 2391-2395.

SHILLINGER, G. L., PALACIOS, D. M., BAILEY, H., BOGRAD, S. J., SWITHENBANK, A. M., GASPAR, P., WALLACE, B. P., SPOTILA, J. R., PALADINO, F. V., PIEDRA, R., ECKERT, S. A. & BLOCK, B. A. 2008. Persistent leatherback turtle migrations present opportunities for conservation. *Plos Biology,* 6, Pp 1408-1416.

SLATKIN, M. 1993. Isolation by distance in equilibrium and nonequilibrium populations. *Evolution,* 47, 264-279.

SODHI, N. S., BUTLER, R. & RAVEN, P. H. 2011. Bottom-up Conservation. *Biotropica,* 43**,** 521-523.

STENSETH, N. C., JORDE, P. E., CHAN, K. S., HANSEN, E., KNUTSEN, H., ANDRE, C., SKOGEN, M. D. & LEKVE, K. 2006. Ecological and genetic impact of Atlantic cod larval drift in the Skagerrak. *Proceedings of the Royal Society B-Biological Sciences,* 273**,** 1085-1092.

STOCKER, T. & SCHMITTNER, A. 1997. Influence of CO2 emission rates on the stability of the thermohaline circulation. *Nature,* 388**,** 862-865.

STOOKEY, L. L. 2004. *Thematic Guide to World Mythology,* Westport, CT USA, Greenwood Press.

SUNNUCKS, P. 2000. Efficient genetic markers for population biology. *Trends in Ecology & Evolution,* 15**,** 199-203.

SUNNUCKS, P. & HALES, D. F. 1996. Numerous transposed sequences of mitochondrial cytochrome oxidase I-II in aphids of the genus Sitobion (Hemiptera: Aphididae). *Molecular Biology and Evolution,* 13**,** 510-524.

SWIMMER, Y., ARAUZ, R., MCCRACKEN, M., MCNAUGHTON, L., BALLESTERO, J., MUSYL, M., BIGELOW, K. & BRILL, R. 2006. Diving behavior and delayed mortality of olive ridley sea turtles *Lepidochelys olivacea* after their release from longline fishing gear. *Marine Ecology Progress Series,* 323**,** 253-261.

TAYLOR, A. C., HORSUP, A., JOHNSON, C. N., SUNNUCKS, P. & SHERWIN, B. 1997. Relatedness structure detected by microsatellite analysis and attempted pedigree reconstruction in an endangered marsupial, the northern hairy-nosed wombat *Lasiorhinus krefftii*. *Molecular Ecology,* 6**,** 9-19.

TEACHER, A. G. F., ANDRÉ, C., JONSSON, P. R. & MERILÄ, J. 2013. Oceanographic connectivity and environmental correlates of genetic structuring in Atlantic herring in the Baltic Sea. *Evolutionary Applications,* 6**,** 549-567.

TIWARI, M. 2002. An evaluation of the perceived effectiveness of international instruments for sea turtle conservation. *Journal of International Wildlife Law & Policy,* 5**,** 145-156.

TRIPATHY, B. & PANDAV, B. 2007. Beach Fidelity and internesting movements of olive ridley turtles (*Lepidochelys olivacea*) at Rushikulya, India. *herpetological Conservation and Biology,* 3**,** 40-45.

WALLACE, B. P., DIMATTEO, A. D., HURLEY, B. J., FINKBEINER, E. M., BOLTEN, A. B., CHALOUPKA, M. Y., HUTCHINSON, B. J., ABREU-GROBOIS, F. A., AMOROCHO, D., BJORNDAL, K. A., BOURJEA, J., BOWEN, B. W., DUENAS, R. B., CASALE, P., CHOUDHURY, B. C., COSTA, A., DUTTON, P. H., FALLABRINO, A., GIRARD, A., GIRONDOT, M., GODFREY, M. H., HAMANN, M., LOPEZ-MENDILAHARSU, M., MARCOVALDI, M. A., MORTIMER, J. A., MUSICK, J. A., NEL, R., PILCHER, N. J., SEMINOFF, J. A., TROENG, S., WITHERINGTON, B. & MAST, R. B. 2010a. Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS ONE,* 5**,** e15465.

WALLACE, B. P., KOT, C. Y., DIMATTEO, A. D., LEE, T., CROWDER, L. B. & LEWISON, R. L. 2013a. Impacts of fisheries bycatch on marine turtle populations worldwide: toward conservation and research priorities. *Ecosphere,* 4**,** 40.

WALLACE, B. P., LEWISON, R. L., MCDONALD, S. L., MCDONALD, R. K., KOT, C. Y., KELEZ, S., BJORKLAND, R. K., FINKBEINER, E. M., HELMBRECHT, S. & CROWDER, L. B. 2010b. Global patterns of marine turtle bycatch. *Conservation Letters,* 3**,** 131-142.

WALLACE, B. P., TIWARI, M. & GIRONDOT, M. 2013b. *Dermochelys coriacea. The IUCN Red List of Threatened Species.* [Online]. Available: http://www.iucnredlist.org [Accessed Downloaded on 09 December 2014.

WANG, I. J., GLOR, R. E. & LOSOS, J. B. 2013. Quantifying the roles of ecology and geography in spatial genetic divergence. *Ecology Letters,* 16**,** 175-182.

WANG, I. J. & SUMMERS, K. 2010. Genetic structure is correlated with phenotypic divergence rather than geographic isolation in the highly polymorphic strawberry poison-dart frog. *Molecular Ecology,* 19**,** 447-458.

WAPLES, R. S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity,* 89**,** 438-450.

WHITING, S. D., LONG, J. L. & COYNE, M. 2007. Migration routes and foraging behaviour of olive ridley turtles *Lepidochelys olivacea* in northern Australia. *Endangered Species Research,* 3**,** 1-9.

WILKINS, D., VAN SEBILLE, E., RINTOUL, S. R., LAURO, F. M. & CAVICCHIOLI, R. 2013. Advection shapes Southern Ocean microbial assemblages independent of distance and environment effects. *Nature communications,* 4.

WILLETT, C. S., LEBEN, R. R. & LAVÌN, M. F. 2006. Eddies and tropical instability waves in the eastern tropical Pacific: a review. *Progress In Oceanography,* 69**,** 218-238.

WILLIAMSON-NATESAN, E. 2005. Comparison of methods for detecting bottlenecks from microsatellite loci. *Conservation Genetics,* 6**,** 551-562.

WITZELL, W. N. 1994. The origin, evolution and demise of the US sea turtle fisheries. *Marine Fisheries Review* 8–23.

WRIGHT, S. 1943. Isolation by Distance. *Genetics,* 28**,** 114-138.

ZUG, G. R., CHALOUPKA, M. & BALAZS, G. H. 2006. Age and growth in olive ridley seaturtles (*Lepidochelys olivacea*) from the North-central Pacific: a skeletochronological analysis. *Marine Ecology,* 27**,** 263-270.