Contrast in the density and biomass of fish in a reef system with different fishing intensity in the Mexican Caribbean
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Contrast in the density and biomass of fish in a reef system with different fishing intensity in the Mexican Caribbean

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A wide range of fish species are caught in reef fisheries. However, fishing efforts tend to be highly selective in favor of large species, which generally have low population growth rates, making them more vulnerable to overfishing. When the decline of large predators occurs, fishing efforts start to focus on catching species from lower trophic levels, which can cause a trophic cascade effect.The objective of this research was to detect changes in the density and biomass of fish communities in areas with different fishing intensity in the study area.This study was carried out in the Banco Chinchorro Biosphere (BCBR) in the Mexican Caribbean and analyze the effect of fishing intensity on fish density and biomass, comparing data obtained from visual censuses with dependent information of the fishery. Evidence was found of a relationship between high fishing exploitation and low levels of density and biomass for *Epinephelus striatus, E. guttatus and Lachnolaimus maximus*. The decline of predators of non-commercial species had no effect on the density and biomass of these species. The density and biomass of commercially important fish species were influenced by the presence of algae, octocorals, hydrocorals and by variations in their catch per unit of effort (CPUE).This study detected that density and biomass have decreased in some species belonging to the Serranidae and Lutjanidae families in areas with high fishing intensity. On the other hand, little evidence was found that the density and total biomass of families of noncommercially important species increased through the decline of their predators. These results are consistent with previous work documenting how fishing activity affects fish species with high trophic levels. The information generated will help the Reserve's managers make decisions towards better management and conservation of fishery resources.

1 **Contrast in the density and biomass of fish in a reef system with different fishing intensity**
2 **in the Mexican Caribbean.**

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Abstract

A wide range of fish species are caught in reef fisheries. However, fishing efforts tend to be highly selective in favor of large species, which generally have low population growth rates, making them more vulnerable to overfishing. When the decline of large predators occurs, fishing efforts start to focus on catching species from lower trophic levels, which can cause a trophic cascade effect.The objective of this research was to detect changes in the density and biomass of fish communities in areas with different fishing intensity in the study area.This study was carried out in the Banco Chinchorro Biosphere (BCBR) in the Mexican Caribbean and analyze the effect of fishing intensity on fish density and biomass, comparing data obtained from visual censuses with dependent information of the fishery. Evidence was found of a relationship between high fishing exploitation and low levels of density and biomass for *Epinephelus striatus, E. guttatus and Lachnolaimus maximus*. The decline of predators of non-commercial species had no effect on the density and biomass of these species. The density and biomass of commercially important fish species were influenced by the presence of algae, octocorals, hydrocorals and by variations in their catch per unit of effort (CPUE).This study detected that density and biomass have decreased in some species belonging to the Serranidae and Lutjanidae families in areas with high fishing intensity. On the other hand, little evidence was found that the density and total biomass of families of noncommercially important species increased through the decline of their predators. These results are consistent with previous work documenting how fishing activity affects fish species with high trophic levels. The information generated will help the Reserve's managers make decisions towards better management and conservation of fishery resources.

Keywords: coral reef; artisanal fishing; fish assemblage structure; Banco Chinchorro biosphere reserve; México.

Introduction

The increase in global fishing levels has generated environmental problems that are of public interest (*Pauly et al., 2002*), such as trophic cascade effects that weaken habitat and key species (*Scheffer et al., 2005*), encourage the proliferation of invasive species (*Daskalov, 2002*),), impact sustainability of other exploitation efforts (*Libralato et al., 2004*) and enhance the negative effects of climate change to the ocean (*Gaines et al., 2018*). There is wide recognition that fish stocks throughout the world are under stress because of overfishing, coastal development, human population growth and climate change (*Savo, Morton & Lepofsky, 2017*; *Russ et al., 2021*).

Small-scale fisheries, including those in reef systems, are an important source of livelihood and food security for more than 1 billion people worldwide (*Adam et al., 2015*; *Babcock, Tewfik & Burns-Perez, 2018*). In the western Caribbean, more than a million people depend on the integrity and health of the Mesoamerican Reef System (MRS) for their livelihoods. The national economies of four countries (Belize, Guatemala, Honduras, and Mexico) benefit substantially from reef fishery resources and attractiveness as international tourist destinations (*Zeller, Graham & Harper, 2011*); however, there have been few studies on the effects of fisheries on reef fish communities in the Caribbean (*Pauly et al., 2002*; *Adam et al., 2015*).

Although a wide range of fish species are caught in reef fisheries, fishing efforts tend to be highly selective in favor of large species, which generally have low rates of population growth, making them more vulnerable to overfishing (*Sadovy de Mitcheson et al., 2013*). Commercial species often include higher predators, such as serranids (groupers), lutjanids (snappers) and balistids (trigger fish). The decline of these species can increase the abundance of prey, leading to trophic cascade effects that influence the base of the food chain (*Mumby et al., 2006*; *Ruppert et al., 2017*). When large predators decline, fishing efforts shift to targeting species from lower trophic levels, which can lead to the depletion of these species as fisheries move down the food web (*Jackson et al., 2001*; *Mumby et al., 2006, 2012*). On the other hand, in recent years, it has been found that coral bleaching in large areas of reefs due to the effect of climate change (*Hoegh-Guldberg et al., 2018*) and the increase in the frequency or intensity of environmental disturbances such as hurricanes (*Knutson et al., 2010*) has much more direct effects on fish (*Graham et al., 2020*) and on benthos (*Cheal et al, 2017*; *Hughes et al., 2018*; *Russ et al., 2021*) than fishing. The coral reef systems of the Banco Chinchorro Biosphere Reserve (BCBR) support many different species, which are the main component of fisheries in the area. These fisheries are generally small-scale, artisanal and multispecific; however, economic progress, increasing coastal tourism, and an increase in human population have led to greater competition for fishing resources and possible overfishing. Most of the fishers live in the City of Chetumal, but spend 15 to 30 days in Cayo Centro in the RBBC to carry out their fishing activities. Approximately 41 motor boats powered by an outboard motor operate in the study area. The capture is made daily and freediving equipment is used for it. This shows that fish in this reserve face various threats, both local and global, and understanding these impacts is crucial for developing effective management strategies.

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104 The fisheries in the BCBR are closely associated with the extraction of the spiny lobster

105 (*Panulirus argus*) and the queen conch (*Aliger gigas*), although several species of fish are also

106 caught throughout the year, including fishing conducted during spawning aggregations of

107 different species, such as *Lutjanus analis* and *Baliste capriscus* (*Castro-Pérez, González &*

108 *Arias-González, 2011*). The federal and state governments of Mexico declared the BCBR a

109 marine protected area on July 19, 1996, with the purpose of conserving and protecting mangrove

110 and coral ecosystems. However, the management program that was established for these

111 purposes was carried out with few scientific studies of the flora and fauna in this complex reef

112 (INE-SEMARNAP, 2000). However, to improve the fishing management plans in marine

113 protected areas, it is necessary to incorporate technical and scientific opinions as well as the

114 knowledge of users and handlers. In the study area, there are few works on the ecology of

115 commercially important fish and their fisheries (*e.j., Sosa-Cordero et al. 1991*; Loreto, *Lara &*

116 *Schmitter-Soto 2003*; *Castro-Pérez, González & Arias-González, 2011*; *Fulton, Caamal &*

117 *Bourillón, 2014*; *Fulton et al 2016*; *Rodríguez-Zaragoza et al., 2016*; *Castro et al., 2018*) and

118 there is no information on the effect of fishing activity on fish communities. For this reason, the

119 present research proposes the ==following hypothesis==: are there changes in the density and biomass

120 of commercially important fish species in areas with different fishing intensities in the BCBR?

121

Materials & methods

Area of study

124 The BCBR is part of the Mesoamerican Reef System, which covers 1000 km along the coasts of

125 Honduras, Guatemala, Belize and Mexico, and it is located in southeastern Mexico in the state of

126 Quintana Roo, 42 km from the Mahahual coast (18°47'- 18°23' N & 87°14' - 87°27' W). This

127 reef was declared a marine protected area under the category of biosphere reserve in 1996. (Fig.

128 1A). Oval in shape, the BCBR covers an area of approximately 814.2 km² (45 km long and 18

129 km wide) and is composed of three cays: *Cayo Norte* (0.4 km²), *Cayo Centro* (5.4 km²), and

130 *Cayo Lobos* (0.1 km²) (*Chávez & Hidalgo, 1984*; *Jordán & Martin*, 1987). The reef lagoon

131 covers approximately 553.7 km², its depth gradually decreases from south to north with values

132 ranging from 2 to 12 m (*González et al., 2003*).

Data collection.

134

135 ==This study analyzed data obtained from samplings carried out in 2007 and 2008. However, the==

136 ==resulting information is of great relevance to understanding how fish communities are affected==

137 ==by fishing in the study area, mainly due to how difficult the sampling logistics are to carry out==

138 ==this type of study.==

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Sampling of the fishery.

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143 We used data from fishing cooperative to identify sites with different fishing intensities in the
144 study area. Although three cooperatives operate in the study area, only the Langosteros del
145 Caribe cooperative was sampled due to the complexity of working with all of them
146 simultaneously. For this purpose, a monthly record of fish species caught was maintained from
147 August 2007 to June 2008. During one week each month, the catches from the boats that arrived
148 at the vessel that received the product were recorded. The weight was measured with a top
149 loading balance with a capacity of 20 kg and an accuracy of 5 g. The fishing locations were
150 recorded by consulting the position with the captain and using a map of the study area divided
151 into 36 fishing quadrats (Fig. 1C). The catch per unit of effort (CPUE) was calculated as
152 kilograms of fish caught per fisher per hour (kg$\cdot$ fisher $^{-1}\cdot$ hr^{-1}) for each quadrant.

153 **Sampling of fish communities**
154 The underwater visual census (UVC) method was used to record the abundance and size of the
155 reef fish using the linear transect technique proposed by *Brock (1954)*. Five UVCs (replicas)
156 were carried out at each sampling station, during the same day and time. Within a 50 m transect,
157 the observer recorded the species detected at a distance of 2 m on each side of the transect and 5
158 m in front of him. For each observation, the diver recorded the abundance per species and
159 estimated the total length of the fish. Fish lengths were estimated in 1 cm intervals for fish 0 to
160 10 cm TL and in 5 cm intervals for fish >10 cm TL. A total of 650 UVCs were performed
161 throughout the study area between August and September 2008 (Fig. 1B).
162
163 **Sampling of the benthic groups in the reef habitats**
164
165 The benthic cover was estimated to evaluate the characteristics of the habitat on the same date
166 and in the sampling stations where the biological data of the reef fishes were obtained with
167 UVCs. A video camera was used to film the benthic substrate at each sampling station along five
168 linear 50 m transects, with the footage then analyzed by stopping the image at specific time
169 intervals, until 40 frames per transect are obtained. In each frame, at a series of 13 marked points
170 (520 points per transect) that were systematically distributed around the monitor, the benthic
171 organisms were identified according to six higher levels, known as morphostructural groups
172 (MSG): scleractinian corals; octocorals; hydrocorals; algae; seagrass; and sponges (*Arias-*
173 *González et al., 2011*).
174
175 It is important to mention that this working group currently has permission (Oficio No.
176 F00.9/DRBBCH/151/2024) to carry out research work without collecting or handling specimens
177 of species not considered at risk within the Banco Chinchorro Biosphere Reserve.
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184 **Data analysis**
185
186 **Areas with different fishing intensities**
187

188 *Castro-Pérez, González & Arias-González (2011)* identified seven fishing zones in the BCBR
189 using the CPUE values for fish of commercial importance in 30 fishing quadrants. Six other
190 quadrants were not used in the analyses because no catches were recorded (Fig. 1C). In the
191 present study, with the purpose of reducing the effect of the structural complexity of the benthos
192 to detect the direct and indirect effects of fishing, 21 fishing quadrants were used, located mainly
193 on the reef slope and in the southern section of the reef lagoon, which are characterized by high
194 structural complexity. Combining the CPUE data of the 10 commercially important species of
195 the 21 quadrants, belonging to the 5 zones identified through multidimensional scaling analysis
196 (MDS) by Castro-Pérez, González & Arias-González (2011), being the following zones: Zone 1
197 (Quadrants 4, 34 and 36); Zone 2 (Quadrant 5); Zone 5 (Quadrant 25); and Zone 7 (Quadrants 2,
198 10, 15, 19, 21, 23, 24, 24, 26, 27, 28, 29, 30, 31, 32, 33 and 35). The similarity between quadrats
199 was calculated using the Bray-Curtis index. The similarity coefficients were used to construct the
200 similarity dendrogram; subsequently, data were permutated 999 times for a distribution to
201 determine ANOSIM's R statistic (R = 0 is identical, R = -1 or 1 is most divergent), which
202 facilitated the discovery of patterns among the quadrats and, thus, the detection of areas with
203 different fishing intensities. Both analyses were performed with PRIMER 6.0 software (*Clarke &*
204 *Gorley, 2001*).

Changes in the density and biomass of fish species due to fishing

207 The density (individuals/100 m^2) and biomass (kilogram/100 m^2) of each of the species were
208 estimated to determine changes in these variables due to the fishing of species of commercial and
209 non-commercial importance using data obtained from UVCs. The fish biomass was calculated
210 via the exponential function $W = aL^b$, where W is the weight in kilograms, L is the length (class
211 mark) obtained from the length intervals and a and b are the constants from the length-weight
212 relationship obtained from both *Claro & García-Arteaga (1994)* and *FishBase*, and where no
213 relationship was available for species, that of a closely related species as applied. The average
214 density and total biomass of commercially and noncommercially important species were
215 compared among areas with different fishing intensities (detected via the similarity dendrogram)
216 by means of a one-way analysis of variance (ANOVA). Subsequently, a multiple range test
217 (Fisher's least significant difference, or LSD) (*Zar, 1999*) was applied to ascertain which areas
218 presented differences. The data were log(x)-transformed to fulfill both normality assumptions
219 (Shapiro–Wilk test) and homoscedasticity (Levene's test) (*Zar, 1999*). The same statistical tests
220 were used to verify the average density and biomass differences among areas with different
221 levels of fishing intensity for each of the eight species caught with the most frequency in the
222 study area: *Epinephelus striatus*, *Epinephelus guttatus*, *Lachnolaimus maximus*, *Lutjanus analis*,
223 *Lutjanus griseus*, *Mycteroperca bonaci*, *Ocyurus chrysurus*, and *Sphyraena barracuda* (*Castro-*
224 *Pérez, González & Arias-González, 2011*). Moreover, differences in the average density and
225 biomass of the noncommercial species were tested among areas of different fishing intensities.
226 For this purpose, these species were grouped into twelve families: Acanthuridae, Balistidae,
227 Chaetodontidae, Haemulidae, Holocentridae, Kyphosidae, Labridae, Malacanthidae, Mullidae,
228 Pomacanthidae, Scaridae, and Serranidae.

Relationship of density and biomass with fishing pressure and benthic variables.

230 The fish assemblages found in the different UVCs can vary for at least three reasons: fishing
231 effort, differences in environmental conditions, and random variation (*Clua & Legendre, 2008*).
232 Two redundancy analyses (RDA) were carried out using the CANOCO v4.5 program (*Ter Braak*

233   *& Smilauer, 2002*), which separately related the density and biomass of the eight commercially
234   important fish species with the coverage data for the different benthic morphostructural groups
235   and the CPUE values for the species of greatest commercial interest. These multivariate methods
236   were applied following the gradient length criterion, the species response models pertaining to
237   the environment and the linear-type CPUE data. The density and biomass values were
238   transformed via the Hellinger distance (*Legendre & Gallagher, 2001*), while the statistical
239   significance was tested by means of Monte Carlo permutations (N = 9999).
240
241   **Results**
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243   **Areas with different fishing intensities**
244
245   Based on the dendrogram using the CPUE values of the most commercially important species,
246   the formation of three groups was detected with a similarity index of 60 % (Fig. 2A). The
247   ANOSIM test provided statistical support to determine that the three groups were different in
248   their composition and abundance (R = 0.99; P < 0.05). Considering this spatial separation and
249   the distribution of the CPUE values for these quadrants, it was observed that Group 1 included
250   quadrants that mainly belonged to the reef lagoon in the southern section of the study area (Cayo
251   Lobos), which presented high CPUE values. Group 2 was formed by quadrats located on the reef
252   slope, with intermediate CPUE values, while Group 3 generally contained quadrats located on
253   the reef slope, with high CPUE values. In accordance with the above and to detect changes in the
254   density and biomass of the fish species caused by the fishing activity, three areas with different
255   fishing intensities were classified in the BCBR: Forereef Moderate Level Fishing (FRMLF);
256   Forereef High Level Fishing (FRHLF); and Reef Lagoon High Level Fishing (RLHLF) (Fig.
257   2B).
258
259   **Changes in the density and biomass of fish species due to fishing**
260   Analysis of the group of commercially important species among the areas of different fishing
261   intensities revealed that the average density and biomass values showed significant differences
262   (one-way ANOVA, P < 0.05). The highest values for these variables were recorded in the
263   moderate fishing area and differed (LSD, P < 0.05) from the density and biomass of fish found in
264   the high fishing areas (FRHLF and RLHLF), which were like each other (LSD, P > 0.05) (Fig.
265   3A). The analysis of the group of noncommercial species did not reveal differences between the
266   density and biomass values for the areas that presented different fishing efforts (one-way
267   ANOVA, P > 0.05) (Fig. 3B).
268   The individual analysis of the eight commercially important species found that *E. guttatus*, *E.*
269   *striatus* and *L. maximus* showed significant differences in their density and biomass values (one-
270   way ANOVA, P < 0.05). The values of these variables decreased in the high fishing areas, which
271   did not show significant differences between them (LSD, P > 0.05) but differed (LSD, P < 0.05)
272   from the moderate fishing zone (FRMLF) that showed high values of density and biomass of
273   these species (Fig. 4).
274   The density and biomass per family of noncommercial species in the areas with different fishing
275   intensities did not show significant differences (one-way ANOVA, P > 0.05), except for the
276   Scaridae family (one-way ANOVA, P < 0.05). The analysis with the LSD test showed that the
277   lowest values of density and biomass were present in the moderate fishing zone, but it differed (P

278 < 0.05) from the zones where the highest catches occurred (FRHLF and RLHLF), which were
279 statistically similar (P > 0.05) (Fig. 5).

280 **Relationship of density and biomass with fishing pressure and benthic variables.**

281 The results of the redundancy analysis (RDA) showed low correlations (0.32 to 0.45) between
282 the benthic coverage (seagrass, octocorals, hydrocorals and algae) and the CPUE fishing variable
283 with the density and biomass of commercially important fish species. The percentage of variance
284 explained was 78.1 to 88.0.

285 The arrangement of the density and environmental variables in the RDA undertaken in the
286 present study revealed that along the first axis, the seagrass cover was associated with the
287 quadrats belonging to the FRMLF and RLHLF areas and had a positive relationship with the
288 density of *S. barracuda* and *L. griseus*. The hydrocoral cover was related to the quadrats in the
289 FRHLF area. The octocoral cover and the grouped CPUE quadrats in the FRHLF area were
290 detected along the second axis, with these variables revealing a strong positive association with
291 the density of *O. chrysurus*. Algae cover was linked to the quadrats in the FRMLF area (C4 and
292 C2), presenting a positive relationship with *B. capriscus* and a negative relationship with the
293 density of *L. analis* (Fig. 6A).

294 Finally, the results of the RDA, considering biomass and environmental variables, show that
295 within the first axis there is a relationship between the highest algal cover with the quadrats (C4
296 and C21) belonging to the FRMLF area, which have a negative relationship with the biomass of
297 *L. analis*. The second axis showed that the octocoral, hydrocoral and CPUE cover was associated
298 with the quadrats mainly pertaining to the FRHLF area, with the hydrocorals and the biomass of
299 *E. striatus, E. guttatus, L. griseus* and *S. barracuda* showing a negative relationship among the
300 CPUE results (Fig. 6B).

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309 **Discussion**

310 **Areas with different fishing intensities**

311 This study used CPUE values to detect and analyze three areas with different fishing intensities
312 within the BCBR to identify changes in the biomass and density of reef fish. Although the
313 fishing quadrats of the areas were found in structurally complex habitats, their location and type
314 of habitat within the system influenced their fishing intensity. The quadrats of the areas with high

315 intensities of fish exploitation (FRHLF and RLHLF) were located mainly on the reef slope and
316 the southern part of the reef lagoon (*Cayo Lobos*), where a great variety of habitats provide the
317 fishing communities a greater surface area in which to search for the target resource, namely, the
318 spiny lobster. In contrast, the quadrats in the area with the least fishing intensity (FRMLF) were
319 located primarily in the middle and northern part of the reef complex, in which fishing efforts are
320 carried out less frequently. In reference to the above, *González et al. (2003)* mention that there is
321 a north-south bathymetric gradient in the RBBC. Shallow depths are defined by extensive sandy
322 bottoms in the central and northern portion of the lagoon, while the southern area of the lagoon is
323 deeper, with more frequent coral ridges and patches. The well-developed barrier reef in the
324 southern portion of the lagoon is attributed to the greater influence of the Cayman Current in this
325 area.

Changes in the density and biomass of fish species due to fishing

327 The results of the present study provide evidence that fishing activity has caused detectable
328 changes in the density and biomass of commercially important fish species in the BCBR. The
329 lower density and biomass of the commercial species in the areas of high fishing intensity reflect
330 the extraction of top predators, such as species belonging to the Serranidae and Lutjanidae
331 families. This may be related to the selectivity of the fishing equipment used in the reef complex,
332 which usually consists of harpoons (*Castro-Pérez, González & Arias-González, 2011*), via which
333 the fishers catch the most expensive and in-demand species in local markets (*Mumby et al.,
334 2012*; *Kadison et al., 2017*). Therefore, the reduction of the species most valuable to fishing
335 communities may be imminent, leading to the exploitation of other less economically important
336 species, such as scarids, balistids and pomacanthids, which could lead to future fishing down the
337 food web. Various studies have found that the decrease in the density and biomass of carnivorous
338 and piscivorous species (Serranidae, Lutjanidae and Caranidae) is caused by an increase in
339 fishing pressure (*Friedlander & DeMartini, 2002*; *Williams et al., 2011*; *Valdivia, Cox & Bruno,
340 2017*). However, it cannot be ruled out that other factors may be involved in the changes in these
341 ecological variables, such as the effects of habitat characteristics (*e.j.,* Bell & Galzin, 1984;
342 Graham &Nash, 2013; Bertocci, Sousa-Pinto & Duarte, 2017; Helder, Burns & Green, 2022).

343 Individual analysis of the eight commercially important species found that *E. striatus*, *E. guttatus*
344 and *L. maximus* showed a lower density and biomass in areas with high fishing intensity. The
345 latter can be attributed to the fact that these species have a high economic value in local markets
346 (US$ 7.79 kg-1), and for this reason, they are caught all year round throughout the reef system
347 through selective fishing, although the highest captures of the first two species were in
348 November, December and January (*J. Castro, 2011, pers. comm.*), months in which these species
349 have been documented to aggregate for reproduction (*Aguilar-Perera & Aguilar-Davila, 1996*;
350 *Sala, Ballesteros & Starr, 2001*; *Dahlgren et al., 2016*). It has been reported in several locations
351 in the Caribbean that these three species form an essential part of the small-scale fishery (*Sadovy
352 de Mitcheson et al., 2013*; *Sherman et al., 2018*). *E. striatus* and *E. guttatus* have been highly
353 exploited due to their reproductive aggregations that facilitate their capture at predictable sites
354 and seasons (*Sadovy De Mitcheson et al., 2013*; *Cheung et al., 2013*; *Sherman et al., 2017*),
355 which is why *E. striatus* is currently listed as threatened by the International Union for
356 Conservation of Nature Red List (IUCN), while *E. guttatus* is considered a minor concern. *L.
357 maximus* is a monandric and protogynous hermaphroditic species (*McBride & Johnson, 2007*),

358   characteristics that have led to a decrease in its population due to overfishing (*Ault, Smith &*
359   *Bohnsack, 2005*); therefore, at the regional level, this condition is classified as vulnerable by the
360   IUCN.

361

362   In the Mexican Caribbean, there is little information on the biology and fisheries of many
363   commercially important species; therefore, there is an urgent need to implement fisheries
364   management and regulation strategies for these species. The only federal law concerning
365   commercially important fish species in the study area is for the Nassau grouper *E. striatus*, which
366   is associated with the closed season for the Red grouper *Epinephelus morio* and other species of
367   grouper from the Gulf of Mexico and Caribbean Sea, which runs from 01 February to 31 March
368   of each year.

369

370   The present research found little evidence that the density and total biomass of families of
371   noncommercially important species increased through the elimination of their predators. This
372   may be due to the small number of predatory species that are captured in the BCBR, causing a
373   moderate indirect effect on the prey populations (*Jennings & Polunin, 1997*; *Roff et al., 2016*).

374   The differences in the density and biomass values found in the Scaridae family between areas
375   with different fishing intensities may be linked to the size of the organisms that make up the
376   family. These organisms are generally large in size (e.g., *Scarus vetula* and *Sparisoma viride*),
377   causing them to be less susceptible to predation. In this reef system, organisms (*E. striatus*, *M.*
378   *bonaci*, *L. analis* and *S. barracuda*) that are capable of consuming large prey are eliminated,
379   leaving smaller predatory species (mesopredators) limited in their capacity to prey on larger
380   organisms. This may have caused an increase in the density and biomass of the scarids in the
381   highly fished areas (FRHLF and RLHLF). While some studies have found that families of large-
382   bodied organisms are more vulnerable to fishing than families of smaller organisms (*Friedlander*
383   *& DeMartini, 2002*; *Hawkins & Roberts, 2004*), there is little scientific evidence that species of
384   the Scaridae family are being caught in the BCBR. The foregoing is the result of the
385   implementation of awareness programs on the protection of parrotfish by the authorities of the
386   reserve toward the fishers. These species are currently on the list of protected species in the
387   Official Mexican Standard NOM-059-SEMARNAT.

388

389   **Relationship of density and biomass with fishing pressure and benthic variables.**

390   The density and biomass of the main commercially important fish species in the areas with
391   different fishing intensities were mainly influenced by the presence of algae, octocorals,
392   hydrocorals and CPUE. Although some of these benthic groups contributed to the structural
393   complexity of the reefs, the most important component was the scleractinian corals, which
394   showed no association with the ecological variables of the fish species. This was because the
395   fishing quadrants were located on reefs with high structural complexity. Although attempts were
396   made in this study to reduce the effect of structural complexity on fish species density and
397   biomass (Luckhurst & Luckhurst, 1978; Chabanet et al., 1997; Darling, 2017), it was evident that
398   specific benthic groups and CPUE explained the observed changes in the density and biomass of
399   fish assemblages in the BCBR. The effect of fishing was based on the negative relationship

400 found between CPUE and the density and biomass of highly exploited species such as *E.*
401 *striatus*, *E. guttatus*, *L. griseus* and *S. barracuda*.

402

403 Although there was a detectable effect of fishing on certain commercially important fish species,
404 there was no evidence that this activity affected the structure of the fish community (top-down
405 trophic cascade effect) that could cause a phase change of benthic groups, as found on highly
406 exploited reefs (*Jackson et al., 2001*; *Mumby et al., 2006*; *Mumby & Steneck, 2008*). *Castro-*
407 *Pérez, González & Arias-González (2011)* mentioned that reef-fish fishing in this reserve was
408 moderate because the target species was usually the spiny lobster *Panulirus argus* and fish were
409 only occasionally caught. This is reflected in the results of this study, where it is observed that
410 there are effects of fishing on some high trophic level species belonging to the Lutjanidae and
411 Serranidae families, and no evidence was found that fishing is affecting noncommercial species,
412 although fishers are now beginning to target these species for sale as grouper fillets. It is
413 therefore important that reserve managers adopt a range of general management and
414 conservation measures to protect top predators that are highly valued in markets, as well as large
415 herbivores. Species-specific measures (e.g. size limits, closes during the reproductive season,
416 fishing moratoria, etc.) may also be implemented.

Conclusion

418 In the BCBR throughout the year, the largest fishing exploitation is for the spiny lobster, but in
419 the months when this crustacean begins to be scarce, the fishers focus their greatest fishing
420 efforts on the main species of commercially important fish. Due to the above, this study has
421 detected evidence that the density and biomass have decreased in some species belonging to the
422 Serranidae and Lutjanidae families in areas with higher fishing intensity along BCBR, therefore,
423 there is an urgent need to implement fisheries management and regulation strategies for these
424 species. On the other hand, little evidence was found that the density and total biomass of
425 families of noncommercially important species increased through the elimination of their
426 predators. This may be due to the small number of predatory species that are captured in the
427 BCBR, causing a moderate indirect effect on the prey populations. Finally, although attempts
428 were made to reduce the effect of structural complexity on the density and biomass of fish
429 species, it was found that certain benthic groups and CPUE explained the observed changes in
430 the density and biomass of fish assemblages in the BCBR.

431

References

433 Adam TC, Burkepile DE, Ruttenberg BI, Paddack MJ. 2015. Herbivory and the resilience of
434   Caribbean coral reefs: knowledge gaps and implications for management. *Marine Ecology*
435   *Progress Series* 520:1–20 http://doi.org/10.3354/meps11170

436 Aguilar-Perera A, Aguilar-Dávila W. 1996. A spawning aggregation of Nassau grouper
437   *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environmental Biology of*
438   *Fishes* 45:351–361 https://doi.org/10.1007/BF00002527

439 Arias-González J, Núñez-Lara E, Rodríguez-Zaragoza F, Legendre P. 2011. Reefscape proxies for
440 the conservation of Caribbean coral reef biodiversity. *Ciencias Marinas* 37(1):87–96
441 https://doi.org/10.7773/cm.v37i1.1746

442 Ault JS, Smith SG, Bohnsack J. 2005. Evaluation of average length as an estimator of exploitation
443 status for the Florida coral-reef fish community. *ICES Journal of Marine Science* 62(3):417–423
444 https://doi.org/10.1016/j.icesjms.2004.12.001

445 Babcock EA, Tewfik A, Burns-Perez V. 2018. Fish community and single-species indicators
446 provide evidence of unsustainable practices in a multi-gear reef fishery. *Fisheries Research*
447 208:70–85 https://doi.org/10.1016/j.fishres.2018.07.003

448 Bell J, Galzin R. 1984. Influence of live coral cover on coral-reef fish communities. *Marine*
449 *Ecology Progress Series* 15:265–274 http://dx.doi.org/10.3354/meps015265

450 Bertocci I, Sousa-Pinto I, Duarte P. 2017. Spatial variation of reef fishes and the relative
451 influence of biotic and abiotic habitat traits. *Helgoland Marine Research* 71:20
452 https://doi.org/10.1186/s10152-017-0500-4

453 Brock VE. 1954. A preliminary report on a method of estimating reef fish populations. The
454 *Journal Wildlife Management* 18(3):297–308 https://doi.org/10.2307/3797016

455 Castro-Pérez JM, González GA, Arias-González JE. 2011. Characterizing spatial and temporal
456 reef fisheries in Chinchorro Bank Biosphere Reserve, northern Mesoamerican Reef System.
457 *Hidrobiológica* 21(2):197–209

458 Castro-Pérez JM, Arias-González JE, Acosta-González G, Defeo O. 2018. Comparison of catch,
459 CPUE and length distribution of spawning aggregations of mutton snapper (Lutjanus analis) and
460 grey triggerfish (Balistes capriscus) on a Mesoamerican coral reef. *Latin american journal of*
461 *aquatic research* 46(4):717–726 https://dx.doi.org/10.3856/vol46-issue4-fulltext-9

462 Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R. 1997. Relationships between
463 coral reef substrata and fish. *Coral Reefs* 16**:**93–102 https://doi.org/10.1007/s003380050063

464 Chávez EA, Hidalgo E. 1984. Spatial structure of benthic communities of Banco Chinchorro,
465 México. *Advances in reef sciences. A join meeting of the Atlantic Reef Committee an The*
466 *International Society for Reef Studies*. Univesity of Miami.

467 Cheal AJ, MacNeil MA, Emslie MJ, Sweatman H. 2017. The threat to coral reefs from more
468 intense cyclones under climate change. *Global Change Biology* 23:1511–
469 1524 https://doi.org/10.1111/gcb.13593

470 Cheung WWL, Sadovy de Mitcheson Y, Braynen MT, Gittens LG. 2013. Are the last remaining
471 Nassau grouper *Epinephelus striatus* fisheries sustainable? Status quo in the Bahamas.
472 *Endangered Species Research* 20:27–39 https://doi.org/10.3354/esr00472

473 Clarke KR, Gorley RN. 2001. PRIMER v5: *User manual/ tutorial*. *PRIMER-E*, Plymouth, UK.,
474 192 pp.

475 Claro R, García-Arteaga JP. 1994. Crecimiento. In: Claro R, ed. *Ecología de los peces marinos de*
476 *Cuba*. Instituto de Oceanología Academia de Ciencias de Cuba and Centro de Investigaciones de
477 Quintana Roo, México.

478 Clua E, Legendre P. 2008. Shifting dominance among scarid species on reefs representing a
479 gradient of fishing pressure. *Aquatic Living Resources* 21(3):339–348
480 https://doi.org/10.1051/alr:2008036

481 Dahlgren CP, Buch K, Rechisky E, Hixon MA. 2016. Multiyear tracking of Nassau grouper
482 spawning migrations. *Marine and Coastal Fisheries* 8:522–535
483 https://doi.org/10.1080/19425120.2016.1223233

484 Darling ES, Graham NAJ, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK. 2017.
485 Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*
486 36**:**561–575 https://doi.org/10.1007/s00338-017-1539-z

487 Daskalov GM. 2002. Overfishing drives a trophic cascade in the Black Sea. *Marine Ecology*
488 *Progress Series* 225:53–63 https://www.int-res.com/abstracts/meps/v225/p53-63/

489 FISHBASE. World Wide Web Electronic Publication. Available et http://www.fishbase.org

490 Friedlander AM, Demartini EE. 2002. Contrasts in density, size, and biomass of reef fishes
491 between the northwestern and the main Hawaiian Islands: the effects of fishing down apex
492 predators. *Marine Ecology Progress Series* 230:253–264 https://doi.org/10.3354/meps230253

493 Fulton S, Caamal J, Bourillón L. 2014. *Evaluación del Refugio Pesquero de Banco Chinchorro,*
494 *2012-2014*. Comunidad y Biodiversidad A.C. Guaymas, Sonora, México. Available et
495 https://cobi.org.mx/wp-content/uploads/2016/03/Evaluacion-de-los-Refugios-Pesqueros-de-
496 Banco-Chinchorro-2012-2014.pdf

497

498 Fulton S, Caamal J, Marcos S, Nalesso E. 2016. *Reporte técnico de los resultados de validación y*
499 *monitoreo de los sitios de agregación reproductiva de pargos y meros en el centro y sur de*
500 *Quintana Roo*. Comunidad y Biodiversidad A.C., Guaymas, Sonora, México. Available et
501 https://gigantesdelpasado.org/wp-content/uploads/2018/08/COBI-2016-Reporte-tecnico-de-los-
502 resultados-de-agregaciones.pdf

503 Gaines SD, Costello C, Owashi B, Mangin T, Bone1 J, García-Molinos J, Burden M, Dennis, H,
504 Halpern B, Kappel CV, Kleisner KM, Ovando D. 2018. Improved fisheries management could
505 offset many negative effects of climate change. Science Advances, 4: eaao1378
506 https://www.science.org/doi/10.1126/sciadv.aao1378

507 González A, Torruco D, Liceaga A, Ordaz J. 2003. The shallow and deep bathymetry of the Banco
508 Chinchorro reef in the Mexican Caribbean. *Bulletin Marine Science* 73(1):15–22

509 Graham NAJ, Nash KL. 2013. The importance of structural complexity in coral reef
510 ecosystems. *Coral Reefs* 32:315–326 https://doi.org/10.1007/s00338-012-0984-y

511 Graham NAJ, Robinson JPW, Smith SE, Govinden R, Gendron G, Wilson SK. 2020. Changing
512 role of coral reef marine reserves in a warming climate. *Nature Communications* 11:2000
513 https://doi.org/10.1038/s41467-020-15863-z

514 Hawkins JP, Roberts CM. 2004. Effects of artisanal fishing on Caribbean coral reefs.
515 *Conservation Biology* 18(1):215–226 https://doi.org/10.1111/j.1523-1739.2004.00328.x

516 Helder NK, Burns JHR, Green SJ. 2022. Intra-habitat structural complexity drives the distribution
517   of fish trait groups on coral reefs. *Ecological Indicators* 142:109266
518   https://doi.org/10.1016/j.ecolind.2022.109266

519 Hoegh-Guldberg O, Kennedy EV, Beyer HL, Mcclennen C, Possingham HP. 2018. Securing a
520   long-term future for coral reefs. *Trends in Ecology & Evolution* 33(12):936–944
521   https://doi.org/10.1016/j.tree.2018.09.006

522 Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum, JK,
523   Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs
524   JA, Hoey AS, Hoogenboom M, Lowe RJ, …Wilson SK. 2018. Spatial and temporal patterns of
525   mass bleaching of corals in the Anthropocene. *Science* 359:80–83
526   https://doi.org/10.1126/science.aan8048

527 INE-SEMARNAP. (2000). Programa de Manejo de la Biosfera Banco Chinchorro, México.
528   Available et https://simec.conanp.gob.mx/pdf_libro_pm/53_libro_pm.pdf

529 Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Louis W, Botsford LW, Bourque BJ,
530   Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan, HS,
531   Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR. 2001. Historical overfishing
532   and the recent collapse of coastal ecosystems. *Science* 293.629–638
533   https://doi.org/10.1126/science.1059199

534 Jennings S, Polunin NVC. 1997. Impacts of predator depletion by fishing on the biomass and
535   diversity of non-target reef fish communities. *Coral Reefs* 16(2): 71–82
536   https://doi.org/10.1007/s003380050061

537 Jones GP, Mccormick MI, Srinivasan M, Eagle JV. 2004. Coral decline threatens fish biodiversity
538   in marine reserves. *The Proceedings of the National Academy of Science (PNAS)* 101(21):8251–
539   8253 https://doi.org/10.1073/pnas.0401277101

540 Jordán E, Martin E. 1987. Chinchorro: morphology and composition of a Caribbean atoll. *Atoll
541   Research Bulletin* 310:1–20 https://doi.org/10.5479/si.00775630.310.1

542 Kadison E, Brandt M, Nemeth R, Martens J, Blondeau J, Smith T. 2017. Abundance of
543   commercially important reef fish indicates different levels of over-exploitation across shelves of
544   the U.S. Virgin Islands. *PLoS ONE* 12(7):e0180063
545   https://doi.org/10.1371/journal.pone.0180063

546 Kleypas JA, Yates KK. 2009. Coral Reefs and Ocean Acidification. *Oceanography* 22(4):108–117
547   http://www.jstor.org/stable/24861028

548 Knutson T, Mcbride J, Chan J, Emanuel K, Holland G, Landsea C, Held I, Kossin JP, Srivastava
549   AK, Sugi M. 2010. Tropical cyclones and climate change. *Nature Geoscience* 3:157–163
550   https://doi.org/10.1038/ngeo779

551 Legendre P, Gallagher ED. 2001. Ecologically meaningful transformations for ordination of
552   species data. *Oecologia*, 129(2):271–280 https://doi.org/10.1007/s004420100716

553 Libralato S, Pranovi F, Raicevich S, Da Ponte F, Giovanardi O, Pastres R, Torricelli P, Mainardi
554   D. 2004. Ecological stages of the Venice Lagoon analysed using landing time series data.
555   *Journal of Marine Systems* 51:331–344 https://doi.org/10.1016/j.jmarsys.2004.05.020

556 Loreto RM, Lara M, Schmitter-Soto JJ. 2003. Coral reef fish assemblages at Banco Chinchorro,
557   Mexican Caribbean. *Bulletin of Marine Science* 73(1):153–170.

558 Luckhurst BE, Luckhurst K. 1978. Analysis of the influence of substrate variables on coral reef
559   fish communities. *Marine Biology* 49**:**317–323 https://doi.org/10.1007/BF00455026

560 McBride RS, Johnson MR. 2007. Sexual development and reproductive seasonality of hogfish
561   (Labridae: *Lachnolaimus maximus*), an hermaphroditic reef fish. *Journal of Fish Biology*
562   71:1270–1292 https://doi.org/10.1111/j.1095-8649.2007.01580.x

563 McClure EA, Sievers KT, Abesamis RA, Hoey AS, Alcala AC, Russ GR. 2020. Higher fish
564   biomass inside than outside marine protected areas despite typhoon impacts in a complex
565   reefscape. *Biological Conservation* 241:108354 https://doi.org/10.1016/j.biocon.2019.108354

566 Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE,
567   Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB. 2006. Fishing,
568   trophic cascades, and the process of grazing on coral reefs. *Science* 311(5757):98–101
569   https://doi.org/10.1126/science.1121129

570 Mumby PJ, Steneck RS. 2008. Coral reef management and conservation in light of rapidly
571   evolving ecological paradigms. *Trends in Ecology & Evolution* 23:555–563
572   https://doi.org/10.1016/j.tree.2008.06.011

573 Mumby PJ, Steneck RS, Edwards AJ, Ferrari R, Coleman R, Harborne AR, Gibson JP. 2012.
574   Fishing down a Caribbean food web relaxes trophic cascades. *Marine Ecology Progress Series*
575   445:13–24 https://doi.org/10.3354/meps09450

576 Pauly D, Christensen V, Guénette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R, Zeller D.
577   2002. Towards sustainability in world fisheries. *Nature* 418:689–695
578   https://doi.org/10.1038/nature01017

579 Rodríguez-Zaragoza FA, Ortiz M, Berrios F, Campos L, de Jesús-Navarrete A, Castro-Pérez J,
580   Hernández-Flores A, García-Rivas M, Fonseca-Peralta F, Gallegos-Aguilar E. 2016. Trophic
581   models and short-term dynamic simulations for benthic-pelagic communities at Banco
582   Chinchorro Biosphere Reserve (Mexican Caribbean): a conservation case. *Community Ecology*
583   17:48–60 https://doi.org/10.1556/168.2016.17.1.7

584 Roff G, Doropoulos C, Rogers A, Bozec YM, Krueck NC, Aurellado E, Priest M, Birrell C,
585   Mumby PJ. 2016. The ecological role of sharks on coral reefs. *Trends in Ecology & Evolution*
586   31(5):395–407 http://dx.doi.org/10.1016/j.tree.2016.02.014

587 Ruppert JLW, Vigliola L, Kulbicki M, Labrosse P, Fortin MJ, Meekan MG. 2017. Human
588   activities as a driver of spatial variation in the trophic structure of fish communities on Pacific
589   coral reefs. *Global Change Biology* 24:e67-79 https://doi.org/10.1111/gcb.13882

590 Russ GR, Rizzari JR, Abesamis RA, Alcala AC. 2021. Coral cover a stronger driver of reef fish
591   trophic biomass than fishing. *Ecological Applications* 31(1):e02224.
592   https://doi.org/10.1002/eap.2224

593 Sadovy de Mitcheson Y, Craig MT, Bertoncini AA, Carpenter KE, Cheung WWL, Choat JH,
594   Cornish AS, Fennessy ST, Ferreira BP, Heemstra PC, Liu M, Myers RF, Pollard DA, Rhodes
595   KL, Rocha LA, Russell BC, Samoilys MA, Sanciangco J. 2013. Fishing groupers towards

596   extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish and*
597   *Fisheries* 14(2):119–136 https://doi.org/10.1111/j.1467-2979.2011.00455.x

598   Sala E, Ballesteros E, Starr RM. 2001. Rapid decline of Nassau grouper spawning aggregations in
599   Belize: fishery management and conservation needs. *Fisheries* 26:23–30
600   https://doi.org/10.1577/1548-8446(2001)026<0023:RDONGS>2.0.CO;2

601   Savo V, Morton C, Lepofsky D. 2017. Impacts of climate change for coastal fishers and
602   implications for fisheries. *Fish and Fisheries* 18(5):877–889 https://doi.org/10.1111/faf.12212

603   Scheffer M, Carpenter S, de Young B. 2005. Cascading effects of overfishing marine systems.
604   *Trends in Ecology and Evolution* 20:579–581 https://doi.org/10.1016/j.tree.2005.08.018

605   Sherman KD, King RA, Dahlgren CP, Simpson SD, Stevens JR, Tyler CR. 2017. Historical
606   processes and contemporary anthropogenic activities influence genetic population dynamics of
607   Nassau Grouper (*Epinephelus striatus*) within the Bahamas. *Frontiers in Marine Science* 4:393
608   https://doi.org/10.3389/fmars.2017.00393

609   Sherman KD, Shultz AD, Dahlgren CP, Thomas C, Brooks E, Brooks A, Brumbaugh DR, Gittens
610   L, Murchie KJ. 2018. Contemporary and emerging fisheries in The Bahamas–Conservation and
611   management challenges, achievements, and future directions. *Fisheries Management and*
612   *Ecology* 25:319–331 https://doi.org/10.1111/fme.12299

613   Sosa-Cordero E, Ramírez A, Domínguez-Viveros M, Aguilar-Perera A. 1991. Peces y pesquerías.
614   In: Camarena-Luhrs T, Salazar-Vallejo SI, eds. *Estudios ecológicos preliminares de zona sur de*
615   *Quintana Roo*. Centro de Investigaciones de Quintana Roo (CIQRO), México.

616   Ter Braak CJF, Smilauer P. 2002. *CANOCO reference manual and CanoDraw for Windows*
617   *user's guide: Software for Canonical Community Ordination* (version 4.5). Biometris,
618   Wageningen. Available et https://edepot.wur.nl/405659

619   Valdivia A, Cox CE, Bruno JF. 2017. Predatory fish depletion and recovery potential on
620   Caribbean reefs. *Science Advances* 3(3):e1601303 https://doi.org/10.1126/sciadv.1601303

621   Veron JEN. 2011. Ocean acidification and coral reefs: An emerging big picture. *Diversity*
622   3(2):262–274 https://doi.org/10.3390/d3020262

623   Williams ID, Richards BL, Sandin SA, Baum JK, Schroeder RE, Nadon MO, Zgliczynski BJ*,*
624   Craig P*,* McIlwain JL, Brainard RE. 2011. Differences in reef fish assemblages between
625   populated and remote reefs spanning multiple archipelagos across the central and western
626   Pacific. *Journal of Marine Science* 1–14 https://dx.doi.org/10.1155/2011/826234

627   Zar JH. 1999. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, pp. 672.

628   Zeller D, Graham R, Harper S. 2011. Reconstruction of total marine fisheries catches for Belize,
629   1950-2008. In: Palomares MLD, Pauly D, eds. *Too Precious to Drill: The Marine Biodiversity*
630   *of Belize*. Fisheries Centre, University of British Columbia, 142–151
631   http://www.seaaroundus.org/doc/publications/books-and-reports/2011/Palomares-and-Pauly-too-
632   precious-to-drill-Belize.pdf

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Figure 1

Location of the study area. (B) Distribution of the sampling stations for fish and benthic organisms. (C) scheme of the fishing quadrats
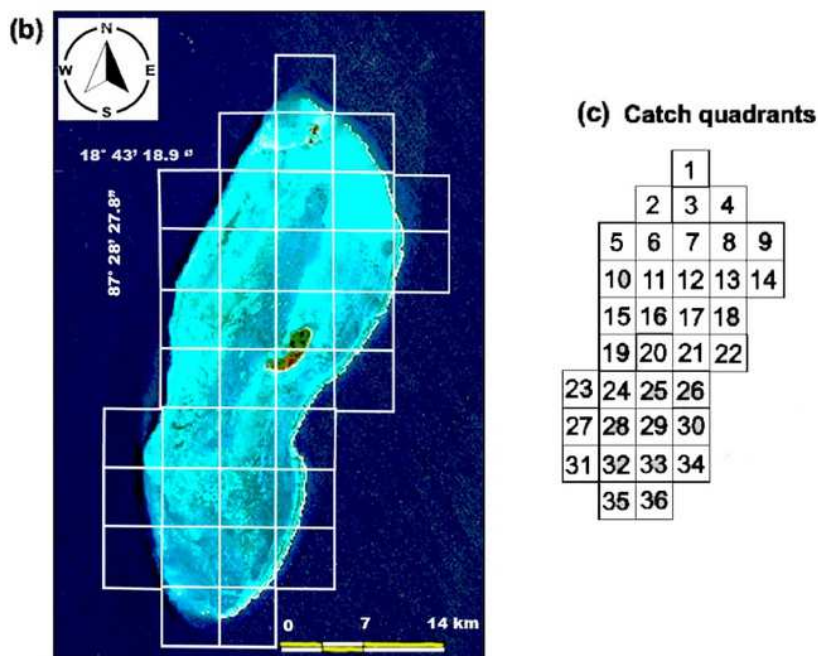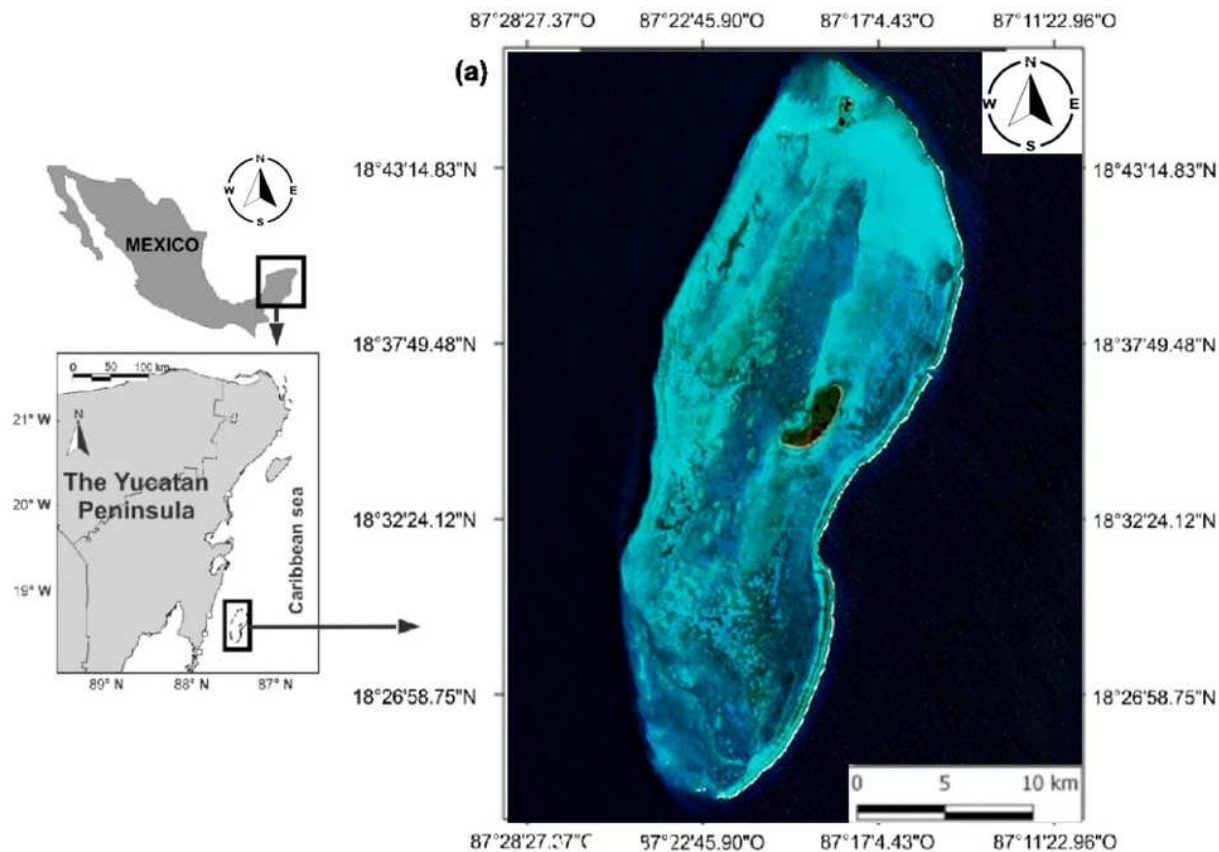
Figure 2

(A) Dendrogram obtained from the Bray–Curtis similarity coefficients and used for identifying quadrats with different fishing intensities based on the CPUE data. (B) Location of the areas with different fishing intensities.

FRMLF = forereef moderate-level fishing; FRHLF = fore-reef high-level fishing; and RLHLF = reef lagoon high-level fishing.
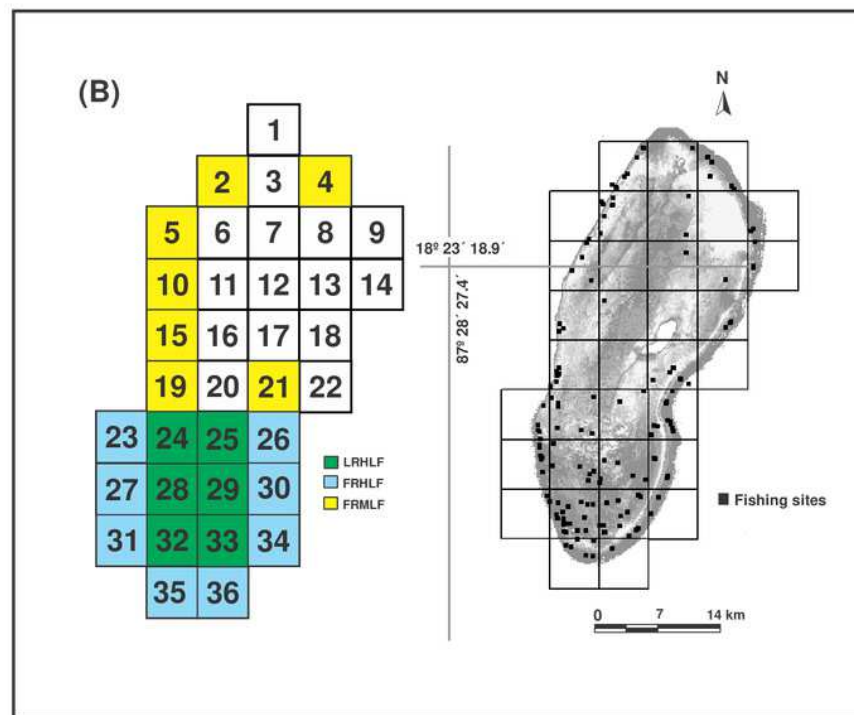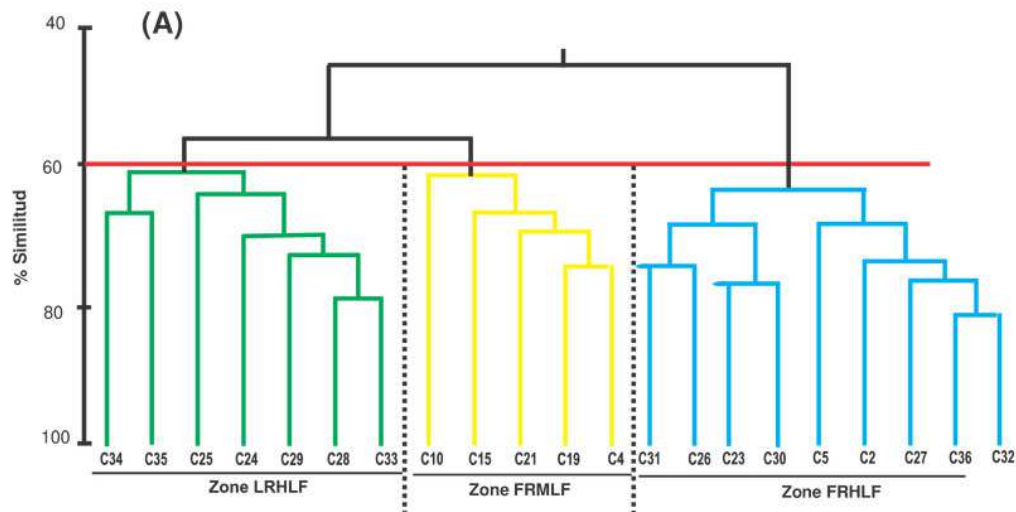
Figure 3

Comparison of the average (± SE) density and biomass among areas with different fishing intensities. (A) commercial species. (B) noncommercial species.

The homogeneous groups (LSD test, P > 0.05) are shown by the same letters for each treatment (areas): FRMLF = forereef moderate-level fishing; FRHLF = forereef high-level fishing; and RLHLF = reef lagoon high-level fishing.
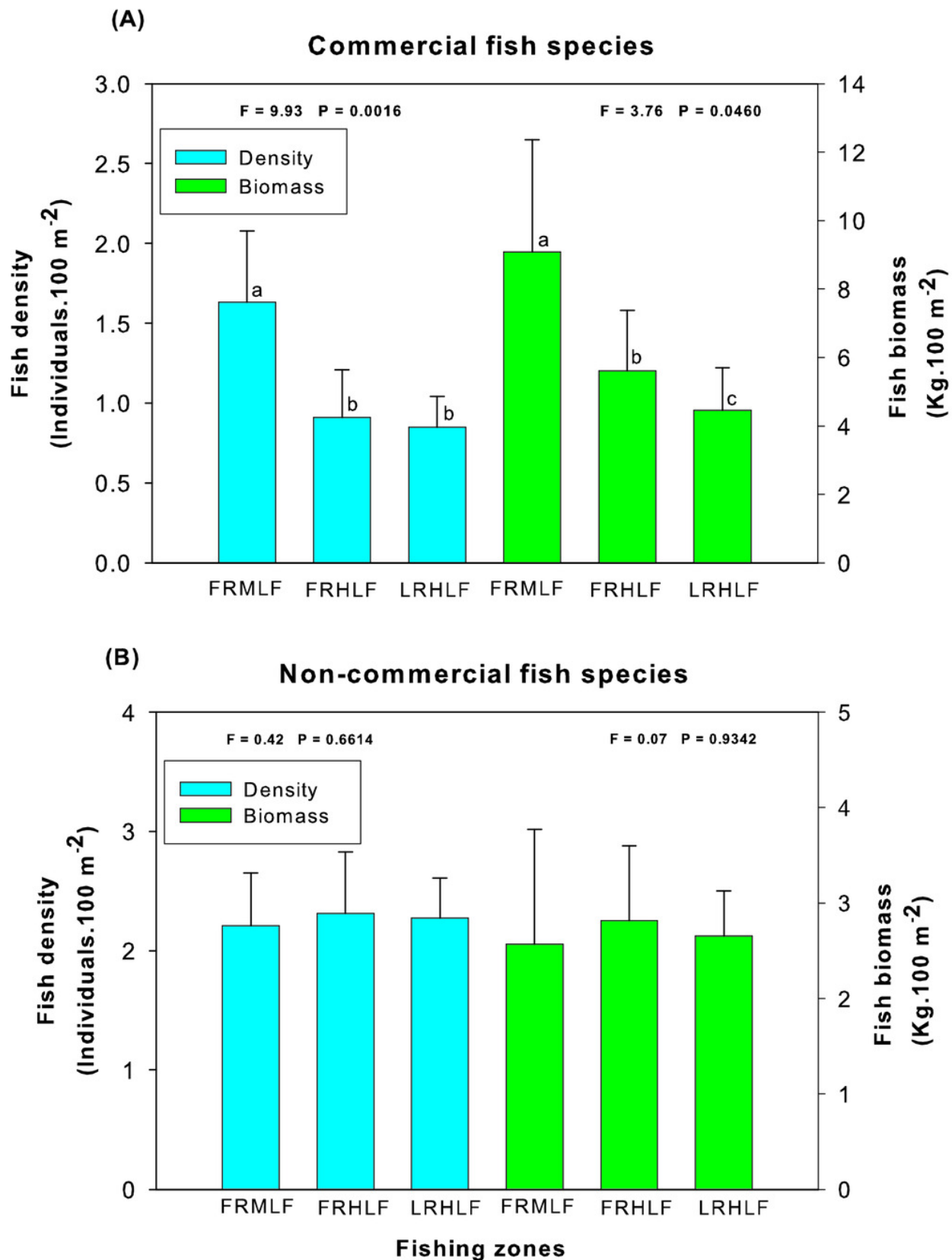
Figure 4

Comparison of the average (± SE) density and biomass per species of commercial importance among areas with different fishing intensities.

The homogeneous groups (LSD test, p > 0.05) are shown by the same letters for each treatment (areas): FRMLF = forereef moderate-level fishing; FRHLF = forereef high-level fishing; and RLHLF = reef lagoon high-level fishing.
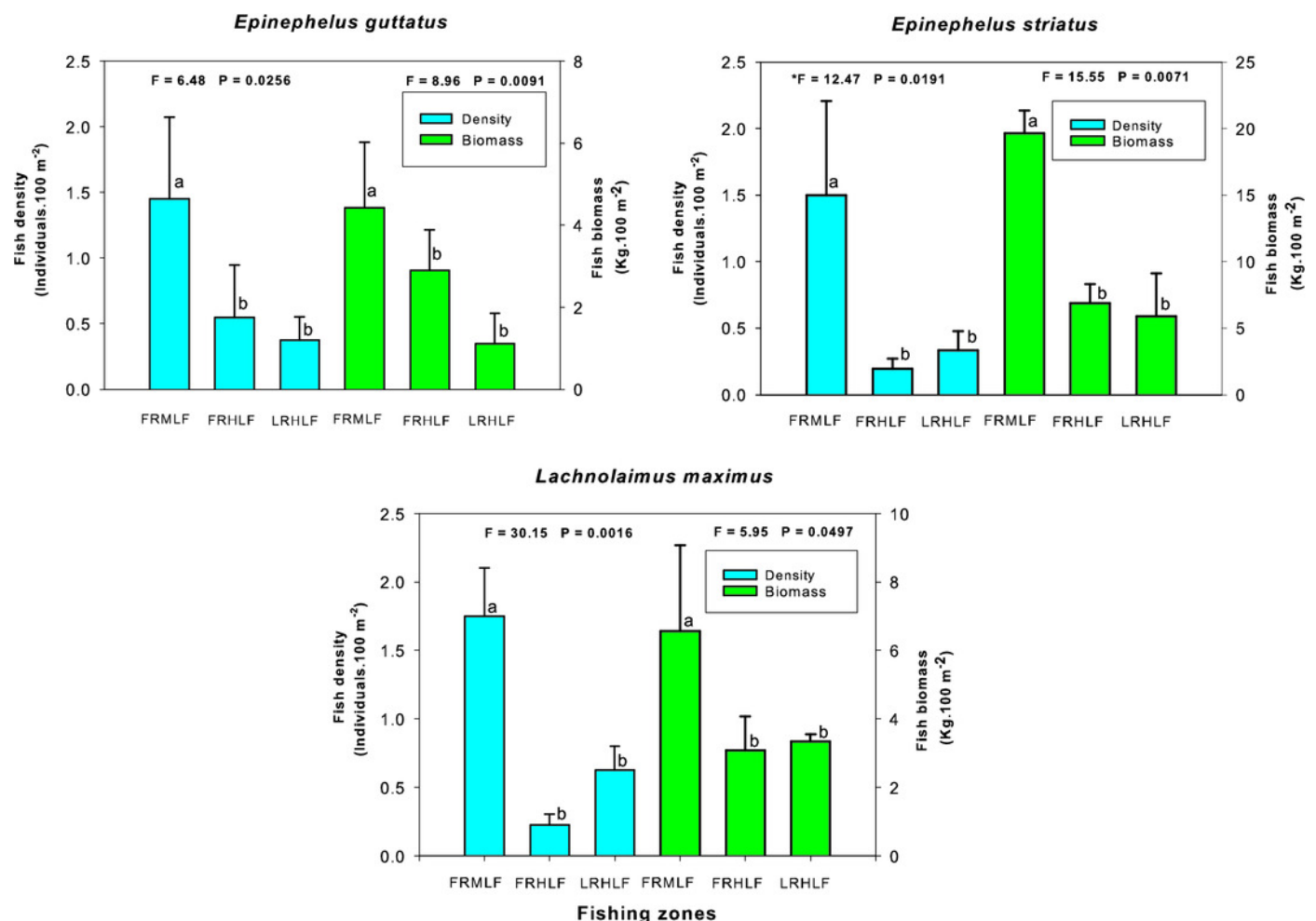
Figure 5

Comparison of the average (± SE) density and biomass of the *Scaridae* family caught among the areas with different fishing intensities.

The homogeneous groups (LSD test, p > 0.05) are shown by the same letters for each treatment (areas): FRMLF = forereef moderate-level fishing; FRHLF = forereef high-level fishing; and RLHLF = reef lagoon high-level fishing.
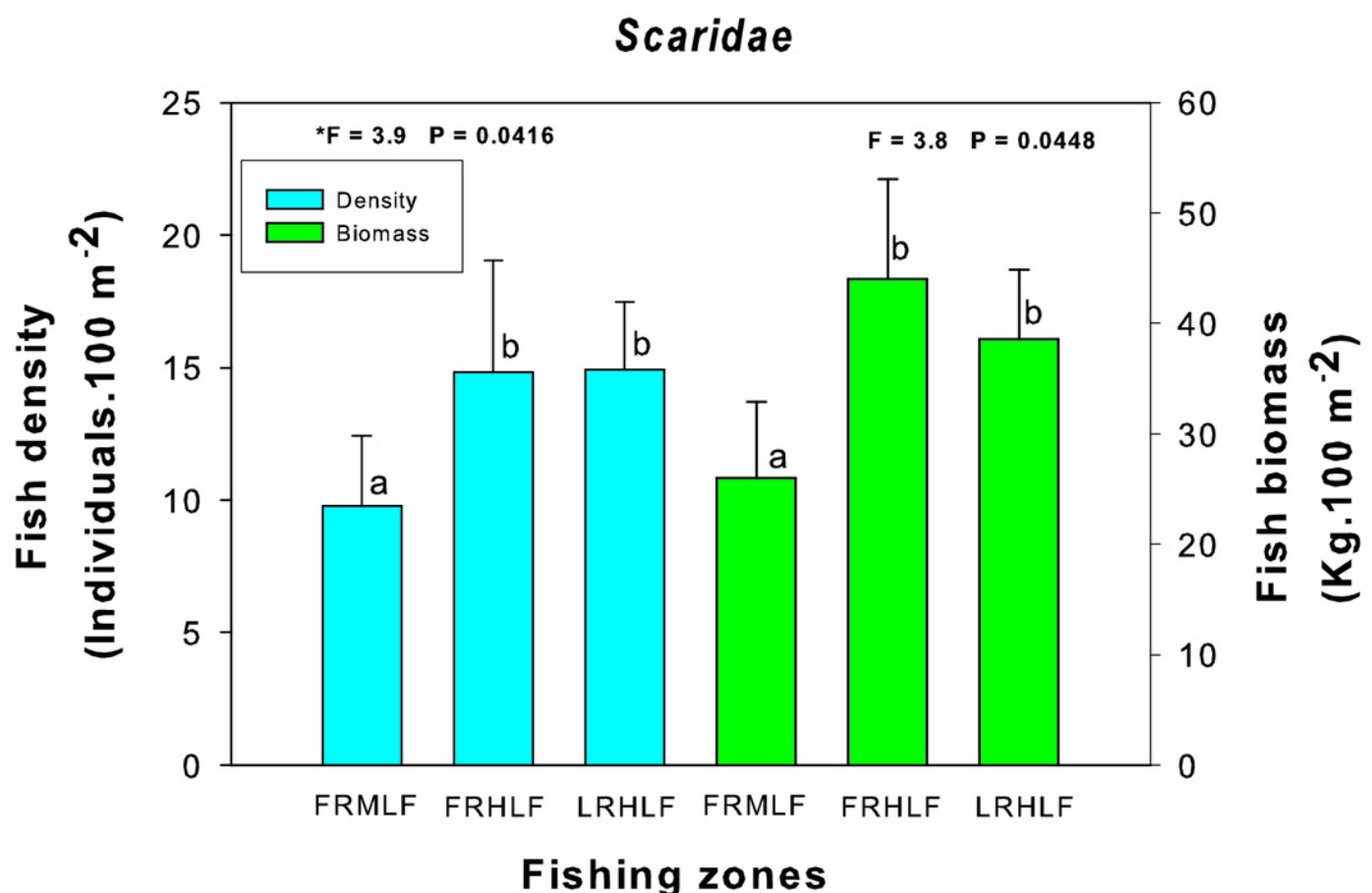
Figure 6

Ordination of the RDA data for the density (A) and biomass (B) of commercial fish with benthic coverage and the CPUE. The symbols represent the areas with different fishing intensities: (red circle) FRMLF; (green square) FRHLF; and (yellow circle) RLHLF.

The abbreviations corresponding to the species are the following: *Balcap* (*Balistes capriscus*); *Epigut* (*Epinephelus guttatus*); *Epistr* (*Epinephelus striatus*); *Lacmax* (*Lachnolaimus maximus*); *Lutana* (*Lutjanus analis*); *Lutgri* (*Lutjanus griseus*); *Mycbon* (*Mycteroperca bonaci*); *Ocychr* (*Ocyurus Chrysurus*); and *Sphbar* (*Sphyraena barracuda*). The letter C = fishing quadrat; FRMLF = forereef moderate-level fishing; FRHLF = forereef high-level fishing; and RLHLF = reef lagoon high-level fishing.