

1 Article

2 Changes in the Fish Community of a Western 3 Caribbean Estuary after the Expansion of an Artificial 4 Channel to the Sea

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11 **Abstract:** Increased connectivity between coastal lagoons and the sea is expected to entail a greater
12 proportion of marine species in the former. Chetumal Bay, estuary of the Hondo river into the
13 Caribbean, had a limited access to the sea until the opening of the Zaragoza Canal. We sought
14 changes in the fish community from 1999-2001 (just after an expansion of the canal) to 2015-2018.
15 The same fishing gear was used, in the same localities, during all seasons. Total fish abundance and
16 mean local richness decreased, although total abundance increased in the polyhaline zone. Diversity
17 was greater in the oligohaline zone in 1999-2001, but in the mesohaline zone in 2015-2018. Three
18 guilds were absent in 2015-2018: medium-sized herbivores, large piscivores, and medium-sized
19 planktivores. Abundance of small benthivores decreased by decade; medium-sized piscivores and
20 small planktivores became more abundant in 2015-2018 in the polyhaline zone. These changes may
21 be due to the opening of the channel, but illegal fishing outside the bay may explain the decrease in
22 juveniles of large piscivores, and erosion in the innermost part may be destroying important
23 habitats. Our findings can be a reference for similar situations, as coastal development and climate
24 change interact and affect tropical estuaries.

25

26 **Keywords:** ichthyofauna; trophic guilds; salinity-tolerance; connectivity; Chetumal Bay; Mexico

27

28 1. Introduction

29 Chetumal Bay (known as Corozal Bay in Belize) is the estuary of the Hondo River and minor
30 affluents, connecting them to the Caribbean Sea, at the border between Mexico and Belize. This
31 large water body (about 3500 km² in area) is protected by both countries [1]. For thousands of years,
32 the narrow and winding natural passage of Bacalar Chico was the connection of the Mexican part of
33 the bay to the Caribbean Sea (a much wider opening exists near the Belize-Guatemala border, about
34 300 km south). However, between 1999 and 2004 an artificial channel was dredged and expanded
35 for navigation, the Zaragoza Canal, opened initially in 1901, but never made deep enough for larger
36 vessels. This direct communication started having a strong influence on the abiotic and biotic
37 conditions of the system, including the intrusion of corals and other reef organisms to formerly
38 brackish areas of the bay [2].

39 Many of the fishes found in this system are important resources. Most relevant for recreational
40 fisheries in Belize and Mexico are the bonefish *Albula vulpes*, but also permit *Trachinotus falcatus*,
41 snook *Centropomus undecimalis*, and tarpon *Megalops atlanticus* [3]. Other species are fished mostly
42 for local markets: snappers (*Lutjanus* spp., especially *L. griseus* and *L. apodus*), mojarras (*Gerres*
43 *cinereus*, *Eugerres plumieri*), mackerels (*Scomberomorus maculatus* and other species), and barracuda

44 *Sphyraena barracuda* [4]. Other mojarras (*Eucinostomus* spp.) are also abundant, as are needlefishes
45 (*Strongylura* spp.), pupfishes (Cyprinodontidae), flatfishes (several families), sea catfishes (Ariidae),
46 gobies (Gobiidae), the puffer *Sphoeroides testudineus*, and, under the influence of freshwater, also
47 cichlids, poeciliids, and the tetra *Astyanax bacalarensis*, among others [5]. A recent addition to this
48 ichthyofauna is the lionfish *Pterois volitans*, an exotic invader (pers. obs.).

49 Qualitative and quantitative data on the fishes of Chetumal Bay are available from the time just
50 before the expansion in depth and width of the Zaragoza Canal [5,6]. Our aim in this paper is to
51 evaluate ichthyological changes almost two decades later, in terms of composition, diversity
52 (including richness, evenness, beta-diversity), abundance of species, trophic guilds, and salinity-
53 tolerance categories, maximum length, and distribution through the salinity gradient of the bay,
54 from the river mouth to the Zaragoza Canal. We discuss possible processes to explain the patterns
55 found.

56 2. Materials and Methods

57 2.1 Study Area

58 The region has a warm humid climate, with summer rains and an average temperature greater
59 than 26.5 °C, with an annual precipitation of 1000-1500 mm; the bay is shallow, its maximum depth
60 5 m (mean 3.2 m), with scattered, much deeper, sinkholes [7]. Most of the bay is mesohaline (13 to
61 22 psu), but freshwater can occur near the mouth of the Hondo River, and marine salinity close to
62 the Zaragoza Canal [8]. Salinity varies seasonally, increasing in the dry season (February to April)
63 and decreasing during the rains (May to October) and during the colder “north winds” season
64 (November to January); however, three areas can be recognized year-round, and we term them here
65 Oligohaline, Mesohaline, and Polyhaline (Fig. 1). Except in winter, southeasterly trade winds
66 predominate, with a mean wind speed of 3.1 m·s⁻¹ [7].

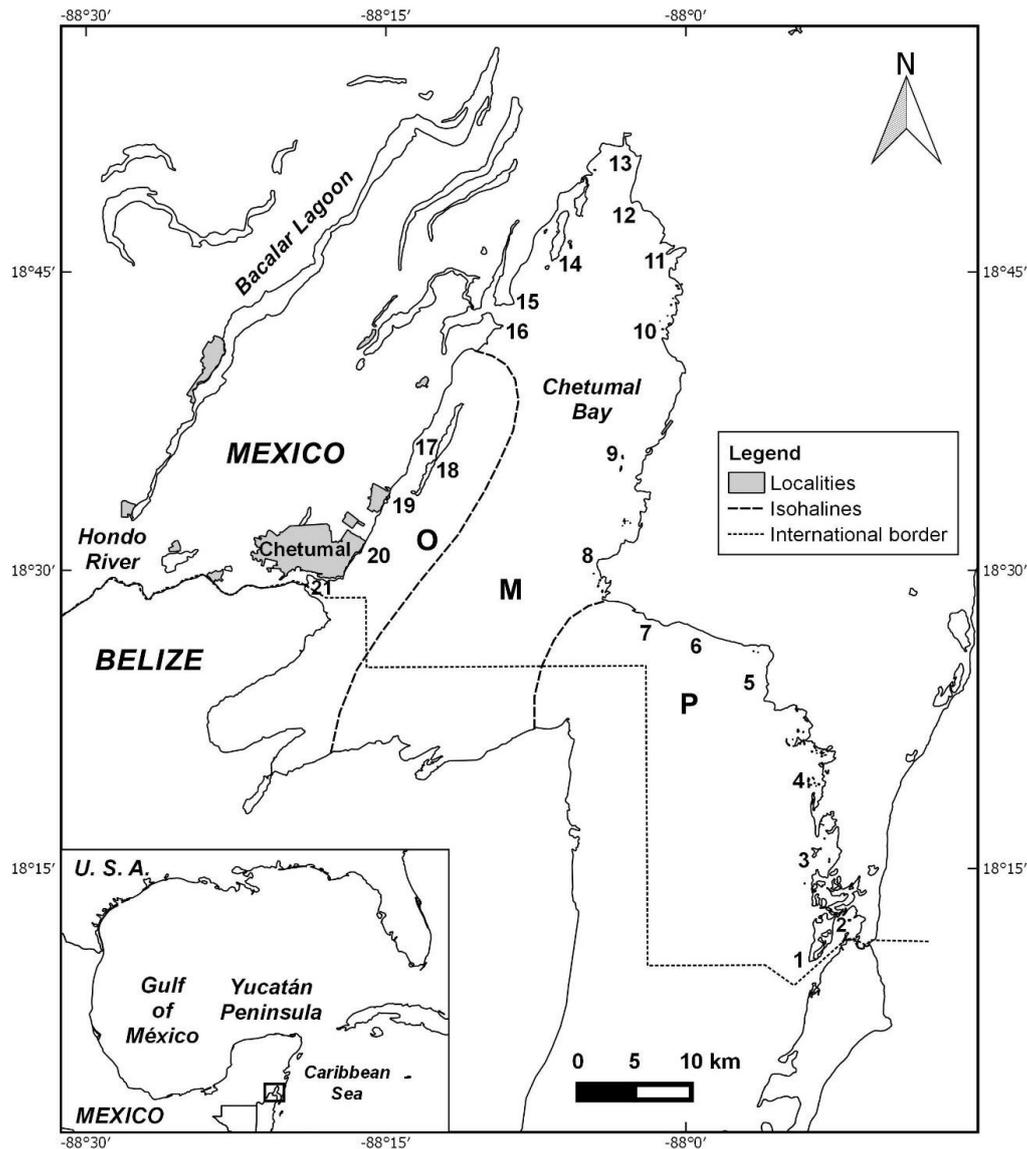
67 Tides are semidiurnal, with water level changing no more than 0.5 m, but nevertheless
68 inducing inward or outward currents at the Zaragoza Canal and minor channels. Water
69 temperature fluctuates between 22 °C at the peak of the north-winds season and 31 °C in August.
70 Bottoms are mostly sandy or sandy-muddy, rocky near the “puntas” (points), usually without
71 vegetation but often with seagrass and algae. Mangrove rims the coast and *Avicennia germinans* can
72 reach heights of 10 m [9], with occasional patches of exotic *Casuarina equisetifolia* trees.

73 There are no human settlements in the northern half of the bay. Chetumal City lies at the
74 mouth of the Hondo river (Figure 1), and just to the south is the Belizean town of Sarteneja.
75 Pesticides from agricultural fields along both banks of the river and organic matter from Chetumal
76 are a pollution problem [10], although largely confined to the river mouth by winds and currents.

77 2.2 Field and Laboratory Work

78 We sampled the bay for fishes at the same 21 localities explored a decade and a half ago by
79 ourselves [6] (Figure 1). Expeditions took place in April 13-15 and July 6-8, 2016, and in April 23-24,
80 2018, and more than 13,000 specimens from 162 samplings were collected, using the same fishing
81 gear and effort (a beach seine, 20 m long, 1.2 m tall, 1 cm diagonal mesh, 2-5 seinings per site, until
82 no new species were found, and each seining lasting ~3 min).

83 Fish were identified and counted *in situ* and then liberated; voucher specimens were kept only
84 for those species which could not be determined in the field, among them all *Eucinostomus*, which
85 were deposited in the fish collection of ECOSUR (acronym ECO-CH). Abundance was controlled by
86 the number of seinings per site/date, as catch per unit effort (CPUE). Collected specimens were
87 measured (standard length) to the nearest millimeter with a vernier caliper or an ichthyometer.



88

89 **Figure 1.** Study area, the northern (Mexican) part of the Bay of Chetumal (known as Bay of Corozal
 90 in Belize). Localities: 1 Cayo Chelem; 2 Zaragoza Canal; 3 Dos de Abril; 4 Mala Noche; 5 Punta Jas; 6
 91 Mainada; 7 Punta Calentura; 8 Punta Flor; 9 Dos Hermanos; 10 Mogote Barlovento; 11 Siete Esteros;
 92 12 Tollocan; 13 Río Krik; 14 Cayo Venado; 15 Punta Pol Box; 16 Punta Lagarto; 17 Isla Tamalcab
 93 (leeward); 18 Isla Tamalcab (windward); 19 Punta Catalán; 20 UQROO; 21 ECOSUR. Abbreviations
 94 for salinity zones: O-oligohaline; M-mesohaline; P-polyhaline (see text). Map by Janneth Padilla.

95 Composition included data from the literature [11, 12], revision of collection specimens, and
 96 observations or captures outside seinings.

97 2.3 Data Analysis

98 We compared the following variables between decades (1999-2001 vs. 2015-2018) and by
 99 salinity areas (Oligohaline, Mesohaline, and Polyhaline – hereafter zones O, M, P): a) composition
 100 (i.e., presence/absence of species); b) richness; c) diversity, both alpha and beta; d) abundance (i.e.
 101 CPUE) of dominant species; e) abundance by guild (see below); f) abundance by salt-tolerance
 102 category [13]: marine stenohaline, marine euryhaline, estuarine resident, freshwater primary or
 103 secondary; g) maximum observed length of selected species; h) frequency (i.e. proportion of
 104 localities where present); i) environmental abiotic variables, mainly temperature, salinity, and wind
 105 at the time of capture. Differences in salinity (refractometer, to 1 psu), temperature (digital

106 thermometer, to 1 °C) and wind force (Beaufort scale) were examined controlling by season (dry,
107 rainy, north-winds; see Study Area) and time of day (morning 07-10:59, noon 11-14:59, afternoon
108 15-19 h: time when sampling started). Fourteen guilds were defined as combinations of feeding
109 habits and three body-size categories [14–16].

110 In addition to analyzing pooled data, the above listed variables were examined separately by
111 salt-tolerance category of the fishes. Abundance was log-transformed. Only species that made up
112 75% of total abundance were analyzed separately. The test used was a two-way ANOVA (by
113 decade and by salinity area), with an interaction term; post-hoc comparisons were performed using
114 Tukey Honest Distance. Frequencies were compared by a Kolmogorov-Smirnov test (KS). Diversity
115 ($H'n$, Shannon index, in nats) and its components (richness, as number of species; $J'n$, Pielou's
116 equity) were calculated by locality and controlled by rarefaction. Beta-diversity as turnover was
117 explored via the Sørensen index and plotted in the triangular graph suggested by Koleff et al. [17].
118 The software used to analyze data and prepare graphs was R [17], with $p < 0.05$ (instances where
119 $p > 0.05$ but $p < 0.10$ are also mentioned and discussed); the package “vegan” was used for diversity
120 analyses [18].

121 We sampled under Permit PPF/DGOPA-053/15 from the Comisión Nacional de Pesca (the
122 Mexican Commission for Fisheries), with further authorization by the protected area “Bahía de
123 Chetumal Santuario del Manatí”. Accession to our database will be provided during review.

124 3. Results

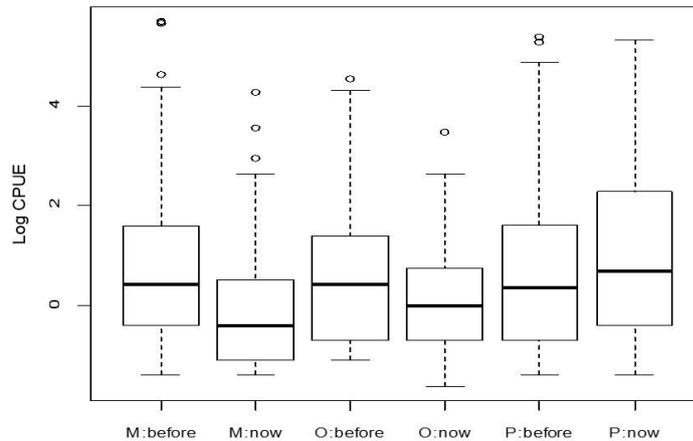
125 Sampling effort, with emphasis on the mesohaline zone (samplings: 140 O, 261 M, 215 P) due
126 to the greater number of localities (5 O, 8 M, 7 P), did not vary between decades (KS, $D=0.67$). Every
127 locality was sampled on average 29 times between both decades. The mean number of fish by
128 species per sampling was 9; the maximum, 294.

129 Salinity varied from 1 to 36 psu, mean 10.9 psu; water temperature, 25-34 °C, mean 29 °C.
130 Wind force in the Beaufort scale was 1 to 4, with a mode of 2. Controlling by season, salinity varied
131 significantly between decades ($F=10.9$), changing from a mean of 10.4 psu in 1999-2001 to 11.8 psu
132 in 2015-2018. Controlling by season and by time of day, water temperature also changed between
133 decades ($F=6.9$), from 29.2 °C to 28.7 °C. Wind force increased as well ($F=21.6$), from 1.9 to 2.4 in the
134 Beaufort scale.

135 General abundance of fish decreased from 1999-2001 to 2015-2018, except in zone P ($F=5.82$ by
136 decade, $F=8.05$ for the interaction decade:zone; Figure 2, Appendix A). By zone, an “estuary effect”
137 is apparent, with greater abundance in zone P than in O, but greater in O than in M ($F=5.97$).

138 There were few changes in composition (Appendix B). The most conspicuous novelty is the
139 lionfish *Pterois volitans*, absent in 1999-2001, now confirmed in the zone P, closest to the Zaragoza
140 Canal. Among the species that were captured in 1999-2001 but not in 2015-2018 are *A. vulpes*,
141 *Ariopsis assimilis*, *Centropomus undecimalis*, *Jenkinsia lamprotaenia*, *Opsanus beta*, and *Opisthonema*
142 *oglinum*; however, all of them are still present in the area, as observed outside our seinings. On the
143 contrary, species that were not seined in 1999-2001 but yes in 2015-2018 include *A. bacalarensis*,
144 *Coroula sanctaeluciae*, *Hypanus* spp., *Diapterus auratus*, and *Lutjanus* spp. Juveniles of *Trachinotus*
145 *falcatus*, not found in the quantitative samplings in 1999-2001, were captured in all three salinity
146 zones in 2015-2018. Three species of *Strongylura* were seined in 1999-2001, but in 2015-2018 only *S.*
147 *notata*. Also exclusive to the older decade were usually reef-dwelling species, as *Holocentrus rufus*
148 and *Sparisoma rubripinne*, freshwater secondary species, as *Poecilia kykesis*, and others (*Syngnathus*
149 spp., *Selene vomer*, *Haemulon* spp., *Chaetodipterus faber*, *Chilomycterus schoepfi*, *Bothus ocellatus*,
150 *Acanthurus* spp.). One case of concern was *Gobiosoma yucatanum*, the only species endemic to

151 Chetumal Bay (Dawson 1971; Greenfield and Thomerson 1997), which we found in 1999-2001, but
 152 not in the most recent expeditions.



153

154 **Figure 2.** General abundance of fishes by decade and salinity area in Chetumal Bay. Abundance
 155 (CPUE) log-transformed. Posthoc significant differences between M:before and M:now, P:before and
 156 M:now, M:now and P:now, and O:now and P:now. Abbreviations for salinity zones: O-oligohaline;
 157 M-mesohaline; P-polyhaline; “before” is 1999-2001 and “now” means 2015-2018.

158 Changes in dominance were clearer than changes in composition. *Atherinomorus stipes* and
 159 *Harengula jaguana* were always abundant and frequent, the former especially in the windward
 160 (sandy) side of mangrove islands, whereas *Floridichthys polyommus*, in both decades, predominated
 161 in the leeward (silty) side. *Bairdiella ronchus* and *Cyprinodon artifrons* decreased (in frequency, 3 to 1);
 162 in 1999-2001, *C. artifrons* was more abundant than the ecologically similar *Jordanella pulchra*, which
 163 increased in frequency from 1 to 3. Concerning another ecologically similar pair, *Eugerres plumieri*
 164 was more abundant than *Gerres cinereus* in 1999-2001 (especially in zone O), but not in 2015-2018 (*G.*
 165 *cinereus* increased in frequency from 2 to 3). The five species of *Eucinostomus* kept their relative
 166 abundances similar, except that *E. melanopterus* was not seined in 1999-2001.

167 Few species displayed significant changes by decade or salinity zone (Table 1). Most increases
 168 occurred in zone P, most decreases in zone M. The flatfish *Achirus lineatus* decreased in abundance in
 169 all three salinity zones; among zones, it preferred O to P, in spite of being a marine species. The
 170 silverside *Atherinomorus stipes* was almost absent from zone O back in 1999-2001, and in 2015-2018 it
 171 preferred P to M. As stated above, *E. plumieri* decreased, especially in zone O, which it used to prefer
 172 in 1999-2001. The needlefish *Strongylura notata* became more abundant in zone P in 2015-2018.

173 Diversity was not uniform by locality. In 1999-2001 most of the sites with greater diversity
 174 belonged in zone O, such as Punta Catalán ($H'n = 2.47$ nats) and UQROO (2.14 nats), same as equity
 175 ($J'n=0.84, 0.97$, respectively) and richness (up to 19 spp.), whereas in 2015-2018 most diverse localities
 176 were in zone M, e.g. Siete Esteros (2.32 nats) and Punta Flor (2.19 nats), same as equity (0.90, 0.88,
 177 respectively) and richness (up to 14 spp., although Chelem, in zone P, reached 15 spp.).

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181 **Table 1.** Fish species whose abundance changed significantly by decade (1999-2001 vs. 2015-2018)
 182 and/or between salinity zones (Oligohaline, Mesohaline, Polyhaline) in Chetumal Bay.

<u>Species</u>	<u>F</u>	<u>Difference</u>
<i>Achirus lineatus</i>	12.70	Decreased by decade at all zones
<i>Achirus lineatus</i>	3.41	Greater abundance in O than in P
<i>Atherinomorus stipes</i>	4.97	Decreased by decade in M
<i>Eugerres plumieri</i>	6.11	Decreased by decade in O and M, not in P
<i>Gerres cinereus</i>	3.44	Decreased by decade in M
<i>Harengula jaguana</i>	7.97	Greater abundance in P in 2015-2018
<i>Strongylura notata</i>	2.47	Greater abundance in P in 2015-2018

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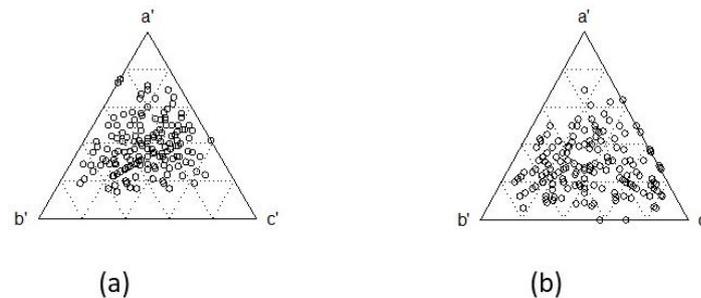
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Total diversity or equity did not differ between decades ($t=0.36$ and $t=1.10$, respectively), but richness yes ($t=2.30$), decreasing from a mean of 11.8 spp. in 1999-2001 to 9.3 spp. in 2015-2018. Beta-diversity (turnover) did not differ between decades, although the graph shows a somewhat greater dispersion in 2015-2018 than in 1999-2001 (Figure 3). Turnover varied slightly between decades, from 0.78 to 0.79, and nestedness from 0.06 to 0.08.



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Figure 3. Beta-diversity of fishes in Chetumal Bay by decade: (a) 1999-2001, (b) 2015-2018. Circles are pairwise comparisons of species turnover derived from the Sørensen formula, where a' are shared species, b' are species exclusive to the focal locality and c' are species exclusive to the compared locality.

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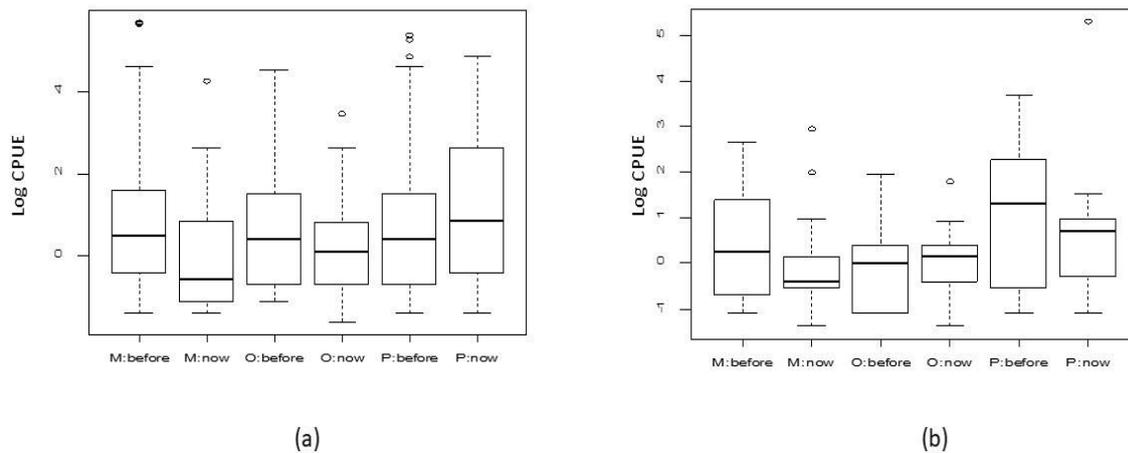
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The most frequent guilds were benthivores, small and medium-sized, followed by small planktivores and medium-sized piscivores. No large benthivores occurred in our samplings in 1999-2001 and three guilds were absent in 2015-2018: medium-sized herbivores, large piscivores, and medium-sized planktivores. Although medium-sized and small benthivores always predominated, the proportions for the 14 guilds changed significantly between decades ($\chi^2=106.75$; Table 2). However, significant changes in abundance by guild between decades and/or zones occurred only for small benthivores ($F=5.27$: decreased by decade), medium-sized piscivores ($F=4.03$: greater in zone P than zone M in 2015-2018), and small planktivores ($F=8.00$: greater in zone P than in zones M and O in 2015-2018, mostly due to juveniles of *H. jaguana*).

Table 2. Fish guild occurrences in Chetumal Bay in 1999-2001 and 2015-2018. Figures are number of samplings.

Guild	1999-2001	2015-2018
Large benthivores	0	4
Middle-sized benthivores	63	46
Small benthivores	157	97
Medium-sized detritivores	8	1
Small detritivores	8	6
Medium-sized herbivores	1	0
Small herbivores	9	3
Medium-sized omnivores	3	2
Small omnivores	11	12
Large piscivores	1	0
Medium-sized piscivores	45	42
Small piscivores	1	6
Medium-sized planktivores	1	0
Small planktivores	63	26

208 By salinity-tolerance, the most frequent species were marine euryhaline, followed by
 209 resident estuarine, freshwater, and very few marine stenohaline, the latter only in the most saline
 210 localities of zone P. Freshwater fishes appeared not only in zone O, but also in stream mouths
 211 within zone M (not only secondary freshwater species, but also primary, i.e. *A. bacalarensis*),
 212 especially during the rainy season. The proportions did not change between decades (KS, D=0.25).
 213 Marine euryhaline species decreased between decades in zones O and M, but increased in zone P
 214 (F=9.54; Figure 4a). Estuarine species decreased in zones M and P, and increased in zone O, but, in
 215 spite of that trend, they always tended to prefer areas of greater salinity (F=2.85, p = 0.06; Figure 4b).



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217 **Figure 4.** Abundances of salinity-tolerance groups of fishes by decade and salinity area in Chetumal
 218 Bay. Abundance (CPUE) log-transformed; (a) marine euryhaline fishes; (b) estuarine resident fishes.
 219 Posthoc significant differences for (a): M:now against M, O, and P:before and P:now; P:now against
 220 O:now; (b) P vs. O and M. Abbreviations for salinity zones: O-oligohaline; M-mesohaline; P-
 221 polyhaline; “before” is 1999-2001 and “now” means 2015-2018.

222 Only two species exhibited significant differences in maximum length observed in seinings.
 223 *Strongylura notata* decreased in size between decades, from 268.9 to 181.7 mm ($F=6.15$).
 224 *Eucinostomus gula* increased ($F=8.49$), but only in zone O, from a mean maximum length of 56.4 mm
 225 in 1999-2001 to 87.3 mm in 2015-2018; by zones, only in 2015-2018, it was larger in zone O than in
 226 zone P (50.8 mm), whereas in 1999-2001 there was no spatial difference in size. Another mojarra, *E.*
 227 *argenteus*, also seemed to increase marginally in size in all zones, from 42.4 mm in 1999-2001 to 50.0
 228 mm in 2015-2018 ($F=3.6$, $p=0.07$).

229 4. Discussion

230 We expected the expansion of the Zaragoza Canal after 1999-2001 to induce changes in
 231 composition and diversity of fishes in Chetumal Bay, some of them perhaps positive (greater access
 232 of marine fishes, at least to zone P, and better development of sea grasses due to increased salinity
 233 [1]), others probably negative, not just because of the entrance of lionfish and sargasso (pers. obs.),
 234 but also due to the methods required for the expansion. The bottom of the canal is mostly bedrock,
 235 so explosives are needed to deepen it, thus putting sediment in suspension that may affect habitats
 236 in the bay itself and in the adjacent reef; moreover, widening the canal implies destroying mangrove,
 237 an important habitat for fishes within and outside the bay [22].

238 The increase in abundance between decades specific to the polyhaline zone, as well as the
 239 increase of the guilds of medium-sized piscivores and small planktivores, and the group of marine
 240 euryhaline fishes, were in line with our expectations, given the expansion of Zaragoza Canal. When
 241 an artificial channel was opened in the El Carmen-Machona coastal lagoon system in the southern
 242 Gulf of Mexico, the composition of the estuary included more marine and fewer estuarine species
 243 over the course of one decade [23].

244 Large schools of the sardine *Harengula jaguana*, a planktivore that we classified as “small”
 245 because we captured mostly juveniles, occurred in zone P in 2015-2018 apparently as often as they
 246 do in the adjacent coast, usually over seagrass meadows (pers. obs.), whereas in former decades they

247 were more abundant in zones O and M (Table 1, Appendix A). In addition, the most diverse area was
248 the oligohaline zone in 1999-2001, but the mesohaline zone in 2015-2018, also shifting dominance
249 towards the seaward opening of the system. Notwithstanding, no general change in composition or
250 diversity was apparent, and several trends that may cause concern were detected, e.g. decreases in
251 total abundance, mean local richness, and number of guilds.

252 Excessive illegal fishing outside the bay may explain the decrease in juveniles of large piscivores.
253 The negative trend for this guild exists as well in the reefs adjacent to Chetumal Bay [24]. The probable
254 shift from *E. plumieri* to *G. cinereus* may also reflect the fact that the former is preferred as a fishery
255 resource in the bay [4].

256 As for the increased size of *E. gula*, and perhaps also *E. argenteus*, especially in zone O, it could
257 be a by-product of the decline in abundance of other benthivores in that area, maybe implying less
258 competence, although this is highly speculative. In contrast, *S. notata* became smaller in length in zone
259 P, where diversity increased. Body size strongly influences trophic level and habitat use of fishes [25].

260 The changes in zone P may reflect the salinity increase in Chetumal Bay during the last decade,
261 a process that had been noted already by other workers [26]. However, the reason for this salinization
262 is not only the expansion of Zaragoza Canal: there is a general trend in the region for the dry season
263 to be longer, thus increasing evaporation and decrease freshwater input from rains (Carrillo, pers.
264 comm.). As for the lower local water temperature in the face of increasing regional heat [27], the
265 increased wind force may offer a straightforward explanation.

266 The differences in freshwater and estuarine species are harder to explain, except for the catfish
267 *A. assimilis*, which in 1996 suffered a massive mortality that was attributed to pollution and specific
268 pathogens [28]; the species seemingly has not recovered ever since. The interdecadal decrease for the
269 guild of small benthivores, many of them estuarine, especially strong in zone M, is not explainable
270 by predation, because medium-sized and large piscivores also declined; we speculate that this decline
271 can be explained, at least in zone O, by the loss of habitat due to the continued erosion of the western
272 coast of the bay, a process that has been ongoing for centuries, as attested by Classic Mayan fishery
273 structures that should have been in contact to the shore, but now are hundreds of meters away from
274 the coast (pers. obs. R.L.H.P.; [29]).

275 The artificial opening of seaward channels strongly alters benthic communities of plants and
276 invertebrates in lagoons [30], which in turn should affect herbivores and benthivores; in addition to
277 the entrance of marine organisms, in the case of Chetumal Bay even stony corals [2], one of the
278 mechanisms for this is the action of invasive lionfish preying on macroinvertebrates [31]. The
279 zooplankton can be affected as well, especially if the salinity and the trophic state of the estuary
280 change [32].

281 On the other hand, and although we did not detect any interdecadal difference in beta-diversity,
282 the increased abundance of freshwater species, even primary, in zone M, and of marine species in
283 zone O, may signal a faunistic homogenization of the bay. In fact, part of our original rationale for
284 defining these three areas was to follow approximately the isolines of 9 ups, upper salinity tolerance
285 of the primary freshwater characid *A. bacalarensis* and lower limit for juveniles of the marine
286 euryhaline snapper *L. apodus*, and 19 ups, upper bound for the secondary freshwater molly *P.*
287 *mexicana* [33], and yet, in 2015-2018, many of these species were recorded outside their preferred
288 salinity area.

289 As observed by Rahel [34], “[h]abitat and flow homogenization are major drivers of biotic
290 homogenization.” At a planetary level, biotic homogenization implies invasion by nonnative species
291 [35], a process enhanced by global warming [36]. Locally, however, impact factors, such as hurricanes,
292 can also make the fauna more homogeneous [37].

293 The expansion of the Zaragoza Canal may be ethically ambiguous. On the one hand, it is
 294 allowing the entry of invaders and may be inducing faunal homogenization, in addition to the
 295 probable loss of such important guilds as large piscivores; on the other hand, making the opening
 296 wider and deeper might have a positive role for the seasonal migratory movements of bonefish [12],
 297 barracuda [22] and other species between the Caribbean sea and the bay. Such optimism
 298 notwithstanding, if habitat destruction is not controlled, especially the flats and mangrove cays that
 299 are favorite feeding grounds for bonefish and permit, the damage would be both ecological and
 300 socioeconomical, as these species support an important fishery both in Belize and in Mexico [3].

301 **Author Contributions:** Conceptualization, J.J.S.S.; methodology, J.J.S.S. and R.L.H.P.; software, J.J.S.S.;
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314 Appendix A

315 Quantitative sampling: Fish species of Chetumal Bay by salinity zone (Oligohaline, Mesohaline,
 316 Polyhaline) and decade. Figures are mean abundances (CPUE).

Species	Zone	1999-2001	2015-2018
<i>Anchoa cayorum</i>		0.5	0.5
	O	0	0.5
	P	0.5	0
<i>Achirus lineatus</i>		68.3	13.4
	M	45.4	2.0
	O	19.0	9.7
	P	3.8	1.7
<i>Albula vulpes</i>		3.5	0
	P	3.5	0

Species			
	Zone	1999-2001	2015-2018
<i>Anchoa colonensis</i>		0.3	0
M		0.3	0
<i>Anchoa cubana</i>		19.2	10.0
M		3.0	0
O		11.7	0
P		4.5	10.0
<i>Ariopsis assimilis</i>		2.3	0
M		1.0	0
O		1.3	0
<i>Astyanax bacalarensis</i>		0	45.2
M		0	38.0
O		0	1.2
P		0	6.0
<i>Atherinomorus stipes</i>		2306.3	590.7
M		1542.2	90.8
O		167.7	0.3
P		596.5	499.5
<i>Bairdiella ronchus</i>		43.3	2.0
M		21.5	0
O		21.3	0

Species			
	Zone	1999-2001	2015-2018
	P	0.5	2
<i>Bathygobius curacao</i>		0	1.2
	M	0	1.2
<i>Bothus ocellatus</i>		0.3	0
	P	0.3	0
<i>Canthigaster rostrata</i>		0	0.3
	P	0	0.3
<i>Centropomus undecimalis</i>		1.0	0
	M	1.0	0
<i>Chriodorus atherinoides</i>		9.8	2.5
	M	8.2	0
	P	1.7	2.5
<i>Corvula sanctaeluciae</i>		0	0.7
	P	0	0.7
<i>Cyprinodon artifrons</i>		45.2	6.0
	M	1.5	0.7
	O	0	1.5
	P	43.7	3.8
<i>Diapterus auratus</i>		0	23.3
	P	0	23.3

Species			
	Zone	1999-2001	2015-2018
<i>Eucinostomus argenteus</i>		34.2	63.6
	M	9.5	3.3
	O	4.5	0.5
	P	20.2	59.8
<i>Eucinostomus gula</i>		269.8	53.8
	M	38.8	12.3
	O	9.5	5.0
	P	221.5	36.5
<i>Eucinostomus harengulus</i>		15.7	30.7
	M	3.3	11.2
	O	0.3	1.0
	P	12	18.5
<i>Eucinostomus jonesii</i>		257.5	72.8
	M	155.3	13.8
	O	45.3	34.1
	P	56.8	24.8
<i>Eucinostomus melanopterus</i>		0	1.7
	M	0	0.3
	P	0	1.3
<i>Eugerres plumieri</i>		78.4	7.8

Species			
	Zone	1999-2001	2015-2018
	M	23.6	1.0
	O	52.3	2.9
	P	2.5	3.8
<i>Floridichthys polyommus</i>		133.4	266.7
	M	78.3	34.4
	O	12.5	5.5
	P	42.7	226.8
<i>Gerres cinereus</i>		1.8	31.2
	M	1	4.3
	O	0	20.3
	P	0.8	6.5
<i>Gobiosoma yucatanum</i>		1.5	0
	O	1.5	0
<i>Gambusia sexradiata</i>		0.5	0
	O	0.5	0
<i>Gambusia yucatanana</i>		9.8	1.5
	M	8.5	1.0
	P	1.3	0.5
<i>Harengula clupeola</i>		9	30
	P	9	30

Species			
	Zone	1999-2001	2015-2018
<i>Harengula humeralis</i>		6	0.3
	P	6	0.3
<i>Harengula jaguana</i>		174.7	149.0
	M	37.3	1.0
	O	74.3	0
	P	63.0	148.0
<i>Hippocampus erectus</i>		0.3	0
	P	0.3	0
<i>Hypanus americanus</i>		0	0.3
	M	0	0.3
<i>Hyporhamphus roberti</i>		1.5	0.25
	M	0	0.25
	O	1.5	0
<i>Jenkinsia lamprotaenia</i>		2.5	0
	P	2.5	0
<i>Jordanella pulchra</i>		8.0	8.9
	M	8.0	2.0
	O	0	6.25
	P	0	0.7
<i>Lophogobius cyprinoides</i>		13.8	2.8

Species			
	Zone	1999-2001	2015-2018
	M	7.3	0
	O	6.5	2.8
<i>Lutjanus griseus</i>		0	13.3
	P	0	13.3
<i>Mayaheros urophthalmus</i>		4.2	1.5
	M	4.2	0
	O	0	1.5
<i>Monacanthus tuckeri</i>		0	0.3
	M	0	0.3
<i>Oligoplites saurus</i>		1.2	0.3
	M	0.7	0
	P	0.5	0.3
<i>Oostethus lineatus</i>		0	0.3
	M	0	0.3
<i>Opisthonema oglinum</i>		9.8	0
	O	5	0
	P	4.8	0
<i>Opsanus beta</i>		1.7	0
	O	1.7	0
<i>Paraclinus fasciatus</i>		0.5	0

Species			
	Zone	1999-2001	2015-2018
	O	0.5	0
<i>Poecilia mexicana</i>		20.2	0.4
	M	19.2	0
	O	2.0	0.4
<i>Sphoeroides testudineus</i>		36.0	47.8
	M	6.0	27.4
	O	25.2	11.7
	P	4.8	8.7
<i>Sphyaena barracuda</i>		24.8	12.0
	M	8.8	4.6
	O	5.2	3.5
	P	10.8	4.0
<i>Strongylura marina</i>		0.5	0
	P	0.5	0
<i>Strongylura notata</i>		51.9	150.5
	M	25.3	27.2
	O	5.8	1.5
	P	20.8	121.8
<i>Strongylura timucu</i>		1.5	0
	M	1.5	0

Species	Zone	1999-2001	2015-2018
<i>Syngnathus floridae</i>		0.25	0
M		0.25	0
<i>Syngnathus scovelli</i>		0.5	0
O		0.5	0
<i>Trachinotus falcatus</i>		0	1.2
M		0	0.3
O		0	0.5
P		0	0.3
<i>Trichromis salvini</i>		0	3.5
O		0	3.5
<i>Vieja melanurus</i>		2.0	0
O		2.0	0

317 Appendix B

318 Qualitative records: Fish species of Chetumal Bay by salinity zone (Oligohaline, Mesohaline,
 319 Polyhaline) and decade (2005 and *Before*, vs. 2006 up to *Now*). Voucher numbers (at ECO-CH, or else
 320 acronym given for other fish collections) or literature sources (in *italics*) given, when the species was
 321 not recorded in this study. Records not assignable with precision to one of the three salinity zones,
 322 or known only from ichthyoplankton, not considered.

Species	Before			Now		
	O	M	P	O	M	P
<i>Acanthurus bahianus</i>			4222			
<i>Achirus lineatus</i>	X	X	X	X	X	X
<i>Aetobatus narinari</i>			pers. obs.			

Species	Before			Now		
	O	M	P	O	M	P
<i>Albula vulpes</i>	4221		X		[12]	[12]
<i>Anchoa cayorum</i>			X	X		
<i>A. colonensis</i>		X				
<i>A. cubana</i>	X	X	X			X
<i>Archosargus probatocephalus</i>	4219					
<i>A. rhomboidalis</i>	4217					
<i>Ariopsis assimilis</i>	X	X	4261			
<i>Astyanax bacalarensis</i>	7815	1301		X	X	X
<i>Atherinomorus stipes</i>	X	X	X	X	X	X
<i>Bagre marinus</i>		3143				
<i>Bairdiella ronchus</i>	X	X	X			X
<i>Bathygobius curacao</i>					X	
<i>Bothus ocellatus</i>			X			
<i>Canthigaster rostrata</i>						X
<i>Caranx latus</i>	4214				X	
<i>Centropomus undecimalis</i>	4216	X				
<i>Chaetodipterus faber</i>		4213				
<i>Chilomycterus schopfi</i>		4047				
<i>Chriodorus atherinoides</i>		X	X	8020		X
<i>Conodon nobilis</i>				CNPE 3221		

Species	Before			Now		
	O	M	P	O	M	P
<i>Coroula sanctaeluciae</i>		1703				X
<i>Cribroheros robertsoni</i>	X					
<i>Cyprinodon artifrons</i>	X		X	X	X	X
<i>D. guttata</i>		4194				
<i>Diapterus auratus</i>						X
<i>Echeneis neucratoides</i>		2785	X			
<i>Elops saurus</i>			[38]			
<i>Epinephelus itajara</i>		pers. obs.	pers. obs.			
<i>Eucinostomus argenteus</i>	X	X	X	X	X	X
<i>E. gula</i>	X	X	X	X	X	X
<i>E. harengulus</i>	X	X	X	X	X	X
<i>E. jonesii</i>	X	X	X	X	X	X
<i>E. melanopterus</i>					X	X
<i>Eugerres plumieri</i>	X	X	X	X	X	X
<i>Floridichthys polyommus</i>	X	X	X	X	X	X
<i>Gambusia sexradiata</i>	X					
<i>G. yucatanana</i>		X	X		X	X
<i>Gerres cinereus</i>		X	X	X	X	X
<i>Gobiosoma yucatanum</i>	X					
<i>Gymnothorax funebris</i>						pers. obs.

Species	Before			Now		
	O	M	P	O	M	P
<i>Haemulon sciurus</i>			pers. obs.			
<i>Harengula clupeiola</i>		2061	X			X
<i>H. humeralis</i>			X	7806		X
<i>H. jaguana</i>	X	X	X		X	X
<i>Hippocampus erectus</i>			X			
<i>Holocentrus rufus</i>		4224				
<i>Hypanus americanus</i>					X	
<i>Hyporhamphus roberti</i>	X				X	
<i>Jenkinsia lamprotaenia</i>			X			
<i>Jordanella pulchra</i>		X		X	X	X
<i>Kyphosus incisor</i>						pers. obs.
<i>Lachnolaimus maximus</i>						pers. obs.
<i>Lobotes surinamensis</i>	4218					
<i>Lophogobius cyprinoides</i>	X	X		X		
<i>Lupinoblennius vinctus</i>	4134					
<i>Lutjanus analis</i>			[38]			
<i>L. apodus</i>			4236			
<i>L. cyanopterus</i>			pers. obs.			
<i>L. griseus</i>			4384			X
<i>L. jocu</i>						[39]

Species	Before			Now		
	O	M	P	O	M	P
<i>L. mahogoni</i>			pers. obs.			
<i>L. synagris</i>			X			
<i>Mayaheros urophthalmus</i>	X	X		X		
<i>Megalops atlanticus</i>		3139				4381
<i>Monacanthus tuckeri</i>					7838	
<i>Mugil cephalus</i>		pers. obs.				
<i>Narcine brasiliensis</i>						pers. obs.
<i>Ocyurus chrysurus</i>						[39]
<i>Oligoplites saurus</i>		X	X			X
<i>Oostethus lineatus</i>					X	
<i>Opisthonema oglinum</i>	X		X			
<i>Opsanus beta</i>	X					
<i>Paraclinus fasciatus</i>	X	3169				
<i>Poecilia kykesis</i>		1246				
<i>P. mexicana</i>	X	X		X		
<i>Pristis</i> sp.	pers. obs.		pers. obs.			
<i>Pterois volitans</i>						pers. obs.
<i>Scomberomorus maculatus</i>		4768			pers. obs.	
<i>Selene vomer</i>		4215				
<i>Sparisoma viride</i>		pers. obs.				

Species	Before			Now		
	O	M	P	O	M	P
<i>Sphoeroides testudineus</i>	X	X	X	X	X	X
<i>Sphyraena barracuda</i>	X	X	X	X	X	X
<i>Strongylura marina</i>			X			
<i>S. notata</i>	X	X	X	X	X	X
<i>S. timucu</i>	5063	X		8025		
<i>Styracura schmardae</i>			3799			
<i>Symphurus diomedeanus</i>	4137					
<i>Syngnathus floridae</i>		X				
<i>S. scovelli</i>	X					
<i>Trachinotus falcatus</i>				X	X	X
<i>Trichromis salvini</i>				X		
<i>Vieja melanurus</i>	X	4302				

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