

1 Complex reef architecture supports more small-bodied fishes and longer food chains on
2 Caribbean reefs

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1 **Abstract:** Coral community shifts towards reefs dominated by stress-resistant corals have
2 contributed to rapid declines in the architectural complexity of reefs throughout the
3 Caribbean. Complex reef architecture provides important niches and refuges for many reef
4 fishes and thus widespread declines in reef complexity could have important consequences
5 for the structure and function of fish assemblages. We explore the influence of reef
6 architecture on fish assemblages by comparing the size and trophic structure of reef fishes
7 along a 20 km-long 15-reef gradient of coral cover, coral species dominance and architectural
8 complexity in Cozumel, Mexico. Our results show that reefs with high architectural
9 complexity, in particular those dominated by robust *Montastraea* corals, supported fish
10 assemblages with larger numbers of individuals in the smallest size classes (< 20 cm) and
11 longer food chains (higher mean trophic levels). The association between coral complexity
12 and fish communities is highly size-structured and is greatest for smallest size classes. The
13 greater abundance of both small fish and the key early life stages of larger fishes on more
14 complex reefs suggests that architectural complexity may influence entire reef fish
15 assemblages, even though larger fish are less dependent on reef complexity. Key reef-
16 building corals such as *Montastraea* are thus likely to be disproportionately important for
17 maintaining reef fish communities, and shifts in Caribbean coral communities may
18 compromise fish recruitment and truncate food chains, reducing resilience and inhibiting reef
19 recovery from degradation.

20

21 **Keywords:** bottleneck, food web, foundation species, habitat complexity, rugosity, size
22 spectra

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1 INTRODUCTION

2 Habitat architecture is known to profoundly influence the abundance and diversity of
3 species through the provision of niches and diverse ways of exploiting environmental
4 resources (e.g. MacArthur and MacArthur 1961, Tews et al. 2004). In many ecosystems, the
5 architecture of the habitat is defined by the abundance and morphological attributes of certain
6 foundation species. Many of these species, such as numerous overstorey trees, reef-building
7 corals and kelp, have experienced or are experiencing widespread declines (Steneck et al.
8 2002, Gardner et al. 2003, Ellison et al. 2005). These declines commonly result in dominance
9 shifts towards more stress-resistant species that often have rapid growth rates and are likely to
10 provide fewer structural benefits (Ellison et al. 2005, Steneck et al. 2009). Understanding the
11 influence of changes in the relative abundance of different foundation species on associated
12 biodiversity can therefore provide valuable insights into the potential consequences of
13 changing habitat structure resulting from environmental disturbances.

14 In tropical coral reef ecosystems, the architectural complexity of coral species is
15 important for providing a wide variety of refuge spaces, such as crevices, holes and branches,
16 which can influence the diversity and structure of reef-associated communities (Bell and
17 Galzin 1984, Jones and Syms 1998). For instance, at small spatial scales (< 1 km), the
18 recruitment of fish larvae depends in part on the availability of suitable refuges, and the post-
19 settlement movements of fish recruits are largely influenced by the availability of
20 microhabitat structures (Jones 1991, Tolimieri 1995, Caley and John 1996, Caselle and
21 Warner 1996, Schmitt and Holbrook 1999, Johnson 2007). In juvenile and adult fishes, levels
22 of competition and predation can also be influenced by the complexity of reef habitats, as
23 more complex habitats may reduce competition by providing a greater spectrum of resources,
24 and reduce predation by providing more prey refuges and/or reducing encounter rates

1 between predators and prey (Holbrook and Schmitt 1988, Hixon and Beets 1993, Almany
2 2003, 2004).

3 Currently, coral reefs are changing very rapidly, particularly in the Caribbean where
4 structurally complex reefs are becoming increasingly scarce, at least partly as a consequence
5 of the loss of key reef-building, morphologically-complex corals (Alvarez-Filip et al. 2009a,
6 2011a, b). Such rapid declines in reef complexity are thought to have severe consequences for
7 biodiversity and associated environmental services. The consequences for coral reef fishes
8 are of particular concern because reef fisheries are extremely valuable and are an important
9 source of protein and livelihood for many vulnerable coastal human communities (Newton et
10 al. 2007, Allison et al. 2009). Declines in reef architectural complexity may therefore result in
11 reductions in overall species richness, particularly of reef specialists, with potential long-term
12 consequences for large-bodied species (Beukers and Jones 1997, Graham *et al.* 2007). The
13 implications of habitat-driven changes in fish assemblages are only just beginning to be
14 understood. However, it is likely that the loss of some services generated by fish populations
15 can have negative consequences for ecosystem functioning and human societies. For
16 example, the reduction of large-bodied is likely to reduce the yield of local fisheries (Graham
17 *et al.* 2007). The loss of key functional groups (e.g. herbivorous) may also be manifested in
18 the reduction of resilience on coral reefs (Mumby *et al.* 2009).

19 As different species of coral vary in their vulnerability to environmental perturbations,
20 the variety of natural and human disturbances can greatly impact the relative abundance of
21 key coral species, potentially resulting in a differential loss of specific microhabitats. For
22 example, in the Caribbean, rapid declines in live coral cover have been accompanied by a
23 shift in communities towards reefs dominated by stress-resistant and less architecturally
24 complex corals (e.g. Hughes 1994, Green et al. 2008). In this region, mid-water reefs are now
25 dominated by stress-resistant corals such as *Porites* and *Agaricia* which provide consistently

1 less architectural-complex reefs in comparison to *Montastraea*-dominated sites (Alvarez-Filip
2 et al. 2011b). These shifts in coral community composition can potentially have severe
3 consequences for associated reef fishes; hence there is a pressing need to understand the
4 response of fish communities to the changes in coral community composition and associated
5 loss of reef complexity.

6 Here we test whether more structurally-complex coral reefs support greater
7 abundances or diversity of fish along a 15-reef gradient of architectural complexity in
8 Cozumel, Mexico. As the architectural complexity of reef-building corals may be especially
9 important for small-bodied fishes, including recruits and juveniles from larger species that
10 rely directly on reef microhabitat features to settle and feed, we explore these relationships
11 using both size-based and trophic-guild perspectives.

13 **METHODS**

15 *Field surveys*

16 Cozumel is a continental island located 22 km off the east coast of the Yucatán
17 Peninsula in the North-Western Caribbean. The island is approximately 46 km long on the
18 north-south axis and 16 km wide (Fig. 1). Cozumel is surrounded by coral reefs, the most
19 developed of which are on the western side of the island and primarily comprise shelf-edge
20 reefs (mostly in the southwestern area), which typically have a complex framework formed
21 by calcareous formations of several meters height, and barrier reefs, mostly in the central part
22 of the island, which are less well-developed. Unlike many other Caribbean reefs that were
23 originally primarily comprised of Acroporid species, Cozumel reefs have been built mainly
24 by *Montastraea* (Muckelbauer 1990). The southwestern coast of Cozumel has been under

official protection since 1980 (Alvarez-Filip *et al.* 2009b; Fig. 1), and while visitation and tourist activities are permitted, fishing is banned on the western coast of the marine reserve.

Description of fish assemblages and reef structure

Benthic composition, architectural complexity and reef fish assemblages were surveyed in 15 mid-depth reefs (10-15 m) within Cozumel's protected area between October 2007 and February 2008 (Fig. 1). The surveyed area in each reef (i.e. transects and the area between them) covered ca. 2000 m², and the 15 reefs sites were all at least 500 m apart. Between three and eight 30 x 5 m transects (150 m²; number of transects per reef is given in Fig. 2) were surveyed on each reef, within the constraints due to logistics and weather conditions during the time available for study. In each transect, a plastic tape measure was unrolled as the diver moved forward, identifying all the conspicuous fishes that crossed the transect line. Individuals were counted in an instantaneous manner to minimise double-counting and inflated density estimates (Ward-Paige *et al.* 2010). The fork length of each fish was estimated within 10 cm categories (≤ 10 , 10 – 20, 20 – 30, 30 – 40, 40 – 50 cm), which is well within the precision possible with minimal training (Darwall and Dulvy 1996; Dulvy *et al.* 2004). The surveyor was previously trained in fish identification and size estimation, and has carried out similar surveys in the study area for several years. Count time was not standardized because this was dependent on fish abundance, diversity and subsequent habitat measures. All transects were haphazardly located within the reefs and surveyed between 09:00 and 15:00 h by the same observer.

Benthic community structure was characterized using the point intercept method (Loya 1972) in each 30 m transect once the fish census was complete. The percentage cover of each benthic component (live coral species, soft coral, turf algae, macroalgae, sponges, bare rock and sand) was identified every 25 cm, resulting in 120 estimates per 30 m transect.

1 Architectural complexity was measured with two complementary methodologies: a
2 chain measure of local reef-relief and a larger-scale visual categorical estimate. For the small
3 scale we used the rugosity index, which is the ratio of a length of chain moulded to the reef
4 surface to the linear distance between its start and end point (Risk 1972). A perfectly flat
5 surface would have a rugosity index of one, with larger numbers indicating more complex
6 surfaces. A three-meter chain (0.7 cm link-length) was used to estimate reef rugosity five
7 times evenly distributed along each 30 m transect, and the average was calculated as a
8 measure of transect-level rugosity. The reefscape-scale visual assessment of architectural
9 complexity consists of assigning the area surrounding each transect a score from 0 (flat
10 surface) to 5 (exceptionally complex reef with numerous caves and overhangs) (Wilson et al.
11 2007).

12

13 *Description of fish assemblages*

14 Fish assemblages were characterized using three univariate metrics that describe the overall
15 fish community (total number of species, total number of individuals and total biomass) and
16 four metrics that describe food-web structure (mean trophic level, trophic guilds and the slope
17 and intercept of the size spectra). Although aggregating data has the disadvantage of
18 overlooking species-specific responses, these metrics were selected as our aim was to identify
19 community-wide functional effects of reef structure on energy flow and foodweb structure.
20 The three community metrics were calculated at the transect level and then averaged across
21 transects to produce reef-level fish community metrics. Total fish biomass was calculated by
22 converting the estimates of fish length to weight using species-specific length-weight
23 conversions (Froese and Pauly 2009).

24 Mean trophic level was used as a proxy of the food chain length, and was calculated
25 for each reef by averaging the trophic level (obtained from Fishbase; Froese and Pauly 2009)

1 of each individual recorded on all transects within each reef. Although, in theory, food chain
2 length could be measured as the trophic level of the largest apex predator, this is difficult to
3 estimate in practice because such ‘asymptotic’ values are highly sensitive to census effort.
4 However, as the combination of the efficiency of energy transfer between trophic levels and
5 size spacing between trophic levels (predator-prey mass ratio) tend to be constant across
6 marine ecosystems (Barnes et al. 2010), it is expected that the mean trophic level of the
7 community will be highly correlated to the maximum trophic level. As mean trophic levels
8 were calculated consistently across reefs, this metric allows comparison of relative
9 differences in food chain length among reefs. In addition to the mean trophic level, fishes
10 were also grouped into six major trophic guilds (planktivores, herbivores, omnivores,
11 invertivores, carnivores and piscivores) following Paddack et al. (2009); these guilds
12 represent important differences in behavioral, functional and ecological responses to habitat
13 variation.

14 In aquatic environments, organismal function varies more with the size of individuals
15 rather than the identity of species, particularly for fishes that grow by several orders of
16 magnitude during their life (Jennings 2005). Ontogenetic size change has profound ecological
17 implications, because most life history and ecological characteristics, such as growth
18 schedules, age at maturity, lifespan, reproductive output, density-dependence in juvenile
19 survival and relative prey sizes are related to body size in marine fishes (Jennings et al. 1999,
20 Denney et al. 2002, Barnes et al. 2010). The size-frequency distribution (size spectrum) of
21 fish captures the size distribution of energy in the ecosystem and describes the flow and
22 depreciation of energy toward larger individuals and species. The size spectrum represents, in
23 effect, the total amount of energy in the ecosystem with the intercept reflecting the overall
24 productivity or energy entering the community (Jennings 2005, Jennings et al. 2008, Wilson
25 et al. 2010) and the slope representing the flow and depreciation of energy across fish size

1 classes (Boudreau and Dickie 1992, Kerr and Dickie 2001, Jennings 2005). The size
2 spectrum of the fish community on each reef was calculated by summing the total number of
3 individuals in each of the five 10 cm length categories, up to 50 cm. Individuals larger than
4 50 cm were very rare ($n = 3$) and therefore were excluded from the analyses. The fish size
5 spectrum was then described by the slope and intercept of a linear regression of this size
6 frequency distribution (Dulvy et al. 2004). Body length data were $\log_{10}(x + 1)$ transformed
7 before analysis, and the midpoint of size classes was rescaled to zero to remove the
8 correlation between slope and intercept (Daan et al. 2005). Steeper slopes indicate an increase
9 in the relative abundance of small fish (a combination of recent recruits of larger bodied
10 species and larger size classes of small species), a decrease in large fish abundance, or both,
11 and this in turn can be disentangled by examining the relative contribution of each size class
12 along the environmental or impact gradient (Dulvy et al. 2004).

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14

15 *Data analyses*

16

17 Benthic data were averaged within transects and then within individual reefs, and the
18 average percentages of cover of the benthic components were arcsine square root
19 transformed. Exploratory analyses revealed strong positive covariation between the
20 percentage cover of coral and both measures of architectural complexity (chain and visual
21 estimation methods; table 1) across the 15 reefs. Hence, we calculated a combined index of
22 “coral cover-complexity” from the first axis of a principal component analysis of these three
23 variables. This first PCA axis explained 99.6% of the variance and comprised coral cover
24 (coefficient = 0.11), chain rugosity (coefficient = 0.23) and the visual estimation of habitat

1 complexity (coefficient = 0.97), such that positive PCA1 scores reflect high coral cover and
2 high architectural complexity and the converse for negative scores.

3 The influence of different components of reef structure and benthic community on all
4 fish assemblage metrics were first explored with hierarchical partitioning analysis (Mac Nally
5 2000, 2002). The metrics that were identified from these analyses as responding to variation
6 in reef structure were then included in analyses (also using hierarchical partitioning) of the
7 influence of different dominant coral types on the structure of fish assemblages. We restricted
8 this second analysis to four categories: the three most dominant coral genera in Cozumel,
9 *Montastraea*, *Agaricia* and *Porites*, and one category including all the other remaining coral
10 genera. Previously, it has been shown that these coral genera differ in colony and size
11 structure, and hence differ in their contribution to reef complexity, with the large and massive
12 nature of *Montastraea* corals disproportionately increasing reef complexity (Alvarez-Filip et
13 al. 2011b). Species from the genera *Agaricia* and *Porites* have variable morphologies (e.g.
14 encrusting, branching). However, the most architecturally complex species of the both genera
15 (*Porites porites* complex and *Agaricia tenuifolia*) had relative low cover during our study
16 period. These two genera are therefore represented mainly by small encrusting and massive
17 species (Alvarez-Filip et al. 2011b).

18 Hierarchical partitioning is a multiple-regression technique that calculates goodness
19 of fit measures for all possible combinations of independent variables in linear models, in
20 order to calculate the average contribution of each predictor (Chevan and Sutherland 1991,
21 Mac Nally 2000). Hierarchical partitioning provides both the independent and the joint
22 effects of each predictor, with independent values representing the explanatory power
23 associated with a single predictor and joint values representing the explanatory power of the
24 parameter of interest in combination with other variables (Mac Nally 2002). In some
25 situations, significant independent effects can be suppressed by antagonistic joint effects, in

1 which case hierarchical partitioning technique converts antagonistic effects into negative joint
2 contributions, effectively unmasking the independent contributions (Chevan and Sutherland
3 1991). Independent effects of the explanatory benthic variables on the fish assemblages were
4 tested with 1000 permutations of the data matrix and significance was evaluated at the 5%
5 level (Mac Nally 2002). We used hierarchical partitioning rather than traditional multiple
6 regressions or other multivariate analysis, because this method deals well with
7 multicollinearity of predictor variables (Mac Nally 2000, 2002). We conducted hierarchical
8 partitioning within R using the *hier.part* package (R Development Core Team. 2011; Walsh
9 and Mac Nally 2008). Hierarchical partitioning does not calculate the direction of the effects
10 of the explanatory variables, so these were derived from Pearson correlations.

11

12 **RESULTS**

13

14 *Fish and habitat description*

15 In Cozumel there was a gradient of increasing coral cover from the north to the south of the
16 island (Fig. 2), and the reefs are largely dominated by *Agaricia*, *Montastraea* and *Porites*,
17 although the surface cover of these genera varied considerably between reef sites with the
18 northernmost and southernmost reefs having a particularly high relative cover of *Montastraea*
19 species (Fig. 2). The major reef-building corals of the genus *Acropora* accounted only for
20 1.1% of the total cover of scleractinian corals in Cozumel.

21 A total of 10,965 individuals from 93 species of fish were recorded across the 15 reefs
22 (appendix 1). The most common fishes were those that mainly feed on plankton and algae
23 (appendix 1, Fig. 2), and there was a clear trend of decreasing abundance with body size; the
24 smallest individuals (< 10 cm) represented 48.1 % of the total abundance while larger
25 individuals (> 40 cm) accounted for only 0.7 % of total abundance.

1

2 *Influence of benthic components on fish assemblages*

3 Fish species richness and total fish abundance were both positively (but not
4 significantly) associated with cover-complexity and negatively associated with the percentage
5 cover of bare rock and sand (Fig. 3), and total fish biomass was unrelated to any of the
6 benthic community components or structure (Fig. 3). However, much stronger links were
7 apparent between reef structure and the trophic and size structure of fish assemblages. The
8 food chain length (as indexed by mean trophic level) and the size spectra slope and intercept
9 of fish communities were significantly related to increasing cover complexity but not to any
10 of the other benthic components (Fig. 3). The intercept of the fish size spectra increased and
11 the slope of the size spectra decreased with increasing cover-complexity (Fig. 3). While mean
12 trophic level and size spectra slope were related only to cover-complexity, the size spectra
13 intercept was also influenced by a joint contribution from different benthic components (Fig.
14 3), suggesting that, while the overall productivity of fish communities is influenced by
15 several different benthic components, the food chain length is mainly driven by ‘coral cover-
16 complexity’.

17

18 *Influence of coral identity on size and trophic structure of fish assemblages*

19 The abundance of the two smallest fish size classes (< 20 cm) was significantly
20 greater on reefs with greater cover of *Montastraea*, whereas other coral genera had no
21 significant effect on the abundance of fishes from any size categories (Fig. 4). The positive
22 relationship between the abundance of small fishes and scleractinian corals suggests that the
23 pattern indicated by the size spectra analyses (i.e. higher intercept and steeper slope on reefs
24 with greater coral cover-complexity; Fig. 3) is likely to result from greater densities of the
25 smallest size class (<10 cm) on complex reefs. The association between fishes and coral

1 cover and complexity was highly size-dependent. Initially the smallest fishes (< 10 cm)
2 appear to be most dependent on the presence of the most architecturally-complex corals (i.e.
3 *Montastraea*), and this relationship decays for increasingly larger size classes, suggesting a
4 strong ontogenetic detachment from scleractinian corals. Fishes in the second size-category
5 (10 to 20 cm) were also more abundant in the presence of *Montastraea*, but the presence of
6 other types of corals also appear to influence their abundance, given the considerable positive
7 contribution of the joint effects to the variation in abundance of this size-class. Although
8 abundance of fish in size classes greater than 20 cm were not significantly related to the cover
9 of any coral genera, those in size classes 20 – 30 and 30 – 40 cm tend to be positively
10 associated with the cover of all coral genera while the largest fish (40 – 50 cm) tend to be
11 negatively associated with coral cover (Fig. 4).

12 Although recruit and juvenile phases were not distinguished from adult phase in our
13 surveys, our results suggest that *Montastraea* corals may indeed favor the presence of the
14 early-stages (recruits) of larger species of fishes. While the number of small fish species
15 (maximum fork length, $L_{\max} < 20$ cm) was not significantly correlated with the cover of
16 *Montastraea* corals (Size class <10 cm: $r = -0.36$, $P = 0.18$; Size class 10-20 cm: $r = 0.45$, P
17 $= 0.09$), small individuals of species with larger maximum body size ($L_{\max} > 20$ cm) were
18 significantly more abundant on sites with greater cover of *Montastraea* (Size class <10 cm: r
19 $= 0.56$, $P = 0.03$; Size class 10-20 cm: $r = 0.66$, $P < 0.01$).

20 The abundance of carnivores, omnivores and herbivores all increased significantly
21 with increasing cover of *Montastraea* corals (Fig. 5) but the cover of *Porites*, *Agaricia* or
22 other coral species did not significantly influence the abundance of fish species of any trophic
23 group.

24

25 **DISCUSSION**

1 The identity, cover and complexity of coral reefs have profound implications for the
2 fundamental processes structuring coral reef fish communities. Here, we show that coral
3 cover and reef architectural complexity positively influence the abundance of small fishes
4 and presumably the food chain length and energy flow through the unfished Caribbean fish
5 assemblages of Cozumel, Mexico. Across reefs varying greatly in coral species composition,
6 coral cover and complexity, greater abundances of small-bodied reef-associated fishes are
7 supported on 'healthier' more architecturally-complex reefs, in particular those dominated by
8 robust *Montastraea* corals. However, the community-wide dependence of fishes upon
9 complex reef structures declines for larger-bodied fish size classes. This suggests that
10 complex reef structures are most important for maintaining reef fish communities mainly by
11 facilitating the presence of key early-life stage individuals and small-bodied fishes that are in
12 turn preyed upon by larger fishes (Caley and John 1996, Beukers and Jones 1997).

13 In contrast to size-based analyses, the variation in species richness, abundance and
14 biomass across reef sites was weakly and non-significantly explained by 'coral cover-
15 complexity' and other benthic components. One possible explanation for this is that the
16 spread and quantity of data was insufficient to detect such sample-size-dependent
17 relationships (see also Jennings *et al* 2001; Dulvy *et al* 2008). In this context, our analyses
18 suggest that an aggregated size-based food web view of coral reef ecology may have more
19 power to detect variation in fish communities, and therefore provide more insights into coral
20 reef community structure, function and energy flow than the classical terrestrial species-based
21 functional perspective.

22 The positive influence of 'coral cover-complexity', and particularly of the genus
23 *Montastraea*, on reef fishes is most evident in small-bodied individuals and probably at small
24 spatial scales. This suggests that the complexity provided by reef-building corals is an
25 important mediator of the energy entering the reef system and the productivity of the reef-fish

1 community. These results are consistent with experimental and observational analyses
2 showing that, at small spatial scales (< 1 km), the recruitment of fish larvae depends in part
3 on the availability of suitable refuges, and the post-settlement movements of fish recruits are
4 largely related to the availability of microhabitat structures (Jones 1991, Tolimieri 1995,
5 Caselle and Warner 1996, Schmitt and Holbrook 1999, Johnson 2007). The steepness of the
6 size spectra on more complex reefs has been attributed to the depleted abundances of apex
7 predators. For example, fishing can change the size distribution of fish communities by
8 directly reducing the number of large-bodied fishes that in consequence will result in prey
9 release (Dulvy et al. 2004, Graham et al. 2005, Wilson et al. 2010). However, Cozumel reefs
10 have been under protection for 30 years (Alvarez-Filip et al. 2009b), and have relatively high
11 abundances of apex predators (relative to other Caribbean reefs; Knowlton and Jackson
12 2008). Therefore the steepening of the slope in the size-spectrum, in combination with the
13 elevated intercept, is likely to result from a stronger association of small-bodied fishes with
14 ‘coral cover – complexity’ rather than an effect of fisheries exploitation of larger fish.

15 The dependence of reef fishes on complex reef structures declines gradually with
16 increasing body length, which suggests an increase in home range size of larger-bodied
17 species and individuals, and the inevitable increasing use of adjacent reef-associated habitats.
18 This observation coincides with the general theory that home range size scales positively with
19 body size, and the degree of exclusivity of habitat use declines with increasing body size due
20 to the metabolic scaling of energy acquisition (Jetz et al. 2004). Small-bodied fishes are
21 strongly related to coral complexity, and particularly to cover of *Montastraea*, probably
22 because coral colonies from this genus develop many holes and crevices that may function as
23 shelter for small fishes. For example, these corals are known to attract high numbers of
24 damselfishes of the genus *Stegastes* that commonly recruit and ‘garden’ algae in these corals
25 (Precht et al. 2010). Indeed, the small-scale pre-and-post settlement processes of reef-fishes

1 are more likely to be explained by the presence of *Montastraea* than by other corals such as
2 those from the genus *Porites*, likely due to the more suitable microhabitat characteristics
3 provided by *Montastraea* (Tolimieri 1995). Our results are also consistent with previous
4 studies showing that, at patch scales, *Montastraea*-dominated reefs are the most species-rich
5 habitats on Caribbean reefs and have the greatest intra-habitat variability (Harborne et al.
6 2008). The abundance of fish of body lengths 10 - 30 cm seem to be influenced by the overall
7 cover of reef-building corals, not just *Montastraea* corals. This may be a consequence of
8 increases in the home range size with increasing body size, as larger Caribbean reef fishes
9 tend to also increase in mobility (Kramer and Chapman 1999), and are therefore less likely to
10 be associated with specific attributes of individual coral colonies. The reduction in
11 dependence on reef complexity of large-bodied fishes suggests that factors such as the
12 availability of prey (Hixon and Beets 1993) and/or reef conditions at larger scales (e.g. the
13 effect of protection at Marine Reserve scales; Kramer and Chapman 1999) or connectivity to
14 adjacent habitats (Mumby et al. 2004; Harborne et al. 2008) may be stronger influences on
15 the abundance of these adult fishes.

16 The increase in mean trophic level with ‘coral cover – complexity’, in addition to the
17 strong and positive influence of *Montastraea* on higher-trophic level (especially carnivorous)
18 fish, suggests that reefs with greater architectural complexity support longer food chains with
19 more predator-dominated fish communities compared to flatter reefs with lower coral cover.
20 The ratio of the abundance of high-trophic guilds (carnivores and piscivores) to low-trophic
21 guilds (herbivores and planktivores) is indeed significantly correlated to ‘coral cover –
22 complexity’ ($r = -0.50$; $P = 0.03$) indicating that relatively flat reefs are largely dominated by
23 low-trophic level fish. However, we caution that the species-based trophic levels used here do
24 not take account of ontogenetic diet shifts, and do not entirely describe trophic relationships
25 (e.g. some small-bodied zooplanktivores fishes can have a trophic categorization similar to

1 some large predators; Froese and Pauly 2009). A more definitive test of our findings would
2 require individual-level estimates of trophic level using stable isotopes.

3 The cover of *Montastraea* corals also appears to positively influence the abundance
4 of fishes of lower trophic guilds such as omnivores and herbivores. The omnivorous fishes
5 recorded in this study are commonly recognized as reef-dependent species that feed on reef
6 benthic flora and fauna (appendix 1; Froese and Pauly 2009). The greater number of refuges
7 for small invertebrates and benthic algae provided by the massive structures of *Montastraea*
8 may therefore support a greater number of food items for these fishes (e.g. Idjadi and
9 Edmunds 2006). The relationship between herbivorous fishes and *Montastraea* cover is more
10 complex; the complex structures and ramets of *Montastraea* may support greater algal
11 diversity and biomass (Mumby et al. 2005, Piñón-Gimate and Collado-Vides 2008), and thus
12 be attractive to herbivorous fishes. In addition, some herbivorous fish such as *Sparisoma*
13 *viridie* and *Stegastes planiformis* are common grazers of *Montastraea* colonies (Mumby 2009,
14 Precht et al. 2010) and may therefore also be attracted by the live tissue of these corals.

15 The ongoing decline in reef architectural complexity throughout the Caribbean may
16 have profound effects on fish communities (Alvarez-Filip et al. 2009a, Paddack et al. 2009).
17 In particular, our findings suggest that recent declines in the overall density of fish
18 communities (Paddack et al. 2009) may be in part a consequence of ongoing declines in the
19 cover of *Montastraea* in reefs through the entire region (Hughes and Tanner 2000, Bruckner
20 and Bruckner 2006, Steneck et al. 2009). Our study suggests that changes in the abundance of
21 *Montastraea* populations could have significant and direct detrimental effects on the
22 abundance of small-bodied fish, with subsequent impacts on the abundance of adult fishes
23 through failures in recruitment and reductions on the transfer of energy through the food web
24 (Graham et al. 2005, Graham et al. 2007, Wilson et al. 2010). This may result in bottlenecks
25 limiting the flow of energy and production of fish assemblages and fisheries yields.

1 *Montastraea* historically ranked in importance with *Acropora palmata* and *A.*
2 *cervicornis* in overall contribution to Western Atlantic reef structure (Jackson 1992).
3 Acroporids have now almost vanished from Caribbean reefs and important functional
4 attributes have been lost with the demise of these highly complex coral structures. Both
5 acroporid species are now listed as *Critically Endangered* by the International Union for the
6 Conservation of Nature (Bruckner 2003, Aronson and Precht 2006). More recent declines in
7 the abundance of *Montastraea* populations and increases in the relative abundance of stress-
8 resistant coral species are further compromising the capacity of reefs to provide habitat for
9 reef-associated biodiversity (Green et al. 2008, Steneck et al. 2009, Alvarez-Filip et al.
10 2011b). Our findings indicate that these recent changes in coral composition on Caribbean
11 reefs may result in very little high quality recruitment habitat for fish species. The importance
12 of these fish populations in sustaining thousands of livelihoods across the region highlights
13 the urgent need to identify and implement means of preserving and improving reef habitat
14 quality throughout the Caribbean.

15

16 **Acknowledgements**

17 Field work was carried out with the permission and support of the Parque Nacional Arrecifes
18 de Cozumel (PNAC) and the Comisión Nacional de Áreas Naturales Protegidas of México. In
19 particular we are grateful to R. Hernandez-Landa, M. Millet-Encalada, and A. Brito-
20 Bermudez who helped with data collection. This research was funded by the Mexican
21 Council for Science and Technology (CONACYT) and the Mexican Secretary of Public
22 Education (SEP) scholarships to L.A-F. NKD is supported by Natural Science and
23 Engineering Research Council of Canada Discovery grants.

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1 Table 1. Associations between the percentage cover of different benthic components of the
2 reefs and reef architecture. Values on the lower left of the table are Spearman-correlation
3 coefficients and values in the upper right of the table (in italics) are *P* values. Visual = visual
4 estimate of reef complexity.

	Rugosity	Visual	Rock	Sand	Coral	Macroalgae	Turf	Sponges
Rugosity	-	<i><0.001</i>	<i>0.523</i>	<i>0.002</i>	<i><0.001</i>	<i>0.269</i>	<i>0.486</i>	<i>0.209</i>
Visual	0.909	-	<i>0.378</i>	<i>0.001</i>	<i><0.001</i>	<i>0.199</i>	<i>0.694</i>	<i>0.178</i>
Rock	-0.167	-0.228	-	<i>0.073</i>	<i>0.363</i>	<i><0.001</i>	<i>0.181</i>	<i>0.174</i>
Sand	-0.703	-0.750	0.446	-	<i><0.001</i>	<i>0.021</i>	<i>0.830</i>	<i>0.001</i>
Coral	0.907	0.915	-0.235	-0.801	-	<i>0.252</i>	<i>0.619</i>	<i>0.149</i>
Macroalgae	0.284	0.328	-0.892	-0.554	0.294	-	<i>0.125</i>	<i>0.051</i>
Turf	-0.181	-0.103	0.341	0.056	-0.130	-0.387	-	<i>0.277</i>
Sponges	-0.321	-0.343	0.346	0.738	-0.365	-0.480	-0.279	-

- 1 Electronic supplement
- 2 Appendix 1. Fish species recorded Cozumel during this study

Species	Relative abundance (n = 10,965)	% occurrence per transect (n = 85)	Trophic group ^a	Individuals in each size class ^b				
				1	2	3	4	5
<i>Chromis cyanea</i>	17.67	91.25	Planktivore	1109	828	0	0	0
<i>Thalassoma bifasciatum</i>	14.27	96.25	Planktivore	1186	379	0	0	0
<i>Stegastes partitus</i>	8.5	95	Herbivore	932	0	0	0	0
<i>Stegastes adustus</i>	6.34	88.75	Herbivore	230	465	0	0	0
<i>Halichoeres garnoti</i>	5.85	72.5	Invertivore	491	151	0	0	0
<i>Acanthurus coeruleus</i>	4.82	93.75	Herbivore	57	86	240	145	0
<i>Clepticus parrae</i>	2.95	28.75	Planktivore	132	169	23	0	0
<i>Sparisoma viride</i>	2.93	88.75	Herbivore	125	12	88	72	24
<i>Haemulon sciurus</i>	2.8	25	Invertivore	23	46	185	53	0
<i>Haemulon flavolineatum</i>	2.75	53.75	Invertivore	1	60	211	30	0
<i>Lutjanus apodus</i>	2.46	23.75	Carnivore	5	8	103	152	2
<i>Lutjanus mahogoni</i>	2.22	17.5	Carnivore	10	14	142	77	0
<i>Chromis multilineata</i>	1.8	28.75	Planktivore	95	102	0	0	0
<i>Stegastes planifrons</i>	1.78	62.5	Herbivore	91	104	0	0	0
<i>Scarus iserti</i>	1.68	55	Herbivore	109	4	52	19	0
<i>Sparisoma aurofrenatum</i>	1.61	66.25	Herbivore	74	14	53	35	0
<i>Abudefduf saxatilis</i>	1.6	33.75	Omnivore	46	118	11	0	0
<i>Caranx ruber</i>	1.38	27.5	Carnivore	1	32	108	10	0
<i>Haemulon plumieri</i>	1.23	27.5	Invertivore	0	8	109	18	0
<i>Acanthurus chirurgus</i>	0.96	33.75	Herbivore	6	24	37	38	0
<i>Acanthurus bahianus</i>	0.92	33.75	Herbivore	2	10	54	35	0
<i>Microspathodon chrysurus</i>	0.78	43.75	Herbivore	32	38	15	0	0
<i>Scarus taeniopterus</i>	0.69	40	Herbivore	18	11	29	18	0
<i>Melichthys niger</i>	0.67	36.25	Omnivore	0	15	48	11	0
<i>Stegastes variabilis</i>	0.67	20	Herbivore	34	39	0	0	0
<i>Kyphosus spp</i>	0.62	20	Herbivore	0	9	2	54	3
<i>Stegastes diencaeus</i>	0.6	33.75	Herbivore	40	26	0	0	0
<i>Haemulon aurolineatum</i>	0.59	7.5	Invertivore	0	61	4	0	0
<i>Ocyurus chrysurus</i>	0.58	23.75	Carnivore	0	1	22	34	7
<i>Canthigaster rostrata</i>	0.57	32.5	Omnivore	60	3	0	0	0
<i>Cephalopholis cruentatus</i>	0.52	28.75	Carnivore	5	33	17	2	0
<i>Halichoeres maculipinna</i>	0.51	13.75	Invertivore	45	11	0	0	0
<i>Chaetodon capistratus</i>	0.47	27.5	Invertivore	51	0	0	0	0
<i>Haemulon carbonarium</i>	0.42	10	Invertivore	0	3	37	6	0
<i>Paranthias furcifer</i>	0.39	5	Planktivore	2	9	32	0	0
<i>Haemulon melanurum</i>	0.32	12.5	Invertivore	0	9	26	0	0
<i>Holacanthus ciliaris</i>	0.32	23.75	Invertivore	1	1	7	19	7

<i>Haemulon striatum</i>	0.29	12.5	Planktivore	9	3	16	4	0
<i>Pomacanthus paru</i>	0.26	20	Omnivore	0	13	7	6	3
<i>Cephalopholis fulvus</i>	0.24	21.25	Carnivore	2	19	5	0	0
<i>Halchoeres bivittatus</i>	0.22	7.5	Invertivore	13	11	0	0	0
<i>Pomacanthus arcuatus</i>	0.21	16.25	Omnivore	1	0	5	13	4
<i>Cantherhines macrocerus</i>	0.2	12.5	Omnivore	0	0	1	18	3
<i>Holacanthus tricolor</i>	0.19	16.25	Invertivore	0	4	10	7	0
<i>Lutjanus analis</i>	0.19	2.5	Carnivore	0	0	20	0	1
<i>Haemulon album</i>	0.18	2.5	Invertivore	0	15	5	0	0
<i>Anisostremus virginicus</i>	0.16	15	Invertivore	0	0	5	12	0
<i>Mulloidichthys martinicus</i>	0.16	6.25	Invertivore	0	0	14	3	0
<i>Chaetodon striatus</i>	0.15	10	Invertivore	0	16	0	0	0
<i>Scarus vetula</i>	0.15	12.5	Herbivore	0	0	1	12	3
<i>Holocentrus rufus</i>	0.14	8.75	Invertivore	0	5	10	0	0
<i>Lutjanus griseus</i>	0.14	6.25	Carnivore	3	5	7	0	0
<i>Bodianus rufus</i>	0.13	7.5	Invertivore	0	9	0	5	0
<i>Haemulon macrostomum</i>	0.12	2.5	Invertivore	0	11	2	0	0
<i>Lutjanus campechanus</i>	0.12	2.5	Carnivore	2	0	3	8	0
<i>Sparisoma chrysopterygum</i>	0.12	11.25	Herbivore	3	1	4	2	3
<i>Chaetodon aculeatus</i>	0.11	3.75	Omnivore	12	0	0	0	0
<i>Haemulon parra</i>	0.11	3.75	Invertivore	0	0	10	2	0
<i>Serranus tigrinus</i>	0.11	11.25	Carnivore	7	5	0	0	0
<i>Aluterus scriptus</i>	0.09	6.25	Omnivore	9	0	0	0	1
<i>Canthidermis sufflamen</i>	0.09	6.25	Invertivore	4	3	2	0	1
<i>Mycteroperca venenosa</i>	0.09	2.5	Carnivore	0	3	0	7	0
<i>Holacanthus bermudensis</i>	0.06	5	Invertivore	0	1	5	1	0
<i>Scarus guacamaia</i>	0.06	3.75	Herbivore	0	0	1	1	5
<i>Chaetodon ocellatus</i>	0.05	1.25	Invertivore	2	4	0	0	0
<i>Gramma loreto</i>	0.05	3.75	Invertivore	5	0	0	0	0
<i>Holocentrus adscensionis</i>	0.05	3.75	Invertivore	0	4	1	0	0
<i>Stegastes leucostictus</i>	0.05	5	Herbivore	6	0	0	0	0
<i>Hypoplectrus puella</i>	0.04	3.75	Carnivore	0	4	0	0	0
<i>Lactophrys triqueter</i>	0.04	3.75	Invertivore	0	0	3	1	0
<i>Sparisoma atomarium</i>	0.04	3.75	Herbivore	1	0	3	0	0
<i>Sparisoma rubripinne</i>	0.04	5	Herbivore	0	0	1	3	0
<i>Balistes vetula</i>	0.03	3.75	Invertivore	0	0	0	2	1
<i>Mycteroperca bonaci</i>	0.03	3.75	Piscivore	1	0	0	0	2
<i>Scarus coelestinus</i>	0.03	1.25	Herbivore	0	0	0	0	3
<i>Trachinotus falcatus</i>	0.03	3.75	Carnivore	0	0	1	0	2
<i>Xanthichthys ringens</i>	0.03	2.5	Invertivore	0	3	0	0	0
<i>Acanthostracion polygonia</i>	0.02	2.5	Invertivore	0	0	1	1	0
<i>Calamus calamus</i>	0.02	1.25	Invertivore	0	0	2	0	0
<i>Chaetodon sedentarius</i>	0.02	2.5	Omnivore	0	2	0	0	0
<i>Diodon holocanthus</i>	0.02	2.5	Invertivore	2	0	0	0	0
<i>Diodon hystrix</i>	0.02	2.5	Invertivore	2	0	0	0	0

<i>Hypoplectrus nigricans</i>	0.02	1.25	Carnivore	0	2	0	0	0
<i>Sphyraena barracuda</i>	0.02	2.5	Piscivore	0	0	0	0	2
<i>Cantherhines pullus</i>	0.01	1.25	Omnivore	0	0	1	0	0
<i>Epinephelus guttatus</i>	0.01	1.25	Carnivore	0	0	1	0	0
<i>Gymnothorax milaris</i>	0.01	1.25	Carnivore	0	0	1	0	0
<i>Gymnothorax moringa</i>	0.01	1.25	Piscivore	0	0	0	1	0
<i>Lutjanus cyanopterus</i>	0.01	1.25	Carnivore	0	0	0	1	0
<i>Lutjanus jocu</i>	0.01	1.25	Carnivore	0	0	0	1	0
<i>Mycteroperca tigris</i>	0.01	1.25	Piscivore	0	1	0	0	0
<i>Pseudupeneus maculatus</i>	0.01	1.25	Invertivore	0	1	0	0	0
<i>Scorpaena plumieri</i>	0.01	1.25	Carnivore	0	0	1	0	0

^a Trophic level is based in diet of adult organism following Paddack et al. (2009). In synthesis, planktivores, feed primarily on macro- and micro-zooplankton; herbivores are fishes that include detritus, turf algae and macroalgae in their diet; omnivores, feed on a mix of animal and plant material; invertivores, feed primarily on invertebrates associated to both hard and soft bottoms; carnivores feed on both mobile invertebrates and fishes; and piscivores feed almost only on fishes.

^b size class 1 = ≤ 10 cm; size class 2 = 10 – 20 cm; size class 3 = 20 – 30 cm; size class 4 = 30 – 40 cm; size class 5 = 40 – 50 cm.

1 Figure legends

2

3 Fig. 1. The location of reef sites on Cozumel Island, Mexico. The continuous line delimits the
4 polygon of the Marine Protected Area (Parque Nacional Arrecifes de Cozumel) and the
5 circles indicate surveyed reefs (Pa= Paraiso, Ch= Chankanaab, Yu= Yucab, Tu= Tunich, Sf=
6 San Francisco, Sr= Santa Rosa, Cd= Cedral, Fr= Francesa, Da= Dalila, Jr= Jardines, Hr=
7 Herradura, Pl= Palancar, Cw= Colombia West, Ce= Colombia East, Ps= Punta Sur).

8

9 Fig. 2. Mean (\pm SE) reef rugosity, cover of *Agaricia*, *Montastraea*, *Porites* and all other coral
10 genera, and abundance (individuals per transect) of six major trophic guilds on the 15
11 surveyed reefs. Reefs are ordered from north to south (see Figure 1). The total number of
12 transects is provided in brackets.

13

14 Fig. 3. Results of hierarchical partitioning analyses of the contribution of reef complexity and
15 the cover of reef benthic components to the community and food-web structure of reef fishes.
16 Bars show the independent (black = statistically significant at $P \leq 0.05$, grey = not significant
17 at $P > 0.05$) and joint (white) effects, and +/- indicates the direction of each relationship. Joint
18 effects are either additive (above the line) or antagonistic (below the line) to the independent
19 effects

20

21 Fig. 4. Results of hierarchical partitioning analyses of the contribution of different coral
22 genera to the abundance of reef fishes of five different size classes. Bars show the
23 independent (black = statistically significant at $P \leq 0.05$, grey = not significant at $P > 0.05$)

1 and joint (white) effects, and +/- indicates the direction of each relationship. Joint effects are
2 either additive (above the line) or antagonistic (below the line) to the independent effects.

3

4 Fig. 5. Results of hierarchical partitioning analyses of the contribution of the cover of
5 different coral genera to the abundance of six major trophic guilds of reef fishes. Bars show
6 the independent (black = statistically significant at $P \leq 0.05$, grey = not significant at $P >$
7 0.05) and joint (white) effects, and +/- indicates the direction of each relationship. Joint
8 effects are either additive (above the line) or antagonistic (below the line) to the independent
9 effects.

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87°6'0" W

86°55'30" W

86°43'30" W

20°35'0" N

20°25'0" N

20°15'0" N









