School of Molecular and Life Sciences
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Spatial and Temporal Variation of Reef Fish Assemblages in the Galapagos Archipelago: The Influence of Biogeography, Management and ENSO

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The thesis is presented for the Degree of
Doctor of Philosophy
of
Curtin University

March 2022

Author's Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council Australian code for the care and use of animals for scientific purposes 8th edition (2013). The proposed research study received animal ethics approval from the Curtin University Animal Ethics Committee, Approval Number # AEC_2014_09.

Etienne Yves Marie Rastoin,
18 March 2022

Acknowledgement of Country

I would like to acknowledge the traditional owners and custodians of the land on which I have had the extraordinary privilege to live and study for the past four years. This land has kept me safe, allowing me to stay focused on my work during the COVID-19 world crisis, while also providing ample opportunities to elevate my spirit. For that, I will be forever grateful. I therefore wish to pay my deepest respects to the Whadjuk Noongar ancestors and members of their communities, past, present, and to their emerging leaders. I add my voice to Curtin University’s commitment to work with all Australians and peoples from across the world, including the First Nations peoples. As a graduate I will strive to exemplify Curtin’s values and be an agent of pacification and reconciliation in Australia and the world at large.

Abstract

The unique oceanographic setting of the Galapagos Islands has created a thriving and unique marine ecosystem which attracts researchers, fishers, and visitors alike. The creation of the Galapagos Marine Reserve (GMR) in 1998 was an attempt to balance increasing human use and conservation priorities. Yet, the decline of key fisheries resources in the archipelago raises questions about the adequacy of the GMR. The predicted intensification of El Niño Southern Oscillation (ENSO) under climate change scenarios may threaten the long-term resilience of the islands' ecosystems. Based on a dataset of ~158 000 observations of fish counted from ~1200 baited remote underwater stereo-video systems (stereo-BRUVs) surveys, the four chapters of this thesis aim to contribute ecological insights which can be used to improve the management of the Galapagos fish populations.

While the GMR management plan (1999) established the need for adequate protection of all biogeographical regions, Edgar et al. (2004a) found that some bioregions were underrepresented in the current zoning scheme. I re-evaluate spatial patterns in fish biogeography in the Galapagos using stereo-BRUVs data (Chapter 2). I found that the patterns in fish biogeography from the stereo-BRUVs data were consistent with that of Edgar et al. (2004a) recorded from UVC surveys in 2000-01. However, my sampling also targeted coastal pelagic fishes using mid water stereo-BRUV systems. I found a similar biogeographical separation for the coastal mid-water environment, but with less well-defined zonation. My findings support the need to adjust the GMR zoning and provides new information for the management of the coastal mid-water environment where fishing effort is redirected as traditionally exploited benthic species decline.

To date there has been no assessment of the impact of the GMR zoning on finfish. Using stereo-video length-based metrics I assess the effects of different levels of fishing pressure, both inside and outside no-take zones for a range of species (Chapter 3). Data analysis and interpretation show that while certain species were larger within no-take zones when compared to fished zones, they did not display the steep recovery that would be expected in well-enforced marine reserves. Epinephelid species are of particularly concern, as no significant

increase in the percentage of mature and mega-spawner individuals was found within no-take zones. This suggests that fish populations managed by the GMR zoning would benefit from changes in the design and enforcement of the GMR and that alternative management measures need to be considered.

Finfish assemblages in the Galapagos islands are threatened by the dual effects of fishing and extreme ENSO events which can have devastating impacts on the marine environment and may intensify under climate change scenarios. I assess the effects of the 2015-16 ENSO on finfish populations (chapter 4). The 2015-16 ENSO was considered to be of moderate strength in the Eastern Tropical Pacific. I found that small pelagic fish populations displayed strong fluctuations with mackerels (i.e. *Trachurus murphyi* and *Decapterus* spp.) showing a five-fold higher biomass, 229% greater relative abundance, and a 20.6% greater average size during the La Nina build-up compared to onset of El Nino. Over 30 other species displayed abundance fluctuations that were probably associated with the different ENSO phases. These findings have important implications as small pelagic fish are an important basis of the marine trophic chain while sustaining major fisheries operations in the Eastern Tropical Pacific.

Fish spawning aggregations urgently require improved management globally as they are crucial event in reef fish reproduction. The targeting of spawning aggregations has impacted finfish populations globally and in the Galapagos. I assess the potential of diver-operated stereo-video surveys (stereo-DOVs) to characterize and monitor reef fish spawning aggregation using stereo-video recordings of the labrid *Bodianus diplotaenia* in the Galapagos (Chapter 5). Using stereo-DOVs I was able to accurately collect key metrics for the monitoring and characterization of spawning aggregations (e.g. size distribution and abundance), making it an ideal but underutilized non-invasive tool in the fisheries managers' toolkit.

Acknowledgments

In my eyes, my PhD journey started well before my enrolment at Curtin University. It was a path of perseverance from the beginning to the end of the academic curriculum. I carry gratitude, love, and deep respect for the many people in my life who gave me the strength to start and supported me until the end. Through these words, I want to acknowledge the people and institutions who were pivotal in creating the fertile and firm ground for this formative part of my life to unfold.

My first thoughts go to my parents, Nathalie and Antoine. From the beginning through to the end of my academic journey, they have been nothing but a voice of loving support, making it possible for me to even think that a PhD was something I was fit to tackle. From granting me the liberty to choose my own path at every crossroads, to their invaluable guidance in times of struggle, they continuously play the most fundamental role in shaping who I am in this world. My love also goes to my siblings, Mathilde and Romain. I could not have hoped for better companions to grow up with and our relationship is one of the most precious thing in my life. I also have deep gratitude for my step-mum, Sylvie and step-dad Jean-Paul, for fostering a loving family environment which allowed me to recharge on home grounds when it was necessary. I will not name each of my uncle or aunts, neither my 42 first-degree cousins, but I cherish many beautiful relationships in this family circle.

A very special acknowledgment goes to my girlfriend Yappo. Meeting you has been the most unexpected and beautiful gift I could have hoped for during my PhD time. Your presence in my life has given me clarity about the kind of person I want to be. Your daily support and love (and delicious cooking) has allowed me to stay afoot and rejoice in knowing that you would be waiting for me at home after the long computer days. I am deeply grateful for your patience and capacity to put up with the never ending “*just one more month*”, followed with the “*just one more week*”. I could not be more excited about what we will create together as a new life chapter begins. I love you and could not have completed this PhD without you.

Along the path, many friends have been significant influences and supports, providing me with opportunities to grow and stimulating the desire to be a positive force in society. Around my hometown, Marseille, this includes Sylvain, Jeanne, all the Guillaumes, Helena, Pierre, Marianne, Thibault, Fred, Remi, Manue, Fatou, Fanny, Claude, Anne, and Jeremy. From my Masters degree, Aude, Adrien, Arthur, Yohann, Corto, Florian, Camille are among the people with whom I built strong friendships, which lasted to this day. In Galapagos, a whole group of people contributed to creating three of the most remarkable and unforgettable years of my life, including Valeria, Suelen, Lisa, Julio, Jorge, Jose, Danni, Gonzalo Salome, Natalie, Elena and Lola, David, Juanito, and Rose. In Perth, my PhD friends, Esteban, Johanna, Lisa, Miwa, Clara, Damien, Simon, Melissa, Alishum, Jason, David, and Maarteen have provided an opportunity to share experiences and tame worries, creating a sense of togetherness which made this experience relatable and less daunting. Also in Perth, Marcelo, Richard, Simon, Chu, Jing, Yang, Tagrid, Peter, Jackson, Joshua, Dannisa, Naiti, Amy, Libby, Ulli and the Haus Anna crew, as well as the dance community, have all contributed to a supportive environment, providing occasions to unplug and recharge away from the white page. All these amazing people deserve a warm and wholehearted thank you and I am no doubt forgetting a few.

A few people played a crucial role and allowed me to initiate, nurture, and grow my relationship with this amazing place that is the Galapagos Archipelago. Oddly so, I would likely never have arrived in the Enchanted Islands without the very brief, but pivotal help of Dr. Sylvia Earle. Back at the 3rd International Marine Protected Areas Congress (IMPAC3), I attended her Mission Blue keynote presentation and followed with a daring ask for professional contacts in the Galapagos. Through her, I was introduced to Dr. Pelayo Salinas de León from the Charles Darwin Foundation. He was also attending IMPAC3 and our fortuitous encounter would soon lead me to join his marine research team. To prepare for my Galapagos job interview, Nicolas and Alexandra, welcomed me into their Barcelona home for 5 weeks of intense Spanish practice as an au-pair. Their trust and decision to welcome me into their family at a three-day's notice is top-of-the-list of the most beautiful things that someone has done to support my professional development. Once in Galapagos, Dr Pelayo Salinas de León played a central role, as a friend and mentor. He challenged me to grow professionally at fast speed and develop a strong work ethic. He also helped me develop a wide range of fieldwork skills which led to some of the most mind-blowing experiences and encounters a young marine biologist could dream of. I will live with those memories my entire life. Without his passion and dedication for operational research, I would never have entertained the thought I could pursue a PhD and my project would not have started without him believing in my capacities. I also want to thank him for the critical feedback and perspectives he's given me as a

PhD supervisor as this led me to push further and improve my research. Also in Galapagos, Dr Arturo Izurieta, former Charles Darwin Foundation Director, also showed great trust and supported me in taking responsibility for the large video dataset that constituted the basis of my PhD research. Lastly, I cannot downplay the influence of Dr. Enric Sala, Bob Ballard, and Thomas Peschak in giving me insights into the kind of professional endeavours that could arise from doing a PhD. To all those remarkable individuals, I want to express my most heartfelt gratitude. None of this would have been possible without your support and benevolent eye on me.

At Curtin University, my most special and warm acknowledgement goes to my main supervisor Professor Euan Harvey. Professor Harvey has perhaps been the most amazing mentor I have had the privilege to interact with. His dedication to training the young generation of marine scientists is truly admirable. Throughout my entire project, his presence has consistently allowed me to stay on track and grow as a scientist. He also has an unusual gift to diffuse the anxieties that naturally build up along the PhD path. So much so, that any work meeting with him would end with the strange impression that everything was under control, all the way back to our first meeting in Ecuador. When I hear about the experiences of some colleagues with their main supervisors, I feel incredibly grateful for the supervisory hand I was dealt. I would also like to thank my Curtin University co-supervisors, Dr. Jordan Goetze and Dr. Benjamin Saunders, for their in-depth critical feedback, as well as their in-person assistance all along my PhD. It has been a pleasure to work under your guidance.

I would also like to give thanks to Curtin University staff, students, and institution at large for making my PhD life such a vibrant, memorable, and well-supported experience. I want to specially thank Carey Ryken-Rapp for her countless contributions to facilitating my PhD administrative journey, she went above and beyond and her kind presence made a substantial difference from day one. I would also like to thank my two thesis Chair, Professor Kate Trinajstic and Professor Damien Arrigan who have always been supportive and available when I needed to talk to them. I express my gratitude to the Graduate Research School team for providing prompt and well-meaning assistance through my time at Curtin and having supported my PhD project from start to finish. My thanks also go to the Fish Ecology Lab team, Laura Fullwood and Demon Driessen especially, for their kind and patient help in trouble shooting the most glitchy stereo-video analysis of all time. I also want to express my sincere gratitude to each of the volunteers who helped with the video analysis over the years, in large or small ways, including, Hannah, Megan, Sasha, Simon, Andrea, Courtney, Corinna, Nicole, Martha, Jorja, and Kyler. At the school of Molecular and Life Sciences, I want to thank the various research staff for the stimulating conversations and encouragements received, including, Nicole, Monique, Shane, Zoe, Claus, Bill, and Kingsley. I would also like to acknowledge all the people who have supported the C3 Project, the side gig sustainability project I launched at Curtin. This project involved far too many people to name them all, but I'd like to thank all the collaborators from Curtin Properties, Curtin place activation, Curtin sustainability policy institute, Curtin research office, Curtin Careers, employment and leadership, Curtin guild, as well as the researchers from the School of marketing, Design and built environment, and Molecular and life sciences. I would also like to thank my co-founder Joshua for his support and the great friendship we developed along the way. Leading the C3 Project has taught me a lot and I will carry those insights into the next big projects I intend to create. I also learned a lot from participating in the Curtin Three Minute thesis and Famelab academic public speaking competitions and would like to thank the amazing teams behind these initiatives. I have also been tremendously supported during my entire PhD project from the amazing people at Curtin Counselling, they all deserve a heartfelt acknowledgement. Finally, I would like to warmly thank all the Curtin gardeners who keep this place so beautiful for students and staff to enjoy and rejuvenate outside the office doors. I have taken innumerable head-clearing walks and gotten to know the gardens of this campus so intimately that I will miss them dearly. Overall, all of these teams and individuals contributed to turning my PhD into the most invigorating and richest study experience I have had, and I feel deeply privileged for this opportunity.

I keep fond memories of certain teachers whom I met along my academic curriculum and that I would like to acknowledge for the difference they made in getting me interested in the natural world or for the role they played in my development. Mr. Davin, my unconventional middle school English teacher, is responsible for sparking a keen interest in the English language and some of the most enjoyable classroom experiences I can remember. My highschool biology teacher was also a remarkably engaging knowledge keeper, and while her name now escapes me, I would like to give her my thanks for being such a relatable teacher. My higschool physics and chemistry teacher, Ms. Grognu, was one of my biggest supporter and I keep very fond memories of the interactions in her classroom. During my Undergraduate Degree in Toulon, Dr. Pirat, my microbiology teacher, awakened in me a keen eye for the infinitely small. She has supported me through the years since I left her classroom and I would like to thank her for always having something kind and encouraging to say to me. Also from my undergrad, I would like to thank Dr. Grillasca, my genetics and population biology teacher, for first introducing fishes in the classroom. During my AgroParisTech Master's Degree, my fondest memories and warmest acknowledgment go to Professor Mariojouls. Her class on coastal zone management was one of the nicest I followed and the first one to really challenge me to think critically about coastal and marine management. For her on-going support after graduation and what she thaught me, I would like to express my gratitude. Lastly, during my final years in Rennes, Professor Didier Gascuel was the most engaging teacher and the first one to get me interested in high-level fisheries science. To all those amazing teachers who believed in me, as well as those I'm certainly forgetting, I want to say a heartfelt thank you.

I would also like to acknowledge other individuals who enabled specific parts of my PhD project. For their in-person support during the different Galapagos fieldwork campaigns, I want to thank Nicolas Moity, Tyler Eddy, Derek Tittensor, Daniel Boyce, Salomé Buglass, Naiti Morales, Amy Rose Coghlan, Magdalena Mossbrucker, Frida Lara, Natalie Tellwright, Ana Belen Suarez, and more. I also want to thank the crews of MVs "Valeska" and "Queen Mabel" for ensuring the safety of our team and equipment during fieldwork. All the rangers of the Galapagos National Park who took turns to accompany us on the water also deserve a sincere acknowledgment. I also want to give special thanks to Dr. David Acuña-Marrero for his kindness and demonstrating state-of-the-art fieldwork practice which inspired me to follow the path he opened. My gratitude also goes to Stuart Banks, Mathias Espinoza and Fernando Rivera for kindly sharing their knowledge on the Galapagos underwater world and providing useful guidance. A warm thank you also goes to the team of expert ichthyologists at "*Shorefishes of the Eastern Pacific online information system*" as their platform was invaluable to identify the different fish species encountered during my surveys. I am also grateful for the help they provided to confirm problematic identification and kindly allowing me to use fish silhouettes sourced from the platform for my thesis. Lastly, my thanks go to Philippe Béarez for providing complementary data for my fifth chapter.

To finish, I would like to acknowledge all the key institutions who contributed to making this project a reality. I am indebted to the Galapagos National Park Directorate for authorising and granting the various research permits that enabled this project. I would like to express my gratitude for the institutional support provided by the Charles Darwin Foundation and Curtin University as my PhD project was executed under their dual umbrella and financial support. This is contribution number 2451 of the Charles Darwin Foundation for the Galapagos islands. This research was conducted under Galapagos National Park Directorate permits (PC-40-14, PC-25-14, PC-26-15 and PC-28-16) granted to Pelayo Salinas-de-León. I also express my gratitude for the Curtin Research Training Program for having provided the majority of the funding for my scholarship. I was also awarded a Curtin Publication Grant to facilitate the publication of my chapters in the scientific peer-reviewed literature and would like to thank the grant committee for supporting my PhD research outcomes. The funding for the field-based part of the project in Galapagos was provided by grants from the Save Our Seas Foundation, Disney Worldwide Conservation Fund, Mohamed Bin Zayed and Lindblad-National Geographic Conservation Funds as well as the Helmsley Charitable Trust. My PhD project would not have been possible without the strong support from all these institutions. They deserve my heartfelt acknowledgments, so do the people behind them.

I may well have omitted people who deserve to be acknowledged. If this happens, this is not intentional, and I hope you will recognize the role you have played in helping me reach the end of this PhD.

With all my sincerity, thank you.

Statement of Contributions

Chapters 2 to 5 of this thesis have been prepared as manuscripts for publication in peer-reviewed journals. These chapters are reproductions of submitted, published, or in-preparation manuscripts, with the exception of formatting consistent with the thesis. Signed author statements can be found in Appendix A and follow the Contributor Role Taxonomy (CRediT) authorship contribution standards. I have obtained permission from the copyright owners to use any third-party copyright material reproduced in this thesis, and to use any of my own published work in which the copyright is held by another party. Permission for paper reproductions in this thesis can be found in Appendix B.

The study presented in **Chapter 2** is in review within the peer-reviewed journal "*Journal of Biogeography*"

Rastoin, E., Salinas-de-León, P., Acuña-Marrero, D., Goetze, J., Saunders, B.J., Ashe, H., Cundy, M., Garcia, R., & Harvey, E.S. Comparative biogeography of benthic and mid-water shore fish communities of the Galapagos: stereo-BRUVs surveys support the use of bioregions for management. *Journal of Biogeography. In Review.*

Authorship contribution statement

To whom it may concern, I, Etienne Rastoin, led and conducted the large majority of the work for this chapter and contributions were as follow. **Etienne Rastoin**: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data curation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Pelayo Salinas-de-León**: Conceptualization, Methodology, Investigation, Resources, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition. **David Acuña-Marrero**: Investigation, Writing – Review & Editing. **Jordan Goetze**: Conceptualization, Methodology, Writing – Review & Editing, Supervision. **Benjamin J. Saunders**: Conceptualization, Methodology, Writing – Review & Editing, Supervision. **Hannah Ashe**: Investigation, Data curation, Writing – Review & Editing. **Megan Cundy**: Investigation, Data curation, Writing – Review & Editing. **Garcia Rodrigo:** Methodology, Software. **Euan S. Harvey**: Conceptualization, Methodology, Resources, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition.

The study presented in **Chapter 3** is in preparation for submission for publication within the peer-reviewed journal "*ICES Journal of Marine Science*".

Rastoin, E., Salinas-de-León, P., Goetze, J., Saunders, B.J., Ayton, S., Zimmerhackel, J., Newman, S., & Harvey, E.S. Length-based metrics suggest limited benefits of Galapagos coastal no-take areas for reef fishes after 15 years of protection. *In preparation for submission.*

Authorship contribution statement

To whom it may concern, I, Etienne Rastoin, conducted the large majority of the work for this chapter and contributions were as follow. **Etienne Rastoin**: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data curation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Pelayo Salinas-de-León**: Conceptualization, Investigation, Resources, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition. **Jordan Goetze**: Conceptualization, Methodology, Software, Writing – Review & Editing, Supervision. **Benjamin J. Saunders**: Conceptualization, Methodology, Software, Writing – Review & Editing, Supervision. **Sasha Ayton**: Investigation, Data curation, Writing – Review & Editing. **Johanna Zimmerhackel:** Conceptualization, Methodology, Writing – Review & Editing. **Steven Newman:** Writing – Review & Editing. **Euan S. Harvey**: Conceptualization, Methodology, Resources, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition.

The study presented in **Chapter 4** is in preparation for submission for publication within the peer-reviewed journal "*Scientific Reports*".

Rastoin, E., Salinas-de-León, P., Goetze, J., Saunders, B.J., McKinley, S., Mattingly, A., Norris, C., Gosby, C., Garcia, R., & Harvey, E.S. Fluctuations of Galapagos mid-water and benthic reef fish populations during the 2015-16 **ENSO.** *In preparation for submission.*

Authorship contribution statement

To whom it may concern, I, Etienne Rastoin conducted the large majority of the work for this chapter and contributions were as follow. **Etienne Rastoin**: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data curation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Pelayo Salinas-de-León**: Conceptualization, Methodology, Investigation, Resources, Writing – Review & Editing, Project Administration, Funding Acquisition. **Jordan Goetze**: Conceptualization, Methodology, Writing – Review & Editing. **Benjamin J. Saunders**: Conceptualization, Methodology, Software, Writing – Review & Editing. **Simon McKinley:** Investigation, Data curation, Writing – Review & Editing. **Mattingly Andrea:** Investigation, Data curation, Writing – Review & Editing. **Courtney Norris:** Investigation, Data curation, Writing – Review & Editing. **Gosby Corinna:** Investigation, Data curation, Writing – Review & Editing. **Rodrigo Garcia:** Methodology, Software, Writing – Review & Editing. **Euan S. Harvey**: Conceptualization, Methodology, Resources, Writing – Review & Editing, Project Administration, Funding Acquisition.

The study presented in Chapter 5 was published within the peer-reviewed journal "*Estuarine, Coastal, and Shelf Science"* on the 30th September 2020.

Rastoin, E., Goetze, J., Harvey, E.S., Acuña-Marrero, D., Fernique, P., & Salinas-de-León, P. (2020). A diver operated stereo-video approach for characterizing reef fish spawning aggregations: The Galapagos Marine Reserve as case study. *Estuarine, Coastal and Shelf Science, 243*, 106629. https://doi.org/10.1016/j.ecss.2020.106629.

Authorship contribution statement

To whom it may concern, I, Etienne Rastoin, conducted the large majority of the work for this chapter and contributions were as follow. **Etienne Rastoin:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Jordan Goetze:** Methodology, Writing - review & editing, Supervision. **Euan S. Harvey:** Resources, Writing - review & editing, Supervision, Project administration. **David Acuña- Marrero:** Investigation, Writing - review & editing, Visualization, Funding acquisition. **Pierre Fernique:** Methodology, Software, Formal analysis, Writing - original draft, Visualization. **Pelayo Salinas-de- León:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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List of Abbreviations

CAP	Canonical analysis of principal coordinates
DNPG	Galapagos National Park Directorate
ENSO	El Niño Southern Oscillation
FL	Fork length
GLM	Generalized linear model
GMR	Galapagos Marine Reserve
KDE	Kernel density estimate
Maxn	Maximum number
MPA	Marine protected area
nm	Nautical mile
nMDS	Non-metric multidimensional scaling
NTZ	No-take Zone
PERMANOVA	Permutational multivariate analysis of variance
PERMDISP	Permutational analysis of multivariate dispersions
SIMPER	Similarity percentage analysis
SIMPROF	Similarity profile test
Stereo-BRUVs	Baited remote underwater stereo-video system
Stereo-DOVs	Diver-operated stereo-video survey
TEP	Tropical Eastern Pacific
UVC	Underwater visual censuses

Chapter 1 Introduction

1.1 Background and Rationale

1.1.1 Brief history of the Galapagos Marine Reserve and its management

The Galapagos Islands are home to some of the most unique marine and terrestrial ecosystems in the world (DPNG, 2005, 2014) and have inspired many generations of scientists since the visit of Charles Darwin in 1832 (Trueba et al., 2013; Walsh & Mena, 2013). Significant efforts from first generation conservationists were pivotal in the creation of the Galapagos National Park in 1959 and their inclusion as the very first UNESCO World Heritage Site in 1978 (Quiroga, 2013). However, the Galapagos Marine Reserve (GMR) as we know it today was enacted much later in 1998 (DPNG, 1998; Heylings et al., 2002; Reck, 2014). Unlike the creation of its terrestrial counterpart which set aside 97% of the islands' area as National Park, this world-renown marine protected area has been shaped through a long and laborious iterative process with several key stages as outlined below.

1986: The creation of the Galapagos Marine Resources Reserve with the primary aim of regulating marine resources extraction and artisanal versus industrial fisheries uses in the archipelago. The reserve encompassed the area within 15 nautical miles of the Galapagos baseline, an imaginary line connecting the outer most islands of the archipelago.

1992: The adoption of the Galapagos Marine Resources Reserve Management Plan which segregated fisheries spatially through:
i) excluding industrial fishing from within 5 nautical miles of the baseline,
ii) granting exclusive fishing rights to locally registered artisanal fishers along the coastal fringe.

1998-99: The creation of the 138 000 km^2 Galapagos Marine Reserve (GMR) and adoption of the Galapagos Marine Reserve Management Plan. The GMR Management plan led to:

i) expanding the exclusion of industrial fisheries to 40nm of the baseline and grant exclusive fishing rights to locally licensed fishers within this area,
ii) establishing a new participatory fisheries co-management regime,
iii) regulating authorized fishing gear within the reserve,
iv) setting time targets for the development of a spatial zoning for fishing, tourism, and conservation zones, and
iv) establishing adaptive management as a guiding principle for the GMR with the need to assess and monitor its success based on socio-economic and biological indicators.

2002: The provisional zoning scheme within the Galapagos Marine Reserve is ratified setting aside 18% of the coastline fringe within 2 nautical miles or 0.8% of the total GMR surface as no-take.

2014: Initiation of the re-zoning process of the GMR to better integrate land/ocean connectivity and maintain key ecosystem services in the Galapagos Archipelago. At sea, zoning reform resulted in the proposed expansion of no-take zones areas to include large extents of open ocean beyond 2 nautical miles.

Despite this existing management framework, the ideology of the Galapagos being a pristine environment devoid of human impacts where discrete visitors can observe evolutionary processes is far from reality (Hennessy & McCleary, 2011; Valle, 2013). Exponential increases in population and tourism at the turn of the century, combined with collapsed fisheries, increasing rates of invasive species and overwhelmed management institutions, led to the temporary listing of the Galapagos on the UNESCO endangered world heritage sites between 2007 and 2010 (Hennessy & McCleary, 2011). This listing focussed the attention of the international community on this iconic archipelago and highlighted the inadequacies between long-term sustainability and conservation goals on one hand, and the current globalized development trends of the islands on the other hand (Orellana & Smith, 2016). To address this conflict, it was recognised that the Galapagos needed to be managed as a complex socio-ecological system instead of trying to dissociate humans from nature, as had been done in the past (González et al., 2008; Denkinger & Vinueza, 2014; Castrejón et al., 2014). This change in management strategy has created opportunities to develop more inclusive management policies by making it clear that long-term human well-being on the islands cannot be dissociated from a well-preserved insular environment.

This link between people's well-being and ecosystem health is apparent in the overarching goal of the Galapagos Marine Reserve established in 1998. That is "*Protecting and conserving the marine coastal ecosystems of the Galapagos Archipelago and its biological diversity for the benefit of humanity, the local populations, science, and education"* (DPNG, 1998). To fulfil this mandate, adaptive management is a guiding principle both in the original 1998 GMR Management Plan and its successor, the 2009 GMR Management Plan Fisheries Chapter (DPNG, 1998; Comisión Técnica Pesquera, 2009). These plans acknowledge the importance of evaluating the success of specific management measures, based on biological and socio-economic indicators generated through sound scientific inquiry, and adapting them if necessary. In particular, the Fisheries Chapter states: "*The management measures for each fishery (e.g. finfish, lobsters, see cucumbers) will be periodically evaluated and adapted based on the new scientific information generated regarding the status of the resource and the socio-economic situation of the fisheries*".

1.1.2 Conservation Biogeography in the Galapagos

The Galapagos archipelago is located at the confluence of four major ocean currents in the Tropical Eastern Pacific (Figure 1.a) (Snell et al., 1996; Glynn, 2002; Palacios, 2004; Liu et al., 2013). Three predominantly cold currents (i.e. Equatorial Under Current, Equatorial Counter Current, and Humbolt Current) and the warm Panama current impinge on the steep topographic features of the Galapagos platform, creating localized upwellings and distinct environmental conditions throughout the Galapagos archipelago (Palacios, 2004; Liu et al., 2013). In response to this unique oceanographic and topographic setting, distinct biological communities have emerged across the archipelago (Bustamante et al., 2002; Edgar et al., 2004a; Edgar et al., 2008).

The principle of biogeographic representation (Whittaker et al., 2005) has guided the spatial management planning of the Galapagos Marine Reserve since its inception in 1998 (Heylings et al., 2002). To conserve important marine communities and sustain key ecosystems functions in the archipelago, each of the recognised marine bioregions was supposed to receive adequate protection under the newly developed no-take zones network. When the zoning was developed and enacted in 2002, there was still no comprehensive understanding of the Galapagos biogeographical subdivisions and it was based on the best data available at that time (Edgar et al., 2004a; Castrejón & Charles, 2013). As a consequence the bioregionalization was based on the work of Harris (1969) which used regional ocean temperature characteristics rather than species distributions to define the distinct regions of the archipelago. The challenges with this approach became evident when Edgar et al. (2004a) published a complete marine bioregionalization of the Galapagos which highlighted important differences in contrast to that based off Harris's work. Edgar et al. (2004a) identified five distinct bioregions based on surveys of reef fish and marine invertebrates and determined that two of the bioregions they identified were underrepresented in the GMR zoning scheme (i.e the Far North and Elizabeth bioregions). The five bioregions identified included the Far North, the North, the Center-southeast, the West, as well as Elizabeth (Figure 1.b).

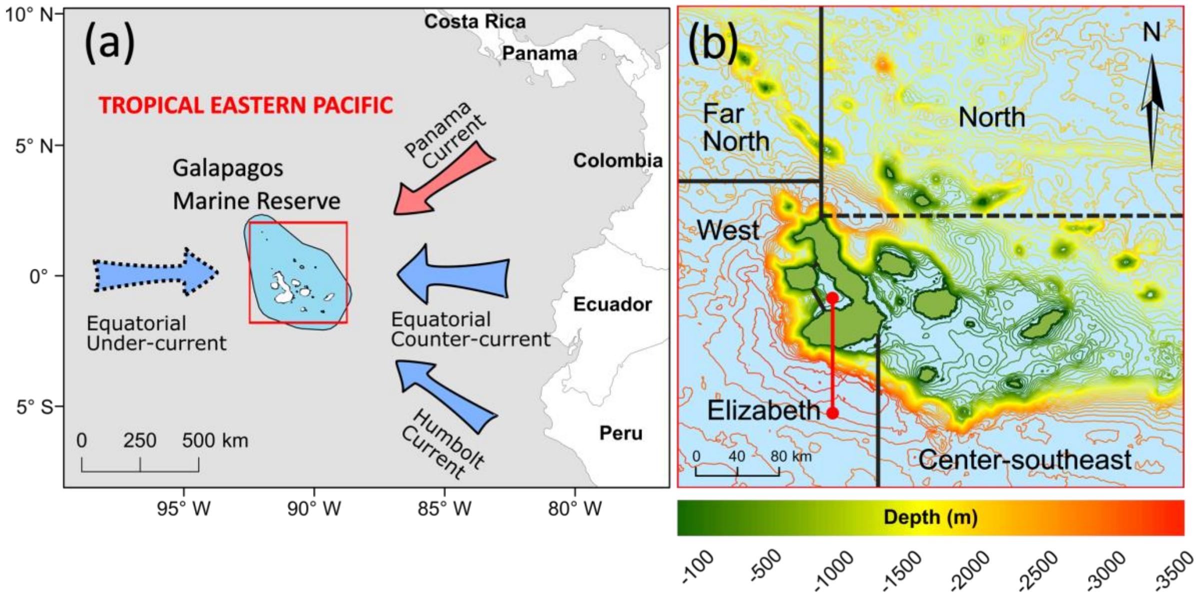


Figure 1.1 a. Location of the Galapagos Marine Reserve in the Tropical Eastern Pacific with schematic view of the prevailing currents converging at the Galapagos. Blue arrows denote predominantly cold currents and red arrow denotes predominantly warm current. Dashed arrow outline denotes deep current while solid outline denotes surface current. b. Bathymetry of the Galapagos platform based on 100 m isobath with the five main bioregions identified by Edgar et al. (2004) based on benthic surveys of reef fish and invertebrates.

Despite Edgar’s observations and the initiation of the GMR re-zoning process, the shortcomings of the GMR zoning remain unaddressed to this day (Castrejón & Charles, 2013; Ministerio del Ambiente del Ecuador, 2018). This is presumably due to a lack of communication during the re-zoning process and push-back from local fishers regarding the proposed zoning adjustments (Burbano et al., 2020; Burbano & Meredith, 2020).

While the research of Edgar et al. (2004a) covered spatial biogeography in detail, it did not consider the potential influence of seasonal fluctuations on biogeographical patterns and only surveyed the benthic habitats. With the over-exploitation of key benthic resources, local fishers are now increasingly targeting the Galapagos pelagic habitat (Zapata, 2006; Ramírez-González & Reyes, 2015; Cerutti-Pereyra et al., 2020). Based on global patterns of benthic and pelagic bioregionalisation of the world’s ocean (Spalding et al., 2007, 2012), it is likely the biogeography of the Galapagos coastal pelagic environment is distinct from that of the benthic habitat. In addition, these is increasing evidence that biogeographical boundaries can shift with ocean warming (Albouy et al., 2013; Villarino et al., 2015; Barton et al., 2016; Frainer et al., 2017; Goldsworthy et al., 2020; McGinty et al., 2021). This suggests it is important to re-examine the current patterns in fish biogeography given Edgar et al. (2004a) surveys were conducted over two decades ago. While Edgar et al. (2004a) used Underwater Visual Censuses, it has been demonstrated that baited remote underwater stereo-video systems (stereo-BRUVs), can also sample the mid-water coastal pelagic environment and give a more comprehensive insight into species diversity than diver based sampling (Watson et al., 2005; Langlois et al., 2010; Watson et al., 2010). Expanding surveys to the mid-water pelagic habitat in coastal areas will help inform the management of the evolving local fisheries.

1.1.3 Shortcomings and evolution of Galapagos fisheries management

Although the 1998 GMR Management Plan established provisions to regulate the activity of artisanal fishers, two important invertebrate and finfish resources continued to decline (Hearn & Pinillos, 2006; Hearn, 2008; Bucaram et al., 2013; Bucaram & Hearn, 2014; Schiller et al., 2014). The over-exploitation of sea cucumbers and lobsters driven by the exponential growth of the fishing sector in the late 90s is well documented and established a premise for mismanagement (Merlen, 1995; Hearn, 2008; Bucaram et al., 2013; Ramírez-González, Moity, Andrade-Vera, & Reyes, 2020). In addition to gear restrictions and zoning measures, a combination of quotas, size limits, and fishing seasons were implemented for key invertebrate species in an attempt to mitigate fishers' impact (Comisión Técnica Pesquera, 2009). These management tools do not apply to any of the key finfish resources in the GMR. There is evidence of a decline in finfish species with a suggestion of a shifting baseline syndrome (Burbano et al., 2014) and the effects of fishing down the food web (Schiller et al., 2014). The most notable case of decline is that of the endemic Galapagos sailfin grouper, *Mycteroperca olfax* (Reck, 1983; Usseglio et al., 2014, 2015, 2016; Eddy et al., 2019; Pontón-Cevallos et al., 2020; Sulaiman et al., 2021). Historically, this species has supported the most economically important artisanal finfish fishery and it is now estimated that there has been a seven fold reduction of its original biomass (Burbano et al., 2014). It is also been suggested that its role as a keystone species in the archipelago has been lost or diminished (Eddy et al., 2019). The decline of traditionally exploited benthic finfish resources led the fishing sector to search for new high value species in the pelagic environment or the deep-sea (Ramírez-González & Reyes, 2015; Marin Jarrin et al., 2018; Cerutti-Pereyra et al., 2020) with the fear that unsustainable exploitation patterns may occur once again (Marin Jarrin et al., 2018; Cerutti-Pereyra et al., 2020).

To address the issue of unsustainable fisheries in the Galapagos, participatory management was proposed as a potential solution (Grenier, 2000; Macdonald, 1997). Years of efforts from conservation actors and social scientists eventually led to the creation of a Participatory Management Board (PMB) which included all Galapagos stakeholders (i.e fishery, conservation and tourism) around the question of fisheries sustainability (Hearn, 2008; Llerena et al., 2017). At the beginning, co-management was seen as the answer to the tense relationship between management institutions and Galapagos fishers and was celebrated as a major conservation success. However, the on-going decline of key resources that the participatory management framework aimed to remediate led to questioning its efficacy (Hearn, 2008; Jones, 2013). The co-management system was eventually described as having failed in its mandate (Castrejón & Charles, 2013) and the PMB was dissolved in 2015 (Llerena et al., 2017).

The other important evolution of fisheries use in Galapagos relates to the significant zoning reform process that was initiated in 2014 (DPNG, 2014), yet has not been implemented. The proposed zoning would expand the total area of no-take zones in Galapagos from ~0.8% to ~33% (Burbano et al., 2020). This important increase is due to the proposed inclusion of large extents of open ocean to protect areas of pelagic and seamount habitats. This reform has received a lot of resistance and has not been implemented (Ministerio del Ambiente del Ecuador, 2018). To date there are no assessments of the effectiveness of the current zoning on fish assemblages and populations which limits the information available for the adaptive fisheries and conservation management. This precludes drawing important lessons from the success or failures of the network of no-take zones in its current form, information which may be important to ensure the success of the proposed reform.

1.1.4 Impact of ENSO on the Galapagos marine environment

El Nino Southern Oscillation (ENSO) is the largest source of inter annual climate fluctuation globally (McPhaden et al., 2006; Santoso et al., 2017), and affects the Galapagos marine environment in profound ways (Valle, 2013). The ENSO related decrease in trade winds and ocean currents in the Tropical Eastern Pacific (Firing et al., 1983; Wang & Fiedler, 2006; Rudnick et al., 2020; Trenberth, 2020) generally leads to an accumulation of warm waters and a decrease in the primary productivity in the archipelago (Barber & Chavez, 1983; Barber & Chávez, 1986; Banks, 2002). These environmental changes have a knock-on influence across the entire marine food web. The impacts of historical ENSO events (i.e. 1982-83, 1997-98) range from massive die-offs of marine mega-fauna (Trillmich, 1985; Valle et al., 1987; Laurie, 1990; Trillmich & Dellinger, 1991; Boersma, 1998; Vinueza et al., 2006), wide-spread bleaching and reduction or coral populations (Glynn, 1984, 1994, 2000 ; Fong & Glynn, 2000), as well as drastic shifts in benthic habitat structure (Edgar et al., 2010). While ENSO is a naturally recurring phenomenon with species evolving to cope with its influence (Stenseth, 2002; Lu et al., 2018; Emile-Geay et al., 2020), the likely intensification of ENSO events under climate change scenarios may threaten species capacity to recover from those perturbations (Cai et al., 2014; Oliver et al., 2018; Cai et al., 2020). The main concern lies in the cumulative effect of natural and anthropogenic impacts (Botsford, 1997; Heithaus et al., 2008; Baum & Worm, 2009; Edgar et al., 2010; Salinas-de-León et al., 2020). For example, Galapagos artisanal fisheries reduced the biomass of species fulfilling important ecosystems functions, which may in turn exacerbate the effects of ENSO (Edgar et al., 2010). While the impact of ENSO on the Galapagos marine environment is strongly mediated by finfish taxa (Wolff et al., 2012), there has been no assemblage-wide in-situ assessment of ENSO influence on finfish. Information on the effects of ENSO on finfish populations and assemblages are needed to better understand how they respond to ENSO and to develop adaptive management measures to mitigate its impact to marine ecosystems.

1.1.5 Towards managing spawning aggregations in Galapagos

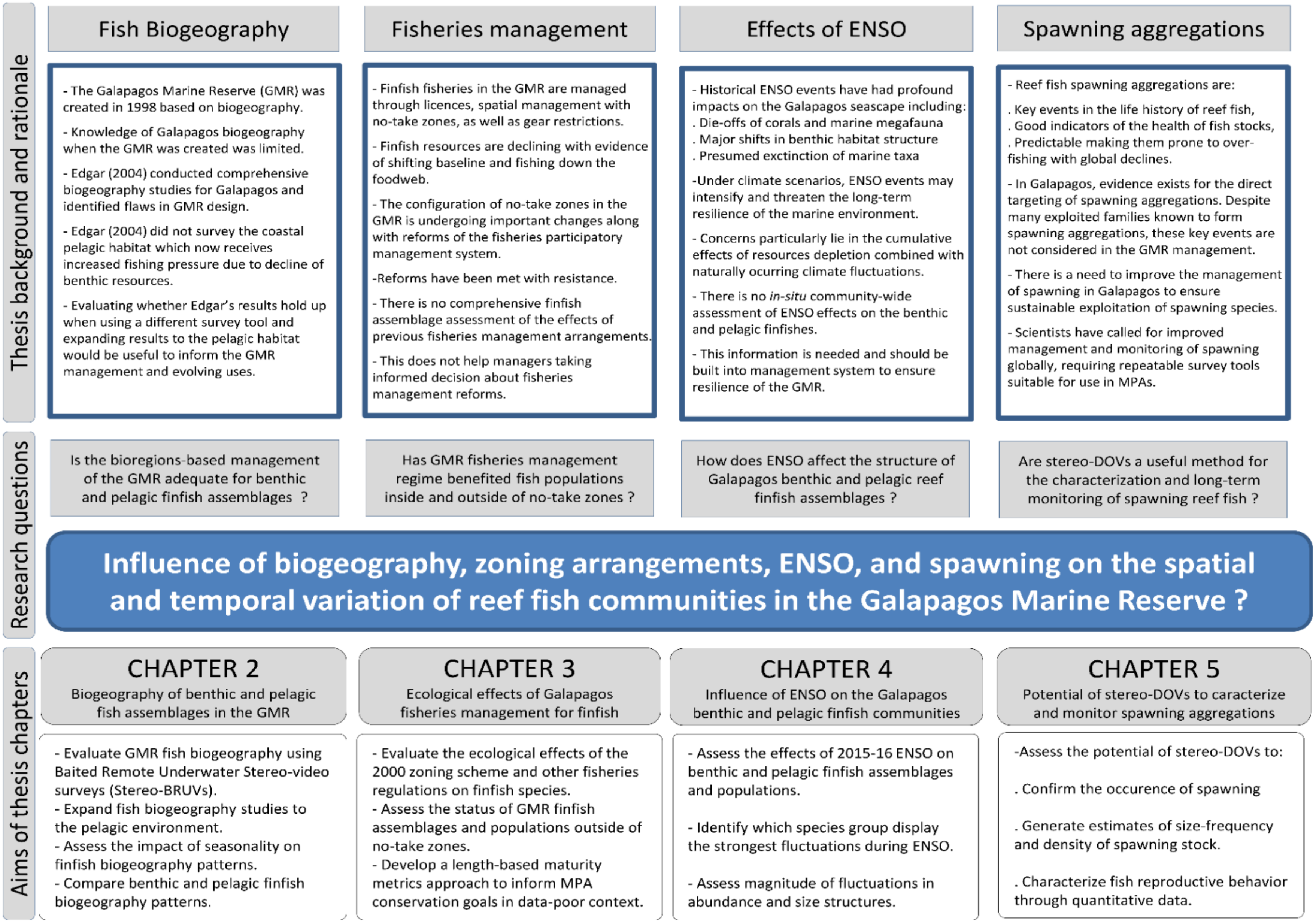
Fish spawning aggregations are events where fish aggregate in space and time to reproduce, and are key features in the life cycle of many commercially exploited reef fish throughout the world (Domeier & Colin, 1997; Grüss et al., 2014; Erisman et al., 2017). Their predictable nature makes them vulnerable to over-fishing which has led to a globalized decline in spawning aggregations (Beets & Friedlander, 1998; Sala et al., 2001; Hamilton et al., 2005; Sadovy de Mitcheson & Domeier, 2005; Aguilar-Perera, 2006; Buckley et al., 2017; Erisman et al., 2019). There is a need to develop methods to monitor spawning aggregations to ensure the sustainability of reef-fish fisheries (Grüss et al., 2014; Erisman et al., 2017; Heyman et al., 2019).

Even though there is evidence for the direct targeting of spawning aggregations in the Galapagos (Salinas-de-León et al., 2015), very little research exists. Salinas-de-León et al. (2015) found that aggregations of Galapagos sailfin grouper were directly exploited in the Far North bioregion, highlighting that seasonal closures and size limits may be needed to safeguard the species’ reproductive events. Unfortunately, spawning aggregations are not considered in the management plan of the GMR (Comisión Técnica Pesquera, 2009). To ensure the long-term sustainability of Galapagos reef-fish fisheries there is a need to improve the management of spawning aggregations in the archipelago and implement robust tools for monitoring spawning aggregations of fish.

1.2 Research Questions and Aims

In this PhD thesis, I explore a series of questions relevant to the adaptive management of finfish assemblages and populations in the GMR. Specifically, I investigate temporal and spatial distribution patterns of finfish assemblages in the Galapagos Marine Reserve and how these are influenced by biogeography, fisheries management, ENSO and spawning (Figure 2).

Through my research, I aim to generate new scientific information about finfish assemblages and populations which can be used to inform their management. My PhD research is a collaborative initiative between Curtin University and the Charles Darwin Foundation. Consequently, my research is designed to align with the Charles Darwin Foundation mission which is: "*to provide knowledge and assistance through scientific research and complementary action to ensure the conservation of the environment and biodiversity in the Galapagos Archipelago*".



	Fish Biogeography	Fisheries management	Effects of ENSO	Spawning aggregations
Thesis background and rationale	- The Galapagos Marine Reserve (GMR) was created in 1998 based on biogeography. - Knowledge of Galapagos biogeography when the GMR was created was limited. - Edgar (2004) conducted comprehensive biogeography studies for Galapagos and identified flaws in GMR design. - Edgar (2004) did not survey the coastal pelagic habitat which now receives increased fishing pressure due to decline of benthic resources. - Evaluating whether Edgar's results hold up when using a different survey tool and expanding results to the pelagic habitat would be useful to inform the GMR management and evolving uses.	- Finfish fisheries in the GMR are managed through licences, spatial management with no-take zones, as well as gear restrictions. - Finfish resources are declining with evidence of shifting baseline and fishing down the foodweb. - The configuration of no-take zones in the GMR is undergoing important changes along with reforms of the fisheries participatory management system. -Reforms have been met with resistance. - There is no comprehensive finfish assemblage assessment of the effects of previous fisheries management arrangements. - This does not help managers taking informed decision about fisheries management reforms.	- Historical ENSO events have had profound impacts on the Galapagos seascape including: . Die-offs of corals and marine megafauna . Major shifts in benthic habitat structure . Presumed exctinction of marine taxa -Under climate scenarios, ENSO events may intensify and threaten the long-term resilience of the marine environment. - Concerns particularly lie in the cumulative effects of resources depletion combined with naturally ocurring climate fluctuations. - There is no *in-situ* community-wide assessment of ENSO effects on the benthic and pelagic finfishes. - This information is needed and should be built into management system to ensure resilience of the GMR.	- Reef fish spawning aggregations are: . Key events in the life history of reef fish, . Good indicators of the health of fish stocks, . Predictable making them prone to over-fishing with global declines. - In Galapagos, evidence exists for the direct targeting of spawning aggregations. Despite many exploited families known to form spawning aggregations, these key events are not considered in the GMR management. - There is a need to improve the management of spawning in Galapagos to ensure sustainable exploitation of spawning species. - Scientists have called for improved management and monitoring of spawning globally, requiring repeatable survey tools suitable for use in MPAs.
Research questions	Is the bioregions-based management of the GMR adequate for benthic and pelagic finfish assemblages ?	Has GMR fisheries management regime benefited fish populations inside and outside of no-take zones ?	How does ENSO affect the structure of Galapagos benthic and pelagic reef finfish assemblages ?	Are stereo-DOVs a useful method for the characterization and long-term monitoring of spawning reef fish ?
Aims of thesis chapters	CHAPTER 2 Biogeography of benthic and pelagic fish assemblages in the GMR	CHAPTER 3 Ecological effects of Galapagos fisheries management for finfish	CHAPTER 4 Influence of ENSO on the Galapagos benthic and pelagic finfish communities	CHAPTER 5 Potential of stereo-DOVs to caracterize and monitor spawning aggregations
	- Evaluate GMR fish biogeography using Baited Remote Underwater Stereo-video surveys (Stereo-BRUVs). - Expand fish biogeography studies to the pelagic environment. - Assess the impact of seasonality on finfish biogeography patterns. - Compare benthic and pelagic finfish biogeography patterns.	- Evaluate the ecological effects of the 2000 zoning scheme and other fisheries regulations on finfish species. - Assess the status of GMR finfish assemblages and populations outside of no-take zones. - Develop a length-based maturity metrics approach to inform MPA conservation goals in data-poor context.	- Assess the effects of 2015-16 ENSO on benthic and pelagic finfish assemblages and populations. - Identify which species group display the strongest fluctuations during ENSO. - Assess magnitude of fluctuations in abundance and size structures.	-Assess the potential of stereo-DOVs to: . Confirm the occurence of spawning . Generate estimates of size-frequency and density of spawning stock. . Characterize fish reproductive behavior through quantitative data.

Influence of biogeography, zoning arrangements, ENSO, and spawning on the spatial and temporal variation of reef fish communities in the Galapagos Marine Reserve ?

Figure 1.2 Thesis flow diagram with rationale, research questions, and aims for each chapter.

Chapter 2: Biogeography of benthic and mid-water reef fish assemblages of the Galapagos.

I seek to address the question "*Is the bioregion-based management of the Galapagos Marine Reserve adequate? How do benthic bioregions translate to the mid-water environment?"*

I aim to investigate whether the documented patterns in the Galapagos biogeography are the same as Edgar et al. (2004a) when a different sampling method (stereo-BRUVs) is used. I also aim to evaluate how benthic biogeographical patterns translate to the mid-water coastal environment. Lastly, I aim to compare benthic and mid-water biogeography patterns and evaluate how they are influenced by seasonal fluctuations.

Chapter 3: Evaluation of the ecological effects of GMR fisheries management for finfish.

The question I address in this chapter is: "*Have current GMR fisheries management measures benefited finfish populations*?"

My aim is to evaluate the ecological effects of the Galapagos zoning 2000 for a range of fish species under varying levels of fishing pressure (i.e. high, medium, low). I also aim to assess the overall status of fish assemblages and populations of the GMR outside no-take zones. My last goal is to test a new methodology to inform MPA conservation goals using a stereo-video length-based maturity metrics approach.

Chapter 4: Effects of the 2015-16 ENSO on Galapagos benthic and mid-water reef fish assemblages.

My question in this chapter is**:** "*How does ENSO affect the abundance and size structure of Galapagos reef fish communities*?"

I aim to assess the effects of the 2015-16 ENSO on benthic and mid-water fish assemblage structure, including abundance and sizes. My second goal is to identify which fish species are most impacted by ENSO.

Chapter 5: Potential of diver-operated stereo-video for the characterization and monitoring of fish spawning aggregations.

In this chapter, I asked the question is: "*Is diver-operated stereo-video systems (stereo-DOVs) a useful method for the characterization and long-term monitoring of spawning reef fish?*"
I aim to assess the potential of stereo-DOVS to i) confirm the occurrence of spawning aggregations, ii) generate estimates of size-frequency and density in spawning fish, and iii) characterize fish reproductive behaviour through quantitative data.

Each data chapters in this thesis is formatted as a peer-reviewed journal article. As a consequence, there is some repetitition between the chapters, particularly in the introductions, materials and methods sections.

Chapter 2 Comparative biogeography of benthic and mid-water shore fish communities of the Galapagos: stereo-BRUVs surveys support the use of bioregions for management

2.1 Abstract

We aimed to strengthen our understanding of patterns of marine biogeography in the Galapagos Archipelago by assessing whether currently accepted benthic bioregions translate to the mid-water environment for fishes. I used baited remote underwater stereo-video systems to conduct archipelago-wide surveys of benthic and mid-water fish communities. Locations were sampled during the cold and warm seasons, yielding 598 deployments which were analysed to compare multivariate patterns between bioregions and environments. Bioregion partitioning based on benthic fish community data was more distinct than in previous studies with the Far Northern, Northern, Central-south-eastern, and Western bioregions displaying significantly different community compositions. The main Galapagos bioregions also displayed distinct coastal mid-water fish communities. However, the Northern bioregion was not clearly defined, suggesting three coastal mid-water subdivisions for the archipelago, namely the Far North, North and Central-southeast combined, and the West. Mid-water fish communities displayed higher heterogeneity, lower species richness and were dominated by species with extensive distribution ranges. My study builds upon previous biogeographic studies in the Galapagos by accounting for previous limitations and assessing both benthic and mid-water environments. My results support the currently accepted bioregion scheme, but suggest that the coastal mid-water environment could be divided into three, not four bioregions. Mid-water baited remote underwater stereo-video systems represent a useful tool to study mid-water biogeographical patterns and we recommend its application in other regions of the world to improve our understanding of biogeography in this understudied environment.

2.2 Introduction

Understanding the distributional dynamics of species across space to inform adequate conservation measures forms the basis of conservation biogeography research (Whittaker et al., 2005). Central to this field is the notion that ecosystems are heterogeneous and can be divided into distinct biogeographical regions, named bioregions, where ecological processes shape cohesive biological communities. Accounting for the patchy nature of ecosystems is crucial to develop representative networks of protected areas and ensure the long-term conservation of all biodiversity. This principle of biogeographic representation has guided protected area planning across the world for over half a century (Dasmann, 1972; Diamond, 1975; Udvardy, 1975; Austin & Margules, 1984) and continues to influence the allocation of conservation funds and research efforts to this day (Lourie & Vincent, 2004; Kukkala & Moilanen, 2013; Larrea-Alcázar et al., 2016; Rodríguez et al., 2016; Goldsworthy et al., 2020).

The unique conservation value and oceanographic setting of the Galapagos Islands has long driven research into their marine regionalization to guide the development of management strategies. The islands lie at the confluence of the four main oceanic currents in the tropical eastern pacific (Banks, 2002), where both cold nutrient rich and warm oligotrophic currents drive distinct biological communities across the archipelago. This leads to highly heterogeneous benthic sessile communities developing in different regions of the archipelago (Bustamante et al., 2000), providing distinct habitats for fish assemblages to thrive. Harris (1969) was the first to propose a subdivision of the archipelago into five distinct regions (north, center, center mixed, south, and west) based on consistent differences in sea surface temperature patterns. However, this regionalization relied mainly on abiotic factors and lacked an appropriate biological underpinning. Wellington (1984; 1975) documented archipelago-wide inventories of subtidal marine species, with a particular focus on invertebrates, and suggested that only four main bioregions existed; north, center, south, and west. Complementing those early works, Jennings (1994) conducted Underwater Visual Censuses (UVC) of fishes at ten locations distributed across the different regions initially proposed by Harris (1969). Despite the small sample size, those surveys revealed significant differences in fish community composition supporting a sub-division of the archipelago into five distinct regions. Such inconsistencies became problematic in 1998, as the long-awaited creation of the Galapagos Marine Reserve (GMR) highlighted the lack of comprehensive biogeographical data to guide the development of an adequate zoning scheme (Bustamante et al., 2000; Edgar et al., 2002). Indeed, the GMR aimed at protecting marine biodiversity through a network of no-take marine reserves representative of all bioregions (Heylings et al., 2002), yet the lack of consensus on the actual number and clear definition of boundaries of bioregions made it difficult to direct conservation efforts in the archipelago.

To provide an unequivocal marine bioregionalisation of the Galapagos, Edgar (Edgar et al., 2002, 2004a) completed the most extensive surveys of fish and macro-invertebrate communities to date. This work yielded a clear sub-division of the archipelago into five main bioregions, namely Far Northern, Northern, Central-Southeastern, Elizabeth and Western, which differed substantially from the scheme proposed by Harris (1969). The prime difference was the relative proportion of species with distinct distribution ranges. More specifically, each bioregion is comprised of a unique mix of Peruvian, Panamic, Indo-pacific, widespread, and endemic species, presumably a result of the different currents prevailing in each area. For example, the Northern bioregion, heavily influenced by the Panama Current, showed the highest species richness with Panamic and Indo-pacific taxa dominating. By contrast, the Western and Elizabeth bioregions, where cold currents are prevalent, show the lowest level of species richness, but also the highest proportion of endemic and Peruvian species. Edgar’s work was pioneering, and the large sampling effort provided a much finer definition of boundaries between bioregions whilst identifying areas overlooked by the provisional zoning scheme of the GMR. While this study was a milestone for the Galapagos Islands, it faced a few limitations. The sampling spanned nearly two years but did not account for potential seasonal variations. This is problematic as Galapagos displays two marked seasons with distinct oceanographic regimes (Palacios, 2004). Fish species have been shown to respond to these changes (Llerena-Martillo et al., 2018), potentially blurring the boundaries between bioregions. In addition, Edgar’s surveys mainly sampled benthic rocky reefs habitat. Sampling both benthic and mid-water habitats increases the diversity of species sampled providing better representation of fish assemblages (Clarke et al., 2019). Edgar et al. (2004a) contributed crucial information that advanced marine conservation planning in the Galapagos Islands. Through the use of both mid-water and benthic baited remote underwater stereo-video systems (stereo-BRUVs) we aim to build upon this work, accounting for seasonal variations and encompassing both mid-water and benthic fish species.

Historically, fish biogeography studies have focused on reef-associated species rather than pelagic (Briggs, 1974; Kulbicki, 2007; Rosenblatt, 1967; Sandin et al., 2008; Thomson et al., 1979; Walker, 1960) due to their high diversity, and advanced taxonomic and distribution data (Kulbicki et al., 2013). Attempts to assess marine regionalization of the pelagic environment have predominantly relied on planktonic communities or disregarded biological systems altogether, discriminating different ocean regions using abiotic factors (Spalding et al., 2012). Pelagic fish species are generally gregarious, fast-swimmers and display strong spatial and temporal variability in their distribution which makes them difficult to sample with fisheries-independent methods (Fréon & Misund, 1999). These characteristics also mean that surveys of pelagic fishes tend to yield patchy data which are challenging to analyse statistically (Heagney et al., 2007; Santana-Garcon et al., 2014). In addition, pelagic fish communities display low diversity patterns driven by broad-scale oceanographic processes (Angel, 1993; Gray, 1997) and have a lower level of bentho-pelagic coupling (Grober-Dunsmore et al., 2008). This results in less static boundaries between generally larger pelagic regions (Angel, 1993) as illustrated by a markedly lower number of pelagic sub-divisions of the world’s oceans, with 37 pelagic provinces compared to 62 provinces for coastal and shelf areas (Spalding et al., 2007, 2012). Despite the elusive nature of pelagic species and the variability of their habitat, a number of empirical studies show that it is possible to elicit regional scale spatial differences in pelagic fish communities using stereo-BRUVs (Heagney et al., 2007; Letessier, Meeuwig, et al., 2013; Santana-Garcon et al., 2014) suggesting that stereo-BRUVs may be a useful tool for assessing regional biogeography patterns in mid-water coastal pelagic waters.

Here, we aimed to validate and build upon the previous biogeography studies of the Galapagos Islands (Edgar et al., 2004a) by sampling both the benthic and mid-water environments while accounting for seasonal variability in fish communities. We also aimed at evaluating how benthic and mid-water fish communities compared in terms of composition, diversity, and dispersion. We hypothesized that the main bioregions identified in Galapagos would be significantly different from one another in both habitats. However, we expected biogeographical patterns to be less clearly defined in the mid-water environment compared to benthic habitats. Finally, we anticipated significant difference between benthic and mid-water fish communities with lower diversity and higher dispersion levels for the latter due to the increased presence of pelagic and bentho-pelagic species.

2.3 Materials and Methods

2.3.1 Video surveys

Baited remote underwater stereo-video systems (stereo-BRUVs) were used to survey fish communities around the Galapagos Archipelago. Stereo-BRUVs are now widely recognized as a reliable, low-impact technique for the systematic sampling of fish assemblages with broad applications in MPAs (Cappo et al., 2006; Harvey et al., 2018; Langlois et al., 2020). While it does have biases associated with the use of bait (Harvey et al., 2007) and sampling of low-mobility species (Watson et al., 2005; Stat et al., 2019), this technique mitigates biases associated with diver-based methods while providing robust fish length, distance, and abundance data (Cappo et al., 2003; Shortis et al., 2009).

Each system comprised two GoPro Hero 4 HD cameras (field-of-view: medium, frame rate: 60 fps, video resolution: 1080 p) enclosed in waterproof housings, mounted 70 cm apart on a stainless-steel triangular base bar with a 7 degrees converging angle to allow field of views to overlap (Figure 2.1c) (Acuña-Marrero et al., 2018). Stereo-BRUV systems were calibrated before and after the surveys using a 3D calibration cube for improved measurements accuracy (Boutros et al., 2015). A bait canister made of a cross-section PVC pipe (25 cm l x 8 cm w) drilled with water-circulation holes was placed 1 m in front of the system and filled with 800 g of chopped bait. Yellowfin tuna (*Thunnus albacares*) was used as bait as traditional stereo-BRUVs bait type (i.e. pilchards) were not available in Galapagos. The general design of the systems was adapted from (Santana-

Garcon et al., 2014) to allow the cameras to float above the substrate, operating efficiently in complex-habitat structure and mitigating entanglement issues with large marine animals (Acuña-Marrero et al., 2018). The cameras were moored at a target bottom depth of 25 m using ballast weights (~30 kg), a mooring line and two sets of buoys that maintained the system above the bottom and marked its position at the surface. To sample both the benthic and mid-water fish communities, the mooring lines and buoys were adapted to allow the cameras to hover at two different depths in the water column. “Benthic” cameras floated at 24 m depth ~1 m above the substrate while “Mid-water” cameras floated at 10 m depth ~15 m off the bottom (Figure 2.1d).

At each site surveyed, four benthic and four mid-water camera systems were deployed in alternation with 500 m between drops to maintain independence between samples (Santana-Garcon et al., 2014). Cameras were deployed for a minimum of 100 min as previous pelagic and mid-water BRUVs studies recommend soak time longer than the 60 min which is more common in benthic studies (Letessier, Kawaguchi, et al., 2013; Santana-Garcon et al., 2014; Clarke et al., 2019). This combination of replicates and soak time was also identified as optimum for the Galapagos environment during a preliminary pilot study (Acuña-Marrero et al., 2018). Surveys were conducted during daytime hours while avoiding the dawn and dusk period (Myers et al., 2016).

2.3.2 Sampling design

Sampling occurred in 2015 and was spread across the Galapagos Archipelago with 45 sites selected along the 25 m depth contour following a spatially stratified random design (Figure 2.1a). The Galapagos Marine Reserve was divided into two types of topographic features: Islands and Islets. Islands were individual land feature with a perimeter greater than 5000 m, and “Islets” pooled groups of emerged rocks together whose cumulated perimeter within a 4 km radius was greater than 5000 m. All features with a cumulated perimeter <5000 m were excluded as they did not allow sufficient spatial replication. Islands constituted the largest pool of candidate sites and were further subdivided into 19 representative locations according to orientation, exposure to predominant currents as well as proximity to the 1000 m isobath. Within each location, two sites were randomly selected among a systematic series of points along the 25 m depth contour to allow the deployment of 8 stereo-BRUVs (i.e. 4 Mid-water and 4 Benthic stereo-BRUVs replicates per site, 500 m distant from one another). The location of Pinta, Marchena and Genovesa Islands yielded 5 sampling sites to account for its larger size. The Islets features constituted two additional locations and yielded 4 sites. This selection process resulted in the selection of 45 sites representative of the diverse marine environments and oceanographic conditions present across the Galapagos Marine Reserve. Since rocky reefs account for over 90% of the shallow subtidal habitats in the archipelago below 50 m depth (Bustamante et al., 2002), this was the main benthic habitat surveyed.

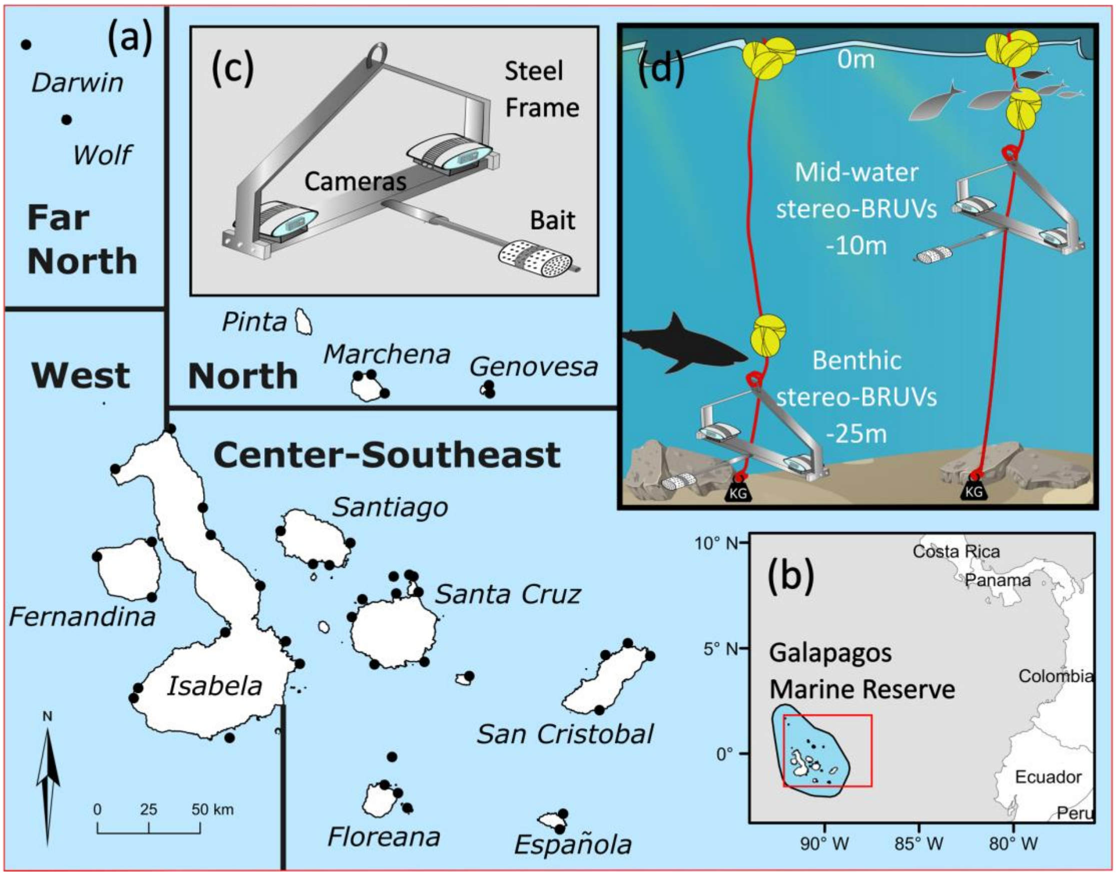


Figure 2.1 a. Map of the Galapagos Archipelago with sites surveyed using stereo-BRUVs during both cold and warm seasons. Each dot represents 8 deployments (4 benthics, 4 mid-waters) deployed 500 m apart from each other over 3.5 km of coastline. The four main bioregions as identified by Edgar et al. (2004) are in bold font and main islands are in italic. b. Location of the Galapagos Marine Reserve (blue surface) 1000 km off the coast of Ecuador in the Tropical Eastern Pacific. Both maps use Aïtoff projection. c. Schematic view of the stereo-BRUVs system used for the surveys. d. Schematic view of the benthic and mid-water stereo-BRUVs configurations.

To account for seasonal variation, the full set of sites was sampled during the warm season (January-June) and cold season (July-December). The resulting sampling design had 4 different factors: bioregions (Far North, North, Center South, Cold West, 4 levels, fixed), sites (45 levels, random, nested in bioregions), sampling environment (Benthic/Mid-water, 2 levels, fixed, fully crossed), and season (Warm/Cold, 2 levels, fixed, fully crossed). Note that the deployments falling in the Elizabeth bioregion were simply considered as part of the wider western bioregion, of which Elizabeth is a local sub-division, due to sites spanning across boundaries between these two zones (Edgar et al., 2004a).

2.3.3 Video analysis

All video footage was analyzed with EventMeasure Stereo SeaGIS software that is specifically designed to process stereo-video data. The videos were analyzed for a period of 90 min with a 5 min delay after the ballast weight reached the bottom to mitigate boat disturbance following Acuña et al. (2018). Species of bony and cartilaginous fish were identified to species level where possible or to broader taxonomic level in the case of a species complex or due to unreliable species level identification. The species complexes considered were *Calamus spp.*, which comprised *Calamus taurinus* and *Calamus brachysomus*, and *Orthopristis spp*., which comprised *Orthopristis forbesi*, *Orthopristis lethopristis*, and *Orthopristis cantharinus.* The two other important species complex categories used were “Mackerels”, which comprised *Decapterus* spp. and *Trachurus murphyi,* and “Skipjack/Bonitos”, which included *Euthynnus lineatus* and *Sarda orientalis* (see Appendix C and D for rare species complexes). Species were individually counted using the dot point function in EventMeasure and *MaxN* were computed (i.e. maximum number of individuals of a given species in a single video frame) following Priede (1994) and Langlois et al. (2020).

To obtain fish distance data, all fish were then 3D pointed at *MaxN* time using the 3D point function in EventMeasure Stereo. The same function was used to obtain the distance of the most distant substrate feature visible in benthic deployments or most distant fish visible in mid-water deployment to estimate visibility. When no fish was present in mid-water deployments, visibility was visually estimated aided by visibility measurements in neighboring deployments. Deployments with less than 4 m visibility were excluded as well as individual fish more than 10 m away from the camera. Data exploration showed that visibility explained less than 3% of the fish community structure and would therefore not confound the results across sites with varying turbidity.

All the above procedures were conducted in three successive steps. A first analyst conducted an initial identification and counts of all the species present. The second analyst reviewed the counts and proceeded to measure, and 3D point all the individuals at MaxN. A third experienced analyst reviewed all the identifications, measurements and 3D points and corrected any mistake to ensure an optimum consistency throughout the dataset. Note that fish length data was also collected through a complementary procedure performed in conjunction with the steps detailed above. Since BRUVs-based fish size information in only used in Chapter 3 and Chapter 4, the detailed method for size collection is provided in the respective methods section of those chapters.

2.3.4 Statistical Analysis

2.3.4.1 Multivariate analysis

Multivariate statistical analyses were conducted in the Primer-E software environment (Clarke & Gorley, 2015) with PERMANOVA+ add-on (Anderson et al., 2008). *MaxN* data was aggregated at site level within depth treatment by summing all *MaxN*s for the 4 benthic deployments and 4 mid-water deployments separately. The resulting data was then presence/absence transformed and a zero-adjusted resemblance matrix was constructed based on the Jaccard similarity measure (Jaccard, 1900). This choice of transformation and similarity measure achieved two complementary goals. First, this removed the influence of heterogeneous dispersion patterns between species therefore producing comparable data between benthic and mid-water communities, the latter typically exhibiting higher dispersion (Fréon & Misund, 1999; Santana-Garcon et al., 2014). In addition, this allowed a meaningful exploration of multivariate dispersion patterns in direct link with faunal composition and traditional biodiversity measures (Anderson et al., 2006).

Following the above, a non-metric multidimensional scaling nMDS ordination procedure was performed. This unconstrained ordination method allows to visualize multivariate data structure without assuming any a-priori groups (Kruskal & Wish, 1978). Differences between bioregions, seasons and benthic and mid-water communities were tested using a distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) and pairwise post-hoc comparisons were used to tease out group-to-group differences. For these tests, the set of H_0 null hypothesis tested were “fish community multivariate structure is the same between bioregions, seasons, and environments (i.e. Benthic and Mid-water)”, with the alternative hypothesis H_A corresponding to “fish community multivariate structure is different between bioregions, seasons, and environments (i.e. Benthic and Mid-water)”.

In addition, a test of homogeneity of multivariate dispersion around group centroids (PERMDISP, Anderson 2006) with post-hoc pairwise comparisons served to determine whether benthic and mid-water fish communities had distinct dispersion patterns. H_0 null hypothesis tested was “no difference in multivariate dispersion between benthic and mid-water fish communities” with the alternative hypothesis H_A corresponding to “multivariate dispersion of benthic and mid-water fish communities is different”. Those estimates of multivariate dispersion were also used to compare non-directional beta-diversity levels between benthic and mid-water environments using the procedure described in Anderson et al. (2006). Since mid-water and benthic fish communities exhibited marked differences, the data was then split to conduct two separate Canonical Analysis of Principal coordinates (CAP, Anderson and Willis 2003) to further investigate group differences. When combined with a leave-one-out allocation procedure, this constrained ordination method allows to explore the robustness of know a-priori groups, in our case bioregions. The H_0 null hypothesis tested by the CAP was “no differences in fish community multivariate structure between bioregions” with H_A alternative hypothesis corresponding to “the fish community multivariate structure differs across bioregions”. Finally, we used a SIMPER analysis to compare levels of similarities across bioregions and habitat (Clarke, 1993). The CAP and SIMPER procedures used a zero-adjusted Bray-Curtis similarity matrix (Bray & Curtis, 1957) rather than a Jaccard (1900) based matrix, as the benthic and mid-water samples were analyzed separately.

2.3.4.2 Species diversity measures, frequency, and distribution ranges

To complement the multivariate procedures, a series of descriptive measures were computed including species frequency of occurrence as well as alpha (α), gamma (ɣ) and beta diversity (βw) (Whittaker, 1960, 1972). Alpha and gamma diversity are both measures of inventory diversity (or species richness), the former being concerned with richness at community level (i.e. site level), while the latter quantifies regional species richness (i.e. bioregion level) (Anderson et al., 2011; Whittaker et al., 2001). Comparisons of alpha diversity between bioregions allows an assessment of the differences in the size of the local species pool which can reveal specific microenvironmental and biotic interactions (Whittaker et al., 2001). Gamma diversity is indicative of the range of environments available within a cohesive geographical extent (Whittaker, 1960). By contrast, beta diversity, computed as [$\beta w=(ɣ/\ \alpha) - 1$], is a differentiation diversity measure which links alpha and gamma diversity (Anderson et al., 2011; Whittaker et al., 2001). Beta diversity quantifies the variability in community structures among sampling units, which can arise from distinct dispersion patterns or habitat heterogeneity (Anderson et al., 2006, 2013). The combination of alpha, gamma, and beta diversity measures can provide insights on micro and macro level ecological processes across bioregions and sampling environments, adequately complementing the multivariate analysis.

In addition, species were classified according to their distribution range following the Tropical Eastern Pacific (TEP) biogeographical categories presented in Robertson & Cramer (2009). The categories were Galapagos endemic (i.e. species strictly endemic to the Galapagos), ocean islands endemic (i.e. species endemic to the islands of Galapagos, Malpelo, and Cocos), Peruvian/Californian/Cortez (i.e. species predominantly distributed in southernmost colder TEP latitudes of the Peruvian region and sometimes also present in the northernmost Californian, and Cortez regions), Panamic/Cortez (i.e. species predominantly distributed in the warmer TEP latitudes of the Panamic and Cortez regions), widespread (i.e. species likely to be encountered in all regions of the TEP, both warm and cold), indo-pacific (i.e. species distributed through the indo-pacific region), circumtropical (i.e. species distribution in the tropical latitudes of all ocean basins). The frequency of occurrence of the most common species were plotted using balloon plots (Wickham, 2016). To optimize the clarity of the balloon plots, we arbitrarily set the minimum frequency of occurrence levels to 30% and 10% for benthic and mid-water species respectively (see Appendix C and D for the full species list frequencies). All data visualization were performed in R (R Core Team, 2013) under the ggplot2 package (Wickham, 2016).

2.4 Results

2.4.1 Data summary and diversity measures

We observed a total of 142 species of fish from 47 families across the archipelago (598 stereo-BRUVs deployments, with 321 benthic and 277 mid-water deployments). At the archipelago level, benthic gamma diversity was over twice that of the pelagic environment with a total of 139 and 66 fish taxa respectively. Overall gamma diversity was similar across bioregions except in the Central-southeast were it was nearly twice as high as in the other bioregions (Table 2.1a). Benthic gamma diversity followed a similar pattern whereas mid-water gamma diversity was twice as high in the Far North and Center-southeast than in the North and West. Within bioregions, benthic gamma diversity levels were markedly higher than mid-water gamma diversity, namely 60%, 242%, 147% and 149% higher in the Far North, North, Center-Southeast, and West bioregions respectively (Table 2.1a). Benthic mean species richness at site level followed a similar pattern and was between two to five-fold higher compared to the mid-water environment. Benthic mean species richness levels were similar in the Far North, North, and Centre-southeast bioregions but ~40% lower in the West (Table 2.1a). By contrast, mid-water mean species richness was comparable between the West, Centre-southeast, and North while it was nearly four times higher in the Far Northern sites (Table 2.1a). Whittaker’s beta diversity measures showed opposite trends to mean species richness with consistently higher levels for the mid-water environment in all bioregions (Table 2.1a). More specifically, mid-water beta diversity was 64%, 115%, 118%, and 191% higher in the Far North, West, North, and Center-southeast respectively.

Table 2.1 a. Mean species richness (α) across sites (n), total species richness or gamma diversity (ɣ), and Whittaker's beta diversity measure [βw=(ɣ/ α) – 1]. b. Distance-based pairwise tests for homogeneity of multivariate dispersion (PERMDISP) testing for difference in mean distance to group centroid between Benthic and Mid-water environments. Bold font denotes significant test. PERMDISP uses zero-adjusted Jaccard-based similarity matrix on Presence/Absence data aggregated at site level (n).

Bioregion	Environment	Sites (n)	Mean Species Richness (α ± SE)	Gamma Diversity (ɣ)		Beta Diversity (βw)	Mean Distance to Centroid (±SE)	PERMDISP P-value
Far North	Benthic	4	39.8 (± 1.9)	61	66	0.53	25.6 (± 1.2)	0.169
	Mid-water	4	20.3 (± 3.3)	38		0.87	31.9 (± 3.7)	
North	Benthic	6	34.5 (± 2.2)	65	69	0.88	30.9 (± 1.5)	0.106
	Mid-water	6	6.5 (± 1.7)	19		1.92	40.8 (± 4.3)	
Central-SE	Benthic	55	34 (± 0.8)	119	125	2.50	39.5 (± 0.7)	**<0.001**
	Mid-water	54	5.8 (± 0.5)	48		7.28	50.4 (± 0.8)	
West	Benthic	16	21.4 (± 1.2)	62	66	1.90	40.3 (± 1.8)	0.078
	Mid-water	16	4.9 (± 0.6)	25		4.10	45.9 (± 2.1)	

(a) (b)

2.4.2 Community structure

The nMDS illustrated a difference in mid-water and benthic fish community structure in multivariate space (Figure 2.2). When looking at the benthic environment, there was a clear separation between the four bioregions with minimal overlap between clusters of sites (Figure 2.2). There was a gradient in benthic community structure from Far North to North to Center-southeast to West (Figure 2.2). However, differences between bioregions in the mid-water environment were not as evident with important overlap between clusters and only the Far North bioregion clearly separated. In the Far North, benthic and mid-water clusters of sites also appeared closer in multivariate space compared to the other three bioregions (Figure 2.2). In addition, the nMDS displayed a generally higher multivariate dispersion within mid-water clusters. Similarly, mean distance to centroid, which quantifies multivariate dispersion and beta diversity, was 14% to 32% higher in the mid-water environment (Table 2.1b). However, the PERMDISP revealed that the Centre-southeast was the only bioregion where mid-water beta diversity was significantly higher than benthic (Table 2.1b).

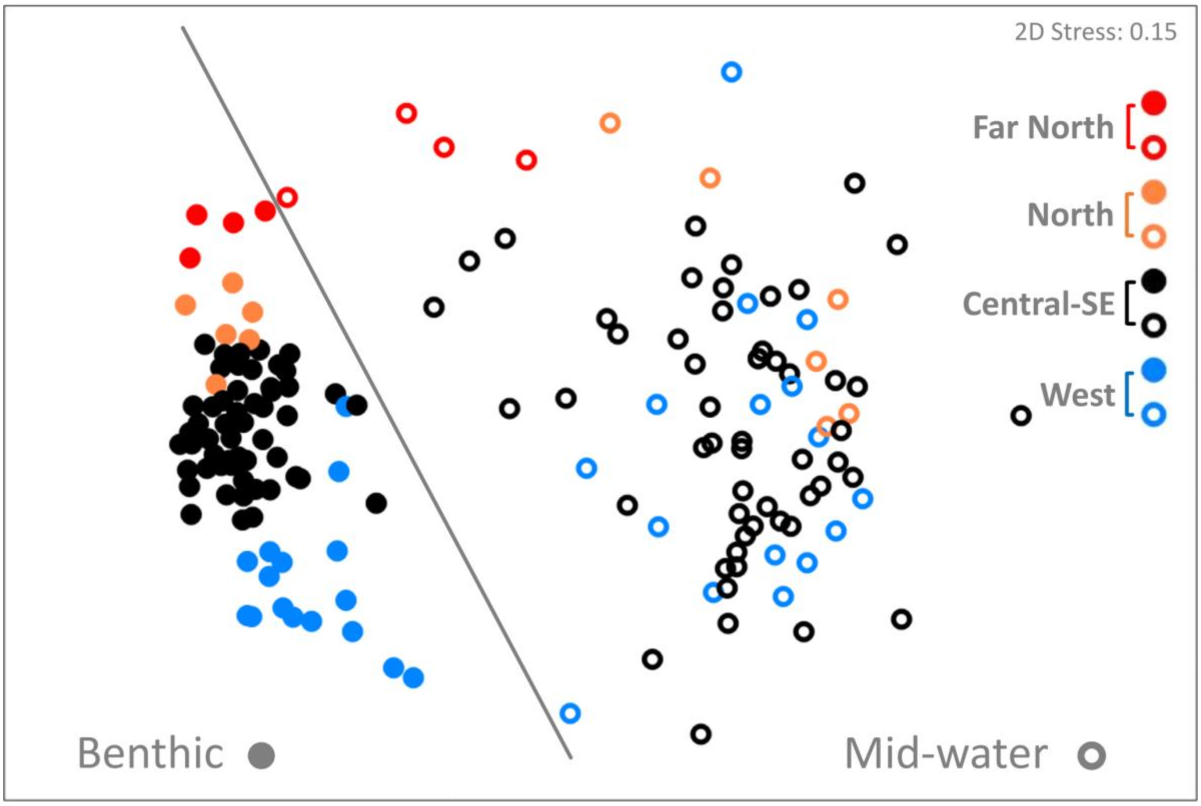


Figure 2.2 Non-metric multi-dimensional scaling showing differences in multivariate patterns of Benthic and Mid-water fish assemblages across the four bioregions considered (Far North, North, Central-Southeast, and West). Ordination based on zero-adjusted Jaccard similarity matrix using Presence/Absence data aggregated at site level (each dot represents 4 Benthic or Mid-water deployments).

There was a significant interaction between bioregion and environment (Table 2.2). All relevant PERMANOVA pairwise comparisons of fish community structures between bioregions and environments were significant at α=0.05, suggesting that the interaction is likely due to difference in the magnitude of the bioregion effect between environments.

Table 2.2 PERMANOVA results for the influence of Season, Bioregion, Environment (i.e Benthic or Mid-water), and associated interactions on the structure of fish assemblages sampled with stereo-BRUVs. Significant effects are in bold. All tests are based on zero-adjusted Jaccard similarity matrix using Presence/Absence data aggregated at site level, type III sums of squares, and 9999 permutations under a reduced model.

Source	df	MS	Pseudo-F	P(perm)
Warm vs. Cold Season	1	2313.8	1.1291	0.279
Bioregion	3	15138	7.3871	**<0.001**
Environment (Benthic vs. Mid-water)	1	40100	19.568	**<0.001**
Season x Bioregion	3	1687.5	0.82348	0.873
Season x Environment	1	1744.2	0.85115	0.699
Bioregion x Environment	3	7230.1	3.5281	**<0.001**
Season x Bioregion x Environment	3	1103.1	0.5383	0.999
Residual	139	2049.3		

Table 2.3 Summary of the similarity of percentages procedure (SIMPER) showing average similarities across and within bioregions and environments (i.e. B: Benthic, and M: Mid-water). Values within coloured outlines indicate similarities of percentage within bioregion whereas values outside show similarities across bioregions. Bold font indicate within group similarities, normal font indicate similarities for similar environment while italic font denotes similarities across different environments. Colours are consistent with figure 2 and 3 for comparison purposes. Procedure based on Bray-Curtis similarity matrix and Presence/Absence data aggregated at site level.

Bioregion/ Environment	Far North B	Far North M	North B	North M	Center-SE B	Center-SE M	West B	West M
Far North - B	**72.89**	-	-	-	-	-	-	-
Far North - M	*52.06*	**62.18**	-	-	-	-	-	-
North - B	56.53	*35.21*	**67.5**	-	-	-	-	-
North - M	*12.25*	21.25	*12.29*	**44.2**	-	-	-	-
Center-SE - B	41.47	*27.69*	54.1	*10.67*	**59.27**	-	-	-
Center-SE - M	*11.71*	18.61	*14.55*	32.17	*15.28*	**31.64**	-	-
West - B	25.15	*20.75*	33.11	*10.1*	44.65	*14.13*	**55.39**	-
West - M	*8.62*	15.67	*8.49*	29.19	*19.65*	28.23	*20.17*	**37.27**

Within group levels of similarities were systematically higher in the benthic environment across all bioregions and decreased gradually from the Far North to the West (Table 2.3). Within bioregion, the Far North was distinct with a percentage of similarity between benthic and mid-water environment over twice that of the other bioregions (Table 2.3). In addition, a decreasing gradient of similarities between bioregions from Far North to West was also apparent for both environments. Interestingly, the similarity between the Center-southeast and North mid-water environments was as high as the mid-water within group similarity of the Center-southeast, a pattern not seen for any other combinations of bioregions and environments.

2.4.3 Separate analysis of benthic and mid-water fish communities

The separation between the four bioregions was best achieved in the Benthic environment as seen in the CAP analysis (Figure 2.3a,c). The Benthic CAP shows virtually no overlap between the four clusters of points, achieving separation of all four bioregions. Moreover, the four benthic clusters (Figure 2.3a) accurately retain the relative geographical positions of the Galapagos bioregions (Figure 2.1). By contrast, the bioregions clusters overlap substantially in the mid-water CAP, in particular the North and Center-southeast bioregions display a full overlap (Figure 2.3c). Therefore, the mid-water CAP shows three main clusters, namely the Far North, the West, and the North and Center-southeast combined. Similarly, attempts to allocate individual Benthic sites to their respective bioregions neared 100% for all bioregions with only two sites misclassified (Table 2.3). The two misclassified benthic sites were the northernmost and southernmost sites at Isabela island which are also the closest to the transition zones between the West and Center-southeast bioregions (Figure 2.1). Those misallocations occurred only in one of the two seasons. In comparison, 14 mid-water sites were misclassified. Failure to properly allocate mid-water sites to their bioregion was highest in the North with a 50% chance to misallocate a site, and in the West with a 25% chance of misallocation. The highest proportions of misallocations were for Northern and Western sites wrongly allocated to the Center-southeast bioregion. In addition, a small percentage of mid-water Central-southeastern sites were also incorrectly allocated to the North and West.

Species correlation analysis revealed distinct clusters of species with clear correspondence to the different bioregions' clusters in both environments (Figure 2.3b,d). Species correlated with the Far Northern bioregion exhibited the strongest correlations, while correlations with the Center-southeast bioregions were the lowest, especially for the mid-water environment. Most species displaying high correlations in the CAPs were also found amongst the common species in the frequency of occurrence analysis with a few exceptions (Figure 2.4 and Figure 2.5). In particular, the wrasse *Halichoeres nicholsi,* porcupine fish *Chilomycterus reticulatus*, moray *Muraena argus*, smooth hound shark *Triakis* spp., bullhead shark *Heterodontus quoyi*, sierra *Scomberomorus sierra*, and sunfish *Mola alexandrini* showed high correlations in the Benthic CAP (Figure 2.3b) although they occurred in less than 30% of the drops (Figure 2.4). In the mid-water environment the chromis *Chromis alta,* mobula *Mobula* spp*., ray Rhinoptera steindachneri,* jack *Seriola rivoliana*, camotillo *Paralabrax albomaculatus* and wrasse *Semicossyphus darwini* had high CAP correlations (Figure 2.3d) but did not cross the 10% frequency threshold (Figure 2.5).

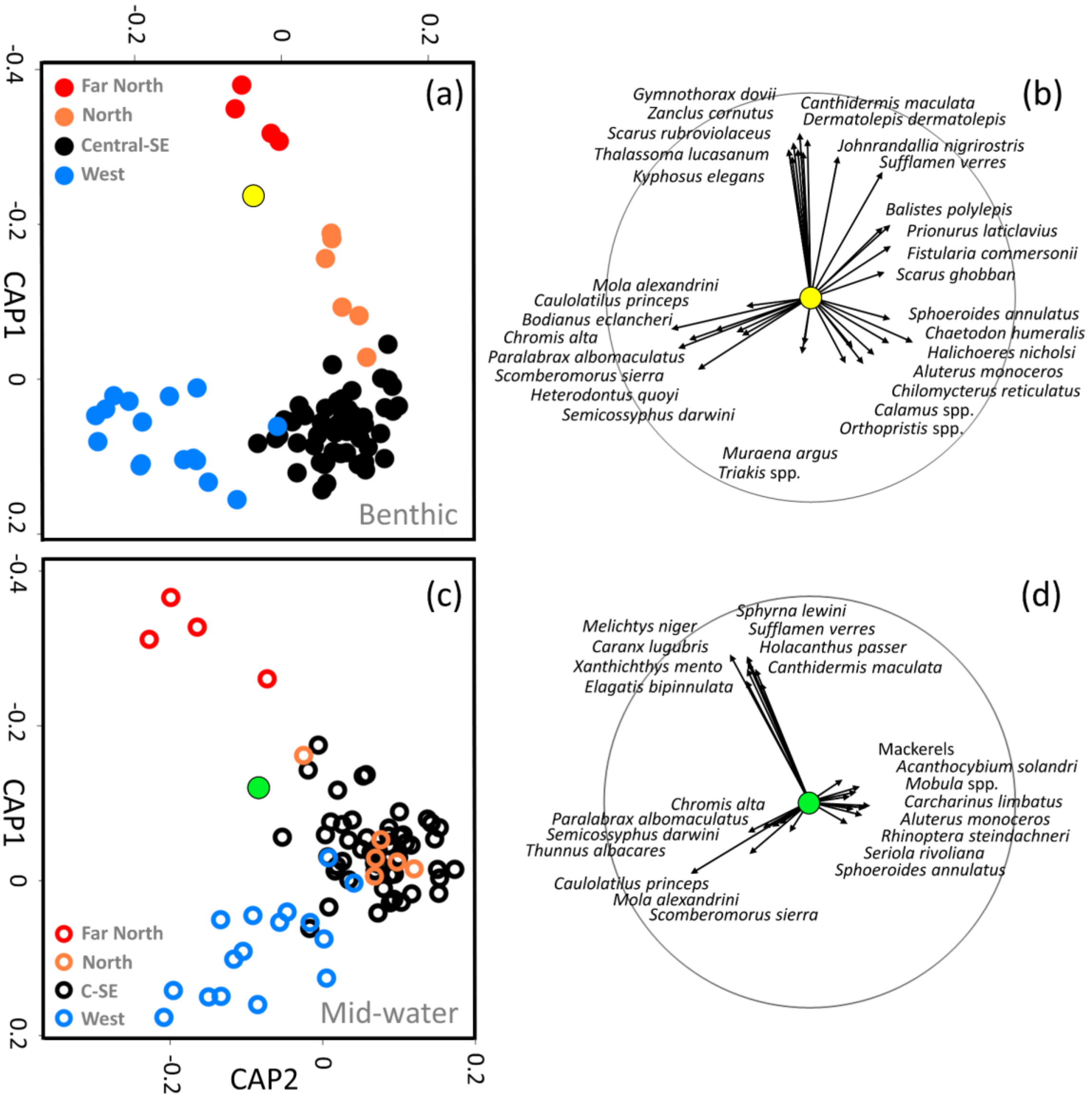


Figure 2.3 Results of the canonical analysis of principal coordinates for benthic environment (a, b) and pelagic environment (b, c). Right panels show the species with the 8 highest positive and negative Pearson correlations with both CAP axis (full radius corresponds to a Pearson correlation of 1). Yellow and green points indicate matching origins of correlation vectors between left and right panels. Outputs are based on zero-adjusted Bray-Curtis similarity matrix using Presence/Absence data aggregated at site

Table 2.4 Classification success of the sites surveyed in the four bioregions using the canonical analysis of principal coordinates leave-one-out allocation procedure in the benthic and mid-water (MID) environment. Classifications based on zero-adjusted Bray-Curtis similarity matrix using Presence/Absence data aggregated at site level.

	Bioregion	Far North	North	Central-SE	West	Total	Correct (%)
BENTHIC	Far North	4	0	0	0	4	100
	North	0	6	0	0	6	100
	Central-SE	0	0	54	1	55	98.2
	West	0	0	1	15	16	93.8
MID	Far North	4	0	0	0	4	100
	North	0	3	3	0	6	50
	Central-SE	0	4	47	3	54	87
	West	0	0	4	12	16	75

The species frequency of occurrence analysis highlighted marked gradients in species distribution across the four bioregions. In the case of the benthic environment, the Far Northern region was distinct and displayed several commonly encountered (high frequency) species only rarely present or absent in the other three bioregions while completely lacking species prevalent in most other regions (Figure 2.4). Far Northern characteristic species included triggerfishes *Xanthichthys mento* and *Melicthys niger,* parrotfish *Scarus rubroviolaceus*, moorish idol *Zanclus cornutus,* trumpetfish *Aulostomus chinensis,* blenny *Ophioblennius steindachneri,* chub *Kyphosus elegans,* and wrasse *Thalassoma lucasanum.* The Center-southeast and Western bioregions both displayed high prevalence of Peruvian/Californian/Cortez and endemic species that were much less frequently recorded in the North and absent from the Far North. This included the porgies *Calamus* spp., Galapagos grunts *Orthopristis* spp. and camotillo *Paralabrax albomaculatus* for the endemics and wrasses *Bodianus eclancheri*, *Semicossyphus darwini, Caulolatilus princeps, and Chromis alta* for the Peruvian/Californian/Cortez species. Despite their commonalities, the West lacked several Central-southeastern common species like the snappers *Lutjanus argentiventris* and *Hoplopagrus guentherii,* the goatfish *Mulloidicthys dentatus,* the grunt *Anisotremus interruptus,* the filefish *Aluterus monoceros* and cornetfish *Fistularia commersonii*. Several widespread and Panamic/Cortez taxa had a high prevalence in all four bioregions including the groupers *Mycteroperca olfax* and *Epinephelus labriformis,* the hogfish *Bodianus diplotaenia*, the angelfish *Holacanthus passer*, creole fish *Paranthias colonus.* Lastly, rare species that were recorded in two deployments or less amounted to 31%, 43%, 25% and 29% of all species recorded in the Far North, North, Centre-southeast, and West bioregions respectively (see Appendix C for full list of species).

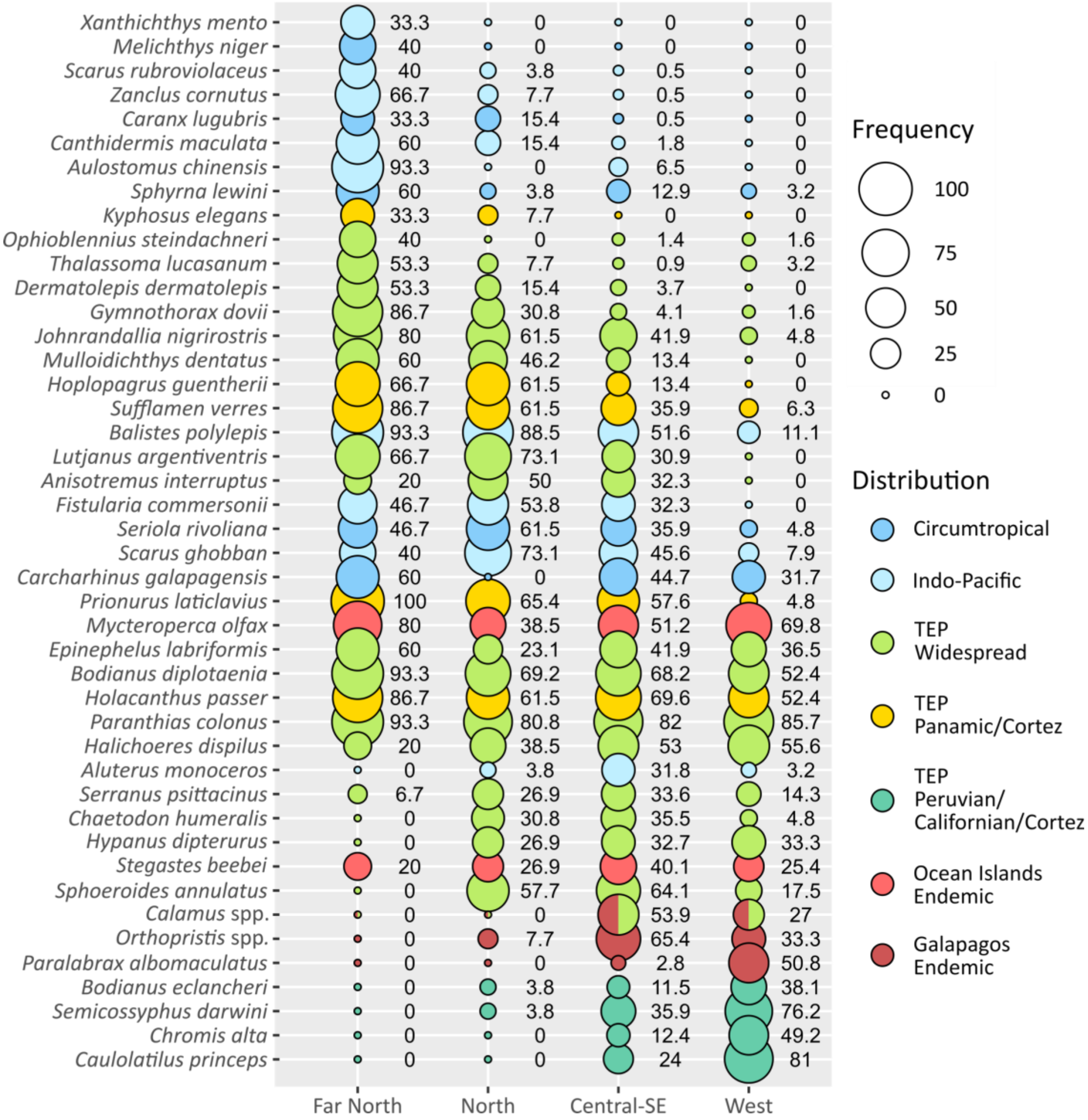


Figure 2.4 Benthic frequency of species occurrence across the four bioregions at single deployment level. Species for which highest overall frequency was lower than 30% are not included (see Appendix C for the full species list).

The mid-water environment showed similar trends to the benthic in terms of relative differences between bioregions, but mid-water species displayed overall lower frequencies of occurrence (Figure 2.5). The Far North did appear to have a higher number of common species compared to the other three bioregions. *Mycteroperca olfax* was the only ocean islands endemic species occurring above 10% frequency and only two Peruvian species occurred with greater than 10% frequency, namely the jack mackerel *Trachurus murphyi* that was highly prevalent in the North and *Caulolatilus princeps* which was most present in the West. The only species prevalent in all bioregions was the creole fish *Paranthias colonus.* Other taxa present in all bioregions but less common included triggerfish *Balistes polylepis*, bonitos, hammerhead shark *Sphyrna lewini,* blacktip shark *Carcharhinus limbatus,* wahoo *Acanthocybium solandri,* and yellowfin tuna *Thunnus albacares.* Rare taxa that were recorded in two deployments or less amounted to 55%, 63%, 43%, and 44% of all species recorded in the Far North, North, Center-southeast, and West bioregions respectively (see Appendix D for full list of species).

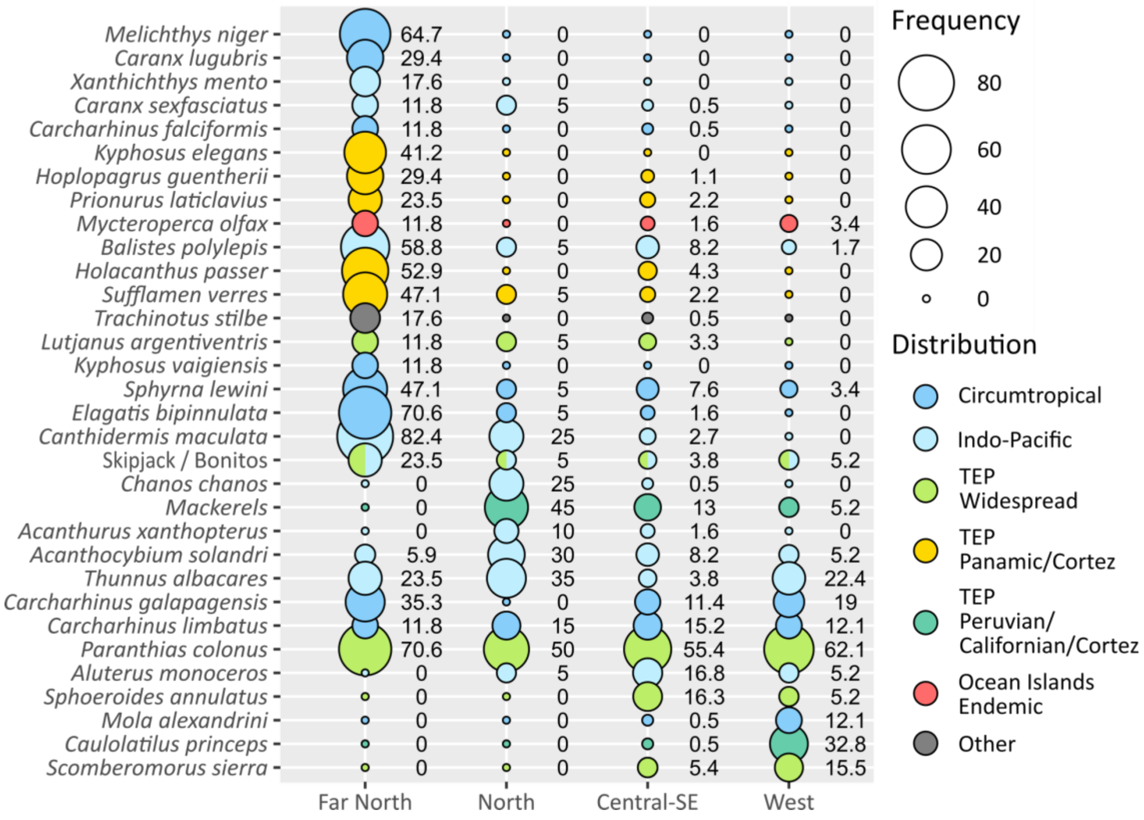


Figure 2.5 Mid-water frequency of species occurrence across the four bioregions at single deployment level. Species for which highest overall frequency was lower than 10% are not included (Appendix D for the full species list).

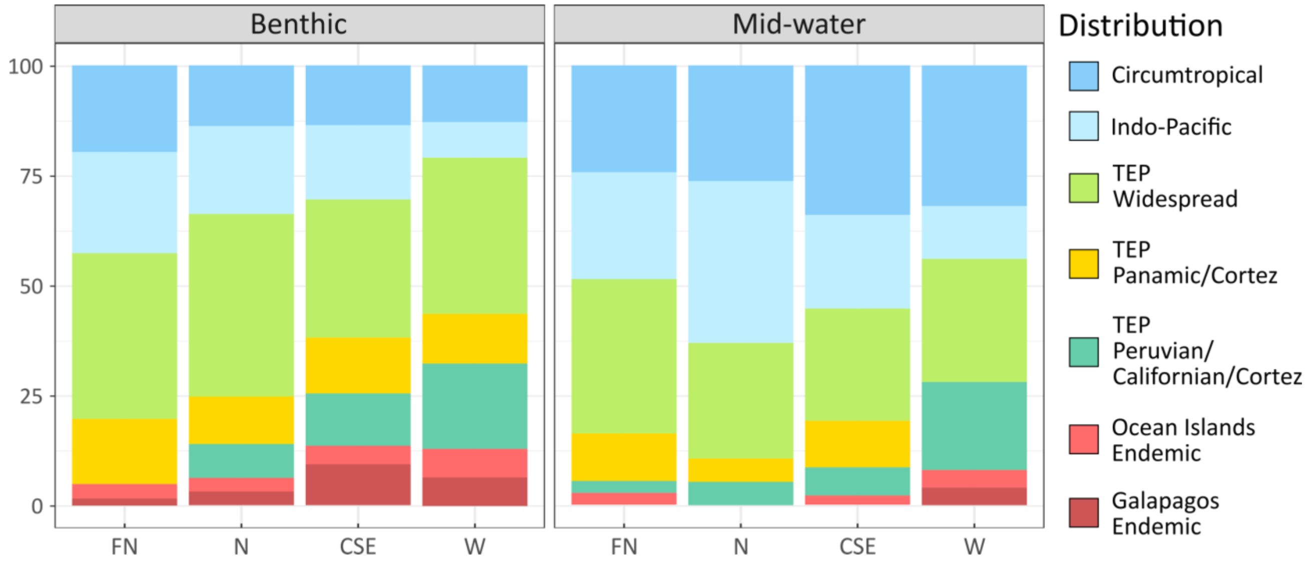


Figure 2.6 Proportion of Endemic, Peruvian, Panamic, Widespread, and Indo-Pacific species recorded in the Far Northern (FN), Northern (N), Central-Southeastern (CSE), and Western (W) bioregions for the Benthic and Mid-water environments.

The benthic and mid-water environments had different proportions of fish belonging to the five major distributions (Figure 2.6). In the benthic environment, the combined proportion of Indo-Pacific and Circumtropical species was the highest in the Far North (42.6%) and decreased gradually going south, being the lowest in the Western bioregion (20.9%). Widespread species and Panamic/Cortez species accounted for ~30-40% and ~10-15% of all benthic species recorded in each of the four bioregions. In addition, Peruvian/Californian/Cortez, Galapagos endemic, and ocean islands endemic species jointly accounted for 32.3% of benthic species in the Western bioregion and gradually decreased in proportion with northern latitudes to reach 4.9% in the Far North. The joint proportion of Indo-Pacific and Widespread species increased in the mid-water environment compared to the benthic environment, with an 6%, 29.3%, 24.8%, and 23% higher proportion in the Far North, West, North, and Center-south respectively. Such increases were associated with an overall decrease in Panamic, Peruvian, and Endemic species proportions. In the mid-water environment, Galapagos endemic species were only recorded in the West, whereas all bioregions displayed Galapagos endemic species in the benthic environment.

2.5 Discussion

As we hypothesized, we identified distinct biogeographical patterns for coastal mid-water bentho-pelagic fish assemblages in Galapagos, largely aligned with benthic environment patterns. The marked differences we found between bioregions are likely explained by the strong bentho-pelagic coupling prevailing in near shore rocky reefs shallower than 50 m depth (Grober-Dunsmore et al., 2008). In coastal shallow waters, predator-prey interactions between bentho-pelagic and benthic species are often direct, each environment influencing the other without the need for intermediary species (Field et al., 2006; Paine, 1992; Wootton, 1997). Since species habitat preference drives the occurrence of specific benthic reef fish taxa (Buxton & Smale, 1989; Carr, 1991), it is reasonable to expect that changes in benthic habitats shapes bentho-pelagic fish communities preying near the bottom. In Galapagos, rocky reefs represent >90% of shallow subtidal habitats below 50m with significant spatial differences in cover of sessile organisms such as macroalgae, soft corals, and hard corals (Bustamante et al., 2002). For example, macroalgal beds are a prevalent feature of the Cold West (Edgar et al. 2004, 2010), while structural hard coral reefs are confined to the Far North (Glynn et al. 2015, 2018). Such differences in substrate types across bioregions likely influence both mid-water bentho-pelagic and benthic coastal fish communities. With Galapagos fishers increasingly targeting the pelagic environment (Ramírez-González & Reyes, 2015; Cerutti-Pereyra et al., 2020) our results highlight the importance of considering the characteristics of each bioregion when designing fisheries management strategies for pelagic and bentho-pelagic species.

Benthic biogeographical patterns were clearly defined, strengthening the case for the currently accepted Galapagos bioregionalization scheme proposed by Edgar et al. (2004a). Interestingly, the bioregional separation achieved in our study was more distinct than Edgar's original biogeography exercise based on the comparison of multivariate re-allocation procedures (CAP). One potential explanation for this is that stereo-BRUVs proved particularly effective at sampling diver-shy species (Chapman et al., 1974; Watson & Harvey, 2007; Lindfield et al., 2014) which have been previously under sampled in the Galapagos archipelago. For example, we found that porgies *Calamus* spp. and filefish

Aluterus monoceros played an important role in discriminating between bioregions while going unreported in Edgar's seminal work. Although more likely due to differences between sampling methods, an alternative explanation is that those species have become more established in the past 15 years. This could be due to changes in environmental conditions or reflect an indirect effect of protection following the local implementation of full no-take marine reserves in 2000 (Heylings et al., 2002). We found that *Calamus* spp., which was most prevalent in the Center-south, tended to associate strongly with rocky reefs characterized by the presence of interspersed sandy patches, a feature most observed in this bioregion that likely contributes to its distinctiveness. Adequately accounting for seasonal variability is another factor which might have contributed to the increased discriminating power of our data. Here, we sampled both in the cold and warm season over a narrow sampling window, accounting for and reducing potential biases associated with seasonal variability in fish communities (Llerena-Martillo et al., 2018) and oceanographic conditions (Palacios, 2004). This influence was noticeable in transition areas between the West and Central-southeastern bioregions with certain sites successively displaying characteristics of each bioregion depending on the season. It seems likely that the exact transition points between bioregions shift slightly with changing seasonal oceanographic conditions and will shift even more so under the effect of climate change (Salinas-de-León et al., 2020). Overall, baited remote underwater stereo-video systems (stereo-BRUVs) proved effective to elicit clear biogeographical differences in the benthic environment, providing increased support for the currently accepted Galapagos marine bioregionalization scheme.

While stereo-BRUVs surveys elicited unequivocal biogeographical patterns in both environments, we acknowledge that there are limitations and biases associated with this sampling technique. First, stereo-BRUVs potentially under sample low-mobility and cryptic species which could have biased species occurrence patterns (Watson et al., 2005; Stat et al., 2019). Stereo-BRUVs surveys are also subject to variation in sampling area due to spatial differences in current dynamics driving uneven bait plume dispersion (Harvey et al., 2007). Although we did not measure water current, differences in water flow between Benthic and Mid-water deployments may have arisen due to interactions with topographic features, leading to potential discrepancies in fish abundances. For this reason, stereo-BRUVs are limited to relative estimates rather than density and in our case, we aggregated abundances at site level, across deployments for each environment, and then used a presence/absence data transformation. This enabled us to describe broad biogeographical patterns while smoothing out fine-scale variability.

While we found evidence for the bioregionalization of mid-water coastal waters, differences in community structure were less clear when compared to benthic bioregions. Indeed, the Far North, North, Center-southeast, and West bioregions were distinct in the benthic environment. The mid-water environment was different in that it was difficult to distinguish the North from the Center-southeast, which also showed greater overlap with the West, suggesting three rather than four mid-water coastal pelagic subdivisions. This fits our understanding of global scale pelagic biogeography patterns which display a lower number of pelagic subdivisions of the world's oceans compared to the shelf areas (Spalding et al., 2007, 2012). Globally, pelagic species distributions are closely related to large scale movements of water masses (Angel, 1993; Barton et al., 2010) with important horizontal feeding and reproductive migrations (Barbaro et al., 2009; Leis & McCormick, 2003; Nøttestad et al., 1999) which contributes to blurring the boundaries between bioregions. This is exacerbated in the open-ocean with the weakening of bentho-pelagic coupling compared to shallow coastal areas below 100 m depth (Grober-Dunsmore et al., 2008). We restricted our sampling to the mid-water coastal environment, and it is likely that biogeographical patterns would have been less clear if we had targeted open-ocean pelagic environment. Future pelagic surveys away from the shore would complement our study to provide a more complete picture of the Galapagos pelagic fish communities. Another clear indication of the coastal setting of our study was the complete absence of large open-ocean pelagic species like marlin (*Makaira mazara*), swordfish (*Xiphias gladius),* escolar (*Lepidocybium flavobrunneum*), mahi-mahi (*Coryphaena hippurus*), thresher shark (*Alopias superciliosus*), and blue shark (*Prionace glauca*), among others, which are regularly caught or bycaught in Galapagos high-seas pelagic fisheries (Ramírez-González & Reyes, 2015; Cerutti-Pereyra et al., 2020). Our study suggests that Galapagos mid-water coastal waters could be subdivided into three bioregions, namely the West, the Far North, and the Center-southeast plus North combined. However, a more complete sampling of the Northern bioregion coastal mid-water environment would be needed to validate this finding.

Pelagic fish communities are often described as being highly heterogeneous (Angel, 1993; Fréon & Misund, 1999; Gray, 1997; Heagney et al., 2007; Letessier, Meeuwig, et al., 2013; Santana-Garcon et al., 2014). These claims are generally based on comparisons of pelagic fish assemblage research against studies conducted in the benthic environment, while attempts to sample both environments are rare, owing in part to the lack of versatile and low-cost sampling methods (Fréon et al., 2005; Fréon & Misund, 1999; Heagney et al., 2007). Here, stereo-BRUVs allowed a direct comparison of mid-water coastal pelagic and benthic fish assemblages, providing substantiated evidence for the high variability in pelagic communities. Beta diversity measures were consistently higher in the mid-water environment which is indicative of higher community heterogeneity (Anderson et al., 2006, 2011, 2013). Furthermore, most mid-water species occurred infrequently compared to benthic taxa. This pattern was also observed by May and Blaber (1989) on the Tasmanian shelf, when comparing both environments using commercial-sized trawls. However, the ecological impact and high cost of trawling operations precludes the wide use of this method. The chief reason for high dispersion in pelagic fish lies in their generally gregarious and highly mobile nature (Fréon et al., 2005; Fréon & Misund, 1999; Santana-Garcon et al., 2014). Indeed, pelagic fish species use their habitats in markedly different ways, with important horizontal and vertical feeding migrations, resulting in strong spatial and temporal variability (Letessier et al., 2013; Santana-Garcon et al., 2014). By contrast, reef fish are predominantly sedentary with limited home-range (Kramer & Chapman, 1999; Leis & McCormick, 2003; Nash et al., 2015), which reduces dispersion and variability in benthic communities. Our study provides a clear reference point for the distinct dispersion patterns of pelagic fish species in mid-water assemblages across a range of ecologically distinct regions.

Lower species richness was the second consistent difference distinguishing mid-water coastal pelagic communities. Here again, previous attempts to empirically compare benthic and pelagic fish community richness are scarce. Clarke et al. (2019) is the only BRUVs study to directly compare Benthic and Pelagic fish assemblages and found lower richness in the latter. However, this study was limited to a single bioregion, precluding a generalization of their results. Most general conclusions drawn on pelagic fish diversity comes from analysis of global patterns, showing that low diversity appears to be the rule in pelagic ecosystems (Briggs, 1960; Angel, 1993; Gray, 1997; Eschmeyer et al., 2010; Gaither et al., 2016). Estimates show that ~8.3% marine fish, are bathypelagic and only 2.14% are open-ocean pelagic species (Eschmeyer et al., 2010; Gaither et al., 2016). From a theoretical standpoint, it seems plausible that lower pelagic fish speciation could stem from low level of habitat heterogeneity and high mobility of species in the open ocean. To describe this, Gaither et al. (2016) coined the term "lonely genus hypothesis", proposing that speciation is reduced in fishes with extensive distribution ranges and high gene flow, particularly pelagic and bathypelagic species. In our case, it was clear that species with extensive distribution range dominated Galapagos mid-water coastal pelagic fish assemblages; but how crucial is pelagic habitat variability? Attempts to model global diversity patterns of pelagic fish, while limited to top predators, suggest that mid-latitudes are the most diverse, owing to strong mesoscale habitat heterogeneity (Boyce et al., 2008; Tittensor et al., 2010; Worm, 2005). In Galapagos, the highest mid-water gamma diversity was found in the Center-southeast bioregion which coincidentally displays the strongest SST spatial gradients (Banks, 2002; Harris, 1969). The link between habitat heterogeneity and biological diversity in the pelagic environment clearly deserves further exploration. Combining stereo-BRUVs surveys with oceanographic data and recently developed environmental DNA techniques (DiBattista et al., 2017; Stat et al., 2019; West et al., 2020) could provide the tool to investigate such questions and improve our understanding of pelagic biogeographical and speciation drivers.

We observed a Central-southeastern gamma diversity twice as high as in any other bioregion. One likely explanation is the difference of spatial extent between bioregions as species richness patterns are certainly scale-dependant (Palmer & White, 1994; Whittaker et al., 2001). The Center-southeast bioregion is the largest of all four bioregions, its coastline orders of magnitude bigger than the Far North or Northern bioregion. However, the West and Center-southeast have a comparable extent and yet the latter harbours nearly twice as many species. Habitat variability might be another potential driver for a higher species richness

(Gratwicke & Speight, 2005; Hewitt et al., 2008). This bioregion was historically divided into three distinct regions in Harris (1969) seminal work which was based on physical characteristics, chiefly SST. But our data clearly showed that those three subdivisions are actually one cohesive unit when looking at biological communities. This finding is consistent with Edgar et al. (2004a). Nevertheless, the variability in environmental conditions likely gives rise to a wider range of available ecological niches in this bioregion. The Center-southeast bioregion presents characteristics of both the West and the Northern regions, acting as a transition zone. While we did not quantify habitat, it can be expected that habitat variability in this region would be higher than in the others therefore driving gamma diversity up.

The Far North bioregion also displayed distinct characteristics with unusually high similarities between Benthic and mid-water communities compared to the other three bioregions. Darwin and Wolf islands have previously been shown to harbour the largest global shark biomass due to their high level of protection and unique oceanographic setting (Salinas-de-León et al., 2016). Those islands display a large near-shore depth gradient, highly dynamic current and local upwelling conditions and are often visited by ocean-going pelagic species (Acuña-Marrero et al., 2014; Hearn et al., 2010; Peñaherrera et al., 2013; Riegl et al., 2019). Such dynamic conditions likely contributed to higher species overlap between benthic and mid-water environments compared to the other Galapagos bioregions. It is also possible that benthic species could swim more easily towards mid-water camera systems due to the strong bathymetry gradients. Comparing benthic and mid-water communities at other isolated oceanic islands would allow to investigate whether similar patterns are common.

It is not entirely clear why the western bioregion displayed considerably lower alpha diversity (species richness at site level) than the other bioregions. This bioregion displays the lowest SST in the archipelago (Banks, 2002) and therefore hosts the largest proportion of Peruvian species with cold-water affinities. It could be that the cold-water conditions of the West limit the establishment of species due to thermal tolerance limitations (Payne et al., 2016). Another reason could be that habitat and environmental conditions are more homogeneous in the west compared to the other bioregions. Indeed, fish diversity of benthic communities increase with habitat diversity (Gratwicke & Speight, 2005; Hewitt et al., 2008). This means that ecosystems functions are fulfilled by fewer species compared to the other bioregions (Hewitt et al., 2008). Complementing our study with an in-depth comparison of habitat variability and functional diversity across the archipelago would provide insight into the low site species richness found in the West.

Historically, marine conservation planning in the Galapagos islands has been strongly guided by the principle of representation, central to the field of conservation biogeography (Whittaker et al., 2005). However, the imprecise bioregionalization of the archipelago led to important areas being underrepresented under the first GMR zoning scheme established in 2000. To address this issue, Edgar et al. (2004a) refined marine bioregions in the Galapagos and highlighted the shortcomings of the zoning. In 2014, a comprehensive rezoning of the Galapagos Marine Reserve was initiated, and the proposed reform would increase the level of protection in the historically underrepresented bioregions. (Burbano et al., 2020). Our study supports those management choices and highlights that the coastal pelagic mid-water environment reflects, in large parts, the biogeographical patterns of benthic communities. With Galapagos small-scale fisheries increasingly expanding into pelagic waters, it is important to consider those regional characteristics to effectively manage pelagic resources.

Chapter 3 Ecological effects of the Galapagos Marine Reserve fisheries management on finfish populations

3.1 Abstract

This study assessed the ecological effect of the Galapagos Marine Reserve 2000 spatial management plan for a range of fish species under high, medium, and low fishing pressure. A modified multivariate length-based approach was used to analyse fish abundance and length data from visual baited underwater video surveys. A total of 9968 length measurements from 34 species collected from 605 baited remote underwater stereo-video surveys across both no-take zones and fished areas were analysed. At a species level, lengths distributions were compared using a combination of kernel density estimates and a suite of fish maturity metrics, including the proportion of juveniles, individuals of sub-optimum size, individuals of optimum size, and individuals considered to be mega-spawners. We found that the Galapagos Marine Reserve (GMR) management has had mixed effects on exploited and non-exploited fish taxa. Although three highly targeted taxa (i.e. *Mycteroperca olfax, Lutjanus argentiventris, Caulolatilus princeps)* were significantly larger in no-take zones compared to fished areas, size differences were inconsistent across species and no-take zones types and were not characteristic of a well-enforced MPA after 15 years of protection. Five species considered to be in low and medium fishing pressure areas also displayed significantly different size structures between zones. Overall, no-take zones where no tourism occurred had greater numbers of large fish than those where tourists were present. Epinephelid species generally had low numbers of mature individuals and mega-spawners in high fishing pressure areas compared to a large number of species in medium and low fishing pressure areas that displayed healthy maturity metrics level across the archipelago. This study suggests the zoning has provided species-specific effects of varying scale, with further actions needed beyond the boundaries of no-take zones to rebuild critical stocks.

3.2 Introduction

While the Galapagos waters are often portrayed as pristine, there are substantial fishing activities impacting this iconic archipelago (Merlen, 1995; Hearn, 2008; Schiller et al., 2014). Its unique ecological values have long bolstered scientific and political efforts to reconcile conservation and economic objectives (Broadus & Gaines, 1987; Kenchington, 1989; Bustamante et al., 2000). As a result, the Galapagos Marine Reserve (GMR) was established in 1998 with a mandate to "*protect and conserve the coastal-marine ecosystems of the archipelago and their biological diversity for the benefit of humanity, the local population, science and education"* and was accompanied by a series of major fisheries management outcomes (Castrejón & Charles, 2013; Reck, 2014). Firstly, industrial fisheries operations were excluded from the reserve, which extended 40 nautical miles from the outermost islands, covering a total area of 138,000 km^2. Within the reserve, exclusive fishing rights were granted to the 1035 locally registered artisanal fishermen and specific gears were banned (i.e. gillnets, longlines, spearguns). Secondly, the zoning scheme for the GMR included a network of full no-take zones (NTZs), amounting to 18% of the coastline (~1% of the GMR total surface) (Moity, 2018). Finally, a participatory co-management regime involving all major stakeholders was established with a mandate to ensure the sustainable exploitation of local marine resources. Those achievements, despite being considered world's best practice at the time (Edgar et al., 2004b), did not meet the expected management outcomes and several key resources continued to decline. The overexploitation of sea-cucumber (Hearn, 2008; Hearn & Pinillos, 2006; Ramírez-González et al. 2020), and lobster populations (Bucaram et al., 2013; Bucaram & Hearn, 2014; Hearn, 2008) is well documented with several invertebrate fisheries having reached historical lows (Jones, 2013). Catches of finfish species have also changed significantly over time, with early evidence of fishing-down marine food webs, and shifting baseline effects across multiple species (Burbano et al., 2014; Schiller et al., 2014). This impact is most visible in epinephelid species as illustrated by recent evidence showing that *Mycteroperca olfax,* the most common and economically important grouper species has now lost its function as keystone species in the archipelago (Eddy et al., 2019).

The overexploitation of marine resources in the archipelago, combined with increasing threats to the terrestrial environment, led researchers to call for a renewed era of governance to better integrate the human components that were often overlooked by conservation biologists (Castrejón & Charles, 2013; González et al., 2008; Vinueza et al., 2014). As a consequence, the Galapagos National Park Services released a new management plan hinging on a cohesive framework, understanding Galapagos as a complex socio-ecological system where human well-being and ecosystem health were intertwined (DPNG, 2014). The most direct effect on the marine environment was the initiation of rezoning process with a proposed NTZs increase from ~1% to 33% of the total extent of the reserve. The proposed rezoning is not strictly restricted to the narrow coastline fringe and would essentially expand the existing zones to include open-water areas such as seamounts and shoals, as well as a large sanctuary around the northernmost islands of Darwin and Wolf. During the development of the rezoning proposal, the fisheries participatory co-management regime was reformed and reduced to a non-binding consultative role leaving government institutions in charge of fisheries executive decisions (Llerena et al., 2017). In this major management transition, there has been minimal assessment of the ecological effects of the first Galapagos Marine Reserve zoning scheme to inform the new governance regime.

Attempts to evaluate the effectiveness of the first Galapagos Marine Reserve zoning in protecting and restoring fish populations are scarce. Banks (2007) detected early signals of larger Galapagos sailfin groupers (*Mycteroperca olfax*) found within NTZs, although this information was not published. Another study found evidence of a fisheries-related trophic cascade with higher abundance of Mexican hogfishes (*Bodianus diplotaenia)*, a species of low commercial importance, within NTZs (Sonnenholzner et al., 2009). However, the latter study only covered two (14%) of the fourteen largest Galapagos islands and collected data less than a year after the zoning was enacted. Consequently, this data should be interpreted with caution. In addition, the zoning was only demarcated in 2006 due to stakeholder conflict and institutional shortcomings, leading to important compliance and enforcement issues until that time (Viteri & Chávez, 2003, 2007; Hearn, 2008; Castrejón & Charles, 2013; Bucaram & Hearn, 2014). Lastly, Edgar (2011) looked at the Galapagos Marine Reserve zoning effectiveness as part of a broad meta-study covering the entire Tropical Eastern Pacific and found no significant differences in fish biomass between zones. Here again, the study used data collected shortly after the zoning was demarcated, and pooled fish biomass at the trophic level, hence limiting the detectability of species-specific effects. This is problematic, as it may take up to five years to detect the initial effects of protection on target species and over a decade for cascading effects (Babcock et al., 2010; Edgar et al., 2009; Edgar, 2011; Micheli et al., 2004). In this context, the only study evaluating the 2000 zoning scheme under an appropriate time frame, although focusing on lobsters and not fish, is by Buglass et al. (2018). While their study only covered four (29%) of fourteen main islands, they found no significant evidence of reserve effect, which suggests that low compliance may have continued even after the zoning was demarcated in 2006. Overall, studies and data on the ecological effects of Galapagos NTZs is limited, with spatial and temporal-scale issues, which can mask trends of fish community recovery (Nash & Graham, 2016).

The absence of a fine-scale, archipelago-wide integrated study into the effectiveness of the 2000 marine zoning is problematic given the 1998 GMR management plan was based on adaptive management and included clear objectives to evaluate and revise the NTZ design based on their initial performance (DPNG, 1998; Heylings et al., 2002). These objectives were not met, which has undermined the credibility of the GMR for a range of stakeholders including fishermen, management bodies, and the conservation sector (Castrejón & Charles, 2013). Considering the on-going rezoning process, a robust multi-species assessment of the ecological impact of the previous zoning would be beneficial for informing Galapagos fisheries management arrangements. For example, an assessment revealing that NTZs successfully rebuilt fish populations, would improve the credibility of the past zoning, and likely contribute to increasing the legitimacy of the new one. This is important, as current perceptions and acceptance of NTZs in the fisheries sector are very poor (Burbano et al., 2020; Burbano & Meredith, 2020), which has previously led to low compliance in the GMR (Viteri & Chávez, 2007; Castrejón & Charles, 2013). Pushbacks by fishers, fuelled by feelings around a lack of inclusiveness in the decision-making process, and doubts in relation to the actual socio-economic benefits of conservation measures (Ministerio del Ambiente del Ecuador, 2018;

Burbano et al., 2020), effectively led to the repeated postponing of the zoning reform implementation to this day (Ministerio del Ambiente del Ecuador, 2018). This resistance could be mitigated if fishermen witness tangible benefits which positively impact their livelihoods (Leleu et al., 2012; Jentoft et al., 2012; Di Lorenzo et al., 2016). To date, no comprehensive evidence has been provided. The alternative case, namely, a zoning assessment revealing no ecological effects of NTZs for any of the commercially exploited species, may suggest either a lack of compliance, or an inadequate zoning design, or a combination of both. This would highlight the importance of addressing compliance issues in the GMR and would strengthen the case for the expanded protection in the new spatial management regime to warrant tangible long-term benefits.

As part of the assessment process, it is important to choose appropriate methods and indicators that accurately detect impacts to fisheries and the recovery of fish communities (Rochet & Trenkel, 2003; Nash & Graham, 2016; Goetze et al., 2017; Jaco & Steele, 2020). The ecological impact of NTZs can be assessed through monitoring the abundance, size, and biomass of fish assemblages since the establishment of regulations, although important caveats exist (Mosquera et al., 2000; Halpern & Warner, 2002; Halpern, 2003; Guidetti et al., 2014; Nash & Graham, 2016; Sala & Giakoumi, 2018). Indeed, most assessments of NTZs lack adequate baseline measures against which changes can be monitored. This is problematic since inherent imbalances in abundance can exist prior to protection due to environmental heterogeneity (Rochet & Trenkel, 2003; Edgar et al., 2004b; Nash & Graham, 2016). If such biases are not accounted for, this can lead to erroneous interpretation of asymmetrical trends between fished areas and NTZs. In the case of the Galapagos 2000 zoning, Edgar et al. (2004b) showed that zone selection bias existed with pre-existing species abundance imbalances across the three main zone types (i.e. fished zones, conservation NTZs, and tourism NTZs). For example, sea cucumbers were three times more abundant in fished zones, and shark abundance was five times higher in tourism NTZs than in conservation NTZs and fished zones. As a result, an abundance-based approach to evaluate the zoning may face limitations when interpreting differences between zones. This also suggests that conservation and tourism NTZs may have responded differentially to protection.

Length-based indicators are model candidates to evaluate the ecological impact of NTZs, as they are often the most sensitive to differences in fishing pressure (Rochet & Trenkel, 2003; Nash & Graham, 2016; Jaco & Steele, 2020). The impact of exploitation on fish-length distributions leads to truncation effects with removal of larger fish and a decrease in the proportion of mature fish (Hall, 1999; Sharpe & Hendry, 2009). On this premise, Froese (2004) proposed three simple indicators to assess fishing pressure in a data-poor context, which are calculated directly from size distributions, namely, the proportion of mature fish, the optimum size fish, and numbers of mega-spawners. While intended for catch-data, those indicators could be adapted to length distributions collected through underwater surveys and yield meaningful insights on fish population health or stock recovery under a range of management scenarios (e.g. seasonal closures, gear restrictions, no-take MPAs). For this purpose, baited remote underwater stereo video systems (stereo-BRUVs) provide an appropriate method as studies have shown they can yield fish length distributions comparable to catch data (e.g. Langlois et al., 2012, 2015) while also providing the high-level measurement accuracy necessary to detect small size changes (Harvey et al., 2010). In addition, stereo-BRUVs can be operated within MPAs where fisheries-dependant methods are often prohibited. Combining Froese's (2004) approach with fisheries-independent surveys may expand on existing MPA evaluation methods while meeting the need for multi-species indicator methods to support the ecosystem-based management of fisheries.

This study aimed to: i) evaluate the ecological effects of the Galapagos zoning 2000 for a range of fish species under varying levels of fishing pressure (i.e. high, medium, low); ii) assess the overall status of fish populations of the GMR in areas open to fishing; and iii) test a new methodology to inform MPA conservation goals through adapting the approach of Froese (2004) to stereo-BRUVs data.

A priori, we hypothesized that highly targeted fish species would show evidence of a reserve effect, with an increase in larger individuals inside no take zones compared to outside, while non-target species would display a mixed response. Furthermore, we also hypothesized that fish species that experience higher fishing pressure would display lower levels of mature individuals and mega-spawners than those under medium or low fishing pressure.

3.3 Materials and Methods

3.3.1 Characteristics of Galapagos finfish fisheries

3.3.1.1 Fishers population and fishing fleet

As of October 2007, there was 1023 registered fishers in the Galapagos (Castrejón, 2011), licensed to extract any legally authorized finfish or invertebrate species. Of that 1023, 436-466 fishers are active during the year, but only approximately 323 are full-time fishers. This discrepancy between the number of registered and full-time fishers in the Galapagos is the aftermath of the "boom-and-bust" exploitation of sea-cucumber resources in the 90s and early 2000s. With the collapse of the Galapagos sea-cucumber fisheries and the decline in the lobster fisheries, the number of active fishermen decreased by ~65% since the onset of the 2000 spatial management scheme (Castrejón, 2011). The fishermen who remain active have been described as generalists and adapt their fishing effort and target species based on resource availability, market incentives, and management regulations (Bucaram & Hearn, 2014; Burbano et al., 2014; Castrejón & Charles, 2020). The Galapagos fishing fleet is comprised of 447 artisanal fishing vessels which belong to three categories: wooden boats called "*pangas*" (3.8 to 8.3 m length), fast speed fiber-glass boats called "*fibras*" (5 to 9.6 m length), and wooden mother boats called "*botes*" (up to 18 m length) (Castrejón, 2011). This fleet allows fishers to easily conduct multi-days fishing trips across the entire archipelago.

3.3.1.2 Fishing gear

The Galapagos Marine Reserve Management Plan (DPNG, 1998) details the different fishing gears allowed in the reserve. In their respective rank of fishing effort, these include hook and line, trolling with lure, hookah, Hawaiian sling as well as artisanal nets such as seines and cast nets. Shore trammel nets and gillnets are also allowed under restricted conditions. Among those gears, the hook and line technique locally referred to as "empate" has historically been the prime fishing technique and continues to constitute the bulk of the fishing effort (Peñaherrera, 2007; Zimmerhackel et al., 2015). Despite being illegal to operate, the use of spearguns (which are distinct from Hawaiian slings under GMR regulations) is commonly reported in the GMR (Ruttenberg, 2001; Peñaherrera, 2007; Usseglio et al., 2016; Pontón-Cevallos et al., 2020). In addition, while longlining is officially banned, five longlining pilot programs have been conducted in the GMR to evaluate the potential of this gear to increase fisher revenue following the depletion of coastal resources (Cerutti-Pereyra et al., 2020). Such programs revealed high megafauna bycatch levels (e.g. list some species here), which confirmed the need to ban this practice. There are anecdotal reports that although there is a ban in place, longline fishing gears continue to be used.

3.3.1.3 Fishing grounds

Outside of no-take zones (NTZs), fishing activities occur throughout the GMR but have historically been largely restricted to the coastline fringe (Peñaherrera, 2007; Reck, 1983; Usseglio et al., 2016, 2016). In addition, fishing effort is not equally distributed between Galapagos bioregions. The central south-eastern region receives over 60% of the total fishing effort, while the northern and western regions receive about 20% and 10%, respectively (Peñaherrera, 2007). Although the majority of finfish catches come from the 0 to 30 m depth range, hook and line fishing occurs as deep as 300 m and there is an on-going trend to fish deeper and further offshore as traditional resources become depleted (Schiller et al., 2014; Marin Jarrin et al., 2018).

3.3.1.4 Target species

The Galapagos sailfin grouper (*Mycteroperca olfax*), locally known as “Bacalao” represented nearly 100% of the finfish catch in the 1920s and 1940s. In the 1970s, epinephelid species still accounted for ~89% of the catch, although only ~40% of landings was Bacalao (Reck, 1983). This species has now lost its key-stone role (Eddy et al., 2019), and only accounts for ~17% of landings (Usseglio et al., 2015). With the depletion of traditional resources, catch composition has changed and a wide-range of up to 87 species may now be targeted (Murillo-Posada, 2003; Peñaherrera, 2007; Schiller et al., 2014), with about 20 species of high-commercial importance (Molina et al., 2004; Zimmerhackel et al., 2015). Commercially important demersal and benthopelagic species include the Galapagos sailfin grouper (*Mycteroperca olfax),* white spotted sandbass or “Camotillo” (*Paralabrax albomaculatus*), leather bass or “Cagaleche”

(*Dermatolepis dermatolepis*), oceanic whitefish or “Blanquillo” (*Caulolatilus princeps*), yellow and dog snapper (*Lutjanus argentiventris* and *Lutjanus novemfasciatus*), spheephead wrasse (*Semicossyphus darwini*), as well as deeper species such as the mottled scorpionfish or “Brujo” (Pontinus clemensi), the olive grouper (*Epinephelus cifuentesi*) and the misty grouper (*Hyporthodus mystacinus*). Commercially important large pelagic species include tuna species (*Thunnus albacares, Thunnus obesus, Euthynnus lineatus*), wahoo (*Acanthocybium solandri*), amberjack (*Seriola rivoliana*), sierra (*Scomberomorus sierra*) and billfishes (*Makaira indica, Makaira mazara, Tetrapterus audax).* Among other smaller pelagic species, mullets (*Xenomugil thoburni* and *Mugil galapagensis)* make up the majority of the landed biomass in the Galapagos artisanal fisheries (Nicolaides et al., 2002; Peñaherrera, 2007; Schiller et al., 2014).

3.3.2 Galapagos Marine Reserve 2000 zoning scheme

The 1998 GMR Management Plan aimed both at preserving the unique biodiversity value of Galapagos marine ecosystems and safe-guarding the socio-economic benefits of its users in a sustainable way (DPNG, 1998). This led to the development of the GMR Zoning scheme, approved in 2000, in the form of a multi-use area (Heylings et al., 2002; Castrejón & Charles, 2013b). Waters above 300m depth were listed as multiple-use zones where all activities were allowed. The coastline fringe, extending 2 nm from shore, was subdivided into three main management subzones broken down as follow:

- Comparison and Protection, referred to here as “Conservation NTZs” (14 subzones in total).
- Conservation and Non-extractive Use, referred to here as “Tourism NTZs” (62 subzones in total).
- Conservation and Extractive and Non-extractive Use, referred to here as “Fishing Zones” (45 subzones in total).

When considering the linear measure of coastline, fished subzones account for 77% of the coastline whilst NTZs account for 18% (8% conservation and 10% tourism) (Heylings et al., 2002). When considering total surface area, fished zones account for 99.04% of the GMR whilst NTZs account for 0.96% (0.30% conservation and 0.66 % tourism)(Moity, 2018).

3.3.3 Stereo-BRUVs surveys

Stereo baited remote underwater video systems (stereo-BRUVs) were used to survey coastal fish assemblages throughout the GMR (Figure 3.1). Stereo-BRUVs are increasingly adopted around the world to generate reliable estimates for a broad range of fish population metrics, including relative abundance, size distribution, and behaviour (Langlois et al., 2020). Each stereo-BRUV system used two GoPro Hero 4s encased in SeaGIS PVC housings, mounted 70 cm apart on a rigid steel frame with seven degrees of inward convergence to allow for an overlap of the two fields of view. GoPro cameras were set to film with a 1080p resolution at 60 frames per second to mitigate the influence of the rolling shutter effect. Stereo-video calibration was performed before and after field campaigns using a 3D calibration cube to optimize measurement accuracy (Boutros et al., 2015). A bait arm protruded in front of the cameras with a bait cannister (25 cm L x 8 cm W) drilled with water-circulation holes mounted 1 m away from the frame. Approximately 800 g of chopped yellowfin tuna (*Thunnus albacares*) was used as bait, a suitable replacement for the common stereo-BRUVs bait type (e.g. pilchards), which is not available in the Galapagos.

The systems were designed to float above, rather than sit on the bottom like traditional stereo-BRUVs, following designs in Santana-Garcon et al. (2014) and Acuna-Marrero et al. (2018). This reduced entanglement issues with large animals, which were commonly observed during the pilot phase of the project. This design also minimised the loss of gear due to interactions with large sharks displacing the gear into deeper water when coming into contact with the bait cannister (Acuna-Marrero et al. 2018a), and they performed well in the complex habitat structure and steep topography often encountered in the Galapagos. The stereo-BRUVs frames were deployed along the 25 m depth contour using a ballast weight (~30 kg), a mooring line, and two sets of buoys to achieve buoyancy and mark the position of the system at the surface. Adapting the length of the line between the cameras and the anchor allowed us to deploy the systems at two different target depths, 1 m above the substrate (benthic systems, ~24 m depth), and 15 m above the substrate (mid-water systems ~10 m depth). This combination facilitated the sampling of both demersal and benthopelagic species. However, stereo-BRUVs may under sample low-mobility and cryptic species which can bias species occurrence patterns (Watson et al., 2005; Stat et al., 2019). While stereo-BRUVs are particularly efficient at sampling carnivorous species, they also survey herbivorous species adequately (Watson et al., 2005; Harvey et al., 2007).

At each site surveyed, eight stereo-BRUVs system were deployed successively (i.e. four benthic and four mid-water), allowing 500 m between adjacent deployments to mitigate pseudo-replication issues (Santana-Garcon et al., 2014). The target soak time was 100 min to allow for a minimum of 90 min of suitable footage for analysis. This combination of eight replicates and 90 min of video was chosen based on preliminary surveys (Acuña-Marrero et al., 2018). All surveys were conducted during daytime hours, avoiding dusk and dawn (Myers et al., 2016) and potential diel sampling biases (Newman and Williams, 1995).

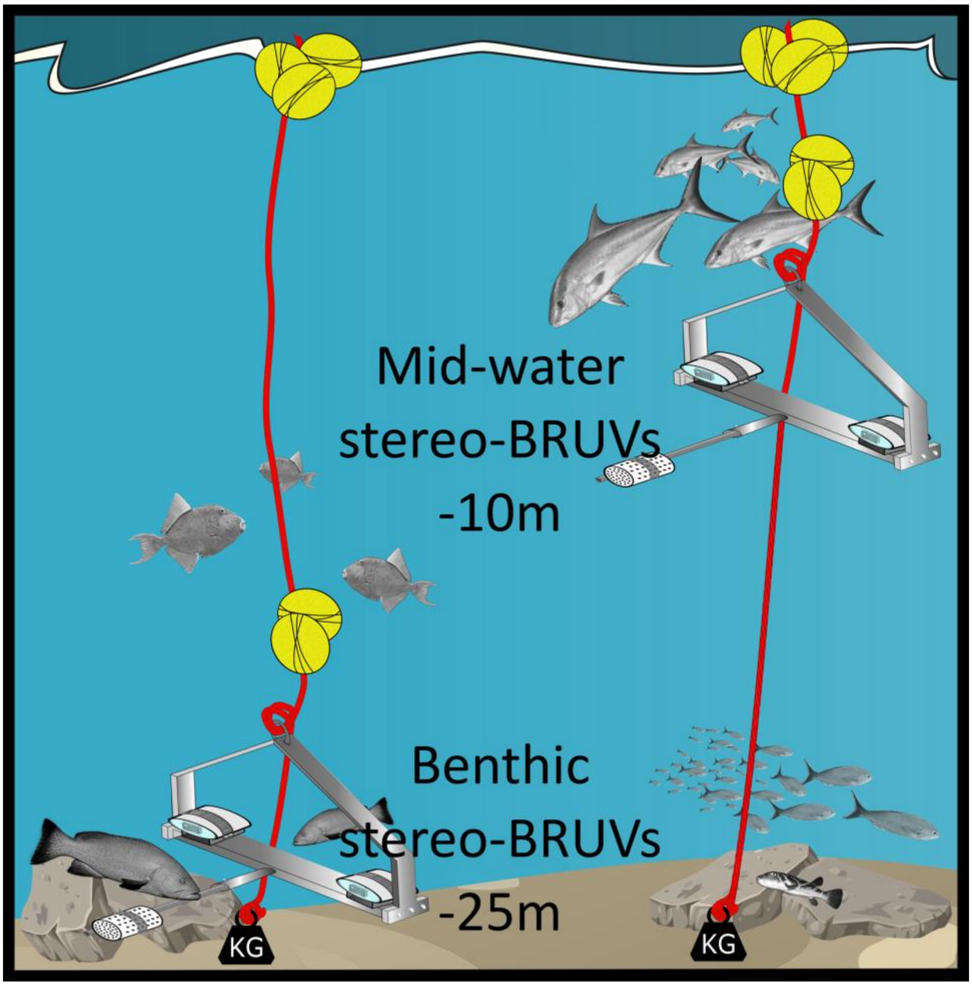


Figure 3.1 Schematic representation of the two stereo-BRUVs configurations used to survey Galapagos coastal fish assemblages. Adjacent deployments were separated by 500 m.

3.3.4 Sampling design

Sampling was carried out in 2015 following a spatially stratified random design along the 25 m depth contour (Figure 3.2). The design included 45 rocky-reef sites representative of NTZs and fished zones across the main Galapagos biogeographical regions, Far North, North, Central-southeastern and West (Edgar et al., 2004a). All sites were sampled twice, once during the warm season (January-June 2015), and once during the cold season (July-December 2015; see Acuña-Marrero et al. 2018 for further details). This amounted to a total of 605 stereo-BRUVs deployments, 411 in fished zones and 195 in NTZs (Note: the slightly larger deployments sampling size in Chapter 3 compared to Chapter 2 is due to the more stringent deployments QA/QC and exclusion process necessary in Chapter 2 and detailed in section 2.3.3). To elicit the potential ecological effect of management subzones on fishes, NTZ deployments were categorized as tourism NTZs (covering 8 individual zones) and conservation NTZs (covering 19 individual zones), using the Galapagos zoning GIS layers provided in Moity (2018). Sampling in NTZs accounted for 27 out of the 60 Galapagos NTZs, representing 57% of conservation NTZs and 41% of tourism NTZs.

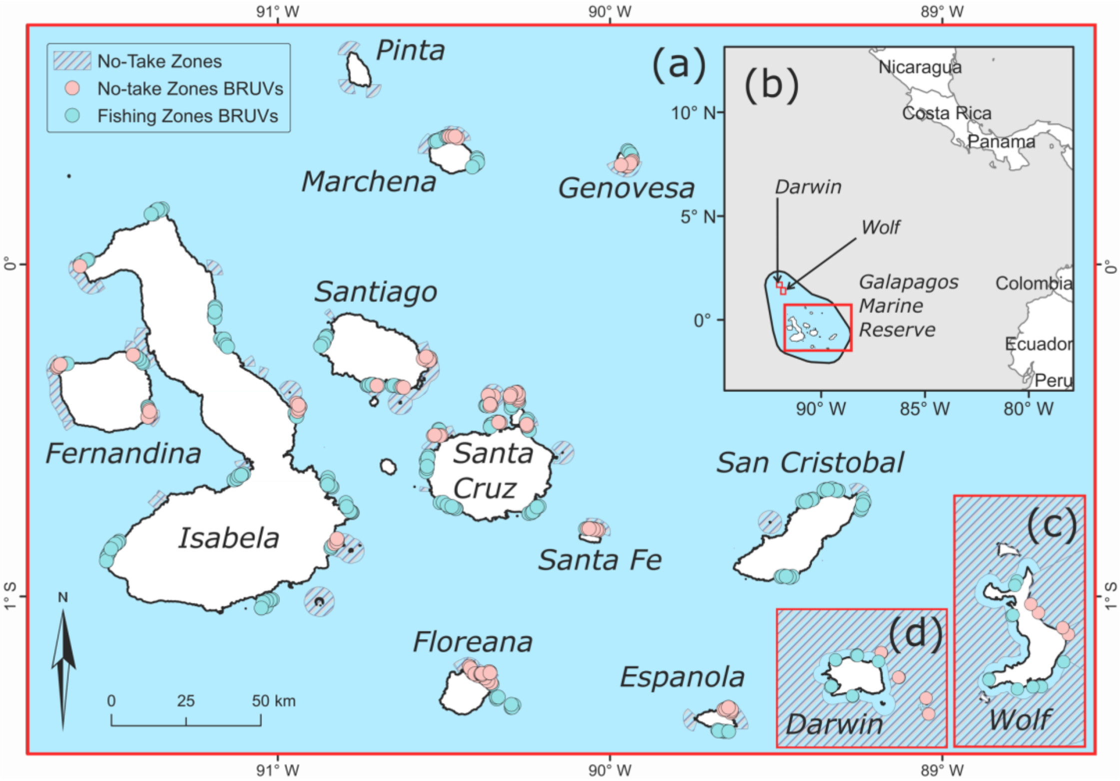


Figure 3.2 a. Locations of the 605 stereo-BRUVs deployments and no-take zones under the Galapagos Marine Reserve 2000 Zoning scheme (GIS zoning layer source from Moity 2018). b. Location of the Galapagos Marine Reserve in the Tropical Eastern Pacific, 1000 km off the coast of Ecuador with extent indicator of the main map in red. Detail of northernmost islands of Darwin and Wolf are provided in the c and d insets.

3.3.5 Video analysis

All stereo-video footage was analysed using the EventMeasure Stereo SeaGIS software package following the methods outlined in Langlois et al. (2020). A video analyst reviewed the imagery to identify and count all species present and calculate MaxN (i.e. the maximum number of individuals of a given species present in a single video frame) using EventMeasure. All bony fish were identified to species level where possible or to broader taxonomic categories in the case of a species complex or due to unreliable species level identification. The species complexes considered were *Calamus* spp., which comprised *Calamus taurinus* and *Calamus brachysomus*, as well as *Orthopristis* spp., which comprised

Orthopristis forbesi, *Orthopristis lethopristis*, and *Orthopristis cantharinus.* Species identifications were then reviewed by a single experienced (chief) analyst to ensure consistency across the data. For all fish species identified and counted, length measurements were made at MaxN to avoid pseudo-replication. To ensure measurement accuracy, EventMeasure Stereo precision to length ratio and residual mean square threshold values were set to 10% and 20 mm, respectively. To account for schooling behavior and high-density species, measurement sub-setting rules were established. For MaxN values below 20 individuals, all fish were measured. For MaxN values between 20 and 50 individuals, a subset of 50% of the school with no less than 20 individuals was measured. The same rule applied for MaxN values above 50 individuals with a cap at 50 measurements. When sub-setting, an analyst measured fish across the entire school to obtain a representative length-distribution. Output measurements data was then checked by the chief analyst to identify and mitigate any discrepancies in the final dataset.

3.3.6 Species selection and categorization

The species selection process aimed to: i) retain species representative of the full gradient of exploitation in the GMR to evaluate both direct and indirect effect of fishing; and ii) select a range of species with a large adequate sample size and corresponding reliable length measurements to allow for a robust interpretation of the results. Sparse species with less than 10 length measurements and small sample sizes (i.e. below 10 to 15 cm average length) were excluded, as along with cryptic species, as they tend to be underrepresented in stereo-BRUVs surveys (Watson et al., 2005; Stat et al., 2019). Elasmobranch species were also excluded as sharks were previously covered in detail in Acuna Acuña-Marrero et al. (2018), while rays could not be measured consistently (due to a large wingspan). This selection process yielded a list of 34 species, which were then categorized according to the level of fishing pressure they received in the Galapagos (high, medium or low, see Appendix E for species list and details). This categorization process followed a combination of expert opinion (Wilson, 1995; Edgar, et al., 2004a; Claudet et al., 2010) with a review of the relevant literature (Reck, 1983; Nicolaides et al., 2002; Murillo-Posada, 2003; Molina et al., 2004a, 2004b; Schiller et al., 2014; Zimmerhackel et al., 2015). The high fishing pressure category included all species regularly reported as commercially important or making up a significant proportion of the fisheries catch. Medium fishing pressure included common bycatch species as well as species occasionally landed, although not primarily targeted. Low fishing pressure included all non-fished species as well as rare bycatch species. Since this fishing pressure categorization is based on patterns of species exploitation within the Galapagos artisanal fisheries context, translating these categories elsewhere would require location-specific adjustments. Out of the 34 species, 17 species had a large adequate sample size to allow a comparison of the length distributions of fish measured within NTZs versus individuals measured in fished zones. Such species had a minimum of 25 individuals measured in fished subzones and conservation subzones (i.e. tourism NTZs and conservation NTZs combined).

3.3.7 Maturity metrics approach

For each species, a series of maturity metrics were computed based on the approach presented in Froese (2004). The first step involved aggregating the length at first sexual maturity (L_{mat}), the optimum length (L_{opt}), and the maximum length (L_{max}) for all species. L_{opt} is defined by Froese (2004) as the length where the number of fish in a given unfished year class multiplied with their mean individual weight is a maximum and where thus the maximum yield and revenue can be obtained. L_{opt} is indicative of the fisheries potential of a given species. L_{max} for each species was obtained from FishBase (Froese & Pauly, 2000). In the case of species complexes with differing L_{max}, we selected the largest L_{max} to yield the most conservative metrics estimates. For several species, the FishBase L_{max} did not match the largest individuals recorded in our data. In this case, the stereo-BRUVs L_{max} was given priority over the FishBase L_{max}. In the case of *Paralabrax albomaculatus*, L_{max} was obtained from the Charles Darwin Foundation landing monitoring data (Marin Jarrin & Salinas-de-León, 2018) as it exceeded both Fishbase and our stereo-BRUVs L_{max}. L_{mat} and L_{opt} were then derived from L_{max} using the empirical equations in Froese & Binohlan (2000) and the associated spreadsheet wizard available on FishBase (see Appendix E for species list and metrics details). Combining those metrics with our length distributions we computed a series of indicators, which were later used for statistics and data visualization purposes:

- Percentage of juveniles (i.e. proportion of individuals below size at first sexual maturity);
- Percentage of mature fish (i.e. proportion of individuals above size at first sexual maturity;
- Percentage of optimum length fish (i.e. proportion of individuals within the optimum length interval, L_{opt} ± 10% L_{opt});
- Percentage of sub-optimum individuals (i.e. proportion of individuals between L_{mat} and optimum length interval lower bound);
- Percentage of megaspawners (i.e. proportion of individuals larger than the optimum length interval higher bound). Mega-spawners are old and large individuals which contribute exponentially to the reproductive success and population stability of a fish species (Froese, 2004; Hixon et al., 2014; Barnett et al., 2017).

Certain interdependencies exist between the above metrics. The percentage of juveniles combined with the percentage of mature fish is equal to 100% allowing to infer each metric using the other. In general, the percentage of mature fish is comprised of the sum of sub-optimum, optimum-size, and mega-spawner individuals, with rare exceptions when the optimum-size interval has minor overlaps with the juveniles segment (see Figure 3.6).

It is important to be aware that Froese's (2004) metrics were originally designed for catch data. Froese (2004) proposed that when metrics reflect the size structure of the whole fish population, a population with 30-40% mega-spawners is considered a healthy population level, while values below 20% should be of concern. Froese (2004) further suggests that all individuals in the catch should be above the length at first sexual maturity (L_{mat}) with the aim of having 100% of the catch falling within the optimum length interval. Herein, this study assumes that stereo-BRUVs generate length information comparable to catch data that is reflective of the size structure of the whole fish assemblage (see also Langlois et al. 2012, 2015). This implies that what constitute healthy levels for the different stereo-BRUVs derived metrics remains indicative at this stage. Interpretations and conclusions based on maturity metrics are therefore relative (i.e. comparing groups of species) rather than absolute.

3.3.8 Statistical analysis of no-take zones ecological effects

The ecological impact of the 2000 spatial management regime on a suite of fish species was evaluated by comparing fish length distributions across fished zones and NTZs. Here, we are interested in detecting whether specific management zones (presumably no-take zones) were associated with mature old-growth length structure in the selected species with high proportions of sexually mature fish and mega-spawners. Such length structures are indicative of high spawning potential and population resilience and stability (Froese, 2004; Hixon et al., 2014; Barnett et al., 2017), potentially revealing a positive ecological effect of protection measures. By contrast, management zones where length structures are truncated and lack sexually mature and large individuals (presumably fished zones) could reveal a detrimental ecological effect of fishing on certain species.Three separate statistical analyses were conducted using the subset of the 17 large sample size species described in the “Species Selection” section. This work was performed within the R statistical computing environment (R Core Team, 2013).

First, we compared length frequency distributions inside/outside for each species following the Kernel Density Estimates (KDEs) approach detailed in Langlois et al. (2012), where KDEs essentially smooth-out length-distributions. This approach involved constructing two separate KDEs for each management status (i.e. “Fished” and “No-take”) and comparing them using a permutation test with an H_0 null model of “no differences between KDEs”, meaning no impact of management status on fish length-distribution. The alternative model H_A was “KDEs differ significantly across management status”. This test is robust to an unbalanced design and does not require underlying assumptions about the length-distributions being compared (Langlois et al., 2012). In addition, this procedure assesses differences in both the “Shape” as well as the “Location” of the length-distributions. The “Shape” test is interested in differences in the overall shapes of the distributions and is influenced by variation in humps, down crests, and skewness. The “Location” test is primarily evaluating whether the two KDEs are shifted or overlap each other.

Secondly, we tested for differences in maturity metric indicators across management zones, by computing the indicators separately for fished zones and NTZs and comparing them using a Chi-square non-parametric test. The H_0 null hypothesis was “there is no difference in the proportion of individuals within each maturity metrics category between fished zones and NTZs” with the H_A alternative hypothesis corresponding to “the proportion of individuals within each maturity metrics category differs significantly between fished zones and NTZs”. Lastly, for species which had significant differences in the shape or location ($p\text{-value}<0.05$) for KDEs, the NTZs length-distribution data was further divided between “tourism NTZs” and “conservation NTZs” and compared against fished zones using a Kruskal-Wallis non-parametric test. To test for zone-to-zone differences in length data, we performed Wilcoxon Ranked Sum tests for each pair of zones. For the above tests, the H_0 null hypothesis was “there is no difference in fish length distributions across zone types” with the H_A alternative hypothesis corresponding to “fish length distributions differ significantly across zone types”. This allowed us to assess whether both no-take management subzones were driving differences equally or perhaps performed differently, and pirate plots (Phillips, 2017) were used to visualize this data. The Galapagos sailfin grouper, *Mycteroperca olfax*, was also included in this analysis as its KDE test was fringing significance.

3.3.9 Comparative analysis of fish population status in fished zones

To compare the status of fish populations in areas open to fishing, and identify groups of species with similar management needs (or comparable conservation status), a multivariate analysis was conducted using the suite of maturity metrics calculated from the fished zone length distributions using the PRIMER-7 statistical software (Clarke & Gorley, 2015). A similarity matrix based on Euclidean distances was computed and a non-metric multidimensional scaling procedure (nMDS; Kruskal & Wish, 1978) was used to visualize the structure of the data. A cluster analysis with group average linkage was subsequently undertaken in combination with a SIMPROF test to assess whether differences between emerging groupings were statistically significant (Clarke & Gorley, 2015). Here, the H_0 null hypothesis was “no coherent groupings of individual species exist based on their maturity metrics” with the H_A alternative hypothesis corresponding to “individual species can be grouped in statistically significant coherent clusters based on their maturity metrics”. Statistically significant groupings were then superimposed to the nMDS for visualization purposes. All figures and tables were created using a combination of R (R Core Team, 2013) and InkScape graphic design environment (Inkscape Project, 2020).

3.4 Results

Video-analysis yielded 9968 individual measurements, 37% and 63% from no-take zones (NTZs) and fished zones, respectively.

3.4.1 Comparison of fished zones versus no-take zones

3.4.1.1 KDEs and maturity metrics comparison

Based on the KDE tests, five species were significantly larger inside NTZs compared to outside. These included two high fishing pressure species, *Lutjanus argentiventris, and Caulolatilus princeps,* and three low fishing pressure species, *Orthopristis* spp*., Prionurus laticlavius,* and *Aluterus monoceros* (Table 3.1, Figure 3.3)*.* Two species exhibited the opposite trend and were significantly smaller in NTZs, (*Lutjanus viridis* and *Paranthias colonus*)*.* Both KDE tests for location and shape were significantly different in all those instances except for *Lutjanus viridis*, *Orthopristis* spp., and *Prionurus laticlavius* where shape was not significant (Table 3.1).

The maturity metrics comparison differed slightly from KDE results as only five species in total displayed significant differences in metrics. *Lutjanus argentiventris* was the only high fishing pressure species, which had a significantly higher proportion of optimum size and mega-spawner individuals in NTZs compared to fished areas, 22% and 13.6% higher respectively. Three low fishing pressure species exhibited a comparable trend including *Orthopristis* spp*., Prionurus laticlavius*, and *Aluterus monoceros*, whereas *Paranthias colonus* had higher proportions in optimum size fish and mega-spawners in fished areas.Maturity metrics values were highly variable from species to species. Juvenile maturity metric values ranged from 100% for *Caulolatilus princeps* to 0.6% for *L. viridis,* with the lowest values reported in the low fishing pressure category (Table 3.1, Figure 3.3)*.* Mega-spawner maturity ranged from 90.2% in NTZs for *L. viridis* to 0% for *Mycteroperca olfax, C. princeps,* and *Melichtys niger*, with four other species scoring less than 5% for that metric including *Anisotremus interruptus*, *Calamus* spp*., Balistes polylepis,* and *P. laticlavius* (Table 3.1, Figure 3.3). Overall, species in the medium and low fishing pressure categories displayed the highest optimum size metric values (Table 3.1, Figure 3.3).

Table 3.1 Data and statistical summary for species included in the fished versus no-take zones comparison. Species are ordered top to bottom in categories according to fishing pressure received (i.e. high, medium, low). Significance for the Kernel Density Estimates (KDE) and Chi-square tests is indicated with bold red font.

No-Take Zones
Fishing Zones

	Sample size (n)	Mean length (cm) ± SE	Juveniles (%)	Sub-optimum (%)	Optimum size (%)	Mega-spawners (%)	Chi-square	KDE (SHAPE / LOCATION)	
			Maturity metrics				p-values		
Mycteroperca olfax	61	48.2 ± 1.4	90.2	4.9	4.9	0	0.2395	0.52	HIGH
Sailfin grouper	220	44.7 ± 0.7	95.5	1.8	2.3	0		0.079	
Lutjanus argentiventris	93	46 ± 1	24.7	7.5	38.7	29.0	**<0.001**	**0.01**	
Yellow snapper	156	41.1 ± 0.8	54.5	13.5	16.7	15.4		**<0.001**	
Caulolatilus princeps	115	37.2 ± 0.5	100	0	0	0	0.6109	**0.02**	
Ocean whitefish	309	37.5 ± 0.3	100	0	0	0		**0.002**	
Semicossyphus darwini	28	45.5 ± 2.3	53.6	3.6	21.4	21.4	0.8499	0.79	
Sheephead wrasse	101	48.3 ± 1.1	44.6	11.9	19.8	23.8		0.161	
Anisotremus interruptus	130	31.6 ± 0.4	58.5	6.9	31.5	3.1	0.3443	1	MEDIUM
Burrito grunt	187	30.6 ± 0.4	67.4	5.9	23.0	3.7		0.259	
Lutjanus viridis	167	25.1 ± 0.2	1.2	0	12.0	87.4	0.8057	0.62	
Blue-and-Gold snapper	163	25.6 ± 0.2	0.6	0	9.2	90.2		**0.03**	
Calamus spp.	87	35.1 ± 0.5	47.1	6.9	44.8	1.1	0.784	0.48	
Galapagos/Pacific porgies	109	33.1 ± 0.6	54.1	7.3	36.7	1.8		0.1	
Balistes polylepis	50	40.7 ± 1.2	56.0	16.0	24.0	4.0	0.3196	0.59	LOW
Finescale triggerfish	82	43 ± 0.7	41.5	17.1	39.0	2.4		0.183	
Sphoeroides annulatus	75	26.5 ± 0.5	36.0	0	53.3	10.7	0.8773	0.63	
Bullseye puffer	143	27.3 ± 0.3	31.5	0	58.0	12.6		0.492	
Scarus ghobban	44	44.5 ± 1.7	40.9	9.1	31.8	18.2	0.5027	0.15	
Blue-barred parrotfish	65	48.4 ± 1	26.2	10.8	36.9	26.2		0.152	
Holacanthus passer	40	23.3 ± 0.7	40.0	0	32.5	35.0	0.3331	0.96	
King angelfish	79	21.2 ± 0.6	53.2	0	34.2	21.5		0.134	
Melichthys niger	37	29.1 ± 0.5	48.6	45.9	5.4	0	0.276	0.81	
Black triggerfish	65	28.9 ± 0.3	46.2	53.8	0.0	0		0.68	
Orthopristis spp.	115	30 ± 0.4	19.1	0	34.8	50.4	**<0.001**	0.32	
Grunts	302	28 ± 0.3	31.5	0	41.7	27.2		**<0.001**	
Prionurus laticlavius	144	33.8 ± 0.4	45.8	14.6	38.9	0.7	**<0.001**	0.44	
Razor surgeonfish	277	31.8 ± 0.3	64.3	12.3	22.4	1.1		**0.002**	
Paranthias colonus	1667	26.7 ± 0.1	52.1	0	33.3	14.6	**<0.001**	**<0.001**	
Pacific creolefish	2856	27.2 ± 0.1	45.6	0	34	20.4		**<0.001**	
Aluterus monoceros	140	42.9 ± 0.4	2.1	0	37.9	60.0	**<0.001**	**<0.001**	
Unicorn filefish	166	39.1 ± 0.7	26.5	2.4	22.3	48.8		**<0.001**	

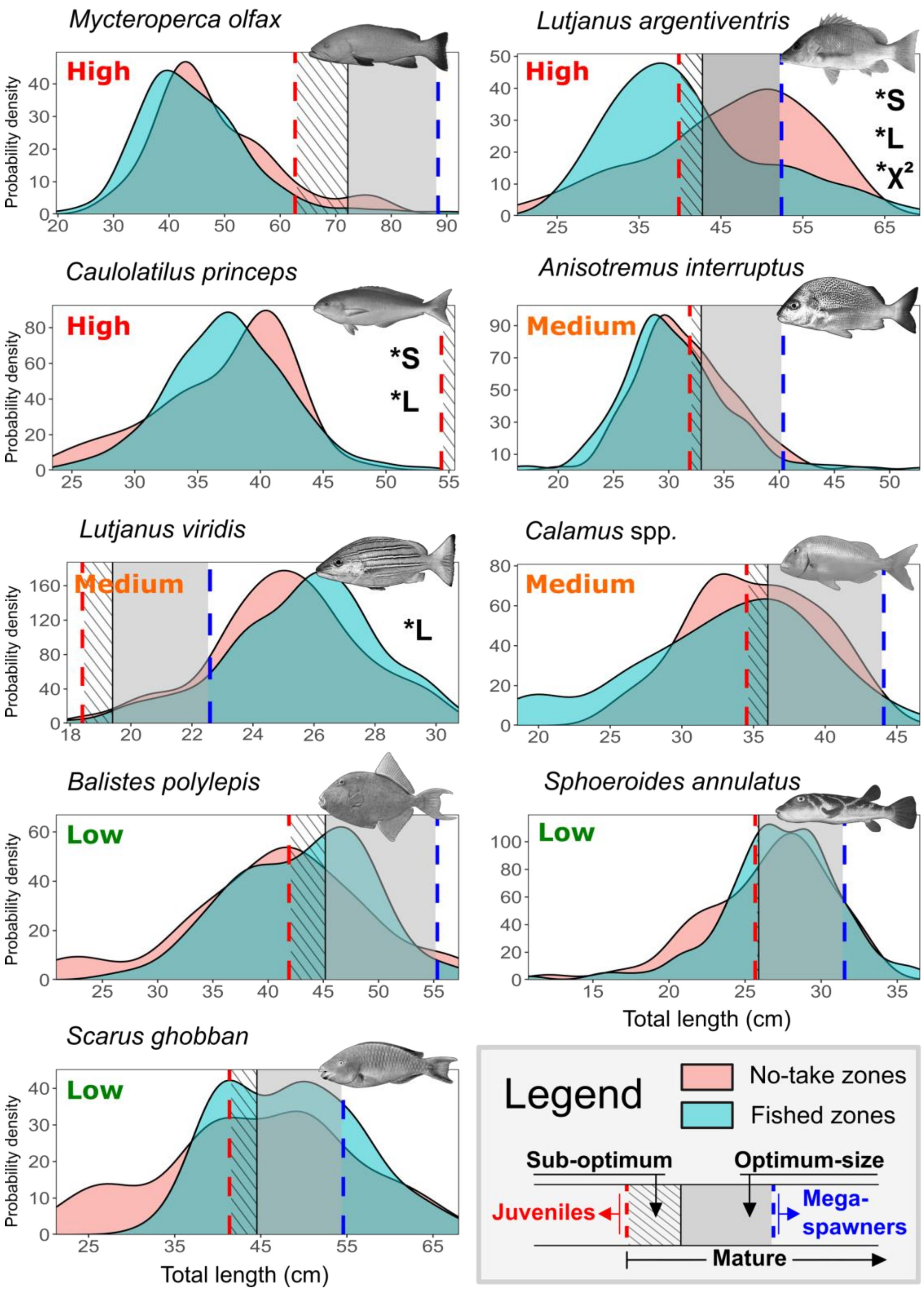
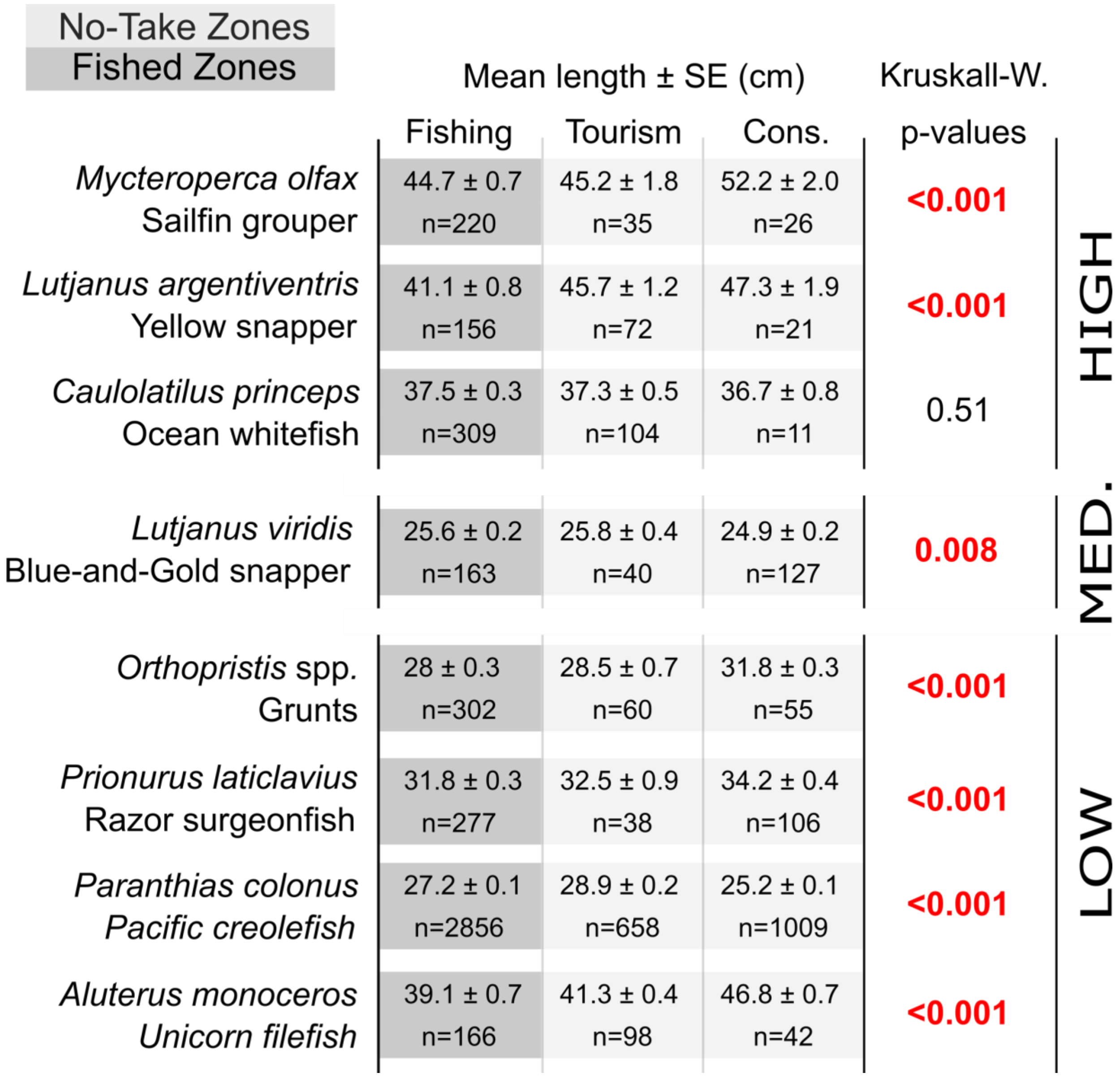


Figure 3.3 Kernel Density Estimates (KDE) plots comparing size distributions of a selection of high, medium, and low fishing pressure species inside and outside of no-take zones. Threshold of maturity metrics categories are indicated with blue and red dashed lines and dashed and shaded areas. Bold black letters denote significant differences between fished and no-take zones as follow; *S for KDE Shape, *L for KDE Location, and *X^2 for maturity metrics (Chi-square).

3.4.1.2 Tourism and conservation no-take zones break-down

All species which had significant KDE tests also displayed significant differences between management zones once NTZs were further divided between tourism and conservation subzones (Table 3.2, Figure 3.4). This additional break down revealed important asymmetries between subzones with five species displaying significant differences between conservation and tourism NTZs including, *Mycteroperca olfax*, *Lutjanus viridis*, *Orthopristis* spp*., Paranthias colonus*, and *Aluterus monceros*. For most species, conservation NTZs displayed the largest fish on average apart for *Lutjanus viridis* and *Paranthias colonus*. As high fishing pressure species, *Mycteroperca olfax*, and *Lutjanus argentiventris* were on average 16.5%, 14.9% larger in conservation NTZs compared to fished zones. *Caulolatilus princeps* was not larger in conservation NTZs, noting the small samples size effect with only 11 fish sampled. Low fishing pressure species, *Orthopristis* spp., *P. laticlavius*, and *A. monoceros* were 13.6%, 7.5%, and 19.5% larger in conservation NTZs compared to fished areas. Tourism NTZs were statistically different from fished zones only in the case of *Lutjanus argentiventris* and *Paranthias colonus*. The latter species were 11% and 6.3% larger in tourism zones compared to fished zones.

Table 3.2 Data summary break-down of fish length by management subzone for species which displayed significance in KDE comparisons. Bold font denotes significant differences (Kruskall-wallis) between management subzones (i.e. fished zones, tourism no-take, and conservation no-take).



No-Take Zones
Fished Zones

	Mean length ± SE (cm)			Kruskall-W.	
	Fishing	Tourism	Cons.	p-values	
Mycteroperca olfax Sailfin grouper	44.7 ± 0.7 n=220	45.2 ± 1.8 n=35	52.2 ± 2.0 n=26	**<0.001**	HIGH
Lutjanus argentiventris Yellow snapper	41.1 ± 0.8 n=156	45.7 ± 1.2 n=72	47.3 ± 1.9 n=21	**<0.001**	
Caulolatilus princeps Ocean whitefish	37.5 ± 0.3 n=309	37.3 ± 0.5 n=104	36.7 ± 0.8 n=11	0.51	
Lutjanus viridis Blue-and-Gold snapper	25.6 ± 0.2 n=163	25.8 ± 0.4 n=40	24.9 ± 0.2 n=127	**0.008**	MED.
Orthopristis spp. Grunts	28 ± 0.3 n=302	28.5 ± 0.7 n=60	31.8 ± 0.3 n=55	**<0.001**	LOW
Prionurus laticlavius Razor surgeonfish	31.8 ± 0.3 n=277	32.5 ± 0.9 n=38	34.2 ± 0.4 n=106	**<0.001**	
Paranthias colonus *Pacific creolefish*	27.2 ± 0.1 n=2856	28.9 ± 0.2 n=658	25.2 ± 0.1 n=1009	**<0.001**	
Aluterus monoceros *Unicorn filefish*	39.1 ± 0.7 n=166	41.3 ± 0.4 n=98	46.8 ± 0.7 n=42	**<0.001**	

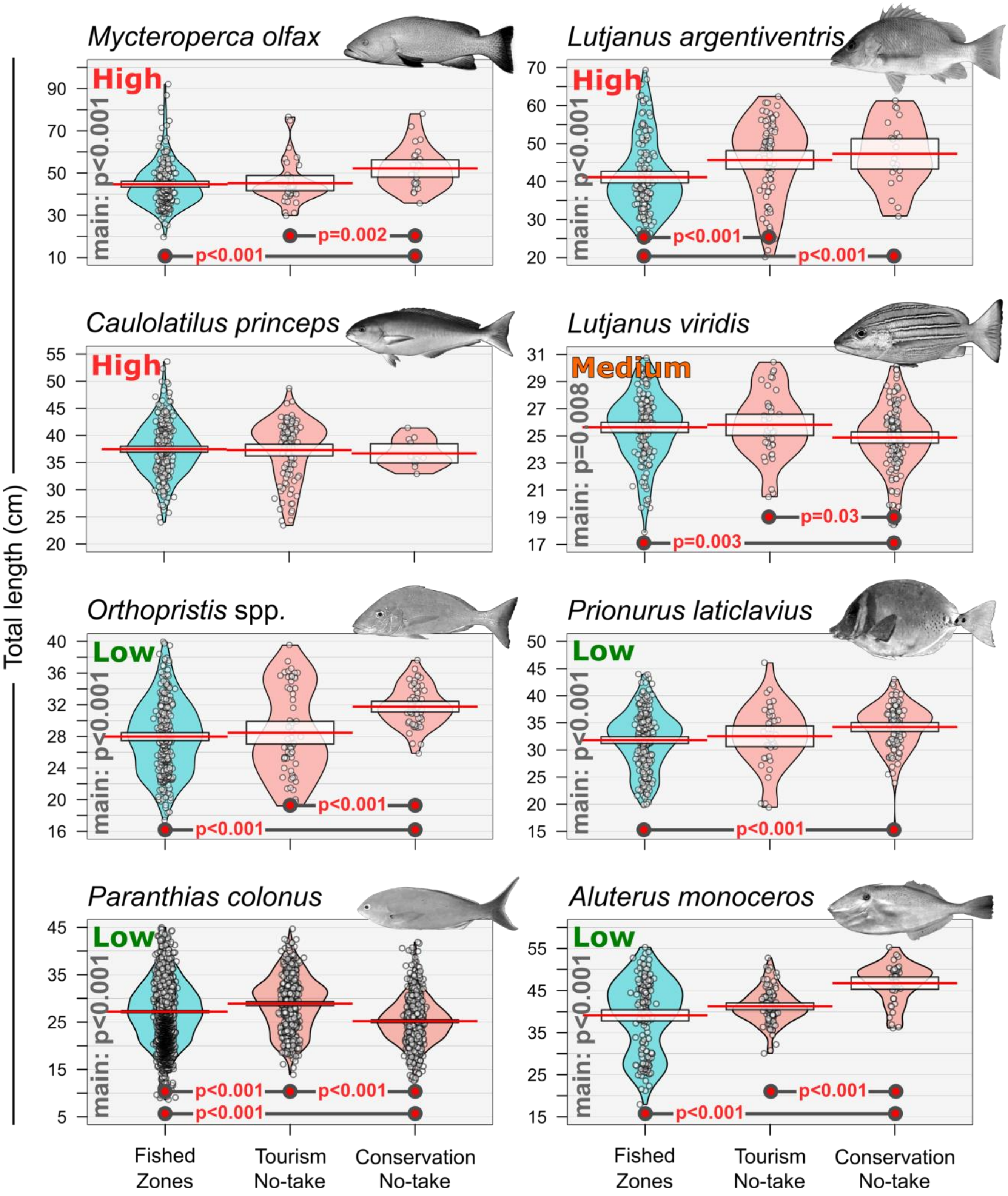


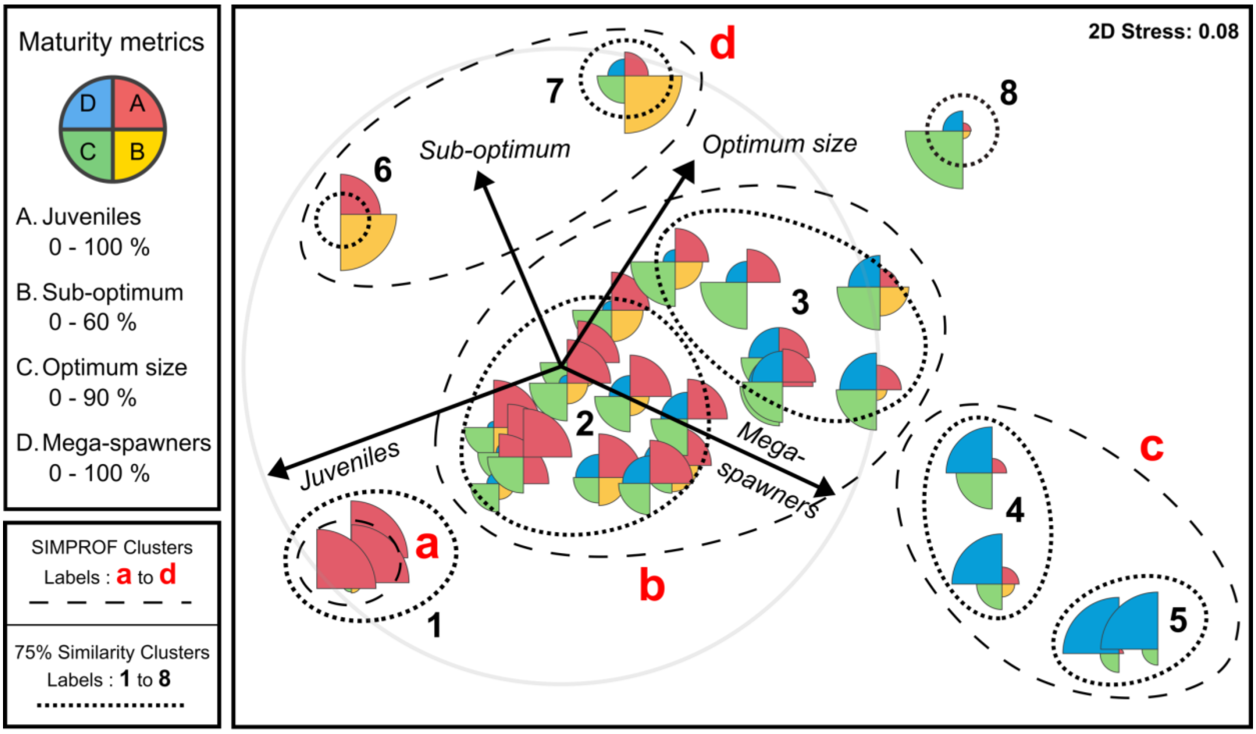
Figure 3.4 Pirate plots break-down of fish lengths by management subzones for species which displayed significance in KDE comparisons. Overall significant differences between subzones is indicated in vertical grey font (Kruskal-Wallis) and subzones pairwise significant differences are indicated in bold red font (Wilcoxon Ranked Sum). Mid red lines mark mean fish size of sample (see Table 3.2 for details) and shaded white area is 95% confidence interval of the population mean.

3.4.2 Overall fish population status in fished zones

3.4.2.1 Maturity metrics non-metric multidimensional scaling (nMDS)

The nMDS analysis revealed marked multivariate patterns with five statistically distinct main groups emerging from the cluster analysis with SIMPROF tests (Figure 3.5). Overlaid 75% similarity clusters reveal that the SIMPROF clusters present varying levels of dispersion between species although each SIMPROF cluster had no less than 50% similarity between species. The juveniles and mega-spawners spearman rank correlation vectors values are nearing 1, indicating distinct multivariate gradients (Figure 3.5). More specifically, the further to the left the clusters lie, the higher the proportion of juveniles they contain. In contrast, the further to the right the clusters, the higher the proportion of mega-spawners present, while also displaying an increased proportion of optimum-sized fish.

Cluster 1 matched SIMPROF cluster (a) and was strictly comprised of high fishing pressure species characterized by a high proportion of immature fish and negligible proportions of optimum size fish or mega-spawners including *Mycteroperca olfax*, *Caulolatilus princeps*, *Dermatolepis dermatolepis*, and *Lutjanus novemfasciatus*. Cluster (b) included species from all fishing pressure categories with high proportions of juveniles, and non-negligible fractions of optimum size fish and some mega spawners in the case of cluster 3, which included some high fishing pressure species like *Lutjanus argentiventris* or *Semicossyphus darwini*. Cluster (d) was characterized by a dominance of sub-optimum size fish. Clusters (c) presented disproportionately high proportions of mega-spawners. No high fishing pressure species were found in the rightmost clusters (c), (3).



1
Mycteroperca olfax (Serranidae) - H
Caulolatilus princeps (Malacanthidae) - H
Dermatolepis dermatolepis (Serranidae) - H
Lutjanus novemfasciatus (Lutjanidae) - H

2
Haemulon scudderii (Haemulidae) - M
Prionurus laticlavius (Acanthuridae) - L
Anisotremus interruptus (Haemulidae) - M
Paralabrax albomaculatus (Serranidae) - H
Balistes polylepis (Balistidae) - L
Lutjanus argentiventris (Lutjanidae) - H
Semicossyphus darwini (Labridae) - H
Aluterus monoceros (Monacanthidae) - L
Caranx caballus (Carangidae) - M
Paranthias colonus (Serranidae) - L
Holacanthus passer (Pomacanthidae) - L
Calamus spp. (Sparidae) - M

3
Epinephelus labriformis (Serranidae) - M
Sphoeroides annulatus (Tetraodontidae) - L
Scarus ghobban (Scaridae) - L
Orthopristis spp. (Haemulidae) - M
Bodianus eclancheri (Labridae) - L
Hoplopagrus guentherii (Lutjanidae) - M
Mulloidichthys dentatus (Mullidae) - L

4
Scomberomorus sierra (Scombridae) - M
Sufflamen verres (Balistidae) - L

5
Lutjanus viridis (Lutjanidae) - M
Canthidermis maculata (Balistidae) - L

6
Melichthys niger (Balistidae) - L

7
Sphyraena idiastes (Sphyraenidae) - M

8
Uraspis helvola (Carangidae) - L

Figure 3.5 Non-metric multivariate dimensional scaling of fish maturity metrics in areas open to fishing for all species. One species is represented by four joint slices, with each slice accounting for one metric and slice size proportional to the metric's percentage value (note the different maximum values of each metric and absence of slice when the metric is equal to zero). Long dash ellipses mark significant SIMPROF clusters while short dash ellipses mark 75% similarity clusters, also used to annotate species in each cluster bellow the graph. Fishing pressure of each species is indicated with H (high), M (medium), and L (low) after its family and scientific name. Black arrows indicate spearman ranked correlation vector for each metric marking gradient from highest metric values (in the direction of the arrow), and lowest metric values (opposite direction). Grey circle indicates magnitude of correlation

3.4.2.2 Maturity metrics bar chart

Overall, nearly two thirds of all species are characterized by a majority of mature individuals (i.e. sub-optimum, optimum and mega-spawners combined) with less than 50% juveniles. The top third of the bar chart is comprised of high and medium fishing pressure species, while the bottom quarter is comprised of low and medium fishing pressure species. Despite most high fishing pressure species being characterized by a majority of juveniles, some displayed fair levels of optimum size individuals such as *Epinephelus labriformis,* and *Semicossyphus darwini.* Most species in the medium fishing pressure categories displayed high levels of optimum size and mega-spawners like *Lutjanus viridis, Scomberomorus sierra, Hoplopagrus guentherii,* and *Sphyraena idiastes* although the grunts *Anisotremus interruptus* and *Haemulon scudderii* displayed an opposite trend. Most epinephelids, namely *Mycteroperca olfax, Dermatolepis dermatolepis, Paralabrax albomaculatus*, and *Epinephelus labriformis* displayed less than 5% mega-spawners. Certain low fishing pressure species, including *Melichthys niger*, *Prionurus laticlavius*, or *Aluterus monoceros* had negligible levels of mega-spawners.

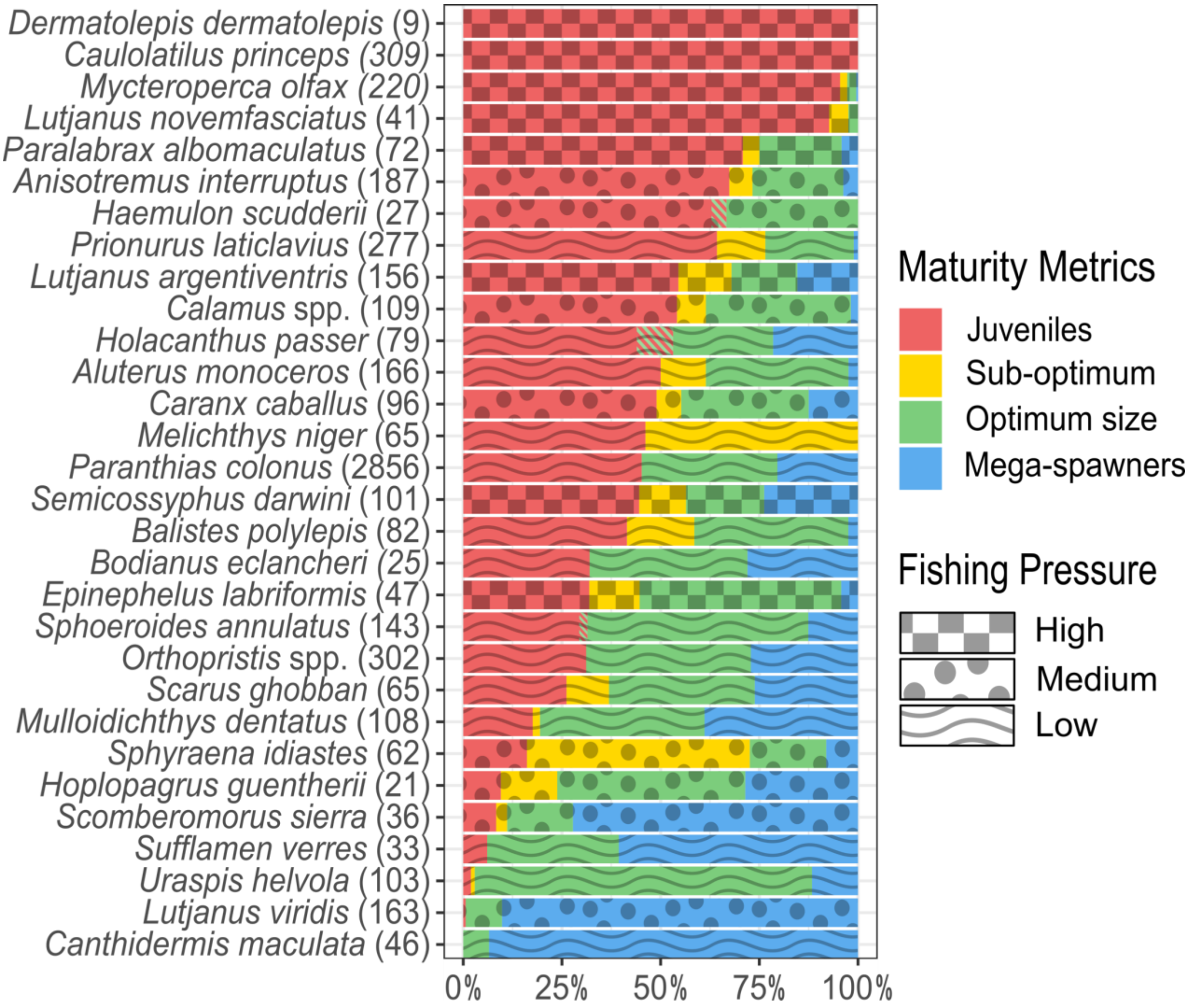


Figure 3.6 Maturity metrics bar chart break-down in areas open to fishing for all species. Species are ranked top to bottom from highest to lowest value of the juvenile maturity metric. Sample size is in bracket following species scientific name. Fishing pressure is marked with overlaid shaded pattern.

3.5 Discussion

This study revealed that the Galapagos Marine Reserve (GMR) management has had mixed effects on exploited and non-exploited fish taxa. On the positive side, a number of highly targeted fish species displayed larger individuals within no-take zones (NTZs) compared to fished areas while medium and low fishing pressure species tended to present fair levels of mature individuals. However, most exploited epinephelid species with sensitive life histories (e.g. *Mycteroperca olfax, Dermatolepis dermatolepis, Paralabrax albomaculatus*) presented very low proportions of mega-spawners and mature individuals, both inside and outside

NTZs, suggesting their status remains preoccupying after 15 years of protection. Based on existing research on effective MPAs and the age of the GMR, it appears that the differences in size detected for such species are not characteristic of a well-enforced MPA with good compliance levels (Russ & Alcala, 2003b; Russ et al., 2005; Edgar et al., 2014; Giakoumi et al., 2017; Friedlander et al., 2017, Goetze et al. 2021).

Interestingly, conservation and tourism NTZs had disproportionate ecological effects for highly targeted species, the latter showing generally weaker or no effects in the case of sailfin groupers. One explanation could be differences in zone design as conservation no-take zones were on average 50% larger than tourism NTZs under the 2000 zoning scheme. Larger MPAs typically perform better as they provide enhanced protection of mobile species across their range (Claudet et al., 2008, 2010; Edgar, 2011; Palumbi, 2004). Alternatively, it could be that compliance is lower in tourism NTZs and that some level of fishing pressure persists in these areas. By contrast, yellow snapper were significantly larger in both tourism and conservation NTZs which might be due to differences in fishing gear. In the Galapagos, snappers are generally caught via spearfishing, which is prohibited throughout the GMR, while sailfin grouper are mostly fished with authorized hook and line (Peñaherrera, 2007). In the Galapagos, non-compliance with fisheries regulations is driven in part by the risk of infringement detection (Viteri & Chávez, 2007). This risk is arguably higher for illegal fishing gear like spear-guns compared to legal gears, irrespective of zone type, likely leading to more homogeneous protection of snapper species across no-take subzones. While the oceanic whitefish (*Caulolatilus princeps*) were also significantly larger in no-take zones, a finer analysis of no-take sub-zone performance is not possible as only a handful of individuals were sampled in conservation NTZs. With the implementation of expanded NTZs in 2019, potential issues associated with zone design will likely be mitigated. However, potential issues related to compliance within tourism zones require further investigation.

A range of medium and low fishing pressure species also displayed significant differences between fishing zones and NTZs, with positive as well as negative impacts of protection. For example, blue and gold snappers (*Lutjanus viridis*), which are small-bodied and unexploited, were significantly smaller in conservation NTZs compared to fished zones. This effect, whereby a non-commercial species is negatively affected by MPAs, is not uncommon and can be indicative of a potential predator-prey interaction (Claudet et al., 2010). This is plausible as conservation NTZs also host the largest sailfin groupers, yellow tail snappers and amberjacks. The planktivorous creole fish (*Paranthias colonus*), the most abundant fish in the Galapagos, are largest in tourism NTZs and smallest in conservation NTZs, with fished zones sitting in the middle. Similar, to *Lutjanus viridis*, *Paranthis colonus* likely receives an increased predation pressure in conservation no-take zones. However, the significantly larger size in tourism no-take zones might be due to environmental factors. Indeed this species displays marked habitat preferences for areas receiving high current and nutrient input (Salinas-de-León et al., 2016). Such habitats were disproportionately picked as tourism NTZs under the 2000 zoning scheme, as they generally harboured higher shark biomass with potentially higher tourism value (Edgar et al., 2004b). By contrast, three low fishing pressure species, namely, the leatherjacket (*Aluterus monoceros*), Galapagos grunts (*Orthopristis* spp.), and razor surgeonfish (*Prionurus laticlavius*), displayed the largest individuals in NTZs, indicating indirect benefits from protection. In the case of the razor surgeonfish, Ruttenberg (2001) found similar results when comparing heavily fished areas and lightly fished areas prior to the establishment of the 2000 zoning. This suggests that NTZs allow for natural trophic dynamics to be restored or maintained, leading to lower urchin densities and higher algal cover, which support populations of surgeonfish (Hay & Taylor, 1985; Robertson, 1991). Similarly, leatherjackets and Galapagos grunts, likely benefit indirectly from protection, as do numerous non-exploited and low trophic level species in other MPAs (Claudet et al., 2010; Halpern, 2003). Despite the above, most medium, and low fishing pressure species did not appear to be significantly affected by the zoning scheme. Our results add to the existing literature on indirect effect of MPAs on non-target species (Claudet et al., 2010; Halpern, 2003), suggesting effects are diverse and species-specific in scale and direction.

The maturity metrics in fished areas suggest that a large proportion of highly targeted species, such as epinephelid species in particular, had concerning maturity metric levels. Specifically, sailfin groupers (*Mycteroperca olfax*), leather bass (*Dermatolepis dermatolepis),* and white spotted sand bass (*Paralabrax* *albomaculatus)* metrics were largely dominated by immature individuals with no or negligible fractions of mega-spawners both inside and outside no-take zones. For reference, Froese (2004) suggests that when metrics reflects the size structure of the whole population, 30-40% of mega-spawners is considered a healthy level and values below 20% should be of concern. The cabrilla (*Epinephelus labriformis*), while presenting almost 75% of mature individuals, also had only ~4% of mega-spawners. By contrast, creole fish (*Paranthias colonus*), the most abundant epinephelid in the Galapagos, had more than 20% mega-spawners and is therefore considered to be of least concern. These results are not surprising as multiple studies have questioned the sustainability of epinephelid fisheries in the Galapagos (Burbano et al., 2014; Pontón-Cevallos et al., 2020; Salinas-de-León et al., 2015; Usseglio et al., 2016). The biomass of bacalao has presumably decreased 85% compared to virgin stocks (Eddy et al., 2019). In addition, while no historical baseline survey exists, abundances of leather bass appear very low with only 23 individuals recorded (none of which were mega-spawners) in over 600 baited remote underwater stereo-video systems (stereo-BRUVs) deployments, compared to 400 sailfin groupers and 100 white-spotted sand bass. Other non-epinephelid species deserve further attention due to high levels of immature individuals and low levels of mega-spawners, including the oceanic whitefish (*C. princeps*), dog snapper (*Lujanus novemfasciatus*), and burrito grunt (*Anisotremus interruptus*).

While the maturity metrics of some species are concerning, a larger number of species surveyed in all fishing pressure categories displayed healthy population metrics levels. This was the case for several fish families including scaridae, balistidae, tetraodontidae, mullidae, labridae. Furthermore, this also included species in highly targeted family groups like the lutjanidae (e.g. *Lutjanus argentiventris* and *Hoplopagrus gentherii*), scombridae (e.g. *Scomberomorus sierra*), or labridae (e.g. *Semicossyphus darwini*). This reveals that a number of species commercially targeted elsewhere have healthy population levels in the Galapagos, owing to two main drivers. The low market value of some of these species likely leads to a moderate or absence of exploitation, in accordance with studies showing how market forces and profitability shape the behaviour of Galapagos fishermen (Bucaram & Hearn, 2014; Castrejón & Charles, 2020; Viteri & Chávez, 2007). In addition, most Galapagos fishermen in activity today have participated in the highly lucrative sea cucumber fisheries era of the late 1990s early 2000s with revenue levels unmatched since the collapse of the fishery. As a result, current efforts to expand the finfish artisanal fisheries are focusing on high-value fisheries such as deep-sea fisheries or long-lining (Cerutti-Pereyra et al., 2020; Marin Jarrin et al., 2018), rather than lower-value species commonly targeted in subsistence fisheries globally. Furthermore, large industrial gears such as gillnets, drift FADs, purse seine, long-lines, and bottom or mid-water trawls are banned from the GMR, while being commonly used in adjacent regions (Avila-Forcada et al., 2012; Castro et al., 2020; Clarke et al., 2018, 2020; Duffy et al., 2019; Essington et al., 2002; Lin & Zhu, 2020; Márquez-Farías, 2011; Martínez-Ortiz et al., 2015; Villalobos-Rojas et al., 2020). These important gear restrictions prevent large scale exploitation of certain fish families routinely caught in the tropical eastern pacific, including parrotfishes (Taylor and Choat 2014; Taylor et al. 2015), puffer fishes (Ojeda-Ruiz et al., 2016; Sánchez-Cárdenas et al., 2011), scads and small jacks (Costa et al., 2020; Mair et al., 2012; Shiraishi et al., 2010), filefishes (Ghosh et al., 2011; Ul Hassan et al., 2020), grunts (Ruiz-Ramírez et al., 2012), and triggerfishes (Salinas-de-León, Andrade, et al., 2020). The overall good conservation status of these species contributes to enhancing the resilience of the GMR in the anthropocene (Salinas-de-León, Andrade, et al., 2020) and reflects important historical governance choices to exclude industrial fisheries and favour local artisanal fisheries.

Combining the Froese (2004) fisheries indicators approach with stereo-video multivariate data analysis offers exciting potential in terms of new approaches contributing to management advice. Visualizing the metrics using a multidimensional scaling analysis (nMDS) allows for cohesive groups to emerge, making it possible to identify the species in need of management. This could be used to easily convey information to different stakeholder groups to help prioritize actions or illustrate the impact of fishing activities, whether recreational or industrial. Compared to fish biomass or abundance data, which have limited applications for inter-taxa comparison due to inherent species to species variation, the proportion of mature fish or mega-spawners data is comparable between species and more relatable (Froese, 2004). In addition, stereo-video surveys are increasingly used around the world (Goetze et al., 2019; Langlois et al., 2020; Whitmarsh et al., 2017), yielding accurate length datasets which could be used for assemblage-wide maturity metrics analysis. Applying this approach within old well-designed and managed MPAs (Edgar et al., 2014) could help determine what optimum maturity metrics look like and provide appropriate targets for new protected areas. Expanding on those findings through implementation in other parts of the world is a prerequisite to validate this method and make it available as an additional easily interpretable fisheries management tool globally.

An important point in the process of validating the maturity metrics benchmark values is understanding whether stereo-BRUVs length distributions accurately represent the age and size structure of each species. This is particularly important as Froese's (2004) original approach was designed for catch data and its applicability to underwater survey data will rely on setting adequate thresholds values to interpret metrics. Initial studies have shown that stereo-BRUVs can provide size-frequency distributions comparable to catch data in fisheries using trawls, traps or hook and line (Cappo et al., 2004; Langlois et al., 2012, 2015). However, Langlois et al. (2012) point out that interpreting length-frequency data requires careful consideration of species life history as well as sampling biases. Indeed, many commercially important reef-fish species display ontogenetic migrations (Aburto-Oropeza et al., 2009; Grüss et al., 2011, 2017; Moura et al., 2011; Nakamura et al., 2008) or depth refuge effects (Lindfield et al., 2014; Pereira et al., 2018; Tyler et al., 2009). Hence, it appears that to obtain representative fish size distributions and allow a meaningful interpretation of maturity metrics, it is crucial to survey habitats that are representative of the adult population habitat range. Future research should focus on validating maturity metrics target values and evaluate the applicability of the method to different species groups in relation to their life history strategy.

The other source of uncertainty which calls for further work lies in the discrepancies surrounding the maximum size of species. The maximum size is a crucial data point which feeds into the empirical equations developed by Froese and Binohlan (2000) and allows the computation of estimates of the size at first sexual maturity, the optimum length interval, and the size of mega-spawners. Here, we opted to use the maximum size found on FishBase as this is the most consistent and complete source of information on the life history of fishes.

However, in several instances, this study observed several individuals above the FishBase recorded max size and thus this value was used. This is consistent with meta analysis by Patrick et al. (2014) and Thorson et al. (2014) which show that Fishbase maximum size values tend to slightly under represent true values and that other discrepancies exist for auto-generated information. In addition, density and latitudinal dependant growth (Helser & Brodziak, 1998; Lorenzen & Enberg, 2002; Wakefield et al., 2020) or life history changes in exploited fish populations (Hall, 1999; Sharpe & Hendry, 2009) do occur, suggesting that FishBase maximum length estimates may not accurately represent all populations or locations. For example, the max size of oceanic whitefish (*Caulolatilus princeps*) on FishBase is 100cm although only reaching a maximum of 53.6cm in our stereo-BRUVs data. This discrepancy is unlikely to be explained by habitat preferences as Galapagos landing catch data for the species indicates a max size of 62cm with fishermen exploiting the species across its entire depth range (Marin Jarrin & Salinas-de-León, 2018). Besides, *C. princeps* of 80cm and above are commonly reported along the Californian coast (Milton Love 2020, pers. comm.). This suggests that multiple sub-populations with varying max length may be found in the eastern pacific although only a populations genetic study would confirm that hypothesis. Alternatively, there might be a disproportionately higher fishing effort in the Galapagos resulting in strong size truncation of the population. By default, choosing FishBase maximum size information results in conservative estimates of maturity metrics for most species. However, if important within-population variability exists in terms of maximum size, the interpretation of maturity metrics would need to be location-dependant or might otherwise be overly concerning, as such results must always be interpreted with caution and reference to available local population data. Resolving such questions will help develop a standard, best-practice approach for the interpretation of maturity metrics.

This study shows that this zoning has not been sufficient to ensure population recovery of the most impacted species groups outside NTZs, with epinephelids being of particular concern. A rezoning process was initiated in 2014 and the proposed scheme may address some of the design flaws of the previous scheme through expanding existing zones and creating new NTZs in areas previously underrepresented (Edgar et al., 2004a). These changes, if implemented, would increase the total NTZ area from ~1% to 33% of the GMR (Burbano et al., 2020). Based on our results, it is likely that expanding the size of NTZs will yield long-term benefits for fish populations. Indeed, herein the largest NTZs (i.e. conservation NTZs) likely contribute more to reproductive success in the GMR as they harbour the largest individuals for several highly targeted species (Barneche et al., 2018; Berkeley et al., 2004; Bohnsack, 1994; Hixon et al., 2014; Palumbi, 2004). With adequate enforcement and compliance, ecological spill-over may increase in the future under the new zoning and help re-build impacted populations beyond NTZ boundaries (Di Lorenzo et al., 2020).

In combination with spatial management, complementary measures must be considered to help rebuild epinephelid populations. Despite ongoing discussions for over 20 years, no species-specific measures, such as minimum and maximum landing size or seasonal closures during reproduction, are in place for any exploited Galapagos finfish species. This has often been attributed to weak governance and ineffective fisheries management structures (Castrejón, 2011; Castrejón & Charles, 2013b; Hearn, 2008; Jones, 2013). Alternative routes to reduce fishing pressure on epinephelids could consist of implementing market restrictions, such as an export ban, as market incentives is a key driver for marine resource exploitation in the Galapagos (Viteri & Chávez, 2007; Bucaram & Hearn, 2014; Castrejón & Charles, 2020). For example, the Galapagos sailfin grouper (*Mycteroperca olfax)* is one of the main ingredients of the traditional *Fanesca*, a dish which millions of Ecuadorians consume for Easter (Salinas-de-León et al., 2015; Usseglio et al., 2016; Zimmerhackel, 2013). Regrettably, this species forms spawning aggregations right before those festivities, and as such is heavily targeted by fishermen who salt and dry the fish before exporting most of the catch. A ban on the exportation of epinephelid species would mean that they could still be consumed locally while significantly reducing the pressure on the stock. Another epinephelid, the leatherbass (*Dermatolepis dermatolepis),* also requires urgent action. Since this species arguably represent a negligible fraction of fishermen revenue, a landing moratorium could be enacted to provide optimum conditions for this species to rebuild while having virtually no impact to fishers' livelihoods. As a wide range of non-epinephelid species exhibit healthy population levels, bio-economic assessments are needed to determine which of these species could replace traditionally caught species in need of stronger protection.

The Galapagos marine environment can undoubtedly support moderate levels of subsistence fisheries for local consumption. Whether these iconic islands can indefinitely withstand an exploitation geared towards national and international exports of high-value species is questionable. Without strengthening both market regulations and fisheries management, the resilience of the Galapagos Marine Reserve may continue to decline, aided by climate change.

Chapter 4 Fluctuations of Galapagos mid-water and benthic reef fish populations during the 2015-16 Enso

4.1 Abstract

El Nino Southern Oscillation (ENSO) events have impacted the marine environment in Galapagos, causing massive die-offs or corals and megafauna, benthic habitat shifts, and presumed species extinctions. With ENSO events predicted to intensify under climate change scenarios, it is important for managers to have an evidence-based understanding of how these events may affect fish assemblages in the Galapagos. We assess the abundance and size fluctuations in benthic and mid-water shore fishes associated with the 2015-16 ENSO using data from baited remote underwater stereo-video surveys collected at four times during 2015-16. We found significant differences in the assemblage structure between the pre-El Nino, El Nino onset, El Nino receding, and La Nina onset sampling periods. Mackerels (i.e. *Trachurus murphyi* and *Decapterus* spp.), the second most abundant recorded taxa, displayed a ~480% greater relative biomass, 229% greater relative abundance, and 20.6% greater size during La Nina onset compared to El Nino. La Nina onset was also associated with a several fold increase in the mid-water abundance of large Carangids, medium-size Scombrids, elasmobranchs (i.e. *Sphyrna lewini*, *Carcharhinus galapagensis*) as well as several other bentho-pelagic taxa. We also found evidence of repeated seasonal fluctuation patterns across years in Scarids, Haemulids, Labrids, Chaetodontids, and Carangids which suggests that ecological regulating processes such as ontogeny persisted despite ENSO. Although the 2015-16 ENSO appears to have had a lesser impact on the Tropical Eastern Pacific compared to historical events, we documented fluctuations in the abundance of several species of key ecological and economic importance in the region. Knowledge about fluctuations in species abundance and the knock-on effects in marine ecosystems should be incorporated into management strategies to enable resilience within the Galapagos Marine Reserve.

4.2 Introduction

El Nino-Southern Oscillation (ENSO) is the largest year-to-year climate fluctuation on earth, with a warm (El Nino) and cold (La Nina) phase occurring naturally every 2-7 years (McPhaden et al., 2006; Santoso et al., 2017; McPhaden et al., 2020). Driven by ocean-atmosphere interactions, ENSO originates in the tropical Pacific Ocean where anomalous pressure gradients trigger a self-reinforcing loop between weakening trade winds and increasing sea-surface temperature (SST) (Wang & Fiedler, 2006; Trenberth, 2020). ENSO's teleconnections with local climates are global, driving extreme weather events with dramatic impact to socio-economic and biological systems (Brönnimann, 2007; Babcock et al., 2019; Whitfield et al., 2019; Cai et al., 2020). At sea, ENSO leads to extensive marine heatwaves and sharp decreases in primary productivity, with knock-on effects across the entire marine ecosystem (Barber & Chavez, 1983; Oliver et al., 2018; Holbrook et al., 2020). The magnitude of these impacts varies greatly, being moderate during weak ENSO, or very strong during extreme ENSOs such as the 1982-83, 1997-98, or 2015-16 events (Santoso et al., 2017; Capotondi et al., 2020). Extreme effects include diebacks of habitat forming species such as mangrove forests, kelp forests, seagrass meadows and coral reefs, as well as population-level impacts to marine mammals, seabirds, invertebrates, and fish assemblages (Quillfeldt & Masello, 2013; Avila et al., 2018; Babcock et al., 2019; Holbrook et al., 2020; Holbrook et al., 2020; Lehodey et al., 2020). Due to their recurring nature and strong influence on environmental conditions, ENSO events have shaped terrestrial and marine ecosystems alike for millennia (Stenseth, 2002; Lu et al., 2018; Emile-Geay et al., 2020). With extreme ENSOs projected to increase under climate change scenarios, the capacity of ecosystems to recover from increased environmental variations is in question (Cai et al., 2014, 2018; Oliver et al., 2018; Cai et al., 2020).

Due to its oceanographic setting, the Galapagos Archipelago offers a unique window to study the response of marine ecosystems to ENSO (Salinas-de-León et al., 2020). Located in the Tropical Eastern Pacific 1000 km off the coast of Ecuador, these islands lie across the Equatorial line at the epicentre of a major cold and warm current system (Figure 4.1a) (Pak & Zaneveld, 1974;

Houvenaghel, 1978; Lukas, 1986; Banks, 2002; Palacios, 2004). Coming from the west, the Equatorial Under Current flows deep and upwells cold nutrient-rich waters to the archipelago, fuelling high levels of primary productivity (Jakoboski et al., 2020). Cold waters also arrive from the east and southeast with the Equatorial Counter Current and Humboldt current while the Panama current brings warm oligotrophic waters from the Northeast. The relative strength of these currents varies during the year, giving rise to a warm season generally from December to June and a cold season between July and November (Harris, 1969; Palacios, 2004). This dynamic oceanographic setting sustains distinct marine assemblages adapted to unique environmental conditions, with five biogeographical regions identified (Edgar et al., 2004a, Chapter 2). This makes Galapagos marine ecosystems particularly vulnerable to the changing oceanographic conditions under ENSO.

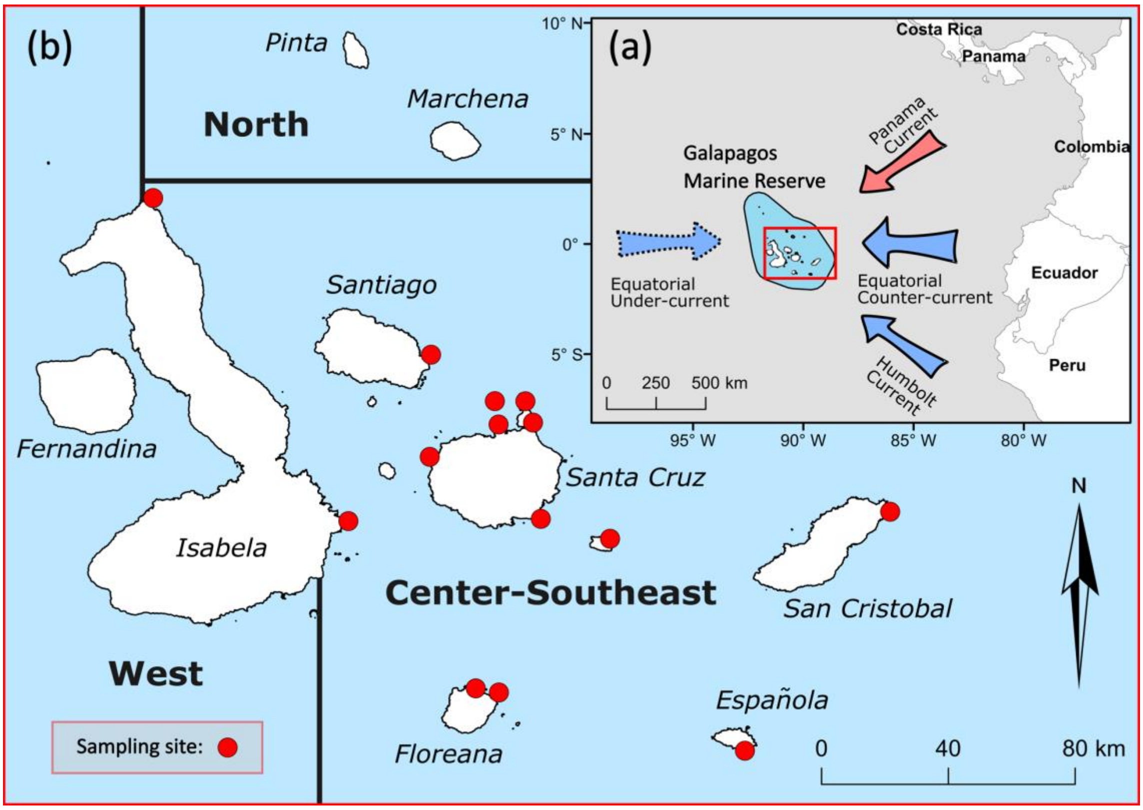


Figure 4.1 a. Location of the Galapagos archipelago in the Tropical Eastern Pacific region and its prevailing currents. Dashed-outline arrow denotes deep flowing currents while solid outline denotes predominantly surface current. b. Location of the stereo-BRUVs survey sites in the Galapagos center-southeast bioregion with all sites sampled twice in 2015 and twice in 2016.

In the Galapagos and wider Tropical Eastern Pacific region ENSO drives decreased easterly trade winds, increased thermocline depth, weakened Equatorial Counter Current and weakened, or even halted Equatorial Under Current (Figure 4.1a, Firing et al., 1983; Wang & Fiedler, 2006; Trenberth, 2020). This leads to a sharp decrease in nutrient and cold water inputs to the archipelago with associated drops in primary productivity and warm water build-up (Figure 4.2a) (Barber & Chavez, 1983; Barber & Chávez, 1986; Banks, 2002). The warm oligotrophic “El Nino” phase generally peaks from October/November through to December/January where temperature anomalies may exceed +4°C and primary productivity decrease by an order of magnitude (Barber & Chavez, 1983; Glynn, 1984, 2000). Following peak anomalies, “El Nino” progressively recedes and gives rise to the cold “La Nina” phase where previously weakened currents regain strength, cool waters flow in and primary productivity rebounds (Figure 4.2b). The impact of a complete ENSO cycle on the Galapagos marine trophic chain can be major and have long-lasting ecosystem-wide effects (Edgar et al., 2010; Glynn et al., 2018).

Extensive research has documented the impact of ENSO on iconic marine taxa in Galapagos, while its impact to local fish populations is less studied. Impact to coral populations is well understood as ENSO-related bleaching episodes have reduced Galapagos coral reefs populations by 97-99% following the 1982-83 event (Glynn, 1984, 1994, 2000; Fong & Glynn, 2000; Edgar et al., 2010; Glynn et al., 2018; Riegl et al., 2019). Similarly, population declines in seabirds (Valle et al., 1987; Valle & Coulter, 1987; Anderson, 1989; Boersma, 1998; Vargas et al., 2006), marine iguanas (Laurie, 1990; Wikelski & Wrege, 2000; Vinueza et al., 2006), and pinnipeds (Trillmich, 1985; Trillmich & Dellinger, 1991; Salazar & Bustamante, 2003; Salazar & Denkinger, 2010) following the 1982-83 and 1997-98 ENSO has been well documented. The wide-spread and strong negative impacts of ENSO on these emblematic species and the existence of population baseline data (Laurie, 1990; Trillmich & Dellinger, 1991; Glynn, 1994; Boersma, 1998) has led to their dominance in the Galapagos ENSO research panorama. In contrast, research investigating the influence of ENSO on fish populations is limited.

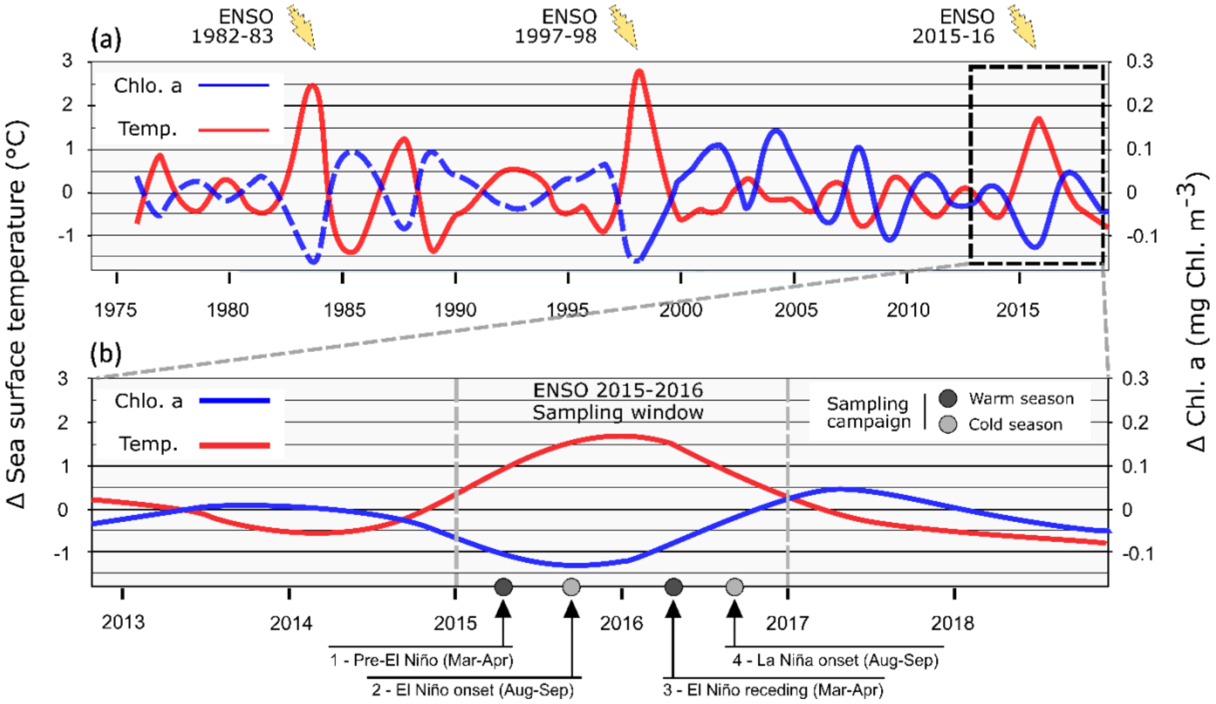


Figure 4.2 a. Sea surface temperature and chlorophyll-a anomalies in the Galapagos region (Latitude 89–92 ° W; longitude 1.5 °S –1 °N) between 1975 and 2018 with timing of the last three extreme ENSO events. b. Detail of environmental fluctuations during the 2015-2016 ENSO in Galapagos with timing of the four sampling periods and their association with the specific ENSO phase and the warm or cold Galapagos season. Time series were re-drawn based on Salinas-de-León et al. (2020).

There are several reasons why there is limited research investigating the impact of ENSO on Galapagos fishes. Robust monitoring of fish assemblages and populations in Galapagos commenced following the establishment of the Galapagos Marine Reserve around 2000 (DPNG, 1998; Heylings et al., 2002; Edgar et al., 2004b; Banks et al., 2016). Therefore, before/after fish assemblage data for the 1982-83 and 1997-98 extreme ENSO events is limited. Additionally, the most direct impacts of ENSO on fish populations are presumably in small pelagic fish populations (Barber & Chavez, 1983; Barber & Chávez, 1986; Sharp & Mclain, 1993; Stenseth, 2002) which are notoriously difficult to sample due to their high-mobility and patchy distributions (Fréon & Misund, 1999; Heagney et al., 2007; Santana-Garcon, Newman, et al., 2014). Small pelagic species respond sharply to decreases in their planktonic prey during ENSO (Barber & Chavez, 1983; Barber & Chávez, 1986), resulting in shifts in foraging grounds or body size as reported along the coast of South America (Dioses et al., 2002; Alheit & Niquen, 2004; Peña-Torres & Agostini, 2007). The likely decline of these prey resources in Galapagos during ENSO would explain the starvation observed in seabirds and pinnipeds, although robust in-situ evidence is still lacking.

These limitations led researchers to use models (Wolff et al., 2012; Bucaram et al., 2018; Eddy et al., 2019), perception surveys (Cavole et al., 2020), or catch data (Marin Jarrin & Salinas-de-León, 2018) to assess the impact of ENSO on fish populations. Additionally, studies using underwater surveys were generally limited to a few benthic species (Ruttenberg, 2001; Lamb et al., 2018). Trophic models suggests that ENSO can decrease the biomass of jacks and mackerels, small planktivorous fish, and mullets by up to 50% because of plankton population declines, although those results are confined to the small Elizabeth bioregion in the west (Wolff et al., 2012). Archipelago-wide models of tuna fisheries productivity indicate that those species may also be negatively affected by ENSO (Bucaram et al., 2018). Similarly, fishers' general perceptions suggest a decreased abundance of pelagic species, but also changes in behaviour of piscivorous fish (Cavole et al., 2020). For example, the Galapagos sailfin grouper, which may migrate to deeper waters (Cavole et al., 2020). Studies of hook-and-line fisheries landing during ENSO years suggest that the proportion of large piscivorous fish in the catch (e.g. groupers, snappers) increases (Marin Jarrin & Salinas-de-León, 2018). This may be due to changes in fish behaviour, whereby reduced prey availability during ENSO may lead to increased predation and bait strike (Marin Jarrin & Salinas-de-León, 2018). In addition, underwater visual surveys of goat fish and bump head parrotfish suggests they may have benefitted from the warm 1998-97 ENSO conditions through increased recruitment (Ruttenberg, 2000). While ENSO may lead to increases in the abundance of some fish species, it can also be detrimental. For example, warm conditions during the 2015-16 ENSO drove an ulcerative skin disease outbreak in fish, causing short-term local declines in angel fish and damsel fish populations (Lamb et al., 2018). Grove (1984) also documented fluctuactions in the frequency of certain fish taxa associated with the warm temperature anomalies during the 1982-83 ENSO. Overall, it appears that ENSO has mixed effects on Galapagos fish species. However, the absence of large-scale in-situ assessment of its influence on benthic and pelagic fish assemblages makes it difficult to make any conclusions about the fish assemblage.

This study aimed to assess the effect of the 2015-16 ENSO on benthic and mid-water fish assemblages' composition and size structure in the Galapagos. We hypothesized that the assemblage composition would be significantly different after El Nino compared to before with a lower abundance of pelagic and bentho-pelagic species during El Nino compared to La Nina.

4.3 Materials and Methods

4.3.1 Stereo-video surveys

We used baited remote underwater stereo-video systems (stereo-BRUVs) to sample fish assemblages at 14 rocky reef sites in the centre southeast Galapagos bioregion (Figure 4.1b). Stereo-BRUVs deployments were carried as detailed in Chapter 2, with half benthic (~25 m) and half mid-water (~10 m) deployments. For full detail about the surveys, camera specifications and video analysis please refer to the Material and Methods section in Chapter 2.

4.3.2 Sampling periods

Sampling was completed twice in 2015 and when the rise of ENSO was confirmed, we opportunistically repeated the sampling in 2016 following a similar schedule. This specific timing allowed us to distinguish between seasonal and ENSO effects (Figure 4.3). Therefore, four sampling periods were carried out to visit all sampling sites with the following timing: March-April 2015 “pre-El Nino”, August-September 2015 “El Nino onset”, March-April 2016 “El Nino receding”, and August-September 2016 “La Nina onset” (Figure 4.2b).

To evaluate potential differences in environmental conditions during sampling, we measured temperature on site using a CTD (SBE 19plus V2 SeaCat Profiler). The CTD was deployed at benthic and mid-water stereo-BRUVs sites to a depth of ~30 m and profiles were processed in Python. The 24 m temperature reading was used as temperature for Benthic deployments while the 10 m temperature reading was used for Mid-water.

4.3.3 Statistical Analysis

4.3.3.1 Multivariate Procedures

We used species MaxN (i.e. the maximum number of individual fish of a given species in one single video frame through the deployment) as data input for the multivariate analysis. MaxN data was aggregated at site level by calculating the mean of individual species MaxNs across the four benthic or four mid-water deployments in each sampling season. To mitigate the effects of uneven dispersion between schooling and non-schooling species, we used a dispersion-based weighting of species count (Clarke et al., 2006) in both Benthic and Mid-water habitats and applied a square root transformation to the mid-water data.

To analyse fish assemblages multivariate patterns across seasons, we used a Canonical Analysis of Principal Coordinates (CAP, Anderson & Willis, 2003) and Permutational Analysis of Variance (PERMANOVA, Anderson, 2001). The PERMANOVA design had two factors: year (2 levels, 2015 and 2016, fixed, fully crossed) and season (2 levels, Warm and Cold, fixed, fully crossed). For the CAP, the H0 null hypothesis was “there is no difference in fish assemblage structure between sampling periods” with the HA alternative hypothesis corresponding to “fish assemblage structure differ significantly between sampling periods”. For the PERMANOVA, the H0 null hypothesis was “there is no difference in fish assemblage structure between years or seasons” with the HA alternative hypothesis corresponding to “fish assemblage structure differ significantly between years and seasons”. To identify species driving differences between sampling periods and which may be most influenced by ENSO, we used a Similarity of Percentage test (SIMPER, Clarke, 1993). All three procedures were performed separately in each habitat in the Primer-E software environment (Clarke & Gorley, 2015) with PERMANOVA+ add-on (Anderson et al., 2008).

4.3.3.2 Species abundance and length comparisons

We used balloon plots (Wickham, 2016) to illustrate and compare species abundance data across seasons for species driving differences between sampling periods based on the SIMPER test. To enhance readability of the balloon plots and allow comparisons of trends between species with different aggregating behaviours (e.g. schooling, gregarious, solitary), we used mean MaxN data standardized by the highest average MaxN recorded for each species. This standardized mean MaxN was not used for any statistical analysis.

To compare species size distributions across seasons, we used pirate plots (Phillips, 2017) to illustrate patterns and Dunn's test (Dinno, 2015) for statistical comparisons. Pirate plots allowed to display the raw data points and the length frequency distribution for each fish species while also presenting the mean and 95% confidence interval of the mean. The Dunn's test produces multiple non-parametric Kruskal-Wallis pairwise comparisons (Kruskal & Wallis, 1952) and we used a benjamini-hochberg adjustment to mitigate false discovery rate (Benjamini & Hochberg, 1995). Here, the H_0 null hypothesis tested was "there is no difference in fish size distribution between sampling periods" with the H_A alternative hypothesis corresponding to "fish size distribution differ significantly between sampling periods". All data visualization were performed in R (R Core Team, 2013).

4.4 Results

4.4.1 Ocean temperature patterns

Mean benthic seasonal temperature was always significantly cooler than mid-water samples, except during the El Nino receding season which also had the warmest mean benthic temperature. Mean seasonal benthic temperatures were 2.71°C, 1.04°C, 1.29°C, and 2.53°C lower than mean seasonal mid-water temperature for the pre-El Nino, El Nino onset, El Nino receding, and La Nina onset respectively. The coldest mean benthic and mid-water temperatures were recorded during the La Nina onset season with a 21.29°C and 18.86°C for the mid-water and benthic samples respectively (Figure 4.3).

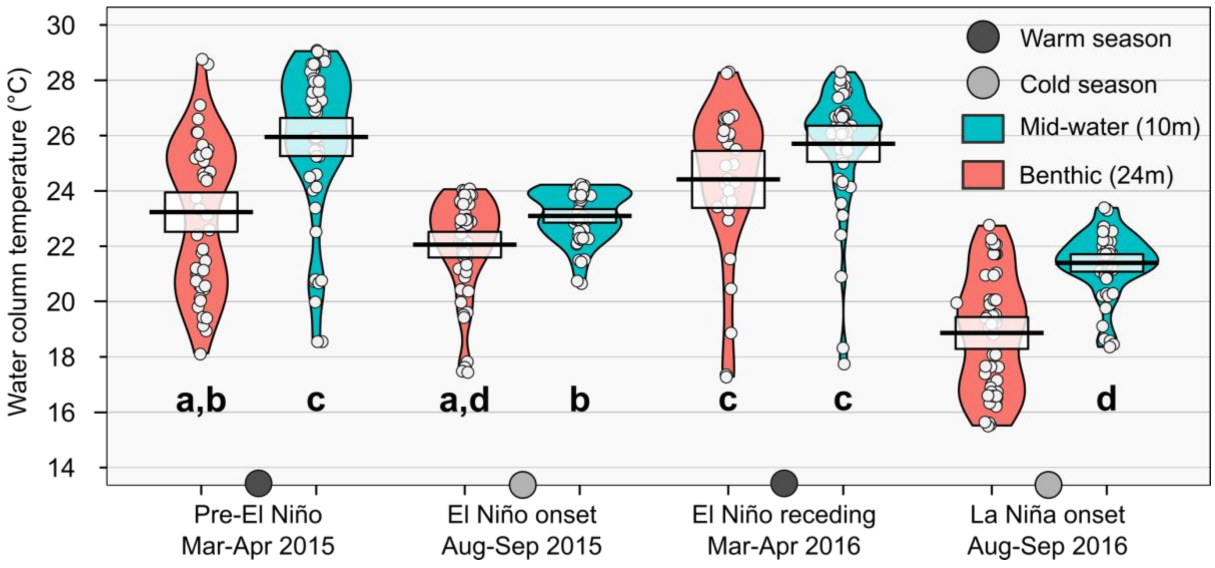
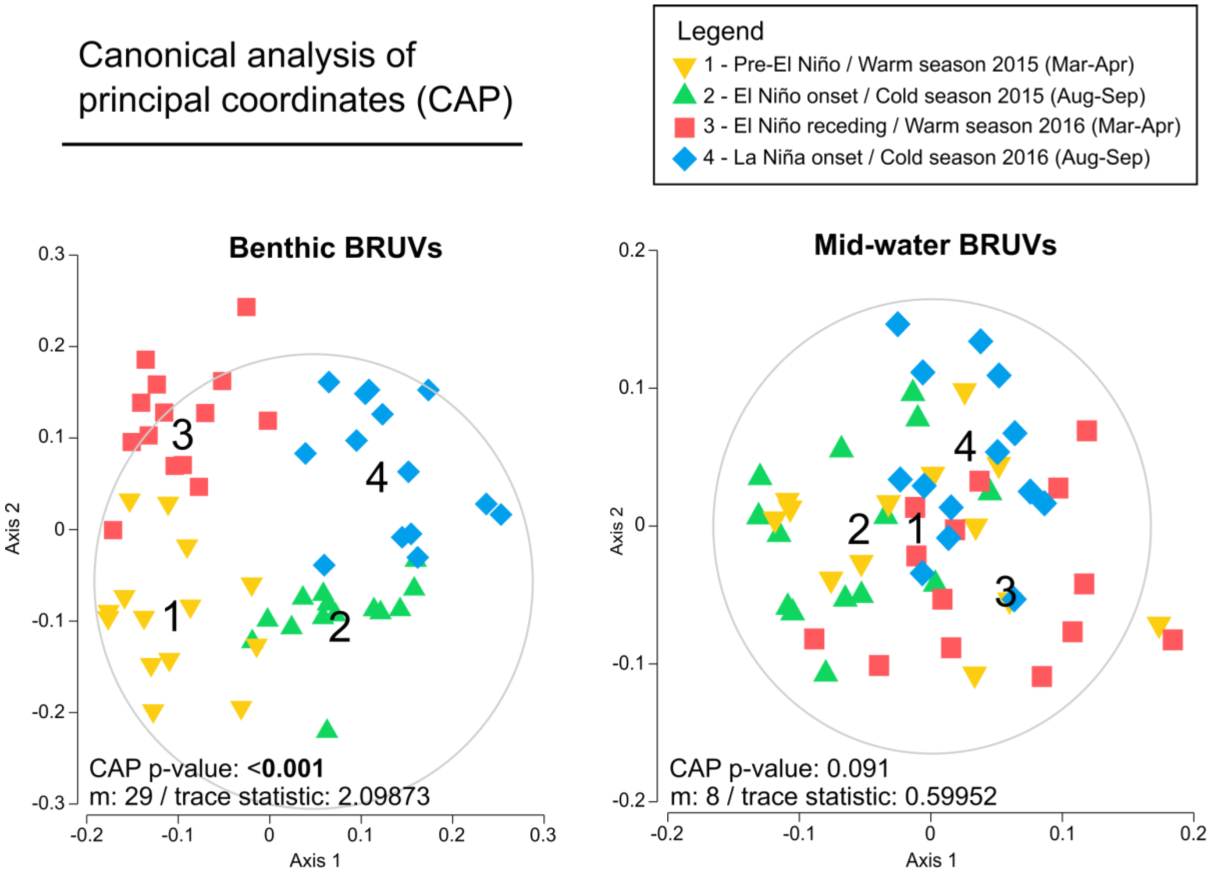


Figure 4.3 CTD water temperature readings for the benthic and mid-water habitats during the four sampling periods. Pirate plots sharing the same bold letters denotes no statistical difference (Dunn's test).

4.4.2 Assemblage patterns

The PERMANOVA detected a year-to-year significant difference based on benthic surveys (p-value: 0.027), but not based on mid-water surveys (p-value: 0.060). In both habitats, no statistical seasonal difference was detected.

The CAP results indicated significant differences between sampling periods based on benthic surveys (CAP p-value: <0.001), but not based on mid-water surveys (CAP p-value: 0.091). All four sampling periods clusters were clearly separated based on the benthic CAP (Figure 4.4). Although there was overlap between clusters in the mid-water CAP, there appeared to be some segregation between the year clusters as well as between the “El Nino receding” and “La Nina onset” clusters (Figure 4.4).



Permutational analysis of variance (PERMANOVA)

Benthic BRUVs

Source	df	MS	F	p-value
Year	1	3352.2	1.7642	**0.027**
Season	1	1804.1	0.94947	0.509
Year x Season	1	1569.2	0.82585	0.682
Res	52	1900.1		
Total	55			

Mid-water BRUVs

Source	df	MS	F	p-value
Year	1	3254.7	1.7328	0.060
Season	1	1945.2	1.0356	0.405
Year x Season	1	1960.1	1.0435	0.399
Res	51	1878.4		
Total	54			

Figure 4.4 Benthic and mid-water fish assemblage multivariate statistical patterns. Analysis based on zero-adjusted bray-curtis similarity matrix using dispersion weighted data aggregated at site level (each symbol represents 4 benthic or mid-water deployments). Mid-water data was also square root transformed.

4.4.3 Abundance fluctuation patterns

We found several trends of fluctuating species abundance between sampling periods with differences between the mid-water and benthic habitats (Figure 4.5 and 4.6).

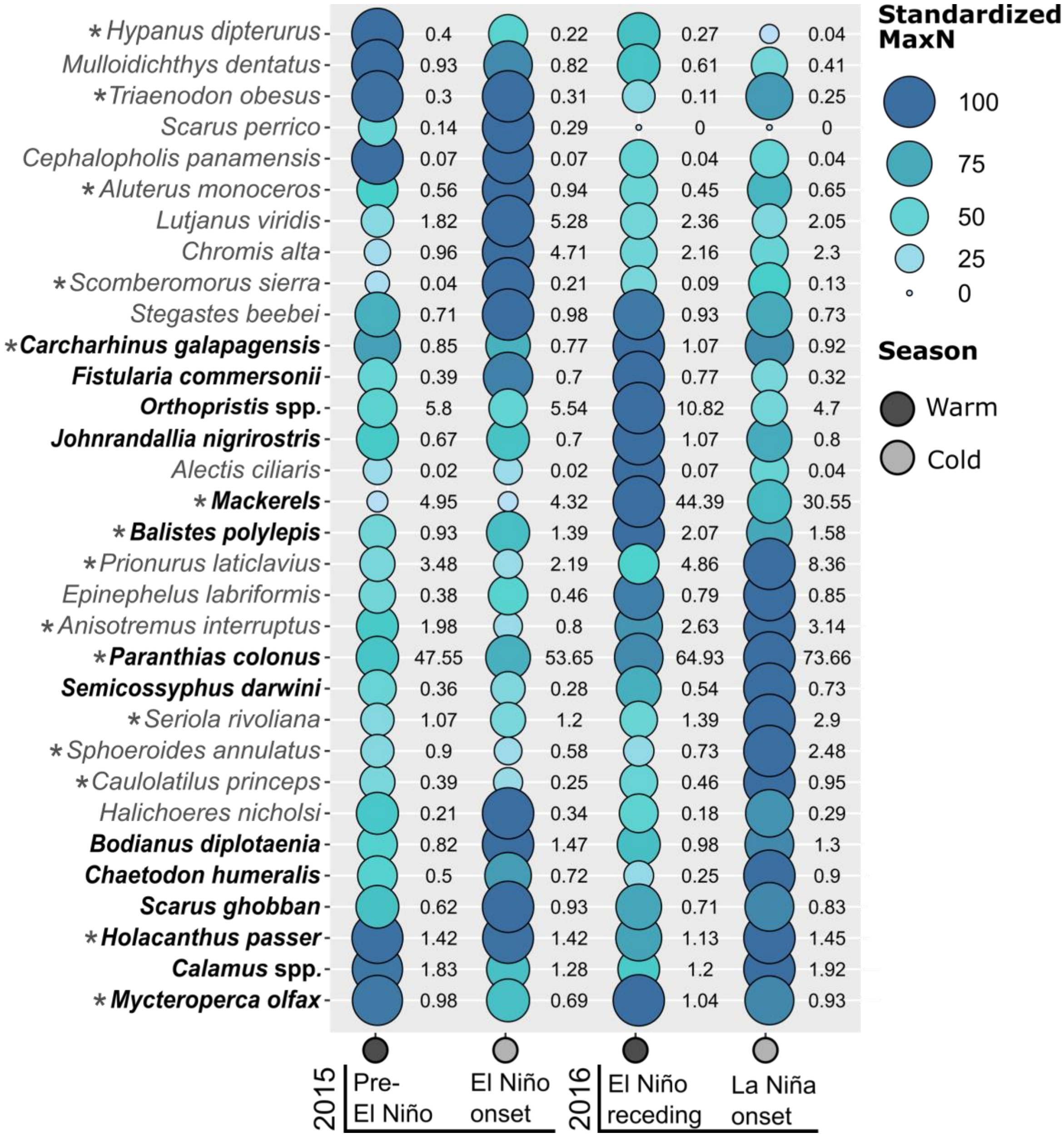


Figure 4.5 Benthic habitat sampling period average MaxN for species accounting for the highest dissimilarities between sampling periods based on the Similarity of Percentage multivariate test (SIMPER). Bold type species ranked highest in terms of dissimilarity percentage. Dot size is proportional to standardized MaxNs for each individual species, with values standardized against highest MaxN average across sampling periods (e.g. *Dasyatis brevis* highest MaxN average was 0.4 in the first sampling period, giving it a standardized value of 100. In the fourth sampling period, this species average MaxN dropped to 10% of the maximum MaxN, giving it a standardized MaxN value of 10). Asterisk next to species name indicate that the species also accounts for the highest dissimilarities between sampling periods in the mid-water domain.

Overall, the magnitude of greatest sampling period to sampling period abundance fluctuations was lower in the benthic habitat as ~70% of species displayed a less than threefold maximum fluctuation (Figure 4.5). By contrast, >75% of species displayed a greater than threefold maximum fluctuation in the mid-water habitat with several order of magnitude fluctuations (Figure 4.6).

Mackerels (i.e. *Trachurus murphyi* and *Decapterus* spp.) and *Paranthias colonus* displayed the highest abundance in both habitats, driving high sampling period to sampling period dissimilarities. In the benthic habitat, Mackerels displayed a greater average MaxN in 2016 compared to 2015 while *P. colonus* displayed a gradual increase of ~50% from first to last sampling period (Figure 4.5). In the mid-water habitat, Mackerels displayed increase in La Nina onset compared to the three previous sampling periods while *P. colonus* displayed its highest average MaxN during the pre-El Nino period, with a lower average MaxN during El Nino onset (Figure 4.6).

Several other species displayed higher abundance during La Nina onset compared to the other sampling periods. In the mid-water habitat, this included, Bonitos, *Lutjanus argentiventris*, *Anisotremus interruptus*, *Rhinoptera steindachnerii*, *Sphoeroides annulatus*, *Seriola rivoliana*, *Seriola peruana*, *Sphyrna lewini*, and *Carcharhinus galapagensis* (Figure 4.6). While relatively sparse, *Thunnus albacares*, *Mycteroperca olfax*, and *Trianodon obesus* had increased sightings during the onset of La Nina. In the benthic habitat, this included, *Prionurus laticlavius*, *Anisotremus interruptus*, *Semicossyphus darwini*, *Seriola rivoliana*, *Sphoeroides annulatus*, and *Caulolatilus princeps* (Figure 4.5).

Some species appeared in higher abundance during the sampling periods closest to peak ENSO conditions. In the mid-water habitat, this included, *Acanthocybium solandri*, *Scomberomorus sierra*, *Prionurus laticlavius*, and *Mobula* spp. (Figure 4.6). In the benthic habitat, this included, *Orthopristis* spp., *Fistularia commersonii*, *Scomberomorus sierra*, *Scarus perrico*, and *Lutjanus viridis* (Figure 4.5). By contrast, some species appeared in lower abundance during the periods closest to peak ENSO conditions. This included, *Mycteroperca olfax*, *Calamus* spp., and *Aluterus monoceros*.

There also appeared to be some seasonality trend in both habitats with species being more abundant in one season or the other (i.e. cold or warm). In the mid-water habitat, *Suflamens verres* and *Caranx caballus* were more abundant in both warm seasons compared to the cold seasons while no individuals were recorded during the cold seasons for both *Elagatis bippinulata* and *Aetobatus narinari* (Figure 4.6). The trend was opposite in the benthic habitat with *Halichoeres nicholsi*, *Bodianus diplotaenia*, *Chaetodon humeralis*, and *Scarus ghobban* displaying a higher abundance during the cold seasons compared to warm (Figure 4.5).

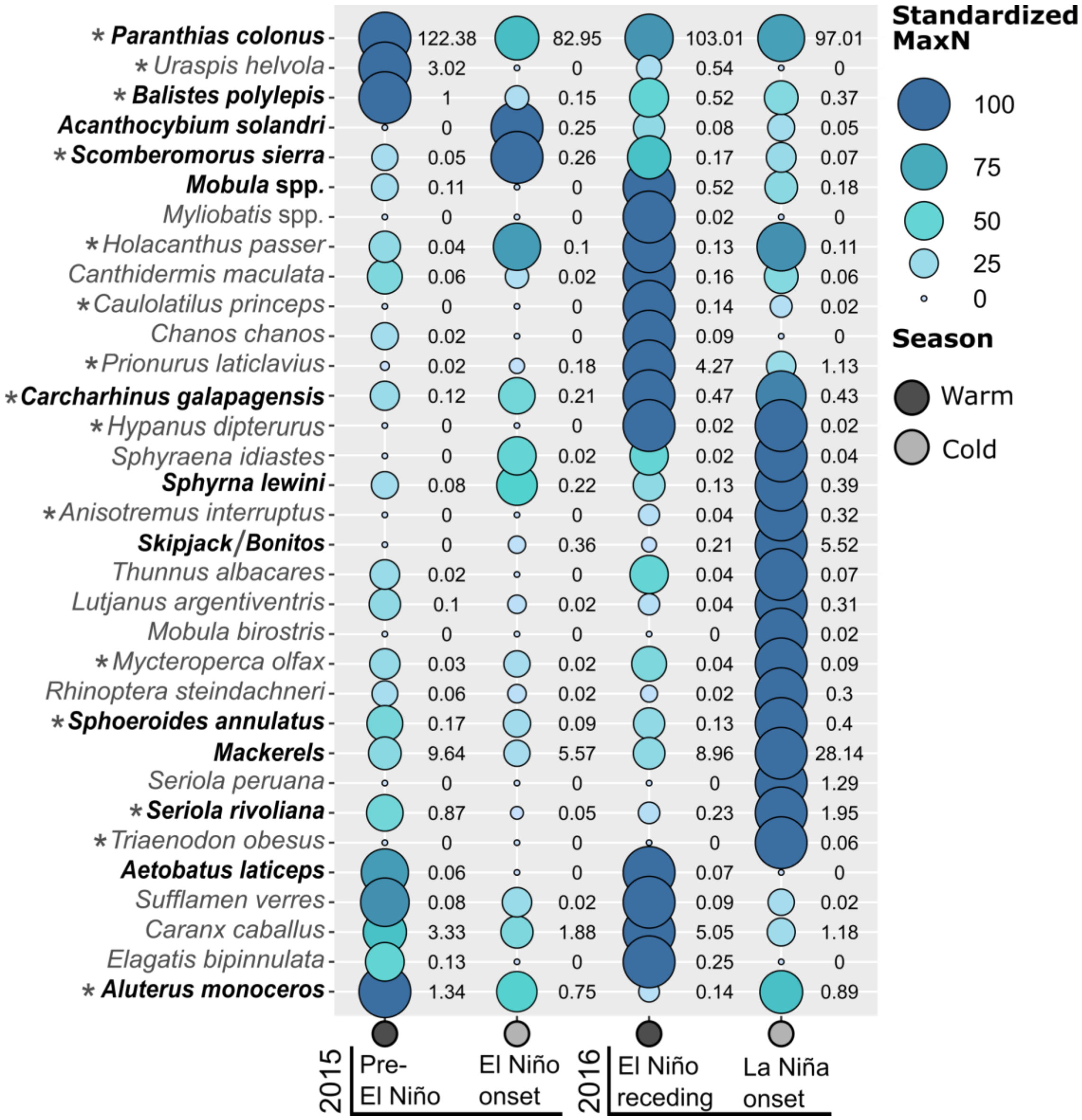


Figure 4.6 Mid-water habitat sampling period average MaxN for species accounting for the highest dissimilarities between sampling periods based on the Similarity of Percentage multivariate test (SIMPER). Bold type species ranked highest in terms of dissimilarity percentage. Dot size is proportional to standardized MaxNs for each individual species, with values standardized against highest MaxN average across sampling periods. Asterisk next to species name indicate that the species also accounts for the highest dissimilarities between sampling periods in the benthic domain.

4.4.4 Small bentho-pelagic species schools fluctuations

4.4.4.1 Paranthias colonus

The proportion of deployments with schools of *Paranthias colonus* displayed little variation in both habitats with a ~60% and ~80% frequency of occurrence across sampling periods in the mid-water and benthic habitat respectively (Figure 4.7). While mid-water schools were less frequent, they were however ~2-3 fold larger on average than benthic schools. Total abundance of this species in mid-water environment was the highest during the pre-El Nino sampling period and was about ~20-30% lower during the other three periods (Figure 4.7). Total abundance in benthic environments was highest during La Nina onset and was 43%, lower during pre-El Nino, and lower again during El Nino onset and El Nino receding (Figure 4.7). Combined benthic and mid-water total abundance remained relatively stable over time (6312, 5850, 5300, and 6180 individual fish chronologically), although was 16% lower during El Nino receding than Pre El Nino.

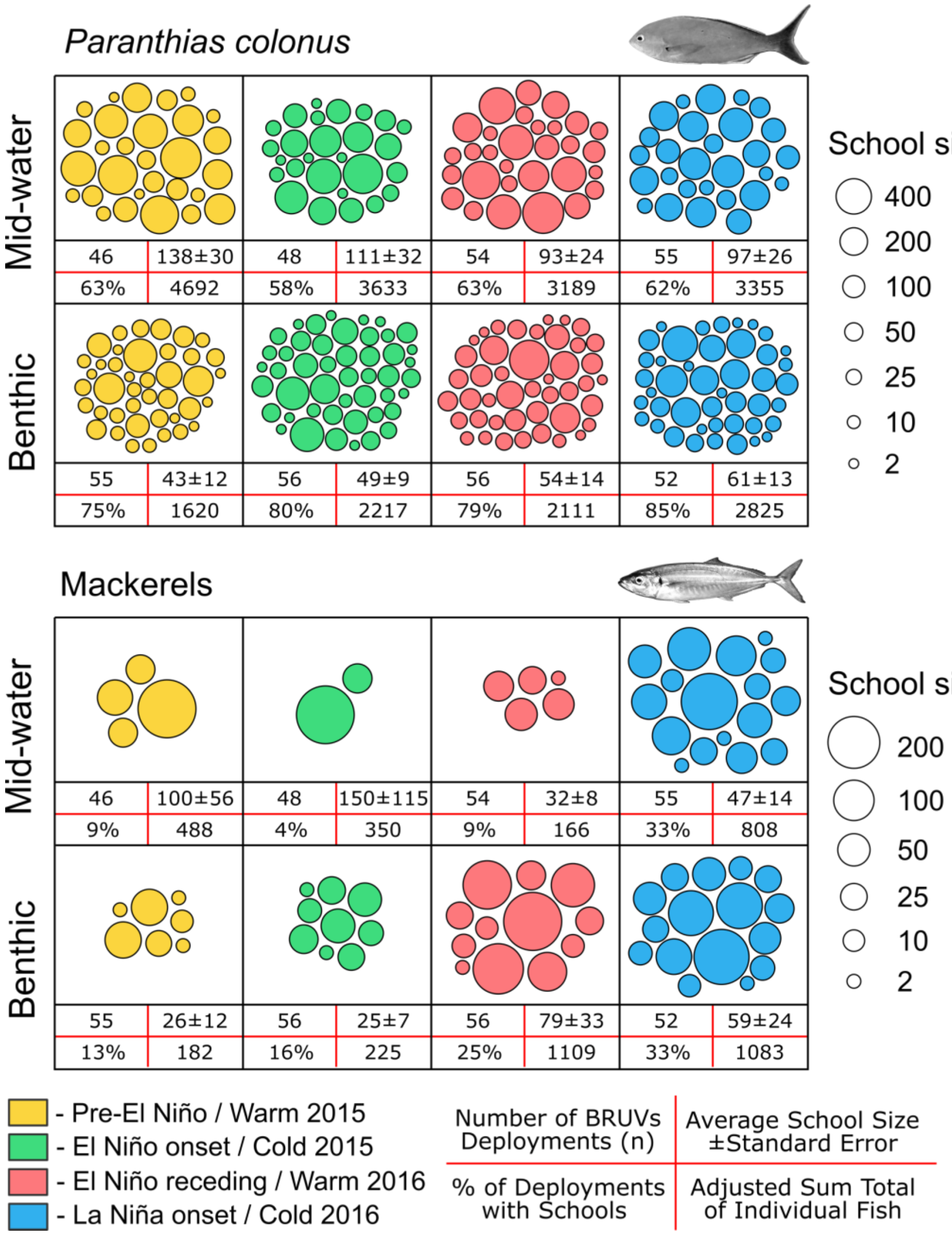


Figure 4.7 Data visualisation of small bentho-pelagic schooling species across seasons. All recorded schools are represented for each season/habitat. Sum total of individual fish is adjusted to account for the uneven sample size.

4.4.4.2 Mackerels (*Trachurus murphyi*, *Decapterus* spp.)

In the mid-water habitat, mackerels schools were recorded in the greatest proportion of deployments during La Nina onset compared to the previous three sampling periods with the lowest frequency of occurance of schools during El Nino onset (Figure 4.7). In the benthic habitat, mackerel schools were 2-3 fold more frequent in both 2016 periods compared to 2015 with the highest frequency found during La Nina onset. Average mid-water school size was 2-5 times greater in 2015 compared to 2016 while average benthic school size was 2-3 times greater in 2016 compared to 2015. Mid-water total abundance was highest in La Nina onset and having gradually increased over the previous three seasons. Total abundance in Benthic environments was ~80% lower during pre-El Nino and El Nino onset compared to both El Nino receding and La Nina onset (Figure 4.7). Combined benthic and mid-water total abundance increased across the sampling period with 670, 575, 1275, and 1891 individual fish recorded during pre-El Nino, El Nino onset, El Nino receding and La Nina onset respectively.

4.4.5 Size structure fluctuations

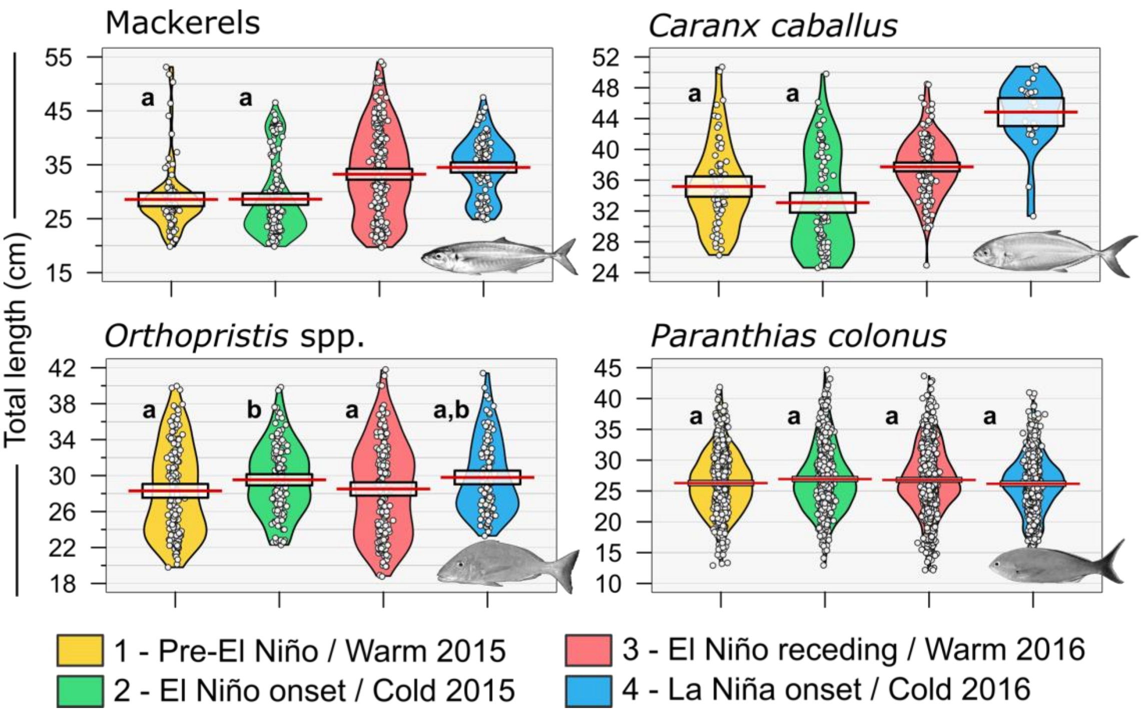


Figure 4.8 Size distributions of species displaying significant size differences between seasons (Dunn's test). Pirate plots sharing the same letter denotes no significant size difference between seasons. Each dot is a fish, red line denotes mean size, and white shaded area denotes 95%CI of the mean. Note that *Paranthias colonus* shows no significant difference between seasons but is included in this panel to provide a point of comparison for Mackerels and *Caranx caballus*, as they all fit in the small bentho-pelagic species category.

Only Mackerels, *Caranx caballus* and *Orthopristis* spp. had statistically different size structure across sampling periods (Figure 4.8 and Figure 4.9). Mackerels and *Caranx caballus* were significantly larger in both 2016 seasons compared to 2015 as well as significantly larger in La Nina onset compared to El Nino receding while no statistical difference was detected for the two 2015 periods (Figure 4.8). In contrast to these two species, the mean size of other pelagic species did not change much over time. Although the mean size of *Orthopristis* spp*.* was significantly greater during El Nino onset than in pre-El Nino and El nino receding sampling periods, the magnitude of the difference was small, and the mean sizes and size distributions relatively consistent over time (Figure 4.8). Similarly, the mean size and size distribution of the small pelagic species *Paranthias colonus* did not change between sampling periods (Figure 4.8).

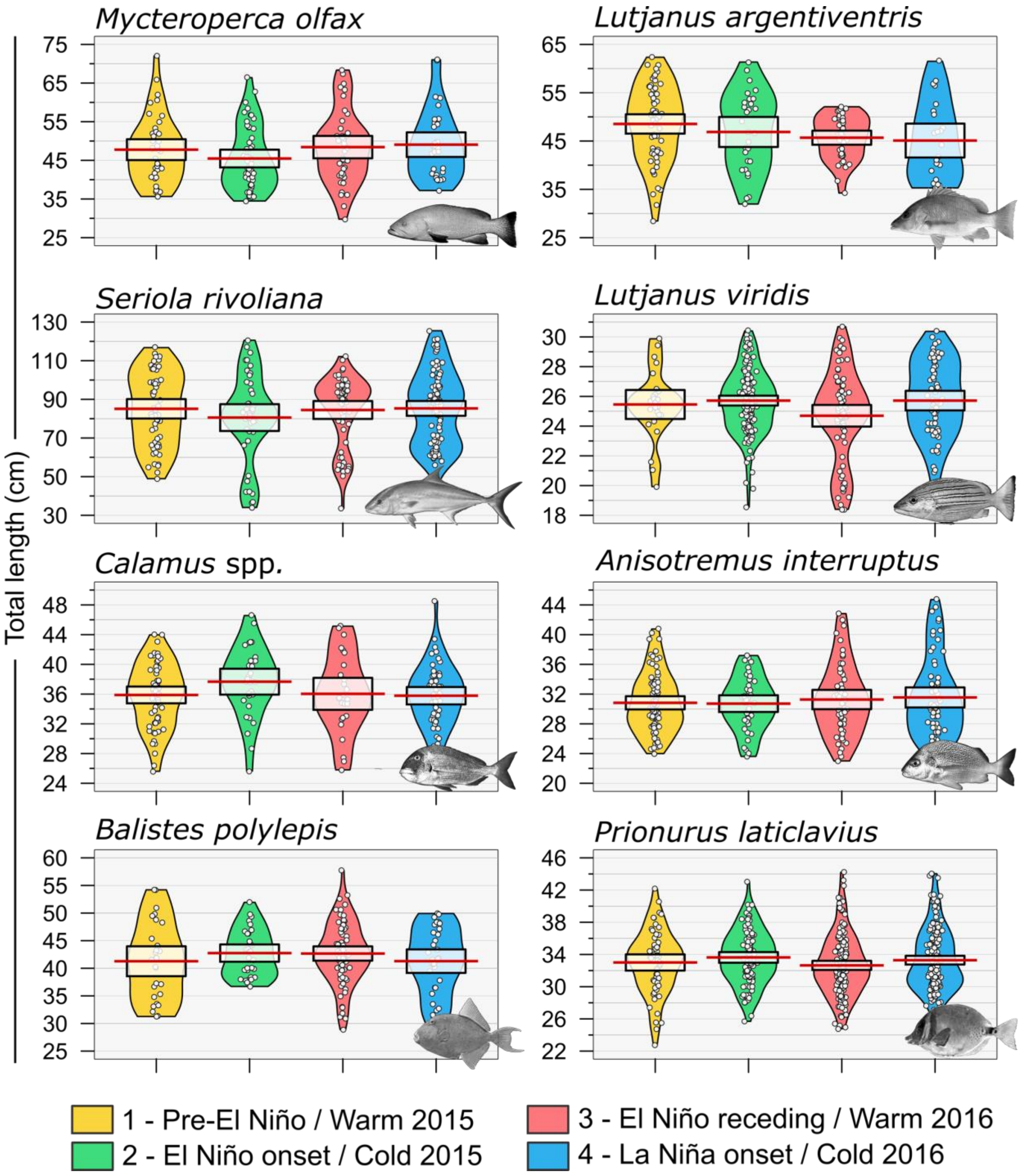


Figure 4.9 Size distributions of species displaying no significant size differences between seasons (Dunn's test).

4.5 Discussion

We found significant fluctuations in the fish assemblage structure, abundance, and length associated with the changes in environmental conditions observed during the 2015-16 ENSO. However, the 2015-16 ENSO did not affect the Eastern Tropical Pacific region as markedly as the historical extreme events of 1982-83 or 1997-98 ENSOs (L'Heureux et al., 2017; Santoso et al., 2017; Xue & Kumar, 2017). These extreme ENSO events led to major die-offs of top predators and coral bleaching in Galapagos, but no such reports followed the 2015-16 ENSO in the archipelago. The 2015-16 ENSO displayed characteristics of Central Pacific ENSO events as opposed to Eastern Pacific events, explaining why its effects were weaker in the Eastern Tropical Pacific with nearly 2°C weaker SST anomalies compared to the 1997-98 event in this region. While the 2015-16 ENSO did not hit Galapagos as forcefully, SST and Chlorophyll-a anomalies in the archipelago reached ~1.8°C and -0.14 $mg.m^{-3}$ and our in-situ temperature data revealed that water stratification was reduced close to peak ENSO conditions with a significant decrease in temperature once conditions were close to normal during the La Nina onset period. Despite the comparatively lower environmental anomalies of the 2015-16 ENSO, we still observed marked fluctuations in the fish assemblage structure, abundance, and length, suggesting that even moderate ENSO conditions can affect the Galapagos marine environment.

The clearest fluctuation signal was associated with the small bentho-pelagic mobile species, Mackerels in particular which was a species complex of *Trachurus murphyi* and *Decapterus* spp.. When converting size and abundance to biomass, this group, the second most abundant recorded taxa in both mid-water and benthic habitat after *Paranthias colonus*., displayed a ~480% increase in the "La Nina onset" period compared to "El Nino onset". *Trachurus murphyi* is capable of adapting to unfavourable warm plankton-poor oceanographic conditions by shifting to better foraging grounds over hundreds of kilometres (Barber & Chavez, 1983; Bertrand et al., 2004; Peña-Torres & Agostini, 2007). Mackerels are predominantly zooplanktivorous, with euphausiids, copepods, and amphipods commonly reported as dominant prey items (Konchina, 1979, 1981; Ben Salem, 1988; Quiñones et al., 1997; Huh & Cha, 1998; Jardas et al., 2004;

Bertrand et al., 2004; Šantić et al., 2005; Rahmani et al., 2020) with small teleosts increasingly present in the diet of larger size classes (Šantić et al., 2005; Rahmani et al., 2020). The availability of zooplankton prey decreases in low-productivity warm water conditions characteristic of ENSO (Barber & Chavez, 1983; Barber & Chávez, 1986). In fact, the Galapagos ENSO trophic models indicate herbivorous zooplankton biomass may be reduced by more than 50% in the western part of Galapagos and predicts a subsequent decrease of jacks and mackerels biomass of a similar scale (Wolff et al., 2012). Baited remote underwater stereo-video systems (stereo-BRUVs) data collected in the Northern and Western bioregion (Rastoin unpublished data), although not included in this study due to sampling limitations, indicate mackerel abundance fluctuations of similar scale and direction. This suggests mackerel populations may shift to more distant foraging grounds during ENSO as was reported elsewhere (Valdivia & Arntz, 1985; Peña-Torres & Agostini, 2007; Peña-Torres et al., 2017). Overall, our results for the central Galapagos region concur with the western region models and suggest the magnitude of mackerel biomass decrease during the onset of 2015-16 ENSO may be even higher.

The fluctuations in mackerel populations we documented, in terms of both size and abundance, are supported by similar reports along the South-American pacific coast region. In this region, the jack mackerel (*Trachurus murphyi)* is of commercial importance and so has been the focus of targeted research into how it responds to ENSO and the implications for national fisheries (Valdivia & Arntz, 1985; Sharp & Mclain, 1993; Arcos et al., 2001; Dioses et al., 2002; Bertrand et al., 2004; Peña-Torres & Agostini, 2007; Peña-Torres et al., 2017). Reports indicate a negative impact of ENSO on *Trachurus murphyi* abundance leading to a decrease, or even disappearance from the Peruvian and Chilean landed catch during ENSO (Barber & Chavez, 1983; Valdivia & Arntz, 1985; Barber & Chávez, 1986; Peña-Torres & Agostini, 2007). Poorer body condition was also reported from the 1982-83 and 1997-98 ENSOs due to lower foraging opportunities (Dioses et al., 2002). Since *Trachurus murphyi* has been the most landed species in Chile by volume for the past 30 years, the effects of ENSO on *Trachurus murphyi* distribution drive large scale shifts in the decisions about where Chilean industrial fleet operates (Peña-Torres et al., 2017). There are also reports of size-increase following ENSO (Alheit & Niquen, 2004). Our data on the influence of

ENSO on the Galapagos mackerel population size and abundance complements a cohesive body of literature for the Eastern Tropical Pacific at the northern end of *Trachurus murphyi's* distribution range.

The timing of fluctuation of mackerel size and abundance poses questions. The low mackerel biomass we found even during the pre-ENSO period may be due to the background of warm conditions in the Eastern Pacific, known as the Blob (Leising et al., 2015; Peterson et al., 2015b, 2015a; Jiménez-Quiroz et al., 2019). The Blob contributed to triggering the 2015-16 ENSO and had pervasive effects in the region, including the reduction of zooplankton abundances (Leising et al., 2015; Cavole et al., 2016; Tseng et al., 2017). This suggests that part of the mackerel population may have shifted its distribution prior to peak ENSO conditions to increase foraging opportunities. In addition, we recorded a marked increase in the abundance and size of mackerels when El Nino started receding, at a time where temperatures anomalies were still important, but chlorophyll-a had started to re-bound. This productivity increase is likely associated with the strengthening of the ocean currents across the Pacific, which occurs during the ENSO receding phase (Firing et al., 1983). The increase of mackerel biomass culminated during the La Nina onset period when chlorophyll-a values were nearly back to normal with only minor SST positive anomalies (Figure 2). Evidence suggests that food availability may be the key driver of mackerel population distribution in the Tropical Eastern Pacific (Bertrand et al., 2004). The re-bound of primary productivity in the archipelago during the ENSO receding phase likely boosted the marine trophic chain and zooplankton abundance, gradually increasing planktonic food availability for mackerels. In conjunction, the increase in mackerel average size we found from the El Nino receding period onwards may also be indicative of an increase in prey favoured by the larger mackerels. Rhamani et al. (2020) and Šantić et al. (2005) found that Clupeiformes (i.e. sardines, anchovies) became increasingly prevalent in the diet of mackerels above 30cm total length. Here, we found that the mean size of mackerels was over 33cm in both 2016 periods which suggest that teleosts may be have been an important food items for them at this time. In addition, *Caranx caballus,* which shares similar prey items with the larger mackerels (Saucedo-Lozano et al., 2012), showed a similar trend of size increase once ENSO started receding. The re-bound of primary productivity during the El Nino receding period (Figure 2) supports this hypothesis of increased clupeiform abundance at this point even though the stereo-BRUVs failed to adequately sample sardines and anchovies populations. Moreover, the mackerel schools we observed did not actively feed and their aggregating behaviour in small schools fits the description of resting behaviour described by Bertrand (2004). *Trachurus* spp*.* typically perform diel feeding migration at dusk or night (Hecht, 1990; Bertrand et al., 2004) suggesting their preys, whether plankton or small teleosts, were not located where we recorded the mackerel schools. Alternatively, the larger mackerels sizes observed in 2016 may be due to the growth of the cohorts present in 2015 as *Trachurus* spp. is a fast growing genus (Kaiser, 1973; Horn, 1993; Horn & Ó Maolagáin, 2021). However, this explanation is not fully satisfying as one would also expect to find large size classes in 2015 in a non-ENSO year while the concordant abundance increase in several other taxa in 2016 suggest that other phenomenon are at play. Overall, it appears that temperature fluctuation alone may not be sufficient to explain mackerel population fluctuations and that prey availability driven by primary productivity may be a more important population bottom-up driver.

Together with mackerels, the abundance of the several other bentho-pelagic and pelagic mobile taxa increased in the mid-water habitat as El Nino started receding, in particular during La Nina onset. This was the case for large carangids (*Seriola rivoliana* and *Seriola peruana*), small scombrids (*Sarda orientalis* and *Euthynnus linneatus*), myliobatids (*Mobula* spp*.* and *Rhinoptera steindacherii*), as well as sharks (*Sphyrna lewini* and *Carcharhinus galapagensis).* Given this common trend across many species it is likely that mid-water conditions were more favourable during this period. It appears that those species may have benefitted from increased abundance of mackerels as well the prey mackerels feed on as there are important predator-prey interrelations between these species. *Seriolas* spp*.* are commonly reported feeding on *Trachurus* spp. (Schmitt & Strand, 1982; Barreiros et al., 2003; Vergani et al., 2008). Particularly, Barreiros (2003) reported that *Trachurus* spp. comprised nearly 65% of the weight and 86% of prey numbers in *Seriola rivoliana* in the Azores during the 1997-98 ENSO while Vergani (2008) found that *Seriola lalandi* fed almost exclusively on young *Trachurus* spp*.* along the coast of Uruguay. Small scombrids have also been reported to rely heavily on *Trachurus* spp. as food source (Dragovich, 1969; Bailey, 1989; Young et al., 1997; Karakulak et al., 2009; Itoh et al., 2011; Logan et al., 2011; Varela et al., 2014; Yoon et al., 2015; Romero et al., 2021) as well Euphausiids and other small teleosts that *Trachurus* spp*.* feed on (Alverson, 1963; Young et al., 1997; Logan et al., 2011; Varela et al., 2014; Páez-Rosas et al., 2020). *Mobula* spp*.* predominantly feeds on euphausiids (Sampson et al., 2010; Rohner et al., 2017; Masangcay et al., 2018) and *Rhinoptera steindachneri* has also been found to feed heavily on macro-zooplankton species such as small mysid shrimps in certain regions of the gulf of California (Ehemann et al., 2019). *Sphyrna lewini* in the mexican Eastern Tropical Pacific consume small carangids and scombrids (e.g. *Scomber japonicus*, *Euthynnus linneatus*, *Auxis* spp*.*, *Decapterus* spp . (Torres-Rojas et al., 2010; Torres Rojas et al., 2015; Flores-Martínez et al., 2017). Our results show that both these groups had increased abundance during La Nina onset period. *Caracharhinus galapagensis* feeds on a diverse diet of teleost and cephalopods (Wetherbee et al., 1996; Papastamatiou et al., 2006) including several families that increased during La Nina onset, such as carangids, scombrids, and tetraodontids. Besides the above, it is likely that the increased presence of predominantly benthic taxa in the mid-water habitat such as lutjanids, serranids, haemulids, or tetreodontids is a likely indicator of increased prey availability for them in the water column. For example, *Lutjanus* spp. have been reported feeding on soft bodied preys like salps, ctenophores, or comb jellies (Takahashi et al., 2020; Valle-Lopez et al., 2021) which were likely more abundant in the colder richer waters of the La Nina onset period. Overall, it appears that the return to normal oceanographic conditions as El Nino receded provided bottom-up benefits across the entire marine food chain.

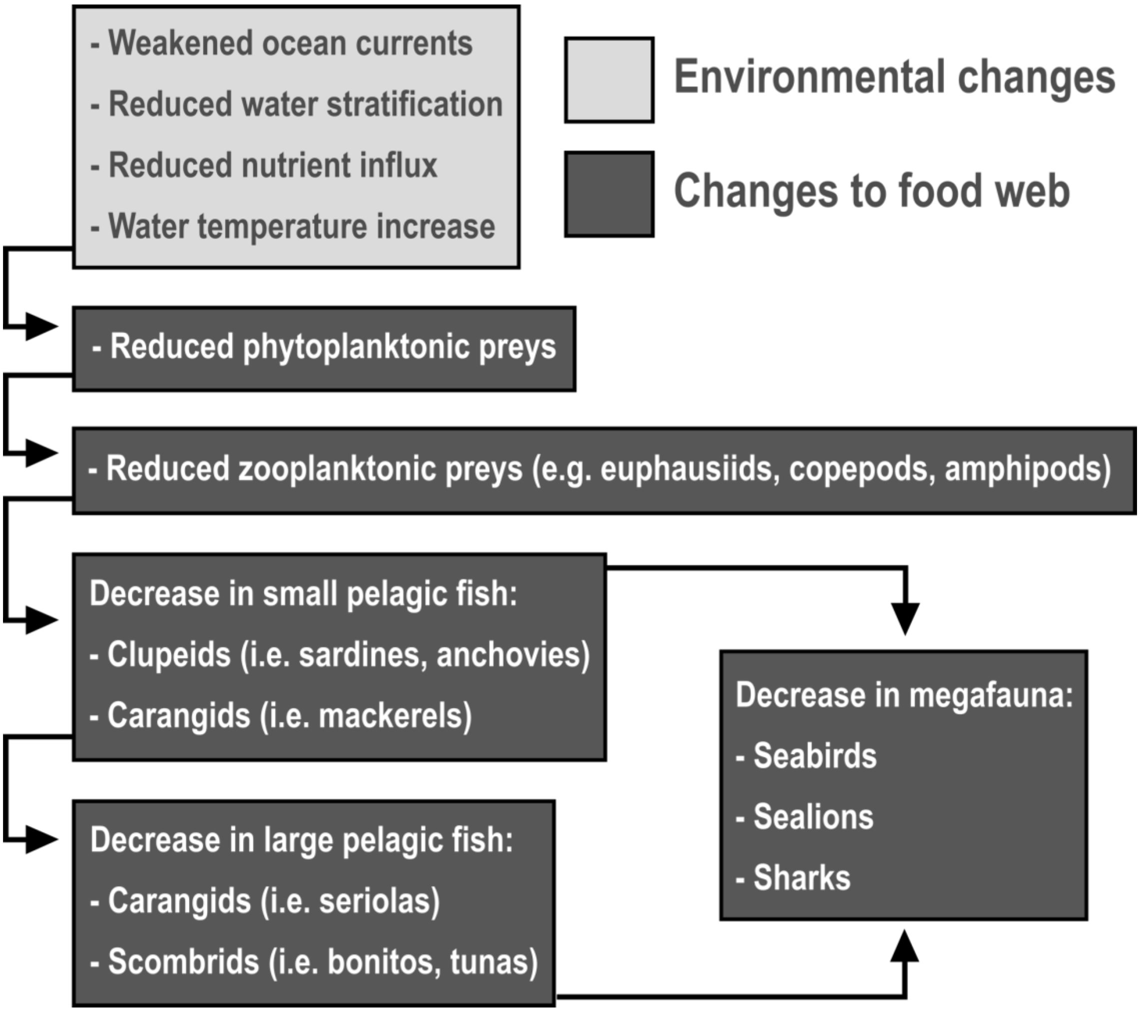


Figure 4.10 Schematic flow-diagram of the main cascading effects on the marine food web caused by environmental changes associated with ENSO warm phase.

We did not see major fluctuations in *Paranthias colonus* as we anticipated. While no comprehensive diet study exists for this species, it is often seen feeding on plankton in mid-water high-current areas and is generally referred to as predominantly planktivorous (Humann & DeLoach, 1993; Grove & Lavenberg, 1997; Okey, 2004; Salinas-de-León et al., 2016). Across the four sampling periods, this species remained particularly stable in terms of size structure and total abundance. Regardless, our results do not provide evidence for a major impact of the 2015-16 ENSO on *Paranthias colonus,* in particular when compared to the fluctuation observed in mackerels. Compared to the mackerels highly mobile behaviour, *Paranthias colonus* range of movements is much more limited. It typically dwells above the reef or in the water column above the reef where it benefits from local currents and upwellings which transport its planktonic prey (Okey, 2004; Salinas-de-León et al., 2016). *Paranthias colonus* may feed on smaller planktonic prey than mackerels, and it is possible that those prey did not decrease beyond the point of creating a food shortage for the species. This concurs with the general consensus that in Galapagos the 2015-16 ENSO was less detrimental than the 1997-98 and 1982-83 ENSO with overall weaker effects.

There are other clues suggesting that the 2015-16 ENSO did not strongly disturb the regular processes regulating the Galapagos marine environment. In particular, *Scarus ghobban*, *Chaetodon humeralis*, *Orthopristis* spp, *Caranx caballus*, *Elagatis bippinulata*, *Bodianus diplotaenia, Halichoeres nicholsi, Aetobatus narinari, Sufflamen verres* among others, displayed discernible warm/cool season fluctuation patterns that were consistent in 2015 and 2016. Interestingly those patterns were the opposite between habitats, with higher abundances in the mid-water habitat observed during the warm seasons while they were observed during the cold seasons in the benthic habitat. The seasonal patterns of habitat use in reef fish may be caused by seasonal fluctuation of foraging resources, periodic predation avoidance strategies, as well ontogenetic migration cycles (Mellin et al., 2007) and are commonly reported in the families we observed including Scarids, Carangids, Labrids, Chaetodontids, Haemulids (Cocheret de la Morinière et al., 2002, 2003; Mumby et al., 2004; Gratwicke & Speight, 2005; Dorenbosch et al., 2006; Mellin et al., 2007; Nagelkerken, 2007; Appeldoorn et al., 2009; Sievers et al., 2020). In a study including 161 reef fish species from 46 families, (Mellin et al., 2007) found that 53% of species in their juvenile life phase used different habitats across seasons while 39% displayed habitats shifts as they grew. In all likelihood, the influence of the 2015-16 ENSO has blurred many seasonal patterns which may have appeared more clearly had we sampled in two non-ENSO years. Yet the persistence of seasonal habitat use patterns suggest such phenomena persisted despite the changes brought by ENSO.

Our data provides some evidence for the positive and negative influence of ENSO on different taxa. For example, *Fistularia commersonii,* a taxa favouring the warmer conditions of the northern Galapagos regions (see Chapter 2) displayed increased benthic abundance closer to peak ENSO conditions, which suggests it may have benefited. *Holacanthus passer* dip in abundance just after peak-ENSO which may be related to the ulcerative skin disease that affected the species during the warmest months at the beginning of 2016 (Lamb et al., 2018). This skin disease outbreak may have benefited the cleaner fish *Johnrandallia nigrirostris* populations. This would explain the higher *J.nigrirostris* abundance we found after peak-ENSO conditions as Lamb et al. (2018) found the cleaning stations of this species were particularly active during the outbreak with increased feeding opportunities as more fish required cleaning of ulcerated skin. Separately, we found that *Caulolatilus princeps* and *Semycossyphus darwini,* two species with cold water preferences and prevalent in the western bioregions (see Chapter 2), displayed lower abundances in benthic habitats during the three seasons with the warmest temperatures. This suggests they may have shifted to deeper colder habitats during ENSO only to resume their normal behaviour once normal conditions returned. While the above cases are consistent with the ecological knowledge about those species, additional interpretation of individual species fluctuations would only be speculative. To better understand which fluctuations are naturally occurring due to seasonal changes versus which are caused by ENSO, it would be necessary to sample in a non-ENSO year to provide a reference point.

The fluctuations we have observed have important implications for the management of the Galapagos Marine Reserve fish populations. The 2015-16 ENSO was reported as being of moderate magnitude for the Tropical Eastern Pacific (L'Heureux et al., 2017; Santoso et al., 2017; Xue & Kumar, 2017) and our surveys did not cover the height of the fluctuation. This suggests we did not measure the peak effects of the 2015-16 ENSO and that the impact of extreme magnitude events in the archipelago are likely much greater. Yet, we have found the 2015-16 ENSO was associated with important fluctuations for multiple species of high commercial and ecological value in the region (Figure 4.10). The near 5-fold mackerel biomass difference between the El Nino onset and La Nina onset period is particularly relevant since this species plays a top-down control on lower trophic levels while being an important prey for several large pelagic species of commercial importance including Scombrids and Carangids. These taxa are increasingly targeted by the local artisanal fisheries sector (Ramírez-González & Reyes, 2015; Cerutti-Pereyra et al., 2020) as coastal benthic resources decline. In addition, perception surveys indicate that local fishers are aware that large pelagic species are impacted during ENSO (Cavole et al., 2020).

This is important as marine heatwaves, for which ENSO is a dominant driver in the Pacific, are projected to become more frequent (Cai et al., 2018; Oliver et al., 2018; Holbrook et al., 2020; Cai et al., 2020) with research suggesting that frequency may double globally (Cai et al., 2014). This is particularly concerning for the marine megafauna of the archipelago considering the strong declines in populations of seabirds (Valle et al., 1987; Valle & Coulter, 1987; Anderson, 1989; Boersma, 1998; Vargas et al., 2006), marine iguanas (Laurie, 1990; Wikelski & Wrege, 2000; Vinueza et al., 2006), and pinnipeds (Trillmich, 1985; Trillmich & Dellinger, 1991; Salazar & Bustamante, 2003; Salazar & Denkinger, 2010) that can occur under regular ENSO regimes due to disrupted foodwebs. An increased ENSO frequency may threaten the establishment of these taxa in Galapagos or lead to permanently reduced populations size, likely affecting the archipelago's attractiveness for tourism and the livelihood of local populations. To date, no strategies exist to mitigate the short-term and long-term effects of ENSO on the socio-ecological systems in the Galapagos Marine Reserve under climate change scenarios. Our results, along with a growing body of evidence from around the world, highlight the urgency of tackling this issue.

Chapter 5 A diver operated stereo-video approach for characterizing reef fish spawning aggregations: the Galapagos Marine Reserve as case study

The study presented in this chapter was published within the peer-reviewed journal “*Estuarine, Coastal, and Shelf Science”* on the 30th September 2020.

5.1 Abstract

The alarming decline of spawning aggregations across the world highlights the need to improve their long-term monitoring and protection. We examined the ability of diver operated stereo-video to characterize reef fish spawning aggregations, using an opportunistic encounter with the first spawning aggregation of the Mexican hogfish, *Bodianus diplotaenia,* recorded in the Galapagos Marine Reserve. We aimed to provide estimates of total density, length, and reproductive behaviour, using quantitative surveys and 3D representation of the spawning event. 3D scenes of aggregating fish in relation to reef substrate were produced to compute distances between individuals (of the same and different sex), and between individuals and the substrate. Males swam significantly higher in the water column and further away from each other when compared to females, which displayed sociable behaviour closer to the bottom. The mean fork length of males (39.79 ± 6.98 cm) was nearly twice the size of females (24.14 ± 5.39 cm). We show that diver operated stereo-video system can provide accurate baseline measures of fish length, density, and reproductive behaviours. Our study offers a new method to characterize fish mating systems and contributes to expanding the range of easily repeatable low-impact tools for the long-term monitoring of spawning events.

5.2 Introduction

Spawning aggregations are critical events in the life history of many commercially targeted fish species throughout the world (Domeier & Colin, 1997; Grüss et al., 2014; Erisman et al., 2017). The majority of these events are predictable in time and space which makes them particularly susceptible to overfishing (Sadovy & Domeier, 2005). Despite regular warnings from the scientific community, many reported aggregations have now disappeared (Beets & Friedlander, 1998; Sala et al., 2001; Aguilar-Perera, 2006), or are in severe decline due to overfishing (Buckley et al., 2017; Erisman et al., 2019; Hamilton et al., 2019), driven in part by the highly lucrative live reef fish trade (Muldoon et al., 2016; Sadovy de Mitcheson et al., 2017; Khasanah et al., 2019). As a result, fish biologists have highlighted the urgent need to establish large-scale programs to better monitor, manage and conserve spawning events (Erisman et al., 2017; Grüss et al., 2018; Heyman et al., 2019). Achieving this goal will require a range of easily repeatable methods available to decision makers to assess the status of spawning events.

Methods involving the direct capture of fish have commonly been used to gather valuable data on the length structure of mating individuals (Heppell et al., 2012; Farmer et al., 2017; Castro Perez et al., 2018). However, the invasive nature and high-mortality rates associated with these techniques poses concerns and prevents their application in most Marine Protected Areas (MPAs), or for vulnerable/endangered species (Rand et al., 2006; Heppell et al., 2012). To mitigate these issues, experts have recommended the use of diver based Underwater Visual Censuses (UVC) as a fishery-independent, non-destructive sampling method to monitor spawning aggregations (Colin et al., 2003a; Sadovy de Mitcheson & Colin, 2012a). However, inaccuracies in the length and distance estimates made by divers, could potentially compromise the ability to detect changes in the spawning stock over time (Harvey et al., 2001a, 2001b; Harvey et al., 2004). For example, Harvey et al. (2002a) questioned the reliability of scaling UVC estimates of length to biomass, while Kulbicki (2005) demonstrated how a 10% error estimate on length could generate a weight error of up to 25% for a mature grouper, resulting in serious inaccuracies when characterizing the spawning stock biomass. Visual estimates of abundance also become increasingly unreliable for large spawning aggregation due to the difficulty of visually counting up to thousands of individuals (Sadovy de Mitcheson & Colin, 2012). These potential biases and inaccuracies in the use of UVC and the destructive nature of direct capture methods for studying spawning aggregations, highlights the importance of exploring alternative non-destructive methods facilitated by advancements in technology.

Underwater stereo-video systems use two cameras mounted on a rigid frame and are calibrated to provide accurate measurement of the length of, and distance to a fish (Harvey & Shortis, 1995, 1998). Stereo-video technology can also provide repeatable and consistent fish counts and meaningful insights into fish behaviour (Harvey et al., 2001a,b; Goetze et al., 2017). However, this approach has rarely been used to examine spawning aggregations, and to an even lesser extent, to investigate spawning behaviours. To our knowledge, Rand et al. (2006) was the first to document the potential of early stage stereo-video to monitor spawning aggregations, following on from past attempts to use stereo-photography to study schooling behaviour (Cullen et al., 1965; Dill et al., 1981; Klimley & Brown, 1983). Since then, stereo-video technology and software has improved greatly, allowing researchers to explore a wider range of metrics with increased accuracy (Goetze et al., 2019). The only other published applications using this technology to document a spawning event were by Salinas de León et al. (2015) and Robinson et al. (2017). However, their studies were mainly management-oriented and did not aim at developing new ways to apply this method more broadly. The scarcity of research applying stereo-video methods to spawning aggregations is surprising considering the fast development and major technical progress made in the field of underwater video surveys in the past decade (Shortis et al., 2009; Mallet and Pelletier, 2014). Given the high accuracy in length and distance estimates made by latest-generation high definition stereo video systems (Goetze et al., 2019; Harvey et al., 2010), it is likely that these systems will be suitable for examining the behaviour, abundance and size structure of mating individuals in a spawning aggregation.

Using an opportunistic sighting of a spawning event in a sexually dimorphic labrid reef fish (*Bodianus diplotaenia*), we aimed to assess the potential of diver-operated stereo-video systems (stereo-DOVs) to:

i. Generate size-frequency distributions from a sample of free-swimming *B. diplotaenia* individuals and provide estimates of density for the spawning stock,
ii. Characterize the reproductive behaviour of *B. diplotaenia* using quantitative surveys and explicit 3D representation of the spawning event; and
iii. Investigate differences in fish density when comparing the spawning aggregation site with non-aggregation sites.

We hypothesized that males *B. diplotaenia* would be larger in size compared to females and that their reproductive behaviour would be significantly different. We also anticipated that fish density would be higher at the spawning aggregation site than at the non-aggregation sites.

5.3 Materials and Methods

5.3.1 Study area

Located approximately 1,000 km west of mainland Ecuador, the Galapagos Islands straddle the equator in the Tropical Eastern Pacific and are surrounded by the 138,000 km^2 Galapagos Marine Reserve (GMR) (Figure 5.1a) (Snell et al., 1996). In 2014, an archipelago-wide stereo-DOVs survey was conducted and sampled 88 sites throughout the GMR (Salinas-de-León, Unpubl. data). The present study utilizes a subset of three rocky reef sites randomly selected along the coastline of Espanola Island to the south of the archipelago were *B. diplotaenia* was observed mating in large numbers (Figure 5.1 b-c.). All surveys presented here were conducted on the 16th of March 2014.

5.3.2 Study species

The Mexican hogfish (*Bodianus diplotaenia*) is a labrid commonly found on reefs of the Tropical Eastern Pacific from Baja California to the North of Peru (Grove & Lavenberg, 1997; Thomson et al., 2000). *Bodianus diplotaenia* is a protogynous hermaphrodite with sex change from female to male occurring between 220-256 mm standard length (Hoffman, 1985). *B. diplotaenia* exhibits a clear sexual dimorphism with males generally larger and displaying a range of specific morphological traits (Humman & Deloach, 2003). Mature males are easily distinguished from females as they display elongated fins, a rounded snout, a protruding forehead, and a distinctive colour pattern (Figure 5.6). *B. diplotaenia*, like many other labrid species, form predictable local spawning aggregations on a daily bases during the reproductive season and over small geographic areas (Hoffman, 1985; Viotti Orsili, 2013). These resident spawning groups forming throughout the range of the species have been well described in the Gulf of California (Hoffman, 1980; Viotti Orsili, 2013). Detailed information on the reproductive biology and foraging behaviour of *B.diplotaenia* and other closely resembling labrid species can be found in the literature (Hoffman, 1983; Warner, 1984; Hoffman, 1985; Hoffman et al., 1985).

5.3.3 Stereo-DOV surveys

The surveys used a stereo-DOV system comprised of two Canon LEGRIA HFG25 high-definition video cameras. Cameras were placed in SeaGIS waterproof housings mounted horizontally on a metal frame at a distance of 0.7 m inwardly converged at 8 degrees and were calibrated both before and after surveys using the CAL SeaGIS software. This stereo configuration of the video cameras allows for accurate measurements of fish length and 3D position of fish in the water column (Harvey et al., 2002b). Using a similar configuration, Harvey et al. (2010) obtained absolute mean errors of less than 1% of the length for targets within 8 m of the stereo-video system.

Surveys were conducted by two SCUBA divers following a standardized approach for stereo-DOV surveys (Goetze et el. 2019) with modifications to capture the spawning aggregation. Specifically, one diver operated the stereo-video system while the other towed a GPS (Garmin GPS Map 78) secured to a buoy to create a detailed track of the area sampled which was subsequently used to calculate the distance travelled for each transect (Salinas-de-León et al., 2016). Divers swam timed transects of 2 min at a depth of 15 to 20 m, 1.5 m from the bottom, and with the cameras slightly tilted downward. Survey start and end times were recorded and synchronized with the GPS internal clock. For the subset of transects used in the present study, this equated to an average of 40.4 ± 3.8 m travelled for each transect.

The spawning aggregation was observed at Bahia Gardner Norte on two separate transects, due to the large size of the aggregation as well as its location on an outcrop (Figure 5.1d). This meant a separate portion of the aggregation was recorded on each transect as the divers travelled down each side of the outcrop. To obtain footage of the entire aggregation, without breaking the protocol for normal transects, the team of divers returned to the aggregation and ascended above it to collect complementary footage of the reproductive event (video available online in published article: Link). The divers filmed the spawning aggregation for a total of 10 minutes from a range of different angles, which enabled the selection of multiple unobstructed views, knowing that it would facilitate counts and length measurements at a later stage.

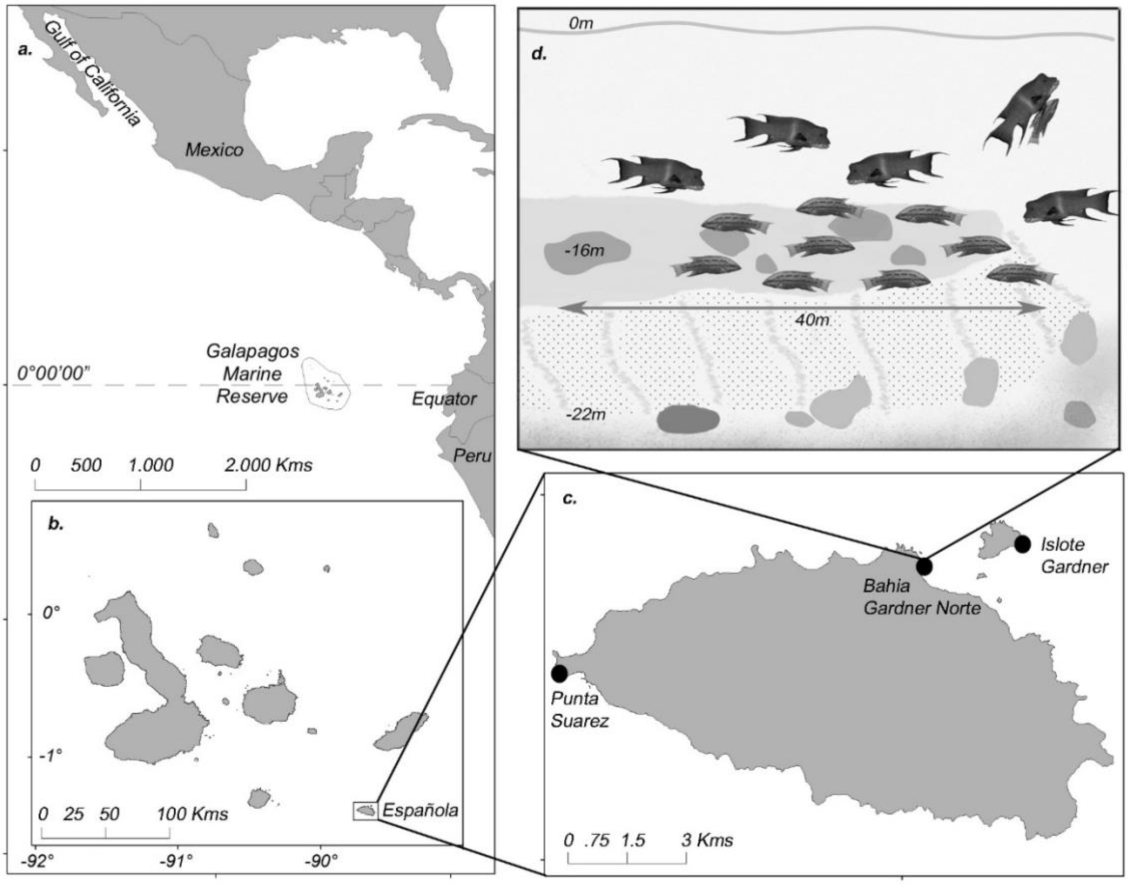


Figure 5.1 a. Location of the Galapagos Marine Reserve (GMR) and distribution range of *B. diplotaenia,* from Baja California to the south of Peru. b. Location of Española Island within the GMR. c. The three survey sites at Española Island are represented with a black dot. d. Schematic representation of the aggregation site at the end of a rocky-reef ledge. Large dark-grey fish are males and small light-grey fish are females

5.3.4 Experimental design

To compare the size of the aggregation observed on two separate stereo-DOV transects to regular *B. diplotaenia* abundances around the island, three non-aggregation locations with three transects at each location were included (Figure 5.3).

5.3.5 Image analysis

5.3.5.1 Transect based video

Pairs of videos were processed using EventMeasure Stereo SeaGIS software. All *B. diplotaenia* inside the transect area (200 m^2 as defined by the 40 m transect length and a cut off of measurements 2.5 m either side of the transect) were located and measured to the nearest millimetre (i.e., fork length, FL) with a maximum residual mean square (RMS) error of 20 mm. In stereo-video surveys, the RMS serves as a threshold for the reliability of a measurement (Shortis and Harvey, 1998). Similarly, fish were measured within 8 m from the camera to ensure the accuracy of the measurements (Harvey et al., 2010). Fish density was calculated as the number of individuals per 100 m^2. Finally, length data were converted to weight to elicit total biomass for each transect using the equation $W = a\ FL^b$, where FL and W are respectively fork length in centimetre and weight in grams. The parameters a and b were respectively 0.015 and 3 and were obtained using length and weight data from a sample of *B. diplotaenia* collected on the Ecuadorian coast. Full details of the calculation of those parameters are available in Appendix F

5.3.5.2 Spawning behaviour video

Male and female fish were measured (FL) throughout the 10 min of spawning footage, taking advantage of the cameras focusing on different areas of the mating ground. Individuals angled at more than 80° or swimming in and out of the field of view were excluded to optimize accuracy and avoid pseudo-replication. In EventMeasure Stereo, fish are marked when a successful measurement is made, and this marking was used to ensure the same individual was not measured multiple times by moving the video back and forwards when a new measurement was made to ensure it hadn’t been measured already. The measurements of unique individuals were used to produce length-frequency distributions and compare sizes between males and females.

A total of 15 still images were selected throughout the 10 min video sequence and later analyzed in EventMeasure Stereo. In four still images, divers were specifically situated directly above the aggregation, filming downward with the reef no further than 6 m away in the background. This configuration facilitated measurements of 3D coordinates of fish in the water column in relation to a set of evenly distributed background substrate points and produced 3D representations of the spawning event. The eleven other still images were from the side of the aggregation, clear from the substrate, and only served to compute distances between mating individuals. Due to the extent of the spawning aggregation (~30 to 40 m) and the relatively low visibility (~12 m), it was not possible to capture the entire aggregation within a single frame. Highlights of the spawning footage are available in the online version of the published article (Link).

5.3.5.3 3D reconstruction of the aggregation

Three types of analysis were run using the still images. Fish and substrate coordinates were used to reconstruct the still images in the form of a 3D visual representation using Python bindings of the Visualization Toolkit software (Schroeder et al., 2006). Substrate was represented using a yellow smoothed surface corresponding to the 2D Delauney triangulation of available substrate points. Males were represented using blue spheres and females using red spheres. Second, a set of three specific distances was computed using Python to characterize the spawning aggregation (Figure 5.2).

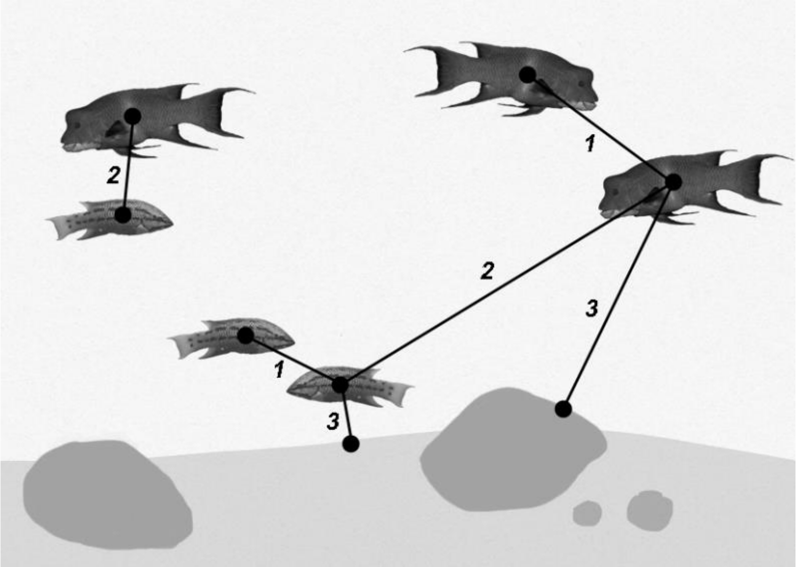


Figure 5.2 Schematic representation of a hypothetical still image with different distances computed: 1. Intra-distance; 2. Inter-distance; 3. Distance to the reef. Large fish with elongated fins and bulging forehead are males and small light-grey fish are females.

Intra-distance was defined as the minimum distance of one individual to another individual of the same sex. Inter-distance was defined as the minimum distance of one individual to another individual of the opposite sex. Distance-to-the-reef represented the shortest distance between a given fish and the closest substrate point.

Third, to investigate territoriality and gregarious habits, volumetric densities of aggregating fish were computed separately for males and females. In each scene, this was achieved by dividing the total number of individuals in a given group of fish by the volume of the convex hull (smallest volume containing a set of 3D points) enclosing the entire group (De Berg et al., 2008). This process is later referred to as "convex hull analysis". All analyses were conducted using Python (Jones et al., 2001; Arbuckle, 2010) and R (R Core Team, 2013) software and are available online in a Python package and IPython Notebook (Perez & Granger, 2007) on GitHub [https://github.com/pfernique/RGHAFS20]. Plots were made with the Matplotlib package (Hunter, 2007) and communication between Python and R was facilitated by the pandas and RPy2 packages (McKinney, 2014).

5.3.6 Statistical analysis

Length-frequency distributions for both sexes were computed, and mean length compared using a generalized linear model (GLM) with length being the response (dependent) variable and gender being the explanatory (independent) variable. The GLM structure was “Length = Intercept + Slope*Gender + Error”. The null model (H_0) was “no difference between male lengths and female lengths” with the alternative model (H_A) being “male lengths and female lengths are significantly different”. Underlying assumptions of homoscedasticity and normality of errors were verified for length, but not for distances. Distances are positive numbers, characterized by right-skewed distributions. Thus, the normality assumption of distances was violated. To highlight statistical differences for a given distance between males and females, two complementary statistical procedures were conducted. First, Wilcoxon rank sum tests with continuity correction were used, then GLMs with Gamma distributions (Dobson & Barnett, 2008) with the distance being the response (dependent) variable and the gender being the explanatory (independent) variable. The GLM structure was “Distance = Intercept + Slope*Gender + Error”. This enabled the statistical comparison of distances either by testing if the parameter associated with gender was significantly different from 0 (p-value <0.05) or using information criterion such as Akaike Information Criterion to compare the model with gender as an explanatory variable to the model without an explanatory variable. Because both approaches gave similar results only the p-values associated to the non-parametric tests were retained. The null model (H_0) was “no difference between male and female distances (i.e. Intra-distance, Inter-distance, and Distance to the reef) with the alternative model (H_A) being “male and female distances are significantly different”.To compare male and female volumetric densities, a non-parametric Wilcoxon rank sum test was used. The null model (H_0) was “no difference between male and female volumetric densities” with the alternative model (H_A) being “male and female volumetric densities are significantly different”. The values presented in the results are means and standard deviation unless otherwise stated.

5.4 Results

5.4.1 Length frequency distribution

A total of 307 individuals (142 females and 165 males) were measured (Figure 5.3). The length of females ranged between 11.4 cm and 45.5 cm with and estimated mean length of 24.14 ± 5.39 cm. The length of males ranged between 20.5 cm and 58.3 cm with and estimated mean length of 39.79 ± 6.98 cm, which differed significantly from females (GLM, d.f. = 305, p-value: <0.001). On average, males were nearly twice the size of females.

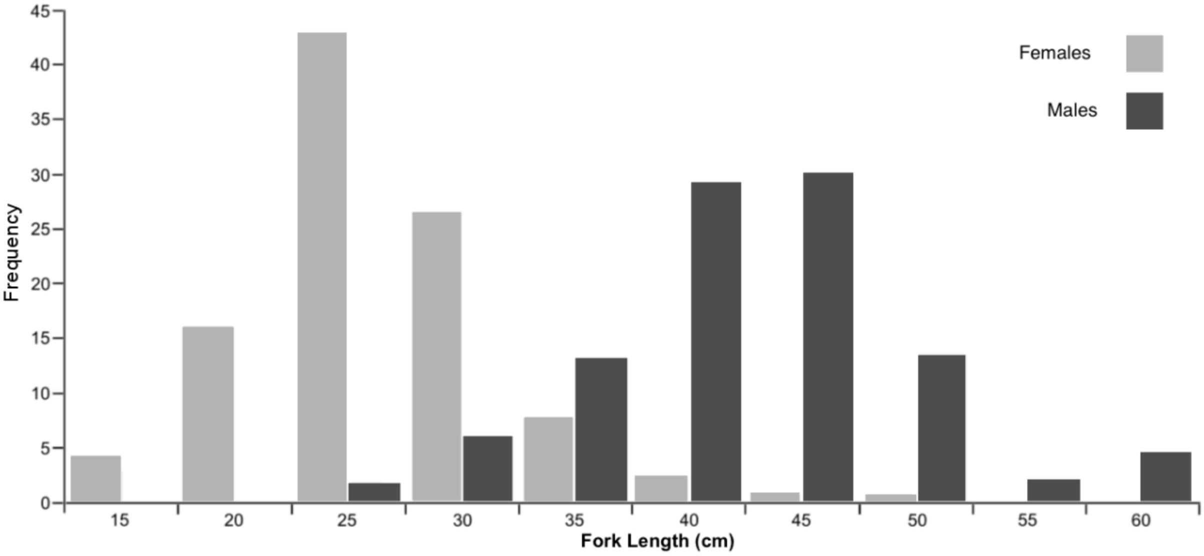


Figure 5.3 ***B. diplotaenia*** **length (FL) frequency distribution for female (n=142) and male (n=165) fish measured at the aggregation site obtained with stereo-video measurements.**

5.4.2 Abundance and biomass at survey sites

Abundances recorded at the two aggregation transects were respectively four and eight times greater than the largest abundance recorded for non-aggregation transects (Figure 5.4). Similarly, biomass recorded for aggregation transects were more than ten times greater than the largest biomass in non-aggregation transects.

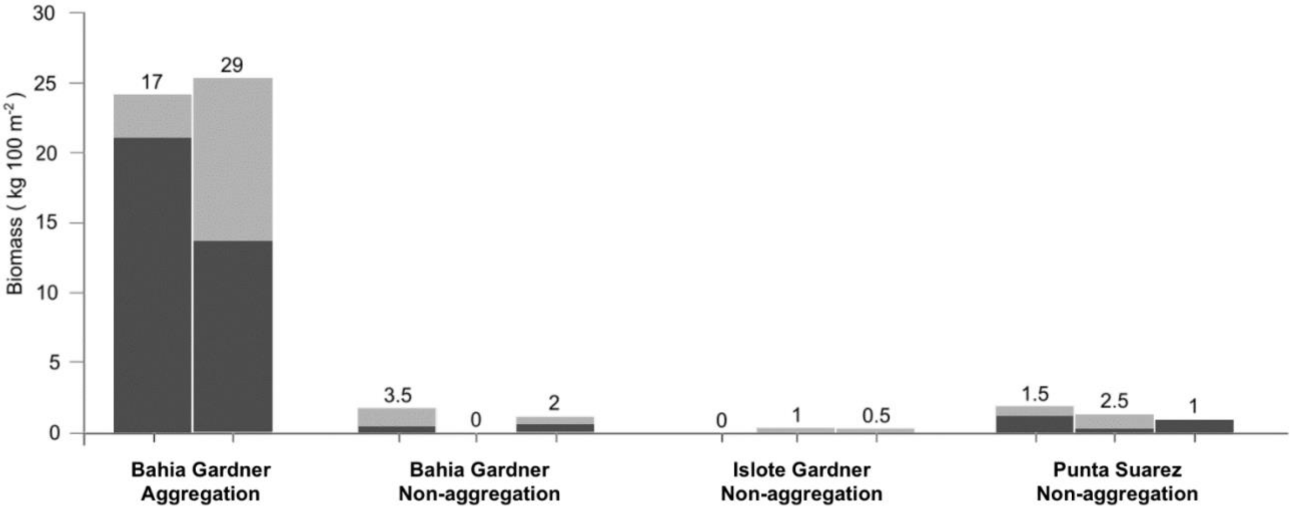


Figure 5.4 Biomass and abundance of *B. diplotaenia* at four survey locations around Espanola Island with two transects for the aggregation site and three transects for each non-aggregation site. Bars represent biomass in kilogram per 100 m^2 where dark grey is male biomass and light grey is female biomass. Abundances are presented above the bars, males and females combined, in individuals per 100 m^2.

5.4.3 Spatial characteristics of the spawning aggregation

Across the 15 different frames analysed, 164 males, 214 females and 387 substrate points coordinates were collected and used to compute mean distance-to-the reef, mean intra-distance and mean inter-distance (Table 5.1).

Table 5.1 Mean distances values (mm ± SD) computed to quantitatively characterize the structure of the spawning event. Distance-to-the-reef is the shortest distance between a given fish and the closest substrate point. Intra-distance is the minimal distance of one individual to another individual of the same sex. Inter-distance is the minimal distance of one individual to another individual of the opposite sex. Statistical difference is represented by * and > indicates which of the two distances is significantly greater.**

	 Males		 Females
Distance-to the reef (mm)	716 ± 401	> ***	496 ± 303
Intra-distance (mm)	1632 ± 874	> ***	1113 ± 713
	∨***		∨***
Inter-distance (mm)	780 ± 450		747 ± 325

Males swam 45% further away from the reef with a mean distance-to-the-reef significantly greater than females (Wilcoxon rank sum test, W=3065, p-value: <0.001). Males also swam 45% further apart from each other than females did as confirmed by a significantly higher mean male intra-distance (Wilcoxon rank sum test, W = 11759, p-value <0.001). Females showed a tendency to swim 40% closer to males than to other females with female mean inter-distance significantly lower than intra-distance (Wilcoxon rank sum test, W = 17152, p-value <0.001). Similarly, males swam around 70% closer to females than to other males, with male mean inter-distance significantly lower than mean intra-distance (Wilcoxon rank sum test, W = 2292, p-value <0.001).

Convex hull analyses showed that females formed groups up to twice as dense as males with densities of 3.5 ± 1.2 ind.m^{-3} compared to 2.0 ± 0.8 ind.m^{-3} for males; (Wilcoxon rank sum test, W = 60, p-value 0.014).

5.4.4 3D reconstruction of the spawning aggregation

Once a two-dimensional still image was reconstructed, it became possible to rotate and observe it in three dimensions from different perspectives. Figure 5.5 presents both a downward-looking frame with the rocky reef plunging to the left of the image (Figure 5.5a) and its 3D reconstruction viewed from the side showing the sharp dip associated with the declination of the substrate (Figure 5.5b). The reader can consult the online version of the published article to access the rest of the reconstructed still images (Link).

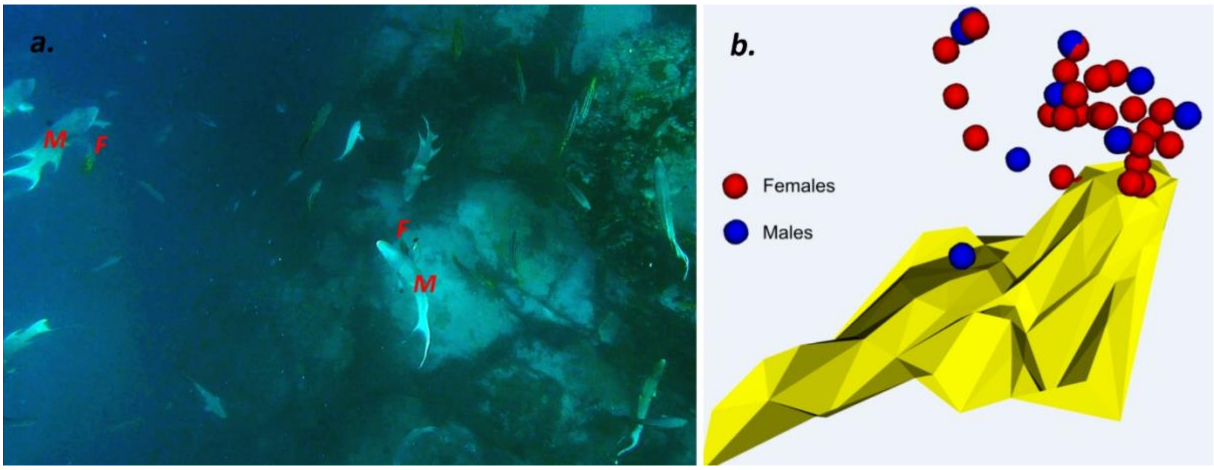


Figure 5.5 a. Downward-looking still image selected from the spawning aggregation video b. 3D reconstruction of the left image produced using Visual Tool Kit Software viewed from the side. The seafloor is represented by a smoothed yellow surface. The upper-most blue-red overlapping dots of the reconstruction represent the two pairs of male-female courting annotated on the left image. Non-courting individuals were not annotated for clarity. Notice the greater spacing between males compared to females. The rest of the reconstructed still images can be accessed in the online version of the published article (Link).

5.4.5 Spawning behaviour

The majority of females aggregated close to the reef while most males were swimming higher in the water column and slightly off the edge of the reef. Males were displaying exaggerated swimming motions, occasionally swimming to the upper water column with fully stretched out fins and fluttering their elongated filaments to attract females. Encounters between males occasionally resulted in “mouth fighting” and chases. A few males were observed swimming amongst females closer to the bottom to try to gain their attention. Conversely, females periodically separated from the group, swimming up the water column where they were courted successively by different males. More specifically, a male would approach a given female and positioned himself above her, straddling her dorsal surface with his extended pelvic fins placed on both sides in order to keep her close (Figure 5.6a). They initially swam together horizontally, parallel to a given depth where the male used his caudal fin and one of his two pectoral fins for propulsion. Most often this behaviour was observed and subsequently the pair split up. However, a second interaction pattern occurred whereby male, and female stayed together for longer periods. In this case, the horizontal sequence was followed by a second swimming pattern where they both rapidly rose vertically in parallel for about two meters. The ascent concluded by quickly revolving simultaneously and bringing their abdomens close together as a white cloud of eggs was observed (Figure 5.6b). Then males and females separated and swam back down to the lower part of the water column with their respective group. Finally, creole fish (*Paranthias colonus*) were observed a number of times feeding on released eggs. The reader can refer to the video available online in the published article to view the range of behaviour previously described (Link).

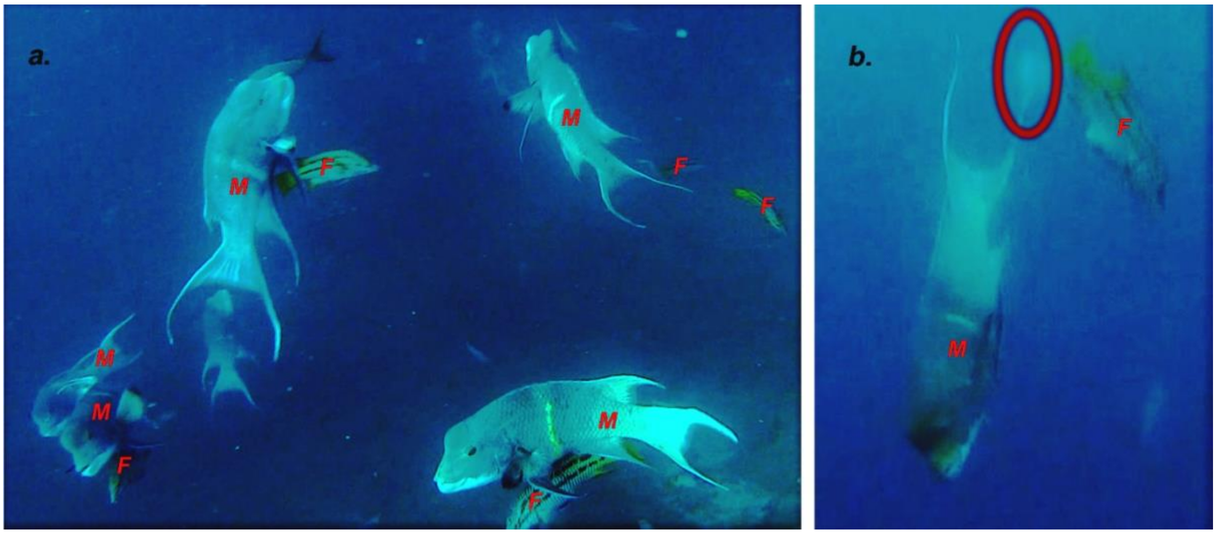


Figure 5.6 a. Male (M) and female (F) *B. diplotaenia* fish displaying courting behaviour. The two males at the forefront and the one at the bottom left each court a different female located right underneath their pectoral fins. b. A pair of *B. diplotaenia* separating immediately after spawning. The red circle indicates a white cloud of gametes.

5.5 Discussion

We present the first record of a spawning aggregation for *B. diplotaenia* in the Galapagos Marine Reserve (GMR). This is confirmed by the direct observation of spawning behaviour (Colin et al., 2003a). Stereo-DOVs surveys showed that the density of this spawning aggregation was at least six times greater than normal levels at non-aggregation sites. Although rarely witnessed, two similar events have been reported in the Islands of Floreana and Marchena by experienced Galapagos divers (M. Espinoza, F. Rivera, Pers. Comm.). These reports, combined with our observation in Española Island, indicate that *B. diplotaenia* forms spawning aggregations across the Galapagos Islands.

Stereo-video technology provides an effective tool to generate the data needed to characterize and manage spawning aggregations. We showed that diver-operated stereo-video can be used to provide baseline measurements of the length distribution and fish density as well as behavioural characteristics of a spawning aggregation. Such baseline measurements, while unlikely to be at pristine levels, are essential to monitor the size and composition of spawning events through time (Beets & Friedlander, 1998; Colin et al., 2003b; Nemeth, 2005a). Moreover, detecting small changes in size or numbers over time is crucial to provide managers and researchers with the relevant feedback to inform the management of spawning stocks (Heppell et al., 2012). Therefore, the high-accuracy of stereo-video technology combined with advantages over traditional visual survey methods and reproducibility (Harvey et al., 2001a, b, Goetze et al., 2019) makes it an optimal technique for the study and long-term monitoring of spawning aggregations.

The benefit of using stereo-video techniques to investigate spawning aggregations largely relies on the possibility to measure fish with great precision, under variable field conditions, and in a non-invasive fashion (Harvey et al., 2000; Harvey et al., 2001a, b). Using the latest stereo-video systems we were able to measure mating fish with absolute mean errors of less than 1% of the length (Harvey et al., 2010). The improved accuracy of stereo-video when compared to Underwater Visual Censuses (UVC) represents a considerable advantage (Harvey et al., 2000). Similarly, the permanent record and systematic analysis of stereo-video data provides a clear advantage over UVC for long-term spawning aggregation monitoring as inter-observer bias can preclude the detection of small changes in fish length (Harvey et al., 2001a, b). Stereo-video systems also offer greater flexibility when compared to underwater laser calliper for generating reliable fish size-distributions. Indeed, while both methods are non-invasive and offer comparable accuracy at short distance, stereo-video maintains measurement accuracy for fish angled up to 80 degrees within 8 m of the system (Harvey et al., 2010) whereas laser calliper accuracy drops significantly past 10 degrees and have not been proven effective past 2.5m in spawning aggregations (Heppell et al., 2012). Comparable size data can be obtained with the direct capture of fish (Colin et al., 2003; Nemeth, 2005b). However, these methods should be avoided due to the high mortality rates and potential disruption to the reproduction of the species (Rand et al., 2006; Heppell et al., 2012). For example, we measured 307 *B. diplotaenia* individuals with no noticeable disruption of the reproductive event whereas Hoffman (1980) harvested 109 *B. diplotaenia* to generate a reliable size frequency distribution for the same species. Thus, we recommend the use of diver-operated stereo-video to monitor the size structure of spawning events.

Beyond the possibility to generate accurate length data with little impact, there are advantages to using stereo-video with the transect approach to improve the accuracy of fish density estimates in a spawning aggregation. While density estimates might be obtained using UVC, transects counts or GPS density surveys (Colin et al., 2003; Golbuu and Friedlander, 2011), these methods become increasingly biased as spawning stock increases largely due to the great difficulty of visually estimating numbers for large groups of fish in situ (Sadovy and Colin, 2012). Similarly, while hydroacoustic methods have shown promises to assess fish numbers in spawning aggregations (Cimino et al., 2018; Egerton et al., 2017), the abundance estimates they generate present large confidence intervals and cannot be used as absolute abundance (Egerton et al., 2017). This is problematic since a recovering or declining trend in a spawning stock can be masked by large confidence intervals, which prevents the effective evaluation of management measures (Heppell et al., 2012). Another issue arising with UVC is the over-estimation of sampling area also leading to inflated fish counts and blurred population trends (Harvey et al., 2004). In contrast, the stereo-video software (EventMeasure Stereo) allowed us to define an accurate sample area therefore yielding comparable density estimates between aggregation and non-aggregation sites. Changes in fish density across a reef area also provide indirect evidence of a spawning aggregation, highlighting the importance of properly estimating densities (Sadovy and Colin, 2012). Using diver-operated stereo-video techniques, Salinas-de-Leon et al. (2016) developed an approach which provided reliable density estimates in groups of fish with over 1000 individuals and that could easily be applied to spawning aggregations. Using stereo-video to characterize spawning events both removes the difficulty of counting fish in situ while allowing a standardized sampling area to produce accurate density estimates for the spawning aggregation.

Following a novel stereo-video approach, we were able to successfully quantify the reproductive behaviours of *B. diplotaenia* previously described through observational studies (Hoffman, 1980; Hoffman, 1985; Viotti-Orsili, 2013). Our approach used EventMeasure Stereo software to define 3D coordinates of swimming fish and substrate, allowing the calculation of the intra and inter-distances, distances-to-the-reef and to create 3D spatial representation. This provided several valuable insights on the territoriality and male-female interdependencies in line with the mating strategy described for that species (Hoffman, 1980; Hoffman, 1985). This mating strategy is known as polygyny with male dominance, where males compete for female's attention through defending a reproductive territory known as "lek" (Emlen & Oring, 1977; Viotti Orsili, 2013). Stereo-video data and convex-hull analysis confirmed that males kept their distances with other dominant males and swam about 50% further apart than females which formed schools twice as dense as males just above the reef platform (Figure 5.5). The segregation between males, swimming high in the water column, and females, staying close to the reef, was also quantified with male distance-to-the-reef nearly 50% greater for males. By staying close to the reef, the females can feed when they are not engaged in mating activities which was specifically observed by Hoffman (1980) in the Gulf of California. The stereo-video spatial approach presented here makes it possible to go beyond visual observations to explicitly quantify reproductive behaviours and shows great promises to answer a wider range of questions on fish mating systems.

Our study presents several novelties compared to Rand et al. (2006) and Salinas de León et al. (2015), who both used stereo-video to assess spawning aggregations of grouper species. *B. diplotaenia*, unlike most grouper species, expresses a strong sexual dimorphism which allowed a finer break-down of male-female interdependencies, reproductive behaviour and size-structure of mating individuals. In addition, the inclusion of the substrate in the 3D analysis, facilitated the investigation of spatial characteristics of the spawning aggregation in relation to habitat. We also present the first attempt to combine stereo-video methodology with Python and Visual Toolkit, producing interactive 3D visual representations that could be rotated and observed from multiple angles. Furthermore, the on-going advances in stereo-video technology have improved our ability to process large amount of video data with greater accuracy and flexibility. For example, Rand et al. (2006) used one single still-image including the coordinates of 40 individuals which had to be measured in an optimal perpendicular position while we were able to measure fish angled up to 80 degrees. In contrast, we used 15 still-images and obtained 765 coordinates of fish and substrate points from a simple opportunistic encounter with a spawning aggregation. This illustrates the wide range of possibilities offered by stereo-video for the systematic study of spawning aggregations.

Modern stereo-video techniques offer a range of easily repeatable tools for the baseline study, characterization, and long-term monitoring of reef fish spawning aggregations. We recommend that future studies, specifically target and monitor spawning aggregations using stereo-video and in the case of opportunistic sighting return to obtain multiple views and transects of the entire aggregation.

Chapter 6 General discussion

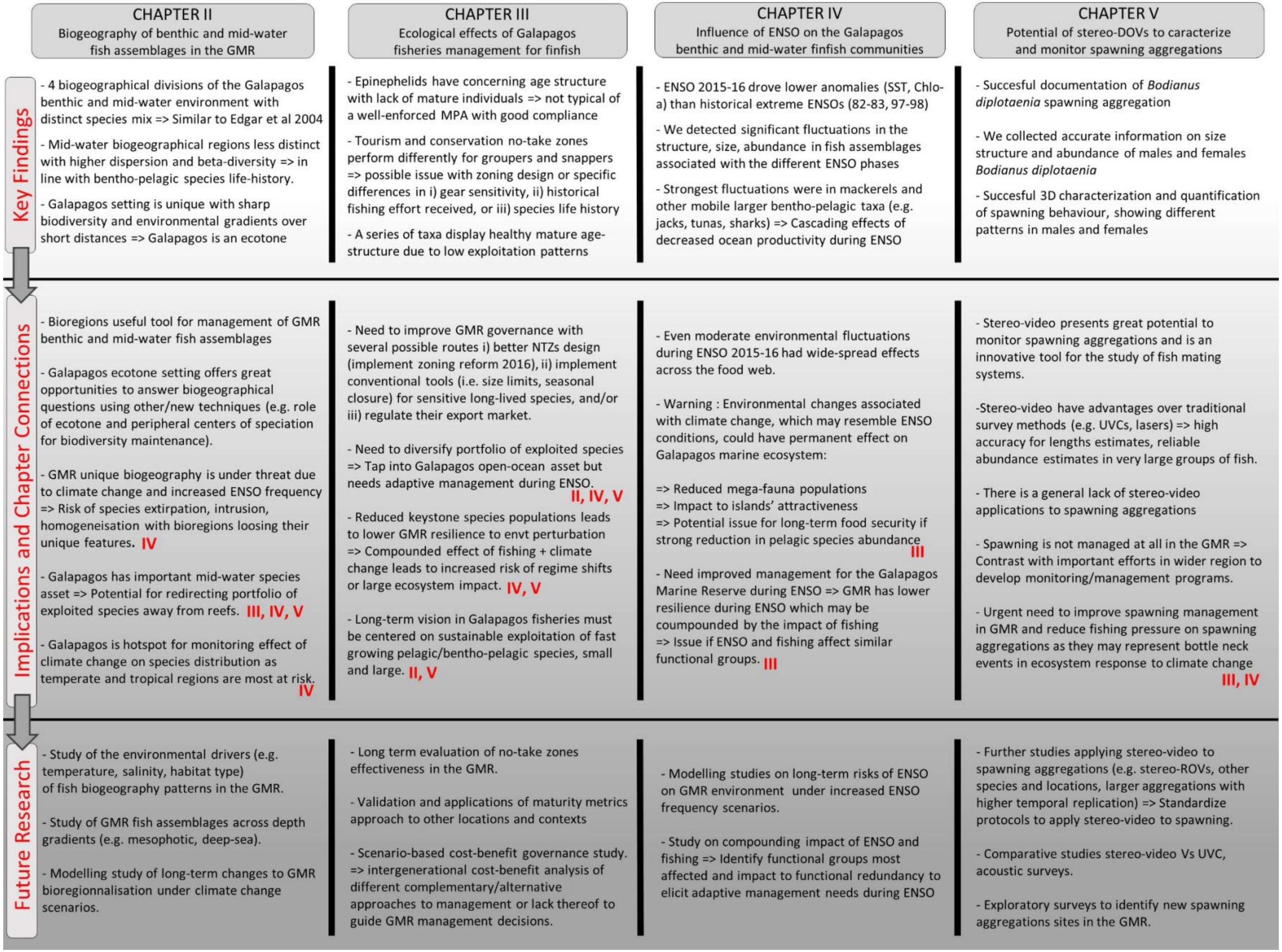
6.1 Summary of findings

In chapter 2, I found a clear biogeographical subdivision of the Galapagos Archipelago benthic fish assemblages. My data separated into four benthic bioregions, which aligned well with the bioregions described by Edgar et al. (2004). I also found that fish data collected from mid-water, separated into four bioregions, although the patterns were less clear suggesting the coastal mid-water environment may be best subdivided into three bioregions. When comparing benthic with mid-water fish assemblages, I found that the latter displayed higher heterogeneity, lower species richness and were dominated by species with extensive distribution ranges.

Under chapter 3, while I found that some exploited species (i.e. *Mycteroperca olfax*, *Lutjanus argentiventris*, *Seriola rivoliana*) were larger inside no-take zones, it appears that the size differences I detected are not characteristic of a well-enforced MPAs after 15 years of protection (Russ et al., 2005; Edgar et al., 2014; Giakoumi et al., 2017; Friedlander et al., 2017, Goetze et al. 2021). In particular, the size structures of *Mycteroperca olfax*, historically the most exploited finfish in Galapagos, were no different between tourism no-take zones and fishing zones suggesting potential issues with compliance or NTZs design. Similarly, no take zones did not harbour a larger proportion of mature or mega-spawner *Mycteroperca olfax* individuals. For *Lutjanus argentiventris* there were larger individuals and higher proportion of mature and mega-spawner fish in no-take zones compared to fishing zones. Outside no-take zones, Epinephelids size structures were dominated by immature fish. Conversely, a series of non-commercially exploited species displayed healthy maturity metrics levels likely owing to gear restrictions measures.

With chapter 4, I found that while the 2015-16 ENSO did not affect the Galapagos Islands as strongly as in 1982-83 or 1997-98, several taxa displayed marked fluctuation patterns associated with changes in environmental conditions. These fluctuations were particularly marked for the small bentho-pelagic mackerels (i.e *Trachurus* spp. and *Decapterus* spp.) and large piscivorous bentho-pelagic taxa such as large Carangids, medium-size Scombrids, elasmobranchs (i.e. *Sphyrna lewini*, *Carcharhinus galapagensis*) which all increased in abundance once El Nino started receding. I also found that mackerels displayed significant changes in size structure with larger individuals as El Nino started receding. This is a probable response to changes in environmental conditions and food availability. Overall, I found that benthic taxa displayed lower magnitude of fluctuation compared to mid-water taxa.

Finally, I found in chapter 5 that a diver operated stereo-video system could be used to collect information about the abundance and size-structure of spawning fish. Using stereo-DOVs I could differentiate between male and female *Bodianus diplotaenia* and measure the size structure of the different sexes. I found that stereo-DOVs could successfully characterize *Bodianus diplotaenia* reproductive behaviour by quantifying the distance between fish, and the distance off the bottom which I used to produce quantitative estimates of relative fish positions in the water column. This shows that stereo-DOVs have great potential to become a standard tool to study and monitor spawning aggregations globally.



	CHAPTER II Biogeography of benthic and mid-water fish assemblages in the GMR	CHAPTER III Ecological effects of Galapagos fisheries management for finfish	CHAPTER IV Influence of ENSO on the Galapagos benthic and mid-water finfish communities	CHAPTER V Potential of stereo-DOVs to caracterize and monitor spawning aggregations
Key Findings	- 4 biogeographical divisions of the Galapagos benthic and mid-water environment with distinct species mix => Similar to Edgar et al 2004 - Mid-water biogeographical regions less distinct with higher dispersion and beta-diversity => in line with bentho-pelagic species life-history. - Galapagos setting is unique with sharp biodiversity and environmental gradients over short distances => Galapagos is an ecotone	- Epinephelids have concerning age structure with lack of mature individuals => not typical of a well-enforced MPA with good compliance - Tourism and conservation no-take zones perform differently for groupers and snappers => possible issue with zoning design or specific differences in i) gear sensitivity, ii) historical fishing effort received, or iii) species life history - A series of taxa display healthy mature age-structure due to low exploitation patterns	- ENSO 2015-16 drove lower anomalies (SST, Chlo-a) than historical extreme ENSOs (82-83, 97-98) - We detected significant fluctuations in the structure, size, abundance in fish assemblages associated with the different ENSO phases - Strongest fluctuations were in mackerels and other mobile larger bentho-pelagic taxa (e.g. jacks, tunas, sharks) => Cascading effects of decreased ocean productivity during ENSO	- Succesful documentation of *Bodianus diplotaenia* spawning aggregation - We collected accurate information on size structure and abundance of males and females *Bodianus diplotaenia* - Succesful 3D characterization and quantification of spawning behaviour, showing different patterns in males and females
Implications and Chapter Connections	- Bioregions useful tool for management of GMR benthic and mid-water fish assemblages - Galapagos ecotone setting offers great opportunities to answer biogeographical questions using other/new techniques (e.g. role of ecotone and peripheral centers of speciation for biodiversity maintenance). - GMR unique biogeography is under threat due to climate change and increased ENSO frequency => Risk of species extirpation, intrusion, homogeneisation with bioregions loosing their unique features. IV - Galapagos has important mid-water species asset => Potential for redirecting portfolio of exploited species away from reefs. III, IV, V - Galapagos is hotspot for monitoring effect of climate change on species distribution as temperate and tropical regions are most at risk. IV	- Need to improve GMR governance with several possible routes i) better NTZs design (implement zoning reform 2016), ii) implement conventional tools (i.e. size limits, seasonal closure) for sensitive long-lived species, and/or iii) regulate their export market. - Need to diversify portfolio of exploited species => Tap into Galapagos open-ocean asset but needs adaptive management during ENSO. II, IV, V - Reduced keystone species populations leads to lower GMR resilience to envt perturbation => Compounded effect of fishing + climate change leads to increased risk of regime shifts or large ecosystem impact. IV, V - Long-term vision in Galapagos fisheries must be centered on sustainable exploitation of fast growing pelagic/bentho-pelagic species, small and large. II, V	- Even moderate environmental fluctuations during ENSO 2015-16 had wide-spread effects across the food web. - Warning : Environmental changes associated with climate change, which may resemble ENSO conditions, could have permanent effect on Galapagos marine ecosystem: => Reduced mega-fauna populations => Impact to islands' attractiveness => Potential issue for long-term food security if strong reduction in pelagic species abundance III - Need improved management for the Galapagos Marine Reserve during ENSO => GMR has lower resilience during ENSO which may be coumpounded by the impact of fishing => Issue if ENSO and fishing affect similar functional groups. III	- Stereo-video presents great potential to monitor spawning aggregations and is an innovative tool for the study of fish mating systems. -Stereo-video have advantages over traditional survey methods (e.g. UVCs, lasers) => high accuracy for lengths estimates, reliable abundance estimates in very large groups of fish. - There is a general lack of stereo-video applications to spawning aggregations - Spawning is not managed at all in the GMR => Contrast with important efforts in wider region to develop monitoring/management programs. - Urgent need to improve spawning management in GMR and reduce fishing pressure on spawning aggregations as they may represent bottle neck events in ecosystem response to climate change III, IV
Future Research	- Study of the environmental drivers (e.g. temperature, salinity, habitat type) of fish biogeography patterns in the GMR. - Study of GMR fish assemblages across depth gradients (e.g. mesophotic, deep-sea). - Modelling study of long-term changes to GMR bioregionnalisation under climate change scenarios.	- Long term evaluation of no-take zones effectiveness in the GMR. - Validation and applications of maturity metrics approach to other locations and contexts - Scenario-based cost-benefit governance study. => intergenerational cost-benefit analysis of different complementary/alternative approaches to management or lack thereof to guide GMR management decisions.	- Modelling studies on long-term risks of ENSO on GMR environment under increased ENSO frequency scenarios. - Study on compounding impact of ENSO and fishing => Identify functional groups most affected and impact to functional redundancy to elicit adaptive management needs during ENSO	- Further studies applying stereo-video to spawning aggregations (e.g. stereo-ROVs, other species and locations, larger aggregations with higher temporal replication) => Standardize protocols to apply stereo-video to spawning. - Comparative studies stereo-video Vs UVC, acoustic surveys. - Exploratory surveys to identify new spawning aggregations sites in the GMR.

Figure 6.1 Thesis overview with detail of the main points developed in the next sections. Red Roman numerals are chapter numbers and indicate a link of findings and implications between chapters.

6.2 Integration of findings and implications in a global and local context

My thesis investigated the spatial and temporal dynamics of Galapagos reef fish assemblages using diversity, abundance, and length data from baited remote underwater stereo-video systems. I generated and presented information in my chapters that describes the ecology and status of Galapagos fish assemblages in relation to key natural and anthropogenic pressures. This information has both local and global implications. These implications include highlighting the unique value of the Galapagos archipelago to the field of biogeography and providing suggestions for possible management to improve the resilience of local fish populations in the face of current and future threats. I also identify gaps in research on spawning aggregations.

The following sections integrate and synthesize my research in both a larger international and smaller local context, and broadly follow the thesis chapters order. However, as part of my learning associated with my thesis these sections encompass larger themes than those developed in the discussions of each chapter. Hence, I will touch on related topics that are not explicitly covered previously in the thesis. In part, this is due to some of the ideas presented here being informed by insights I gathered during the three years I spent working in the Galapagos marine research field prior to starting my thesis. The whole of section 6.2 can be thought of as an integrated piece of scientific writing resembling a book chapter. Figure 6.1 is presented to provide the reader with a succinct graphical overview of the outcomes, implications, and links between chapters.

6.2.1 Galapagos, a living laboratory for biogeography research

Darwin’s biogeographical observations of the Galapagos fauna in 1835 played a key role in developing the Theory of Evolution which still influences the field of biogeography to this day (Sulloway, 1982; Spellerberg & Sawyer, 1999; Briggs, 2009; Valle, 2013). In 1977, research in the Galapagos once again revolutionized our understanding of life on earth with the discovery of hydrothermal vents at the Galapagos, sparking renewed effort to document the marine biogeography of our planet (Rogers et al., 2012; Ebach, 2013). My findings on the biogeography of reef fish communities highlight the unique characteristics of the Galapagos islands in a global context. Like Edgar et al. (2004a), I found that the Galapagos archipelago could be subdivided into four main bioregions (noting that my surveys did not sample the western sub-bioregion of Elizabeth included in their work, which precluded re-assessing it using stereo-BRUVs), each characterized by a distinct mix of tropical, sub-tropical and temperate fish species, and a marked difference in alpha diversity over short distances. In addition, my study highlights that these bioregions arise just as clearly using stereo-BRUVs compared to Underwater Visual Censuses (UVC) and that they are consistent across seasons. These biogeographical transitions from tropical to cold-temperate environment with a subtropical subtraction effect typically unfold over thousands of kilometres, such as in South-Africa (Emanuel et al., 1992; Turpie et al., 2000) or along the Western and Eastern coasts of Australia (Thackway & Cresswell, 1998; Zann, 2000; Fox & Beckley, 2005; Goldsworthy et al., 2020),In the Galapagos, the interaction of various cold and warm currents with the unique geomorphological features of the insular platform drives comparable biogeographical gradients at a considerably reduced scale. Understanding the past and current drivers shaping biodiversity patterns is a central part of biogeographical research (Whittaker, 1972; Spellerberg & Sawyer, 1999; Lourie & Vincent, 2004; Cowman & Bellwood, 2013a; Santos et al., 2016). I believe that as the field of biogeography evolves, the Galapagos Islands with their unique oceanographic setting will continue to yield crucial insights into the spatial and temporal dynamics influencing the distribution of marine life.

From early efforts to map biological resources for exploitation, to a field now predominantly preoccupied with understanding evolutionary processes of biodiversity build-up and optimizing its long-term preservation and management (Whittaker et al., 2005; Ebach, 2013), biogeography research has come a long way. However, many marine biogeography questions remain, or need to be refined, e.g. the drivers of speciation (Rocha et al., 2002; Rocha, 2003; Floeter et al., 2008; Briggs, 2010; Bowen et al., 2013; Cowman & Bellwood, 2013a; Cowman et al., 2017), drivers of community structure (Bellwood & Hughes, 2001;

Hobbs et al., 2012; Parravicini et al., 2013; Hachich et al., 2015; Santos et al., 2016; Bennett et al., 2018), or optimizing protected area design (Turpie et al., 2000; Lourie & Vincent, 2004; Whittaker et al., 2005; Alpine & Hobday, 2007; Game et al., 2009; Briscoe et al., 2016). The rapid advancement of techniques and approaches available to study the dynamics of reef fish populations and assemblages creates opportunities to revisit and build on previous biogeographical knowledge (Ebach, 2013; Joly et al., 2014; Edgar et al., 2016). Expanding fields and tools include functional biogeography methods (Frainer et al., 2017; Olivier et al., 2018), molecular biology sampling techniques such as e-DNA (Joly et al., 2014; Kavanaugh et al., 2016; Edgar et al., 2016; West et al., 2021), as well as information technology and remote approaches (Edgar et al., 2016; Roberson et al., 2017). Applying these new methods to the study of an atypical biogeographical setting, such as the Galapagos, can improve our understanding of the role of ecological transition zones (Schilthuizen, 2000; Spector, 2002; Smith et al., 2005) and peripheral centres of speciation (Lessios & Robertson, 2006; Robertson et al., 2004; Bowen et al., 2013) for biodiversity maintenance. Indeed, there is much to learn about the drivers of diversity build-up through studying atypical environments, as demonstrated by the field of Island biogeography (MacArthur & Wilson, 1967; Whittaker et al., 2008; Santos et al., 2016; Jacquet et al., 2017).

The typical processes driving community structure in the tropics, such as species richness/habitat area relationship, do not apply well to the Tropical Eastern Pacific (Bellwood & Hughes, 2001; Parravicini et al., 2013). This region is largely independent from the rest of the Pacific due to the East Pacific Barrier (Robertson et al., 2004; Lessios & Robertson, 2006; Cowman & Bellwood, 2013b) and is characterized by high productivity and upwelling processes (Fiedler et al., 1991; Pennington et al., 2006; Fiedler & Lavín, 2017). The Galapagos further stands out in the Tropical Eastern Pacific, as it has a much wider range of habitats than the other island groups in the region (Robertson & Cramer, 2009), including sandy beaches and bottoms, mangroves, as well as around 300 shoals and seamounts (Smith, 2014; DPNG, 2014; Salinas-de-León et al., 2020). In addition, the Galapagos archipelago is characterized by much higher rates of endemism and comparably low numbers of eastward migrants compared to the rest of the Tropical Eastern Pacific Oceanic Province (Robertson et al., 2004; Robertson &

Cramer, 2009). The conservation efforts in the Galapagos archipelago have sheltered marine habitats from destructive practices and many taxa and functional groups which have declined globally, such as herbivorous fish or sharks, have a good status in the Galapagos (Edgar et al., 2011; Salinas-de-León et al., 2016, Chapter 3). This means that the Galapagos is likely a less disturbed site to investigate a wide range of biogeographical processes than other more populated regions. The above information highlights the unique value and the potential for further research in the Galapagos which will deepen our understanding of the dynamics influencing a species distribution, a key topic considering the implications of climate change in redistributing life on earth (Hoegh-Guldberg & Bruno, 2010; Poloczanska et al., 2016; Reygondeau, 2019).

6.2.2 Implications for pelagic biogeography research

The field of pelagic biogeography is becoming increasingly important due the growing awareness that the open ocean is underrepresented in conservation schemes (Alpine & Hobday, 2007; Game et al., 2009; Briscoe et al., 2016; Todorović et al., 2019; Boerder et al., 2019). The initial documentation of global scale distribution patterns followed by finer scale regional studies is a recurring process in the field of biogeography (Ebach, 2013) and the pelagic environment is no exception. Early efforts to produce a global bioregionalisation of the open ocean were mostly based on planktonic taxa (Backus, 1985; Beklemishev, 1966; Pierrot-Bults & van der Spoel, 1995) and have now been updated with broader taxonomic information (Spalding et al., 2012; Costello et al., 2017). However, small-scale pelagic biogeography studies have remained scarce compared to their benthic and coastal counterparts. My biogeography findings for the mid-water environment is one of the first to elicit coastal biogeography patterns based on in-situ fisheries-independent data of mid-water fish assemblages mainly comprised of bentho-pelagic and pelagic species. My results suggest three zones of subdivision of the coastal pelagic mid waters, one less than for the benthic environment. While my study is not strictly pelagic and is restricted to the coastal waters, we did sample a large proportion of the coastal pelagic fish assemblage. Hence, my work aligns with other studies, which generally find fewer subdivisions in the pelagic environment in comparable focal areas such as the Caribbean (Robertson and Cramer, 2014), the Tropical Eastern Pacific (Robertson and

Cramer, 2009) for non-endemic pelagic taxa, or on a global scale (Spalding et al., 2007, 2012; Costello et al., 2017). This is generally explained by the larger distribution range of pelagic species and dynamic oceanography of the open ocean (Costello et al., 2017). More regional scale pelagic biogeography studies are needed to mitigate the Wallacean shortfall (Whittaker et al., 2005) which hinders efforts to improve the conservation of pelagic resources. This is particularly relevant as a growing number of studies indicate that, in small islands settings, a sustainable exploitation of pelagic resources may be preferable to exploiting demersal taxa, allowing to meet food security need while accounting for the preoccupying declines of benthic resources. (Bell et al., 2018; Hanich et al., 2018; Wabnitz et al., 2018).

One of the key concerns of pelagic biogeography is how to operationalize the protection of the open ocean (Spalding et al., 2012; Costello et al., 2017; Todorović et al., 2019). The challenge of accurately sampling pelagic fish species, due to their heterogeneous distribution (Angel, 1993; Fréon & Misund, 1999), has long limited using these taxa for in-situ biogeography studies (Spalding et al., 2012). Pelagic camera systems provide a way forward (Heagney et al., 2007; Santana-Garcon, 2014; Santana-Garcon, Newman, et al., 2014), but they are not a panacea. As an alternative, technological improvements have sparked a growing interest in biogeochemical provinces as a means to provide meaningful subdivisions of the pelagic habitat (Longhurst, 2007; Vichi et al., 2011; Reygondeau et al., 2013). This relies on the assumption that high trophic level biological communities emerge coherently as a product of oceanographical processes that include temperature, bathymetry, chlorophyll a concentration, surface temperature, and salinity (Vichi et al., 2011). Dynamic eddies zones and steep temperature gradients have also been used to identify pelagic habitat (Etnoyer et al., 2004). However, using environmental data to model pelagic habitat does require validation with in-situ biological data (Roberson et al., 2017). Molecular genomics technique such as eDNA may provide enough resolution to generate species presence/absence data to confirm biogeographical provinces (Joly et al., 2014; Edgar et al., 2016; West et al., 2021). These techniques do not yet provide relative abundance or biomass data in the same way that pelagic stereo-video systems do. Stereo-video relative abundance data may have greater application for management because fine biogeographical patterns may have applications to predict patterns of fisheries resource exploitation (Chevallier et al., 2021). Overall, studies concerned with the distribution of pelagic taxa need to incorporate their inherent dynamic nature (Angel, 1993; Kavanaugh et al., 2016; Todorović et al., 2019). This is best illustrated by the rapid rise of the field of real-time dynamic ocean management to conserve the pelagic environment and the highly mobile taxa present there (Maxwell et al., 2015; Lewison et al., 2015; Hazen et al., 2018; Ortuño Crespo et al., 2020; Barlow, 2021). This type of management rapidly adapts to changing conditions in the resource system managed as opposed to permanent or static measures which do not change once established unless revised. Considering that climate change is likely to impact the distribution of the most mobile taxa first (Pinsky et al., 2013; Sunday et al., 2015; Frainer et al., 2017, Chapter 4), the field of pelagic biogeography will yield crucial insights to anticipate future changes in species distribution, supporting adaptive management of the open ocean.

6.2.3 Dynamics of fish distributions in the climate change era

Biological records demonstrate that the biogeographical processes at play in the oceans are dynamic (Briggs, 2003; Floeter et al., 2008; Cowman et al., 2017). There has been massive biogeography rearrangements in the past (Cowman et al., 2017) and climate change may well be leading to another dramatic wave of biodiversity redistribution (Hoegh-Guldberg & Bruno, 2010; Poloczanska et al., 2016; Reygondeau, 2019). As climate change progresses, the world’s oceans are predicted to warm up, become more acidic, and oxygen-depleted (Pörtner, 2012; Fiedler & Lavín, 2017; Reygondeau, 2019). Fish taxa respond closely to these changes (Pinsky et al., 2013; Sunday et al., 2015) due to their restrictive physiological oxygen requirements and thermal tolerance (Pörtner & Farrell, 2008; Pörtner, 2012; Payne et al., 2016). Combined with the impact of climate-change on primary productivity and foraging dynamics, this leads to important range expansions or contractions which may fundamentally modify food webs and community structure on a global scale (Perry et al., 2005; Dulvy et al., 2008; Hoegh-Guldberg & Bruno, 2010; Frainer et al., 2017). One of the main threats to communities under global warming is biotic homogenisation, where cold-water biotas grow increasingly similar to warm-water biotas due to non-native and cosmopolitan species taking over specialist and short-range native taxa (Blois et al., 2013; Magurran et al., 2015; Reygondeau, 2019) . The tropical and temperate regions are of particular concern (Asch et al., 2018; Reygondeau, 2019; Lam et al., 2020a) due to higher risks of species extirpation (Pörtner, 2012; Payne et al., 2016; Reygondeau, 2019) or intrusion (Sunday et al., 2015; Frainer et al., 2017; Reygondeau, 2019). In the Tropical Eastern Pacific, the response of marine ecosystems to the temporary warming and primary productivity decrease during ENSO may give us a proxy for how they may respond to climate change in the future. My results have shown that even moderate environmental changes are associated with significant fluctuations in community structure (Chapter 4), which may have major implications if environmental fluctuations are magnified in the future (Cheung & Frölicher, 2020). While the direction of climate-related environmental changes in the Tropical Eastern Pacific remain debated (Belmadani et al., 2014; Rykaczewski et al., 2015), growing evidence suggests that the effects may include increased temperature and acidity, along with decreased primary productivity due to increased stratification and weakened upwelling dynamics (Deser et al., 2010; Fiedler & Lavín, 2017; Manzello et al., 2017). Vecchi and Soden (2007) suggest that ENSO-like conditions may become the default state in the Tropical Pacific which may dramatically affect the marine environment in the region (Fiedler & Lavín, 2017). Regional studies in the Eastern Pacific have already documented wide-spread changes in phenological events (Asch, 2015) as well as a major temperate community restructuring associated with a synergetic shift in temperature and productivity (Holbrook et al., 1997). However, the near absence of long-term climate change studies in the region (Richardson et al., 2012) highlights an important research gap. Improving our understanding of the future changes in this region will be crucial to develop adequate mitigation and adaptation management measures.

There are several reasons why the Galapagos Islands represent a hotspot to monitor the effects of climate change and gather early insights into ecosystem response to warming (Hobday & Pecl, 2014; Salinas-de-León, Andrade, et al., 2020). Regional environmental conditions changes, including above-average warming (Hobday & Pecl, 2014) and acidification (Raven et al., 2005; Manzello et al., 2017) may lead to climate change effects becoming apparent much sooner in the Galapagos archipelago (Hobday & Pecl, 2014). In addition, changes to community structure under climate change may be most visible in regions with marked biogeographical patterns (Whitfield et al., 2016; Frainer et al., 2017). The marked assemblage composition and the distinct biological communities I found across Galapagos bioregions (Edgar et al., 2004, Chapter 2) fit this profile well. In this context, it appears particularly important to monitor changes to the Far North and Western bioregions, as they will likely exemplify the expected ecosystem effects of climate change. The tropical Far North may experience extirpation of species and local extinctions as temperature conditions exceed their thermal tolerance (Pörtner, 2012; Payne et al., 2016; Reygondeau, 2019), and the reduction of coral habitat may well further reduce species richness (Bellwood & Hughes, 2001; Bellwood et al., 2005). By contrast, the cold and productive Western bioregion may highlight the impact of a progressive decrease in productivity and a simplification of food webs (Reygondeau, 2019). Monitoring megafauna populations will be important as they are intimately linked with primary productivity dynamics in this part of the archipelago (Valle et al., 1987; Salazar & Denkinger, 2010; Wolff & Gardener, 2012). This region may also be progressively colonized by species whose establishment is facilitated by warming temperatures (Sunday et al., 2015; Frainer et al., 2017; Reygondeau, 2019). As the Galapagos archipelago hosts a high percentage of endemics (Robertson, 2001; Robertson & Cramer, 2009; Valle, 2013), including the epinephelids *Mycteroperca olfax* (regional endemic) and *Paralabrax albomaculatus* (local endemic), observed changes to these taxa will allow validating the hypothesized higher-sensitivity of short-range endemics to climate change (Sunday et al., 2015). Climate change may well lead to a homogenisation of environmental conditions across Galapagos bioregions, leading to a loss of some the unique characteristics of marine communities in the archipelago. This will likely reduce the long-term attractiveness of the islands and negatively affect the tourism sector and well-being of the local populations, highlighting the need to incorporate these effects into management (McLean et al., 2018).

The compounding effect of climate change and fishing is one of the most serious threats to marine biodiversity globally (Folke et al., 2004; Wernberg et al., 2011; Ainsworth et al., 2011; Staudt et al., 2013; Hoey et al., 2016; Fu et al., 2020). The tropics will likely undergo some of the largest drops in fish biomass in response to climate change under a business as usual scenario, with a decrease in biomass available to fisheries which may range from 15% up to 40% (Cheung et al., 2010; Asch et al., 2018; Lam et al., 2020b). This will have serious consequences for fisheries management and food security across the Pacific (Barnett, 2011; Reygondeau, 2019; Lam et al., 2020b). The large fluctuations in pelagic fish biomass I observed during the moderate 2015-16 ENSO (Chapter 4) may provide some insights into what the Galapagos could permanently look like by the end of the century under a business-as-usual climate change scenario with significant temperature increase. For example, a shift to a prevailing warm climate phase in the North Atlantic likely exacerbated by fishing, abruptly restructured small-pelagic fish populations with large declines in certain regions, likely having major implications for benthic and pelagic ecosystem functioning in this area (McLean et al. 2018). Synergistic effects of climate change and decreased top-predators populations (Estes et al., 2011; Hunsicker et al., 2011; Aschan et al., 2013) may further jeopardize the Galapagos marine environment. Looking at the status of epinephelid populations across the Galapagos Marine Reserve, I found that they are the most impacted taxa with several species displaying concerning maturity metrics status (Chapter 3). This is a real problem as fish communities where the role of keystone top-predator is diminished, through reduced biomass and truncated age-structure, typically display greater variability and sensitivity to environmental fluctuations (Beddington & May, 1977; Hsieh et al., 2006; Anderson et al., 2008; DeMartini et al., 2008), impaired reproductive potential (Longhurst, 2002; DeMartini et al., 2008; Marshall et al., 2019) and reduced genetic diversity (Baskett et al., 2005; Kenchington et al., 2003; Baskett & Barnett, 2015). Hence, the combined effect of fishing and climate change may continue to erode the resilience of Galapagos marine communities unless strong management actions are implemented to restore ephinephelids and preserve key piscivorous reef species. Failing to address this situation and safeguard the resilience of the Galapagos Marine Reserve may result in additional catastrophic regime shifts (Folke et al., 2004; Hsieh et al., 2005; de Young et al., 2008), comparable to the massive habitat restructuring of subtidal habitat which followed the 1982-83 event in the Galapagos archipelago (Edgar et al., 2010). The dire ecological consequences of trophic downgrading and regime shifts (Hughes, 1994; Scheffer et al., 2001; Hughes et al., 2005; Estes et al., 2011) have driven an exponential growth in research to predict, detect, and prevent them (Hughes et al. 2013; Hawkins et al., 2015). This reveals that the erosion of resilience and ecosystem function often occurs at a slow pace, making regime shifts difficult to detect and account for in management (Hughes et al. 2013a, Hughes et al. 2013b). In the face of the ecological complexities associated with regime shifts and climate change, the best management strategy is to mitigate cumulative impacts, adopt a precautionary approach, and manage ecosystems to optimize resilience.

6.2.4 Role of MPAs for marine resilience and implications for Galapagos zoning and management

A representative network of MPAs is essential to maintain resilient marine communities in Galapagos (Allison et al., 1998; Gell & Roberts, 2003; Roberts et al., 2005, 2017; Edgar et al., 2018). Functional MPAs maintain old-growth age structure in fish and insure against deleterious evolutionary effects of fishing and mismanagement (Kenchington et al., 2003; Baskett & Barnett, 2015; Barnett et al., 2017). In addition, there is growing compelling evidence for the role of MPAs to support fish populations in adjacent exploited areas (Roberts, 2001; Harrison et al., 2012; Marshall et al., 2019), in particular when conventional fisheries management is failing (Buxton et al., 2014). MPAs can also provide opportunities for scientific research (Edgar et al., 1997; Angulo-Valdés & Hatcher, 2010), and may be useful to study the effects of climate change without the coumpounded effect of fishing. However, MPA networks need to be biogeographically representative to provide adequate protection to all ecosystems and functional processes (Lourie & Vincent, 2004; Fernandes et al., 2005; Whittaker et al., 2005). My bioregionalisation of the Galapagos reef fish communities support the claim by Edgar et al. (2004) that the Galapagos 2000 zoning scheme left the Far North and Western bioregions underrepresented. Since the revised Galapagos zoning was not enacted (Ministerio del Ambiente del Ecuador, 2018), including the proposed Darwin and Wolf sanctuary, the shortfalls remain. Under the 2000 zoning, less than 1% of the GMR is under strict no-take management, a sharp contrast with the Great Barrier Reef Marine Park which protected 20% of each bioregion as no-take zones following the restructure of the local Marine Spatial Planning (Day et al., 2000). While all Galapagos bioregions require improved protection, the Far North is particularly in need for strong and stable protection of the reef ecosystems. Indeed, the last functional remnants of the Galapagos coral reefs are found in this region (Glynn et al., 2015; Holbrook et al., 2017; Riegl et al., 2019). These reefs need optimum marine community functioning in order to stand the chance to survive in front of the threats facing corals in the TEP (Manzello, 2010; Edgar et al., 2011; Manzello et al., 2017). Yet, despite unrivalled shark biomass there, the piscivorous fish populations have been markedly impacted (Salinas-de-León et al., 2016; Chapter 3) destabilizing the reef ecosystem (Hsieh et al., 2006; Anderson et al., 2008). There is clear evidence that even moderate fishing effort over short period can cancel out the effects of protection and significantly affect fish population (Jupiter et al., 2012; Russ & Alcala, 1996, 2003a). Birkeland (2017) pointed out that considering the generally low productivity of coral reefs, they are not capable of withstanding high fishing efforts in the long term. Considering the unique ecological value, and economic importance of Darwin and Wolf islands to the local tourism economy (Salinas-de-León et al., 2016) and the very limited area of fishing grounds (Snell et al., 1996a), they should realistically not support any kind of fishing activity targeting reef species. Due to their isolation and susceptibility to poaching, a solution may be to follow regional best-practice for high-value oceanic outposts, such as that of Cocos Island National Park (Friedlander et al., 2012) and Malpelo Island Sanctuary (Quimbayo et al., 2017; Claudino-Sales, 2019). Both locations are considered highly protected compared to the Galapagos Far North where fish assemblages reflect the low-protection status of the site (Edgar et al., 2011). In Cocos Island National Park, a complete fishing ban and a permanent warden presence maintains piscivorous fish populations. (Friedlander et al., 2012) although the island is not sheltered from the impact of illegal fishing (White et al., 2015). Implementing a strong protection in Darwin and Wolf would require to improve the governance and capacities of the Galapagos National Park, as closing the Islands to the local fishers but failing to adequately enforce such measures may increase their exposure to illegal, unreported, and unregulated fisheries occurring in the region (White et al., 2015; Arias & Pressey, 2016; Claudino-Sales, 2019). An alternative would be to find ways to maintain some level of fisheries for pelagic species in the Far North while protecting the reefs (Grober-Dunsmore et al., 2008) and vicinity of the Islands, although this would also require strong governance capacities and may not be desirable due to the risks it poses to the large shark populations in this area (Salinas-de-León et al., 2016). The future full protection of Darwin and Wolf was even agreed upon in the

2000 provisional zoning agreement elaborated by managers and fishers through the Participatory Management Board (Heylings et al., 2002).

6.2.5 Galapagos fisheries management beyond the boundaries of no-take zones

While well managed no-take zones are needed to preserve the long-term status of Galapagos marine ecosystems, there are governance obstacles limiting their effectiveness. While I found marginally larger sailfin grouper (*Mycteroperca olfax*) individuals within conservation no-take zones, tourism no-take zones were not distinguishable from fishing zones (Chapter 3). Around the world, well-documented cases of successful grouper populations recovery indicate that such taxa often exhibit the strongest and clearest response to protection in well managed no-take zones (Russ & Alcala, 2003b; Russ et al., 2005; Edgar et al., 2014; Giakoumi et al., 2017; Friedlander et al., 2017). This clearly illustrates that Galapagos no-take zones have not provided effective protection for *Mycteroperca olfax*, 15 years after the establishment of the first zoning. Similarly, Buglass et al. (2018) found that the Galapagos no-take zones had failed to conserve lobster populations in the Galapagos archipelago. Globally, many MPAs also fail to fulfil their mandates (Gill et al., 2017; Giakoumi et al., 2018; Lacarella et al., 2021). In a meta-study of 87 MPAs, Edgar et al. (2014) documented that 59% could not be distinguished from fished adjacent areas. In another meta-analysis of the performance of large-scale MPAs around the world, the Galapagos Marine Reserve ranks poorly, with declining trends in fisheries and local well-being (Ban et al., 2017). Several factors may be responsible for the ineffectiveness of the Galapagos no-take zones, including lack of enforcement, low compliance by fishers, failure to engage stakeholders and community in MPA creation and management, lack of legitimacy and institutional failures (Ban et al., 2017; Dehens & Fanning, 2018; Giakoumi et al., 2018; Humphreys & Clark, 2020; Lacarella et al., 2021,Strati, 2021). MPAs being too small or lacking connectivity can also lead to MPAs not meeting their objectives (Edgar et al., 2014; Goetze et al., 2021). In the Galapagos, lack of legitimacy and stakeholder engagement (Burbano et al., 2020; Burbano & Meredith, 2020), institutional shortfalls (Jones, 2013; Gill et al., 2017; Buglass et al., 2018), and a lack of common sense of resource ownership (Hearn, 2008) are likely the prime reasons why reserves are not meeting their objectives. In 2015 the participatory management board, which was the main mechanism for stakeholder engagement and collaboration, was dissolved (Llerena et al., 2017), which is indicative of the divide between managers and fishers. To remediate these issues, the way forward is to improve the governance of the Galapagos Marine Reserve (Ban et al., 2012; Grafton et al., 2008; Rice et al., 2012; Weigel et al., 2014). This will require finding ways to re-engage and collaborate with the community (Rice et al., 2012; Di Franco et al., 2016; Giakoumi et al., 2018; Balata & Williams, 2020) as well as strong local leadership to generate a real sense of stewardship (Schultz & Fazey, 2009; Rice et al., 2012; Watson et al., 2014; Giakoumi et al., 2018). Clarifying the role and function of no-take zones is also important to improve their acceptance, including, being explicit that their primary role is that of managing biodiversity and resilience maintenance (Jones, 2007; Barnett & Baskett, 2015).

6.2.6 The Galapagos open ocean: an asset for Galapagos fisheries transition

There is a strong rational to promote and develop sustainable pelagic fisheries in the Galapagos to redirect fishing effort away from declining reef species. First, the oceanographic setting of the Galapagos Islands region supports very productive waters with numerous upwelling systems (Barber & Chávez, 1986; Fiedler et al., 1991; Palacios, 2004; Wolff & Gardener, 2012), providing extensive fishing grounds. The very high productivity of the open ocean is one of the reason why they allow a much greater export of fish biomass for pelagic fisheries compared to reef systems (Nixon, 1982; Birkeland, 2015, 2017). Pelagic species are also characterised by life-history traits that generally makes them more resilient to exploitation (Weng & Sibert, 2000; Choat & Robertson, 2002; Roeger et al., 2016), although their exploitation does require careful management (Pikitch et al., 2012; Pikitch et al., 2014). They are typically fast growing, mature early, and have short life spans when compared to reef species. My pelagic stereo-BRUVs data (Chapters 2, 3, and 4) reveals that many species of small and large pelagic fish could be candidates to redirect fishing effort, although a dynamic management approach (Lewison et al., 2015; Maxwell et al., 2015) would be needed during ENSO year to account for decreased pelagic species abundance

(Chapter 4), especially during the warm El Nino phase. By contrast, reef species such as epinephelids, are slow growing, long-lived, and typically mature late (Coleman et al., 2000; Choat & Robertson, 2002; Andrews et al., 2011), making them much less forgiving to mismanagement, as their recovery can take a very long time (Abesamis et al., 2014; McClanahan, 2014; McClanahan & Graham, 2015). This is problematic as they have historically received a large part of the fishing effort geared towards export (Reck, 1983; Usseglio et al., 2016). Reef species are also the go-to species for plate-size fish in tourist restaurants around the islands. For example the scorpion fish Pontinus clemensi, a mesotrophic species with a conservative life history (Marin Jarrin et al., 2018), has now replaced *Mycteroperca olfax* on most display stalls. Considering the growing Galapagos population and tourism (Epler, 2007), it only makes sense to develop a long term strategy leveraging the natural pelagic assets of the archipelago. For example, restaurant menus in Hawaii are now largely dominated by open ocean species, as collapsed reef resources forced a move away from traditional species (Van Houtan et al., 2013). A similar situation may well occur in Galapagos, suggesting that a proactive precautionary approach is the way forward. Several authors argue that the sustainable exploitation of pelagic resources is key to the long-term sustainability and food security of islands communities in the Pacific (Albert et al., 2014; Bell et al., 2015, 2018; Roeger et al., 2016). Pelagic fisheries also allows for the implementation of right-based fisheries management systems centred around FADs (Albert et al., 2014; Sharp, 2014; Bell et al., 2015; Bell et al., 2018). Pilot FAD program have been trialled in Galapagos, but need more support to demonstrate the real potential of this tool as well as conditions for their appropriate use (Moina et al., 2018). Bulk harvesting of near-shore pelagic may also provide a long-term sustainable option (Sokimi, 2014; Bell et al., 2018) as demonstrated by a three decades long stable exploitation of these species in Hawaii (Weng & Sibert, 2000). Other techniques such as pole and line (Sokimi, 2014) or trolling (Boggs & Russel, 1992; Mahon, 1995; Sharma et al., 2003) may provide viable low-bycatch alternatives to account for the prevalence of marine mega-fauna in the Galapagos. Overall there are many options to explore as an alternative to long-lines which have been repeatedly pushed by the fishing sector to exploit large pelagic species which are clearly incompatible with the conservation frameworks (Cerutti-Pereyra et al., 2020). A long-term vision for a sustainable use of Galapagos marine resources aligned with conservation and food security objectives, such as that of Palau (Palau National Marine Sanctuary Act, 2015; Wabnitz et al., 2018), must not overlook the huge pelagic resources asset in the archipelago.

6.2.7 Applications of market-based management regulations in the Galapagos context

The implementation of market regulations may provide a critical tool to mitigate the over-exploitation of piscivorous fish taxa in the Galapagos (Bellwood et al., 2004; Claudet et al., 2010; Collette et al., 2011; Birkeland, 2017) as an alternative or complement to the existing management. Based on my maturity metrics data for epinephelid species (Chapter 3), it is clear that these species urgently require improved management to increase the proportion of mature individuals and mega-spawners in the population. Indeed, when old-growth fish are missing, several deleterious effects may ensue, including, reduced population productivity, decline in trait diversity, loss of resilience to environmental fluctuations, as well as altered community stability (Barnett et al., 2017). This is especially problematic in the case for *Mycteroperca olfax*, which may have also seen a seven times overall reduction in biomass compared to historical baselines (Burbano et al., 2014), hence losing its role as keystone species (Eddy et al., 2019). In addition, no-take zones do not appear to have a major effect in restoring mature age-structure for the species (Chapter 3). This species forms transient spawning aggregations (Salinas-de-León et al., 2015), a period during which mature and mega spawners fish perform important migrations (Sadovy de Mitcheson & Colin, 2012a) and may leave no-take zones. This means that the largest individuals may be fished at unprotected spawning sites as was documented at Wolf Island (Salinas-de-León et al., 2015). Despite concerns that *Mycteroperca olfax* has been over-exploited dating back to the 80s (Reck, 1983), no species specific measures has been implemented to halt its decline in nearly four decades. Therefore, a market regulation, such as a ban on export of species with conservative life history traits, may mitigate institutional failures and prevent further population decrease. This type of measure could also allow over-coming the lack of common resources ownership, which was identified as an important block to implementing technical fisheries management measures in the Galapagos Archipelago (Hearn, 2008). Market regulations can be a powerful tool to manage fishing pressure, as access to markets has often been a key driver for the decline in reef fish populations in other parts of the world (Muldoon et al., 2016; Sadovy de Mitcheson et al., 2017; Khasanah et al., 2019). In the Galapagos, a significant export of salted-dried reef fish supplies ingredients for the “fanesca” (Zimmerhackel et al., 2015; Usseglio et al., 2016; Pontón-Cevallos et al., 2020), a dish served during Easter celebrations, which can sometimes gather nearly a million participants (Ministerio de Turismo, 2013, 2019; Moeller, 2017). *Mycteroperca olfax* has historically been the main species supplying the salted-dried fish export (Usseglio et al., 2016), although other species became progressively incorporated into the trade (Merlen, 1995). Easter celebrations also drive the over-exploitation of the Andean Wax Palm in continental Ecuador (Galárraga & Joselo, 2012), questioning the long-term sustainability of such supply chains as Ecuador’s population grows and demand goes up. In the face of unsustainable demand, several islands nations have already implemented strong market regulations, including total bans, on the export of fragile reef species such as groupers or wrasse (Birkeland, 2017; Khasanah et al., 2019). In Palau, strong local leadership, and the realization that exports of natural resources was jeopardizing the long-term health of the marine environment led to strong decisions being taken to ban all export of reef species (Birkeland, 2017). In the Galapagos, market drivers were associated with a historical collapse of sea cucumber stocks, which finally led to decisions to close the fishery (Merlen, 1995; Wolff, Schuhbauer, et al., 2012; Ramírez-González, Moity, Andrade-Vera, & Reyes, 2020). In the case of finfish species, declines have been gradual, with shifting baseline syndrome occurring over decades (Burbano et al., 2014). This slow decline is much less spectacular than the sea cucumber population collapse and may be the reason why building enough political to do something about it has been so difficult (Hughes et al., 2013). While the island’s complex socio-political situation may not allow implementing such strong measures for epinephelids fisheries, restricting their export may provide an alternative tool to restore and maintain keystone species populations. This would support a diversification of fisheries management tools (de Young & Charles, 2008; Jones et al., 2013; Jones, 2014) congruent with the biology of each species (Birkeland, 2017), and contribute to a long-term vision hinging on resilient Galapagos marine communities.

6.2.8 Spawning aggregations management and research gap

Conserving fish spawning aggregations may be the most effective way to maintain resilient fish populations in Galapagos (Sadovy de Mitcheson & Erisman, 2012; Heyman et al., 2019; Pittman & Heyman, 2020). In fact, it is argued that in a data-deficient context, such as in the Galapagos, preserving spawning migrations and aggregations is likely the single most important step for fisheries and biodiversity management (Erisman et al., 2017). Considering their fundamental ecological function (Johannes, 1978; Sadovy de Mitcheson & Colin, 2012a; Domeier, 2012) the importance to preserve them is recognized in multiple international marine management frameworks (Erisman et al., 2017), driving strong spawning aggregation conservation efforts in a number of countries (Erisman et al., 2018; Taylor et al., 2020; Acevedo et al., 2020). Despite the growing recognition of the key role of spawning, conservation efforts are generally considered to lag behind (Sadovy de Mitcheson et al., 2013; Russell et al., 2014; Erisman et al., 2017), with the most recent status report indicating that 55% of spawning aggregations are declining and 9% have been fully extirpated (Chollett et al., 2020). The status of groupers with aggregation-based reproductive strategy is particularly alarming as 25% of species risk extinction, or are considered near threatened, including *Mycteroperca olfax* (Sadovy de Mitcheson et al., 2013). Information gaps are important obstacles to improving the global conservation of spawning aggregations (Erisman et al., 2017; Grüss et al., 2014; Taylor et al., 2020), an issue exacerbated in temperate environments such as Galapagos since these regions are strongly underrepresented in spawning aggregation research efforts (Russell et al., 2014). My study on *Bodianus diplotaenia* spawning (Rastoin-Laplane et al., 2020, Chapter 5) and that of Salinas-de-León et al. (2015), are the only two publications focusing on these events in the Galapagos Archipelago. In addition, very little (if any) attention is given to the management of spawning aggregations in the current fisheries management framework of the Galapagos Marine Reserve (DPNG, 1998; Comisión Técnica Pesquera, 2009). This is in sharp contrast with other Mesoamerican regions where spawning aggregations conservation is framed as a cornerstone of fisheries management efforts (Erisman et al., 2018; Heyman et al., 2019; Acevedo et al., 2020). This is problematic as many species in the archipelago have congeneric species known to form spawning aggregations elsewhere (Heyman et al., 2004; Sadovy de Mitcheson et al., 2013) and direct targeting of spawning aggregations has already been documented in the Far North (Salinas-de-León et al., 2015). The lack of mature *Mycteroperca olfax* that I identified both inside and outside no-take zones (Chapter 3) could in fact be due to direct targeting of undocumented spawning aggregation sites in other bioregions. Further evidence of direct targeting of grouper spawning aggregations is found in historical photographs of fishing vessel decks filled to the rim with deep-sea groupers (*Epinephelus* spp., Salinas-de-León, pers. comm.). Groupers aggregations may be the most at risk in the Galapagos since these taxa are particularly susceptible to hook-and-line fishing (Robinson et al., 2015), a prevalent technique in the archipelago (Reck, 1983; Zimmerhackel et al., 2015; Pontón-Cevallos et al., 2020). This is further exacerbated since spawning aggregation fisheries may exhibit hyperstability (Erisman et al., 2011), where CPUE does not reflect fish abundance, suggesting fishers can fish out an aggregation without realizing its slow demise (Post et al., 2002). Protecting spawning aggregation sites has huge benefits and successful conservation stories demonstrate that this becomes feasible when strong stakeholder commitment and collaboration occurs (Waterhouse et al., 2020; Pittman & Heyman, 2020; Stock et al., 2021). Recent research further highlights the importance of protecting spawning aggregations and suggest these events represent “bottleneck” playing a major role in how fish populations will respond to climate change (Asch & Erisman, 2018). Support for this claim is found in marked changes to phenological events in the Eastern Pacific region (Asch, 2015). This means that spawning aggregations protection may be particularly important during ENSO, as spawners are particularly sensitive to heightened temperature (Pörtner, 2012; Asch & Erisman, 2018). Protecting spawning species is most effective through a combination of both spatial management measures such as spawning aggregation MPAs, and complementary measures such as seasonal closures, market restrictions, size limits, and harvest regulations (Sadovy de Mitcheson & Colin, 2012a; Russell et al., 2012; Grüss, Robinson, et al., 2014). This will ultimately be context-based and depend on the information available, suggesting that umbrella measures (i.e. sales ban, or seasonal closures) may be most appropriate until significant effort are deployed to identify and manage specific spawning aggregations sites in Galapagos (Grüss et al., 2014).

Considering the global increase in management efforts tailored towards spawning aggregations, and their irreplaceable ecological value, there is an urgent need to give these events appropriate attention within Galapagos management frameworks.

Developing and implementing effective and reliable spawning aggregations monitoring techniques is fundamental to their management (Russell et al., 2012; Sadovy de Mitcheson et al., 2020; Taylor et al., 2020). Ideally, survey tools need to be cost-effective and simple to implement, as capacities and budgets are often a limitation in monitoring efforts (Heyman, 2017; Acevedo et al., 2020; Taylor et al., 2020). My study applying stereo-video to *Bodianus diplotaenia* spawning aggregations, demonstrates that this technique can provide valuable information on the spawning stock, even based on an opportunistic encounter (Chapter 5). This suggests that more structured and planned stereo-video based approaches could yield robust data for the long-term monitoring of spawning aggregations. However, the uptake of stereo-video in the field of spawning aggregation research has arguably been very slow, as to my knowledge, only seven published articles have used stereo-video for spawning aggregations in nearly two decades (Rand et al., 2006a; Salinas-de-León et al., 2015; Robinson et al., 2017; Daly et al., 2018; Rastoin-Laplane et al., 2020; Sadovy de Mitcheson et al., 2020; Williams et al., 2021). Until now, most monitoring efforts have been UVC based (Heyman et al., 2004; Pet et al., 2006; Hughes et al., 2020; Acevedo et al., 2020), and when lengths were not visually estimated, estimates have generally been based on laser callipers (Heppell et al., 2012; Heyman, 2017; Stock et al., 2021). Nevertheless, in a recent workshop presenting frontier tools for the study of spawning aggregations, several conservation groups expressed their interest in stereo-video techniques (Taylor et al., 2020). These groups generally perceive stereo-video as a complementary tool rather than a go-to main survey method. This perception and the slow up-take of stereo-video for spawning aggregations research is likely owing to the lack of methods and feasibility studies comparing stereo-video to other tools. Diver-operated stereo-video offers important advantages of UVC abundance counts, particularly in large groups of fish due to the possibility to standardize sampling area and permanent records (Rastoin-Laplane et al., 2020). Considering that spawning aggregations only host a few species at most, the analysis process is much reduced compared to typical stereo-DOVs analysis of coral reef transects based on my experience. Perhaps the fact that most spawning aggregations have suffered severe declines and abundance are reduced renders UVC counts usable for now. These counts may become a lot less reliable for groups of thousands of fish which is common for healthy grouper aggregations (Mourier et al., 2019; Jublier et al., 2020; Acevedo et al., 2020). Length-measurements also provide key information to detect recovery trends as demonstrated by recent research in Palau (Sadovy de Mitcheson et al., 2020), and the Caribbean (Stock et al., 2021), with the former study using stereo-video while the latter used laser-callipers. Laser-callipers are currently being rolled out extensively across the Mesoamerican region and promoted through capacity building efforts (Acevedo et al., 2020). While laser-callipers can provide usable data (Heppell et al., 2012c; Stock et al., 2021), they are limited by the need to have fish oriented perpendicular to the camera and laser system and working with one individual at a time (Heppell et al., 2012c), thereby limiting the possibility to rapidly build large lengths samples. In addition, the risk of blinding fish with laser callipers is a valid concern, which may not allow implementing this technique in countries with strong animal ethics requirement such as Australia (Euan Harvey, pers. comm.). Stereo-video is likely to overcome the above limitations and significantly cut down post-processing time since software-based measuring is an easy process and allows marking down measured individuals to avoid pseudo-replication (Rastoin-Laplane et al., 2020). The field of acoustic monitoring of spawning aggregations, both passive and active, is also taking major strides forward. While limitations remain and techniques still require refining (Egerton et al., 2017; Wilson et al., 2019; Allen et al., 2020), estimates of abundance, length, and biomass are becoming increasingly accurate (Rowell et al., 2017; Egerton et al., 2018). Acoustic techniques also have applications for extreme size aggregations such as for the Gulf corvina in Mexico, where over a million fish aggregate (Rowell et al., 2017), rendering video-based counts impractical. Acoustic approaches may also be used to cover extensive areas for coarse grain monitoring or spawning aggregations detection work (Rowell et al., 2012; Allen et al., 2020; Caiger et al., 2020; Chérubin et al., 2020), cases where stereo-video is not a viable option. Overall, stereo-video remains well underrepresented in spawning aggregations research, highlighting a clear need for comparative feasibility surveys to demonstrate the applicability of such tools for the long-term monitoring and study of spawning.

6.3 Limitations and opportunities for future research

While my biogeography chapter confirmed historical patterns described by Edgar et al. (2004) and translated those findings to the coastal pelagic environment (Chapter 2), I did not assess the drivers of biogeography patterns. In the future, it would be useful to conduct an evaluation of fish community drivers like this was done in the Tropical Eastern Pacific (Mora & Robertson, 2005), Brazil (Floeter et al., 2001), or the Caribbean (Bouchon-Navaro et al., 2005). This would elicit the specific roles of temperature, salinity, habitat type and area in structuring fish assemblages among bioregions. In particular, assessing the current match between fish assemblages and biogeochemical provinces (Longhurst, 2007; Vichi et al., 2011; Reygondeau et al., 2012) would be very useful, providing a basis to model biogeographical changes under warming scenarios (Reygondeau, 2019). Regarding changes under climate fluctuations, my biogeography chapter did not consider the potential implications of ENSO for the observed biogeographical patterns. While the biogeographical subdivisions were very clear and aligned with previous research, the specific assemblages may have been influenced by the warm conditions of ENSO in 2015. In all likelihood, ENSO would have blurred biogeographical subdivisions between the Far North, North, and Center-south bioregions, as Northern tropical species likely intruded further south than on non-ENSO year. The changes to the pelagic environment highlighted in my 2015-2016 inter-annual comparison suggest that some bentho-pelagic and pelagic taxa exhibited reduced abundance in 2015, which may have further influenced biogeographical patterns. The influence of ENSO on the West/Center-south subdivision may have led to reduced cold-water taxa in the Center-south while increasing the abundance of warm-temperate taxa in the Western region, potentially resulting in a neutral influence. The choice to use presence-absence data rather than relative abundance likely mitigated the influence of ENSO on biogeographical patterns, although ENSO may well have contributed to the less distinct coastal pelagic subdivisions I observed. Considering the important

ENSO-associated fluctuations in piscivorous taxa (Chapter 4), a worthwhile area of research would be to evaluate changes in functional biogeography (Frainer et al., 2017) during ENSO year. Evaluating how ENSO affects functional redundancy in the Galapagos archipelago would elicit which taxa maintain key ecosystem functioning during this time (Baltar et al., 2019; Alabia et al., 2020). This would highlight which species may require dynamic management measures during warming periods, a crucial consideration if such species have already declined in abundance due to fishing.

My length-based evaluation of Galapagos fish populations (Chapter 3) provided a one-off overview of their status across different management zones (i.e. tourism no-take, conservation no-take, fishing zones), but did not consider multi-year trends. A longer-term evaluation of individual no-take zones effectiveness may reveal more information on the asymmetrical patterns I observed across taxa (e.g. *Mycteroperca olfax* vs *Lutjanus argentiventris*) and management status (i.e. tourism no-take vs conservation no-take). This would be best achieved with a sampling design including small and large no-take zones in each bioregions with a corresponding set of control sites in adjacent fishing zones (Smokorowski & Randall, 2017; Kerr et al., 2019). Including habitat as a variable may also take into consideration the biases in zone selection identified in the archipelago (Edgar, Bustamante, et al., 2004). Including different depth strata would facilitate evaluating how communities at different depth benefit from protection (Asher et al., 2017a, 2017b). This information will be important in the Galapagos since fishing effort is partly being redirected towards deeper water (Marin Jarrin et al., 2018). In addition, a recent MPA meta-analysis shows the importance of considering the depth factor when evaluating MPAs performance (Goetze et al., 2021). A long-term monitoring of Galapagos NTZs effectiveness will be crucial to assess the performance of the new zoning when the obstacles blocking its implementation are mitigated (Burbano et al., 2020; Burbano & Meredith, 2020). My length-based maturity metrics approach could provide a useful framework to inform MPA targets and prioritize management efforts, although it would require additional validation to become a tool trusted by managers. This includes identifying the species for which the method is best-suited and for which it should not be used. This means considering the life history of a species as well as their habitat preferences to determine the best spatial and temporal extent of sampling to obtain representative length samples. Additional consideration regarding the minimum sample size required is also needed. Indeed, Froese (2004) suggests that his indicators can be applied to a single fish although the approach is meant to be applied to catch data which typically comprises hundreds of individuals. If the maturity threshold values are calculated using empirical equations based on asymptotic size (Froese & Binohlan, 2000), the question of which source of information is optimum to determine asymptotic size needs to be addressed. In other words, how to mitigate the fact that Fishbase maximum length may sometimes reflect populations parameters estimated decades ago that may have changed due to fishing pressure (Hsieh et al. 2010). Once these points are dealt with, there is one idea of experimental design where the maturity metrics approach may prove useful. This would require selecting a spatial gradient of recreational fishing effort, such as a coastline with marked population gradient, to conduct stereo-video surveys. Species selection would need to include families of high interest for recreational fishers (e.g. serranids, lutjanids, labrid) as well as species of low interest (e.g. kyphosids, haemulids) both distributed along the entire coastline. Under such conditions, we can hypothesize a significant interaction between overall regional fishing effort and whether species are targeted or not. Highly prized families would see poorer maturity metrics levels in highly populated areas compared to areas with low fishing effort whereas non-targeted species would see unaffected maturity metrics levels regardless of the location. This study may help to illustrate the impact of recreational fishing (Freire et al., 2020), helping to improve the management of recreationally over-exploited species.

While my evaluation of the ecological effects of the Galapagos spatial management measures highlights their limitations, especially for *Mycteroperca olfax* (Chapter 3), additional research is needed to identify which alternative management options are best suited to the local context (Young & Gasser, 2002; Ostrom, 2007; Rice et al., 2012; Weigel et al., 2014). This seems particularly relevant considering the governance obstacles surrounding the spatial management reform (Burbano et al., 2020; Burbano & Meredith, 2020), and the recent structural changes to the participatory management regime in the Galapagos archipelago (Llerena et al., 2017). To identify alternatives to NTZs-based management, intergenerational scenario-based cost-benefit approaches may be well-suited (Sumaila, 2001, 2004), paying particular attention to trade-offs between current exploitative uses and long-term resilience and well-being in the islands. Scenarios could explore the long-term socio-economic effect of varying strength and combinations of measures (Gasalla et al., 2010; Pascal, 2011; Read, 2013; Rees et al., 2013). For example scenarios could investigate the present-day and long-term cost and benefits of i) technical measures, such as seasonal closures, harvest regulations of vulnerable finfish, or gear restrictions, ii) market based incentives and regulations, such as a free-market driven exportation-heavy future versus tight market restrictions with a focus on local economy, food security, and climate-resilience, following the example of Palau (Palau National Marine Sanctuary Act, 2015; Birkeland, 2017), or iii) the dominance of reef or pelagic taxa in the future portfolio of exploited species in the islands. Highlighting the winners and losers associated with the different management routes, or lack thereof, may improve the legitimacy of fisheries management in the archipelago, likely benefiting the long-term well-being of the wider Galapagos community.

My stereo-DOVs application to a fish spawning aggregation (Chapter 5) provides a useful reference point, but its scope remains limited. Indeed, I did not address temporal variability in spawning behaviour (Colin, 2012) and the number of fish I counted is around 300, well below the size of healthy grouper aggregations (Mourier et al., 2019; Jublier et al., 2020; Acevedo et al., 2020). The method would need to be scaled up to larger aggregations to evaluate its true potential and limitations against acoustic (Rowell et al., 2011, 2017; Egerton et al., 2018) and UVC (Sadovy de Mitcheson & Colin, 2012a; Sadovy de Mitcheson et al., 2020) alternatives. In addition, stereo-video systems may be mounted on remote operated vehicles (Schramm et al., 2020a, 2020b) to study spawning dynamics at greater depth and during dusk hours, two situations when diver-operated surveys become increasingly risky. Before applying monitoring programs to spawning aggregations sites in Galapagos, a significant effort will be required to identify spawning locations. A good starting point would be to leverage local ecological knowledge as fishers typically possess extensive empirical knowledge of spawning aggregations locations and timing (Johannes, 1978, 1981; Johannes et al., 2000). Alternatively, a combination of modelling approaches and scouting surveys may facilitate the discovery of multi-species aggregations sites (Egerton et al., 2017; Grüss et al., 2018; Heyman et al., 2019; Chérubin et al., 2020). Indeed, aggregation sites share marked topographic characteristics (Heyman et al., 2019), which allows identifying candidate sites via bathymetry glider surveys. Grüss et al. (2018) also used habitat modelling to identify regions most likely to host spawning aggregations in the Gulf of Mexico. This technique may be replicated in the Galapagos to narrow the extent of areas to scout. Based on the timing of known aggregations for similar or sister taxa in the wider region Tropical Eastern Pacific region (Aburto-Oropeza & Hull, 2008; Erisman et al., 2010), a passive acoustic glider survey could also detect aggregations based on courtship fish sounds (Chérubin et al., 2020). Confirming the presence of spawning aggregations at candidate sites will then require ground-truthing via diving surveys. I recommend that these survey teams carry a stereo-DOVs system in case of a successful encounter with an aggregation. Finally, there is a need for a greater integration of the Galapagos managers and fishery scientists to the regional collaborative effort to conserve fish spawning aggregations (Heyman, 2017; Taylor et al., 2020; Acevedo et al., 2020).

6.4 Closing remarks

The biogeographical setting of the Galapagos Islands highlights their unique ecological and conservation value on a global scale. The development and application of new sampling techniques for the study of marine communities will help refine our understanding of life's distribution in the oceans. Yet, the unique oceanographic characteristics of different locations may also exacerbate sensitivity to heightened environmental fluctuations and anthropogenic impacts. Business-as-usual climate change scenarios would likely cause fundamental changes to the Galapagos islands as we know them today. In this context, it is crucial to apply precautionary approaches to manage the Galapagos marine environment and mitigate the risk of unforeseen regime shifts due to cumulative effects of fishing and climate change. Significant habitat shifts have already occurred, and further trophic downgrading could drastically affect local livelihoods, both among fishers as well as for those relying on tourism. To safeguard the resilience of the archipelago, improving the effectiveness and design of no-take zones will be necessary and efforts must be deployed to improve their legitimacy among fishers. However, to improve the status of fisheries in the Galapagos archipelago, the full range of existing management tools must be considered, in congruence with the biology of exploited species and the governance constraints of the Galapagos socio-ecological system. In particular, the deficit of management measures centred on spawning aggregations must be addressed. Leveraging the major collaborative research networks on fish spawning aggregations in the Mesoamerican region would help improve their conservation in Galapagos. Significant management reforms are necessary to pave the way towards long-term marine resilience and mitigate the alarming climate change projections in the region. Such reforms will only succeed under a strong sense of vision and stewardship from the rising generation of Galapagueños. Only then will the well-being of the Galapagos communities be preserved, and the magnificent Galapagos marine life enjoyed by the coming generations.

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Appendix A Statement of contributions

The study presented in **Chapter 2** is in review within the peer-reviewed journal "*Journal of Biogeography*"

Rastoin, E., Salinas-de-León, P., Acuña-Marrero, D., Goetze, J., Saunders, B.J., Ashe, H., Cundy, M., Garcia, R., & Harvey, E.S. Comparative biogeography of benthic and pelagic shore fish communities of the Galapagos: stereo-BRUVs surveys support the use of bioregions for management. *Journal of Biogeography. In Review.*

Authorship contribution statement

To whom it may concern, I, Etienne Rastoin, led and conducted the majority of the work for this chapter and contributions were as follow. **Etienne Rastoin**: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data curation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Pelayo Salinas-de-León**: Conceptualization, Methodology, Investigation, Resources, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition. **David Acuña-Marrero**: Investigation, Writing – Review & Editing. **Jordan Goetze**: Conceptualization, Methodology, Writing – Review & Editing, Supervision. **Benjamin J. Saunders**: Conceptualization, Methodology, Writing – Review & Editing, Supervision. **Hannah Ashe**: Investigation, Data curation, Writing – Review & Editing. **Megan Cundy**: Investigation, Data curation, Writing – Review & Editing. **Garcia Rodrigo:** Methodology, Software. **Euan S. Harvey**: Conceptualization, Methodology, Resources, Writing – Review & Editing, Supervision, Project Administration, Funding Acquisition.

Etienne Rastoin

Signed:

I, as a co-author, endorse that the level of contribution by the candidate stated above is appropriate.

Pelayo Salinas-de-León:

Signed:

David Acuña-Marrero:

Signed:

Jordan Goetze

Signed:

Benjamin J. Saunders:

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Megan Cundy:

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Euan S. Harvey:

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The study presented in **Chapter 3** is in preparation for submission for publication within the peer-reviewed journal "*ICES Journal of Marine Science*".

Rastoin, E., Salinas-de-León, P., Goetze, J., Saunders, B.J., Ayton, S., Zimmerhackel, J., Newman, S., & Harvey, E.S. Length-based metrics suggest limited benefits of Galapagos coastal no-take areas for reef fishes after 15 years of protection. *In preparation for submission.*

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The study presented in **Chapter 4** is in preparation for submission for publication within the peer-reviewed journal “*Scientific Reports*”.

Rastoin, E., Salinas-de-León, P., Goetze, J., Saunders, B.J., McKinley, S., Mattingly, A., Norris, C., Gosby, C., Garcia, R., & Harvey, E.S. **Fluctuations of Galapagos pelagic and benthic reef fish populations during the 2015-16 ENSO.** *In preparation for submission.*

Authorship contribution statement

To whom it may concern, I, Etienne Rastoin conducted the majority of the work for this chapter and contributions were as follow. **Etienne Rastoin**: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data curation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Pelayo Salinas-de-León**: Conceptualization, Methodology, Investigation, Resources, Writing – Review & Editing, Project Administration, Funding Acquisition. **Jordan Goetze**: Conceptualization, Methodology, Writing – Review & Editing. **Benjamin J. Saunders**: Conceptualization, Methodology, Software, Writing – Review & Editing. **Simon McKinley:** Investigation, Data curation, Writing – Review & Editing. **Mattingly Andrea:** Investigation, Data curation, Writing – Review & Editing. **Courtney Norris:** Investigation, Data curation, Writing – Review & Editing. **Gosby Corinna:** Investigation, Data curation, Writing – Review & Editing. **Rodrigo Garcia:** Methodology, Software, Writing – Review & Editing. **Euan S. Harvey**: Conceptualization, Methodology, Resources, Writing – Review & Editing, Project Administration, Funding Acquisition.

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The study presented in Chapter 5 was published within the peer-reviewed journal "*Estuarine, coastal, and shelf science"* on the 30th September 2020.

Rastoin, E., Goetze, J., Harvey, E.S., Acuña-Marrero, D., Fernique, P., & Salinas-de-León, P. (2020). A diver operated stereo-video approach for characterizing reef fish spawning aggregations: The Galapagos Marine Reserve as case study. *Estuarine, Coastal and Shelf Science, 243*, 106629. https://doi.org/10.1016/j.ecss.2020.106629.

Authorship contribution statement

To whom it may concern, I, Etienne Rastoin, conducted the majority of the work for this chapter and contributions were as follow. **Etienne Rastoin:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Jordan Goetze:** Methodology, Writing - review & editing, Supervision. **Euan S. Harvey:** Resources, Writing - review & editing, Supervision, Project administration. **David Acuña- Marrero:** Investigation, Writing - review & editing, Visualization, Funding acquisition. **Pierre Fernique:** Methodology, Software, Formal analysis, Writing - original draft, Visualization. **Pelayo Salinas-de- León:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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I, as a co-author, endorse that the level of contribution by the candidate stated above is appropriate.

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Appendix B Copyright statement

The study presented in Chapter 5 was published within the peer-reviewed journal "*Estuarine, coastal, and shelf science"* on the 30th September 2020.

As per the Elsevier authorship rights (below), I am authorised to include this article in my PhD thesis.

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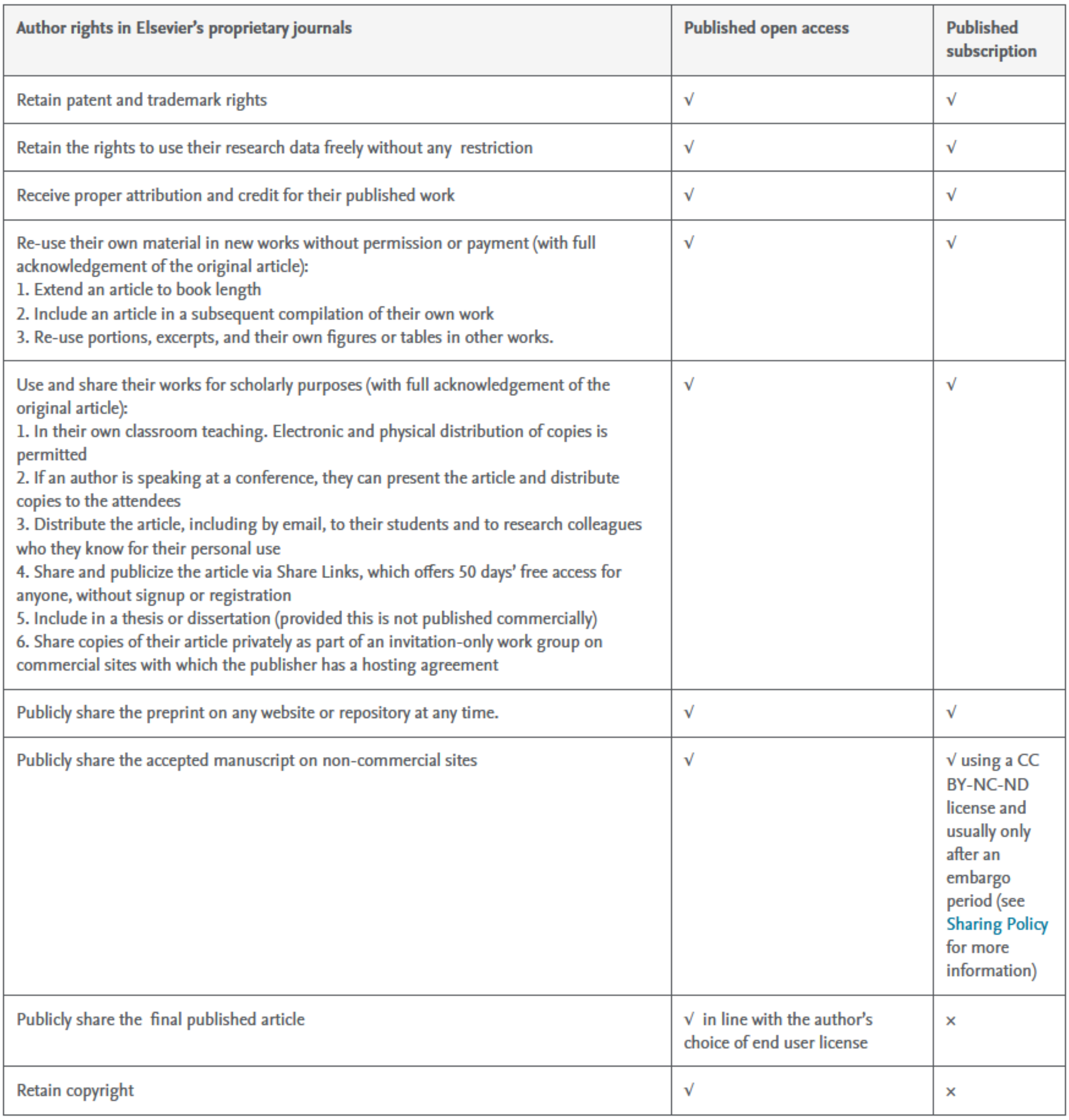

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Appendix C Frequency of occurrence of 2015 benthic BRUVs fish taxa (Chapter 2)

Table A.2 Benthic frequency of species occurrence across the four bioregions at single deployment level.

Species	Distribution	Far North	North	Center-SE	West
Abudefduf troschelii	TEP endemic widespread	-	-	2.8	-
Acanthocybium solandri	Indo-pacific	-	-	0.9	-
Acanthurus nigricans	Indo-pacific	26.7	-	-	-
Acanthurus xanthopterus	Indo-pacific	-	15.4	2.3	-
Aetobatus laticeps	TEP endemic widespread	-	19.2	8.8	3.2
Alectis ciliaris	Circumtropical	6.7	7.7	2.8	-
Alphestes immaculatus	TEP endemic widespread	-	-	4.1	-
Aluterus monoceros	Indo-pacific	-	3.8	31.8	3.2
Aluterus scriptus	Circumtropical	6.7	-	6.0	-
Anisotremus interruptus	TEP endemic widespread	20.0	50.0	32.3	-
Anisotremus scapularis	TEP Peruvian/Calif./Cortez	-	3.8	5.1	12.7
Apogon spp.	TEP endemic widespread	-	-	1.4	-
Archosargus pourtalesii	Galapagos endemic	-	-	3.2	-
Arothron hispidus	Indo-pacific	20.0	7.7	0.9	-
Arothron meleagris	Indo-pacific	13.3	-	4.1	-
Aulostomus chinensis	Indo-pacific	93.3	-	6.5	-
Balistes polylepis	Indo-pacific	93.3	88.5	51.6	11.1
Bodianus diplotaenia	TEP endemic widespread	93.3	69.2	68.2	52.4
Bodianus eclancheri	TEP Peruvian/Calif./Cortez	-	3.8	11.5	38.1
Bonitos	TEP widespread/Indo-P.	6.7	-	1.8	4.8
Bothus leopardinus	TEP endemic widespread	-	-	0.9	-
Calamus spp.	Galapagos end. /TEP wide.	-	-	53.9	27.0
Canthidermis maculata	Indo-pacific	60.0	15.4	1.8	-
Caranx caballus	TEP endemic widespread	6.7	11.5	11.5	-
Caranx lugubris	Circumtropical	33.3	15.4	0.5	-
Caranx melampygus	Indo-pacific	20.0	-	0.5	-
Caranx sexfasciatus	Indo-pacific	20.0	-	0.5	-
Carcharhinus falciformis	Circumtropical	6.7	-	-	-
Carcharhinus galapagensis	Circumtropical	60.0	-	44.7	31.7
Carcharhinus limbatus	Circumtropical	20.0	11.5	14.7	7.9
Caulolatilus princeps	TEP Peruvian/Calif./Cortez	-	-	24.0	81.0
Cephalopholis panamensis	TEP endemic widespread	20.0	11.5	8.8	-
Chaetodon humeralis	TEP endemic widespread	-	30.8	35.5	4.8
Chanos chanos	Indo-pacific	-	3.8	-	-
Chilomycterus reticulatus	Circumtropical	-	11.5	17.5	7.9
Chromis alta	TEP Peruvian/Calif./Cortez	-	-	12.4	49.2

Chromis atrilobata	TEP endemic widespread	26.7	-	2.3	11.1
Cirrhitichthys oxycephalus	Indo-pacific	6.7	3.8	4.1	1.6
Cirrhitus rivulatus	TEP Panamic/Cortez	-	-	0.5	-
Cratinus agassizii	TEP Peruvian/Calif./Cortez	-	-	7.4	7.9
Dermatolepis dermatolepis	TEP Peruvian/Calif./Cortez	53.3	15.4	3.7	-
Elagatis bipinnulata	Circumtropical	20.0	7.7	1.4	-
Enchelycore lichenosa	N/A	-	-	0.5	-
Epinephelus labriformis	TEP endemic widespread	60.0	23.1	41.9	36.5
Euprepocaranx dorsalis	TEP endemic widespread	-	-	0.5	-
Fistularia commersonii	Indo-pacific	46.7	53.8	32.3	-
Galeocerdo cuvier	Circumtropical	-	7.7	8.8	4.8
Girella freminvillii	Galapagos endemic	-	-	5.1	-
Gnathanodon speciosus	Indo-pacific	-	-	0.5	-
Gobioclinus dendriticus	Ocean islands endemic	-	-	2.3	7.9
Gymnothorax dovii	TEP endemic widespread	86.7	30.8	4.1	1.6
Gymnothorax flavimarginatus	Indo-pacific	-	-	0.5	-
Haemulon scudderii	TEP Panamic/Cortez	-	-	24.4	-
Haemulon steindachneri	TEP endemic widespread	-	-	0.5	-
Halichoeres dispilus	TEP endemic widespread	20.0	38.5	53.0	55.6
Halichoeres nicholsi	TEP Panamic/Cortez	6.7	3.8	27.6	3.2
Halichoeres notospilus	TEP Panamic/Cortez	6.7	-	-	-
Hemilutjanus macrophthalmos	TEP Peruvian/Calif./Cortez	-	-	0.5	3.2
Heteroconger klausewitzi	N/A	13.3	23.1	2.3	-
Heterodontus quoyi	TEP Peruvian/Calif./Cortez	-	-	4.1	14.3
Holacanthus passer	TEP Panamic/Cortez	86.7	61.5	69.6	52.4
Hoplopagrus guentherii	TEP Panamic/Cortez	66.7	61.5	13.4	-
Hypanus dipterurus	TEP Panamic/Cortez	-	26.9	32.7	33.3
Hypanus longus	TEP Panamic/Cortez	-	-	0.5	-
Johnrandallia nigrirostris	TEP endemic widespread	80.0	61.5	41.9	4.8
Kyphosus elegans	TEP endemic widespread	33.3	7.7	-	-
Kyphosus ocyurus	TEP endemic widespread	-	3.8	0.5	-
Kyphosus vaigiensis	Circumtropical	20.0	7.7	-	-
Liopropoma fasciatum	TEP Panamic/Cortez	-	-	0.9	4.8
Lutjanus aratus	TEP Panamic/Cortez	-	-	0.9	-
Lutjanus argentiventris	TEP endemic widespread	66.7	73.1	30.9	-
Lutjanus guttatus	TEP endemic widespread	-	-	7.4	1.6
Lutjanus novemfasciatus	TEP endemic widespread	6.7	11.5	8.3	1.6
Lutjanus viridis	TEP Panamic/Cortez	20.0	15.4	21.2	1.6
Mackerels	TEP Peruvian/Calif./Cortez	-	7.7	18.0	11.1
Melichthys niger	Circumtropical	40.0	-	-	-
Mobula birostris	Circumtropical	-	-	0.5	-
Mobula spp.	Circumtropical	-	-	4.6	1.6
Mola alexandrini	Circumtropical	-	-	0.5	4.8
Mugil galapagensis	Galapagos endemic	-	-	0.9	-
Mulloidichthys dentatus	TEP endemic widespread	60.0	46.2	13.4	-
Muraena argus	TEP endemic widespread	-	3.8	11.1	9.5
Muraena clepsydra	TEP Panamic/Cortez	-	-	6.5	3.2
Muraena lentiginosa	TEP endemic widespread	-	-	2.8	-

Mycteroperca olfax	Ocean islands endemic	80.0	38.5	51.2	69.8
Myliobatis spp.	TEP endemic widespread	-	3.8	4.1	3.2
Novaculichthys taeniourus	Indo-pacific	-	-	0.9	-
Ogcocephalus darwini	Galapagos endemic	-	23.1	3.7	-
Ophioblennius steindachneri	TEP endemic widespread	40.0	-	1.4	1.6
Oplegnathus insignis	TEP Peruvian/Calif./Cortez	-	-	1.4	-
Orthopristis forbesi	Galapagos endemic	-	7.7	65.4	33.3
Paralabrax albomaculatus	Galapagos endemic	-	-	2.8	50.8
Paranthias colonus	TEP endemic widespread	93.3	80.8	82.0	85.7
Plagiotremus azaleus	TEP endemic widespread	6.7	3.8	3.7	12.7
Prionotus miles	Galapagos endemic	-	-	1.8	-
Prionurus laticlavius	TEP Panamic/Cortez	100.0	65.4	57.6	4.8
Prognathodes carlhubbsi	Ocean islands endemic	-	-	6.5	12.7
Quassiremus evionthas	Galapagos endemic	-	-	0.5	-
Remora spp.	Circumtropical	-	-	0.5	-
Rhinoptera steindachneri	TEP endemic widespread	6.7	15.4	4.1	1.6
Rypticus bicolor	TEP endemic widespread	6.7	-	1.8	-
Scarus compressus	TEP Panamic/Cortez	-	-	1.4	-
Scarus ghobban	Indo-pacific	40.0	73.1	45.6	7.9
Scarus perrico	TEP endemic widespread	-	7.7	6.0	-
Scarus rubroviolaceus	Indo-pacific	40.0	3.8	0.5	-
Scomberomorus sierra	TEP endemic widespread	-	-	8.3	27.0
Scorpaena histrio	TEP endemic widespread	-	7.7	0.5	-
Semicossyphus darwini	TEP Peruvian/Calif./Cortez	-	3.8	35.9	76.2
Seriola lalandi	Circumtropical	-	-	0.5	-
Seriola peruana	TEP endemic widespread	-	-	-	1.6
Seriola rivoliana	Circumtropical	46.7	61.5	35.9	4.8
Serranus psittacinus	TEP endemic widespread	6.7	26.9	33.6	14.3
Sphoeroides angusticeps	Galapagos endemic	6.7	-	9.7	3.2
Sphoeroides annulatus	TEP endemic widespread	-	57.7	64.1	17.5
Sphyraena idiastes	TEP Peruvian/Calif./Cortez	-	-	1.8	17.5
Sphyrna lewini	Circumtropical	60.0	3.8	12.9	3.2
Stegastes leucorus	Ocean islands endemic	20.0	26.9	40.1	25.4
Sufflamen verres	TEP Panamic/Cortez	86.7	61.5	35.9	6.3
Taeniurops meyeni	Indo-pacific	-	3.8	10.1	6.3
Thalassoma grammaticum	TEP Panamic/Cortez	13.3	-	0.5	-
Thalassoma lucasanum	TEP endemic widespread	53.3	7.7	0.9	3.2
Thunnus albacares	Circumtropical	13.3	-	4.1	-
Triaenodon obesus	Indo-pacific	-	3.8	20.7	-
Triakidae spp.	TEP Peruvian/Calif./Cortez	-	-	10.1	7.9
Umbrina galapagorum	Galapagos endemic	-	-	1.4	-
Uraspis helvola	Circumtropical	6.7	3.8	-	-
Xanthichthys mento	Indo-pacific	33.3	-	-	-
Xyrichtys victori	Ocean islands endemic	-	-	0.9	-
Zanclus cornutus	Indo-pacific	66.7	7.7	0.5	-

Appendix D Frequency of occurrence of 2015 mid-water BRUVs fish taxa across bioregions (Chapter 2)

Table A.3 Mid-water frequency of species occurrence across the four bioregions at single deployment level.

Species	Distribution	Far North	North	Center-SE	West
Abudefduf troschelii	TEP endemic widespread	-	-	0.5	-
Acanthocybium solandri	Indo-pacific	5.9	30.0	8.2	5.2
Acanthurus xanthopterus	Indo-pacific	-	10.0	1.6	-
Aetobatus laticeps	TEP endemic widespread	-	-	5.4	1.7
Alectis ciliaris	Circumtropical	-	-	0.5	-
Aluterus monoceros	Indo-pacific	-	5.0	16.8	5.2
Aluterus scriptus	Circumtropical	-	-	1.1	-
Anisotremus interruptus	TEP endemic widespread	5.9	-	0.5	-
Aulostomus chinensis	Indo-pacific	5.9	-	-	-
Balistes polylepis	Indo-pacific	58.8	5.0	8.2	1.7
Bodianus diplotaenia	TEP endemic widespread	5.9	-	-	-
Bonitos	TEP widespread/Indo-P.	23.5	5.0	3.8	5.2
Canthidermis maculata	Indo-pacific	82.4	25.0	2.7	-
Caranx caballus	TEP endemic widespread	5.9	5.0	7.6	-
Caranx caninus	TEP endemic widespread	-	-	0.5	-
Caranx lugubris	Circumtropical	29.4	-	-	-
Caranx melampygus	Indo-pacific	5.9	-	0.5	-
Caranx sexfasciatus	Indo-pacific	11.8	5.0	0.5	-
Carcharhinus altimus	Circumtropical	5.9	-	0.5	1.7
Carcharhinus falciformis	Circumtropical	11.8	-	0.5	-
Carcharhinus galapagensis	Circumtropical	35.3	-	11.4	19.0
Carcharhinus limbatus	Circumtropical	11.8	15.0	15.2	12.1
Caulolatilus princeps	TEP Peruvian/Calif./Cortez	-	-	0.5	32.8
Chanos chanos	Indo-pacific	-	25.0	0.5	-
Chilomycterus reticulatus	Circumtropical	-	-	0.5	-
Chromis alta	TEP Peruvian/Calif./Cortez	-	-	-	3.4
Elagatis bipinnulata	Circumtropical	70.6	5.0	1.6	-
Epinephelus labriformis	TEP endemic widespread	5.9	-	-	-
Euprepocaranx dorsalis	TEP endemic widespread	-	-	-	-
Fistularia commersonii	Indo-pacific	5.9	-	1.1	-
Forcipiger flavissimus	Indo-pacific	-	-	-	-
Galeocerdo cuvier	Circumtropical	-	-	3.3	1.7
Girella freminvillii	Galapagos endemic	-	-	-	1.7
Gymnothorax dovii	TEP endemic widespread	5.9	-	-	-
Holacanthus passer	TEP Panamic/Cortez	52.9	-	4.3	-

Hoplopagrus guentherii	TEP Panamic/Cortez	29.4	-	1.1	-
Johnrandallia nigrirostris	TEP endemic widespread	5.9	-	-	-
Kyphosus elegans	TEP endemic widespread	41.2	-	-	-
Kyphosus ocyurus	TEP endemic widespread	5.9	-	0.5	-
Kyphosus vaigiensis	Circumtropical	11.8	-	-	-
Lutjanus aratus	TEP Panamic/Cortez	-	-	0.5	-
Lutjanus argentiventris	TEP endemic widespread	11.8	5.0	3.3	-
Lutjanus guttatus	TEP endemic widespread	-	-	-	1.7
Mackerels	TEP Peruvian/Calif./Cortez	-	45.0	13.0	5.2
Melichthys niger	Circumtropical	64.7	-	-	-
Mobula birostris	Circumtropical	-	-	0.5	-
Mobula spp.	Circumtropical	-	-	7.1	-
Mola alexandrini	Circumtropical	-	-	0.5	12.1
Mulloidichthys dentatus	TEP endemic widespread	5.9	-	-	-
Mycteroperca olfax	Ocean islands endemic	11.8	-	1.6	3.4
Paralabrax albomaculatus	Galapagos endemic	-	-	-	1.7
Paranthias colonus	TEP endemic widespread	70.6	50.0	55.4	62.1
Plagiotremus azaleus	TEP endemic widespread	-	-	-	-
Prionotus miles	Galapagos endemic	-	-	-	-
Prionurus laticlavius	TEP Panamic/Cortez	23.5	-	2.2	-
Rhinoptera steindachneri	TEP endemic widespread	-	5.0	4.3	5.2
Scomberomorus sierra	TEP endemic widespread	-	-	5.4	15.5
Scorpaena histrio	TEP endemic widespread	-	-	-	-
Semicossyphus darwini	TEP Peruvian/Calif./Cortez	-	-	-	5.2
Seriola rivoliana	Circumtropical	-	-	7.6	-
Sphoeroides annulatus	TEP endemic widespread	-	-	16.3	5.2
Sphyraena idiastes	TEP Peruvian/Calif./Cortez	5.9	-	1.6	1.7
Sphyrna lewini	Circumtropical	47.1	5.0	7.6	3.4
Sufflamen verres	TEP Panamic/Cortez	47.1	5.0	2.2	-
Thunnus albacares	Circumtropical	23.5	35.0	3.8	22.4
Trachinotus stilbe	N/A	17.6	-	0.5	-
Triaenodon obesus	Indo-pacific	-	-	0.5	-
Uraspis helvola	Circumtropical	-	5.0	0.5	-
Xanthichthys mento	Indo-pacific	17.6	-	-	-
Zanclus cornutus	Indo-pacific	5.9	-	-	-

Appendix E Details of fish taxa used in length-based maturity metrics analysis (Chapter 3)

Table A.4 List of fish taxa used in the maturity-metrics analysis with metrics details and source of the maximum length used to estimate metrics.

Species Name	Fishing Pressure	Source for Max Length	Maximum Length (cm)	Maturity Length (cm)	Optimum Length Interval (cm)
Mycteroperca olfax	high	Fishbase	120	62.9	72.2-88.2
Dermatolepis dermatolepis	high	Fishbase	100	53.5	59.9-73.2
Paralabrax albomaculatus	high	Catch data	74.0	37.0	43.9-53.7
Lutjanus argentiventris	high	Stereo-BRUVs	72.0	40.0	42.8-52.3
Lutjanus novemfasciatus	high	Fishbase	170	85.5	103.1-126.1
Hoplopagrus guentherii	high	Fishbase	92	49.7	54.9-67.1
Thunnus albacares	high	Fishbase	239	115.6	146.3-178.8
Acanthocybium solandri	high	Fishbase	250	120.3	153.1-187.1
Anisotremus interruptus	medium	Stereo-BRUVs	55.9	32.0	32.9-40.3
Calamus spp.	medium	Fishbase	61	34.6	36-44
Caulolatilus princeps	medium	Fishbase	102	54.5	61-74.6
Epinephelus labriformis	medium	Fishbase	60	34.1	35.5-43.3
Lutjanus viridis	medium	Stereo-BRUVs	31.7	19.4	18.5-22.6
Haemulon scuderii	medium	Stereo-BRUVs	41.9	24.8	24.6-30
Semicossyphus darwini	medium	Stereo-BRUVs	80.4	44.1	47.9-58.5
Seriola rivoliana	medium	Fishbase	160	81.1	96.9-118.5
Sphyraena idiastes	medium	Fishbase	91	49.2	54.4-66.4
Scomberomorus sierra	medium	Stereo-BRUVs	115.8	60.9	69.6-85
Orthopristis spp.	medium	Stereo-BRUVs	43.1	25.4	25.2-30.8
Balistes polylepis	low	Fishbase	76	42	45.2-55.2
Sufflamen verres	low	Stereo-BRUVs	40.1	23.9	23.4-28.6
Aluterus monoceros	low	Fishbase	72.6	40.3	43.1-52.7
Bodianus eclancheri	low	Fishbase	61	34.6	36-44
Canthidermis maculata	low	Stereo-BRUVs	54.1	31.1	31.9-38.9
Caranx caballus	low	Stereo-BRUVs	62.1	35.1	36.7-44.9
Holacanthus passer	low	Fishbase	35.6	21.5	20.8-25.4
Melichthys niger	low	Fishbase	50	29	33.5-40.9
Mulloidichthys dentatus	low	Stereo-BRUVs	46.7	27.3	27.5-33.6
Paranthias colonus	low	Stereo-BRUVs	45.1	26.5	26.5-32.3
Prionurus laticlavius	low	Fishbase	60	34.1	35.5-43.3
Scarus ghobban	low	Fishbase	75	41.5	44.6-54.5
Sphoeroides annulatus	low	Fishbase	44	25.9	25.7-31.5
Decapterus spp./*T.murphyi*	low	Stereo-BRUVs	55.6	31.9	32.8-40
Uraspis helvola	low	Fishbase	58	33.1	34.2-41.8

Appendix F Estimation of *Bodianus diplotaenia* length-weight relationship parameters (Chapter 5)

Length and weight from a sample of *B. diplotaenia* collected on the Ecuadorian coast by Bearez (1996) were analyzed. The parameters a and b of relationships of the form W = a FL^b were estimated through a logarithmic transformation, i.e. ln W = ln a + b ln FL, with a and b estimated by ordinary least squares regression (Fig A.1) as described by Kulbicki et al. (2005). FL and W are respectively fork length in centimetre and weight in grams.

The values obtained for a and b were respectively 0.015 and 3.088 with a R^2 for the regression equal to 0.98.

Using the estimated parameters, the weight of each fish entering the estimate was backcalculated, generating an estimated weight W_{est}. The normalized root-mean-square error, denoted CV(RMSE), was then computed to investigate the predictive power of the model and associated error for future estimations.

The CV(RMSE) was computed as follow:

$$CV(RMSE) = \frac{\left(\sqrt{\frac{\sum_{w=1}^{n}(West - W)^2}{n}}\right)}{Mean(W)}$$

The CV(RMSE) value equals 15.2%. Together with the high R^2 for the regression, this indicates that the predictive power for the model is good.

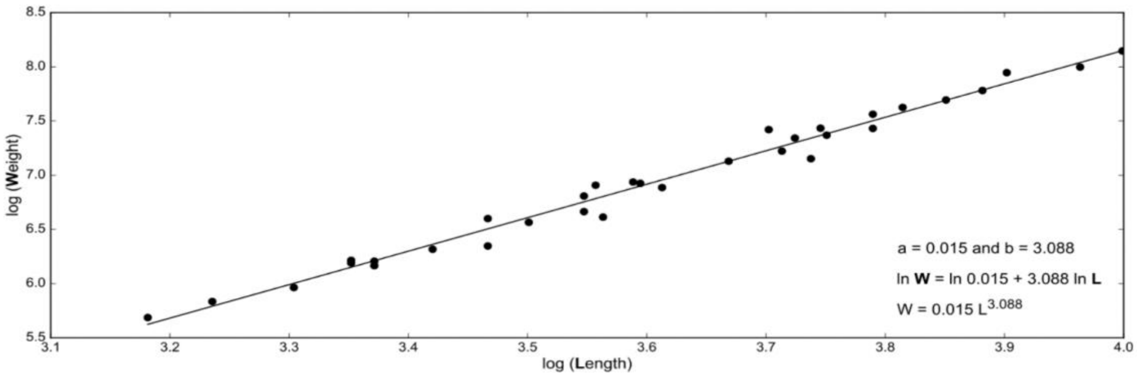

Figure A.1 *B. diplotaenia* length-weight relationship regression curve and estimated parameters for the ordinary least squares regression.

Appendix G Public speaking and community-based outcomes at Curtin University

At Curtin, I invested significant efforts in developing my outreach, leadership, and in-person communication skills. This included participating in co-curricular activities offered to postgraduate students as well as starting a number of campus-based initiatives in line with my interest in sustainability at large. Here is a list of the various endeavors I undertook alongside my PhD research project.

Famelab Australia

- Famelab Australia finalist and People's Choice second place. Link to my three-minute presentation at the Western Australia State Theater during the finals (pictures below): https://www.youtube.com/watch?v=pUmaULvJ3qY

Three-minute thesis

- Curtin Three-minute thesis 2018 Winner with my talk “What’s fishy about the Galapagos”?
- Curtin Three-minute Thesis 2018 People’s Choice first place.
- Asia-Pacific Three-minute Thesis semi-finalist
- Curtin Three-minute Thesis 2019 Heat’s MC and mentor

Curtin Rapid-fire MLS Seminar

I launched and MCed this short-talks ecology seminar series to encourage cross-fertilization of ideas at the School of Molecular and Life Sciences. Around 30 speakers participated until COVID-19 put this initiative on halt. Since in-person meetings are now allowed, the seminar series was recently re-launched by another group of students at the school.

Big Idea Presentation

The Big Issue magazine organizes a social-entrepreneurship start-up contest every year. For the 2019 edition of this event, I was solicited to give a presentation on the fundamentals of public speaking to the participants.

Curtin Advance Science Students

Curtin advance science students are outstanding Curtin students with a track-record of acamedic excellence who follow a more demanding course load with additional industry practice. As part of their co-curriculum, I was solicited to give a presentation on the fundamentals of public speaking to the 2020 second year cohort.

The C3 Project (Curtin Cuts the Cups)

The C3 Project is a flagship social impact project I launched at Curtin University. This gave me a venue to give numerous science-based presentations to a wide variety of stakeholders including, Curtin executives, industry partners and student classrooms. The project aimed at raising awareness about the impact of the single use culture, develop viable alternatives to disposables, and foster a culture shift at Curtin University. Around 200 students in six independent Curtin curriculum worked on the project as part of their course assignments and the project continues to be used as a case study to this day. The project gathered major momentum and institutional support at Curtin with about 130 stakeholders involved. The largest achievement was for the project to be chosen as the basis for the 6-months long project of the John Curtin Leadship Academy (JCLA), Curtin’s extra curricular leadership program which trains 40 of Curtin’s top-ranking students every year. As part of the JCLA efforts, dozens of on-campus outreach and stakeholders engagement activities were planned for the first semester of 2019. Sadly, the project was stopped as Covid-19 hit and the campus was shut down and the momentum died-out although other people are now attempting to revive the project.

C3 interview for Curtin Careers Employment and Leadership program:
https://www.youtube.com/watch?v=08dpCXnkJUY

Article about the C3 Project in Scitech Particle:
https://particle.scitech.org.au/food/cutting-the-cups-how-to-dispose-of-an-everyday-problem/

C3 one-year milestone recap:
https://www.instagram.com/p/B4zlNorHONG/