



DEGRADACIÓN DE MICROHÁBITATS DE CORAL POR INFLUENCIA DE BASURA MARINA Y SU EFECTO SOBRE COMUNIDADES DE MACROINVERTEBRADOS Y PECES EN LA COSTA DE MANABÍ- ECUADOR.



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TESIS DOCTORAL

TITULO: *DEGRADACIÓN DE MICROHABITATS DE CORAL POR INFLUENCIA DE BASURA MARINA Y SU EFECTO SOBRE COMUNIDADES DE MACROINVERTEBRADOS Y PECES EN LA COSTA DE MANABI-ECUADOR*

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Título de la tesis:

Degradación de microhábitats de coral por influencia de basura marina y su efecto sobre comunidades de macroinvertebrados y peces en la costa de Manabí-Ecuador.

Degradation of coral microhabitats by the influence of derelict fishing gear and its effects over macroinvertebrates and fish communities in the coast of Manabi-Ecuador.

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TÍTULO DE LA TESIS:

Degradación de microhábitats de coral por influencia de basura marina y su efecto sobre comunidades de macroinvertebrados y peces en la costa de Manabí-Ecuador.

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INFORME RAZONADO DEL/DE LOS DIRECTOR/ES DE LA TESIS

(se hará mención a la evolución y desarrollo de la tesis, así como a trabajos y publicaciones derivados de la misma).

La tesis se ha desarrollado conforme a lo planteado en el plan de investigación inicial e incluso ampliando algunos objetivos como las comunidades de invertebrados (capítulo IV). El desarrollo de la tesis ha sido el previsto abordando el efecto de las redes de pesca sobre los arrecifes coralinos (abordado en el **capítulo I**), y publicado en Coral Reefs (*Coral fracture by derelict fishing gear affects the sustainability of the marginal reefs of Ecuador*). Posteriormente se investigó un aspecto metodológico clave como es la turbidez y su efecto en la detección y estima de abundancia de comunidades de peces (**capítulo II**), publicado en Ecological Indicators (*Turbidity: A key factor in the estimation of fish species richness and abundance in the rocky reefs of Ecuador*).

Finalmente se desarrollaron dos capítulo para determinar los cambios espaciales y temporales de composición (abundancia y diversidad) de especies de peces (**capítulo III**) e invertebrados marinos (**capítulo IV**) asociados a micro-hábitats de coral con alta presencia y persistencia de materiales y redes de pesca. En este caso el capítulo III ha sido publicado en Marine Pollution Bulletin (*Natural and anthropogenic-induced stressors affecting the composition of fish communities in rocky reefs of Ecuador*), mientras que el capítulo IV se encuentra actualmente bajo revisión en Coral Reefs (*Echinoderms as indicators of disturbance on marginal reefs along the continental coast of Ecuador*).

De acuerdo con lo mencionado anteriormente la tesis ha abordado y cumplido con éxito todos los objetivos planteados inicialmente y con un gran rigor científico avalado por la calidad de las revistas donde se han publicados los artículos.

Por todo ello, se autoriza la presentación de la tesis doctoral.

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A mi esposa Jhesenia por el amor y apoyo durante estos años... me inspiras... te amo!

A mis Abuelos Wilfrido y Lucila, mis tíos Sonia y Roger y mi hermano Wilfrido por el amor, los valores, la paciencia y guia de todos estos años. Los amo!

Cerrar los ojos a la naturaleza solo nos hace ciegos en un paraíso de tontos.

Jacques Cousteau

La naturaleza es siempre más sutil, más compleja y elegante que lo que somos capaces de imaginar.

Carl Sagan

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RESUMEN

Las comunidades coralinas incrementan la complejidad estructural de los arrecifes marginales, proveyendo recursos biológicos y dinamizando las interacciones biológicas y ecológicas entre los organismos del arrecife. La disminución en la complejidad estructural de los arrecifes marginales en relación con la influencia de las actividades antrópicas ha sido recientemente reportada alrededor del mundo y en los últimos años ha empezado a ser entendida en la costa continental del Ecuador. Nuestra tesis se enfoca en determinar los impactos de las redes de pesca abandonadas sobre las comunidades de coral (capítulo I), invertebrados (capítulo IV) y peces (capítulo III) en las zonas geomorfológicas (cresta, pendiente y fondo) de dos arrecifes marginales de la costa central de Manabí-Ecuador, incluyendo la turbidez como covariable en las estimaciones de estas comunidades (capítulo II); con el fin de explicar los procesos de fractura, pérdida de cobertura de coral y los cambios de composición de invertebrados y peces. Los resultados muestran que las crestas de los arrecifes estudiados están altamente afectadas por el enredo de redes e identifican a las redes de pesca abandonadas como un dinamizador clave en la fractura, fragmentación y pérdida de cobertura de corales duros, produciendo además efectos adversos sobre la composición de invertebrados y peces. Los resultados muestran a la turbidez como una variable a tener en cuenta para evitar sesgos en las estimaciones de abundancia de las comunidades peces. Las diferencias en la composición, diversidad, abundancia y densidad de peces y equinodermos estuvieron relacionadas a la complejidad de hábitat, cobertura de coral vivo y algas césped y a la presencia y prevalencia de redes de pesca abandonadas. Se recomiendan evaluaciones periódicas para medir la pérdida de complejidad estructural y cambios de composición. Un programa de recuperación para los arrecifes estudiados involucra educación, participación y colaboración los pescadores artesanales, organizaciones gubernamentales y universidades.

Palabras clave: Actividades antrópicas, Efectos comunitarios, Fractura de coral, Redes de pesca abandonadas

ABSTRACT

Coral communities increase marginal reefs' structural complexity, provide biological resources, ecosystem services and drive biological and ecological interactions among reef organisms. The decline in the structural complexity of marginal reefs concerning the influence of anthropogenic activities has been recently reported around the world and, in the last few years, has started to be understood on the continental coast of Ecuador. Our thesis focused on determining the impacts of derelict fishing gear on hard coral species (chapter I), invertebrates (chapter IV), and fish (chapter III) communities in the geomorphological zones (crest, slope, and bottom) of two marginal reefs of the central coast of Manabi-Ecuador, including turbidity as a covariate in the estimates of these communities (chapter II); to explain the process of fracture, loss of hard coral coverage, and the changes of composition in invertebrates and fish communities. Results show that the crest zones of studied reefs are highly affected by the entanglement of nets and identify derelict fishing gear as a key driver in the fracturing, fragmentation, and loss of hard coral coverage process, also producing an adverse effect on invertebrate and fish composition. Turbidity was an important variable to consider in the assessment to avoiding biases in the estimation of abundance of fish communities. The differences in composition, diversity, abundance and density of fish and echinoderms communities was related to the habitat complexity, live coral and turf algae coverage, and the presence and prevalence of derelict fishing gear. Periodic assessments to measure the loss of structural complexity and composition changes are recommended. A recovery program for the reefs studied involves the education, active participation, and collaboration of artisanal fishermen, governmental organizations, and universities.

Keywords: Anthropogenic activities, Community effects, Coral fracture, Derelict fishing gear

INTRODUCTION

Coral reefs

Coral reefs are complex marine ecosystems that support the highest biological diversity, providing essential services to millions of people worldwide (Burke et al., 2011; Hughes et al., 2017; Camp et al., 2018; Burt et al., 2020). Classical coral reefs (i.e., Caribbean and Australian) can only occur under oligotrophic and stable conditions: shallow habitats with high levels of light penetration; and low fluctuation of temperature, pH and nutrients (Table 1) (Elias, 2018; Soares et al., 2020). Corals are found in all oceans, both in shallow and deep waters. However, reef-building corals, which have a symbiotic relationship with algae (zooxanthellae), need clear, shallow waters that allow light to penetrate for photosynthesis, and they also need tropical or subtropical temperatures, which exist in the 30-degree range north or 30 degrees south of the equator (Figure 1). During the last decades, coral reefs have faced a vast and intensifying array of global and local threats related to direct and indirect human activities: overfishing, coastal development, agricultural runoff, increasing warming and acidification of the ocean (Hill & Hoogenboom, 2022). These threats intensify coral bleaching, the prevalence of diseases and the death of colonies and negatively impact the maintenance of the three-dimensional complexity of the reefs with subsequent reduction of living coral areas, invertebrate and fish diversity and increasing algal turf cover, leading reefs to phase shift and degradation (Alvarez-Filip et al., 2011; Burke et al., 2011; Hughes et al., 2017).

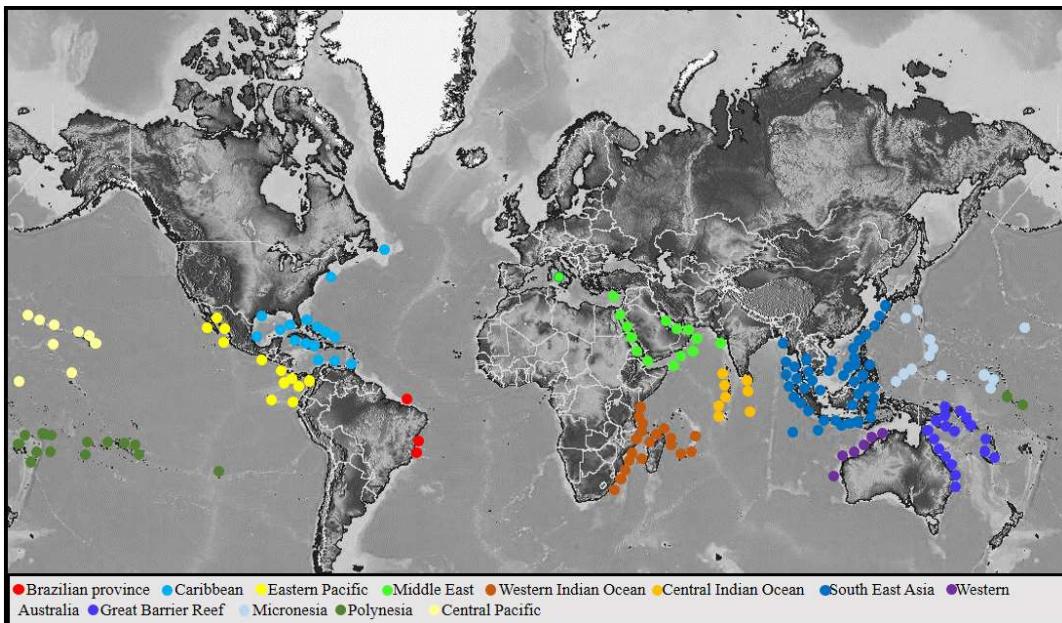


Figure. 1. Worldwide distribution of coral reefs by oceanic province.

Marginal reefs

In contrast to the Caribbean and Australian Coral Reefs, adapted to stable conditions of physical variables (temperature, low levels of sedimentation and nutrients), some reef ecosystems and communities can occur under marginal or suboptimal conditions (Figure 2) (Perry & Larcombe, 2003; Burt et al., 2020; Soares, 2020). These conditions include mesophotic depths, turbid waters, high sedimentation rates and nutrient levels, increased primary productivity, extreme pH fluctuations, and highly variable temperatures (Table 1) (Kleypas et al., 1999; Perry & Larcombe, 2003; Halfar et al., 2005; Schoepf et al., 2015; Chow et al., 2019; Enochs et al., 2020; Soares, 2020). Marginal communities may also occur on hard substrates: intertidal or subtidal rocky reefs, rhodolith beds and estuarine habitats (Soares et al., 2017; Francini-Filho et al., 2018). Recent studies have demonstrated that marginal reefs of High Latitudes and the Eastern Tropical Pacific have adapted to resist the high fluctuations of physical variables that provide them with a

greater capacity to adapt, resist and expand in future climate-changing scenarios (Couce et al., 2013; Freeman, 2015; Manzello et al., 2017; Camp et al., 2018). On the other hand, marginal reefs research in the last decade has increased the knowledge about the structure, functioning, resistance, resilience, and refugia potential of the *marine forest* (Rossi et al., 2017; Bianchi et al., 2017; Camp et al., 2018; Soares, 2020). These essential findings broaden the understanding of the diversity, endemism, ecosystem goods, services, and production of calcium carbonate in coral reefs (Hennige et al., 2010, Pinheiro et al., 2017, Paoli et al., 2017).

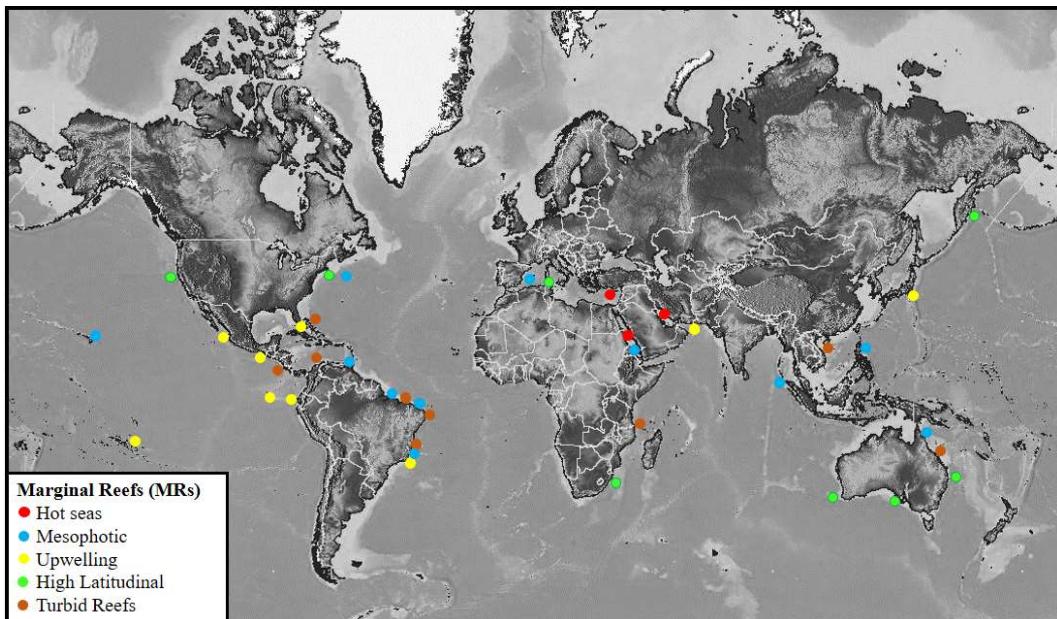


Figure. 2. Map of worldwide distribution of marginal reefs.

Marginal reef biota is very dissimilar to *classical coral reefs* concerning ecological attributes (species richness, diversity, endemism), and it is composed mainly of reef specialists (majorly stress-tolerant species) (Burt et al., 2020; Soares, 2020). In general, biogeographic and suboptimal environmental conditions filtered out marginal reefs species by natural selection, resulting in two conspicuous ecological characteristics: 1) lower species richness (Kleypas et al., 1999; Bak & Meesters, 2000; Perry, 2003) and 2)

dominance of stress-tolerant species (Harriott & Banks, 2002; Bennett et al., 2010; Lybolt et al., 2010; Narayan et al., 2015; Bento et al., 2016; Browne et al., 2019).

Table 1. Comparison of biological and ecological attributes of classical and marginal coral reefs.

Type of reef	Environment	Species richness	Diversity	Dominance	Ecosystem services	Threats
Classical	Oligotrophic and shallow or optimal conditions of T°, pH, low primary production and nutrients, low sedimentation	High	High	Reef generalists and vulnerable species	Partially evaluated	Very vulnerable to global changes: sea acidification, global warming and anthropogenic pressure overfishing, coastal development, and agricultural runoff.
Marginal	Deep and suboptimal: High fluctuation of T°, pH, primary production and nutrients, sedimentation, turbid waters.	Low	Low	Reef specialists and stress-tolerant species	Not evaluated	Theoretically resistant and resilient to global changes: sea acidification, global warming, but highly vulnerable to anthropogenic pressure. Overfishing, coastal development.

Soares (2020) argues that marginal reefs are under *severe anthropogenic pressure* and suggest that their resilience could be lost if proper and urgent conservation actions are not taken at local and global scales in the next few decades as "classical" coral reefs. On the other hand, for Cortés and Reyes-Bonilla (2017), it is evident that Eastern Tropical Pacific (ETP) coral reefs (relatively small and few) need urgent protection from all sectors of society that benefit from the environmental services and aesthetic pleasures they offer.

Ecosystem goods and services of animal forest and coral reefs

Marine animal forests supply ecosystemic goods and services based on multiple ecological functions such as sediment stabilization and reduction of current flow (Sammal

et al., 2017), nursery zones (Cau et al., 2017) and carbon immobilizers (Rossi & Rizzo, 2017) thus generating human benefits (Burke et al., 2011; Paoli et al., 2017, Spalding et al., 2017, Laing et al., 2020). Moberg and Folke (1999) analyzed the ecosystem services of coral reefs, particularly concerning functional groups of species and biological communities in different regions of the world. For these authors, coral reef systems showed poor recovery when they are affected by natural and persistent human disturbances; and their capacity to generate ecological goods and services requires innovative national and international policies, incentives, and adequate institutional arrangements. However, these services and the continued existence of countless species that inhabit reefs depend on stable populations of reef-building corals, many of which have been declining globally due to direct and indirect anthropogenic activities (Alvarez-Phillip et al., 2011; de Groot et al., 2012; Pratchet et al., 2013; Forrester et al., 2015; Mansour et al., 2017; Bruno et al., 2019).

Chronologically, several research attempts have been made globally to value the ecosystem goods and services of coral reefs, all with variable results (Cesar et al., 2003; Paoli et al., 2017; Spalding et al., 2017); due to their intangible nature, the absence of markets to ascribe their relative importance, and multiple ways to analyze and interpret data derived from assessment (de Groot et al., 2012; Laing et al., 2020). Paoli et al. (2017) classified and analyzed the attributes of ecosystemic services for coral reefs in four categories: 1) regulation, 2) provision, 3) habitat, and 4) information services. Primary ecosystem provisional services derived from classical coral reefs include provision services: food (Burke et al., 2011) and economic benefits through fisheries and tourism (Spalding et al., 2017). Cesar et al. (2003) suggests that 32% of the calculated annual value of coral reefs is ascribable to tourism and recreation and 30% to coastal protection and fisheries and biodiversity for slightly less than 20% each. The mean economic value

of reefs (with tourism) is calculated annually at \$482,428 per square kilometer, and the most valuable reefs generate more than \$7 million per square kilometer per year (Spalding et al., 2017). On the other hand, reefs are essential to protect coastal communities from large waves generated by storms or tsunamis (Ferrario et al., 2014; Harris et al., 2018).

Camp et al. (2018) suggest that despite current and evident knowledge gaps, coral colonies from marginal reefs may have an unrecognized (and disproportionately) high research and conservation value concerning trait selection of resident coral populations adapted to extreme conditions that offer genetic rescue (heat-tolerant genotypes across latitudes) and prominent ecosystemic services (not evaluated yet). On the other hand, assessing biota and functional groups on marginal reefs (coral colonies, fish and invertebrate's communities) involves a wide range of technical difficulties and methodological challenges, considering the high fluctuation of local physical parameters like turbidity and temperature related to annual upwelling events, tide regimens and current dynamics (Figueroa et al., 2020a; Soares et al., 2020). These considerations are critical for choosing the assessment method for conspicuous and cryptic fish and invertebrate species and require extra efforts and skills in species identification to obtain optimal results and decrease bias.

The importance of marginal reefs assessment and its relationship with Agenda 2030

Concerning the United Nations Agenda 2030, Sustainable Development Goal 14: Life below water highlights the importance of conserving *and sustainably using the oceans, seas, and marine resources for sustainable development*. More specifically, the goal targets 14.1 and 14.2 urges the signatory governments to: 1) prevent and reduce marine pollution of all kinds significantly from land-based activities, including marine debris and

nutrient pollution, and 2) manage sustainably and protect the marine and coastal ecosystems to avoid significant adverse impacts, strengthen their resilience and take action for their restoration to achieve healthy and productive oceans (United Nations, 2015). In this context, multidisciplinary approaches must include cooperation and engagement with society, in which citizen science can be a powerful tool to achieve conservation goals (Zorrilla-Pujana, 2017).

Direct and indirect anthropic impacts over rocky reefs in the Eastern Tropical Pacific (ETP) Region

Cortés and Reyes-Bonilla (2017) suggest that human impacts on ETP coral communities and reefs are relatively minor compared to other regions. The direct causes of damage to coral and marginal reefs in the ETP region are mainly coral extraction and other reef organisms (overfishing), nonregulated tourist activity, ship groundings, anchor damage, and eutrophication (Cortés & Reyes-Bonilla, 2017) and increasing ghost fishing due to the presence and prevalence of abandoned monofilament nets (the most common type of abandoned gear) over reefs of Ecuador (Figueroa et al., 2016; Povolo, 2021; Wolff et al., 2022). Primary indirect sources of damage to coral and marginal reefs include coastal alteration, sedimentation, pollution (including eutrophication), oil pollution and agrochemicals, plankton blooms (Cortés & Reyes-Bonilla, 2017) and derelict fishing gear over crest zones with negative interactions with coral colonies and fish communities in marginal reefs of Manabi-Ecuador (Figueroa-Pico et al., 2016, 2020a, 2021).

Documented interactions and impacts of DFG in order of importance in Ecuador are 1) entanglement of monofilament nets in the crest and slope zones of the reefs, 2) coverage/smothering of branching coral colonies in the crest zones, 3) colonization of monofilament nets by turf algae, later succeeded by crustose and coralline algae and 4) ghost fishing (Figure 3) (Consoli et al., 2020; Angiolillo & Fortibuoni, 2020).

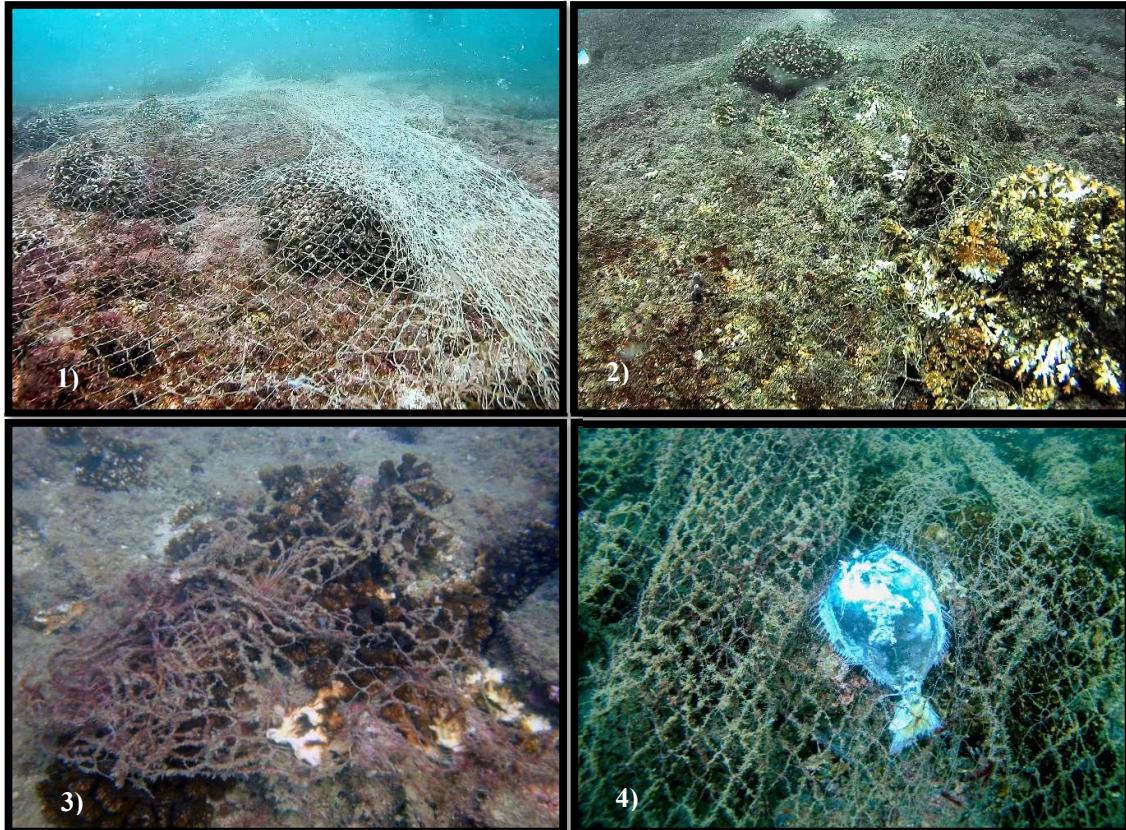


Figure 3. Interactions of monofilament nets in marginal reefs 1) Entanglement 2) Coral fracture 3) Colonization of turf algae and smothering of branching coral colonies by 4) Ghost fishing.

Wolff et al. (2022) suggest that entanglement is the type of interaction with higher occurrence in the reefs of Atacames-Esmeraldas (49%), followed by smothering (28%), colonization (21%) and ghost fishing (2%). While entanglement, smothering and ghost fishing have been demonstrated to cause negative impacts on rocky bottoms and biota, abandoned nets for long periods are progressively damaged and heavily colonized by

encrusting biota (Thomas & Sandhya, 2019), including turf algae consortiums (Figueroa et al., 2020). Galeth-Moreira (2021) documented the interactions of benthic biota with abandoned, lost or otherwise discarded fishing gear (ALDFG) in the Bajo Atacames rocky reef system of Esmeraldas-Ecuador. Interactions included the entanglement effects over sessile and low-motion benthic invertebrates: bivalves (Pteriidae, Spondylidae) and gastropods molluscs (Cypraeidae, Muricidae) and branching coral colonies of the genus Pocillopora spp. Other significant documented interactions of benthic invertebrates with monofilament nets abandoned for long periods in Manabí includes non-identified small sea cucumbers (González, Bluepoint Foundation, pers. comm.).

For Manzello et al. (2017), local impacts are the leading cause of coral reef degradation. These impacts include excessive terrigenous sedimentation, pollution, human-enhanced harmful algal blooms, coral extraction, and overexploitation of associated reef organisms. The author suggests that improved and integrated coastal zone management should reduce terrigenous sediments, pollutants, and nutrients. However, creating and appropriately managing Marine Protected Areas should help improve fish stocks and minimize the extraction of coral reef organisms (Manzello et al., 2017).

Coral reefs and marginal reefs on the continental coast of Ecuador

The continental coast of Ecuador has two marine reserves: Galera-San Francisco Marine Reserve (Esmeraldas) and El Pelado Marine Reserve (Santa Elena), and five protected areas with marine and terrestrial ecosystems: Machalilla National Park, Pacoche Coastal-Marine Wildlife Refuge, Puntilla Santa Elena Coastal-Marine Faunal Production Reserve, Isla Santa Clara Wildlife Refuge and Playas Villamil National Recreational Area (Yanez, 2016) (Figure 4).

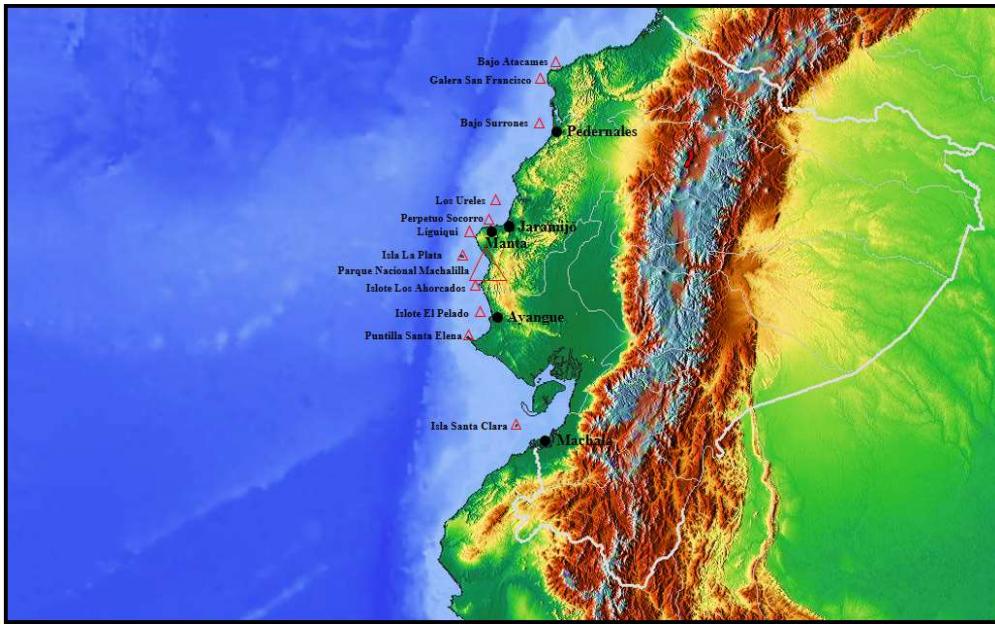


Figure 4.- Map of distribution of coral and marginal reefs along the continental coast of Ecuador.

Small red triangles represent individual reef systems, and big red triangles represent Marine Protected Areas.

Galera-San Francisco Marine Reserve has a high diversity of marine habitats, including mangroves, estuaries, rocky reefs, and coral patch reefs with abundant gorgonian populations, several species of soft and stony corals, and the largest known black coral population on the Ecuadorian continental shelf (Glynn et al., 2017). El Pelado Marine Reserve harbours a variety of fishes and invertebrates, some of which are of high value to local fishing and tourism activities (Cardenas-Calle et al., 2018; Steiner et al., 2019). Machalilla National Park (MNP) represents the southernmost limit of known reef development on the eastern Pacific mainland. Although the low number of endemic species, MNP has the most extensive and diverse coral reefs on the continental coast of Ecuador (Glynn, 2003). The faunal richness and the best-developed coral reefs are present in sites like Isla de la Plata, Isla Salango and La Playita. The Pacoche Refuge (Coastal Marine Wildlife Refuge Pacoche) has various ecosystems, including rocky reefs, sand beaches, and seamounts. None of the mentioned Marine Protected Areas or Marine

Reserves on continental Ecuador has specific guidelines to protect coral reefs or habitats.

On the other hand, the *International Union for Conservation of Nature (IUCN)* classifies several coral species, such as *Pocillopora damicornis*, *Pocillopora capitata*, and *Pocillopora eydouxi* as *least concerned* and *near threatened* (Glynn et al., 2017). In some cases, the legal framework in Marine Protected Areas of Ecuador is ambiguous and confusing and does not support their conservation and preservation.

General *in situ* biodiversity conservation strategies has been established in Marine Protected Areas of Ecuador, including monitoring, enforcement of regulations, environmental education, and well-managed tourism. Nonetheless, the most severe risk to the marine fauna in MNP is the irresponsible and uncontrolled exploitation by commercial and artisanal fisheries and the legal conflicts between MAE and other public entities (Stafford et al., 2016; Narvaez, 2020) (Figure 5).

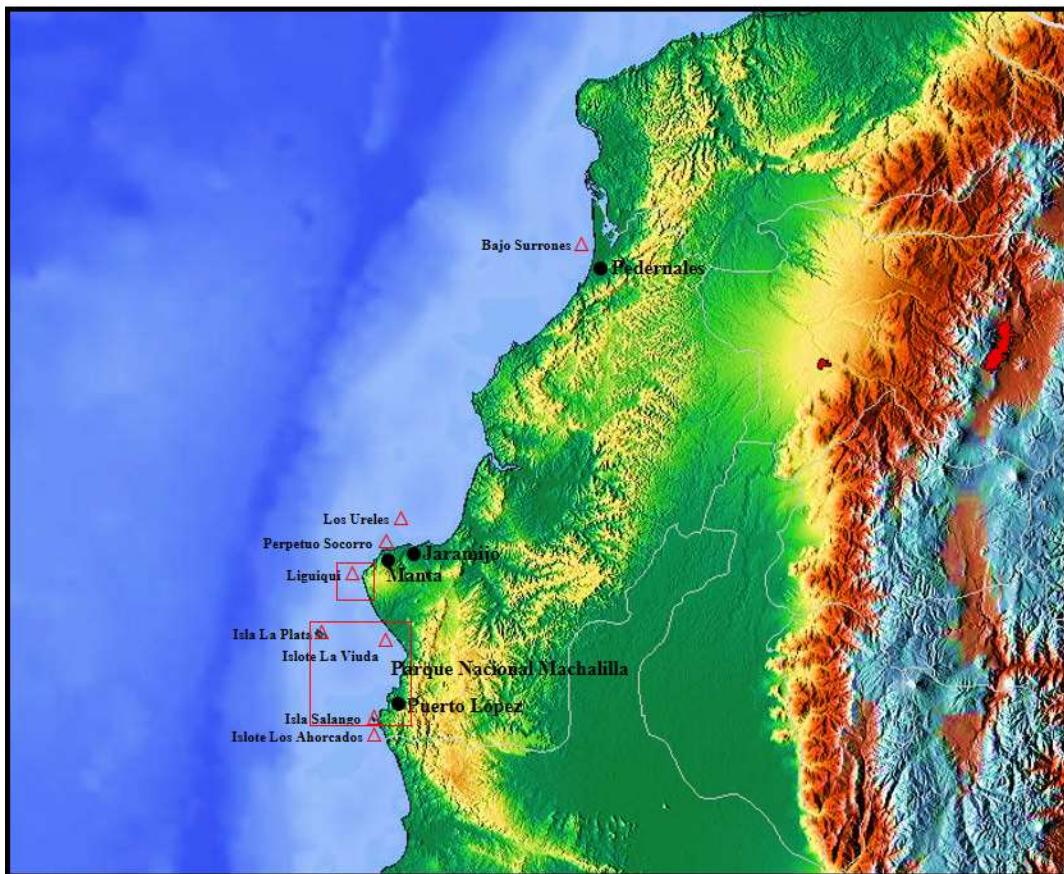


Figure 5. Coral and marginal reefs along the coast of Manabi province. Red triangles represent individual coral and marginal reef systems, while red squares represent Marine Protected Areas.

Derelict fishing gear on the continental coast of Ecuador: Socio-economic issues.

Derelict fishing gear has negative socio-economic implications for local fishermen communities and specific economic sectors through long-term direct or indirect impacts on fisheries, tourism, reduced coastal protection and coral reef degradation (Macfadyen et al., 2009; Watkins et al., 2015). Figueroa-Pico et al. (2016, 2021) and Galeth-Moreira (2021) suggest that the presence and prevalence of abandoned nets over the rocky reefs of Manabí and Esmeraldas could be the effect of the intense extractive pressure and use by the local fishermen communities, leading to direct and indirect impacts on coral and rocky reef communities. Figueroa et al. (2013), Castillo et al. (2013), Povolo (2021),

Castillo et al. (2022) and Wolff et al. (2022) state that artisanal coastal fisheries in Manabi and Esmeraldas are currently unsustainable due to overfishing, illegal fishing, and conflicts among resource users through the years. Furthermore, Povolo (2021) and Wolff et al. (2022) identified four direct and indirect causes associated with the loss of fishing gear and the presence and prevalence of abandoned nets in Esmeraldas concerning social and natural factors: 1) maneuvers that conduct in loss of gear control to avoid robbery from pirates, 2) bottom obstructions, 3) weather and changing currents, and 4) interactions with marine mammals. Frequent fishing gear loss (longlines and nets) (66%) in Esmeraldas represented a considerable economic loss for local fishermen (approx. \$ 521 000 \$) with the subsequent acute poverty cycle (debts, low incomes) that pushed fishermen to get involved in crime and some cases drug trafficking.

The role of turf algae in the degradation process of coral reefs communities

Turf algae are composed of dense, multi-species assemblages of filamentous benthic algae, small individuals of macroalgae, and cyanobacteria (<1 cm in height) (Connell et al., 2014; Swierts & Vermeij, 2016; Fong et al., 2017). Turf algae assemblages have fast growth (Littler et al., 2006) and occupy available spaces quickly (Humphries et al., 2014), including abandoned monofilament nets in marginal reefs (Figueroa et al., 2016, 2020a), and their structure and height make them less vulnerable to grazing and water turbulence (Cheroske et al., 2000; Connell et al., 2014). Turf algae are typically associated with the process of reef degradation, which is the most abundant benthic group (Littler et al., 2006; Sandin et al., 2008; Alcivar, 2015, Alcivar et al., 2021), impacting the branching coral communities negatively through massive colonization and smothering of the colonies (Barott et al., 2012; Figueroa et al., 2020) that provokes critical bleaching processes and cause potential phase shifts on reefs (Cruz et al., 2018) (Figure 6).

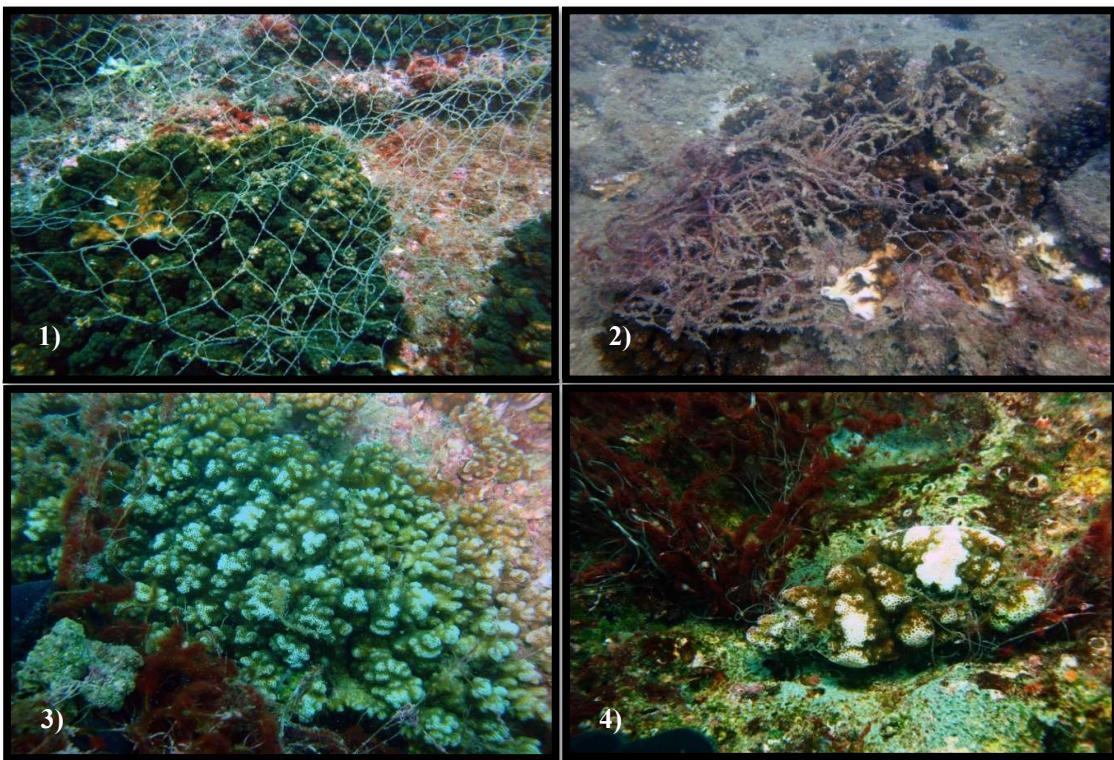


Figure 6. The degradation process of branching coral colonies concerns the presence and persistence of abandoned monofilament nets. 1) Abandoned net over a *Pocillopora* sp. colony, 2) Turf algae colonization over monofilament net, 3) Bleaching signals on *Pocillopora* colony, 4) Severe bleaching signal and death of coral tissues.

Turf algae composition in marginal reefs of the continental coast of Ecuador.

Alcivar et al. (2021) identified six species of turf algae over hard substrates of Perpetuo Socorro rocky reef (a site classified by the author as disturbed) in Manta-Manabí. Turf algae composition included five Rhodophyta species: *Chondracanthus aciculatus*, *Gelidiella tinerensis*, *Jania rubens*, *Polysiphonia* sp., *Pterosiphonia parasitica*, and one Chlorophyte species: *Bryopsis plumosa*. The presence and prevalence of turf algae at this site seem to reach maximum coverage values during the dry season (June-December each year). The author points to high urban development and sedimentation process as the main factor for the persistence and high coverage of turf algae and the low coverage of macro-algae species in reef systems near the coast (Vermeij et al., 2010). Fong et al. (2017)

suggest marked differences between the composition of algae in the geomorphological zones of ETP reefs; flats, for example, are typically dominated spatially by crustose coralline algae and algal turfs, while the crest often supports a slightly higher abundance of foliose macroalgae. The complex structure of branching coral colonies (*Pocillopora*) in the crest zones of the reefs; refuges and protects macroalgae species reducing the intense grazing of the highest biomass of damselfishes, sea urchins and other herbivores; however, there is much reef-to-reef variability concerning nutrients levels and oceanographic dynamics (Smith, 2005).

Preliminary laboratory observations of turf algae species collected on segments of monofilament nets (crest and slope zones of the reefs); suggest a similar composition pattern between hard substrates (Alcivar et al., 2021) and nets. However, it is necessary to focus on the colonization stages and succession process, where the differences in the presence and coverage of turf algae species could be more pronounced.

Turf algae-branching coral competitive interactions

The species composition of branching corals in marginal reefs of the continental coast of Ecuador is represented majorly by three species from *Pocillopora* genus: *Pocillopora capitata*, *P. damicornis* and *P. elegans*. *Pocillopora* is the most frequent reef-builder in the ETP region, and colonies are composed of different species of the genus hosting unique *Symbiodinium* clades that appear to exhibit a higher resilience to bleaching disturbances (Glynn et al., 2001; Baker et al., 2008; La Jeunesse et al., 2010) and fast growth rates. Trujillo (2017) assessed the growth of *P. capitata* y *P. elegans* in the Ureles (UR) marginal reef system of Jaramijo, Ecuador. The author suggests that under suboptimal conditions (high variability of temperature and turbidity), both species have

slow growth, with the highest growth values in the rainy season. On the other hand, branching corals species with fast-growing rates seems to have low success in competing with turf algae, and the decrease in the abundance of branching corals causes the reduction of the structure of the reef, with indirect effects on other reef organisms, i.e. fishes that use the complex structures typical of branching corals as shelters (Swierts & Vermeij 2016).

OBJECTIVES

General Objective

Determinate the impacts of derelict fishing gear in the degradation of marginal reef systems on the continental coast of Manabi-Ecuador.

Specific Objectives

The specific objectives of the present work were:

- i. Determinate the status of conservation of coral colonies and the direct and indirect impacts derived from the presence and persistence of derelict fishing gear on marginal reef systems of the continental coast of Manabí-Ecuador.
- ii. Analyze the influence of physical factors affecting the assessment of fish communities in marginal reef systems of the continental coast of Manabí-Ecuador.
- iii. Determinate the natural and human-induced factors affecting the composition and ecological attributes (species richness, diversity, and abundances) of fish communities in marginal reef systems of the continental coast of Manabí-Ecuador.
- iv. Compare the changes in the composition and ecological attributes (spatial distribution, species richness, diversity, and density) of echinoderm species in marginal and low-impacted reef systems of the continental coast of Manabí-Ecuador.
- v. Determinate the potential resilience capacity of marginal reef systems communities (coral colonies, invertebrates, and fish) as an effect of derelict fishing gear presence and persistence.

CHAPTER I

CHAPTER I: CORAL FRACTURE BY DERELICT FISHING GEAR AFFECTS THE SUSTAINABILITY OF THE MARGINAL REEFS OF ECUADOR.

Figueroa-Pico, J., Tortosa, F.S., & Carpio, A.J., 2020. Coral fracture by derelict fishing gear affects the sustainability of the marginal reefs of Ecuador. *Coral Reefs*, 39(3), 819–827.
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Abstract

Hard coral coverage contributes to increasing the structural complexity of coral reefs, provides biological resources and drives biological and ecological interactions among reef organisms. Declines in the structural complexity and coral diversity of tropical reefs, due to the influence of anthropogenic activities, have been reported around the world in recent decades; however, coral reefs on the continental coast of Ecuador have been poorly studied. From September 2017 to April 2018, the method of permanent belt transects, and quadrats was used to assess the status of coral (percentage of live, dead and fractured coral) to determine the contribution of derelict fishing gear to the process of coral fracture, which causes loss of structural complexity on two marginal coral-rocky reefs in the central coast of Manabi-Ecuador: Perpetuo Socorro and Ureles. Three geomorphological zones [crest (5-7m depth), slope (7-10m depth) and bottom (10-13m depth)] were assessed. Results show that the crest zone in Ureles reef was highly affected by the entanglement of nets compared with Perpetuo Socorro and identify derelict fishing gear as a key driver in the process of the fracturing and fragmentation of coral. Seasonal and site-associated factors also had a significant effect on the structural complexity of the reef studied. Destruction of coral in the crest zones drastically affects invertebrate and fish communities. We recommend a periodical assessment to measure the loss of structural complexity plus the implementation of a recovery program for the reefs studied that involves the education, active participation and collaboration of artisanal fishermen, governmental organizations and universities.

Keywords: anthropogenic activities; community effects; coral fracture; dead coral; derelict fishing gear.

1. Introduction

Over the last few decades, coral reefs worldwide have faced increased threats derived from rising carbon dioxide (CO₂) levels, and ocean temperatures, and lower aragonite saturation levels associated with climate change and anthropogenic stressors (Burke et al., 2011, Hughes et al., 2017). However, recent studies have demonstrated that marginal High Latitude and Eastern Tropical Pacific reefs habitats have adapted to resist the high fluctuations of physical variables (providing them with a greater capacity to adapt, resist and expand in future climate-changing scenarios (Couce et al., 2013; Freeman, 2015; Camp et al., 2018).

Hard corals contribute to the structural complexity of coral reef habitats, providing essential resources (food, shelter, places for reproduction) for many reef organisms and mediating biological interactions among coral-associated organisms (Pratchett et al., 2008; Pratchett et al., 2011; Coker et al., 2012). However, declines in the structural complexity and coral diversity of tropical reefs due to anthropogenic effects have been reported in the Caribbean and the Indo-Pacific regions in the last few decades (Gardner et al., 2003; Bruno and Selig, 2007; Alvarez-Filip et al., 2009; Rogers et al., 2014). By other hand, coral communities in the Eastern Tropical Pacific (ETP) have demonstrated a high degree of resilience to diverse natural biotic and physical disturbances, with robust recovery at several localities in recent years (Glynn et al., 2017a), however, the anthropogenic influence and effects over reefs in this region remain briefly documented (see Cortés and Reyes-Bonilla, 2017).

The negative effects of anthropogenic activities associated with tourism and fishing on coral reefs have been addressed by multiple authors worldwide with the primary description of *i*) the effects of anchoring on coral and marine diversity (Dinsdale and Harriott, 2004; Saphier and Hoffmann, 2005; Fava et al., 2009; Forrester et al., 2015;

Flynn and Forrester, 2019), *ii)* the effects of blast fishing on reefs (Fox and Caldwell, 2006; Raymundo et al., 2007; Praveena et al., 2012; Fuchs, 2013), and *iii)* the effect of faunal removal of fish and benthic invertebrates (Calderon-Aguilera et al., 2019; Eddy et al., 2019; Cáceres et al., 2020). However, the effects of derelict fishing gear or entangled nets on coral, with the subsequent fracture and breakage due to their removal, are poorly documented.

Reefs on the continental coast of Ecuador are mostly rocky subtidal habitats (≤ 20 m in depth) that provide suitable environmental conditions for the occurrence of a few reef-building corals species and the development of coral communities (Glynn, 2003). Coral communities of Ecuador had been described through the years with a focus in the diversity, coverage of coral and associated fauna from Machalilla National Park (MNP) and Galapagos Archipelago (Glynn, 2003) and through recent information about diversity and coral distribution along with the mainland Ecuador and Galapagos (Glynn et al., 2017a). Coral communities on rocky reefs of Ecuador represent the Southernmost distribution in the ETP. Due to their ability to withstand sub-optimal conditions and tolerate the local fluctuation of environmental conditions (but high biological productivity), these reefs can be classified as marginal (Kleypas et al., 1999; Perry and Larcombe, 2003; Wicks et al. 2010). These ecosystems are present in areas of high levels of turbidity (Glynn, 2003; Figueroa-Pico et al., 2020) due to the interaction of marine currents and tides (Vera et al., 2009), and an annual up-welling event (January-April each year) with changes of temperature between 1-10°C (Moreano, 1983). Heavy deposition of sediments occurs locally during the rainy season (Soledispa, 2011) and domestic and industrial wastewaters are released near to these habitats as well (González and González, 2017, Velasco et al., 2019). Concerning anthropogenically induced impacts, Flachier and Sonnenholzner (1997), Terán (1998), Glynn (2003) and Baquero-Gallegos et al. (2006)

identified and briefly described fishing activities with monofilament nets, tourism-associated anchoring on the reefs and the harvesting of corals as the primary threats to the coral-rocky reefs in the Machalilla National Park (PMN). However, no reliable data on this topic is available or has been published yet. Zurita (2007) suggested the lack of economic alternatives as a key factor that forces artisanal fishermen to use non-selective and highly destructive fishing gear, such as monofilament nets which can negatively affect rocky and coral habitats along the continental coast of Ecuador. Figueroa-Pico et al. (2016) described the composition and spatial distribution of marine litter on rocky reefs along the continental coast of Ecuador and showed how the entanglement of monofilament nets could impact coral colonies in the crest zones. The structural complexity of the reefs studied plays an important role in the dynamics of invertebrate and fish communities in the crest zones due to the high coverage provided by branching hard coral such as *Pocillopora elegans*, *P. damicornis* y *P. capitata* (~30-50% average percentage/m²), which tolerate constant changes of turbidity and temperature (Figueroa-Pico et al., 2016). The current study examined two sites where local coral rocky reef exhibit different levels of disturbance relative to direct and indirect anthropogenic impacts. One site (PS, see study area in methods) exhibit intensive sedimentation, high coverage of turf algae (Alcivar, 2015), grazing effects and trophic overlap of sea urchins (Cabanillas-Terán et al., 2016). In the second site (UR), we found low rates of light penetration and slow coral growth rates (Trujillo, 2017). Other impacts identified at both sites include overfishing, anchoring, and persistent of marine debris and derelict fishing gear on the crest zones (Figueroa-Pico et al., 2016).

Considering the implications for future global coral reef management, it is important to put more emphasis on the conservation of marginal reefs to assure their sustainability in time (Couce et al., 2013). The main goal of the present work was to assess the impacts

of derelict fishing gear and entangled nets on patches of hard coral to understand the process of coral fracture and fragmentation at the sites, reef zones, and during different seasons as a potential driver of structural complexity loss on the marginal coral-rocky reefs of Ecuador.

2. Materials and methods

2.1. Study area

The study was conducted in Manabi Province, on the continental coast of Ecuador. Two study sites were chosen: 1) Perpetuo Socorro (PS) ($00^{\circ} 55.637$, S $80^{\circ} 44.353$, W), located 2.3 km off the coast of Manta, and 2) Ureles (UR) ($00^{\circ} 54.113$, S $80^{\circ} 38.863$, W), located 4.6 km from the nearest port in Jaramijo (Figure 1). Both sites are marginal reefs that share structural similarities: rocky bottoms between 5 and 13 m deep, and three geomorphological areas treated here as “zones”: (1) the crest, 5-7 m deep, a rocky substratum with patches of branching coral species such as *Pocillopora* spp.; (2) the slope, 7-10 deep, a rocky substratum with small patches of branching coral colonies such as *Pocillopora* spp. colonies or massive corals such as *Porites lobata*, and (3) the bottom 10-13 m deep, a mixed substratum with rock, sand, gravel, and patches of massive coral species such as *Pavona clavus*, that stabilizes at a maximum depth of 13m.

2.2. Coral status and human-induced variables

Sampling was conducted between 2017 and 2018 in two seasons: 1) the dry season: September-December 2017, with an annual mean rainfall of 2 mm and 2) the rainy season January-April 2018, with an annual mean rainfall of 143 mm. At both sites, we assessed a total of 18 days. We surveyed a total of 270 permanent belt transects of 20 x 2.5m as

survey units (135 per site) each on the crest (CR), slope (SL) and the bottom (BT) zones (45 transects per zone at each site). Percentages of live coral (%LC), dead coral (%DC) and fractured coral (%FC) were estimated as a perspective of 2D area within 5 (1x1-m) quadrats randomly located within every belt transect in all study sites and zones. A mean of %LC, %DC and %FC coral for each belt transect was calculated through the sum of the percentage in each quadrat divided between the five survey units. Plan-viewed photographs of each quadrat were taken always at the same distance (1.5m above from the substrate) and later analyzed with the software ImageJ 1.80 free version (Abramoff et al. 2005). Finally, to assess the impact of derelict fishing gear (DFG) over coral colonies, we counted and recorded the number of DFG segments of monofilament nets in every belt transect in each site and zone. In this category, we only included segments of DFG over coral colonies with a maximum area of 4m² considering the highest area reached by a single coral colony observed in the study sites. For analysis and comparative purposes, the segments were called items of DFG and extrapolated to an area of 100m².

2.3. Statistical analysis

The calculated average of %LC, %FC, %DC and DFG (absences of normal distribution) were primarily analyzed with a Kruskal Wallis non-parametric analysis of variance for the factor “zone” or “geomorphological zone”.

Data for fractured and dead coral were highly correlated, so we performed only one model with fractured coral as the dependent variable. A General Linear Mixed Model (GLMMs) was performed using Infostat (Di Rienzo et al., 2018) with an extension of R software (R Core Team, 2013). Three fixed factors were entered in the model: site with two levels (UR and PS), zone with three levels (BT, SL, and CR), and season with two levels (dry and rainy season). The percentages of live coral (%LC) and derelict fishing gear (DFG)

were entered in the model as covariates. The transects were entered in the model as a random factor. The model was fitted to a Poisson distribution with a log link function. Rather than using criteria based on parsimony to select the 'best model' (which favours precision *vs.* bias) we used the full models: (i) because our models had high degrees of freedom (five explanatory variables) with no need to guard against over-fitting; (ii) to protect from the bias of regression coefficients; and (iii) to preserve the accuracy of confidence intervals while using other non-collinear factors for control purposes (multiplicity adjustment, while our understanding of the underlying biological processes led us to believe that the important variables to control for had been included). The assumptions of normality, homogeneity and independence in the residuals were assessed in models with a normal distribution function (Zuur et al., 2009). The significant *p*-value was set at *p* = 0.05.

3. Results

3.1. Descriptive results

Live coral percentage (%LC) was especially high and variable in the crest zones of both sites (*p*<0.001) (Table 1). Fractured coral (%FC) was high in the crest and bottom zones of the UR site (*p*<0.001) and on the crest of PS site (*p*<0.001) (Figure 1). Dead coral (%DC) was especially high in the BT zone of UR (*p*<0.001) (Table 1). Finally, the amount of derelict fishing gear, such as items of DFG, was 5-31 items x 100m⁻² in UR, while at PS it was 1-16 items x 100m⁻² in the crest zones and had low values for the SL and BT zones with significant differences between sites and zones (*p*<0.001) (Table 1).

Table 1. Descriptive statistics for coral status (%LC=Percentage of live coral and %DC=Percentage of dead coral) and human-induced variables (%FC=Percentage of fractured coral and DFG=Derelict fishing gear) depending on sites (UR=Ureles and PS= Perpetuo Socorro) and zones (CR=Crest, SL=Slope and BT=Bottom). Kruskall Wallis test results, p-value =* <0.05 ; ** <0.01 ; *** <0.001 .

Site	Variables	Zones												H value	p value		
		CR				SL				BT							
		Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max				
UR	%LC	50.11	16.2	25	82	9.49	8	0	19	20.5	3	14	26	111.4	***		
	%DC	15.13	4.08	8	25	0	0	0	0	28	17	11	52	94.3	***		
	%FC	19.09	6.63	12	35	2	2.6	0	7	22.7	8.3	12	38	91.4	***		
	DFG	14.87	6.08	5	31	0.91	0.6	0	2	2.91	1.8	1	8	104.3	***		
PS	%LC	30.84	19.3	4	68	35.3	18	5	67	1.62	1.7	0	5	89.1	***		
	%DC	8.87	4.36	1	18	0	0	0	0	7.91	6.7	0	17	58.8	***		
	%FC	11.38	6.1	4	25	1.76	2.4	0	8	7.91	6.7	0	17	47.1	***		
	DFG	7	3.83	1	16	1.04	0.7	0	3	0.71	0.5	0	1	79.3	***		

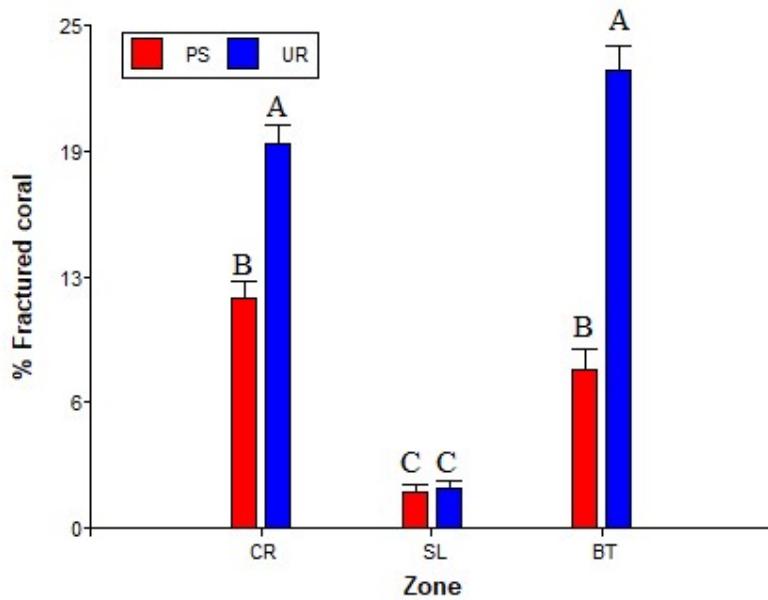


Figure 1. Mean values (\pm S.E.) of fractured coral in different zones (CR= Crest, SL= Slope, and BT=Bottom) in the two study sites (UR=Ureles and PS=Perpetuo Socorro). Capital letters (A, B, C) indicate significant differences ($P = 0.05$) between zones according to Fisher LSD tests.

3.2. The relationship of fractured coral with the study variables

The results of the GLMMs show that the percentage of fractured coral was significantly affected by site and zone factors ($p<0.001$), with the highest values at the UR site and in the crest and bottom zones (Table 2). The percentage of live coral was a strong positive predictor of fractured coral in the study sites ($p<0.001$) (Table 2). We found significant interactions between the DFG and season (higher coral fracture in the rainy season), site (higher coral fracture at the UR site) and zone factors (higher coral fracture on the crest than in the slope zones) that suggest that the fracture of coral colonies in the studied sites, zones and seasons is driven by DFG. (Table 2, Fig. 2).

Table 2. F and P-values and coefficients of the variables included in the mixed model to explain fractured coral. (* $p<0.05$; ** $p<0.01$; *** $p<0.001$). Coefficients for the level of fixed factors were calculated using reference values of Dry in the variable ‘Season’, ‘PS’ in the variable ‘Site’, and ‘BT’ in the variable ‘Zone’.

Variables	F-value	Coefficient \pm S.E.
Season	0.59 n.s.	Rainy = -0.5 ± 0.07
Site	189.12 ***	Site UR = 0.95 ± 0.07
Zone	189.00 ***	Zone CR = -1.11 ± 0.09 Zone SL = -2.50 ± 0.14
%LC	147.23 ***	= 0.22 ± 0.02
DFG	1.75 n.s.	= 0.03 ± 0.02
Season x DFG	6.51 **	Season Rainy DFG 0.01 ± 0.01
Site x DFG	70.83 ***	Site UR DFG -0.08 ± 0.01
Zone x DFG	11.99 ***	Zone CR DFG 0.09 ± 0.01 Zone BT DFG -0.07 ± 0.12

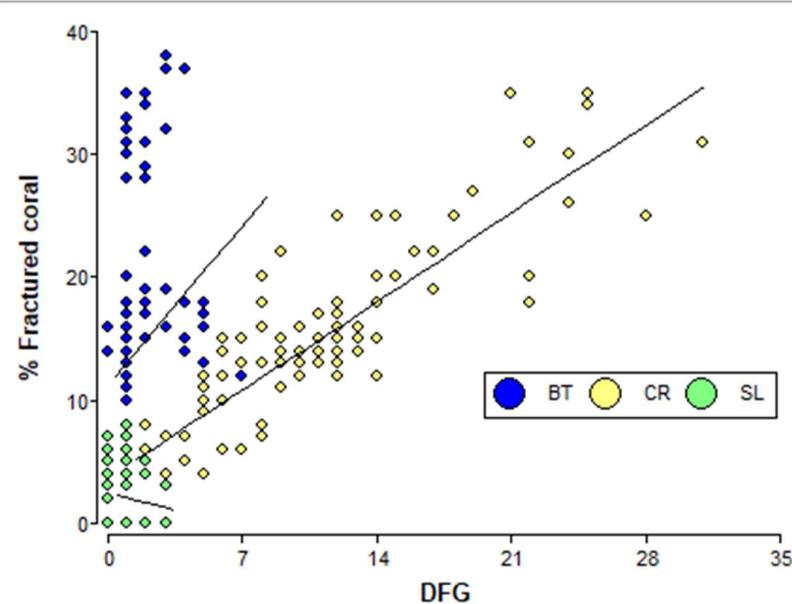


Figure 2. Percentage of fractured coral in relation to derelict fishing gear (DFG= Derelict fishing gear) (items x 100m²) in three 3 zones (CR=Crest, SL=Slope and BT=Bottom)

4. Discussion

Our work is the first systematic initiative to quantify the growing and persistent problem of coral fracture caused by entangled nets over marginal coral-rocky reefs in Ecuador, a topic briefly described by Figueroa-Pico et al. (2016) which primarily focused on explaining the possible impact of monofilament nets on coral colonies in the crest zones. Few, but important, efforts have been made worldwide to explain the mechanisms of the coral fracturing by the anchoring of boats and DFG leading to the subsequent loss of structural complexity in coral reefs (Dinsdale and Harriott, 2004; Saphier and Hoffmann, 2005; Fava et al., 2009; Flynn and Forrester, 2019). However, reliable data about the fracturing of coral by entangled nets worldwide is still poorly known.

In this study, we found a strong effect of the site on fracturing. The UR site showed more coral coverage compared with the PS site (Table 1). The study sites are traditional areas of artisanal fishing activities throughout the year (line and net fishing). However, despite its distance from the coast, the UR site is subject to higher seasonal fishing pressure using monofilament nets than the PS site, due to dependence on available temporal fishing resources, so the probabilities of finding more coral fractured by entanglement increase. The interaction between DFG and site supports the aforementioned conclusions and suggests that the UR site suffered more fishing pressure than the PS site.

Other important predictors of fractured coral were geomorphological zone and the percentage of live corals (Table 1). Crest and slope zones are structurally more complex than the bottom (Figueroa et al., unpublished data) supported higher coverage of branching corals like *Pocillopora* spp., with faster growth rates but fragile and vulnerable to physical damage or massive coral forms such as *Porites lobata*, which are more resistant to physical damage (Dinsdale and Harriott, 2004; Pratchett et al., 2015). Live

coverage of *Pocillopora* spp. corals on the crest zones of the study sites $\sim 130\text{m}^2$ in UR and $\sim 80\text{m}^2$ in PS, which represents about 30 to 50% of the total area of the crest (Table 1). Baums et al. (2014) reported aggregations of 53m^2 , 104m^2 , and 291m^2 in three lava pools of Isabela Island in the Galapagos Archipelago although authors did not mention the total sampled area to estimate the percentage of the area covered by coral. However, the coral aggregations in Isabela Island were at different depth (2-3m) and oceanographic conditions showing the high capacity of *Pocillopora* species to colonize and develop in different habitats and environmental conditions. Therefore, the high coverage of branching corals on the crest zones creates a greater probability of fracturing when artisanal fishermen attempt to remove entangled nets. According to Figueroa-Pico et al. (2016), artisanal fishermen deploy their fishing gear in the areas surrounding the reefs, so temporal changes in speed and direction of the currents at low and high tide could be the factors that cause their entanglement on the reef crests, making removal difficult and contributing to coral breakage by mechanical damage. After the breaking of the coral colony, fragments of *Pocillopora* spp. may remain in the crest zone where has more probabilities to survive or fall down the slope from the crest and, depending on the physical configuration of this zone, remain and colonize the rocks or simply fall directly to the bottom where the lack of optimal biotic and physical conditions, i.e., size of the coral fragment (Baums et al., 2014; Lizcano-Sandoval et al., 2018) and high levels of sedimentation, cause the live fragments to bleach and die due to the action of algae and cyanobacteria (Lizcano-Sandoval et al., 2018) with the subsequent significant effects on the coral and the resilience of the reefs (Fava et al., 2009).

We found high levels of DFG (monofilament nets) on the crests, with 1-31 items $\times 100\text{m}^{-2}$ at the UR site and 1-16 items $\times 100\text{m}^{-2}$ at the PS site (Table 1). Figueroa-Pico et al. (2016) reported similar results at the same study sites and suggested that derelict fishing

gear and ghost nets persist on crest zones over time. We found a strong interaction between DGF and fractured coral on the crest zones that suggest the high vulnerability of these zones to coral fracture with a direct negative effect on coral coverage and indirect effects for invertebrate and fish communities due to the loss of structural complexity. Natural factors influencing the fracturing of branching colonies had been widely reported, e.g. the activity of corallivorous fish and urchins, feeding behavior of turtles (Glynn, 2004) and reef sharks (Jimenez, 1997), and the exposure of the coral colonies to the action of low tides or shallow waters (Castrillón-Cifuentes et al., 2017). Mentioned factors and their interactions are difficult to quantify and their influence was not considered in our study. On the other hand, as a response from environmental pressure, fragmentation is the most common and important asexual reproductive strategy for pocilloporids in the Tropical Eastern Pacific that helps to maintain the integrity of the populations through time and avoid local genetic extinction (Baums et al., 2014; Glynn et al., 2017b; Castrillón-Cifuentes et al., 2017). This fragmentation process is initiated and exacerbated by bioerosion (sponges, mollusks, echinoderms, and endolithic organisms) and corallivorous organisms (pufferfishes) that weakens coral skeletons and makes colonies susceptible to physical damage by the action of waves and storm surge (Reaka-Kudla et al., 1996; Glynn et al., 2017b; Alvarado et al., 2017). The depth range on crest zones (5-7m) in our study sites favours the growth of Pocillopora colonies and could be an important factor limiting the natural fracturing and fragmentation of the colonies by the action of the waves or swells common in shallow water colonies (< 3m depth) (Taebi and Pattiarchi, 2014; Baldok et al., 2019) of Galapagos Archipelago and some localities of Machalilla National Park, also susceptible to anomalies of warm water related to ENSO events (Glynn et al., 2018).

Fava et al. (2009) suggested that the fracturing of coral causes a coral rubble rain that might have a physically negative impact on the reef and create patchiness that leads to habitat fragmentation. Also, Pratchett et al. (2011), Fuchs (2013), and Russ and Leahy (2017) suggested that the fracture and decrease in live coral cover on reefs would lead to a considerable decline in the richness of invertebrate and fish species and abundance, although marginal coastal reefs are inhabited by coral fauna adapted to survive under conditions markedly different from those traditionally accepted as ideal for the optimal functioning of a coral reef (Hennige et al., 2010; Browne et al., 2012). Further, Flynn and Forrester (2019) argued that many reef fish taxa depend on three-dimensional reef structures for shelter and the *flattening process* of reefs with heavy anchorage could explain the reduction in the density of most functional groups of adult fish i.e. scrapers and excavators, spongivorous, benthic carnivorous, piscivorous, and omnivorous. Further, the entangled and derelict nets over the branching coral are gradually colonized by turf and fleshy algae consortiums that change their composition over time and could dynamize the degradation of coral via disruption of ecological processes, detrimental smothering effects, diseases and death of corals, and decline of invertebrate and fish communities (Figueroa-Pico et al., 2016; Galgani et al., 2018; de Carvalho-Souza et al., 2018; Lamb et al., 2018; Valderrama et al., 2018). Barott et al. (2012) suggested that coral-turf algae interaction at the reef scale negatively affects the physiology of coral colonies with a reduction in the production of oxygen of the coral halobiont and the subsequent limitation of growth, lower coral fecundity and inhibition of larval settlement. This may impact corals on multiple spatiotemporal scales and influence the structure of benthic coral reef communities. Swierts and Vermeij (2016) suggest a strong relationship between coral growth forms and their success in competitive interactions with turf algae. These authors argue that branching corals with faster growth rates are the least successful

rate competing with turf algae. This evidence suggests that coral colonies of *Pocillopora* spp., common in the study sites and crest zones, could be highly vulnerable to the detrimental effects of turf and fleshy algae consortiums that grow over DFG. Their interrelationship must be studied in more depth to understand the dynamics and the long-term effects concerning coral traits, invertebrate, and fish communities.

Season by itself was not influential enough to explain coral fracturing on the reefs studied; however, we found an interaction between the presence of derelict fishing gear (DFG) and season (accentuated in the rainy season in UR site). There was a higher presence of DFG in the rainy season compared to the dry season, a repeated pattern observed in the same sites during the last years (Personal observations). An important fishing resource, such as the triggerfish *Balistes polylepis*, an active species that feeds over the sandy bottom adjacent to rocky reefs (Hobson, 1965; Robertson and Allen, 2015) reach the highest abundance in the rainy season (January-April) due to an spawning aggregation process (Erisman et al., 2010), this makes this species a temporary target for the artisanal fleet of Jaramijo. Other fish species with similar aggregation pattern in the rainy season but without commercial importance for the artisanal fleet of Jaramijo are the long spine balloonfish *Diodon holacanthus* and round stingrays *Urobatis* spp. (no published data). At the same time, changes in the direction and intensity of currents and strong groundswells are common in this season (Vera et al., 2009) increasing the probabilities of fishermen losing monofilament nets due to entanglement.

Our findings suggest that derelict fishing gear (entangled nets) is a driver in the fracture and fragmentation of pocilloporid corals on the marginal rocky reefs of the continental coast of Ecuador, which mainly affects the structural complexity of the crest zones with direct implications for the sustainability of resident invertebrate and fish communities. We strongly recommend a periodic assessment of the structural complexity

of the reefs and the implementation of a recovery program for the reefs affected that involves the education and active participation and collaboration of artisanal fishermen, governmental organizations and universities.

CHAPTER II

CHAPTER II: TURBIDITY: A KEY FACTOR IN THE ESTIMATION OF FISH SPECIES RICHNESS AND ABUNDANCE IN THE ROCKY REEFS OF ECUADOR

Figueroa-Pico, J., Carpio, A.J., Tortosa, F.S., 2020. Turbidity: a key factor in the estimation of fish species richness and abundance in the rocky reefs of Ecuador. *Ecol. Indic.* 111, 106021.
<https://doi.org/10.1016/j.ecolind.2019.106021>.

Abstract

The effectiveness of using standardized sampling methods for fish communities in coral and rocky reefs has been widely discussed because it largely depends on the experience and skill of the observer, availability of high-definition equipment and the stability of local environmental parameters. The rocky reefs in Ecuador have highly variable conditions of turbidity, which can generate biases in the sampling of reef fish. The present work compares the effectiveness of detection of two sampling methods: 1) observer-band transects and 2) video-transects, as tools to determine the composition of fish communities in two rocky reefs subjected to high anthropic pressure and high variability in the conditions of turbidity. To achieve this goal, 48 transects of 100 m and variable-width on the dependence of turbidity conditions were performed in three geomorphological reef zones: the crest, slope, and bottom, where a community of fish was sampled from September 2017 to April 2018 using both methods. The results showed significant differences in the fish abundance recorded depending on the sampling method, the video-transect method was more efficient for the estimation of abundance. Comparison of the survey methods in reef zones showed that video-transects are more effective in detecting significant differences in abundance on the slopes of the reefs in comparison with observer-band transects. Turbidity significantly affected the abundance of fish detected by both sampling methods. Our results suggest that the video-transect method is more efficient to record fish abundance with respect to the observer-transect method under different conditions of turbidity.

Keywords: detectability, fish, rocky reefs, survey methods, video-transects

1. Introduction

Coral and rocky reefs are complex and productive marine ecosystems that support high but very sensitive and vulnerable biodiversity (Knowlton, 2001; Kulbicki et al., 2013; Parravicini et al., 2013). The diversity of invertebrates and fish in these ecosystems can be affected by natural stressors (deposition of sediments and turbidity) (Freitas et al., 2019) or by the direct or indirect influence of anthropogenic stressors: overfishing, derelict fishing gear, dredging or sewage pollution (Muthukrishnan and Fong, 2014; Jones et al., 2016; Valderrama et al., 2018; Abaya et al., 2018). In terms of conservation, these ecosystems and their diversity need a suitable way to be assessed (Rotherham et al., 2007), taking into consideration the dynamics of local conditions of physical parameters (Bayley and Mogg, 2018). For coral and rocky reef systems, an underwater visual census (UVC) with strip transects (fixed length and width) is the most frequent method for non-destructively surveying community dynamics (Kulbicki et al., 2010; Bosch et al., 2017).

The effectiveness of the detection of standardized sampling methods for fish communities in coral and rocky reefs has been discussed worldwide because it is closely related to the: experience, skill and swimming speed of the observer (Bernard et al., 2013; Henriques et al., 2013; Jones et al., 2015; Daros et al., 2018), availability of high-definition equipment (Bower et al., 2011; Assis et al., 2013; Mallet and Pelletier, 2014; Warnock et al., 2016; Wilson et al., 2018), stability of local environmental parameters (Edgar et al., 2004; Bozec et al., 2011; Usseglio, 2015; Wartenberg and Booth, 2015) and the activity of the fish group (diurnal or nocturnal), their detectability (conspicuous or cryptic species) and their mobility (Thresher et al., 1981).

The importance of turbidity has been underestimated by some authors as a factor affecting fish detectability (Pais and Cabral, 2017). However, underwater turbidity is a limiting factor for visual techniques, whether UVC, photo or video (Mallet and Pelletier,

2014). Travers et al. (2018), suggest that surveys taking place in locations with high turbidity have only minor possibilities of obtaining reliable data when using methods that require clear visibility, such as remote underwater video systems or underwater visual census (UVC). Our study highlights the need to implement complementary sampling techniques to monitor ecological changes, in the various dimensions of biodiversity (Bosch et al., 2017).

Information about fish community assessment on the continental coast of Ecuador is scarce and is only available through general technical reports of ichthyofauna in Machalilla National Park (MNP) or derived from unpublished data obtained from experienced divers. Flachier and Sonnenholzner (1997) and Terán (1998), describe a total of 106 species associated with rocky reefs and coral patches in MNP using UVC, these reports also describe the diversity of fish according to the significant habitat complexity of the sites studied.

The rocky reefs on the continental coast of Ecuador are present in areas of highly variable conditions of turbidity; some areas maintain good conditions of visibility all around the year whereas in other areas turbidity may change rapidly throughout the year, this variability of conditions may produce errors and biases during fish sampling. Local changes of turbidity mainly occur due to the interaction of physical variables such as marine currents and tides (Vera et al., 2009), an annual up-welling event (January-April each year) (Moreano, 1983), the increase of turbidity caused by deposition of sediments in the rainy season (Soledispa, 2011) and the release of domestic and industrial wastewater. The present work compares the effectiveness of detection of two sampling methods: 1) Observer-Transect Method and 2) Video-Transect Method, to record the fish communities on two rocky reefs under high fluctuations of turbidity and analyze the

influence of the real abundance of fish as determinant in identifying trends in the species richness and abundance of Ecuadorian reefs.

2. Materials and Methods

2.1. Study area

The study was conducted in the province of Manabi, the continental coast of Ecuador. Two study sites were chosen: 1) Perpetuo Socorro (PS) ($00^{\circ} 55.637' S$ $80^{\circ} 44.353' W$), located 2.3 km off the coast of Manta and 2) Ureles (UR) ($00^{\circ} 54.113' S$ $80^{\circ} 38.863' W$), located 4.6 km from the nearest port in Jaramijo (Figure 1). Both sites share structural similarities: rocky reefs between 6 and 13 m in depth. At both sites, we can distinguish three geomorphological areas (crest, slope, and bottom). Identified impacts at both sites include high levels of sedimentation, overfishing, anchoring, marine litter, and derelict fishing gear. The sites described also share similarities in fish diversity (65-70 species associated with rocky reefs) and have high biological productivity (personal observations). Both sites are traditional areas of artisanal fishing activities throughout the year (line and net fishing, autonomous and semiautonomous diving) and tourism (autonomous diving) (Figueroa-Pico et al., 2016).

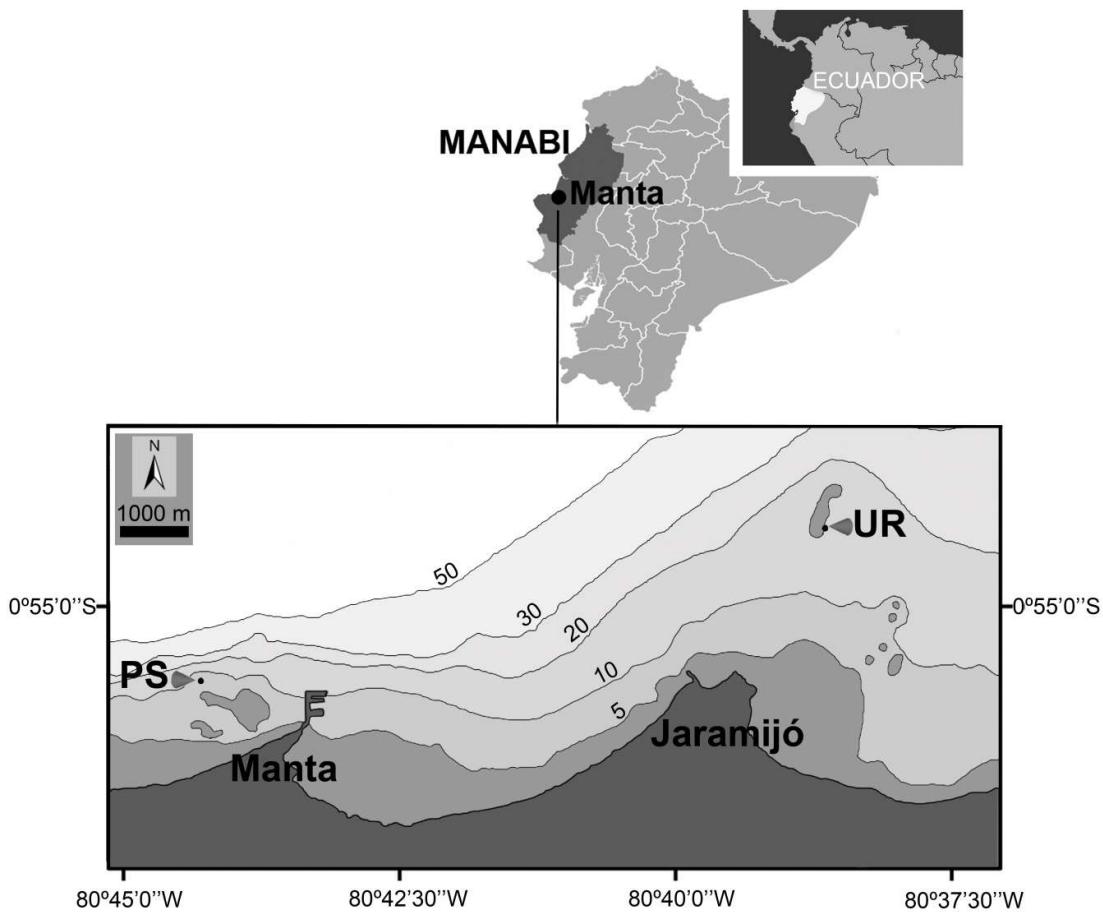


Figure 1. Map of study sites represented as PS (Perpetuo Socorro) in Manta and UR (Ureles) in Jaramijo.

2.2. Survey methods

Sampling was conducted between September 2017 and April 2018 at each study site with a total of 16 hours of data recording. Two methods were simultaneously used to record the species richness and abundance: 1) the Observer-Transect Method (OTM) performed by a diver with experience in the identification of fish species and 2) the Video-Transect Method (VTM) performed by a diver with a GoPro Hero Underwater High Definition camera and Evolve light of 900 lumens. For both methods, 48 permanent transects of 100 m (five subunits of 20 m or 240 transect segments) and variable width

(max. 2.5 meters on each side from the central line of the strip transect) in relation to turbidity levels were used as survey units on the bottom (BT), slope (SL) and crest (CR) zones (16 transects per zone). In order to minimize disturbance, both methods were carried out simultaneously by two divers swimming side by side during the same diving session (standardized speed 0.17 m/s and elevation 1m) in independent surveys in the above-mentioned zones, and the same route was repeated during the study period in each zone. Total survey time was 8 hours for each method with no variations between both methods. During every sampling session, the number and the abundance of every detected fish species were recorded for each method. OTM data was recorded on slates, while, VTM records were later watched by the same experienced observer and the number of fish species and abundance were registered.

Vertical and horizontal turbidity was estimated at the surface and underwater with a Secchi disk, 30 cm in diameter. The range of horizontal turbidity fixed in the present study was 1-7 m, and it was recorded in every survey. No survey was performed when turbidity was less than 1 m.

2.3. Statistical analysis

To evaluate the factors affecting the species richness and abundance of fish, we used four Generalized Linear Mixed Models (GLMMs). In these models, the species richness (model 1) and abundance (model 2) were used as response variables. These set of models were divided into two subsets of models: 1) (model 1a for species richness and model 2a for abundance) for all turbidity conditions ($N=240$) and 2) (model 1b for species richness and model 2b for abundance) for turbidity conditions of less than 2 meters ($N=70$), where we assume that the probability of detection is 1, and therefore we can distinguish the

effects of abundance and detection. In these models, two fixed factors were included: the survey method with two levels (VTM and OTM) and the zone with three levels (BT, SL, and CR). The turbidity was entered in the model as a covariate. The site, transects (nested to the site), and segments (nested to transect) performed during the survey period were entered in the model as random factors. In addition, the interaction zone * survey method and turbidity* survey method were also included in all models. A Poisson distribution with a log-link function was used in all models.

Rather than using criteria based on parsimony to select the 'best model' (which favour precision vs. bias) we used the full models: (i) because our models had high degrees of freedom and there was no need to prevent overfitting, (ii) to protect from the bias of regression coefficients, and (iii) to preserve the accuracy of confidence intervals while using other non-collinear factors for control purposes. Such factors included multiplicity adjustment, while our understanding of the underlying biological processes led us to believe that the important variables to control for had been included. In addition, Fisher's LSD post-hoc test within the mixed analysis was applied to check for response differences among different levels of categorical variables (zone and survey method) and their interaction. Statistical analyses were performed using InfoStats with an extension of R statistical software.

3. Results

A total of 48 transects (16 transects in each zone; BT, SL, and CR) were performed using both methods during the study period. Turbidity had a variation of between 1-7 meters and was highly fluctuated during the study period in the BT zone (Mean \pm SD; 3.54 \pm 0.87) (Figure 2).

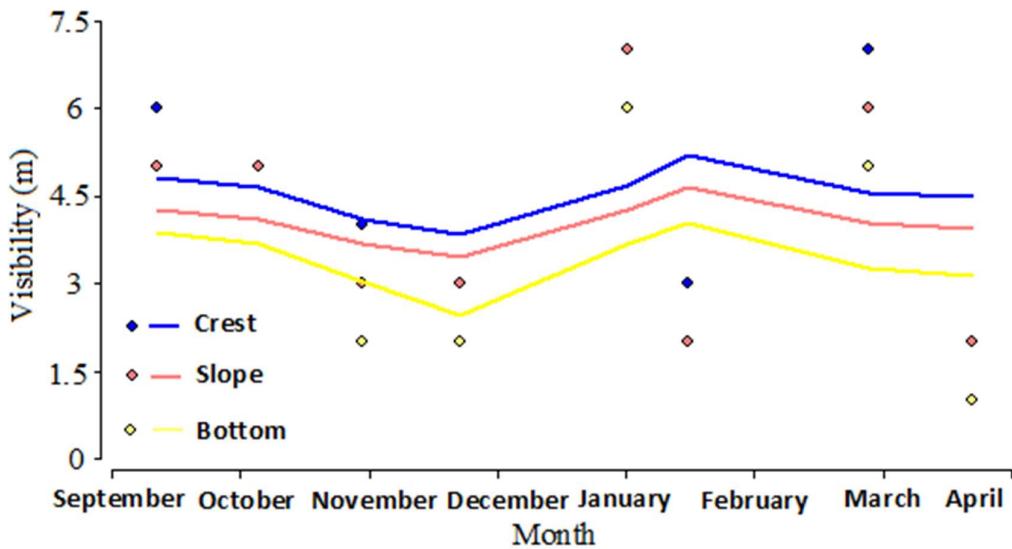


Figure 2. Temporal evolution of the visibility in each zone (crest, slope, and bottom)

3.1. Fish species richness estimation and survey methods.

In the monthly transects performed in the three zones (CR, SL, and BT), we counted a maximum number of 22 species using OTM whereas 31 species were detected with VTM. VTM detected nine species more in comparison with OTM. These were cryptic and nocturnal species such as *Synodon evermanni*, *Plagiotremus azaleus*, *Halichoeres dispilus*, *Alphestes multiguttatus*, *Stegastes flavilatus*, *Cirrhitichthys oxycephalus*, *Apogon pacificus*, *Apogon dovii* and *Sargocentron suborbitalis*. The species richness detected did not differ significantly between survey methods for both the models proposed: 1) all turbidity conditions ($N=240$) and 2) turbidity conditions <2 meters ($N=70$), where we assume that the probability of detection is 1 (Table 1a and 1b). The factor zone had an effect on the detectability of fish species richness in model 1a with all distances (Table 1a, Figure 3), species richness values were lower in CR zones in

comparison with SL and bottom zones. The interaction between survey method and turbidity was not significant, so turbidity equally affected the detection of the fish species in both methods (Table 1a and 1b).

Table 1. General models of sequential hypothesis tests for species richness

- a. Model of sequential hypothesis tests for fish species richness considering all turbidity conditions (N=240)

	numDF	denDF	F-value	p-value
Survey method	1	232	0.01	0.9153
Zone	2	232	8.89	0.0002
Turbidity	1	232	2.37	0.1247
Survey method x zone	2	232	0.18	0.8363
Survey method x <u>turbidity</u>	1	232	0.08	<u>0.7824</u>

- b. Model of sequential hypothesis tests for fish species richness considering turbidity conditions <2m (N=70) and assumption for the probability of detection =1.

	numDF	denDF	F-value	p-value
Survey method	1	62	0.20	0.6575
Zone	2	62	0.78	0.4633
Turbidity	1	62	2.02	0.1602
Survey method x zone	2	62	0.05	0.9508
Survey method x <u>turbidity</u>	1	62	0.22	<u>0.6408</u>

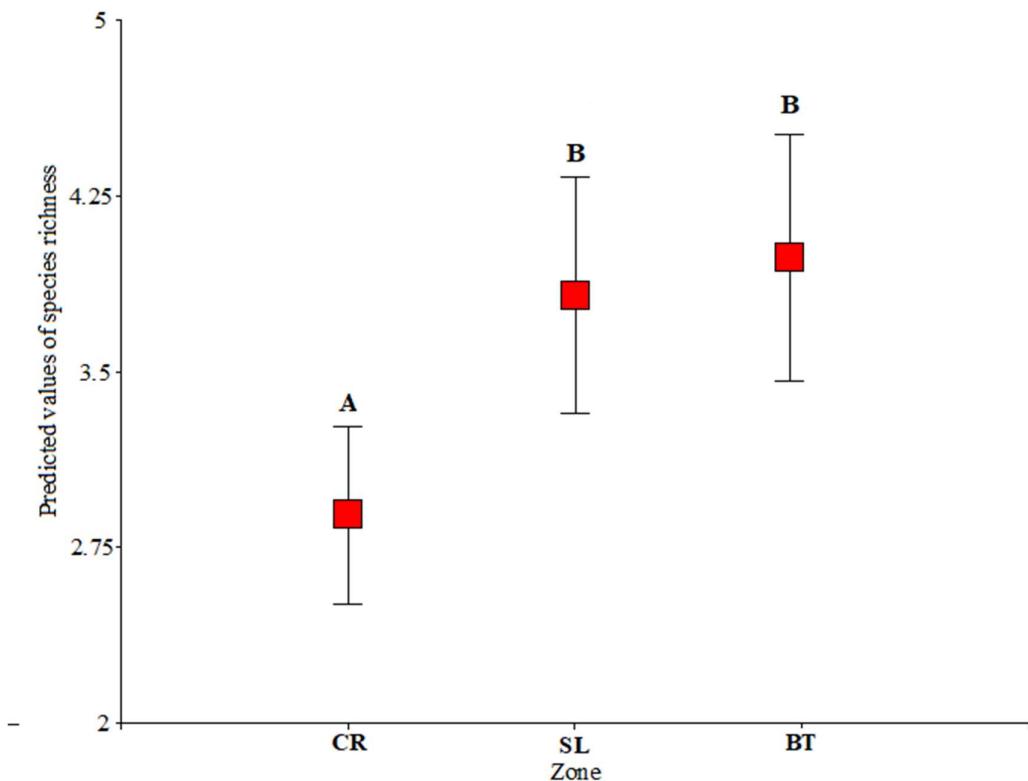


Figure 3. Predicted values (median \pm 95% CI) of species richness (nº of species) as a function of the zone (CR: crest, SL: slope and BT: Bottom). Capital letters indicate significant differences ($P=0.05$) between zones according to Fisher LSD tests.)

3.2. Fish abundance estimation and survey methods.

In all the transects performed monthly, we counted a maximum number of 262 fish using OTM, whereas 535 fish were detected with VTM. The estimation of abundance was significantly different between the survey methods in both the models proposed: 1) all turbidity conditions ($N=240$) and 2) turbidity conditions <2 meters ($N=70$) with the assumption of the probability of detection=1 (Tables 2a and 2b). The zone was another important factor that affected the estimation of fish abundance in both samples (Table 2a, Figure 4). The fish abundance was higher in the SL zones in comparison with the CR and BT zones of the reefs studied. Turbidity was an important factor that affected the

estimation of abundance in both the models proposed (Tables 2a and 2b). We found a significant interaction between the survey methods and the zone (but only in model 2a: with all distances) where VTM was capable of detecting and recording more fish than OTM in the SL zone (Table 2, Fig. 4). The interaction between survey methods and turbidity in both models was not significant (Table 2a and 2b).

Table 2. Model of sequential hypothesis tests for fish abundance

a. Model of sequential hypothesis tests for fish abundance considering all turbidity conditions (N=240)

	numDF	denDF	F-value	p-value
Survey method	1	232	43.37	<0.0001
Zone	2	232	305.52	<0.0001
Turbidity	1	232	534.79	<0.0001
Zone x survey method	2	232	8.43	0.0003
<u>Turbidity x survey method</u>	<u>1</u>	<u>232</u>	<u>0.44</u>	<u>0.5074</u>

b. Model of sequential hypothesis tests for fish abundance considering turbidity conditions <2m (N=70) and assumption for the probability of detection =1.

	numDF	denDF	F-value	p-value
Survey method	1	62	6.31	0.0146
Zone	2	62	3.26	0.0449
Turbidity	1	62	7.11	0.0097
Zone x survey method	2	62	0.23	0.7989
<u>Turbidity x survey method</u>	<u>1</u>	<u>62</u>	<u>2.97</u>	<u>0.0897</u>

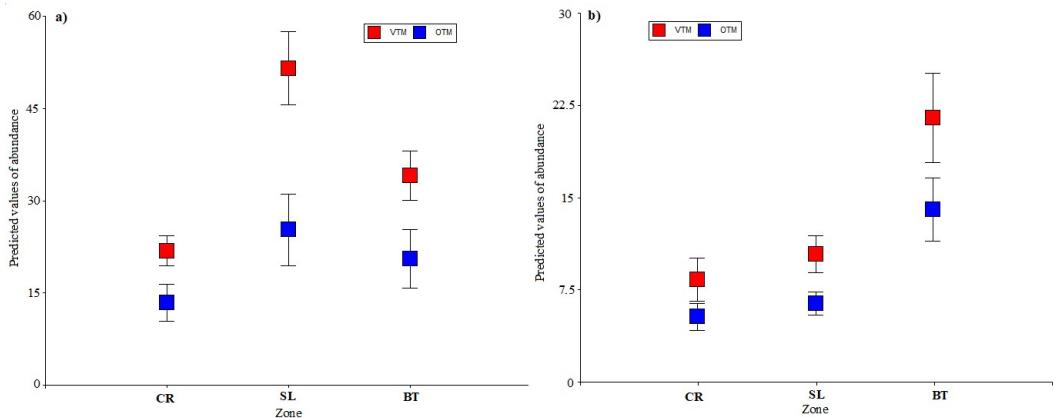


Figure 4. Predicted values of abundance (n° of individuals) as a function of the zone (CR: crest, SL: slope and BT: Bottom) (categorized according to the sampling method: VTM vs OTM). a) predicted values for the global model (model 1a) and b) predicted values for the model <2m (model 1b).

4. Discussion

Our results show that VTM is a better census method than OTM, especially to estimate fish abundance under the different turbidity conditions of the rocky reefs of Ecuador. Wartenberg and Booth (2015), suggested video-transects as the most appropriate underwater visual census method for surveying high-latitude coral reef fish in the southwestern Indian Ocean, based on the low data variability concerning the species richness and fish abundance obtained. Similar conclusions were reached by Pelletier et al. (2011), and in a review by Mallet and Pelletier (2014), who suggest that there is an important increase in the amount of data collected by underwater video systems in comparison with other methods. Thanopoulou et al. (2018), compared the efficiency of detection for strip and line transects methods performed by observers and suggest potential biases derived from the strip transects method, mainly due to the imperfect detectability of fish in transects with >2.5 m in width and the behavioral responses of fish,

especially for shy and secretive species, which are poorly detected by observers in visual counts or due to the limitations of underwater visibility. On the other hand, Video Stereo Systems have been shown to provide more accuracy and precision in the identification of fish and estimation of abundance, length, and distance than visual estimation made by observers (Harvey et al., 2004; Pelletier et al., 2011; Mallet and Pelletier, 2014). However, none of the studies referred to here considered or analyzed the importance of turbidity as a factor affecting survey methods.

We found high variability in the data of fish abundance when comparing both testing methods; however, VTM detected between 147% and 235% more fish than OTM in the surveyed transects. Our results show that OTM may cause an underestimation of the abundance of fish communities that increased when the abundance increased. Wartenberg and Booth (2015), suggest that the use of UVCs, in our case OTM, may underestimate fish abundance, due to the innate challenges in non-destructively detecting all fish present in a community. This underestimation seems to be accentuated when surveying highly heterogeneous systems, such as coral reefs, where the most accurate identification and counting by the observers may be limited by structural complexity. Jones et al. (2015), suggest that variability in abundance is likely to be the greatest determinant of whether monitoring can effectively identify trends concerning abundance in fish communities. Detectability varies considerably across fish species and is mostly affected by biological traits: body size, schooling behavior, shyness, and camouflaging coloration or behavior (MacNeil et al., 2008; Bozec et al., 2011); environmental factors such as habitat complexity (Edgar and Barrett, 1999) and water turbidity (MacNeil et al., 2008) also influence detectability. The schooling behavior of fish is an innate trait that seems to affect their detectability and counting positively (MacNeil et al., 2008); however, we observed that the high levels of schooling of different species in some places

of the reefs studied combined with the high structural complexity and the stability of turbidity conditions could affect negatively the identification and counting of fish by OTM. In our study, permanent strip transects and estimated turbidity avoided the issue of dealing with distance estimation as a source of uncertainty for both survey methods. VTM records may show less error associated with distance estimation than observers and offer a cost-effective tool that allows reducing the biases derived from OTM (Harvey et al., 2004; Pelletier et al., 2011).

Fish abundance in the study sites was affected by the factor zone; we found an interaction between the survey method and zone; VTM was especially effective in detecting differences of fish abundance on the slope (SL) zone with respect to the crest (CR) and bottom (BT) zones of the studied sites (Fig. 3). Gratwicke and Speight (2005) and Fuchs (2013) suggest that factors such as the architectural complexity of reefs may support a great species richness and abundance of fish and invertebrates, so the architectural complexity in the reef slopes may cause an increase in fish abundance (Darling et al., 2017) that could increase the underestimation of fish abundance using OTM.

Turbidity was an important and highly influential factor with a strong effect on detecting the fish abundance. Minimal differences in fish abundance between the VTM and OTM methods were detected with bad conditions (<2m) of visibility at the study sites. Conversely, in transects performed under low levels of turbidity (2-7m), VTM was much more effective for the detection of fish abundance, since the greater the visibility, the more differences between the methods were found.

Comparison of tested models for species richness (sets 1a and 1b) and abundance (sets 2a and 2b) for all turbidity conditions ($N=240$) and turbidity conditions <2 m ($N=70$) showed similar results with differences only for species richness (factor zone) and for abundance (interaction zone x turbidity). We, therefore, conclude that both methods

(VTM and OTM) are capable to detect species richness and changes of abundance without considerable differences in distinct scenarios of turbidity.

Most studies worldwide have been developed under relatively stable conditions of visibility; in these particular cases, traditional methods such as the underwater visual census (UVC) may have led to a possible underestimation of communities with a high abundance of fish. Bozec et al. (2011) found that turbidity had a considerable effect on the detectability of the profile of fish in a study in New Caledonia; however, more generally, turbidity has been an underrated factor during studies of fish communities. A review made by Usseglio (2015), showed that only 5.3% of papers related to assessing fish communities worldwide, consider water clarity as a factor or source of variation, mainly because most of the studies have been developed at sites with stable conditions of visibility (Henriques et al., 2013) or simply because studies and related models consider maximum visibility as a constant (Jones et al., 2015; Pais and Cabral, 2017; Warnock et al., 2016). Even though studies like (Kulbicki, 1998) have shown that when the water is very clear, underwater distances tend to be underestimated, and the opposite occurs when the water is turbid, distances tend to be overestimated. Under fluctuating turbidity conditions, other authors, such as Assis et al. (2013), suggest that VTM using fixed cameras can be a suitable tool to assess fish assemblages, this method seems to increase the efficiency of the efforts in the field and reduces the negative effect of divers changing the composition of the assemblages in the surveys or the “*diver effect*” (Dickens et al., 2011). However, the authors point out a lower accuracy of the fixed camera method (counting of fish and evaluating the species richness) in comparison with the observer and video strip transects when records are made under extreme turbidity conditions.

Our results show that when turbidity levels are low, the probability of detecting fish is increased, especially when VTM is used. Although it may seem obvious, in

environments with high turbidity, visibility could be a key factor for evaluating fluctuations in fish communities during the year and should really be included as a covariate in future studies. Therefore, we recommend recording data of horizontal turbidity prior to every survey and using VTM transects with variable width. This may allow comparable estimated values (derived from the effect of the visibility as a covariate) of fish abundance to be obtained, considering real measurements of turbidity.

VTM could be used to assess fish communities in any zone of the reef. Data recorded by VTM could be analyzed and stored for *a posteriori* spatiotemporal changes or behavioral studies of key species as indicators of reef health. Finally, it is important to note that data obtained from VTM may be especially useful to determine the spatial and temporal changes of fish communities caused by environmental and anthropogenic drivers (Bozec et al., 2011; Wartenberg and Booth, 2015) on the rocky reefs of Ecuador.

CHAPTER III

CHAPTER III: NATURAL AND ANTHROPOGENIC- INDUCED STRESSORS AFFECTING THE COMPOSITION OF FISH COMMUNITIES ON THE ROCKY REEFS OF ECUADOR

Figueroa-Pico, J., Tortosa, F.S., & Carpio, A.J., (2021). Natural and anthropogenic-induced stressors affecting the composition of fish communities on the rocky reefs of Ecuador. Marine Pollution Bulletin, 164 112018. <https://doi.org/10.1016/j.marpolbul.2021.112018>

Abstract

Natural and human-induced stressors have threatened the sustainability of the fish communities of coral-rocky reefs worldwide in the last decades. The composition of the fish communities on the reefs of Ecuador and the factors affecting spatiotemporal changes are unknown. We studied the influence of the descriptors of structural complexity, the current status of coral and human-induced variables over fish communities. A video transect method was used to assess fish communities in three zones (slope, crest, and bottom) of two reefs during two seasons (rainy and dry). The structure of fish communities was highly influenced by the zones and season; rugosity and live coral affected the fish composition on the crest and slope zones. The fractured coral and derelict fishing gear on coral produced an adverse effect on fish composition over the crest. A multifactorial process causing loss of structural complexity and affecting fish composition was identified, however, periodical assessment is required for a greater understanding of this process.

Keywords: Derelict fishing gear, fish communities, reef degradation processes, spatiotemporal composition changes, structural complexity

1. Introduction

Coral and rocky reefs are complex and productive marine ecosystems that support high but very sensitive and vulnerable biodiversity and spatial-seasonal variation (Knowlton, 2001; Kulbicki et al., 2013; Parravicini et al., 2013; Alvarez-Filip et al., 2015; Nelson et al., 2016). The structural complexity of the reefs expressed as rugosity can shape the abundance and diversity of reef fish assemblages across large and small spatial scales (Nash et al., 2013; Ferrari et al., 2016; Darling et al., 2017). The diversity of fish in these ecosystems can be affected by global threats such as climate change (Ateweberhan et al., 2013; Attamimi and Saraswati, 2019) and natural local and regional stressors such as deposition of sediments and turbidity (Freitas et al., 2019). On the other hand, recent declines in the structural complexity and coral diversity of tropical reefs due to anthropogenic stressors like overfishing, derelict fishing gear, dredging or sewage pollution (Muthukrishnan and Fong, 2014; Jones et al., 2016; Valderrama et al., 2018; Abaya et al., 2018) may have consequences for reef fish and fisheries (Alvarez-Filip et al., 2013; Rogers et al., 2014).

Coral-rocky reef biodiversity along the continental coast of Ecuador represents the southernmost distribution in the Eastern Tropical Pacific (ETP); however, it has been rarely studied (Cortés-Núñez, 1997; Cortés, 2011; Alcivar, 2015; Cabanillas-Terán et al., 2016; Trujillo, 2017; Figueroa et al., 2016; Figueroa et al., 2020a, b). The rocky reefs on the continental coast of Ecuador are present in areas of highly variable physical conditions such as high levels of turbidity, the interaction of marine currents and tides (Vera et al., 2009), and an annual up-welling event (January-April each year) (Moreano, 1983). These events have effects on temperature changes, the release of domestic and industrial wastewater, and the local deposition of sediments in the rainy season (Soledispa, 2011).

Information about fish communities on the continental coast of Ecuador is scarce and is only available through general technical reports of ichthyofauna in Machalilla National Park (MNP) or derived from unpublished data obtained from experienced divers. Flachier and Sonnenholzner (1997) and Terán (1998), found 106 species associated with rocky reefs and coral patches in MNP by using underwater visual census (UVC). These reports also describe the diversity of fish according to the significant habitat complexity of the sites studied and analyze the direct influence of fishing and touristic activities on fish communities.

Our research focuses on the spatial and seasonal variation of fish communities and discusses the effect of disturbances and their possible seasonal responses (McClanahan, 2019). The main goals of this study were i) to characterize the fish communities of two coral-rocky reefs on the continental coast of Ecuador with different levels of disturbance and ii) to determine the influence of the environmental and anthropogenic induced variables on the spatiotemporal changes of the composition of the fish communities.

2. Materials and methods

2.1. Study area

The study was conducted in the province of Manabi, the continental coast of Ecuador. Two study sites were chosen: 1) Perpetuo Socorro (PS) ($00^{\circ} 55.637$ S $80^{\circ} 44.353$ W), located 2.3 km off the coast of Manta and 2) Ureles (UR) ($00^{\circ} 54.113$ S $80^{\circ} 38.863$ W), located 4.6 km from the nearest port in Jaramijo (Figure 1). Both sites are traditional areas of artisanal fishing activities throughout the year (line and net fishing, autonomous and semiautonomous diving) and tourism (autonomous diving) and share structural similarities: rocky reefs between 6 and 13 m in depth. We can distinguish three

geomorphological areas: (1) the crest 5-7 m in depth, rocky substratum with patches of branching coral species such as *Pocillopora spp*; (2) the slope 8-10 m in-depth, rocky substratum with small patches of branching coral species such as *Pocillopora spp*. colonies or massive corals such as *Porites lobata*, and (3) the bottom 11-13 m in depth, mixed substratum with rocky, sand, gravel, and patches of massive coral species such as *Pavona clavus*. None of the study sites is considered “pristine” and present different levels of disturbance concerning local sedimentation processes, low rates of light penetration, and direct or indirect anthropogenic impacts i.e.: the PS site shows high-levels of disturbance and sedimentation due to its proximity to the coast, causing high coverage of turf algae (Alcivar, 2015), grazing effects and trophic overlap of sea urchins (Cabanillas-Terán et al., 2016), while the UR site shows mid-levels of disturbance and sedimentation causing slow rates of growth for coral species (Trujillo, 2017). Other important impacts identified in both sites include overfishing, anchoring and the presence and persistence of marine debris and derelict fishing gear (Figueroa-Pico et al., 2016) with effects on coral fracturing processes on the crest zones (Figueroa-Pico et al., 2020b).

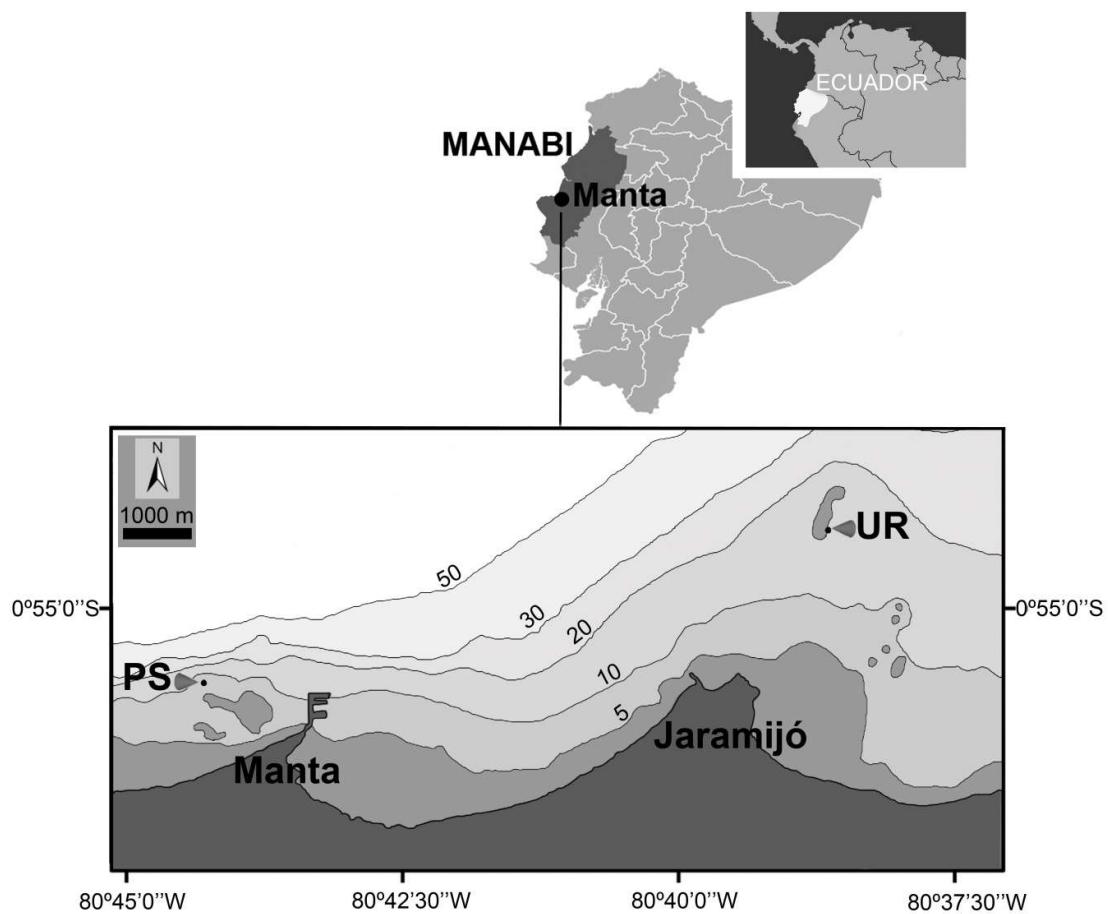


Figure 1. Map of study sites represented as PS (Perpetuo Socorro) in Manta and UR (Ureles) in Jaramijo.

2.2. Fish Community Assessment

Sampling was conducted between September 2017 and April 2018 at each study site with a total of 18 days of data recording, distributed in 9 days in the rainy and the dry season respectively with monthly periodicity (only biweekly for October 2017). The Video-Transect Method (VTM) was used to record the richness of the fish species and their abundance as the best method according to a pilot study performed in the study area (see Figueroa-Pico et al., 2020a). VTM was performed with a GoPro Hero Underwater High Definition camera and Evolve light of 900 lumens. VTM records (~14 hours of video recording) were watched by an experienced observer and the number of fish species and their abundance was registered. We performed a total of 54 permanent transects of 100m divided into 270 segments (135 segments per study site) of 20 m in length and variable width relating to visibility conditions available during the survey time. VTM was carried out in independent surveys (5 segments 20m per day in each zone) in the bottom (BT), slope (SL), and crest (CR) zones (45 segments per zone in each study site), and the same route was repeated during the study period in each zone.

2.3. Descriptors of architectural complexity

The descriptors of architectural complexity were estimated with two complementary methodologies: Rugosity Index (RI) (Risk, 1972; Luckhurst and Luckhurst, 1978) to assess the small-scale relief in each transect, using chains of 3.0 m in length with links of 2.0 cm, and a modified Habitat Assessment Score (HAS), which is a categorical larger-scale visual estimate of the relief (Gratwicke and Speight, 2005; Fuchs, 2013; Lozano-Álvarez et al., 2017). RI is the ratio of the length of a chain attached to the reef surface to the linear distance between its start and endpoints. RI is a measure of substrate complexity because a flat substrate would have an $RI = 1$ and the higher the RI value the

greater the availability of spaces for live organisms (Luckhurst and Luckhurst, 1978; Murray et al., 2002). We performed 10 independent measurements of RI along each permanent transect (two measurements per segment of 20m) in the crest, slope, and bottom zones, and a mean of two IR was calculated for each segment. Modified HAS combines several qualitative measurements of five habitat complexity variables [visual rugosity (VR), hard substratum (HS), live cover (LC), habitat height (HH), and refuge size (RS)], each assessed visually using a five-category scale from 1 (lowest) to 5 (highest) for each variable. A total HAS score was calculated for each transect by adding the scores of each of the five complexity variables. For each permanent transect, we estimated HAS variables in 5m×5m quadrats located in each transect, and averaged the five scores as a measure of transect-level HAS.

2.4. Coral coverage and anthropogenically induced variables

Percentage of live coral (%LC), dead coral (%DC), and fragmented coral (%FC) were estimated in five 1x1 m quadrats located in every transect at the study sites and in the zones. Pictures of quadrats were taken from a horizontal plane and always at the same distance (1.5 m in height from the bottom) and later analyzed with the software ImageJ 1.80 free version (Abramoff et al., 2005). Finally, we recorded the number of segments or pieces of mono and multifilament nets or derelict fishing gear (DFG) along every transect at each site and in each zone.

2.5. Statistical analysis

Data recorded on the abundance of fish species taken with VTM were primarily analyzed with a nonparametric Kruskall Wallis analysis of variance for the factor zone and the Mann Whitney U-test for the factor site. Besides, the Shannon Diversity Index was

calculated for the factors site, zone, and season and later compared with a Diversity Permutation Test using the software PAST version 3.7. The fish community was analyzed with a Permutational Multivariate Analysis of Variance (PERMANOVA). Three fixed factors were entered into the analysis: Site with two levels (UR and PS), zone with three levels (BT, SL, and CR) nested at the site, and season (dry and rainy seasons). Values of quantitative variables RI, %LC, %DC; anthropogenically induced variables %FC and DFG and qualitative complexity HAS descriptors VR, %HS, LC, HH, RS for each transect were entered into the analysis as covariates. Type III Sum of Squares was used since it is appropriate in the case of an unbalanced design. All the tests were performed with 999 permutations to increase the power and precision of analysis (Anderson et al., 2008) of residuals under a reduced model (Anderson and Braak, 2006).

Multicollinearity among architectural complexity and anthropic variables may result in adverse effects in the modeling process, and therefore collinear variables were excluded using the variance inflation factor (VIF), with the threshold cutoff value being set at 3 (Zuur et al., 2010). The VIF was analyzed using the Heiberger method (Heiberger, 2012).

The differences in community structure among the zones were investigated using a posteriori pair-wise test with 999 permutations. The advantage of the permutation approach is that the resulting test is “distribution-free” and not constrained by many of the typical assumptions of parametric statistics (Walters and Coen, 2006).

The relative contribution of each particular fish species to determine differences in the composition of the communities between sites, zones, and seasons were evaluated using a similarity percentage analysis (SIMPER). In this study, SIMPER was employed to identify those fish species that were responsible for more than 90% of dissimilarity among sites, zones, and season. We did not remove *rare species* (<5% of the total

observations in all sampling segments) from the analysis. Although these species may negatively influence multivariate analyses and add little to dissimilarity measures (Rowe and Holland, 2013), they can contribute with important information about vulnerable species for *a priori* redlist.

Finally, to explore the relationship (strength and significance) between the structure of the fish communities and the habitat complexity variables (RI, VR), coral status (%LC), and human-induced variables (%DC, %FC, DFG) in each zone of the study sites, we used a non-parametric distance-based linear model (DISTLM) in combination with distance-based redundancy ordination analysis (dbRDA). The DISTLM models the relationship between the variables mentioned and the multivariate fish community dataset based on a multiple regression model as a way to find the linear combination of variables that explains the greatest amount of variation in the fish community dataset and examines the amount of variance explained by each variable. All the analyses were performed using PRIMER v6 software (Clarke and Gorley, 2006), including the PERMANOVA+ add-on package (Anderson et al., 2008).

3. Results

3.1. Descriptive results

A total of 9431 fish of 49 species and 26 families were identified in the study sites using VTM. 5818 fish were observed at UR and another 3613 at the PS site. (Table 1a). The percentage difference for abundance between sites (UR/PS) was 161% (Table 1a). Concerning the zones, we found more fish abundance in SL and BT at both sites whereas CR always showed the lowest abundances (Table 1a). The percentage difference for abundance between the zones of the sites studied (UR/PS) was 127%, 162%, and 106%

for the CR, SL, and BT zones respectively (Table 1a). Total fish abundance was significantly different between the UR and PS sites ($p < 0.001$), while total fish abundance was significantly different between zones ($p < 0.05$) (Table 1a). Shannon Diversity Index was significantly different between sites ($p < 0.001$), zones CR and SL vs BT of PS site ($p < 0.001$), Dry and rainy and dry season for both sites ($p < 0.001$) (Fig. 2, Appendix 2)

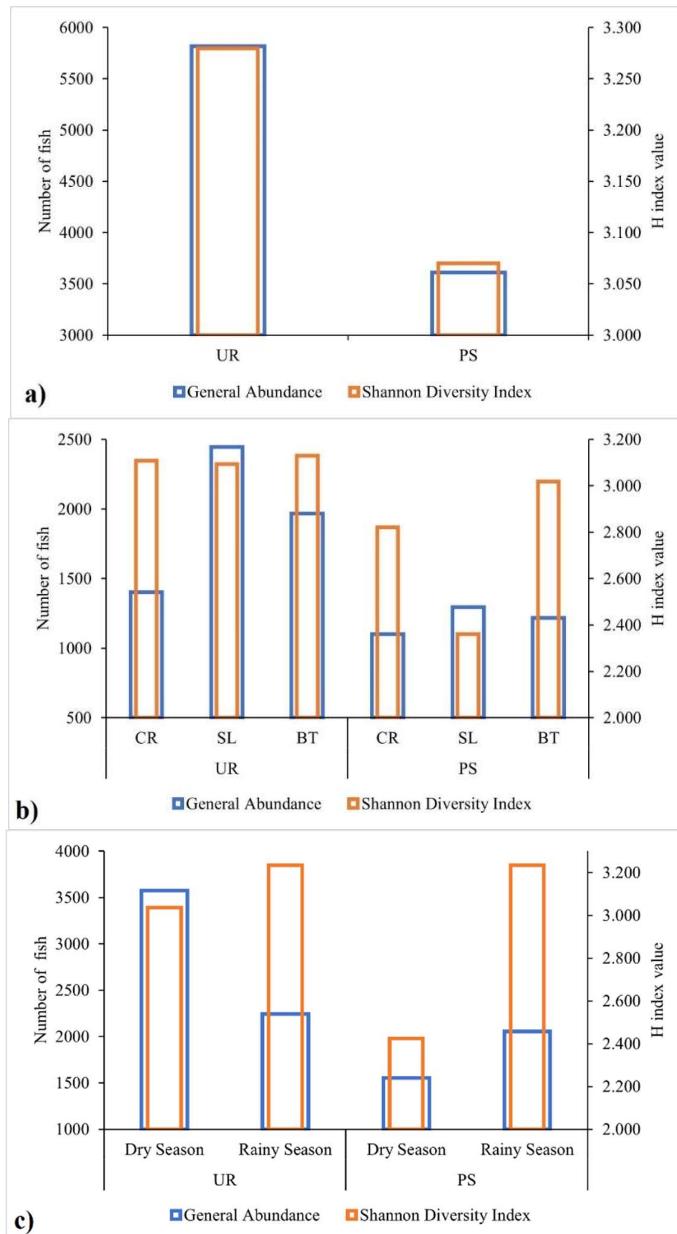


Figure 2. General Abundance and Shannon Diversity Index values per a) study site, b) per zone, and c) per season.

Live coral percentage (%LC) showed a higher abundance in the crest zone compared with the slope and bottom zones at UR ($p <0.001$). Similar results were found in the other study area (PS) where the higher live coral abundance occurs in the crest and the slope zones compared with the bottom zones ($p <0.001$) (Table 1b). Coral colonies of *Pocillopora elegans*, *P. damicornis* and *P. capitata* with 4 to 82% of coverage/ m² were common in the crest zones of the reefs studied, while on the slopes, we found small patches of coral species like *P. damicornis*, *P. capitata*, *Pavona clavus*, and *Porites lobata* with 5 to 67% of coverage/ m² (continuous and complex high bare rocks).

Fractured coral (%FC) was higher on the crest and bottom of both sites compared with the slope zones ($p <0.001$). Dead coral (%DC) was especially high in the bottom zones of both sites ($p <0.001$). Finally, the number of derelict fishing gear as segments of monofilament nets (DFG) was higher in the crest zone of UR and PS compared with the SL and BT zones at both sites ($p <0.001$) (Table 1b).

Table 1. Descriptive statistics for, a) differences in fish abundance between sites and zones, and results for Mann Whitney U (sites) and Kruskal-Wallis tests (zones) and b) structural quantitative (RI) and qualitative HAS (VR, HH, RS, LC, %HS), coral status (%LC, %DC) and human-induced variables (%FC, DFG).

a.		UR						PS											
Total fish per site		5818						3613											
Difference between sites UR/PS		161%																	
Mann Whitney U-test		W= 16118						p <0.001											
		CR		SL		BT		CR		SL		BT							
Total fish per zone		1402		2447		1969		1101		1295		1217							
Difference between zones: CR, SL, BT by site UR/PS		127%		162%		106%													
Kruskal-Wallis test		H=6.3				p <0.05													
Zones																			
b.		CR				SL				BT									
Site	Variables	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	H value	p value				
UR	RI	1.37	0.1	1.2	1.5	1.89	0.2	1.7	2.3	1.21	0.1	1.1	1.4	104.4	***				
	VR	3.4	1.37	2	5	3.4	0.5	3	4	3.4	0.5	3	4	0.57	n.s				
	HH	2.6	0.5	2	3	5	0	5	5	2.6	0.8	2	4	89.5	***				
	RS	3	0.64	2	4	4.4	0.5	4	5	3.2	0.8	2	4	61.5	***				
	LC	3.6	0.81	3	5	1.4	0.5	1	2	2.2	0.8	1	3	82.9	***				
	%HS	5	0	5	5	5	0	5	5	4	0.9	3	5	36.1	***				
	%LC	50.11	16.2	25	82	9.49	8	0	19	20.5	3	14	26	111.4	***				
	%DC	15.13	4.08	8	25	0	0	0	0	28	17	11	52	94.3	***				
	%FC	19.09	6.63	12	35	2	2.6	0	7	22.7	8.3	12	38	91.4	***				
	DFG	14.87	6.08	5	31	0.91	0.6	0	2	2.91	1.8	1	8	104.3	***				
PS	RI	1.32	0.09	1.2	1.5	1.82	0.1	1.7	2	1.22	0.1	1.1	1.4	96.4	***				
	VR	3.6	0.81	3	5	3.4	0.5	3	4	2.6	0.5	2	3	36.8	***				
	HH	2.4	0.5	2	3	5	0	5	5	2.6	0.5	2	3	90.5	***				
	RS	3	0.64	2	4	4.6	0.5	4	5	2.6	0.5	2	3	86.1	***				
	LC	2.6	1.03	1	4	2.6	1	1	4	1	0	1	1	57.1	***				
	%HS	5	0	5	5	5	0	5	5	2.6	0.5	2	3	89.3	***				
	%LC	30.84	19.3	4	68	35.3	18	5	67	1.62	1.7	0	5	89.1	***				
	%DC	8.87	4.36	1	18	0	0	0	0	7.91	6.7	0	17	58.8	***				
	%FC	11.38	6.1	4	25	1.76	2.4	0	8	7.91	6.7	0	17	47.1	***				
	DFG	7	3.83	1	16	1.04	0.7	0	3	0.71	0.5	0	1	79.3	***				

*** highly significant p< 0.001. n.s. no significant

3.2. Sites, zones, and seasonal fish species assemblage.

The PERMANOVA analysis revealed significant differences in the composition of fish species and abundance across sites ($p = 0.003$) and seasons ($p = 0.001$) (Table 2a). We found interactions between factors: zones x site ($p = 0.001$) and site x season ($p = 0.001$) (Table 2a). Variables such as the rugosity index (RI), percentage of live cover (%LC),

and visual rugosity (VR) of HAS were the most important predictors of fish communities ($p<0.05$). Pair-wise test results revealed significant differences in fish compositions between the slope (SL) vs bottom (BT) zones at the UR site and between crest (CR) vs bottom (BT) at the PS site (Table 2b and 2c).

Table 2. a) PERMANOVA for the number of observations for each species based on sites, zones, and season (multivariate data) and b) results of the pair-wise test concerning the number of fish in each species for each zone at the study sites.

a) PERMANOVA test, table of results

Variable	df	SS	MS	Unique Pseudo-F	P(perm)	perms
Si	1	6531	6531	2.7886	0.003	999
Zo (Si)	4	29383	7345.6	3.1365	0.001	999
Season	1	36813	36813	15.719	0.001	997
Si (Time)	1	8660.4	8660.4	3.6979	0.001	998
RI	1	5026.3	5026.3	2.1462	0.019	999
VR	1	29344	29344	12.53	0.001	997
%LC	1	6757.3	6757.3	2.8853	0.002	999
% FC	1	2066	2066	0.88216	0.547	998
DFG	1	3273.5	3273.5	1.3977	0.171	997
Res	257	6.0189E5	2342			
Total	269	8.2646E5				

b) Pair-wise test Term 'Zo(Si)' within level 'UR' of factor 'Site'

Groups	t	Unique P(perm)	perms
CR, SL	0.92703	0.564	998
CR, BT	1.1797	0.156	999
SL, BT	1.6221	0.002	997

c) Pair-wise test Term 'Zo(Si)' within level 'PS' of factor 'Site'

Groups	t	Unique P(perm)	perms
CR, SL	0.58273	0.964	999
CR, BT	2.6356	0.001	998
SL, BT	0.9333	0.557	999

The SIMPER analysis showed considerable average dissimilarity between sites (82.7%), zones (83.19%), and seasons (84.2%). The species with the highest dissimilarity contribution between sites (UR vs PS) were: *Chromis atrilobata*, *Abudefduf troschelli*, *Thalassoma lucasanum*, *Diodon holacanthus*, *Johnrandallia nigrirostris*, and *Balistes polylepis* (See Appendix 3 Table S1). The species with the highest dissimilarity contribution values between CR and SL zones were *C. atrilobata*, *A. troschelli*, *T. lucasanum*, *J. nigrirostris*, *Prionurus laticlavius*, and *D. holacanthus* (See Appendix 3 Table S2). The species with the highest dissimilarity contribution values between CR and BT zones were *C. atrilobata*, *A. troschelli*, *D. holacanthus*, *B. polylepis*, *T. lucasanum*, and *Halichoeres dispilus* (See Appendix 3 Table S2). The species with the highest dissimilarity contribution values between SL and BT zones were *C. atrilobata*, *A. troschelli*, *D. holacanthus*, *J. nigrirostris*, *T. lucasanum*, and *B. polylepis*. Finally, concerning the seasons, the SIMPER showed that sampling in the rainy season had the lowest similarity in the community composition compared with sampling in the dry season. The species with the highest contribution to the dissimilarity between rainy and dry season were: *C. atrilobata*, *A. troschelli*, *D. holacanthus*, *T. lucasanum*, *B. polylepis* and *J. nigrirostris*, which were more abundant in the rainy season.

The sequential test performed by means of the DistLM indicated that 5 variables had a strong effect on the structure and composition of the fish communities in the study zones at the two sites. Visual rugosity contributed to explaining the highest percentual variance, accounting for 12.98% of the variability in the fish communities, followed by a rugosity index with 5.2%, live cover with 4.35%, fractured coral with 2.89%, and derelict fishing gear with 2.32% (Table 3). The dbRDA includes vectors corresponding to these 5 variables in two axes that explained 83.63% of the fitted variation and 17% of the total variation (Fig. 3). The samples corresponding to the crest and bottom zones are distributed

along the dbRDA2 axis, while the samples of the slope are dispersed along the dbRDA1 axis. Concerning architectural complexity and human-induced variables, %FC and VR were related to bottom communities, while DFG is related to both bottom and crest communities. However, the rugosity index and % LC were associated with crest and slope communities.

Table 3. Distance-based linear model for the number of observations for each species based on the zones at the study sites.

Variables	SS(trace)	Pseudo-F	P	Prop.
Rugosity Index	33991	14.412	0.001	5.10
Visual Rugosity	82641	37.963	0.001	12.98
% Live Coral	28995	12.198	0.001	4.35
% Fractured Coral	19264	7.9822	0.001	2.89
DFG in transect	15505	6.3874	0.001	2.32
res.df: 268				

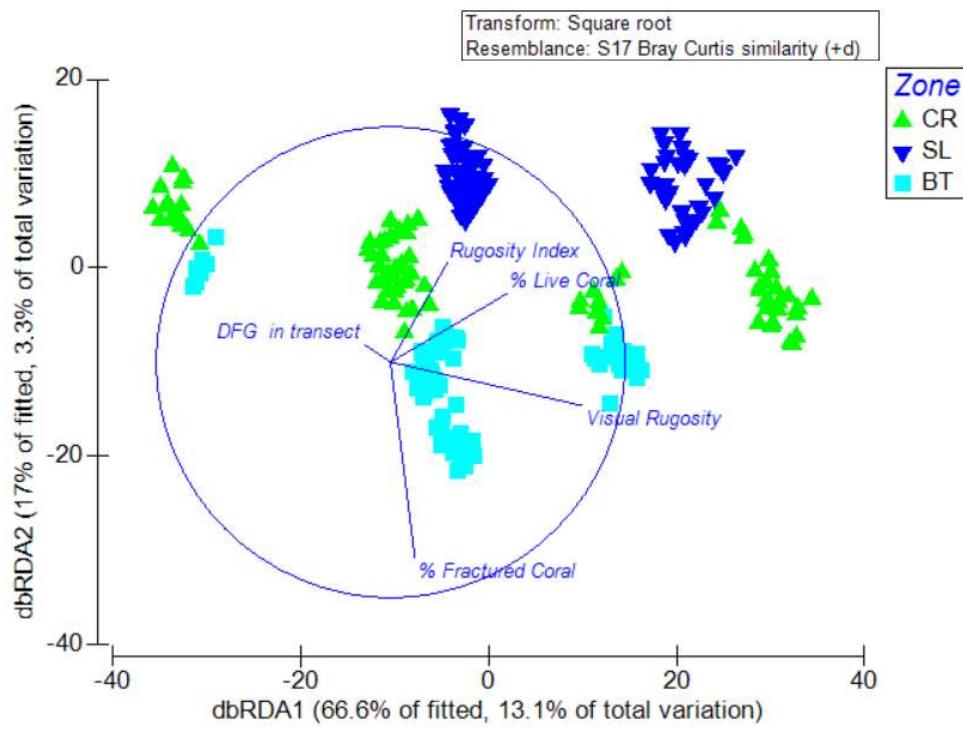


Figure 3. Distance-based redundancy analysis (dbRDA) of the fish communities for each reef zone (CR, SL, BT) showing vector overlays of fish species included in the best model by DistLM analysis.

4. Discussion

Our study is the first systematic initiative to characterize fish communities on the rocky reefs of the continental coast of Ecuador. Our results show differences in the composition of the fish communities between the two study sites, zones, and seasons. The richness of the composition of the species at both study sites is represented by 24 common species from a total of 49 (Appendix 1a). We found 161% more fish in UR than PS (Appendix 1b). The differences in fish composition between the sites studied could be related to a local and multifactorial process of degradation affecting the PS site and explained by its proximity to the coast. This process includes local stressors like high levels of sedimentation due to the discharge of domestic wastewater with the subsequent proliferation of turf algae with adverse effects on algae and invertebrate composition (Alcivar, 2015; Cabanillas-Terán et al., 2016) with direct implications concerning fish communities. Also, overfishing of key herbivore and carnivore species may occur at PS, as well as high anchoring levels and the fracturing of the coral colonies on the crests due to the entanglement of mono and multifilament nets (Figueroa et al., 2020b). Alcivar (2015) found dominance and high coverage of turf algae due to high levels of sedimentation (Virgilio et al., 2006) at the PS site. Further, there is no evidence of the overfishing of herbivore fish that could influence the high coverage of turf algae at the site (Vermeij et al., 2010). Cabanillas-Terán et al. (2016) found a high density of the sea urchin *Eucidaris thouarsi* at the PS site. The population dynamics of this species are related to massive coral mortality and the subsequent proliferation of turf algae on disturbed reefs (Sotelo-Casas et al., 2018). The echinoderm species may also limit coral growth and it has the ability to modify the habitat structure and interfere with the development of the reef frame (Sonnenholzner et al., 2012). This finding is also supported by Ghazilou et al. (2016) who suggest that coral reef fish assemblages may show changes

in response to disturbance levels that result in a decrease in the diversity of a coral reef fish community due to the loss of live coral cover, lower topographical complexity, and/or lower richness of coral species in disturbed areas.

Our results show differences in the abundance of fish between zones per site. Fish abundance was higher on the slope and crest than in the bottom zones (Appendix 1b). When we compared the zones by site, we found that UR shows more abundance of fish: 127% more fish on the crest, 162% on the slope, and 106% on the bottom in comparison with PS (Appendix 1b). Slopes and crests are zones with high structural complexity and live coral coverage, that can provide food, reproduction places, and permanent or temporal shelter for cryptic and conspicuous fish species (Coker et al., 2012; Darling et al., 2017). Darling et al. (2017) suggest that the characteristics of the reef zone reveal the importance of diversity and abundance in the slope and crest zones, typically associated with more abundant and diverse reef fish communities than flat reefs or bottoms. The differences in fish abundance between the slope and bottom zones in UR site and the crest and bottom zones at PS site were especially related to the presence of reef dweller species such as *T. luccasanum*, *J. nigrirostris*, *P. laticlavius*, and *Z. cornutus*.

The season was another factor affecting fish assemblage, suggesting spatiotemporal changes in fish communities at the study sites. Species like *D. holacanthus*, *B. polylepis*, and *U. tumbesensis* had the highest differences in average abundance and were more abundant in the rainy season. The changes in the abundance of these species could be related to the recruitment process (Munro et al., 1973) and spawning aggregations (Erisman et al., 2010), the effects of a low temperature (Hoisington IV and Lowe, 2005; Vaudo and Lowe, 2006; Jirik and Lowe, 2012) and high productivity in the rainy season dynamized by a temporal upwelling event (Rosales-Casián, 2013) occurring between January-April every year on the coast of Ecuador

(Moreano, 1983). La Mesa et al. (2013) suggested that rocky reef habitats are a sort of biodiversity hotspot with significant patterns of broad-scale variation in the composition of fish species and assemblage structure with very fluctuating patterns. On the contrary, Sánchez-Caballero et al. (2019) found great stability of the fish communities on the rocky reefs of Baja California concerning El Niño/La Niña events and that changes in individual species are not strong enough to affect community structure, abundance, or richness. However, the authors also suggest that the abundance of some fish populations is more strongly related to changes in the phytoplankton biomass compared with temperature changes.

The rugosity index (RI) was a strong predictor of abundance for small-scale relief assessment in the slope and crest zones of the reefs studied (Table 1, Fig. 2) in this study. Trebilco et al. (2015) found a similar relationship between the habitat complexity descriptor RI and species richness and abundance of fish in reefs of temperate waters; where substratum rugosity was associated with higher overall fish biomass and small-bodied fish. On the other hand, the estimation of the visual category of larger-scale relief with HAS was only significant for visual rugosity (VR); so this descriptor explains the differences between the richness of species and the total fish abundance between sites and zones of the reefs studied better. Gratwicke and Speight (2005) found a positive relationship between the richness and abundance of fish species with HAS descriptors such as visual rugosity, variety of growth forms, and habitat height. Similar conclusions were reached by Fuchs (2013) in a study that describes the relationship between invertebrate communities with visual rugosity and a variety of growth forms as the principal HAS descriptors. Our results suggest that the composition of fish is dynamized by the high structural complexity of the slope and crest zones of the reefs. Similar results

were found by Darling et al. (2017) who suggest that structural complexity and reef zone are the strongest predictors of fish diversity and abundance.

Rugosity in the crest zones is a function of the high percentage of live cover (%LC), another significant variable in our study (Tables 1 and 2). Pratchett et al. (2015) suggest that the combination of the structural complexity of the reefs and living corals is required for optimal reef fish productivity and diversity, while Darling et al. (2017) specifically argue that the total abundance of reef fish increases with the covering of stress-tolerant corals in crest and slope zones.

The percentage of fractured coral (%FC) and derelict fishing gear (DFG) significantly affected the composition of the fish community. The fracturing of the coral colonies in crest zones occurs because of the efforts to remove entangled nets by local fishermen (Figueroa-Pico et al., 2016, 2020b) and secondly because of the anchoring of boats (Flynn and Forrester, 2019). After the breaking process, coral fractured in the crest zones falls down the slope and depending on the physical configuration of this zone remains and colonizes the rocks or simply falls directly to the bottom where the lack of optimal physical conditions drives the fragments to bleach and die.

We found a high presence and prevalence of derelict fishing gear (monofilament and multifilament nets) on the coral colonies on the crests of the UR and PS sites during the study period (Appendix 2). These results are similar to those reported by Figueroa et al. (2016) for the same study sites and suggest that the problem of derelict fishing gear and ghost nets on crest zones has a high prevalence over time. Our results show a strong relationship between human-induced DGF descriptor and fractured coral on the crest zones and negative effects on the composition of fish. A high percentage of the fish species, (40%) in the study sites, were strongly linked to the coral colonies in the crest and slope zones where they find permanent and temporary shelter and places to feed or

reproduce. So the gradual destruction of coral negatively impacts on the diversity and composition of the fish communities in these zones. Pratchett et al. (2011) and Russ and Leahy (2017) suggest that an absolute decrease in live coral cover on the reefs would lead to a considerable decline in the richness and abundance of fish species. Similarly, Flynn and Forrester (2019) argue that many reef fish taxa depend on a three-dimensional reef structure for shelter, so the “flattening” of highly anchored sites is a plausible explanation for the reduced densities of most (5 of 7) functional groups of adult fish.

A clear example of the above-mentioned issues in our study is the coral hawkfish *Cirrhitichthys oxycephalus* a rare species of the coral reef. This cryptic species is usually found perched on branching coral colonies of *Pocillopora spp.* (Robertson and Allen, 2015) and was especially abundant in the CR and SL zones of the UR site but was absent in the fish composition of the PS site. The presence of *C. oxycephalus* was restricted only to living branching coral colonies that offer protection against predators (Coker et al., 2015) and where the species predate over small cryptic invertebrates and fishes (Palacios-Narváez et al., 2020). The species was never observed in fractured or dead coral colonies. Coral hawkfish is included on the Red List of the International Union for Conservancy of Nature (IUCN) as a species not evaluated with the category of least concern (LC) (Greenfield and Williams, 2016). However, we found evidence that indicates a possible major threat to coral-dependant fish species related to habitat degradation by the indirect effect of human activities.

Finally, important theoretical inputs about the disruption of ecological processes on branching coral colonies concerning the gradual colonization of algae consortiums over the derelict fishing gear and its negative effects on the composition and coverage have been widely discussed (Galgani et al., 2018; de Carvalho-Souza et al., 2018;

Valderrama et al., 2018; Figueroa-Pico et al., 2020b; Beneli et al., 2020). However, the long-term effects on the invertebrate and fish communities remain unknown.

Our findings suggest that the spatio-temporal changes in the composition of fish communities of the rocky reefs of Ecuador are driven by a complex and multifactorial process that includes the positive influence of structural complexity and negative effects of the loss of live coral cover and the subsequent loss of structural complexity by human-induced stressors, affecting both fish diversity and abundance. We strongly recommend a periodical assessment of fish communities, structural complexity descriptors, and human-induced descriptors. New data on the sediment deposition process and temperature fluctuations are also needed as well as the effect of the derelict monofilament nets due to coral-turf algae growth since the effect of the algae on the coral remains poorly known.

CHAPTER IV: ECHINODERMS AS INDICATORS OF DISTURBANCE ON MARGINAL REEFS ALONG THE CONTINENTAL COAST OF ECUADOR.

CHAPTER IV

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Abstract

Echinoderms are key organisms in the development, functionality, and balance of coral and rocky reef ecosystems. The spatiotemporal fluctuation of echinoderm species influenced by natural and anthropic factors is crucial to understanding the capacity of marginal reefs to adapt and be resilient concerning future climate change and ocean acidification scenarios. Scientific information on the spatial distribution and abundance of echinoderms on the continental coast of Ecuador is scarce and limited to a few old systematic studies and technical reports. Our study compared seasonal and geomorphological changes in ecological attributes (species richness, diversity, density, spatial distribution) of echinoderm communities at three study sites: one reef from a marine protected area and two marginal reefs from a non-protected area with different levels of disturbance along the central and south coast of Manabi-Ecuador. Five x five quadrants were performed in each study site considering the geomorphological similarities between reef zones: crest, slope, and bottom. Results suggest that echinoderm communities from marine protected and non-protected areas (marginal reefs) show differences in composition, diversity, and density related to habitat complexity, live coral and turf algae coverage, and the presence and prevalence of derelict fishing gear. Changes in the composition between sites include: a high density of slate pencil sea urchins (*Eucidaris thouarsii*) in the crest zones of marginal reefs with high levels of sedimentation; turf algae coverage; fragmented and fractured branch coral forms; and the presence of derelict fishing gear. We recommend a periodical assessment of echinoderm communities to analyse possible acute phase shift scenarios in Ecuador's coral and rocky reef ecosystems.

Keywords: Bioindicators, community effects, Echinodermata, marginal reefs, reef degradation processes, spatio-temporal composition changes.

1. Introduction

Marginal reefs (MR) are marine ecosystems developed on hard bottoms (coral, rocky) that occur under suboptimal physical conditions: high fluctuation of temperature and pH, high levels of turbidity, sedimentation, and nutrients (Soares et al., 2020). Due to their widely discussed capacity for adaptation and resilience to future climate changes and ocean acidification scenarios, the research on marine populations inhabiting MR is crucial and highly relevant (Camp et al., 2018; Burt et al., 2020; Soares et al., 2020). The scientific basis suggests that marginal reef communities are composed of highly dominant reef specialists and stress-tolerant species with lower species richness and diversity (Soares et al., 2020). However, the limited resistance of MR and their biota make them susceptible to direct and indirect pressures derived from human activities that cause degradation processes and changes within the benthic communities, i.e. coral to algae dominance (phase shift) (Norström et al., 2009; Cortés and Reyes-Bonilla, 2017; de Carvalho-Souza et al., 2018; Cruz et al., 2018; Richmond et al., 2018; Sommer et al., 2021; Thompson et al., 2022)

Echinoderms are an essential and highly diverse group of marine invertebrates inhabiting coral and rocky reefs worldwide (including MR) from which they obtain food, shelter, and reproduction resources (Sonnenholzner et al., 2013; Sotelo-Casas et al., 2018). On the other hand, echinoderm assemblages are affected by seasonal fluctuations in environmental conditions (sediments, upwelling events) and human-induced variables (overfishing, habitat deterioration), usually observed as changes in the species richness and density of organisms between sites, seasons and reef geomorphological zones (Hermosillo-Nunez et al., 2015, Sotelo-Casas et al., 2018).

The functional role of echinoderms on coral reefs and benthic communities has been described and widely discussed by Birkeland (1989), Sonnenholzner et al. (2013), Purcell

et al. (2016), Alvarado et al. (2017), Manzello et al. (2017) and Castelló & Tickell et al. (2022). This role includes the control and regulation of invertebrate populations and coral colonies through direct predation for sea stars (Asteroidea); grazing and bioerosion with biological and geological effects through a generalist diet (crustose and turf algae, coral polyps), and opportunistic feeding behaviour related to food items available for sea urchins (Echinoidea), and the recycling of nutrients through sedimentary deposit and feeding on organic matter by sea cucumbers (Holothuroidea).

The fauna of echinoderms along the continental coast of Ecuador described by Mair et al. (2002), Glynn (2003), Sonnenholzner et al. (2013), and Steiner et al. (2019) includes 8-10 species of sea urchins (Echinoidea); 6-9 species of sea stars (Asteroidea); 2-4 species of brittle stars (Ophiuroidea), and 4-6 species of sea cucumbers (Holothuroidea). Previous studies of reef echinoderms in Ecuador were limited to basic research and taxonomy and do not allow a proper analysis of their distribution and interaction effects between species and the environmental variables (Sonnenholzner et al., 2013). On the other hand, Steiner et al. (2019) highlight the importance of characterizing the spatial distribution of conspicuous echinoderms (sea urchins, sea stars) through stratified bathymetric surveys to explain the influence of physical (habitat complexity, sediment deposition) and oceanographic parameters (temperature, pH).

Our study contributes to filling some of the most critical gaps of knowledge related to the current state of the conspicuous echinoderm populations in marine protected areas and along the marginal reefs of the continental coast of Ecuador, contributing with important information on their spatiotemporal distribution, the influence of biological, physical, direct and indirect human-induced variables and the interactions of echinoderms with the reef community. Therefore, the objectives of the study were: i) to determine the differences in the composition of echinoderm species of two rocky marginal reefs (non-

protected area) with scaling levels of perturbation in comparison with one classical rocky reef system from a marine protected area (MPA) along the central and south coast of Ecuador; ii) to identify the differences in spatiotemporal distribution patterns, and ecological attributes (species richness, diversity, and density) of the sea urchins, sea stars and sea cucumbers at the study sites and in the zones of the reefs and iii) to analyze the influence of physical (habitat complexity), biological (coral and turf algae coverage) and human-induced variables (derelict fishing gear) on the echinoderm communities.

2. Materials and Methods

2.1. Study sites

We conducted our study in the Province of Manabí, on the continental coast of Ecuador. Three study sites were chosen: (1) Perpetuo Socorro (PS) ($00^{\circ} 55.637$, S $80^{\circ} 44.353$, W), located 2.3 km off the coast of Manta; (2) Ureles (UR) ($00^{\circ} 54.113$, S $80^{\circ} 38.863$, W), located 4.6 km from the nearest port in Jaramijo and (3) La Viuda (LV) ($01^{\circ} 24.360$, S $80^{\circ} 46.383$, W), located 2 km off the coast from the commune of Salaite (Fig.1). The PS and UR sites are submerged marginal reefs with different levels of anthropogenic pressure and disturbances located near developing coastal cities (Figueroa et al., 2020; 2021), while the third is an islet (control site) located in the northern sector of Machalilla National Park (MNP), an important Marine Protected Area on the continental coast of Ecuador. The three study sites share structural similarities: rocky substrates between 5 and 14 m in depth and the three geomorphological areas treated here as *zones*: (1) the crest, 5–7 m deep, a rocky substratum with patches of branching coral species such as *Pocillopora* spp.; (2) the slope, 7–10 m deep, a rocky substratum with small patches of branching coral colonies such as *Pocillopora* spp. colonies or encrusted corals such as *Porites lobata*, and (3) the bottom 10–14 m deep, a mixed substratum with rock, sand,

gravel, and patches of massive coral species such as *Pavona clavus*, that stabilises at a maximum depth of 14 m.

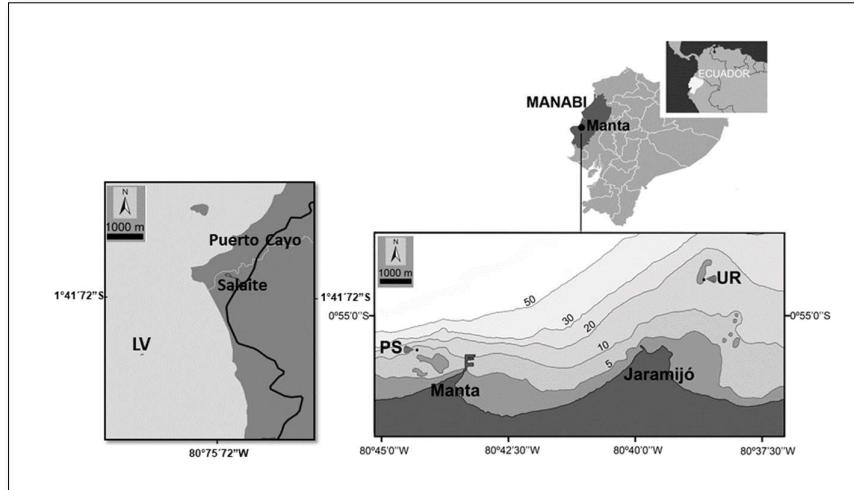


Figure 1.- Map of the study sites. Marginal reefs from Non-Protected Marine Areas Ureles (UR) Jaramijó, Perpetuo Socorro (PS) Manta, and reef from Protected Marine Area La Viuda (LV) Puerto Cayo-Salaite.

The UR and PS sites present different levels of disturbance concerning local sedimentation processes, low rates of light penetration, and direct or indirect anthropogenic impacts, i.e. the PS site shows high levels of disturbance and sedimentation due to its proximity to the coast. These factors cause high coverage by turf algae (Alcivar, 2015; Alcivar-Mendoza et al., 2021), grazing effects, and the trophic overlap of sea urchins (Cabanillas-Terán et al., 2016), while the UR site shows mid-levels of disturbance and sedimentation causing slow rates of growth for coral species (Trujillo, 2017). Other impacts at both sites include: overfishing, anchoring, and the presence and persistence of marine debris and derelict fishing gear (Figueroa-Pico et al., 2016). These stressors at the sites increase coral fracturing processes in the crest zones (Figueroa-Pico et al., 2020a)

and influence spatiotemporal changes in fish diversity and abundance driven by the positive influence of structural complexity and the adverse effects of the loss of live coral cover and the subsequent loss of structural complexity caused by human-induced stressors (Figueroa-Pico et al., 2021). On the other hand, the LV site shows high diversity and abundance of macroalgae, coral species, benthic macroinvertebrates, and fish due to: the presence of hard and complex substrates (Flachier & Sonnenholzner, 1997; Terán, 1998), the dynamics of marine currents (Vera et al., 2009), good conditions of conservation related to the low impact caused by nearby human populations, the control of the MNP authorities over autonomous (touristic), and semiautonomous diving (fishing) activities, and the relative low sedimentation affecting visibility (Terán, 1998; Platt, 2007).

2.2. Assessment of the echinoderm community

Sampling was conducted between September 2020 and August 2021 at each study site with a total of eight days of data recording, distributed over four days in the rainy and four days in the dry season, respectively, with quarterly periodicity. We performed 108 quadrants of 5x5m (a total survey area of 2,700 m²). Fifty-four quadrants were performed in the dry season (DR), while the other 54 were performed in the rainy (RA) season. Three quadrants were performed independently in each zone: crest (CR), slope (SL), and bottom (BT) zones (9 quadrants per day of the survey) and a total of 36 quadrants per study site during the study period. Conspicuous echinoderms of three taxa: echinoids, asteroids, and holothuroids were identified and counted in every survey unit (5x5m quadrant). Pictures of the species were taken using a Canon digital camera with Ikelite housing to avoid mistakes in the identification process (Annex 1).

2.3. Descriptors of architectural complexity

The Rugosity Index (*RI*) (Risk, 1972; Luckhurst & Luckhurst, 1978) was used to assess the small-scale relief in each quadrant using chains of 3.0 m in length with links of 2.0 cm. *RI* is the ratio of the length of a chain touching the reef surface to the linear distance between its start and end points. *RI* is a measure of substrate complexity because a flat substrate would have an *RI* = 1, and the higher the *RI* value, the greater the availability of spaces for live organisms (Luckhurst & Luckhurst, 1978; Murray et al., 2002). We performed ten random independent measurements of *RI* in each quadrant deployed in the crest, slope, and bottom zones, and a mean of *RI* measurements was calculated for each quadrant.

2.4. Coral and turf coverage and anthropogenic-induced variables

The percentage of coral cover (%CC) was estimated in five 1×1 m quadrats, while turf algae cover (%TC) was estimated in five 0.5x0.5 m quadrats in every echinoderm quadrant in the zones at the study sites. Pictures of quadrats for %CC were taken from a horizontal plane and always at the same distance (1.5 m in height from the bottom) and later analyzed with the software ImageJ 1.80 free version (Abramoff et al., 2005), while turf algae cover (%TC) was estimated through direct observation. Finally, we recorded the number of segments or pieces of mono and multifilament nets or derelict fishing gear (*DFG*) in every quadrant at each site and zone.

2.5. Statistical analysis

Explanatory variables *RI*, %CC, %TC and *DFG* were primarily compared between study sites (PS, UR, LV) and zones (CR, SL, BT) and analyzed through a non-parametrical analysis of variance (Kruskal-Wallis).

Raw data of abundance for each echinoderm species in each quadrant was analyzed using the Indices of Dispersion tool of the software Ecological Methodology version 7.4 (Krebs, 2019) to determine possible changes in the spatial distribution patterns between dry seasons (DR) and rainy (RA). We calculated three indices for each echinoderm species: 1) The Variance-to-Mean ratio (VMR), 2) the Morisita Index (MI), and 3) the Morisita Standardized Index (MSI). The spatial distribution patterns for each species were compared using the Chi-squared test.

To determine the underlying anthropic and climatic factors driving the ecological attributes: species richness (S), diversity (H), and density (D) of global and each echinoderm taxa (echinoids, asteroids, and holothurians), eight General Linear Mixed Models (GLMM) and four Generalised Linear Mixed Models (GzLMM) were performed using the variables global S , H and D and of each taxon as response variables. Models were fitted with a normal distribution and identity-link function in the case of density and diversity and a Poisson distribution and log-link function in the case of richness. The variables: (Zo) zone (3 levels), (Si) site (3 levels), and (Se) seasons (2 levels) were added as fixed factors, whereas RI , %CC, %TC, and DFG were included as covariates. The quadrants were included as a random factor. Multicollinearity among architectural complexity and anthropic variables may result in adverse effects in the modelling process, and therefore collinear variables were excluded using the variance inflation factor (VIF), with the threshold cutoff value being set at 3 (Zuur et al., 2010). The VIF was analyzed using the Heiberger method (Heiberger, 2012). The most plausible models were selected by comparing Akaike's information criterion (AIC) in the models following a backward procedure. Fisher's least significant difference test (LSD test) was used to check the differences among the levels of categorical variables retained in the model. The assumptions of normality, homogeneity, and independence in the residuals were assessed

in models with a normal distribution function (Zuur et al., 2009). These statistical analyses were performed using InfoStat software (Di Rienzo et al., 2011).

The echinoderm community was analysed with a Permutational Multivariate Analysis of Variance (PERMANOVA). Three fixed factors and the interactions between them were entered into the analysis: site with three levels (UR, PS, and LV), zone with three levels (CR, SL, and BT), and seasons with two levels (DR and RA). Type III Sum of Squares was used since it is appropriate in the case of an unbalanced design. All the tests were performed with 999 permutations to increase the power and precision of analysis (Anderson et al., 2008) of residuals in a reduced model (Anderson & Braak, 2003). The differences in community structure among the zones were analysed using a posteriori pair-wise test with 999 permutations. The advantage of the permutation approach is that the resulting test is "distribution-free" and not constrained by many of the typical assumptions of parametric statistics (Walters & Coen, 2006). The relative contribution of each particular echinoderm species, to determine the differences in the composition of the communities between sites, zones, and seasons, was evaluated using a similarity percentage analysis (SIMPER). In this study, we used SIMPER analysis to identify those echinoderm species responsible for more than 90% dissimilarity among sites, zones, and seasons. We did not remove rare species (<5% of the total observations in all sampling segments) from the analysis. Although, these species may negatively influence multivariate analyses and add little to dissimilarity measures (Rowe & Holland, 2013), they can contribute to important information about vulnerable species.

Finally, to explore the relationship (strength and significance) between the structure of the echinoderm communities and the habitat complexity variables (*RI*), coral cover (%CC), turf cover (%TC), and derelict fishing gear (*DFG*) in each zone of the study sites,

we used a non-parametric distance-based linear model (DISTLM) in combination with distance-based redundancy ordination analysis (dbRDA). The DISTLM models the relationship between the variables mentioned and the multivariate echinoderm community's dataset based on a multiple regression model to find the linear combination of variables that explains the most significant variation in the echinoderm community's dataset and examines the amount of variance explained by each variable. All analyses used PRIMER v6 software (Clarke & Gorley, 2006), including the PERMANOVA+ add-on package (Anderson et al., 2008).

3. Results

3.1. Descriptive results

A total of 2,408 echinoderms (1,867 echinoids, 418 asteroids, and 123 holothurians) of 11 species and seven families were identified at the study sites from September 2020–August 2021 (Table S1 & S2). We found 1,321 echinoderms in the dry season and the other 1,087 in the rainy season. We observed 712 echinoderms at UR, 878 at PS, and another 818 at the LV site. (Table S2). Concerning the study zones, we found 835 echinoderms in the CR, 952 in the SL and 617 in the BT zone (Table S2).

The rugosity index (*RI*) differed significantly between sites and zones, with the highest values in the CR and SL zones of the LV site (Table S3). Coral cover (%CC) showed the highest values in the crest zones of the LV and UR compared with the CR zones of PS (Table S3) and was represented by branching coral colonies of *Pocillopora elegans*, *Pocillopora damicornis* and *Pocillopora capitata*, common species in the crest zones of the reefs studied. Turf cover (% TC) reached its highest amount in the CR zones of the UR and PS sites compared with the low coverage of turf in the CR zone of the LV site (Table S3). Finally, the number of segments of monofilament nets, such as derelict fishing

gear (*DFG*), was higher in the CR zone of UR and PS compared with the CR zone of the LV site with the lowest number of net segments (Table S3).

Regarding general spatial distribution (all sites), the sea urchin species *Eucidaris thouarsii*, *Diadema mexicanum*, *Astropyga pulvinata*, and the sea star *Pentaceraster cumingi* maintained their aggregated spatial distribution in the dry and rainy seasons (Table S4). In contrast, the sea urchin *Toxopneustes roseous* changed its spatial distribution from random in the rainy season to aggregated in the dry season (Table S4).

A comparison of spatial distribution indices between sites and zones showed similar results, except for *E. thouarsii*'s random distribution in the RA season for the LV site, random distribution of *A. pulvinata* in the DR season for the UR site and *P. cumingi* had an aggregated distribution for both seasons at the UR site (Table S5).

The general species richness (*S*) of echinoderms was affected positively by the rugosity index (*RI*) (Table 1a). General diversity (*H*) was influenced by the zone factor with a significant interaction between site and zone (Table 1b.1. & 1b.2.). The general density (*D*) was positively affected by the rugosity index, which was different between seasons, it was higher in the dry season (Table 1c).

Table 1. *F* and *p* values and coefficients of the variables included in the mixed model to explain general a) species richness (*S*), b) diversity (*H*) and c) density (*D*) of echinoderms.

a. General species richness			
Variables	<i>F</i> value	Coefficient ± S.E.	
RI	9.15***	RI = 0.48 ± 0.16	
b. General diversity			
Variables	<i>F</i> value	Coefficient ± S.E.	
Site	2.85	Site PS = 0.11 ± 0.11 Site UR = 0.02 ± 0.02	
Zone	12.3***	Zone CR = 0.39 ± 0.11 Zone SL = 0.56 ± 0.11	
Zone x Site	3.18*	Zone SL x Site PS = -0.49 ± 0.16 Zone SL x Site UR = -0.45 ± 0.16 Zone CR x Site PS = -0.19 ± 0.16 Zone CR x Site UR = -0.06 ± 0.16	
b.1. General diversity <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$). Adjusted means and standard errors for factor zone. Means with different letters are significantly different.			
Zone	Means	S.E.	
CR	2.58	0.05	A
SL	2.52	0.05	A
BT	2.27	0.05	B
b.2. General diversity <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$). Adjusted means and standard errors for site x zone interactions. Means with different letters are significantly different.			
Site	Zone	Means	S.E.
LV	SL	2.79	0.08
LV	CR	2.62	0.08
UR	CR	2.58	0.08
PS	CR	2.54	0.08
PS	SL	2.40	0.08
UR	SL	2.36	0.08
PS	BT	2.33	0.08
UR	BT	2.25	0.08
LV	BT	2.23	0.08
c. General density			
Variables	<i>F</i> value	Coefficient ± S.E.	
Season	6.68*	Season Rainy = -0.97 ± 0.38	
RI	21.9***	RI = 1.81 ± 0.39	

The diversity of echinoids was significantly different at the season and zone level, higher in the dry season and the bottom zone (Table 2b.1.) and was influenced positively by the *DFG* variable, with interactions between sites and zones (Table 2b). The density of

echinoids was significantly different between seasons (higher in the dry season), sites (higher at PS and LV; Table 2c & 2c.1.), and zones (higher in the slopes; Table 2c.2.), with interactions between sites and zones (Table 2c.3), and the *DFG* influenced its changes positively (Table 2c). The slate pencil sea urchin *E. thouarsii* was the dominant species (highest densities) in the CR zones of the UR and PS sites (Supplementary material, Fig. 3a & 3b). In contrast, the long-spined sea urchin, *D. mexicanum*, showed the highest density values as the dominant species in the CR zone of the LV site (Fig. 3c). In the SL zones of the study sites, the sea urchin *D. mexicanum* showed the highest density values (Table 1b). Finally, the sea urchins *T. roseus* and *A. pulvinata* were the dominant echinoid species in the BT zone of the UR and PS sites, respectively (Table 1, Fig. 2a & 2c).

Table 2. *F* and *p* values and coefficients of the variables included in the mixed model to explain general a) species richness (*S*) and b) diversity (*H*) and c) density of echinoids.

a. Echinoids Species richness		
Variables	<i>F</i> value	Coefficient ± S.E.
DFG	2.2 n.s.	DFG = 0.04 ± 0.02
b. Echinoids Diversity		
Variables	<i>F</i> value	Coefficient ± S.E.
Season	5.33*	Season Rainy = -0.11 ± 0.5
Zone	21.16***	Zone CR = -0.26 ± 0.07 Zone SL = -0.40 ± 0.06
DFG	16.05**	DFG = 0.06 ± 0.01
b.1. Echinoids diversity <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$) Adjusted means and standard errors for factor zone. Means with different letters are significantly different.		
Zone	Medias	S.E.
BT	1.50	0.05 A
CR	1.25	0.05 B
SL	1.11	0.04 C

c. Echinoids Density

Variables	F value	Coefficient ± S.E.	
Season	33.5***	Season Rainy = -0.20 ± 0.03	
Site	11.83***	Site PS = 0.34 ± 0.07 Site UR = -0.09 ± 0.07	
Zone	23.98***	Zone CR = 0.18 ± 0.07 Zone SL = 0.53 ± 0.07	
DFG	7.53*	DFG = 0.04 ± 0.01	
Site x Zone	10.48***	Site PS x Zone CR = -0.22 ± 0.11 Site PS x Zone SL = -0.62 ± 0.10 Site UR x Zone CR = -0.03 ± 0.12 Site UR x Zone SL = -0.11 ± 0.1	
c.1. Echinoids density <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$) Adjusted means and standard errors for factor site. Means with different letters are significantly different.			
Site	Means	S.E.	
PS	3.91	0.16 A	
LV	3.56	0.17 A	
UR	2.90	0.16 B	
c.2. Echinoids density <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$) Adjusted means and standard errors for factor zone. Means with different letters are significantly different			
Zone	Means	S.E.	
SL	4.25	0.15 A	
CR	3.31	0.18 B	
BT	2.81	0.16 B	
c.3. Echinoids density <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$) Adjusted means and standard errors for interaction site x zones. Means with different letters are significantly different.			
Site	Zone	Means	S.E.
LV	SL	5.04	0.27 A
PS	BT	4.11	0.26 B
UR	SL	4.03	0.26 B
PS	CR	3.95	0.30 B C
PS	SL	3.68	0.26 B C
LV	CR	3.27	0.27 C D
UR	CR	2.73	0.34 D E
LV	BT	2.38	0.28 E
UR	BT	1.94	0.26 E

Asteroid species richness was significantly different at the levels of site and zone, higher in the CR and SL zones and at the LV site (Table 3a). Asteroid diversity was significantly

different at the levels of site and zone and was higher in the SL and CR zones and at the LV site (Table 3b.1. & 3b.2.); with interactions between sites and zones (Table 3b.3.). Finally, the density of asteroids was significantly different between sites, higher at LV, followed by UR and PS (Table 3c & 3c.1.), with interactions between sites and zones (Table 3c.2.) with a positive influence of the variable %TC (Table 3c). Seastars such as *Pharia pyramidata* and *Phataria unifascialis* reached the highest density values and were the dominant sea star species in the CR zones of the UR and PS sites (Fig. 3a & 3b), while at the LV site, the densities for both species were similar (Fig. 3b). In the case of the sea star *P. cumingi*, the density reached its highest values in the BT zones of the PS and LV sites (Fig. 3b & 3c).

Table 3. *F* and *p* values and coefficients of the variables included in the mixed model to explain a) species richness (*S*), b) diversity (*H*) and c) density (*D*) of Asteroids.

a. Asteroids Species richness

Variables	<i>F</i> value	Coefficient ± S.E.
Zone	3.55*	Zone CR = 0.39 ± 0.17
		Zone SL = 0.40 ± 0.17
Site	3.88*	Site PS = -0.40 ± 0.16
		Site UR = -0.32 ± 0.15

a.1. Asteroids species richness *a posteriori* LSD Fisher test ($\alpha=0.05$). Adjusted means and standard errors for factor site. Means with different letters are significantly different.

Site	PredLin	E.E.	Media	E.E.
LV	1.02	0.10	2.76	0.28 A
UR	0.69	0.12	1.99	0.23 B
PS	0.62	0.12	1.86	0.23 B

a.2. Asteroids species richness *a posteriori* LSD Fisher test ($\alpha=0.05$). Adjusted means and standard errors for factor zone. Means with different letters are significantly different.

Zone	PredLin	E.E.	Media	E.E.
SL	0.91	0.11	2.49	0.26 A
CR	0.90	0.11	2.46	0.26 A
BT	0.51	0.13	1.67	0.21 B

b. Asteroids Diversity

Variables	F value	Coefficient ± S.E.	
Site	8.9**	Site PS= 0.06 ± 0.2 Site UR = 0.15 ± 0.2	
Zone	19.15***	Zone CR = 1.12 ± 0.20 Zone SL = 1.17 ± 0.20	
Site x Zone	3.66**	Site PS Zone CR = -0.65 ± 0.28 Site UR Zone CR = -0.77 ± 0.28 Site PS Zone SL = -0.90 ± 0.28 Site UR Zone SL = -0.82 ± 0.28	
b.1. Asteroids diversity <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$). Adjusted means and standard errors for factor site. Means with different letters are significantly different.			
Site	Means	S.E.	
LV	1.24	0.08	
UR	0.86	0.08	
PS	0.79	0.08	
b.2. Asteroids diversity <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$). Adjusted means and standard errors for factor zone. Means with different letters are significantly different.			
Zone	Means	S.E.	
CR	1.19	0.08	
SL	1.15	0.08	
BT	0.55	0.08	
b.3. Asteroids diversity <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$). Adjusted means and standard errors for the interaction site x zone. Means with different letters are significantly different.			
Site	Zone	Means	S.E.
LV	SL	1.65	0.14
LV	CR	1.60	0.14
PS	CR	1.01	0.14
UR	SL	0.98	0.14
UR	CR	0.98	0.14
PS	SL	0.81	0.14
UR	BT	0.63	0.14
PS	BT	0.54	0.14
LV	BT	0.48	0.14
c. Asteroids Density			
Variables	F value	Coefficient ± S.E.	
Site	29.7***	Site PS= -0.24 ± 0.22 Site UR = 0.32 ± 0.21	
Zone	1.16 n.s	Zone CR = 0.14 ± 0.04 Zone SL = 0.18 ± 0.04	
% TC	4.8*	%TC = 0.0026 ± 0.0012	
Site x Zone	8.82***	Site PS Zone CR = -0.23 ± 0.06 Site UR Zone CR = -0.30 ± 0.06 Site PS Zone SL = -0.23 ± 0.06 Site UR Zone SL = -0.27 ± 0.06	

c.1. Asteroids density *a posteriori* LSD Fisher test ($\alpha=0.05$) Adjusted means and standard errors for factor site. Means with different letters are significantly different.

Site	Means	S.E.	
LV	2.09	0.09	A
UR	1.45	0.09	B
PS	1.07	0.09	C

c.2. Asteroids density *a posteriori* LSD Fisher test ($\alpha=0.05$) Adjusted means and standard errors for interactions sites x zone. Means with different letters are significantly different.

Site	Zone	Means	S.E.				
LV	SL	2.45	0.15	A			
LV	CR	2.26	0.15	A	B		
UR	BT	1.87	0.15		B	C	
LV	BT	1.55	0.16		C	D	
UR	SL	1.43	0.15			D	E
PS	BT	1.31	0.15			D	F
UR	CR	1.06	0.19			D	F
PS	SL	1.05	0.15			E	F
PS	CR	0.87	0.18				F

The holothuroid species richness was significantly different only between zones, higher in SL. In contrast, holothuroid diversity was significantly different at the level of zone and positively influenced by the RI (Table 4a & 4a.1.). The density of holothuroids was significantly different between seasons and zones (Table 4c & 4c.1.). Density values for the sea cucumber *Isostichopus fuscus* were similar in the SL zone of the PS and LV sites. At the same time, *Cucumaria flamma* was a common species at all the study sites and in the zones, with the lowest density values at the LV site (Table S2b).

Table 4. *F* and *p* values and coefficients of the variables included in the mixed model to explain a) species richness (*S*), b) diversity (*H*) and c) density (*D*) of Holothuroids.

a. Holothoroids species richness

Variables	<i>F</i> value	Coefficient ± S.E.
Zone	10.77**	Zone CR = 1.04 ± 0.35 Zone SL = 1.51 ± 0.33
Season	2.75 n.s.	Season Rainy = 0.35 ± 0.21

b. Holothuroids diversity		
Variables	F value	Coefficient ± S.E.
Zone	3.39*	Zone CR = -0.06 ± 0.09 Zone SL = 0.20 ± 0.15
Rugosity Index	5.60*	Rugosity index = 0.60 ± 0.25
b.1. Holothuroids diversity <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$) Adjusted means and standard errors for factor zone. Means with different letters are significantly different.		
Zone	Means S.E.	
SL	0.34 0.08	A
BT	0.12 0.08	A B
CR	0.08 0.05	B
c. Holothuroids density		
Variables	F value	Coefficient ± S.E.
Season	8.95**	Season Rainy = 0.22 ± 0.07
Zone	24.04***	Zone CR = 0.50 ± 0.09 Zone SL = 0.58 ± 0.09
c.1. Holothuroids density <i>a posteriori</i> LSD Fisher test ($\alpha=0.05$). Adjusted means and standard errors for factor zone. Means with different letters are significantly different.		
Zone	Means S.E.	
SL	0.37 0.03	A
CR	0.18 0.03	B
BT	0.06 0.03	C

3.2. Sites, zones, and seasonal echinoderm species assemblage

The PERMANOVA analysis revealed significant differences in the composition of echinoderm species across seasons, sites and zones (Table 5a). We found interactions between factors: season x zone and site x zone (Table 5a). Pair-wise test results revealed significant differences in echinoderm composition between the dry (DR) vs rainy (RA) seasons, between sites: Ureles (UR) vs Perpetuo Socorro (PS), Ureles (UR) vs La Viuda (LV), and Perpetuo Socorro (PS) vs La Viuda (LV), and between zones: crest (CR) vs slope (SL), crest (CR) vs bottom (BT) and slope (SL) vs bottom (BT) (Table 5b).

Table 5. a) PERMANOVA for the number of observations for each species based on sites, zones, and season (multivariate data) and b) results of the pair-wise test concerning the number of echinoderms in each species for each season, site, and zone at the study sites.

a. PERMANOVA table of results

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Se	1	2483.3	2483.3	70.154	0.001	999
Si	2	8045	4022.5	11.364	0.001	999
Zo	2	49608	24804	70.071	0.001	997
Se x Si	2	572.04	286.02	0.80801	0.59	998
Se x Zo	2	1794	897	2.534	0.017	999
Si x Zo	4	7588.8	1897.2	53.596	0.001	998
Res	94	33274	353.98			
Total	107	103360				

b. PAIR-WISE TESTS

Season			
Groups	t	P(perm)	Uniqu e perms
Dry vs Rainy	2.62	0.001	998

Site			
Groups	t	P(perm)	Uniqu e perms
UR vs PS	2.55	0.001	999
UR vs LV	3.11	0.001	998
PS vs LV	4.25	0.001	999

Zone			
Groups	t	P(perm)	Uniqu e perms
CR vs SL	6.58	0.001	999
CR vs BT	8.53	0.001	998
SL vs BT	8.90	0.001	997

The SIMPER analysis showed important average dissimilarity between seasons (39.55%), between the UR & PS (28.78%), UR & LV (33.20%), PS & LV (33,55%) sites and CR & SL (33.76%), CR & BT (49.75%) and SL & BT (54.03%) zones (Table S6a).

The species with the highest dissimilarity contributions between seasons (DR vs RA) were: *Diadema mexicanum*, *Toxopneustes roseus*, *Astropyga pulvinata*, *Eucidaris thouarsii*, and *Pentaceraster cumingi* (Table S6b). The species with the highest dissimilarity contribution values between the UR & PS sites were: *A. pulvinata*, *T. roseus*, *D. Mexican*, *Phataria unifascialis*, and *E. thouarsii*, for the UR & LV sites: *D. mexicanum*, *T. roseus*, *P. cumingi*, *E. thouarsii* and *A. pulvinata* and for the PS & LV sites: *A. pulvinata*, *E. thouarsii*, *D. mexicanum*, *P. cumingi*, and *T. roseus*. Finally, concerning the zones, the species with the highest dissimilarity contribution values between the CR & SL zones were: *D. mexicanum*, *E. thouarsii*, *A. pulvinata*, *Isostichopus fuscus*, and *P. pyramidata*. In relation to the CR & BT zones, they were: *E. thouarsii*, *T. roseus*, *P. cumingi*, and *D. mexicanum* and regarding the SL & BT zones: *D. mexicanum*, *T. roseus*, *A. pulvinata*, and *P. cumingi*. (Supplementary material Table S6).

The sequential test employing the DistLM indicated that the four variables chosen strongly affected the structure and composition of the echinoderm communities in the study zones at the three sites. The rugosity index (*RI*) explained the highest percentual variance, accounting for 25.63% of the variability in the echinoderm communities, followed by turf cover (%*TC*) with 13.02%, coral cover (%*CC*) with 9.88%, and derelict fishing gear (*DFG*) contributing with 6.76% (Table 6).

Table 6. Distance-based linear model for the number of observations for each species based on the zones at the study sites.

Variable	SS (trace)	Pseudo-F	P	Prop.
Rugosity index	26489	36.53	0.001	25.63
% Coral cover	13463	15.87	0.001	13.02
% Turf cover	10215	11.63	0.001	9.88
DFG in quadrat	6990.8	7.69	0.001	6.76

res.df: 106

The dbRDA includes vectors corresponding to these four variables on two axes that explained 91,9% of the fitted variation and 41,8% of the total variation. The crest and slope zone samples are distributed along the dbRDA1 axis, while the bottom samples are dispersed along the dbRDA2 axis. Concerning the explanatory variables, habitat complexity was related to the crest and slope communities, while coral cover, turf cover, and net segments were only related to the crest communities (Fig.2).

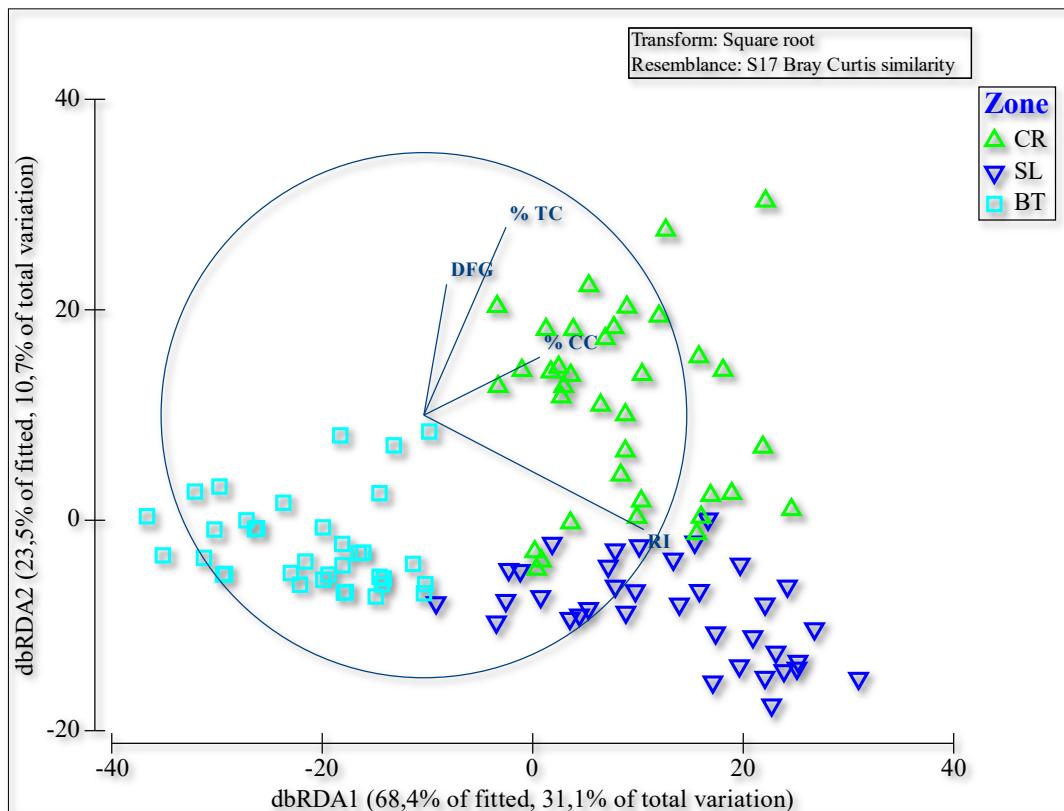


Figure 2.- Distance-based redundancy analysis (dbRDA) of the echinoderm's communities for each reef zone (CR, SL, BT), showing vector overlays of echinoderms species included in the best model by DistLM analysis.

4. Discussion

All the echinoderm species (11) at both study sites (control and disturbed) were conspicuous, and their presence was linked significantly to hard (rocky and coral) and

complex substrates (caves, holes, crevices), and only a few species to soft and mixed substrates (sand and gravel). Our results suggest that these species showed specific spatial distribution patterns, species richness, and density related to the reef features and the level of health or degradation of their habitats. On the other hand, results from the *post hoc* analysis suggest the use of a great diversity of micro niches selected by the echinoderms in the study area, where the interaction between sites and zones showed many different groups of general diversity and Echinoidea and Asteroidea densities. Only the holothuroids behave the same at the three study sites, with differences only due to the zone.

Sonnenholzner et al. (2013) showed that the sea urchins *D. mexicanum*, *E. thouarsii*, and sea stars *P. pyramidata*, or *P. unifascialis* are widely spread species along the central and southern continental coast of Ecuador; however, ecological attributes from the echinoderm communities and species population dynamics differ from reefs in the Marine Protected Areas compared with marginal urban reefs.

Seasonal pattern

In general, echinoderms were more abundant in the dry season (June-December) compared to the rainy (January-May). A similar seasonal pattern was found in the Mexican Pacific Region by Hermosillo-Nuñez et al. (2015) and Sotelo-Casas et al. (2018) and was related to the increase in productivity caused by the upwelling event on the continental coast of Ecuador (Moreano, 1983) that favours the coverage of turf algae (Alcivar, 2015; Alcívar-Mendoza et al., 2021) and sessile invertebrates. The diversity of the sea urchins significantly differed between seasons, and the density of species such as *E. thouarsii* and *D. mexicanum* were slightly different in dry and rainy seasons. We did not find any apparent seasonal pattern that indicates an increase in the density of sea urchins in the rainy season (January-May), despite the increase in fishing activities of the

artisanal fleet of Jaramijo targeting the fine-scale triggerfish *Balistes polylepis* (a sea urchin predator) (Figueroa et al., 2021). The sea urchin *A. pulvinata* was more abundant and gregarious in the upwelling season (February-April) in the CR and BT zones of the study sites; Alvarado (2008) described a similar pattern in Costa Rica and suggested that aggregation could have a possible role in reproduction. On the other hand, sea urchins like *T. roseous*, and sea stars like *P. cumingi*, changed their spatial distribution; increasing their density in the BT zones (sandy bottoms at the edge of rocky reefs) during the dry season (July-September), possibly due to the availability of food items or as a strategy to increase reproductive success (Reyes-Bonilla et al., 2018).

Species distribution

Sea urchins (Echinoidea) were the class with the most significant number of individuals at both the disturbed and control study sites (78%), followed by the sea stars, Asteroidea (18%), and sea cucumbers Holothuroidea (4%) in total density. Terán (1998) reported similar abundance patterns at three localities of the MNP (including the LV site) and Sotelo-Casas et al. (2018) in the Islas Marietas National Park, Central Mexican Pacific Region.

Echinoderms were more abundant at the PS site than at the UR and LV sites. Despite the relative good and healthy conditions of the LV site, the echinoderm species had a relatively low abundance compared with the disturbed PS site and was slightly superior to the UR site; suggesting a change in the composition of echinoderm species and their spatial distribution at disturbed sites (PS); with a high dominance of sea urchins like the *E. thouarsii*, also found by Cabanillas-Terán et al. (2016) (Fig. 3). This species is known to be successful in environments with high levels of fishing (Sonnenholzner, 2009), sediment deposition, and turf algae (Alcivar, 2015; Cabanillas-Terán, 2016; Alcivar et al., 2021). Disturbances to classical and marginal reefs can affect the benthic

communities' ecological attributes (species richness, diversity, evenness) and their functional profile (Mora et al., 2016; Soares et al., 2020). The population dynamics of this species are related to massive coral mortality and the subsequent proliferation of turf algae on disturbed reefs (Sotelo-Casas et al., 2018). *E. thouarsii* may also limit coral growth, modify the habitat structure, and interfere with the development of the reef framework (Sonnenholzner et al., 2013).

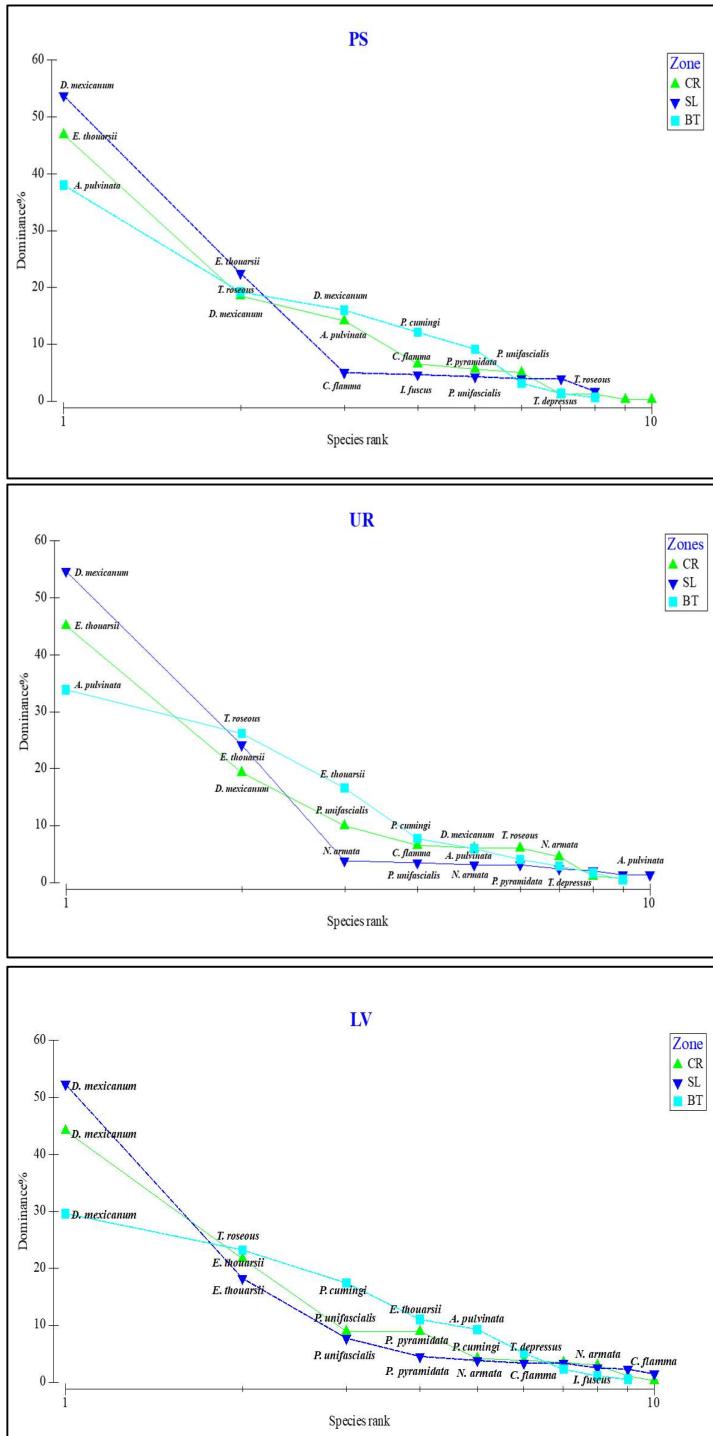


Figure 3. Species-rank of echinoderms for each study site and zone. Sites: a) PS = Perpetuo Socorro, b) UR = Ureles and c) LV = La Viuda. Zones: CR = Crest, SL = Slope, and BT = Bottom.

The *D. mexicanum* sea urchin was the most abundant species; however, its density differed between study sites. At disturbed sites like UR and PS, the most representative species were *E. thouarsii*, *D. mexicanum*, and *A. pulvinata*, while at the LV site they were *D. mexicanum*, *E. thouarsii*, and *T. depressus*.

Aggregated spatial distribution was similar between seasons for three species of sea urchins: *E. thouarsii*, *D. mexicanum* and *A. pulvinata* and one species of sea star *P. cumingi*. We found changes in the spatial distribution for the white sea urchin *T. roseous* from being random in the rainy season, to aggregated in the dry season (stable temperature conditions), which may be related to the increase in the availability of food and intense reproductive activity of the species. Mejía-Gutiérrez et al. (2019) suggest that, in laboratory conditions, *T. roseous* increases fertilization success between May-September every year. The spatial distribution of *T. roseous* was analyzed and discussed by James (2000) as a function of the depth variation: aggregated in shallow and middle depth to random in deep environments, and by Benítez-Villalobos et al. (2015) as a function of temperature and habitat preference. At our study sites, the presence of *T. roseous* was linked to rhodolith beds (food) and gravel substrates with dead coral in the bottom zones, with suitable conditions of protection from surge and hydrodynamics; and where the grazing process can increase the production of carbonate sediments through bioturbation (James, 2000).

Our findings show that the spatial distribution of echinoderms and ecological attributes such as: species richness, abundance, and density in the zones of the study sites are highly influenced by the increasing benthic habitat heterogeneity. Similar patterns have been reported by Flachier & Sonnenholzner (1997) and Terán (1998) on coral and rocky reefs of the MNP and by Hermosillo-Nuñez et al. (2015) in Mexico. Echinoderms reached the highest abundance in the slope (SL) zones compared to the crest (CR) and bottom (BT)

zones of the study sites. The rugosity index (*RI*) explained the physical heterogeneity of the zones and was the most important physical variable, contributing to clues about the spatial distribution, general density, species richness, and diversity of the echinoderms. Coverage of live branching, massive and encrusting coral colonies (%*CC*) from the *Pocillopora*, *Pavona*, and *Porites* genera was higher in the CR zones, and their presence increases the structural complexity of the CR zone, making it a suitable zone for the presence of crucial sessile invertebrate and corallivorous sea star species such as *P. pyramidata* and *P. unifascialis* (Castelló & Tickell et al., 2022); however, these species can also be found on fractured live coral colonies in the SL and BT zones of the UR and PS sites (Figueroa et al., 2020).

On the other hand, the presence of generalist sea star species such as *N. armata* is restricted to the SL zones, while *P. cumingi* is common in the BT zones with mixed substrates (sediment-covered flat rock), surrounded by sandy areas where spatial distribution changes are possibly related to habitat preferences and reproductive strategy (Reyes-Bonilla et al., 2018; Castelló & Tickell et al., 2022).

The long-spined urchin *D. mexicanum* shows an aggregated spatial distribution in zones of the reef with relatively low structural complexity (CR and BT), while the use of reef zones like SL with a high presence of caves, crevices, and holes, provide them with protection against predators (Hereu et al., 2005) like triggerfish (Balistidae) during the day. Surveys at night have proved that *D. mexicanum* sea urchins tend to split from aggregations or leave their refuges to perform low to medium-rate movements (Sonnenholzner et al., 2013) during this period. Food-searching movements include the consumption of green algae or occasionally hard coral colonies (*Pocillopora*) thereby exposing sea urchins to opportunistic night predators like the sea snail *Strombus peruvianus* and the octopus *Octopus mimus* in the crest and slope zones of study sites like

UR (Pers. observations). The slate pencil sea urchin *E. thouarsii* is a cryptic and sedentary species showing different spatial distribution and density patterns at the sites and in the zones studied. This species feeds on coralline crustose algae (Hernández-Almaraz et al., 2022) and coral polyps (Pocillopora) (Sonnenholzner et al., 2013).

The sea urchin *T. depressus* is a low-density and solitary species that was only found in the rocky substrates of the CR and SL zones at the UR and LV sites. Sonnenholzner & Lawrence (2002) and Sonnenholzner et al. (2013) stated that in reef systems of the MNP, *T. depressus* shows aggregated spatial distribution and densities between 1.5-1.8 ind/m², mainly in shallow habitats (<10m in depth). In the case of *T. depressus* populations in disturbed reefs, its presence, low density, and spatial distribution could be influenced by the absence of stable environmental conditions (Lawrence & Agatsuma, 2007) and food availability (coralline macroalgae) that allow the development of life stages. (Hernández-Almaraz et al., 2022)

Solitary individuals or aggregations of *A. pulvinata* were observed in the CR and BT zones of the UR and PS sites and only in the BT zone at the LV site. This species reached the highest density values (0.15-0.36 ind/m²) at the PS site, where maybe local environmental factors (availability of food) and social interactions (reproduction, defense) affect its abundance (Alvarado, 2008). Further, the species adopts different patterns of spatial distribution concerning the age of the individuals of *A. pulvinata*: solitary juveniles tend to occupy crevices and holes in rocky or reef areas (SL zones), while adults prefer to aggregate on BT zones as they have better protection due to the length of their spines Alvarado (2008).

In our study, low-density species such as the brown sea cucumber *I. fuscus* was found regularly in the SL zones of the study sites but rarely in zones like CR. The high intensity of fishing activities in Ecuador has led to a severe depletion of the *I. fuscus* population

(Sonnenholzner et al., 2009; 2013) and it is classified as “endangered” on the Red List of Threatened Species of IUCN (Mercier et al., 2013). In the Galapagos Islands, the catching of *I. fuscus* has been halted indefinitely since 2018, while on the continental coast of Ecuador, populations have not recovered due to illegal and furtive fishing of the species (Sonnenholzner-Varas, 2021). However, some effective management and conservation initiatives for the aquaculture and resettlement of *I. fuscus* have been developed in the last few years (Sonnenholzner-Varas, 2021).

The sea cucumber *C. flamma* is a low-density solitary species that inhabits rocky-sandy sediments (Solís-Marín & Laguarda-Figueras, 1999; Sánchez-Alonso et al., 2021) and was found in all the zones of the sites studied, particularly attached to rocky substrates with different levels of sedimentation.

Key predators like the fish: *Balistes polylepis*, *Sufflamen verres*, *Arothron meleagris*, *Bodianus diplotaenia*, spiny lobsters: *Panulirus gracilis*, *Panulirus penicillatus*, the slipper lobster *Scyllarides astori* and the sea star *P. cumingi* control the population of sea urchins along the continental coast of Ecuador and Galapagos Archipelago (Flachier & Sonnenholzner, 1997; Sonnenholzner et al., 2013; Castelló & Tickell et al., 2022). Removing sea urchin predators (large fish and lobsters) by artisanal fishing has cascade effects and can increase the abundance of sea urchins. Sonnenholzner et al. (2009) suggest that *E. thouarsii* in the Galapagos Marine Reserve show high density at sites with high levels of fishing, where predators like the Mexican hogfish *B. diplotaenia* and spiny lobster *Panulirus penicillatus* are less abundant.

Sea stars, such as *P. unifascialis* and *N. armata*, share a common predator, the harlequin shrimp *Hymenocera picta*, a common species inhabiting the CR and SL zones of the study sites. Harlequin shrimps inhabit holes, crevices, and caves on shallow rocky and coral reefs and prey exclusively upon starfish (Glynn, 1977; Prakash & Kumar, 2013; Valencia-

Mendez et al., 2017), and their role seems to be related to the regulation of the sea star populations (Prakash & Kumar, 2013). *H. picta* was sighted predating these species in zones (crest, slope) mainly dominated by branching coral colonies of the genus *Pocillopora* or in zones (bottom) with a high abundance of fragmented or fractured coral. Other important sea star predators include the parrotfish *Scarus perrico* (Sonnenholzner & Lawrence, 2002) and the blunthead triggerfish *Pseudobalistes naufragium* (Castelló & Tickell et al., 2022).

Turf cover and the effects of derelict fishing gear

Turf cover (%TC) was a critical variable explaining the composition of the echinoderm communities in the CR zones of disturbed reefs such as UR and PS. Turf algae consortiums growing in the CR zones act like natural traps of sediment (Connell et al., 2014) that provide nutrients and allow turf algae species to reach the highest values of coverage in the dry season (Alcívar-Mendoza et al., 2021). Temporal or permanent sediment contribution (domestic wastewater, rivers runoff) indirectly affects the composition of macroalgae and harms sea urchin communities in the CR zones. This leads to the replacement of dominant herbivorous species such as *D. mexicanum* by omnivorous species like *E. thouarsii* (Cabanillas-Terán et al., 2016, Alcívar-Mendoza et al., 2021) whose presence does not affect the structure and abundance of macroalgae and turf consortiums (Sonnenholzner et al., 2009, 2013). Dajka et al. (2021) discussed the function of the sea urchins species as grazers and controllers of macroalgae expansion in degraded coral reefs; based on the low impact of sea urchin aggregations on turf algae coverage and also suggest that Diadematidae species prefer to congregate in patches of reefs with high structural complexity (Hereu et al., 2005; Lee, 2006) and a low algae coverage. In our study, the coverage of turf algae (%TC) seems to have a relatively positive effect on

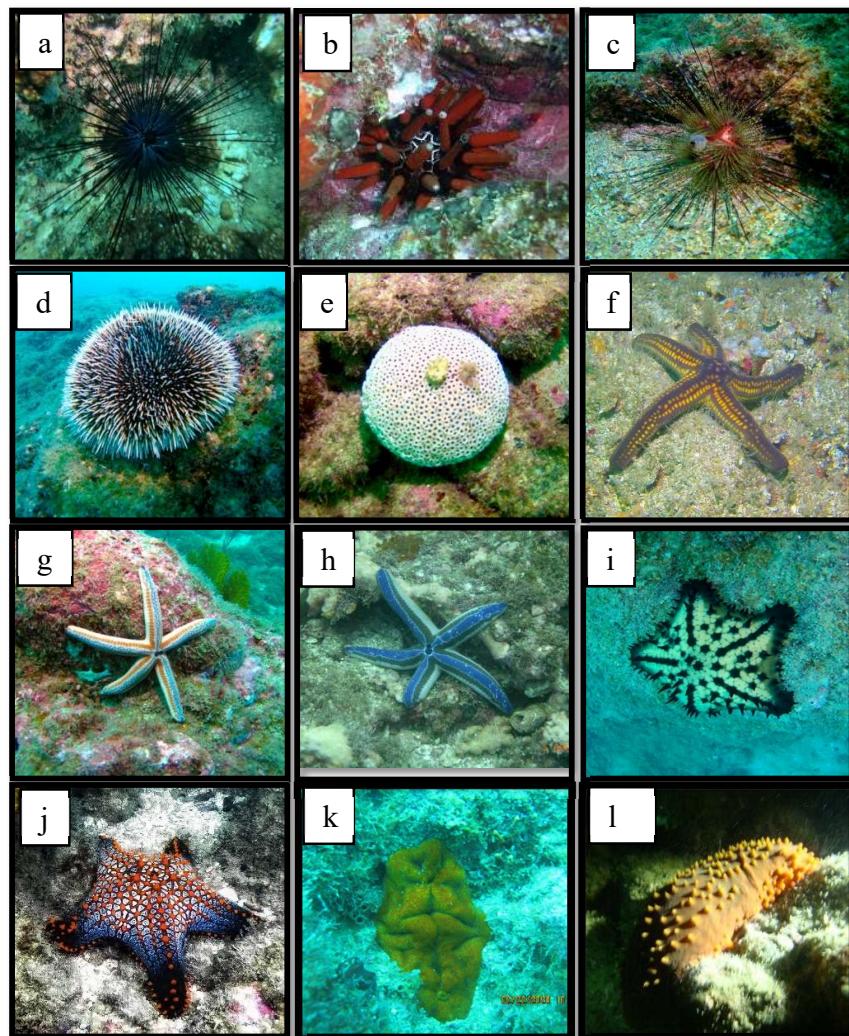
the increase of sea star density, which could be related to the trophic niche amplitude of the species. Most sea stars (excluding *P. cumingi* and *N. armata*) are facultative herbivores. The diets of sea star species are dominated by crustose and turf algae, supplemented by a small proportion of sessile invertebrates (Castelló & Tickell et al., 2021; 2022). On the other hand, turf algae consortiums, functioning as natural sediment traps, become important microhabitats for small infaunal invertebrates (Harris, 2015).

Derelict fishing gear (*DFG*) was an important variable explaining the composition of echinoderm assemblages in the CR zones and influencing the changes in the ecological attributes (diversity and density) of echinoids. De Carvalho-Souza et al. (2018) suggest that echinoderms and cnidarians are the leading marine organisms impacted by the covering and smothering effects of marine litter and *DFG*. The interactions of echinoderms with marine litter include the selective use of particular forms for protection (Amato et al., 2008); however, the high availability and chemical composition of these materials could cause an alteration in the relationships of those animals in their natural habitats (de Carvalho-Souza et al., 2018). Figueroa-Pico et al. (2016) suggest that monofilament nets are the most common form of *DFG* in the CR zones of the PS and UR study sites. Recent studies have proved the deleterious impacts of monofilament nets over branching coral colonies through fracture (Figueroa-Pico et al., 2020a) and the negative impacts on fish communities and cryptic species (Figueroa-Pico et al., 2021) in marginal reefs of Manabí. However, echinoderms need more systematic studies to identify the possible positive (protection) and negative (smothering, loss of structural complexity through coral fracture) effects of *DFG* on sea urchins and stars.

Despite sharing the same composition of species, our results suggest that echinoderm communities of disturbed (PS, UR) sites, and relative healthy reefs (LV) along the continental coast of Ecuador show remarkable differences related to the spatial

distribution and dominance of some sea urchins and sea star species according to the sites and reef zones. Differences in ecological attributes could be the result of direct and indirect anthropogenic activities (overfishing, marine litter, derelict fishing gear, loss of spatial heterogeneity, and increasing sedimentation rates) that can negatively affect the intrinsic autoregulatory capacity of the echinoderm communities for long-term maintenance to respond to global environmental anomalies. We recommend a periodical assessment and interannual analysis of the echinoderm communities as a helpful tool to comprehend the dynamics of disturbance and degradation processes in marginal reef environments.

APPENDIX



Annex 1. Pictures of echinoderms species in marginal reefs of the continental coast of Ecuador. a. *Diadema mexicanum* (Agassiz, 1863), b. *Eucidaris thouarsii* (Agassiz & Desor, 1846), c. *Astropyga pulvinata* (Lamarck, 1816), d. *Tripneustes depressus* (Agassiz, 1863), e. *Toxopneustes roseous* (Agassiz, 1863), f. *Pharia pyramidata* (Gray, 1840), g.-h. *Phataria unifascialis* (Gray, 1840), i. *Nidorellia armata* (Gray, 1840), j. *Pentaceraster cumingi* (Gray, 1840), k. *Cucumaria flamma* (Solis-Marin & Laguarda-Figueras, 1999) l. *Isostichopus fuscus* (Agassiz, 1863). Photos by: Antonio Santos & Juan Figueroa.

Table S1. Taxonomic classification of echinoderms in the study sites

Class	Family	Species	Type of habitat
Echinonidea	Cidaridae	<i>Eucidaris thouarsii</i>	Rocky/Coral
	Diadematidae	<i>Diadema mexicanum</i>	Rocky
		<i>Astropyga pulvinata</i>	Rocky/Gravel
Asteroidea	Toxopneustidae	<i>Tripneustes depressus</i>	Rocky
		<i>Toxopneustes roseus</i>	Rocky/Gravel
Holothuroidea	Ophidiasteridae	<i>Pharia pyramidata</i>	Rocky/Coral
		<i>Phataria unifascialis</i>	Rocky/Coral
	Oreasteridae	<i>Nidorellia armata</i>	Rocky
		<i>Pentaceraster cumingi</i>	Rocky/Gravel
	Stichopodidae	<i>Isostichopus fuscus</i>	Rocky
	Cucumariidae	<i>Cucumaria flamma</i>	Rocky

Table S2. General abundance of echinoderm classes per season, sites and zones.

Class	All sites		Season		Sites		Zones		
	N	Dry	Rainy	UR	PS	LV	CR	SL	BT
Echinoidea	1867	1061	806	543	725	599	641	751	475
Asteroidea	418	213	205	134	100	184	145	138	135
Holothuroidea	123	47	76	35	53	35	49	63	11
Total	2408	1321	1087	712	878	818	835	952	621

Table S3. Results for Kruskal-Wallis tests (sites and zones) for environmental (RI, %CC, %TC) and human-induced variables (DFG)

Variable	UR			PS			LV			Between sites		Between sites		Between sites	
	CR	SL	BT	CR	SL	BT	CR	SL	BT	H value CR	p-value	H value SL	p-value	H value BT	p-value
RI	1.40	1.60	1.20	1.28	1.50	1.08	1.40	1.85	1.25	16.63	**	25.93	***	23.60	***
%CC	27.70	9.00	7.50	15.00	8.50	12.00	27.50	10.00	5.00	18.26	**	2.87	n.s.	15.15	**
%TC	4.50	2.00	1.00	6.00	1.50	1.00	1.00	1.00	0.00	20.57	***	14.75	* ^a	6.80	*
DFG	6.00	2.00	1.00	4.50	1.50	1.00	1.00	1.00	0.00	20.57	***	14.75	**	6.80	*

Significance level: p <0.001 ***, p< 0.01**, p< 0.05*

Table S4. Values of spatial distribution index of echinoderm species per season: VMR = Variance-to-Mean ratio, MI= Morisita Index, and MSI = Morisita Standardized Index of echinoderms. AG= Aggregated, RD=Random and RG= Regular. * Significant Chi-squared Test.

Species	Dry				Rainy			
	VMR	MI	MSI	SD	VMR	MI	MSI	SD
<i>Eucidaris thouarsii</i>	2.21	1.20	0.50	*AG	2.58	1.29	0.50	*AG
<i>Diadema mexicanum</i>	5.11	1.48	0.50	*AG	3.34	1.33	0.50	*AG
<i>Astropyga pulvinata</i>	8.6	4.63	0.53	*AG	7.99	5.58	0.54	*AG
<i>Tripneustes depressus</i>	1.01	1.06	0.02	RD	0.87	0.00	-0.19	RD
<i>Toxopneustes roseus</i>	3.50	1.90	0.51	*AG	0.93	0.90	-0.09	RG
<i>Pharia pyramidata</i>	1.26	1.27	0.30	RD	0.82	0.78	-0.26	RG
<i>Phataria unifascialis</i>	0.99	0.97	-0.01	RG	0.76	0.82	-0.34	RG
<i>Nidorellia armata</i>	0.74	0.39	-0.38	RG	0.89	0.77	-0.16	RD
<i>Pentaceraster cumingi</i>	2.40	2.08	0.51	*AG	2.00	1.85	0.50	*AG
<i>Isostichopus fuscus</i>	0.97	0.90	-0.04	RD	1.13	1.41	0.16	RD
<i>Cucumaria flamma</i>	0.89	0.81	-0.15	RG	0.70	0.72	-0.43	RD

Table S5. Values of spatial distribution index of echinoderm species per site and season: VMR = Variance-to-Mean ratio, MI= Morisita Index, and MSI = Morisita Standardized Index, SD = Spatial distribution of echinoderms. AG= Aggregated, RD=Random and RG= Regular. * Significant Chi-squared Test for aggregated distribution.

Species	LV				PS				UR							
	Dry		Rainy		Dry		Rainy		Dry		Rainy					
	VMI	MI	MSI	SD	VMI	MI	MSI	SD	VMI	MI	MSI	SD	VMI	MI	MSI	SD
<i>Eucidaris thouarsii</i>	1.48	1.10	0.31	*AG	1.20	1.06	0.13	RD	2.55	1.20	0.50	*AG	2.54	1.21	0.50	*AG
<i>Diadema mexicanum</i>	4.01	1.24	0.50	*AG	2.90	1.21	0.50	*AG	4.24	1.43	0.51	*AG	2.86	1.28	0.50	*AG
<i>Astropyga pulvinata</i>	4.00	18.00	1.00	*AG	3.71	5.18	0.59	*AG	7.06	2.10	0.53	*AG	9.04	3.55	0.57	*AG
<i>Tripneustes depressus</i>	0.69	0.59	-0.28	RD	0.71	0.00	-0.26	RG	0.94	0.00	-0.05	RD	0.94	0.00	-0.05	RD
<i>Toxopneustes roseus</i>	2.95	1.90	0.52	*AG	0.99	0.53	0.98	RD	3.79	1.97	0.52	*AG	1.06	1.05	0.04	RD
<i>Pharia pyramidata</i>	1.11	1.06	0.07	RD	0.63	0.69	-0.33	RG	0.80	0.66	-0.18	RD	0.89	0.88	-0.10	RD
<i>Phataria unifascialis</i>	1.11	1.06	0.07	RD	0.77	0.86	-0.20	RG	0.47	0.47	-0.48	RD	0.52	0.60	-0.42	RD
<i>Nidorellia armata</i>	0.68	0.40	-0.29	RD	0.78	0.69	-0.20	RD	0.85	0.64	-0.13	RD	1.05	1.20	0.04	RD
<i>Pentaceraster cumingi</i>	2.21	1.80	0.51	*AG	1.20	1.13	0.13	RD	2.62	2.53	0.52	*AG	1.25	1.71	0.16	RD
<i>Isostichopus fuscus</i>	1.05	1.20	0.04	RD	1.12	1.29	0.08	RD	0.95	0.86	-0.05	RD	1.25	1.71	0.16	RD
<i>Cucumaria flamma</i>	0.88	0.00	-0.11	RD	0.47	0.47	-0.48	RD	0.68	0.66	-0.30	RD	0.92	0.94	-0.07	RD

Table S6. Simper Test Results

SIMPER results of species that contribute more than 5% at dissimilarity between seasons (Dry vs Rainy)

Average dissimilarity = 39.55

Species	Group Dry & Group Rainy					
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Diadema mexicanum</i>	2.62	2.44	6.04	1.26	15.26	15.26
<i>Toxopneustes roseus</i>	1.27	0.74	5.18	1.20	13.10	28.36
<i>Astropyga pulvinata</i>	0.82	0.63	4.47	0.84	11.31	39.66
<i>Eucidaris thouarsii</i>	2.34	2.14	4.36	1.22	11.03	50.69
<i>Pentaceraster cumingi</i>	0.76	0.74	4.12	1.04	10.43	61.11
<i>Cucumaria flamma</i>	0.50	0.87	3.35	1.22	8.46	69.57
<i>Phataria unifascialis</i>	0.93	0.98	3.21	1.09	8.11	77.69
<i>Pharia pyramidata</i>	0.71	0.66	3.01	1.07	7.62	85.31
<i>Nidorellia armata</i>	0.42	0.45	2.50	0.97	6.32	91.62

SIMPER results of species that contribute more than 5% at dissimilarity between season sites (UR vs PS).

Average dissimilarity = 28.78

Group UR & Group PS

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Astropyga pulvinata</i>	0.53	1.41	6.37	0.94	22.14	22.14
<i>Toxopneustes roseus</i>	1.21	1.02	4.02	1.11	13.96	36.10
<i>Diadema mexicanum</i>	2.14	2.39	3.27	1.09	11.37	47.47
<i>Phataria unifascialis</i>	0.89	0.90	2.67	1.02	9.29	56.75
<i>Eucidaris thouarsii</i>	2.30	2.56	2.59	1.14	9.02	65.77
<i>Cucumaria flamma</i>	0.69	0.85	2.54	0.98	8.82	74.59
<i>Pentaceraster cumingi</i>	0.82	0.45	2.28	0.71	7.92	82.51
<i>Pharia pyramidata</i>	0.54	0.52	1.80	0.78	6.26	88.77
<i>Nidorellia armata</i>	0.37	0.36	1.60	0.69	5.55	94.32

SIMPER results of species that contribute more than 5% at dissimilarity between sites (UR vs LV).

Average dissimilarity = 33.20

Group UR & Group LV

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Diadema mexicanum</i>	2.14	3.05	4.91	1.36	14.80	14.80
<i>Toxopneustes roseus</i>	1.21	0.79	3.95	1.21	11.90	26.70
<i>Pentaceraster cumingi</i>	0.82	0.99	3.89	1.10	11.72	38.42
<i>Eucidaris thouarsii</i>	2.30	1.87	3.50	1.11	10.53	48.95
<i>Astropyga pulvinata</i>	0.53	0.22	3.37	0.80	10.15	59.11
<i>Pharia pyramidata</i>	0.54	1.01	3.17	1.05	9.56	68.66
<i>Phataria unifascialis</i>	0.89	1.08	2.89	1.05	8.71	77.38
<i>Cucumaria flamma</i>	0.69	0.52	2.72	1.01	8.20	85.58
<i>Tripneustes depressus</i>	0.06	0.51	2.14	0.90	6.43	92.01

SIMPER results of species that contribute more than 5% at dissimilarity between sites (PS vs LV).

Average dissimilarity = 33.45

Group PS & Group LV

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Astropyga pulvinata</i>	1.41	0.22	6.20	0.90	18.53	18.53
<i>Eucidaris thouarsii</i>	2.56	1.87	4.18	1.23	12.50	31.03
<i>Diadema mexicanum</i>	2.39	3.05	3.81	1.16	11.38	42.41
<i>Pentaceraster cumingi</i>	0.45	0.99	3.76	1.29	11.23	53.64
<i>Toxopneustes roseus</i>	1.02	0.79	3.07	0.96	9.19	62.83
<i>Pharia pyramidata</i>	0.52	1.01	2.66	0.96	7.95	70.79
<i>Cucumaria flamma</i>	0.85	0.52	2.53	1.01	7.57	78.36
<i>Phataria unifascialis</i>	0.90	1.08	2.50	0.98	7.48	85.84
<i>Tripneustes depressus</i>	0.11	0.51	2.01	0.87	6.02	91.86

SIMPER results of species that contribute more than 5% at dissimilarity between zones (CR vs SL).

Average dissimilarity = 33.76

Species	Group CR & Group SL					
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Diadema mexicanum</i>	2.41	3.72	5.94	2.00	17.61	17.61
<i>Eucidaris thouarsii</i>	2.90	2.36	3.75	1.54	11.10	28.70
<i>Astropyga pulvinata</i>	0.83	0.09	3.58	0.85	10.61	39.31
<i>Isostichopus fuscus</i>	0.06	0.79	3.29	1.44	9.75	49.06
<i>Pharia pyramidata</i>	1.18	0.61	3.11	1.22	9.21	58.27
<i>Nidorellia armata</i>	0.33	0.89	2.86	1.23	8.47	66.74
<i>Toxopneustes roseus</i>	0.51	0.61	2.82	1.07	8.35	75.09
<i>Cucumaria flamma</i>	1.00	0.74	2.72	1.10	8.07	83.16
<i>Phataria unifascialis</i>	1.33	1.04	2.47	0.98	7.31	90.47

SIMPER results of species that contribute more than 5% at dissimilarity between zones (CR vs BT).

Average dissimilarity = 49.75

Group CR & Group BT

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Eucidaris thouarsii</i>	2.90	1.46	7.38	1.89	14.83	14.83
<i>Toxopneustes roseus</i>	0.51	1.91	7.26	1.75	14.60	29.43
<i>Pentaceraster cummingui</i>	0.25	1.52	7.10	1.97	14.27	43.70
<i>Diadema mexicanum</i>	2.41	1.44	5.21	1.44	10.48	54.18
<i>Astropyga pulvinata</i>	0.83	1.24	5.17	1.05	10.39	64.57
<i>Pharia pyramidata</i>	1.18	0.28	4.79	1.81	9.62	74.19
<i>Phataria unifascialis</i>	1.33	0.51	4.47	1.38	8.99	83.18
<i>Cucumaria flamma</i>	1.00	0.31	4.10	1.32	8.23	91.42

SIMPER results of species that contribute more than 5% at dissimilarity between zones (SL vs BT).

Average dissimilarity = 54.03

Group SL & Group BT

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Diadema mexicanum</i>	3.72	1.44	11.57	2.36	21.41	21.41
<i>Toxopneustes roseus</i>	0.61	1.91	6.82	1.53	12.62	34.03
<i>Astropyga pulvinata</i>	0.09	1.24	6.11	0.92	11.31	45.34
<i>Pentaceraster cumingi</i>	0.49	1.52	6.01	1.67	11.12	56.46
<i>Eucidaris thouarsii</i>	2.36	1.46	4.68	1.34	8.66	65.12
<i>Nidorellia armata</i>	0.89	0.08	4.15	1.70	7.67	72.79
<i>Phataria unifascialis</i>	1.04	0.51	4.02	1.32	7.45	80.24
<i>Isostichopus fuscus</i>	0.79	0.00	3.84	1.52	7.11	87.35
<i>Cucumaria flamma</i>	0.74	0.31	3.21	1.16	5.95	93.30

CHAPTER V

CHAPTER V: DISCUSIÓN GENERAL Y CONCLUSIONES

La tesis doctoral presentada intenta llenar algunos importantes vacíos de conocimiento relacionados con el estado de conservación de las comunidades coralinas de arrecifes rocosos marginales de la costa continental de la provincia de Manabí, Ecuador. Estos ecosistemas han sido altamente impactados por actividades humanas mayormente derivadas del turismo y las pesquerías artesanales. Figueroa et al. (2016) determinó la presencia y persistencia de basura marina en los sistemas de arrecifes marginales Perpetuo Socorro y Ureles (costa central de Manabí) y sugiere que las redes de monofilamento son la forma más abundante de artes de pesca abandonados en los arrecifes. La presencia de estas redes afecta negativamente a la conservación de las colonias de coral ramificado del género *Pocillopora* con implicaciones directas e indirectas sobre las comunidades de peces e invertebrados en las zonas de cresta y pendiente de los arrecifes.

Nuestro trabajo introduce y analiza el concepto de arrecifes marginales en la investigación de los ecosistemas marinos del Ecuador, una categoría relativamente nueva y poco estudiada de arrecifes que se desarrolla en condiciones subóptimas de parámetros ambientales y que en otras áreas geográficas ha recibido la atención de numerosos investigadores a nivel mundial desde la primera década del nuevo siglo XXI (Kleypas et al., 1999; Perry & Larcombe 2003; Wicks et al., 2010; Camp et al., 2018; Thompson et al., 2022), pero escasamente estudiado en Ecuador (Figueroa et al., 2016, 2020a, 2020b, 2021).

Los primeros estudios en arrecifes marginales se desarrollaron a principios de los años 2000. Estos estudios se enfocaron en analizar y evaluar la capacidad potencial de estos ecosistemas para soportar y enfrentar cambios globales derivados del calentamiento global y la acidificación oceánica (Baker et al., 2008; Freeman, 2015; Rossi et al., 2017; Camp et al., 2018) considerando la resiliencia de sus comunidades bióticas ante la alta

fluctuación de parámetros físicos como temperatura, potencial de hidrógeno y turbidez (Soares et al., 2020).

Nuevas perspectivas de investigación y hallazgos recientes sugieren que, a pesar de la alta capacidad para enfrentar cambios globales, los arrecifes marginales son ecosistemas altamente vulnerables a la influencia antrópica e impactos locales lo cual se describe como la paradoja de los arrecifes marginales analizada por Soares (2020). Por otro lado, los científicos a nivel mundial han remarcado la importancia del estudio sistemático de las comunidades biológicas en los arrecifes marginales. Esto incluye el estado de conservación de colonias coralinas tolerantes al estrés, invertebrados indicadores de la salud de los arrecifes y peces conspicuos de los arrecifes y dependientes del coral que permita establecer la dinámica de estos ecosistemas y sus múltiples interacciones con los factores ambientales (Camp et al., 2018; Soares et al., 2020), aspectos que fueron considerados y desarrollados en los **Capítulos I, III y IV** de la tesis.

Los impactos causados sobre las colonias de coral ramificado del género Pocillopora por la remoción y abandono de la redes de monofilamento (**Capítulo I**) incluyen la fractura, pérdida de complejidad de hábitat y el ahogamiento, con afectación directa e indirecta sobre las especies de invertebrados y peces dependientes del coral en las zonas de cresta de los arrecifes (Valderrama et al., 2018) como se describe en los **capítulos III y IV**. Las colonias de coral ramificado muestran alta capacidad de adaptación y tolerancia al estrés y a pesar de tener la fragmentación como una estrategia de reproducción asexual, se describe que un porcentaje alto de la fractura de coral se encuentra directamente relacionado con las actividades pesqueras sobre las zonas de cresta de los arrecifes marginales de la costa central de Manabí (Figueroa et al., 2020b). La presión pesquera temporal o permanente sobre el arrecife incrementa los eventos de enredo de las redes y la fractura de las colonias de coral ramificado por daño mecánico causado por los intentos

infructuosos de remoción del arte de pesca enredado en los complejos sustratos rocosos de las zonas del arrecife (Povolo, 2021; Wolf et al., 2021).

Por otro lado, la visibilidad es otro factor esencial afectando a la evaluación *in situ* de las comunidades de peces (Freitas, 2019) (**capítulo II**) debido a su alta fluctuación en los arrecifes marginales (Soares et al., 2020), y ha sido poco estudiado o subestimado en estudios realizados en ambientes con condiciones estables propios de los arrecifes clásicos (Bozec et al., 2011; Assis et al., 2013; Bernard et al., 2013; Usseglio, 2015; Thanopoulou et al., 2018). Por tanto, resulta clave determinar su efecto en las estimaciones de abundancia y densidad de las comunidades de peces de arrecifes marginales. Para ello, se comparó la efectividad de dos métodos de muestreo tradicional: Transecto de Video y Transecto de Observador para la obtención y análisis de datos de riqueza de especies, diversidad y abundancia de peces. Esto se llevó a cabo en los dos sistemas de arrecifes marginales estudiados e involucró el efecto de la época del año (seca y lluviosa) y las zonas geomorfológicas de los arrecifes (cresta, pendiente y fondo). El método de Transecto de Video fue más efectivo (Pelletier et al., 2011; Wartenberg & Booth, 2015; Wilson et al., 2018), especialmente al estimar los cambios de abundancia en las zonas geomorfológicas de los arrecifes, donde los cambios derivados de los eventos de surgencia, dinámica de corrientes y régimen de mareas puede producir altas fluctuaciones de visibilidad. El incremento de la turbidez en los arrecifes marginales reduce la detectabilidad de los peces y genera subestimación de abundancia, sesgos y malas interpretaciones de los resultados, especialmente en zonas con mayor complejidad estructural como las crestas y pendientes de los arrecifes (Edgar et al., 2004; Bozec et al., 2011; Pais & Cabral, 2017). Al contrario, niveles bajos de turbidez incrementaron la probabilidad de detección de los peces, especialmente al usar el método del Transecto de Video (Wartenberg & Booth, 2015; Wilson et al., 2018). Importantes recomendaciones

técnicas derivadas del estudio incluyen el registro de datos de visibilidad horizontal previo a cada muestreo y el uso del Transecto de Video con diferentes amplitudes, condiciones que permitirían comparar valores estimados de abundancia de peces con la visibilidad como una covariante y considerando medidas más precisas de turbidez. Este capítulo está enlazado con el **capítulo III** de la tesis pues fue esencial para el desarrollo y análisis de los atributos ecológicos de las comunidades de peces en los arrecifes marginales estudiados.

La determinación de la composición y atributos ecológicos de las comunidades de peces en los arrecifes marginales involucraron el uso del método de muestreo más efectivo (Transecto de Video) (**capítulo II**). Los cambios espaciales y temporales en la composición de las comunidades de peces de los arrecifes marginales de Manabí se dinamizan por un proceso complejo y multifactorial que incluye la influencia positiva de la complejidad estructural de los sitios (Bozec et al., 2011; Trebilco et al., 2015; McClanahan, 2019) y los efectos adversos de la pérdida de cobertura de coral vivo y subseciente pérdida de complejidad estructural analizados en el **capítulo I**, lo cual afecta la diversidad y la abundancia de peces (Pratchett et al., 2011; Rogers et al., 2014; Valderrama et al., 2018). Las zonas geomorfológicas de los arrecifes y la época del año influyen en la estructura de las comunidades de peces en ambos sitios de estudio. Las abundancias de especies conspicuas y dependientes del coral fue más alta en las zonas de pendiente y cresta comparadas con la zona de fondo. Variables como la complejidad estructural del hábitat y la cobertura de coral vivo afectaron positivamente la composición de especies (Gratwicke & Speight, 2005; Darling et al., 2017; Cáceres et al., 2020) en las zonas mencionadas, siendo los más fuertes predictores de la diversidad y abundancia de peces. Por otro lado, la combinación de complejidad estructural en relación a las zonas estudiadas fueron factores esenciales que incrementaron la riqueza de especies,

diversidad y abundancia total en relación a la cobertura de corales tolerantes al estrés (colonias de Pocillopora) en las zonas de cresta y pendiente (**capítulo I**). En contraste, el coral fracturado y la presencia y persistencia de redes abandonadas (descriptores inducidos por actividad antrópica) sobre el coral produjeron un efecto adverso en la composición de peces, especialmente sobre las zonas de cresta.

Un porcentaje elevado de las especies de peces en los sitios de estudio estuvieron fuertemente ligados a las colonias de coral en las zonas de cresta y pendiente donde encuentran refugio temporal y permanente, lugares de alimentación o reproducción, por lo cual la destrucción gradual del coral podría impactar negativamente a la diversidad y composición de las comunidades de peces en las zonas mencionadas (**capítulo I**). Las diferencias en la composición de especies de peces entre los sitios de estudio podrían estar relacionados a un proceso multifactorial local de degradación que afecta especialmente al arrecife Perpetuo Socorro. Esto puede ser explicado por su proximidad a la costa, donde estresores locales como los altos niveles de sedimentación, debido a la descarga de agua residual de carácter doméstico incrementa la proliferación de los consorcios de algas césped (Alcivar-Mendoza et al., 2021), con efectos adversos en la comunidad de peces e invertebrados (**capítulo III y IV**).

La época del año es otro importante factor afectando a la composición de las comunidades de peces, lo cual sugiere cambios espaciales y temporales en los sitios de estudio. Un importante ejemplo es el pez ballesta *Balistes polylepis*, cuyos cambios de distribución espacial y abundancia podrían responder a procesos de reclutamiento por reproducción y al efecto de baja temperatura y alta productividad en la época lluviosa, dinamizados por el evento temporal de surgencia (Rosales-Casián, 2013) descrito anteriormente. Entre enero y abril de cada año, la especie es blanco de la flota pesquera artesanal y su captura incrementa el enredo y abandono de redes monofilamento en las crestas del arrecife

durante las faenas nocturnas, causando en primera instancia fractura y posteriormente competencia y efectos de ahogamiento sobre las colonias coralinas. Este fenómeno tendría implicaciones en la conservación de las especies conspicuas y crípticas dependientes de la presencia de coral en relación a la progresiva degradación de su hábitat por el efecto indirecto de las actividades humanas asociadas a la pesca (Coker et al., 2013; Coker et al., 2015; Ghazilou et al., 2016; Russ & Leahy, 2017; Palacios-Narváez et al., 2020).

La comparación de las comunidades de equinodermos (indicadores del estado de salud) en los arrecifes marginales en contraste con un sistema de arrecife con niveles bajos de perturbación (Parque Nacional Machalilla) (**capítulo IV**) contribuye con importante información sobre la distribución espacial y temporal de los equinodermos y la influencia de variables biológicas, físicas y estresores inducidos por actividad humana y sus múltiples interacciones con las comunidades biológicas de los arrecifes estudiados.

Las comunidades de equinodermos en ambos tipos de sistemas de arrecifes muestran marcadas diferencias en su distribución espacial y dominancia de erizos y estrellas de mar en relación con los sitios estudiados, zonas del arrecife (James, 2000; Hereu et al., 2005; Alvarado, 2008; Amato et al., 2008) y el nivel de salud o degradación que puedan presentar sus hábitats (Cabanillas-Terán et al., 2016; Sotelo-Casas et al., 2018). Las diferencias en los atributos ecológicos (riqueza de especies, diversidad y densidad) son el resultado de actividades antrópicas directas o indirectas como la sobrepesca (Sonnenholzner et al., 2009, 2012; Calderón-Aguilera et al., 2019), presencia y persistencia de basura marina y redes de pesca abandonadas, pérdida de heterogeneidad espacial por fractura de coral y el incremento de las tasas de acumulación de sedimento (Sotelo-Casas et al., 2018). Todos estos estresores afectan negativamente la capacidad

auto regulatoria intrínseca de las comunidades de equinodermos para responder a anomalías ambientales globales a largo plazo.

La abundancia de equinodermos se incrementó en la época seca (junio-diciembre) (Sotelo-Casas et al., 2018) en comparación con la época lluviosa (enero-mayo), un patrón estacional ligado al incremento de la productividad causado por el evento de surgencia en la costa continental del Ecuador que además favorece el incremento en la cobertura de algas césped (Alcivar-Mendoza et al., 2021) e invertebrados sésiles. Los erizos de mar (Echinoidea) fueron la clase más numerosa tanto en sitios perturbados como en el sitio control en comparación con las estrellas de mar (Asteroidea) y pepinos de mar (Holothuroidea).

La cobertura de algas césped (turf) explicó los cambios de composición de la comunidad de equinodermos en las zonas de cresta de los arrecifes perturbados. En estas zonas, los consorcios de algas césped actúan como trampas naturales de sedimento que proveen nutrientes lo que les permite alcanzar los valores más altos de cobertura en la época seca. La contribución temporal o permanente de sedimentos (aguas residuales domésticas y escorrentías) podrían ser un factor importante afectando indirectamente la composición de macroalgas y las comunidades de erizos de mar (Dajka et al., 2021) en las zonas de cresta. Esto trae como consecuencia el reemplazo de especies herbívoras dominantes como los erizos de puntas largas (*D. mexicanum*) por especies omnívoras como los erizos lapiceros (*E. thouarsii*), cuya presencia y dominancia no afecta a la estructura de macroalgas y los consorcios de algas césped, pero limita el crecimiento del coral, ya que puede modificar la estructura del hábitat e interferir en el desarrollo estructural de los arrecifes (Sonnenholzner et al., 2009). Por otro lado, la alta cobertura de algas césped parece tener un efecto positivo sobre el incremento de la densidad de algunas especies de estrellas de mar, lo que podría asociarse a la amplitud de nicho trófico de algunas especies

(herbívoros facultativos), cuyas dietas están dominadas por algas costrosas y césped, complementadas por una pequeña proporción de invertebrados sésiles (Castelló y Tickell et al., 2022). En efecto, los consorcios de algas césped pueden convertirse en importantes micro hábitats para el desarrollo de pequeños invertebrados (Conell et al., 2014) disponibles como alimento para las especies de estrellas de mar en los sitios de estudio.

Finalmente, las redes de pesca abandonadas fueron también un importante factor explicando los cambios de composición de las comunidades de equinodermos en las zonas de cresta e influenciando los cambios de los atributos ecológicos (diversidad y densidad) de los erizos de mar. Sin embargo, el desarrollo de futuros estudios sistemáticos permitiría identificar los posibles efectos positivos (protección) (Amato et al., 2008) y negativos (pérdida de complejidad estructural a través de la fractura, ahogamiento) de las redes de pesca abandonadas sobre los erizos y estrellas de mar (Carvalho-Souza et al., 2018).

Las comunidades coralinas, peces e invertebrados de los arrecifes marginales de la provincia de Manabí se desarrollan exitosamente por su estrecha y vital relación con la alta complejidad estructural de las zonas geomorfológicas de los arrecifes (condición descrita en los **capítulos III y IV**). En las zonas de cresta esta complejidad está mediada por presencia de colonias de coral ramificado, mientras en las zonas de pendiente por las colonias de coral ramificado, masivo e incrustante, paredes y grietas, en ambos casos proporcionando a los organismos de los recursos de protección, alimentación y reproducción que requieren para su supervivencia. Por otro lado, la adición estacional de nutrientes como efecto del evento de surgencia (enero-abril) representan un factor importante que influye directamente en los cambios de composición y distribución espacial de varias especies de peces e invertebrados (recursos alimenticios y reproductivos). La configuración de la estructura de los arrecifes permite además la

retención de masas de agua fría con niveles más bajos de pH y elevada concentración de nutrientes que lejos de ser factores que hacen más lento el crecimiento de las colonias coralinas ramificadas, las han vuelto más tolerantes al estrés y posiblemente más resilientes al calentamiento global y acidificación oceánica. Por otro lado, el rango de profundidad de las zonas de cresta (5-7 m) de los arrecifes de la costa central de Manabí podría ser un factor positivo que limitaría la fractura natural y la fragmentación de las colonias por la acción del oleaje o marejadas (Castrillón-Cifuentes et al., 2017; Lizcano-Sandoval et al., 2018) e incluso disminuiría la susceptibilidad de las colonias coralinas a anomalías causadas por masas de agua con alta temperatura comunes en los eventos como El Niño Oscilación Sur (ENOS) (Glynn et al., 2001; Glynn et al., 2003; Glynn et al., 2018; Manzello et al., 2017).

Los efectos negativos comunes sobre las comunidades coralinas, peces e invertebrados se encuentran asociados directa e indirectamente a las actividades humanas derivadas del desarrollo costero de las ciudades de Manta y Jaramijó, y actividades turísticas y pesqueras de sus pobladores que disminuyen su capacidad de resiliencia. La adición permanente o temporal de sedimentos producto de la liberación de aguas residuales, salida estacional de ríos y escorrentías en las ciudades, dinamizada por las mareas y corrientes genera turbidez (**capítulo II**). Esto, también tiene un efecto de sobrecarga de nutrientes que tiene implicaciones directas sobre el aumento de la cobertura de las algas césped en las zonas de cresta de los arrecifes, generando cambios importantes en la composición de equinodermos (**capítulo IV**) y el reemplazo de importantes especies herbívoras clave en el desarrollo de la configuración del arrecife por especies omnívoras que generan impactos importantes a nivel estructura y funciones.

Los efectos de ahogamiento de las colonias de Pocillopora, causado por las redes abandonadas gradualmente colonizadas por los consorcios de algas césped (turf)

requieren especial atención pues los efectos dañinos de estos consorcios conducen a las colonias de coral al blanqueamiento y muerte (Swierts & Vermeij, 2016; Fong et al., 2018). Sin embargo, la potencial capacidad de resiliencia y recuperación de las colonias cuando el agente estresante (red de monofilamento) es removido y los posibles efectos positivos sobre las colonias con la recuperación de tejido vivo debe ser base para futuras investigaciones.

Por otro lado, los arrecifes estudiados reciben presiones turísticas y pesqueras permanentes y temporales que se han sostenido e intensificado durante las últimas décadas en relación al aprovechamiento de sus servicios ecosistémicos y que alteran su capacidad de resiliencia. Los arrecifes estudiados presentan niveles elevados de fractura de coral por anclaje y redes de pesca (**capítulo I**), además de actividades poco planificadas de buceo turístico y limpiezas submarinas y sobrepesca de especies clave (pargos, meros, langostas o pepinos de mar) con consecuencias en la composición de tallas y abundancias de estas especies consideradas como reguladoras e indicadoras de la salud de los arrecifes.

Finalmente, se remarca que las redes abandonadas sobre los arrecifes de manera accidental o inconsciente representan un factor clave que agudiza los procesos de degradación de las colonias coralinas a través de la fractura por acción mecánica directa o indirectamente como consecuencia de los consorcios de algas césped que encuentran en las redes un sustrato apropiado para su colonización. Estos consorcios algales entran en competencia directa con el tejido vivo del coral y causan el debilitamiento de las colonias, conduciéndolas finalmente al blanqueamiento y a la muerte. Los efectos sobre las comunidades de peces e invertebrados no son menos preocupantes pues la fractura de las colonias influye en la pérdida de complejidad estructural de las zonas de cresta, y subsecuentemente en la desaparición de importantes grupos funcionales de peces e

invertebrados o al reemplazo de especies herbívoras (erizos) importantes para la configuración del arrecife y sus interacciones con otros organismos.

CONCLUSIONES

1. Las colonias coralinas de los arrecifes marginales de la provincia de Manabí-Ecuador presentan una alta vulnerabilidad a las presiones antrópicas derivadas del desarrollo costero (sedimentación) y actividades pesqueras (redes) que causan la fractura de las colonias por enredo, la pérdida de complejidad estructural y el ahogamiento de las colonias por la acción de los consorcios de algas césped que crecen sobre las redes abandonadas.
2. La turbidez es un factor clave a considerarse en la evaluación de las comunidades de peces de los arrecifes marginales, ya que sus efectos pueden causar sesgos y malas interpretaciones en los datos de abundancia en zonas de alta complejidad estructural por lo que debe considerarse como una importante variable en estudios sistemáticos.
3. La composición y atributos ecológicos de las comunidades de peces de los arrecifes marginales de la provincia de Manabí son afectados por la compleja relación de factores naturales de carácter estacional (surgencias), alta complejidad estructural de las zonas geomorfológicas y el nivel de perturbación o degradación de los arrecifes debido a las presiones derivadas del desarrollo costero, y a las actividades turísticas y pesqueras permanentes y temporales.
4. Las comunidades de equinodermos presentan una composición similar de especies en relación con factores de carácter estacional y temporal (surgencias) y alta complejidad estructural de sus zonas geomorfológicas, pero importantes

diferencias en sus atributos ecológicos en relación al nivel de perturbación y degradación de su hábitat (cobertura de algas césped, presencia de redes de pesca).

5. Las comunidades biológicas de los arrecifes marginales de la provincia de Manabí presentan una baja capacidad de resiliencia a presiones derivadas de la presencia y persistencia de redes de pesca abandonadas, las cuales causan efectos sostenidos de pérdida de complejidad estructural (fractura), degradación de hábitat (blanqueamiento y muerte de colonias coralinas) y la consecuente pérdida y sucesión de importantes especies conspicuas y cripticas de peces e invertebrados.

RECOMENDACIONES GENERALES

Nuestro trabajo aporta importante información científica sobre el estado de conservación de los arrecifes marginales de la costa continental de la provincia de Manabí y sienta las bases para futuros estudios de estos ecosistemas que debido a la potencial resistencia y resiliencia de sus comunidades biológicas podrían enfrentar y ser exitosos ante futuros cambios globales. Sin embargo, una serie importante de acciones de protección y recuperación de estos ecosistemas deben ser tomadas a corto y mediano plazo para disminuir las presiones derivadas de las actividades turísticas y pesqueras y de aquellas indirectamente asociadas al desarrollo de las ciudades costeras. Esto involucra la educación de los usuarios directos e indirectos de los arrecifes (pescadores y sus familias, cooperativas pesqueras, turistas, comunidad local) y la acción directa de centros de educación básica, bachillerato, universidades, centros de investigación y organizaciones gubernamentales y no gubernamentales cuyo trabajo mancomunado genere un efecto positivo en la percepción de la comunidad ante los problemas ambientales asociados a los ecosistemas marinos. Las voluntades políticas de los gobiernos autónomos descentralizados locales y de las organizaciones mencionadas podrían ser un factor importante en la sostenibilidad y éxito de propuestas conjuntas, e incidiría en la posible transformación de las personas y su percepción ambiental.

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Mi gratitud eterna para todos...

J.A.F.P

ANEXOS



REPORT

Coral fracture by derelict fishing gear affects the sustainability of the marginal reefs of Ecuador

Juan Figueroa-Pico¹ · Francisco S. Tortosa² · Antonio J. Carpio^{2,3}

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Abstract Hard coral coverage contributes to increasing the structural complexity of coral reefs, provides biological resources and drives biological and ecological interactions among reef organisms. Declines in the structural complexity and coral diversity of tropical reefs, due to the influence of anthropogenic activities, have been reported around the world in recent decades; however, coral reefs on the continental coast of Ecuador have been poorly studied. From September 2017 to April 2018, the method of permanent belt transects and quadrats was used to assess the status of coral (percentage of live, dead and fractured coral) to determine the contribution of derelict fishing gear to the process of coral fracture, which causes loss of structural complexity on two marginal coral-rocky reefs in the central coast of Manabi-Ecuador: Perpetuo Socorro and Ureles. Three geomorphological zones [crest (5–7 m depth), slope (7–10 m depth) and bottom (10–13 m depth)] were assessed. Results show that the crest zone in Ureles reef was highly affected by the entanglement of nets compared with Perpetuo Socorro, and identify derelict fishing gear as a key driver in the process of the fracturing and fragmentation of coral. Seasonal and site-associated factors also had a

significant effect on the structural complexity of the reef studied. Destruction of coral in the crest zones drastically affects invertebrate and fish communities. We recommend a periodical assessment to measure the loss of structural complexity plus the implementation of a recovery program for the reefs studied that involves the education, active participation and collaboration of artisanal fishermen, governmental organizations and universities.

Keywords Anthropogenic activities · Community effects · Coral fracture · Dead coral · Derelict fishing gear

Introduction

Over the last few decades, coral reefs worldwide have faced increased threats derived from rising carbon dioxide (CO_2) levels, and ocean temperatures, and lower aragonite saturation levels associated with climate change and anthropogenic stressors (Burke et al. 2011; Hughes et al. 2017). However, recent studies have demonstrated that marginal High Latitude and Eastern Tropical Pacific reefs habitats have adapted to resist the high fluctuations of physical variables (providing them with a greater capacity to adapt, resist and expand in future climate-changing scenarios (Couce et al. 2013; Freeman 2015; Camp et al. 2018).

Hard corals contribute to the structural complexity of coral reef habitats, providing essential resources (food, shelter, places for reproduction) for many reef organisms and mediating biological interactions among coral-associated organisms (Pratchett et al. 2008, 2011; Coker et al. 2012). However, declines in the structural complexity and coral diversity of tropical reefs due to anthropogenic effects have been reported in the Caribbean and the Indo-

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Pacific regions in the last few decades (Gardner et al. 2003; Bruno and Selig 2007; Alvarez-Filip et al. 2009; Rogers et al. 2014). By other hand, coral communities in the Eastern Tropical Pacific (ETP) have demonstrated a high degree of resilience to diverse natural biotic and physical disturbances, with robust recovery at several localities in recent years (Glynn et al. 2017a); however, the anthropogenic influence and effects over reefs in this region remain briefly documented (see Cortés and Reyes-Bonilla 2017).

The negative effects of anthropogenic activities associated with tourism and fishing on coral reefs have been addressed by multiple authors worldwide with the primary description of (1) the effects of anchoring on coral and marine diversity (Dinsdale and Harriott 2004; Saphier and Hoffmann 2005; Fava et al. 2009; Forrester et al. 2015; Flynn and Forrester 2019), (2) the effects of blast fishing on reefs (Fox and Caldwell 2006; Raymundo et al. 2007; Praveena et al. 2012; Fuchs 2013), and (3) the effect of faunal removal of fish and benthic invertebrates (Calderon-Aguilera et al. 2019; Eddy et al. 2019; Cáceres et al. 2020). However, the effects of derelict fishing gear or entangled nets on coral, with the subsequent fracture and breakage due to their removal, are poorly documented.

Reefs on the continental coast of Ecuador are mostly rocky subtidal habitats (≤ 20 m in depth) that provide suitable environmental conditions for the occurrence of a few reef-building corals species and the development of coral communities (Glynn 2003). Coral communities of Ecuador had been described through the years with a focus in the diversity, coverage of coral and associated fauna from Machalilla National Park (MNP) and Galapagos Archipelago (Glynn 2003) and through recent information about diversity and coral distribution along with the mainland Ecuador and Galapagos (Glynn et al. 2017a). Coral communities on rocky reefs of Ecuador represent the southernmost distribution in the ETP. Due to their ability to withstand sub-optimal conditions and tolerate the local fluctuation of environmental conditions (but high biological productivity), these reefs can be classified as marginal (Kleypas et al. 1999; Perry and Larcombe 2003; Wicks et al. 2010). These ecosystems are present in areas of high levels of turbidity (Glynn 2003; Figueroa-Pico et al. 2020) due to the interaction of marine currents and tides (Vera et al. 2009), and an annual up-welling event (January–April each year) with changes of temperature between 1 and 10 °C (Moreano 1983). Heavy deposition of sediments occurs locally during the rainy season (Soledispa 2011) and domestic and industrial wastewaters are released near to these habitats as well (González Arteaga and González Arteaga 2017; Velasco et al. 2019). Concerning anthropogenically induced impacts, Flachier and Sonnenholzner (1997), Terán (1998), Glynn (2003) and Baquero Gallegos

et al. (2006) identified and briefly described fishing activities with monofilament nets, tourism-associated anchoring on the reefs and the harvesting of corals as the primary threats to the coral-rocky reefs in the Machalilla National Park (PMN). However, no reliable data on this topic are available or have been published yet. Zurita (2007) suggested the lack of economic alternatives as a key factor that forces artisanal fishermen to use non-selective and highly destructive fishing gear, such as monofilament nets which can negatively affect rocky and coral habitats along the continental coast of Ecuador. Figueroa-Pico et al. (2016) described the composition and spatial distribution of marine litter on rocky reefs along the continental coast of Ecuador and showed how the entanglement of monofilament nets could impact coral colonies in the crest zones. The structural complexity of the reefs studied plays an important role in the dynamics of invertebrate and fish communities in the crest zones due to the high coverage provided by branching hard coral such as *Pocillopora elegans*, *P. damicornis* y *P. capitata* ($\sim 30\text{--}50\%$ average percentage/m²), which tolerate constant changes of turbidity and temperature (Figueroa-Pico et al. 2016). The current study examined two sites where local coral-rocky reef exhibits different levels of disturbance relative to direct and indirect anthropogenic impacts. One site (PS, see study area in methods) exhibits intensive sedimentation, high coverage of turf algae (Alcivar 2015), grazing effects and trophic overlap of sea urchins (Cabanillas-Terán et al. 2016). In the second site (UR), we found low rates of light penetration and slow coral growth rates (Trujillo 2017). Other impacts identified at both sites include overfishing, anchoring, and persistent of marine debris and derelict fishing gear on the crest zones (Figueroa-Pico et al. 2016).

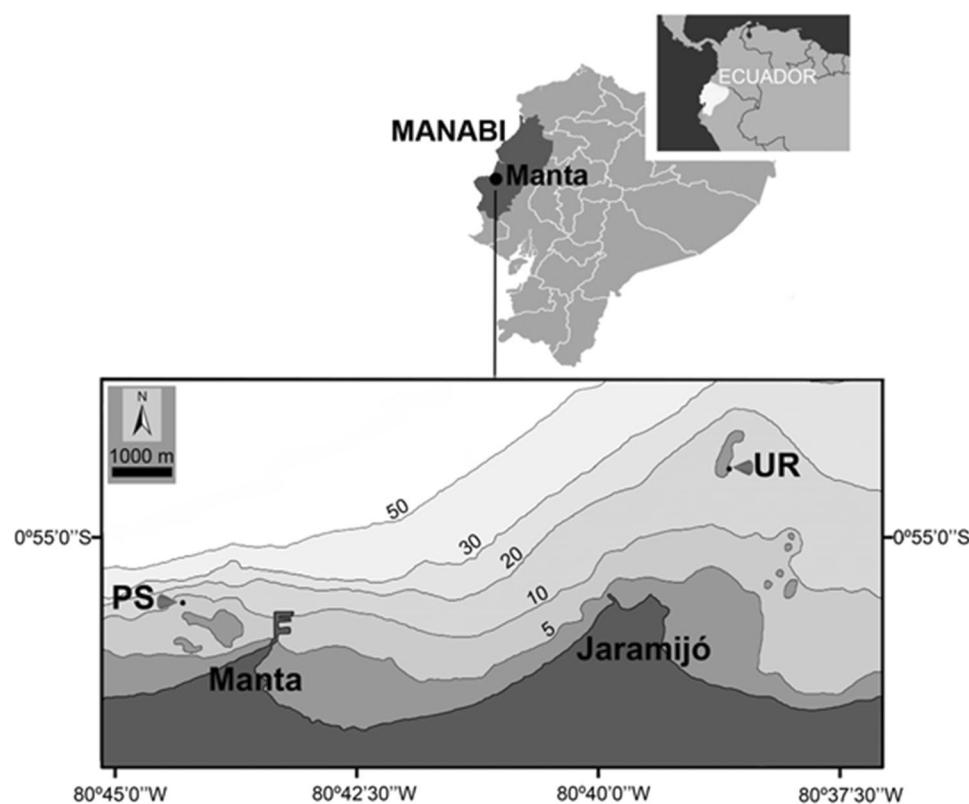
Considering the implications for future global coral reef management, it is important to put more emphasis on the conservation of marginal reefs to assure their sustainability in time (Couce et al. 2013). The main goal of the present work was to assess the impacts of derelict fishing gear and entangled nets on patches of hard coral to understand the process of coral fracture and fragmentation at the sites, reef zones, and during different seasons as a potential driver of structural complexity loss on the marginal coral-rocky reefs of Ecuador.

Materials and methods

Study area

The study was conducted in Manabi Province, on the continental coast of Ecuador. Two study sites were chosen: (1) Perpetuo Socorro (PS) ($00^{\circ} 55.637$, S $80^{\circ} 44.353$, W), located 2.3 km off the coast of Manta, and (2) Ureles (UR)

Fig. 1 Map of study sites represented as PS (Perpetuo Socorro) in Manta and UR (Ureles) in Jaramijo



($00^{\circ} 54.113$, S $80^{\circ} 38.863$, W), located 4.6 km from the nearest port in Jaramijo (Fig. 1). Both sites are marginal reefs that share structural similarities: rocky bottoms between 5 and 13 m deep, and three geomorphological areas treated here as “zones”: (1) the crest, 5–7 m deep, a rocky substratum with patches of branching coral species such as *Pocillopora* spp.; (2) the slope, 7–10 m deep, a rocky substratum with small patches of branching coral colonies such as *Pocillopora* spp. colonies or massive corals such as *Porites lobata*, and (3) the bottom 10–13 m deep, a mixed substratum with rock, sand, gravel, and patches of massive coral species such as *Pavona clavus*, that stabilizes at a maximum depth of 13 m.

Coral status and human-induced variables

Sampling was conducted between 2017 and 2018 in two seasons: (1) the dry season: September–December 2017, with an annual mean rainfall of 2 mm and (2) the rainy season January–April 2018, with an annual mean rainfall of 143 mm. At both sites, we assessed a total of 18 days. We surveyed a total of 270 permanent belt transects of 20×2.5 m as survey units (135 per site) each on the crest (CR), slope (SL) and the bottom (BT) zones (45 transects per zone at each site). Percentages of live coral (%LC), dead coral (%DC) and fractured coral (%FC) were estimated as a perspective of 2D area within 5 (1×1 -m)

quadrats randomly located within every belt transect in all study sites and zones. A mean of %LC, %DC and %FC coral for each belt transect was calculated through the sum of the percentage in each quadrat divided between the five survey units. Plan-viewed photographs of each quadrat were taken always at the same distance (1.5 m above from the substrate) and later analyzed with the software ImageJ 1.80 free version (Abramoff et al. 2005). Finally, to assess the impact of derelict fishing gear (DFG) over coral colonies, we counted and recorded the number of DFG segments of monofilament nets in every belt transect in each site and zone. In this category, we only included segments of DFG over coral colonies with a maximum area of 4 m^2 considering the highest area reached by a single coral colony observed in the study sites. For analysis and comparative purposes, the segments were called items of DFG and extrapolated to an area of 100 m^2 .

Statistical analysis

The calculated average of %LC, %FC, %DC and DFG (absences of normal distribution) was primarily analyzed with a Kruskal–Wallis nonparametric analysis of variance for the factor “zone” or “geomorphological zone”.

Data for fractured and dead coral were highly correlated, so we performed only one model with fractured coral as the dependent variable. A General Linear Mixed Model

(GLMMs) was performed using Infostat (Di Rienzo et al. 2018) with an extension of R software (R Core Team 2013). Three fixed factors were entered in the model: site with two levels (UR and PS), zone with three levels (BT, SL, and CR), and season with two levels (dry and rainy season). The percentages of live coral (%LC) and derelict fishing gear (DFG) were entered in the model as covariates. The transects were entered in the model as a random factor. The model was fitted to a Poisson distribution with a log link function. Rather than using criteria based on parsimony to select the “best model” (which favors precision vs. bias), we used the full models: (1) because our models had high degrees of freedom (five explanatory variables) with no need to guard against overfitting; (2) to protect from the bias of regression coefficients; and (3) to preserve the accuracy of confidence intervals while using other non-collinear factors for control purposes (multiplicity adjustment, while our understanding of the underlying biological processes led us to believe that the important variables to control for had been included). The assumptions of normality, homogeneity and independence in the residuals were assessed in models with a normal distribution function (Zuur et al. 2009). The significant p value was set at $p = 0.05$.

Results

Descriptive results

Live coral percentage (%LC) was especially high and variable in the crest zones of both sites ($p < 0.001$) (Table 1). Fractured coral (%FC) was high in the crest and bottom zones of the UR site ($p < 0.001$) and on the crest of PS site ($p < 0.001$) (Fig. 2). Dead coral (%DC) was

Table 1 Descriptive statistics for coral status (%LC = Percentage of live coral and %DC = Percentage of dead coral) and human-induced variables (%FC = Percentage of fractured coral and DFG = Derelict

Site	Variables	Zones												<i>H</i> value	<i>p</i> value		
		CR				SL				BT							
		Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max				
UR	%LC	50.11	16.2	25	82	9.49	8	0	19	20.5	3	14	26	111.4	***		
	%DC	15.13	4.08	8	25	0	0	0	0	28	17	11	52	94.3	***		
	%FC	19.09	6.63	12	35	2	2.6	0	7	22.7	8.3	12	38	91.4	***		
	DFG	14.87	6.08	5	31	0.91	0.6	0	2	2.91	1.8	1	8	104.3	***		
PS	%LC	30.84	19.3	4	68	35.3	18	5	67	1.62	1.7	0	5	89.1	***		
	%DC	8.87	4.36	1	18	0	0	0	0	7.91	6.7	0	17	58.8	***		
	%FC	11.38	6.1	4	25	1.76	2.4	0	8	7.91	6.7	0	17	47.1	***		
	DFG	7	3.83	1	16	1.04	0.7	0	3	0.71	0.5	0	1	79.3	***		

Kruskall Wallis test results, p value = * < 0.05 ; ** < 0.01 ; *** < 0.001

Table 2 *F* and *p* values and coefficients of the variables included in the mixed model to explain fractured coral

Variables	<i>F</i> value	Coefficient \pm SE
Season	0.59 n.s.	Rainy = -0.5 ± 0.07
Site	189.12***	Site UR = 0.95 ± 0.07
Zone	189.00***	Zone CR = -1.11 ± 0.09 Zone SL = -2.50 ± 0.14
%LC	147.23***	= 0.22 ± 0.02
DFG	1.75 n.s.	= 0.03 ± 0.02
Season \times DFG	6.51**	Season Rainy DFG 0.01 ± 0.01
Site \times DFG	70.83***	Site UR DFG = -0.08 ± 0.01
Zone \times DFG	11.99***	Zone CR DFG 0.09 ± 0.01 Zone BT DFG = -0.07 ± 0.12

Coefficients for the level of fixed factors were calculated using reference values of Dry in the variable ‘Season’, ‘PS’ in the variable ‘Site’, and ‘BT’ in the variable ‘Zone’

* $p < 0.05$; ** < 0.01 ; *** < 0.001

especially high in the BT zone of UR ($p < 0.001$) (Table 1). Finally, the amount of derelict fishing gear, such as items of DFG, was $5\text{--}31$ items $\times 100\text{ m}^{-2}$ in UR, while at PS it was $1\text{--}16$ items $\times 100\text{ m}^{-2}$ in the crest zones and had low values for the SL and BT zones with significant differences between sites and zones ($p < 0.001$) (Table 1).

The relationship of fractured coral with the study variables

The results of the GLMMs show that the percentage of fractured coral was significantly affected by site and zone factors ($p < 0.001$), with the highest values at the UR site

fishing gear) depending on sites (UR = Ureles and PS = Perpetuo Socorro) and zones (CR = Crest, SL = Slope and BT = Bottom)

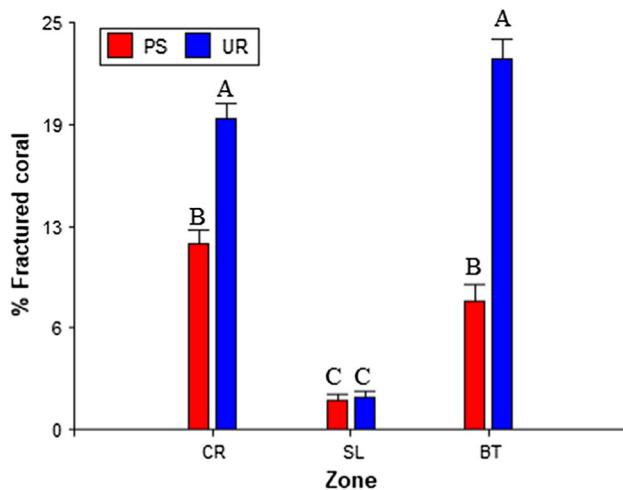


Fig. 2 Mean values (\pm SE) of fractured coral in different zones (CR = Crest, SL = Slope, and BT = Bottom) in the two study sites (UR = Ureles and PS = Perpetuo Socorro). Capital letters (A, B, C) indicate significant differences ($p = 0.05$) between zones according to Fisher LSD tests

and in the crest and bottom zones (Table 2). The percentage of live coral was a strong positive predictor of fractured coral in the study sites ($p < 0.001$) (Table 2). We found significant interactions between the DFG and season (higher coral fracture in the rainy season), site (higher coral fracture at the UR site) and zone factors (higher coral fracture on the crest than in the slope zones) that suggest that the fracture of coral colonies in the studied sites, zones and seasons is driven by DFG. (Table 2, Fig. 3).

Discussion

Our work is the first systematic initiative to quantify the growing and persistent problem of coral fracture caused by entangled nets over marginal coral-rocky reefs in Ecuador, a topic briefly described by Figueroa-Pico et al. (2016) which primarily focused on explaining the possible impact of monofilament nets on coral colonies in the crest zones. Few, but important, efforts have been made worldwide to explain the mechanisms of the coral fracturing by the anchoring of boats and DFG leading to the subsequent loss of structural complexity in coral reefs (Dinsdale and Harriott 2004; Saphier and Hoffmann 2005; Fava et al. 2009; Flynn and Forrester 2019). However, reliable data about the fracturing of coral by entangled nets worldwide are still poorly known.

In this study, we found a strong effect of the site on fracturing. The UR site showed more coral coverage compared with the PS site (Table 1). The study sites are traditional areas of artisanal fishing activities throughout the year (line and net fishing). However, despite its

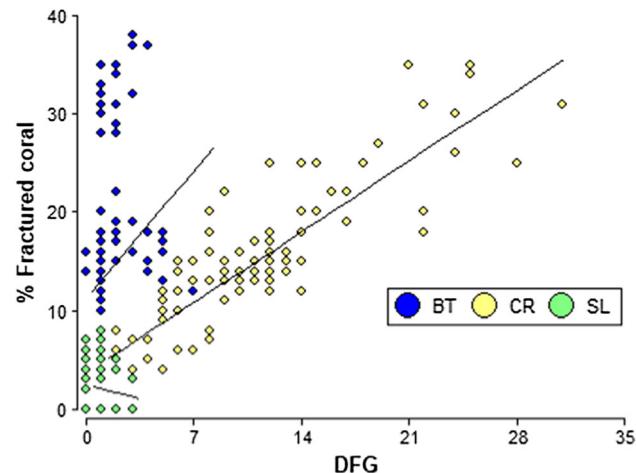


Fig. 3 Percentage of fractured coral in relation to derelict fishing gear (DFG = Derelict fishing gear) (items $\times 100 \text{ m}^2$) in three 3 zones (CR = Crest, SL = Slope and BT = Bottom)

distance from the coast, the UR site is subject to higher seasonal fishing pressure using monofilament nets than the PS site, due to dependence on available temporal fishing resources, so the probabilities of finding more coral fractured by entanglement increase. The interaction between DFG and site supports the aforementioned conclusions and suggests that the UR site suffered more fishing pressure than the PS site.

Other important predictors of fractured coral were geomorphological zone and the percentage of live corals (Table 1). Crest and slope zones are structurally more complex than the bottom (Figueroa et al. unpublished data) supported higher coverage of branching corals like *Pocillopora* spp., with faster growth rates but fragile and vulnerable to physical damage or massive coral forms such as *Porites lobata*, which are more resistant to physical damage (Dinsdale and Harriott 2004; Pratchett et al. 2015). Live coverage of *Pocillopora* spp. corals on the crest zones of the study sites $\sim 130 \text{ m}^2$ in UR and $\sim 80 \text{ m}^2$ in PS, which represents about 30 to 50% of the total area of the crest (Table 1). Baums et al. (2014) reported aggregations of 53 m^2 , 104 m^2 , and 291 m^2 in three lava pools of Isabela island in the Galapagos Archipelago although authors did not mention the total sampled area to estimate the percentage of the area covered by coral. However, the coral aggregations in Isabela island were at different depth (2–3 m) and oceanographic conditions showing the high capacity of *Pocillopora* species to colonize and develop in different habitats and environmental conditions. Therefore, the high coverage of branching corals on the crest zones creates a greater probability of fracturing when artisanal fishermen attempt to remove entangled nets. According to Figueroa-Pico et al. (2016), artisanal fishermen deploy their fishing gear in the areas surrounding the reefs, so

temporal changes in speed and direction of the currents at low and high tide could be the factors that cause their entanglement on the reef crests, making removal difficult and contributing to coral breakage by mechanical damage. After the breaking of the coral colony, fragments of *Pocillopora* spp. may remain in the crest zone where has more probabilities to survive or fall down the slope from the crest and, depending on the physical configuration of this zone, remain and colonize the rocks or simply fall directly to the bottom where the lack of optimal biotic and physical conditions, i.e., size of the coral fragment (Baums et al. 2014; Lizcano-Sandoval et al. 2018) and high levels of sedimentation, cause the live fragments to bleach and die due to the action of algae and cyanobacteria (Lizcano-Sandoval et al. 2018) with the subsequent significant effects on the coral and the resilience of the reefs (Fava et al. 2009).

We found high levels of DFG (monofilament nets) on the crests, with 1–31 items $\times 100\text{ m}^{-2}$ at the UR site and 1–16 items $\times 100\text{ m}^{-2}$ at the PS site (Table 1). Figueroa-Pico et al. (2016) reported similar results at the same study sites and suggested that derelict fishing gear and ghost nets persist on crest zones over time. We found a strong interaction between DGF and fractured coral on the crest zones that suggest the high vulnerability of these zones to coral fracture with a direct negative effect on coral coverage and indirect effects for invertebrate and fish communities due to the loss of structural complexity. Natural factors influencing the fracturing of branching colonies had been widely reported, e.g., the activity of corallivorous fish and urchins, feeding behavior of turtles (Glynn 2004) and reef sharks (Jimenez 1997), and the exposure of the coral colonies to the action of low tides or shallow waters (Castrillón-Cifuentes et al. 2017). Mentioned factors and their interactions are difficult to quantify and their influence was not considered in our study. On the other hand, as a response from environmental pressure, fragmentation is the most common and important asexual reproductive strategy for pocilloporids in the Tropical Eastern Pacific that helps to maintain the integrity of the populations through time and avoid local genetic extinction (Baums et al. 2014; Glynn et al. 2017b; Castrillón-Cifuentes et al. 2017). This fragmentation process is initiated and exacerbated by bioerosion (sponges, mollusks, echinoderms, and endolithic organisms) and corallivorous organisms (pufferfishes) that weakens coral skeletons and makes colonies susceptible to physical damage by the action of waves and storm surge (Reaka-Kudla et al. 1996; Glynn et al. 2017b; Alvarado et al. 2017). The depth range on crest zones (5–7 m) in our study sites favors the growth of *Pocillopora* colonies and could be an important factor limiting the natural fracturing and fragmentation of the colonies by the action of the waves or swells common in

shallow water colonies ($< 3\text{ m}$ depth) (Taebi and Patiaratchi 2014; Baldock et al. 2019) of Galapagos Archipelago and some localities of Machalilla National Park, also susceptible to anomalies of warm water related to ENSO events (Glynn et al. 2018).

Fava et al. (2009) suggested that the fracturing of coral causes a coral rubble rain that might have a physically negative impact on the reef and create patchiness that leads to habitat fragmentation. Also, Pratchett et al. (2011), Fuchs (2013), and Russ and Leahy (2017) suggested that the fracture and decrease in live coral cover on reefs would lead to a considerable decline in the richness of invertebrate and fish species and abundance, although marginal coastal reefs are inhabited by coral fauna adapted to survive under conditions markedly different from those traditionally accepted as ideal for the optimal functioning of a coral reef (Hennige et al. 2010; Browne et al. 2012). Further, Flynn and Forrester (2019) argued that many reef fish taxa depend on three-dimensional reef structures for shelter and the flattening process of reefs with heavy anchorage could explain the reduction in the density of most functional groups of adult fish, i.e., scrapers and excavators, spongivorous, benthic carnivorous, piscivorous, and omnivorous. Further, the entangled and derelict nets over the branching coral are gradually colonized by turf and fleshy algae consortiums that change their composition over time and could dynamize the degradation of coral via disruption of ecological processes, detrimental smothering effects, diseases and death of corals, and decline of invertebrate and fish communities (Figueroa-Pico et al. 2016; Galgani et al. 2018; de Carvalho-Souza et al. 2018; Lamb et al. 2018; Valderrama et al. 2018). Barott et al. (2012) suggested that coral-turf algae interaction at the reef scale negatively affects the physiology of coral colonies with a reduction in the production of oxygen of the coral holobiont and the subsequent limitation of growth, lower coral fecundity and inhibition of larval settlement. This may impact corals on multiple spatiotemporal scales and influence the structure of benthic coral reef communities. Swierts and Vermeij (2016) suggest a strong relationship between coral growth forms and their success in competitive interactions with turf algae. These authors argue that branching corals with faster growth rates are the least successful rate competing with turf algae. This evidence suggests that coral colonies of *Pocillopora* spp., common in the study sites and crest zones, could be highly vulnerable to the detrimental effects of turf and fleshy algae consortiums that grow over DFG. Their interrelationship must be studied in more depth to understand the dynamics and the long-term effects concerning coral traits, invertebrate, and fish communities.

Season by itself was not influential enough to explain coral fracturing on the reefs studied; however, we found an

interaction between the presence of derelict fishing gear (DFG) and season (accentuated in the rainy season in UR site). There was a higher presence of DFG in the rainy season compared to the dry season, a repeated pattern observed in the same sites during the last years (Personal observations). An important fishing resource, such as the triggerfish *Balistes polylepis*, an active species that feeds over the sandy bottom adjacent to rocky reefs (Hobson 1965; Robertson and Allen 2015) reach the highest abundance in the rainy season (January–April) due to an spawning aggregation process (Erisman et al. 2010), this makes this species a temporary target for the artisanal fleet of Jaramijo. Other fish species with similar aggregation pattern in the rainy season but without commercial importance for the artisanal fleet of Jaramijo are the long spine balloonfish *Diodon holacanthus* and round stingrays *Urobatis* spp. (no published data). At the same time, changes in the direction and intensity of currents and strong groundswells are common in this season (Vera et al. 2009) increasing the probabilities of fishermen losing monofilament nets due to entanglement.

Our findings suggest that derelict fishing gear (entangled nets) is a driver in the fracture and fragmentation of pocilloporid corals on the marginal rocky reefs of the continental coast of Ecuador, which mainly affects the structural complexity of the crest zones with direct implications for the sustainability of resident invertebrate and fish communities. We strongly recommend a periodic assessment of the structural complexity of the reefs and the implementation of a recovery program for the reefs affected that involves the education and active participation and collaboration of artisanal fishermen, governmental organizations and universities.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

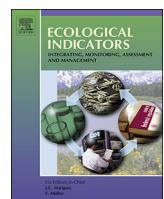
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Turbidity: A key factor in the estimation of fish species richness and abundance in the rocky reefs of Ecuador



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ABSTRACT

The effectiveness of using standardized sampling methods for fish communities in coral and rocky reefs has been widely discussed because it largely depends on the experience and skill of the observer, availability of high-definition equipment and the stability of local environmental parameters. The rocky reefs in Ecuador have highly variable conditions of turbidity, which can generate biases in the sampling of reef fish. The present work compares the effectiveness of detection of two sampling methods: 1) observer-band transects and 2) video-transects, as tools to determine the composition of fish communities in two rocky reefs subjected to high anthropic pressure and high variability in the conditions of turbidity. To achieve this goal, 48 transects of 100 m and variable-width on the dependence of turbidity conditions were performed in three geomorphological reef zones: the crest, slope, and bottom, where a community of fish was sampled from September 2017 to April 2018 using both methods. The results showed significant differences in the fish abundance recorded depending on the sampling method, the video-transect method was more efficient for the estimation of abundance. Comparison of the survey methods in reef zones showed that video-transects are more effective in detecting significant differences in abundance on the slopes of the reefs in comparison with observer-band transects. Turbidity significantly affected the abundance of fish detected by both sampling methods. Our results suggest that the video-transect method is more efficient to record fish abundance with respect to the observer-transect method under different conditions of turbidity.

1. Introduction

Coral and rocky reefs are complex and productive marine ecosystems that support high but very sensitive and vulnerable biodiversity (Knowlton, 2001; Kulbicki et al., 2013; Parravicini et al., 2013). The diversity of invertebrates and fish in these ecosystems can be affected by natural stressors (deposition of sediments and turbidity) (Freitas et al., 2019) or by the direct or indirect influence of anthropogenic stressors: overfishing, derelict fishing gear, dredging or sewage pollution (Muthukrishnan and Fong, 2014; Jones et al., 2016; Valderrama et al., 2018; Abaya et al., 2018). In terms of conservation, these ecosystems and their diversity need a suitable way to be assessed (Rotherham et al., 2007), taking into consideration the dynamics of local conditions of physical parameters (Bayley and Mogg, 2019). For coral and rocky reef systems, an underwater visual census (UVC) with strip transects (fixed length and width) is the most frequent method for

non-destructively surveying community dynamics (Kulbicki et al., 2010; Bosch et al., 2017).

The effectiveness of the detection of standardized sampling methods for fish communities in coral and rocky reefs has been discussed worldwide because it is closely related to the: experience, skill and swimming speed of the observer (Bernard et al., 2013; Henriques et al., 2013; Jones et al., 2015; Daros et al., 2018), availability of high-definition equipment (Bower et al., 2011; Assis et al., 2013; Mallet and Pelletier 2014; Warnock et al., 2016; Wilson et al., 2018), stability of local environmental parameters (Edgar et al., 2004; Bozec et al., 2011; Usseglio 2015; Wartenberg and Booth 2015) and the activity of the fish group (diurnal or nocturnal), their detectability (conspicuous or cryptic species) and their mobility (Thresher and Gunn, 1981).

The importance of turbidity has been underestimated by some authors as a factor affecting fish detectability (Pais and Cabral, 2017). However, underwater turbidity is a limiting factor for visual

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techniques, whether UVC, photo or video (Mallet and Pelletier, 2014). Travers et al. (2018), suggest that surveys taking place in locations with high turbidity have only minor possibilities of obtaining reliable data when using methods that require clear visibility, such as remote underwater video systems or underwater visual census (UVC). Our study highlights the need to implement complementary sampling techniques to monitor ecological changes, in the various dimensions of biodiversity (Bosch et al., 2017).

Information about fish community assessment on the continental coast of Ecuador is scarce and is only available through general technical reports of ichthyofauna in Machalilla National Park (MNP) or derived from unpublished data obtained from experienced divers. Flachier and Sonnenholzner (1997) and Terán (1998), describe a total of 106 species associated with rocky reefs and coral patches in MNP using UVC, these reports also describe the diversity of fish according to the significant habitat complexity of the sites studied.

The rocky reefs on the continental coast of Ecuador are present in areas of highly variable conditions of turbidity; some areas maintain good conditions of visibility all around the year whereas in other areas turbidity may change rapidly throughout the year, this variability of conditions may produce errors and biases during fish sampling. Local changes of turbidity mainly occur due to the interaction of physical variables such as marine currents and tides (Vera et al., 2009), an annual up-welling event (January-April each year) (Moreano, 1983), the increase of turbidity caused by deposition of sediments in the rainy season (Soledispa, 2001) and the release of domestic and industrial wastewater. The present work compares the effectiveness of detection of two sampling methods: 1) Observer-Transect Method and 2) Video-Transect Method, to record the fish communities on two rocky reefs under high fluctuations of turbidity and analyze the influence of the real abundance of fish as determinant in identifying trends in the species richness and abundance of Ecuadorian reefs.

2. Materials and methods

2.1. Study area

The study was conducted in the province of Manabi, the continental coast of Ecuador. Two study sites were chosen: 1) Perpetuo Socorro (PS) ($00^{\circ} 55.637' S$ $80^{\circ} 44.353' W$), located 2.3 km off the coast of Manta and 2) Ureles (UR) ($00^{\circ} 54.113' S$ $80^{\circ} 38.863' W$), located 4.6 km from the nearest port in Jaramijo (Fig. 1). Both sites share structural similarities: rocky reefs between 6 and 13 m in depth. At both sites, we can distinguish three geomorphological areas (crest, slope, and bottom). Identified impacts at both sites include high levels of sedimentation, overfishing, anchoring, marine litter, and derelict fishing gear. The sites described also share similarities in fish diversity (65–70 species associated with rocky reefs) and have high biological productivity (personal observations). Both sites are traditional areas of artisanal fishing activities throughout the year (line and net fishing, autonomous and semiautonomous diving) and tourism (autonomous diving) (Figueroa-Pico et al. 2016).

2.2. Survey methods

Sampling was conducted between September 2017 and April 2018 at each study site with a total of 16 h of data recording. Two methods were simultaneously used to record the species richness and abundance: 1) the Observer-Transect Method (OTM) performed by a diver with experience in the identification of fish species and 2) the Video-Transect Method (VTM) performed by a diver with a GoPro Hero Underwater High Definition camera and Evolve light of 900 lm. For both methods, 48 permanent transects of 100 m (five subunits of 20 m or 240 transect segments) and variable width (max. 2.5 m on each side from the central line of the strip transect) in relation to turbidity levels were used as survey units on the bottom (BT), slope (SL) and crest (CR) zones (16

transects per zone). In order to minimize disturbance, both methods were carried out simultaneously by two divers swimming side by side during the same diving session (standardized speed 0.17 m/s and elevation 1 m) in independent surveys in the above-mentioned zones, and the same route was repeated during the study period in each zone. Total survey time was 8 h for each method with no variations between both methods. During every sampling session, the number and the abundance of every detected fish species were recorded for each method. OTM data was recorded on slates, while, VTM records were later watched by the same experienced observer and the number of fish species and abundance were registered.

Vertical and horizontal turbidity was estimated at the surface and underwater with a Secchi disk, 30 cm in diameter. The range of horizontal turbidity fixed in the present study was 1–7 m, and it was recorded in every survey. No survey was performed when turbidity was less than 1 m.

2.3. Statistical analysis

To evaluate the factors affecting the species richness and abundance of fish, we used four Generalized Linear Mixed Models (GLMMs). In these models, the species richness (model 1) and abundance (model 2) were used as response variables. These set of models were divided into two subsets of models: 1) (model 1a for species richness and model 2a for abundance) for all turbidity conditions ($N = 240$) and 2) (model 1b for species richness and model 2b for abundance) for turbidity conditions of less than 2 m ($N = 70$), where we assume that the probability of detection is 1, and therefore we can distinguish the effects of abundance and detection. In these models, two fixed factors were included: the survey method with two levels (VTM and OTM) and the zone with three levels (BT, SL, and CR). The turbidity was entered in the model as a covariate. The site, transects (nested to the site), and segments (nested to transect) performed during the survey period were entered in the model as random factors. In addition, the interaction zone * survey method and turbidity* survey method were also included in all models. A Poisson distribution with a log-link function was used in all models.

Rather than using criteria based on parsimony to select the 'best model' (which favour precision vs. bias) we used the full models: (i) because our models had high degrees of freedom and there was no need to prevent overfitting, (ii) to protect from the bias of regression coefficients, and (iii) to preserve the accuracy of confidence intervals while using other non-collinear factors for control purposes. Such factors included multiplicity adjustment, while our understanding of the underlying biological processes led us to believe that the important variables to control for had been included. In addition, Fisher's LSD post-hoc test within the mixed analysis was applied to check for response differences among different levels of categorical variables (zone and survey method) and their interaction. Statistical analyses were performed using InfoStats with an extension of R statistical software (Zuur et al., 2009).

3. Results

A total of 48 transects (16 transects in each zone; BT, SL, and CR) were performed using both methods during the study period. Turbidity had a variation of between 1 and 7 m and was highly fluctuated during the study period in the BT zone (Mean \pm SD; 3.54 ± 0.87) (Fig. 2).

3.1. Fish species richness estimation and survey methods

In the monthly transects performed in the three zones (CR, SL, and BT), we counted a maximum number of 22 species using OTM whereas 31 species were detected with VTM. VTM detected nine species more in comparison with OTM. These were cryptic and nocturnal species such as *Synodon evermanni*, *Plagiotremus azaleus*, *Halichoeres dispilus*,

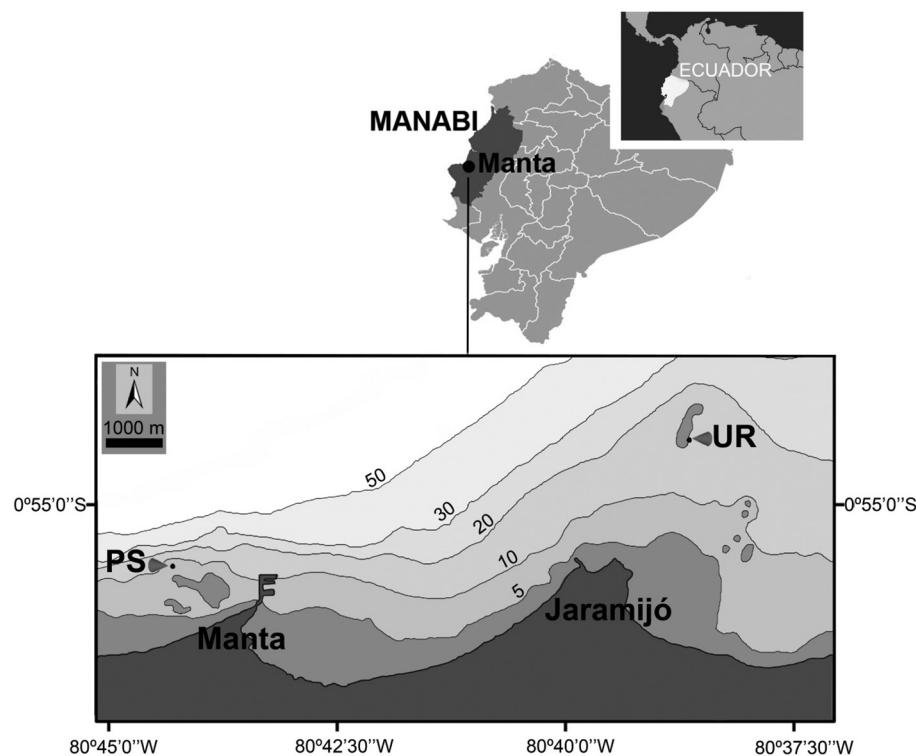


Fig. 1. Map of study sites represented as PS (Perpetuo Socorro) in Manta and UR (Ureles) in Jaramijó.

Alphestes multiguttatus, *Stegastes flavilatus*, *Cirrhitichthys oxycephalus*, *Apogon pacificus*, *Apogon dovii* and *Sargocentron suborbitalis*. The species richness detected did not differ significantly between survey methods for both the models proposed: 1) all turbidity conditions ($N = 240$) and 2) turbidity conditions < 2 m ($N = 70$), where we assume that the probability of detection is 1 (Table 1a and 1b). The factor zone had an effect on the detectability of fish species richness in model 1a with all distances (Table 1a, Fig. 3), species richness values were lower in CR zones in comparison with SL and bottom zones. The interaction between survey method and turbidity was not significant, so turbidity equally affected the detection of the fish species in both methods (Table 1a and 1b).

3.2. Fish abundance estimation and survey methods

In all the transects performed monthly, we counted a maximum

number of 262 fish using OTM, whereas 535 fish were detected with VTM. The estimation of abundance was significantly different between the survey methods in both the models proposed: 1) all turbidity conditions ($N = 240$) and 2) turbidity conditions < 2 m ($N = 70$) with the assumption of the probability of detection = 1 (Tables 2a and 2b). The zone was another important factor that affected the estimation of fish abundance in both samples (Table 2a, Fig. 4). The fish abundance was higher in the SL zones in comparison with the CR and BT zones of the reefs studied. Turbidity was an important factor that affected the estimation of abundance in both the models proposed (Tables 2a and 2b). We found a significant interaction between the survey methods and the zone (but only in model 2a: with all distances) where VTM was capable of detecting and recording more fish than OTM in the SL zone (Table 2, Fig. 4). The interaction between survey methods and turbidity in both models was not significant (Table 2a and 2b).

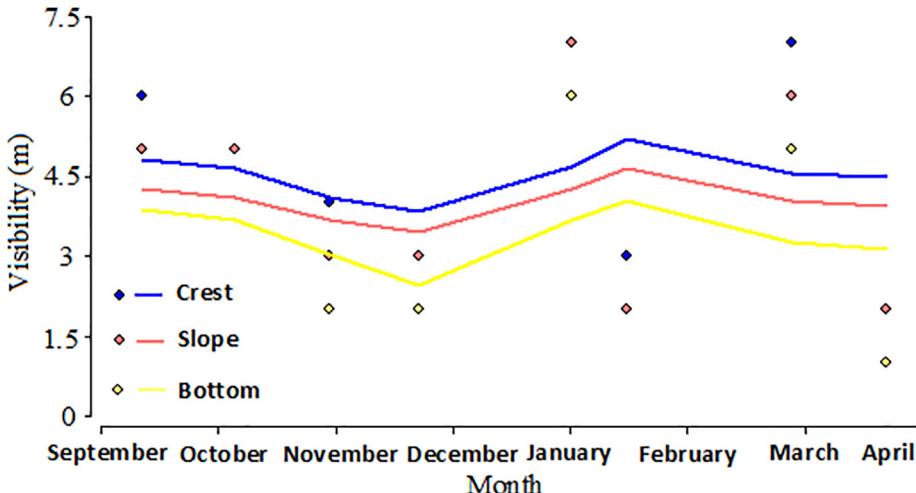


Fig. 2. Temporal evolution of the visibility in each zone (crest, slope, and bottom).

Table 1

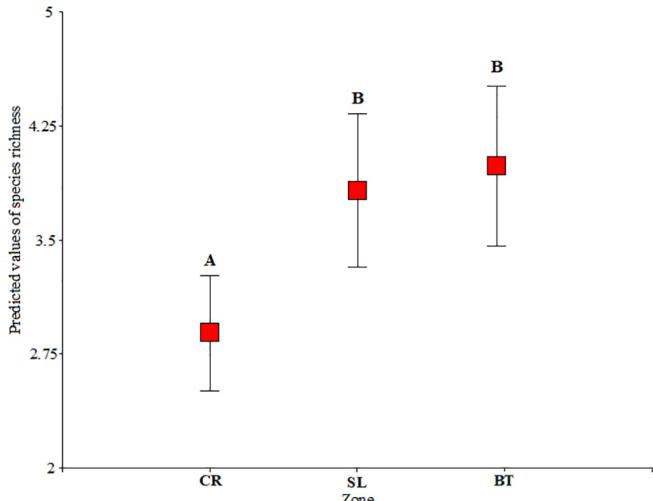
General models of sequential hypothesis tests for species richness.

a Model of sequential hypothesis tests for fish species richness considering all turbidity conditions (N = 240)

	numDF	denDF	F-value	p-value
Survey method	1	232	0.01	0.9153
Zone	2	232	8.89	0.0002
Turbidity	1	232	2.37	0.1247
Survey method × zone	2	232	0.18	0.8363
Survey method × turbidity	1	232	0.08	0.7824

b Model of sequential hypothesis tests for fish species richness considering turbidity conditions < 2m (N=70) and assumption for the probability of detection = 1.

	numDF	denDF	F-value	p-value
Survey method	1	62	0.20	0.6575
Zone	2	62	0.78	0.4633
Turbidity	1	62	2.02	0.1602
Survey method × zone	2	62	0.05	0.9508
Survey method × turbidity	1	62	0.22	0.6408

**Fig. 3.** Predicted values (median ± 95% CI) of species richness (n° of species) as a function of the zone (CR: crest, SL: slope and BT: Bottom). Capital letters indicate significant differences (P = 0.05) between zones according to Fisher LSD tests.)

4. Discussion

Our results show that VTM is a better census method than OTM, especially to estimate fish abundance under the different turbidity conditions of the rocky reefs of Ecuador. Wartenberg and Booth (2015), suggested video-transects as the most appropriate underwater visual census method for surveying high-latitude coral reef fish in the southwestern Indian Ocean, based on the low data variability concerning the species richness and fish abundance obtained. Similar conclusions were reached by Pelletier et al. (2011), and in a review by Mallet and Pelletier (2014), who suggest that there is an important increase in the amount of data collected by underwater video systems in comparison with other methods. Thanopoulou et al. (2018), compared the efficiency of detection for strip and line transects methods performed by observers and suggest potential biases derived from the strip transects method, mainly due to the imperfect detectability of fish in transects with > 2.5 m in width and the behavioral responses of fish, especially for shy and secretive species, which are poorly detected by observers in visual counts or due to the limitations of underwater visibility. On the other hand, Video Stereo Systems have been shown to provide more

Table 2

Model of sequential hypothesis tests for fish abundance.

a Model of sequential hypothesis tests for fish abundance considering all turbidity conditions (N = 240)

	numDF	denDF	F-value	p-value
Survey method	1	232	43.37	< 0.0001
Zone	2	232	305.52	< 0.0001
Turbidity	1	232	534.79	< 0.0001
Zone × survey method	2	232	8.43	0.0003
Turbidity × survey method	1	232	0.44	0.5074

b Model of sequential hypothesis tests for fish abundance considering turbidity conditions < 2m (N = 70) and assumption for the probability of detection = 1.

	numDF	denDF	F-value	p-value
Survey method	1	62	6.31	0.0146
Zone	2	62	3.26	0.0449
Turbidity	1	62	7.11	0.0097
Zone × survey method	2	62	0.23	0.7989
Turbidity × survey method	1	62	2.97	0.0897

accuracy and precision in the identification of fish and estimation of abundance, length, and distance than visual estimation made by observers (Harvey et al., 2004; Pelletier et al., 2011; Mallet and Pelletier, 2014). However, none of the studies referred to here considered or analyzed the importance of turbidity as a factor affecting survey methods.

We found high variability in the data of fish abundance when comparing both testing methods; however, VTM detected between 147% and 235% more fish than OTM in the surveyed transects. Our results show that OTM may cause an underestimation of the abundance of fish communities that increased when the abundance increased. Wartenberg and Booth (2015), suggest that the use of UVCs, in our case OTM, may underestimate fish abundance, due to the innate challenges in non-destructively detecting all fish present in a community. This underestimation seems to be accentuated when surveying highly heterogeneous systems, such as coral reefs, where the most accurate identification and counting by the observers may be limited by structural complexity. Jones et al. (2015), suggest that variability in abundance is likely to be the greatest determinant of whether monitoring can effectively identify trends concerning abundance in fish communities. Detectability varies considerably across fish species and is mostly affected by biological traits: body size, schooling behavior, shyness, and camouflaging coloration or behavior (MacNeil et al., 2008; Bozec et al., 2011); environmental factors such as habitat complexity (Edgar and Barrett, 1999) and water turbidity (MacNeil et al. 2008) also influence detectability. The schooling behavior of fish is an innate trait that seems to affect their detectability and counting positively (MacNeil et al., 2008); however, we observed that the high levels of schooling of different species in some places of the reefs studied combined with the high structural complexity and the stability of turbidity conditions could affect negatively the identification and counting of fish by OTM. In our study, permanent strip transects and estimated turbidity avoided the issue of dealing with distance estimation as a source of uncertainty for both survey methods. VTM records may show less error associated with distance estimation than observers and offer a cost-effective tool that allows reducing the biases derived from OTM (Harvey et al., 2004; Pelletier et al., 2011).

Fish abundance in the study sites was affected by the factor zone; we found an interaction between the survey method and zone; VTM was especially effective in detecting differences of fish abundance on the slope (SL) zone with respect to the crest (CR) and bottom (BT) zones of the studied sites (Fig. 3). Gratwicke & Speight (2005) and Fuchs (2013) suggest that factors such as the architectural complexity of reefs may support a great species richness and abundance of fish and

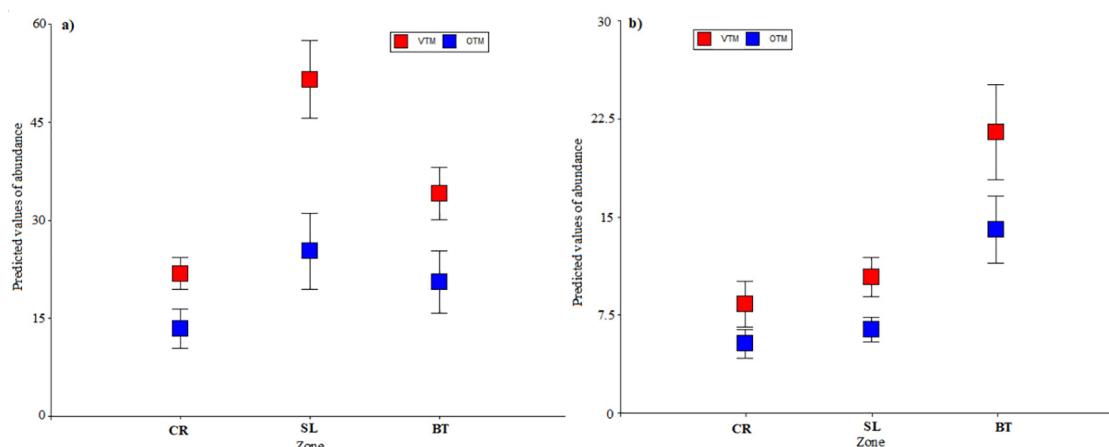


Fig. 4. Predicted values of abundance (n° of individuals) as a function of the zone (CR: crest, SL: slope and BT: Bottom) (categorized according to the sampling method: VTM vs OTM). a) predicted values for the global model (model 1a) and b) predicted values for the model < 2 m (model 1b).

invertebrates, so the architectural complexity in the reef slopes may cause an increase in fish abundance (Darling et al., 2017) that could increase the underestimation of fish abundance using OTM.

Turbidity was an important and highly influential factor with a strong effect on detecting the fish abundance. Minimal differences in fish abundance between the VTM and OTM methods were detected with bad conditions (< 2 m) of visibility at the study sites. Conversely, in transects performed under low levels of turbidity (2–7 m), VTM was much more effective for the detection of fish abundance, since the greater the visibility, the more differences between the methods were found.

Comparison of tested models for species richness (sets 1a and 1b) and abundance (sets 2a and 2b) for all turbidity conditions ($N = 240$) and turbidity conditions < 2 m ($N = 70$) showed similar results with differences only for species richness (factor zone) and for abundance (interaction zone \times turbidity). We, therefore, conclude that both methods (VTM and OTM) are capable to detect species richness and changes of abundance without considerable differences in distinct scenarios of turbidity.

Most studies worldwide have been developed under relatively stable conditions of visibility; in these particular cases, traditional methods such as the underwater visual census (UVC) may have led to a possible underestimation of communities with a high abundance of fish. Bozec et al. (2011) found that turbidity had a considerable effect on the detectability of the profile of fish in a study in New Caledonia; however, more generally, turbidity has been an underrated factor during studies of fish communities. A review made by Usseglio (2015), showed that only 5.3% of papers related to assessing fish communities worldwide, consider water clarity as a factor or source of variation, mainly because most of the studies have been developed at sites with stable conditions of visibility (Henriques et al., 2013) or simply because studies and related models consider maximum visibility as a constant (Jones et al., 2015; Pais and Cabral 2017; Warnock et al., 2016). Even though studies like (Kulbicki, 1998) have shown that when the water is very clear, underwater distances tend to be underestimated, and the opposite occurs when the water is turbid, distances tend to be overestimated. Under fluctuating turbidity conditions, other authors, such as Assis et al. (2013), suggest that VTM using fixed cameras can be a suitable tool to assess fish assemblages, this method seems to increase the efficiency of the efforts in the field and reduces the negative effect of divers changing the composition of the assemblages in the surveys or the “diver effect” (Dickens et al., 2011). However, the authors point out a lower accuracy of the fixed camera method (counting of fish and evaluating the species richness) in comparison with the observer and video strip transects when records are made under extreme turbidity conditions.

Our results show that when turbidity levels are low, the probability of detecting fish is increased, especially when VTM is used. Although it may seem obvious, in environments with high turbidity, visibility could be a key factor for evaluating fluctuations in fish communities during the year and should really be included as a covariate in future studies. Therefore, we recommend recording data of horizontal turbidity prior to every survey and using VTM transects with variable width. This may allow comparable estimated values (derived from the effect of the visibility as a covariate) of fish abundance to be obtained, considering real measurements of turbidity.

VTM could be used to assess fish communities in any zone of the reef. Data recorded by VTM could be analyzed and stored for *a posteriori* spatiotemporal changes or behavioral studies of key species as indicators of reef health. Finally, it is important to note that data obtained from VTM may be especially useful to determine the spatial and temporal changes of fish communities caused by environmental and anthropogenic drivers (Bozec et al., 2011; Wartenberg and Booth, 2015) on the rocky reefs of Ecuador.

CRediT authorship contribution statement

Juan Figueroa-Pico: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration. **Antonio J. Carpio:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing - review & editing. **Francisco S. Tortosa:** Conceptualization, Methodology, Validation, Resources, Writing - review & editing, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Natural and anthropogenic-induced stressors affecting the composition of fish communities on the rocky reefs of Ecuador

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ABSTRACT

Natural and human-induced stressors have threatened the sustainability of the fish communities of coral-rocky reefs worldwide in the last decades. The composition of the fish communities on the reefs of Ecuador and the factors affecting spatiotemporal changes are unknown. We studied the influence of the descriptors of structural complexity, the current status of coral and human-induced variables over fish communities. A video transect method was used to assess fish communities in three zones (slope, crest, and bottom) of two reefs during two seasons (rainy and dry). The structure of fish communities was highly influenced by the zones and season; rugosity and live coral affected the fish composition on the crest and slope zones. The fractured coral and derelict fishing gear on coral produced an adverse effect on fish composition over the crest. A multifactorial process causing loss of structural complexity and affecting fish composition was identified, however, periodical assessment is required for a greater understanding of this process.

1. Introduction

Coral and rocky reefs are complex and productive marine ecosystems that support high but very sensitive and vulnerable biodiversity and spatial-seasonal variation (Knowlton 2001; Kulbicki et al. 2013; Paravicini et al. 2013; Alvarez-Filip et al. 2015; Nelson et al. 2016). The structural complexity of the reefs expressed as rugosity can shape the abundance and diversity of reef fish assemblages across large and small spatial scales (Nash et al. 2013; Ferrari et al. 2016; Darling et al., 2017). The diversity of fish in these ecosystems can be affected by global threats such as climate change (Ateweberhan et al. 2013; Attamimi and Saraswati, 2019) and natural local and regional stressors such as deposition of sediments and turbidity (Freitas et al., 2019). On the other hand, recent declines in the structural complexity and coral diversity of tropical reefs due to anthropogenic stressors like overfishing, derelict fishing gear, dredging or sewage pollution (Muthukrishnan and Fong 2014; Jones et al. 2016; Valderrama et al. 2018; Abaya et al. 2018) may have consequences for reef fish and fisheries (Alvarez-Filip et al. 2013; Rogers et al. 2014).

Coral-rocky reef biodiversity along the continental coast of Ecuador represents the southernmost distribution in the Eastern Tropical Pacific

(ETP); however, it has been rarely studied (Cortés-Núñez 1997; Cortés 2011; Alcivar 2015; Cabanillas-Terán et al. 2016; Trujillo 2017, Figueroa et al., 2016, Figueroa et al., 2020a, 2020b). The rocky reefs on the continental coast of Ecuador are present in areas of highly variable physical conditions such as high levels of turbidity, the interaction of marine currents and tides (Vera et al. 2009), and an annual up-welling event (January–April each year) (Moreano 1983). These events have effects on temperature changes, the release of domestic and industrial wastewater, and the local deposition of sediments in the rainy season (Soledispa, 2011).

Information about fish communities on the continental coast of Ecuador is scarce and is only available through general technical reports of ichthyofauna in Machalilla National Park (MNP) or derived from unpublished data obtained from experienced divers. Flachier and Sonnenholzner (1997) and Terán (1998), found 106 species associated with rocky reefs and coral patches in MNP by using underwater visual census (UVC). These reports also describe the diversity of fish according to the significant habitat complexity of the sites studied and analyze the direct influence of fishing and touristic activities on fish communities.

Our research focuses on the spatial and seasonal variation of fish communities and discusses the effect of disturbances and their possible

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seasonal responses (McClanahan 2019). The main goals of this study were i) to characterize the fish communities of two coral-rocky reefs on the continental coast of Ecuador with different levels of disturbance and ii) to determine the influence of the environmental and anthropogenic induced variables on the spatiotemporal changes of the composition of the fish communities.

2. Materials and methods

2.1. Study area

The study was conducted in the province of Manabi, the continental coast of Ecuador. Two study sites were chosen: 1) Perpetuo Socorro (PS) ($00^{\circ} 55.637\text{ S}$ $80^{\circ} 44.353\text{ W}$), located 2.3 km off the coast of Manta and 2) Ureles (UR) ($00^{\circ} 54.113\text{ S}$ $80^{\circ} 38.863\text{ W}$), located 4.6 km from the nearest port in Jaramijo (Fig. 1). Both sites are traditional areas of artisanal fishing activities throughout the year (line and net fishing, autonomous and semiautonomous diving) and tourism (autonomous diving), and share structural similarities: rocky reefs between 6 and 13 m in depth. We can distinguish three geomorphological areas: (1) the crest 5–7 m in depth, rocky substratum with patches of branching coral species such as *Pocillopora spp.*; (2) the slope 8–10 m in-depth, rocky substratum with small patches of branching coral species such as *Pocillopora spp.* colonies or massive corals such as *Porites lobata*, and (3) the bottom 11–13 m in depth, mixed substratum with rocky, sand, gravel, and patches of massive coral species such as *Pavona clavus*. None of the study sites is considered “pristine” and present different levels of disturbance concerning local sedimentation processes, low rates of light penetration, and direct or indirect anthropogenic impacts i.e.: the PS site shows high-levels of disturbance and sedimentation due to its proximity to the coast, causing high coverage of turf algae (Alcivar 2015), grazing effects and trophic overlap of sea urchins (Caballillas-Terán et al. 2016), while the UR site shows mid-levels of disturbance and sedimentation causing slow rates of growth for coral species (Trujillo 2017). Other important impacts identified in both sites include overfishing, anchoring and the presence and persistence of marine debris and derelict fishing

gear (Figueroa-Pico et al. 2016) with effects on coral fracturing processes on the crest zones (Figueroa-Pico et al. 2020b).

2.2. Fish community assessment

Sampling was conducted between September 2017 and April 2018 at each study site with a total of 18 days of data recording, distributed in 9 days in the rainy and the dry season respectively with monthly periodicity (only biweekly for October 2017). The Video-Transect Method (VTM) was used to record the richness of the fish species and their abundance as the best method according to a pilot study performed in the study area (see Figueroa-Pico et al. 2020a). VTM was performed with a GoPro Hero Underwater High Definition camera and Evolve light of 900 lm. VTM records (~14 h of video recording) were watched by an experienced observer and the number of fish species and their abundance was registered. We performed a total of 54 permanent transects of 100 m divided into 270 segments (135 segments per study site) of 20 m in length and variable width relating to visibility conditions available during the survey time. VTM was carried out in independent surveys (5 segments 20 m per day in each zone) in the bottom (BT), slope (SL), and crest (CR) zones (45 segments per zone in each study site), and the same route was repeated during the study period in each zone.

2.3. Descriptors of architectural complexity

The descriptors of architectural complexity were estimated with two complementary methodologies: Rugosity Index (RI) (Risk 1972; Luckhurst and Luckhurst 1978) to assess the small-scale relief in each transect, using chains of 3.0 m in length with links of 2.0 cm, and a modified Habitat Assessment Score (HAS), which is a categorical larger-scale visual estimate of the relief (Gratwicke and Speight 2005; Fuchs 2013; Lozano-Álvarez et al. 2017). RI is the ratio of the length of a chain attached to the reef surface to the linear distance between its start and endpoints. RI is a measure of substrate complexity because a flat substrate would have an RI = 1 and the higher the RI value the greater the availability of spaces for live organisms (Luckhurst and Luckhurst 1978;

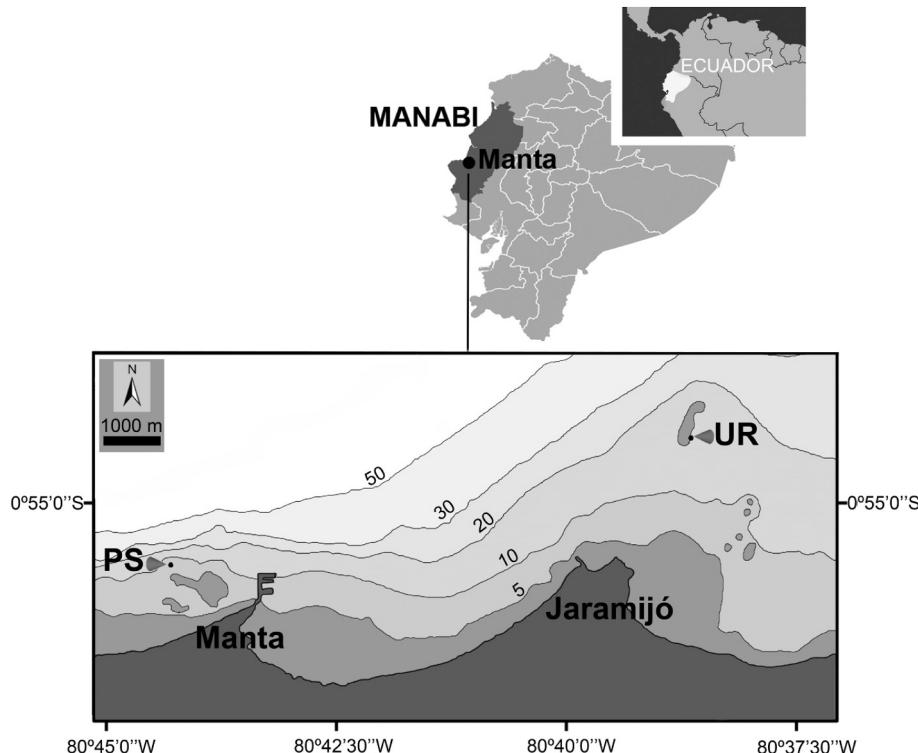


Fig. 1. Map of study sites represented as PS (Perpetuo Socorro) in Manta and UR (Ureles) in Jaramijo.

Murray et al. 2002). We performed 10 independent measurements of RI along each permanent transect (two measurements per segment of 20 m) in the crest, slope, and bottom zones, and a mean of two IR was calculated for each segment. Modified HAS combines several qualitative measurements of five habitat complexity variables [visual rugosity (VR), hard substratum (HS), live cover (LC), habitat height (HH), and refuge size (RS)], each assessed visually using a five-category scale from 1 (lowest) to 5 (highest) for each variable. A total HAS score was calculated for each transect by adding the scores of each of the five complexity variables. For each permanent transect, we estimated HAS variables in 5 m × 5 m quadrats located in each transect, and averaged the five scores as a measure of transect-level HAS.

2.4. Coral coverage and anthropogenically induced variables

Percentage of live coral (%LC), dead coral (%DC), and fragmented coral (%FC) were estimated in five 1 × 1 m quadrats located in every transect at the study sites and in the zones. Pictures of quadrats were taken from a horizontal plane and always at the same distance (1.5 m in height from the bottom) and later analyzed with the software ImageJ 1.80 free version (Abramoff et al. 2005). Finally, we recorded the number of segments or pieces of mono and multifilament nets or derelict fishing gear (DFG) along every transect at each site and in each zone.

2.5. Statistical analysis

Data recorded on the abundance of fish species taken with VTM were primarily analyzed with a nonparametric Kruskall Wallis analysis of variance for the factor zone and the Mann Whitney U test for the factor site. Besides, the Shannon Diversity Index was calculated for the factors site, zone, and season and later compared with a Diversity Permutation Test using the software PAST version 3.7. The fish community was analyzed with a Permutational Multivariate Analysis of Variance (PERMANOVA). Three fixed factors were entered into the analysis: Site with two levels (UR and PS), zone with three levels (BT, SL, and CR) nested at the site, and season (dry and rainy seasons). Values of quantitative variables RI, %LC, %DC; anthropogenically induced variables % FC and DFG and qualitative complexity HAS descriptors VR, %HS, LC, HH, RS for each transect were entered into the analysis as covariates. Type III Sum of Squares was used since it is appropriate in the case of an unbalanced design. All the tests were performed with 999 permutations to increase the power and precision of analysis (Anderson et al. 2008) of residuals under a reduced model (Anderson and Braak, 2003).

Multicollinearity among architectural complexity and anthropic variables may result in adverse effects in the modeling process, and therefore collinear variables were excluded using the variance inflation factor (VIF), with the threshold cutoff value being set at 3 (Zuur et al. 2010). The VIF was analyzed using the Heiberger method (Heiberger 2012).

The differences in community structure among the zones were investigated using a posteriori pair-wise test with 999 permutations. The advantage of the permutation approach is that the resulting test is “distribution-free” and not constrained by many of the typical assumptions of parametric statistics (Walters and Coen 2006).

The relative contribution of each particular fish species to determine differences in the composition of the communities between sites, zones, and seasons were evaluated using a similarity percentage analysis (SIMPER). In this study, SIMPER was employed to identify those fish species that were responsible for more than 90% of dissimilarity among sites, zones, and season. We did not remove rare species (<5% of the total observations in all sampling segments) from the analysis. Although these species may negatively influence multivariate analyses and add little to dissimilarity measures (Rowe and Holland 2013), they can contribute with important information about vulnerable species for a priori redlist.

Finally, to explore the relationship (strength and significance) between the structure of the fish communities and the habitat complexity

variables (RI, VR), coral status (%LC), and human-induced variables (% DC, %FC, DFG) in each zone of the study sites, we used a non-parametric distance-based linear model (DISTLM) in combination with distance-based redundancy ordination analysis (dbRDA). The DISTLM models the relationship between the variables mentioned and the multivariate fish community dataset based on a multiple regression model as a way to find the linear combination of variables that explains the greatest amount of variation in the fish community dataset and examines the amount of variance explained by each variable. All the analyses were performed using PRIMER v6 software (Clarke and Gorley 2006), including the PERMANOVA+ add-on package (Anderson et al. 2008).

3. Results

3.1. Descriptive results

A total of 9431 fish of 49 species and 26 families were identified in the study sites using VTM. 5818 fish were observed at UR and another 3613 at the PS site. (Table 1a). The percentage difference for abundance between sites (UR/PS) was 161% (Table 1a). Concerning the zones, we found more fish abundance in SL and BT at both sites whereas CR always showed the lowest abundances (Table 1a). The percentage difference for abundance between the zones of the sites studied (UR/PS) was 127%, 162%, and 106% for the CR, SL, and BT zones respectively (Table 1a). Total fish abundance was significantly different between the UR and PS sites ($p < 0.001$), while total fish abundance was significantly different between zones ($p < 0.05$) (Table 1a). Shannon Diversity Index was significantly different between sites ($p < 0.001$), zones CR and SL vs BT of PS site ($p < 0.001$), Dry and rainy and dry season for both sites ($p < 0.001$) (Fig. 2, Appendix 2).

Live coral percentage (%LC) showed a higher abundance in the crest zone compared with the slope and bottom zones at UR ($p < 0.001$). Similar results were found in the other study area (PS) where the higher live coral abundance occurs in the crest and the slope zones compared with the bottom zones ($p < 0.001$) (Table 1b). Coral colonies of *Pocillopora elegans*, *P. damicornis* and *P. capitata* with 4 to 82% of coverage/m² were common in the crest zones of the reefs studied, while on the slopes, we found small patches of coral species like *P. damicornis*, *P. capitata*, *Pavona clavus*, and *Porites lobata* with 5 to 67% of coverage/m² (continuous and complex high bare rocks).

Fractured coral (%FC) was higher on the crest and bottom of both sites compared with the slope zones ($p < 0.001$). Dead coral (%DC) was especially high in the bottom zones of both sites ($p < 0.001$). Finally, the number of derelict fishing gear as segments of monofilament nets (DFG) was higher in the crest zone of UR and PS compared with the SL and BT zones at both sites ($p < 0.001$) (Table 1b).

3.2. Sites, zones, and seasonal fish species assemblage

The PERMANOVA analysis revealed significant differences in the composition of fish species and abundance across sites ($p = 0.003$) and seasons ($p = 0.001$) (Table 2a). We found interactions between factors: zones x site ($p = 0.001$) and site x season ($p = 0.001$) (Table 2a). Variables such as the rugosity index (RI), percentage of live cover (%LC), and visual rugosity (VR) of HAS were the most important predictors of fish communities ($p < 0.05$). Pair-wise test results revealed significant differences in fish compositions between the slope (SL) vs bottom (BT) zones at the UR site and between crest (CR) vs bottom (BT) at the PS site (Table 2b and c).

The SIMPER analysis showed considerable average dissimilarity between sites (82.7%), zones (83.19%), and seasons (84.2%). The species with the highest dissimilarity contribution between sites (UR vs PS) were: *Chromis atrilobata*, *Abudefduf troschelli*, *Thalassoma lucasanum*, *Diodon holocanthus*, *Johrandallia nigirostris*, and *Balistes polylepis* (See Appendix 3 Table S1). The species with the highest dissimilarity contribution values between CR and SL zones were *C. atrilobata*,

Table 1

Descriptive statistics for, a) differences in fish abundance between sites and zones, and results for Mann Whitney U (sites) and Kruskal-Wallis tests (zones) and b) structural quantitative (RI) and qualitative HAS (VR, HH, RS, LC, %HS), coral status (%LC, %DC) and human-induced variables (%FC, DFG).

a.	UR								PS						
Total fish per site	5818								3613						
Difference between sites UR/PS	161%														
Mann Whitney U test	W = 16,118 p < 0.001														
a.		CR	SL	BT	CR	SL	BT								
Total fish per zone		1402	2447	1969	1101	1295	1217								
Difference between zones: CR, SL, BT by site UR/PS		127%		162%		106%									
Kruskal-Wallis test			H = 6.3			p < 0.05									
b.	Zones														
Site	Variables	CR	SL				BT								
		Mean	SD	Min	Max	Mean	SD	Min	Max	H value	p value				
UR	RI	1.37	0.1	1.2	1.5	1.89	0.2	1.7	2.3	1.21	0.1	1.1	1.4	104.4	***
	VR	3.4	1.37	2	5	3.4	0.5	3	4	3.4	0.5	3	4	0.57	n.s
	HH	2.6	0.5	2	3	5	0	5	5	2.6	0.8	2	4	89.5	***
	RS	3	0.64	2	4	4.4	0.5	4	5	3.2	0.8	2	4	61.5	***
	LC	3.6	0.81	3	5	1.4	0.5	1	2	2.2	0.8	1	3	82.9	***
	%HS	5	0	5	5	5	0	5	5	4	0.9	3	5	36.1	***
	%LC	50.11	16.2	25	82	9.49	8	0	19	20.5	3	14	26	111.4	***
	%DC	15.13	4.08	8	25	0	0	0	0	28	17	11	52	94.3	***
	%FC	19.09	6.63	12	35	2	2.6	0	7	22.7	8.3	12	38	91.4	***
	DFG	14.87	6.08	5	31	0.91	0.6	0	2	2.91	1.8	1	8	104.3	***
	RI	1.32	0.09	1.2	1.5	1.82	0.1	1.7	2	1.22	0.1	1.1	1.4	96.4	***
	VR	3.6	0.81	3	5	3.4	0.5	3	4	2.6	0.5	2	3	36.8	***
	HH	2.4	0.5	2	3	5	0	5	5	2.6	0.5	2	3	90.5	***
PS	RS	3	0.64	2	4	4.6	0.5	4	5	2.6	0.5	2	3	86.1	***
	LC	2.6	1.03	1	4	2.6	1	1	4	1	0	1	1	57.1	***
	%HS	5	0	5	5	5	0	5	5	2.6	0.5	2	3	89.3	***
	%LC	30.84	19.3	4	68	35.3	18	5	67	1.62	1.7	0	5	89.1	***
	%DC	8.87	4.36	1	18	0	0	0	0	7.91	6.7	0	17	58.8	***
	%FC	11.38	6.1	4	25	1.76	2.4	0	8	7.91	6.7	0	17	47.1	***
	DFG	7	3.83	1	16	1.04	0.7	0	3	0.71	0.5	0	1	79.3	***

*** Highly significant $p < 0.001$. n.s. no significant.

A. troschelli, *T. lucasanum*, *J. nigrirostris*, *Prionurus laticlavius*, and *D. holacanthus* (See Appendix 3 Table S2). The species with the highest dissimilarity contribution values between CR and BT zones were *C. atrilobata*, *A. troschelli*, *D. holacanthus*, *B. polylepis*, *T. lucasanum*, and *Halichoeres dispilus* (See Appendix 3 Table S2). The species with the highest dissimilarity contribution values between SL and BT zones were *C. atrilobata*, *A. troschelli*, *D. holacanthus*, *J. nigrirostris*, *T. lucasanum*, and *B. polylepis*. Finally, concerning the seasons, the SIMPER showed that sampling in the rainy season had the lowest similarity in the community composition compared with sampling in the dry season. The species with the highest contribution to the dissimilarity between rainy and dry season were: *C. atrilobata*, *A. troschelli*, *D. holacanthus*, *T. lucasanum*, *B. polylepis* and *J. nigrirostris*, which were more abundant in the rainy season.

The sequential test performed by means of the DistLM indicated that 5 variables had a strong effect on the structure and composition of the fish communities in the study zones at the two sites. Visual rugosity contributed to explaining the highest percentual variance, accounting for 12.98% of the variability in the fish communities, followed by a rugosity index with 5.2%, live cover with 4.35%, fractured coral with 2.89%, and derelict fishing gear with 2.32% (Table 3). The dbRDA includes vectors corresponding to these 5 variables in two axes that explained 83.63% of the fitted variation and 17% of the total variation (Fig. 3). The samples corresponding to the crest and bottom zones are distributed along the dbRDA2 axis, while the samples of the slope are dispersed along the dbRDA1 axis. Concerning architectural complexity and human-induced variables, %FC and VR were related to bottom communities, while DFG is related to both bottom and crest communities. However, the rugosity index and % LC were associated with crest

and slope communities.

4. Discussion

Our study is the first systematic initiative to characterize fish communities on the rocky reefs of the continental coast of Ecuador. Our results show differences in the composition of the fish communities between the two study sites, zones, and seasons. The richness of the composition of the species at both study sites is represented by 24 common species from a total of 49 (Appendix 1a). We found 161% more fish in UR than PS (Appendix 1b). The differences in fish composition between the sites studied could be related to a local and multifactorial process of degradation affecting the PS site and explained by its proximity to the coast. This process includes local stressors like high levels of sedimentation due to the discharge of domestic wastewater with the subsequent proliferation of turf algae with adverse effects on algae and invertebrate composition (Alcivar 2015; Cabanillas-Terán et al. 2016) with direct implications concerning fish communities. Also, overfishing of key herbivore and carnivore species may occur at PS, as well as high anchoring levels and the fracturing of the coral colonies on the crests due to the entanglement of mono and multifilament nets (Figueroa et al., 2020b). Alcivar (2015) found dominance and high coverage of turf algae due to high levels of sedimentation (Virgilio et al. 2006) at the PS site. Further, there is no evidence of the overfishing of herbivore fish that could influence the high coverage of turf algae at the site (Vermeij et al. 2010). Cabanillas-Terán et al. (2016) found a high density of the sea urchin *Eucidaris thouarsi* at the PS site. The population dynamics of this species are related to massive coral mortality and the subsequent proliferation of turf algae on disturbed reefs (Sotelo-Casas et al. 2018). The

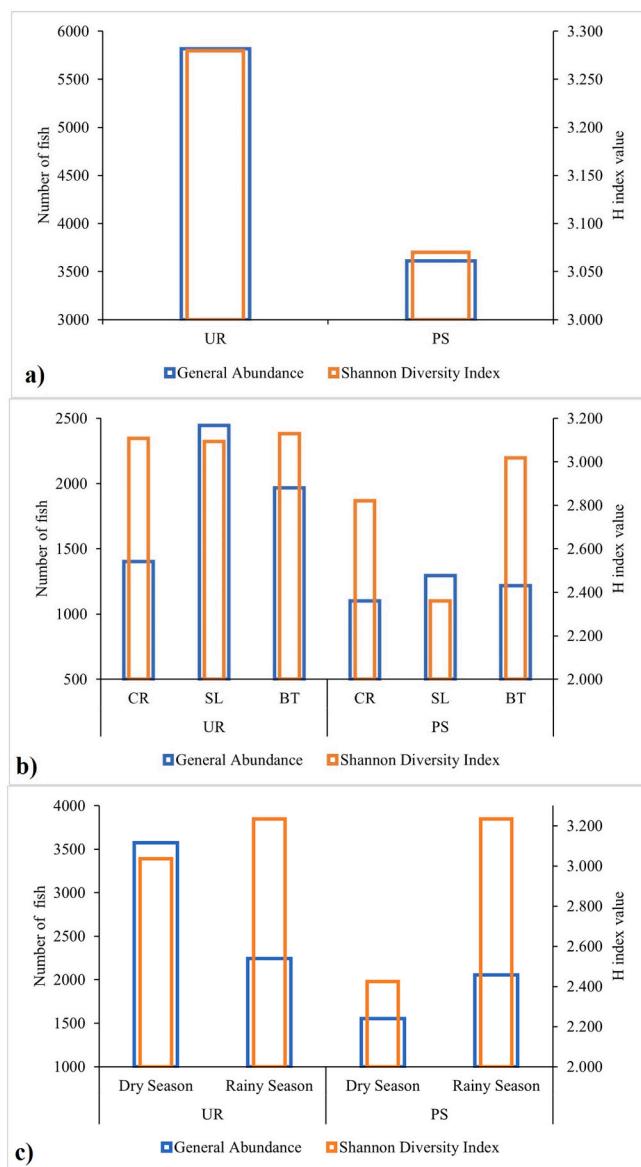


Fig. 2. General Abundance and Shannon Diversity Index values per a) study site, b) per zone, and c) per season.

echinoderm species may also limit coral growth and it has the ability to modify the habitat structure and interfere with the development of the reef frame (Sonnenholzner et al., 2012). This finding is also supported by Ghazilou et al. (2016) who suggest that coral reef fish assemblages may show changes in response to disturbance levels that result in a decrease in the diversity of a coral reef fish community due to the loss of live coral cover, lower topographical complexity, and/or lower richness of coral species in disturbed areas.

Our results show differences in the abundance of fish between zones per site. Fish abundance was higher on the slope and crest than in the bottom zones (Appendix 1b). When we compared the zones by site, we found that UR shows more abundance of fish: 127% more fish on the crest, 162% on the slope, and 106% on the bottom in comparison with PS (Appendix 1b). Slopes and crests are zones with high structural complexity and live coral coverage, that can provide food, reproduction places, and permanent or temporal shelter for cryptic and conspicuous fish species (Coker et al., 2012; Darling et al., 2017). Darling et al. (2017) suggest that the characteristics of the reef zone reveal the importance of diversity and abundance in the slope and crest zones, typically associated with more abundant and diverse reef fish

Table 2

a) PERMANOVA for the number of observations for each species based on sites, zones, and season (multivariate data) and b) results of the pair-wise test concerning the number of fish in each species for each zone at the study sites.

a. PERMANOVA test, table of results

Variable	df	SS	MS	Unique Pseudo-F	P (perm)	Perms
Si	1	6531	6531	2.7886	0.003	999
Zo (Si)	4	29,383	7345.6	3.1365	0.001	999
Season	1	36,813	36,813	15.719	0.001	997
Si (Time)	1	8660.4	8660.4	3.6979	0.001	998
RI	1	5026.3	5026.3	2.1462	0.019	999
VR	1	29,344	29,344	12.53	0.001	997
%LC	1	6757.3	6757.3	2.8853	0.002	999
% FC	1	2066	2066	0.88216	0.547	998
DFG	1	3273.5	3273.5	1.3977	0.171	997
Res	257	6.0189E5	2342			
Total	269	8.2646E5				

b) Pair-wise test Term 'Zo(Si)' within level 'UR' of factor 'Site'

Groups	t	Unique P(perm)	Perms
CR, SL	0.92703	0.564	998
CR, BT	1.1797	0.156	999
SL, BT	1.6221	0.002	997

c) Pair-wise test Term 'Zo(Si)' within level 'PS' of factor 'Site'

Groups	t	Unique P (perm)	Perms
CR, SL	0.58273	0.964	999
CR, BT	2.6356	0.001	998
SL, BT	0.9333	0.557	999

Table 3

Distance-based linear model for the number of observations for each species based on the zones at the study sites.

Variables	SS (trace)	Pseudo-F	P	Prop.
Rugosity index	33,991	14.412	0.001	5.10
Visual rugosity	82,641	37.963	0.001	12.98
% live coral	28,995	12.198	0.001	4.35
% fractured coral	19,264	7.9822	0.001	2.89
DFG in transect	15,505	6.3874	0.001	2.32

res.df: 268.

communities than flat reefs or bottoms. The differences in fish abundance between the slope and bottom zones in UR site and the crest and bottom zones at PS site were especially related to the presence of reef dweller species such as *T. lucasanum*, *J. nigrirostris*, *P. latilobus*, and *Z. cornutus*.

The season was another factor affecting fish assemblage, suggesting spatiotemporal changes in fish communities at the study sites. Species like *D. holacanthus*, *B. polylepis*, and *U. tumbesensis* had the highest differences in average abundance and were more abundant in the rainy season. The changes in the abundance of these species could be related to the recruitment process (Munro et al. 1973) and spawning aggregations (Erisman et al. 2010), the effects of a low temperature (Hoisington IV and Lowe 2005; Vaudo and Lowe 2006; Jirik and Lowe 2012) and high productivity in the rainy season dynamized by a temporal upwelling event (Rosales-Casián 2013) occurring between January–April every year on the coast of Ecuador (Moreano 1983). La Mesa et al. (2013) suggested that rocky reef habitats are a sort of biodiversity hotspot with significant patterns of broad-scale variation in the composition of fish species and assemblage structure with very fluctuating patterns. On the contrary, Sánchez-Caballero et al. (2019) found great stability of the fish communities on the rocky reefs of Baja California concerning El Niño/La Niña events and that changes in individual species are not strong enough to affect community structure, abundance,

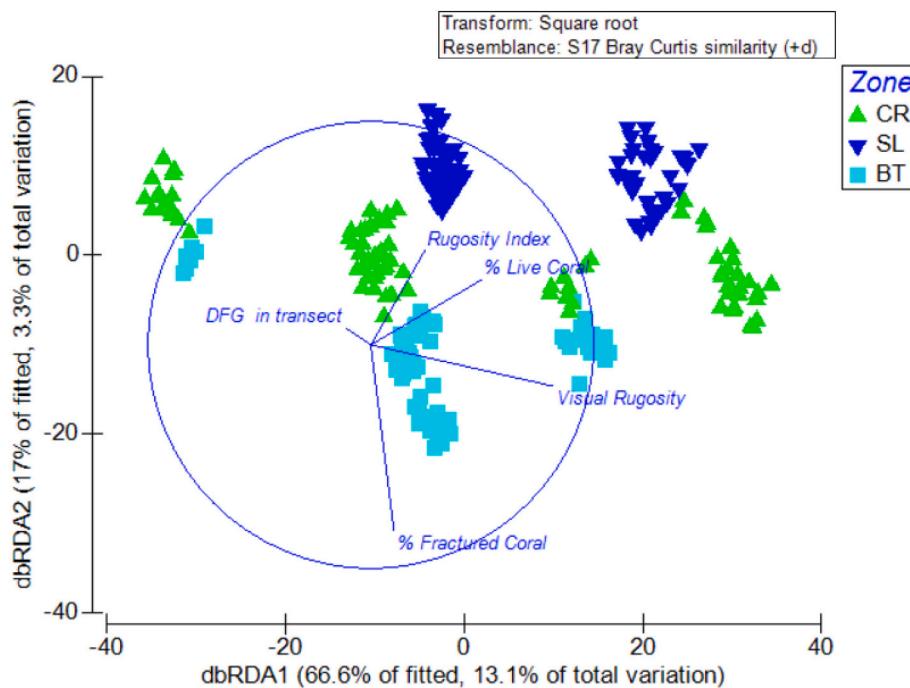


Fig. 3. Distance-based redundancy analysis (dbRDA) of the fish communities for each reef zone (CR, SL, BT) showing vector overlays of fish species included in the best model by DistLM analysis.

or richness. However, the authors also suggest that the abundance of some fish populations is more strongly related to changes in the phytoplankton biomass compared with temperature changes.

The rugosity index (RI) was a strong predictor of abundance for small-scale relief assessment in the slope and crest zones of the reefs studied (Table 1, Fig. 2) in this study. Trebilco et al. (2015) found a similar relationship between the habitat complexity descriptor RI and species richness and abundance of fish in reefs of temperate waters; where substratum rugosity was associated with higher overall fish biomass and small-bodied fish. On the other hand, the estimation of the visual category of larger-scale relief with HAS was only significant for visual rugosity (VR); so this descriptor explains the differences between the richness of species and the total fish abundance between sites and zones of the reefs studied better. Gratwicke and Speight (2005) found a positive relationship between the richness and abundance of fish species with HAS descriptors such as visual rugosity, variety of growth forms, and habitat height. Similar conclusions were reached by Fuchs (2013) in a study that describes the relationship between invertebrate communities with visual rugosity and a variety of growth forms as the principal HAS descriptors. Our results suggest that the composition of fish is dynamized by the high structural complexity of the slope and crest zones of the reefs. Similar results were found by Darling et al. (2017) who suggest that structural complexity and reef zone are the strongest predictors of fish diversity and abundance.

Rugosity in the crest zones is a function of the high percentage of live cover (%LC), another significant variable in our study (Tables 1 and 2). Pratchett et al. (2015) suggest that the combination of the structural complexity of the reefs and living corals is required for optimal reef fish productivity and diversity, while Darling et al. (2017) specifically argue that the total abundance of reef fish increases with the covering of stress-tolerant corals in crest and slope zones.

The percentage of fractured coral (%FC) and derelict fishing gear (DFG) significantly affected the composition of the fish community. The fracturing of the coral colonies in crest zones occurs because of the efforts to remove entangled nets by local fishermen (Figueroa-Pico et al. 2016, 2020b) and secondly because of the anchoring of boats (Flynn and Forrester 2019). After the breaking process, coral fractured in the crest

zones falls down the slope and depending on the physical configuration of this zone remains and colonizes the rocks or simply falls directly to the bottom where the lack of optimal physical conditions drives the fragments to bleach and die.

We found a high presence and prevalence of derelict fishing gear (monofilament and multifilament nets) on the coral colonies on the crests of the UR and PS sites during the study period (Appendix 2). These results are similar to those reported by Figueroa et al. (2016) for the same study sites and suggest that the problem of derelict fishing gear and ghost nets on crest zones has a high prevalence over time. Our results show a strong relationship between human-induced DGF descriptor and fractured coral on the crest zones and negative effects on the composition of fish. A high percentage of the fish species, (40%) in the study sites, were strongly linked to the coral colonies in the crest and slope zones where they find permanent and temporary shelter and places to feed or reproduce. So the gradual destruction of coral negatively impacts on the diversity and composition of the fish communities in these zones. Pratchett et al. (2011) and Russ and Leahy (2017) suggest that an absolute decrease in live coral cover on the reefs would lead to a considerable decline in the richness and abundance of fish species. Similarly, Flynn and Forrester (2019) argue that many reef fish taxa depend on a three-dimensional reef structure for shelter, so the “flattening” of highly anchored sites is a plausible explanation for the reduced densities of most (5 of 7) functional groups of adult fish.

A clear example of the above-mentioned issues in our study is the coral hawkfish *Cirrhitichthys oxycephalus* a rare species of the coral reef. This cryptic species is usually found perched on branching coral colonies of *Pocillopora spp.* (Robertson and Allen, 2015) and was especially abundant in the CR and SL zones of the UR site but was absent in the fish composition of the PS site. The presence of *C. oxycephalus* was restricted only to living branching coral colonies that offer protection against predators (Coker et al. 2015) and where the species predate over small cryptic invertebrates and fishes (Palacios-Narváez et al. 2020). The species was never observed in fractured or dead coral colonies. Coral hawkfish is included on the Red List of the International Union for Conservancy of Nature (IUCN) as a species not evaluated with the category of least concern (LC) (Greenfield and Williams 2016).

However, we found evidence that indicates a possible major threat to coral-dependant fish species related to habitat degradation by the indirect effect of human activities.

Finally, important theoretical inputs about the disruption of ecological processes on branching coral colonies concerning the gradual colonization of algae consortiums over the derelict fishing gear and its negative effects on the composition and coverage have been widely discussed (Galgani et al. 2018; de Carvalho-Souza et al. 2018; Valderrama et al. 2018; Figueroa-Pico et al. 2020b; Beneli et al. 2020). However, the long-term effects on the invertebrate and fish communities remain unknown.

Our findings suggest that the spatio-temporal changes in the composition of fish communities of the rocky reefs of Ecuador are driven by a complex and multifactorial process that includes the positive influence of structural complexity and negative effects of the loss of live coral cover and the subsequent loss of structural complexity by human-induced stressors, affecting both fish diversity and abundance. We strongly recommend a periodical assessment of fish communities, structural complexity descriptors, and human-induced descriptors. New data on the sediment deposition process and temperature fluctuations are also needed as well as the effect of the derelict monofilament nets due to coral-turf algae growth since the effect of the algae on the coral remains poorly known.

CRediT authorship contribution statement

Juan Figueroa-Pico: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration. **Francisco S. Tortosa:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Project administration. **Antonio J. Carpio:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing for financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2021.112018>.

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