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Fisheries Research 44 (2000) 247–260

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Comparative assessment of multispecies reef fish resources in the Lesser Antilles

Bertrand Gobert*

Institut de Recherche pour le Développement, Centre IRD de Brest, BP 70, 29280, Plouzané, France

Received 11 December 1998; received in revised form 29 June 1999; accepted 17 July 1999

Abstract

Reef fish resources and exploitation were compared in four islands of the Lesser Antilles (Saint-Lucia, Martinique, Dominica, and Guadeloupe), using existing fishery statistics and data from a standardized fishery-independent trap survey. Great differences of demersal fishing pressure were found, with fishing effort spanning one order of magnitude between the least exploited sector (Dominica East) and the most exploited one (Martinique). In spite of this, catch per unit effort, species composition, average length, size structure, and total mortality led only to the ranking of sectors along a weak and continuous gradient consistent with the levels of fishing effort. No firm conclusion on the status of stock production could be drawn from the relation between catch and effort, owing to the possibility of biased estimates in one sector. These results contrast somewhat with the generally accepted diagnostic of severe overfishing for most reef fish populations of the Lesser Antilles. However in the long run, a precautionary management is all the more necessary as productivity may also be influenced by other factors such as habitat condition and recruitment sources. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Reef fisheries; Multispecific resources; Stock assessment; Comparative analysis; Lesser Antilles

1. Introduction

The fish resources of coral reefs are intensively exploited all over the world and in many cases overfished (Pauly, 1994). In spite of recent progresses in the ecological understanding of these communities (Sale, 1991), many aspects of the dynamics of their exploitation still remain obscure (Russ, 1991), and successful assessment methods suited to these highly complex fisheries are still to be designed (Appeldoorn, 1996).

While the comparative analysis of existing fisheries increasingly appears as a valuable opportunity to improve the assessment of individual stocks (Russ, 1991), this approach was rarely applied in sustainable fisheries, and across gradients where fishing effort itself could be adequately measured (Jennings and Lock, 1996). Fishing pressure was generally considered only qualitatively (Ferry and Kohler, 1987; Russ, 1985; Russ and Alcala, 1989), with few attempts to quantify it (Munro and Thompson, 1983; Koslow et al., 1994). Even in the most favorable cases, the interpretation was generally hampered by factors such as crudeness of fishing effort units, differences of gear and target species among fisheries,

*Tel.: +33-29822-4516; fax: +33-29822-4514.

E-mail address: gobert@ird.fr (B. Gobert).

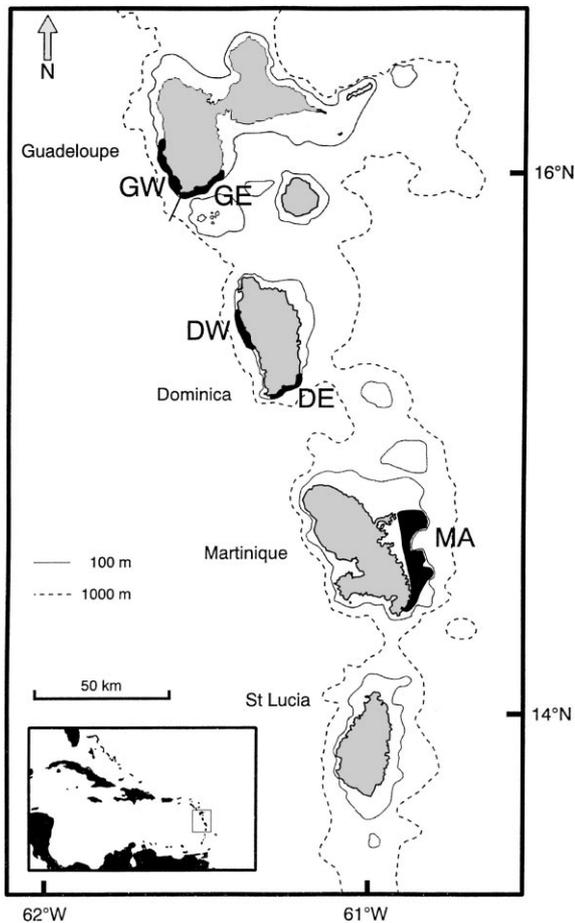


Fig. 1. Map of the four islands with the location and abbreviation of the five sectors sampled.

lack of detailed catch data, or non-equilibrium situations.

A comparative analysis was applied to the reef fisheries of four Lesser Antilles islands (Saint-Lucia, Martinique, Dominica, Guadeloupe) (Fig. 1). These islands are characterized by mountainous relief and narrow shelves (except the Eastern part of Guadeloupe), the absence of significant coral reefs (except in Martinique), a common fish fauna (Randall, 1983), and a similar general biological productivity within the regional Caribbean context. From a common technical and social basis stemming from the same historical background, the fishery sector developed quite differently in the post-colonial period, where

Saint-Lucia and Dominica became independent states, and Martinique and Guadeloupe became French Overseas Departments. All islands recently experienced a development of the pelagic fishery, but the exploitation of bottom species can be considered as relatively stable. The general feeling is that these coastal demersal stocks are highly overexploited (Mahon, 1990, 1993); although the fishing pressure is obviously very high, at least in some of the islands, traditional mono-specific analysis of fisheries have shown their limits (Gobert, 1991) and stock assessments are supported by very few objective data (Appeldoorn and Lindeman, 1985). Management measures (summarized by Chakalall, 1995) are thus not always established on a firm basis (Gobert, 1994a).

2. Materials and methods

2.1. Estimation of landings and fishing effort

In Dominica and Saint-Lucia, statistical data collected by the fisheries division or department (Lawrence et al., 1988; Murray et al., 1988) were processed to estimate fishing activity (number of trips) and landings by gear, month and landing site, for 1990–1993 and 1990–1992 respectively (Guiste et al., 1996; Gobert and Domalain, 1995). As no such data were available in Martinique and Guadeloupe, 1992 fishing effort was estimated indirectly using the statistics of fishing gear materials sold by the cooperatives, and calibrated from an intensive survey conducted in 1987 (Gobert, 1989) and the yearly statistics of the fishermen's professional organization. Using sale statistics was shown to provide a realistic estimate of at least the number of trips (Gobert, in press). Estimates of fishing effort were obtained separately for each gear in the demersal fishery (Gobert, unpublished ms.). The total number of traps hauled was multiplied by the relative fishing power of traps (Munro, 1974) corresponding to the average soak time in the island (ignoring a possible effect of trap shape or size, as all traps used in the islands are variants of the "antillean trap"); the effort expressed in "trap-days" (td) is the number of traps hauled after 24 h that would have yielded the same weight of catch. Fishing effort for the other gears was estimated from that of traps in the same island on the basis of their respective landings.

Table 1
Characteristics of the fishery-independent survey in the five sectors

Sector	Dominica East	Dominica West	Guadeloupe East	Guadeloupe West	Martinique
Abbreviation	DE	DW	GE	GW	MA
Sampling period	04/93–10/93	04/93–10/93	01/93–09/93	01/93–09/93	12/91–12/92
Number of trap hauls	77	138	428	655	412

2.2. Fishery-independent survey

The comparative study of the resource is based on standardized fishery-independent surveys (Gobert, unpublished ms.). Unbaited fish traps were used in standardized conditions: mesh shape (hexagonal) and size (31 mm smallest opening), trap shape (arrowhead with single funnel) and size (2 m × 2.5 m × 0.66 m, with a wooden or, in Guadeloupe, a metal, frame), soak time (seven days, most often between six and nine days). The traps were set at random stations within 10 m depth strata; most of them fished between 10 and 60 m. Five sectors were sampled in three of the islands, from December 1991 to October 1993 (Fig. 1, Table 1). For each trap hauled, information was recorded on date and time, GPS position, depth, soak time, problems occurring (if any). Except in a few isolated cases, each individual in the catch was measured in centimeters and weighted in grams. Occasionally in Guadeloupe, very large catches could not be processed entirely: then only the overall number by species and individual fish weights were measured.

2.3. Methods of analysis

After testing the log-normal distribution of catches in each sector (chi-square tests, $p > 0.1$), the average trap catch was computed with the estimator suitable for log-normal distributions (Dagnelie, 1973) from traps with soak time between six and nine days and non-zero catch. This latter condition was found to be the best way to reject the traps which did not fish in normal conditions (falling upside down on the bottom or with the door not properly closed). Trap dimensions, mesh size, and soak time make the probability of a null catch very low for a trap fishing in normal conditions, so the complete emptiness was considered as an important clue to detect this bias, although errors of both types almost certainly occurred. The effects of

depth, sector and month on catch were tested with a non-parametric analysis of variance (Kruskal–Wallis test).

To cope with the small number of fish caught for most species in each sector, length distributions were processed regardless of catch date or depth, as these factors were not found to have any clear influence on specific size structures. This was shown by visual inspection of distributions and, in the most intensively sampled sectors (Guadeloupe), by analysis of variance of length by depth strata (parametric ANOVA or Kruskal–Wallis tests, followed by length–depth regression analysis for significant species).

No attempt was made to estimate growth parameters from field data, but they were found in Claro and Garcia-Arteaga (1994). The comparison of total mortality coefficients Z among sectors was based on the length-converted catch curve (Pauly, 1980; Sparre and Venema, 1992) using the FAO-ICLARM FISAT software (Gayanilo et al., 1996). Z cannot be estimated when growth parameters are unknown, but the ratio of Z estimates for two distributions is quite independent of these growth parameters if the same input values are used in both analysis (Gobert, 1997). This property was used to estimate ratios of Z among sectors, for species whose growth parameters are not reliably known; the ratio was averaged for sets of combinations of K and L_{∞} chosen within ranges of values considered as possible given the existing biological knowledge (maximum recorded size, likely values for the growth rate K).

Length–frequency analysis is severely limited by the size of samples and therefore leads to discard thousands of fish measurements; processing average lengths allows the use a much larger part of this considerable amount of quantitative information. Sectors were ranked using an approach which does not rely directly on the comparisons of average length, but on the proportion of significant differences among

them. For each combination of species and depth strata, average lengths were compared among sectors with Student *t*-test when sample size was greater than 10, an arbitrarily low value which has little impact on the indirect approach described above. The results were summarized for each sector with two indices: SD (proportion of significant differences among all the possible comparisons involving this sector), and SD+ (proportion of differences where the mean length is greater in the sector, among all the significant ones involving it). Average length was also considered by groups of species reaching a comparable maximum size (i.e. 10–20 cm, 20–30 cm, etc.), thus reflecting the part of the total size range covered by the species groups.

The differences in relative catch composition were tested with the analysis of similarity, a non-parametric analogue of MANOVA (Clarke and Green, 1988; Clarke and Warwick, 1994). Because of the limitations (less than 125 samples) of the Primer software (Plymouth Marine Laboratory, UK), the ANOSIM procedure was applied to data subsets of this size. 15 subsets were randomly extracted from the whole set (25 samples \times 5 sectors), and the results of the 15 analyses were summarized.

2.4. Measurement of shelf areas

Shelf areas were measured from the most precise marine charts available, down to the 100 m isobath because the slopes deeper than 60 m, almost unexploited, are very steep and represent a negligible area. On the eastern shelf of Martinique, areas of flat and unproductive bottom, which support almost no fishing effort (Gobert and Stanisère, 1997), were

excluded in the computation of relative (=per unit area) catch and effort of the fishery at the scale of the whole island. But at the scale of the surveyed sector, taking into account unproductive areas was not necessary to compute average catch, as these areas are mainly located outside the sector, or in its deepest part where very few traps were set.

3. Results

3.1. Modes of exploitation of the resource

The demersal fishery is dominated in all islands by the use of traps, which account for about 60% of both activity and landings (Table 2). Nets and lines include variable proportions of several fishing techniques (gillnets and trammelnets, handlines and longlines) which are generally difficult to separate in statistical data. Initially built with bamboo, traps are increasingly made of galvanized chicken wire on wooden frames, with arrowhead or Z shape and variable size; they are generally set unbaited (or with bread or vegetal bait) and hauled on the average once a week in the French islands and twice in the other two. Minimum mesh sizes are 31 mm (smallest opening) in Martinique and 38 mm in the other islands. At the scale of the whole shelves, the amount of fishing effort differs widely (Table 3), especially between Saint-Lucia/Dominica and Martinique/Guadeloupe. Relative efforts (td/km²) cannot be compared on reliable bases at this scale, as the information on unproductive areas of the kind identified in Martinique is not available in other islands, especially in Guadeloupe where it likely exists.

Table 2
Characteristics of the demersal fishery in Saint-Lucia, Dominica, and Martinique

Island (year)	Saint-Lucia (1993)		Dominica (1992)		Martinique (1987)	
	Activity	Landings	Activity	Landings	Activity	Landings
% of traps	61.1	51.2	62.1	72.7	60.0	63.8
% of bottom lines	23.7	26.8	32.1	20.2	10.2	8.8
% of bottom nets	10.7	14.8	5.8	7.1	21.9	21.6
% of diving	4.4	7.2			7.8	5.8
Total demersal	7670 trips	130 tons	8493 trips	119 tons	92460 trips	1386 tons
Demersal/total (%)	30.4	11.6	35.3	16.7	60.4	42.2

Table 3
Standardized effort (SE) in the four islands

	Saint-Lucia	Dominica	Martinique	Guadeloupe
SE traps (td)	248 570	249 307	2 849 540	3 623 550
SE other gears (td)	155 939	93 592	2 352 466	≥2 300 000
Total SE (×1000 td)	~0.4	~0.3	~5.0	~6.0
Main sources of uncertainty	Traps hauled/trip Line fishery	Trap soak time	Evolution since 1987	All elements

3.2. Results of the fishery-independent survey

3.2.1. Catch per unit effort

Trap catches were usually low, with a mode at values lower than 1 kg/haul followed by steadily decreasing frequencies, except in DE where the frequencies spread more evenly (Fig. 2); the difference with DW (where the sample is also small) suggests that the distribution in DE is more an effect of the structure of the sampled population than of the size of the sample. All the differences between successive means are statistically significant (Student *t*-test, $p < 0.01$) except GE-MA ($t = 0.85$, $p = 0.39$). The sectors can thus be ranked according to the average catch, as follows: DE > GW > (GE – MA) > DW.

Among the main factors potentially accounting for catch variability (depth, sector and month), sector ($K = 83.7$) and month ($K = 35.1$) effects are very highly significant ($p = 0.01$) and depth is not significant ($K = 6.4$, $p = 0.49$). However, month was not considered in the analysis as the monthly catches observed along the year do not show any seasonal evolution, but rather random variations.

3.2.2. Catch composition

A total of 144 different species were identified, ranging from 59 to 111 among sectors in relation with the amount of sampling (number of traps hauled). As expected in these communities, the catch is not dominated by a few species: the most abundant one accounts for 9–14% of the total weight, and 22 different species are found in the first half of the total weight in all sectors (Table 4).

Except Monacanthidae in DE, no family accounts for more than 20% in weight (Fig. 3); Monacanthidae, Muraenidae, Mullidae, Holocentridae, and Haemulidae are important in all sectors but some families are so in some sectors only: Acanthuridae (MA), Caran-

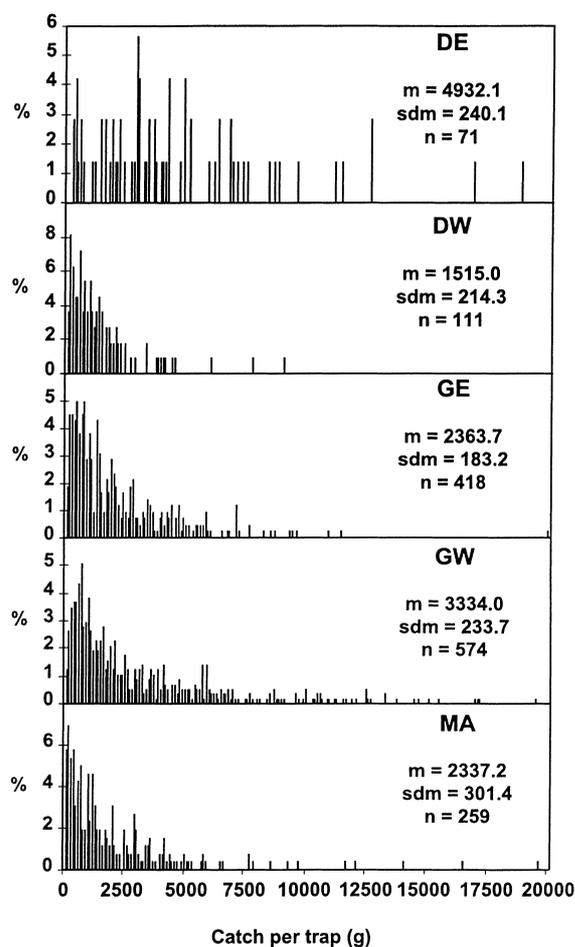


Fig. 2. Relative frequency distribution of the catch per trap (m : mean, sdm : standard deviation of the mean, n : sample size).

gidae (GW), etc. Although the catch composition by family is significantly different among sectors (ANO-SIM, $0.069 < R < 0.167$, $p = 0.01$), the low value of R shows that the overall similarity level is quite high. DE is more different from the rest of the sectors, as shown

Table 4
Overall species composition (%) of the catch for traps hauled after 6 to 9 days (species representing more than 1% of total weight)

DE (59 species)	%	DW (62 species)	%	GE (90 species)	%	GW (111 species)	%	MA (84 species)	%
<i>Cantherhines macrocerus</i>	14.1	<i>Gymnothorax moringa</i>	8.9	<i>Dactylopterus volitans</i>	13.1	<i>Gymnothorax moringa</i>	11.4	<i>Holocentrus rufus</i>	9.9
<i>Dactylopterus volitans</i>	8.6	<i>Pseudupeneus maculatus</i>	7.0	<i>Gymnothorax moringa</i>	11.3	<i>Pseudupeneus maculatus</i>	8.9	<i>Acanthurus bahianus</i>	9.6
<i>Holocentrus ascensionis</i>	8.6	<i>Sparisoma aurofrenatum</i>	4.6	<i>Pseudupeneus maculatus</i>	5.5	<i>Mulloidichthys martinicus</i>	8.8	<i>Sparisoma aurofrenatum</i>	6.9
<i>Epinephelus fulvus</i>	6.4	<i>Dactylopterus volitans</i>	4.4	<i>Panulirus argus</i>	5.4	<i>Lutjanus synagris</i>	7.1	<i>Gymnothorax moringa</i>	4.9
<i>Mulloidichthys martinicus</i>	5.0	<i>Myripristis jacobus</i>	4.1	<i>Holocentrus ascensionis</i>	5.3	<i>Myripristis jacobus</i>	4.3	<i>Holocentrus ascensionis</i>	4.7
<i>Balistes vetula</i>	4.9	<i>Lutjanus mahogoni</i>	4.0	<i>Haemulon plumieri</i>	5.2	<i>Epinephelus fulvus</i>	3.9	<i>Cantherhines macrocerus</i>	4.1
<i>Gymnothorax moringa</i>	4.8	<i>Mulloidichthys martinicus</i>	4.0	<i>Lutjanus synagris</i>	4.3	<i>Rhomboplites aurorubens</i>	3.9	<i>Pseudupeneus maculatus</i>	4.0
<i>Aluterus monoceros</i>	4.1	<i>Gymnothorax funebris</i>	3.9	<i>Mulloidichthys martinicus</i>	4.3	<i>Caranx latus</i>	3.2	<i>Panulirus argus</i>	3.9
<i>Aluterus scriptus</i>	3.5	<i>Lactophrys quadricornis</i>	3.2	<i>Epinephelus fulvus</i>	3.4	<i>Sparisoma aurofrenatum</i>	3.0	<i>Myripristis jacobus</i>	3.8
<i>Balistes spp.</i>	3.0	<i>Scarus taeniopterus</i>	3.1	<i>Caranx crysos</i>	2.6	<i>Caranx ruber</i>	2.7	<i>Cantherhines pullus</i>	3.0
<i>Lactophrys quadricornis</i>	2.9	<i>Diodon holocanthus</i>	3.0	<i>Diodon holocanthus</i>	2.5	<i>Haemulon aurolineatum</i>	2.5	<i>Haemulon plumieri</i>	2.6
<i>Sparisoma aurofrenatum</i>	2.6	<i>Lutjanus synagris</i>	3.0	<i>Haemulon chrysargyreum</i>	2.5	<i>Caranx hippos</i>	2.4	<i>Mithrax spp.</i>	2.3
<i>Haemulon chrysargyreum</i>	2.1	<i>Diodon hystrix</i>	2.5	<i>Holocentrus rufus</i>	2.1	<i>Rypticus saponaceus</i>	2.1	<i>Epinephelus fulvus</i>	2.3
<i>Pseudupeneus maculatus</i>	2.1	<i>Haemulon aurolineatum</i>	2.4	<i>Caranx latus</i>	1.9	<i>Gymnothorax funebris</i>	1.8	<i>Mulloidichthys martinicus</i>	2.1
<i>Pomacanthus paru</i>	1.8	<i>Rypticus saponaceus</i>	2.3	<i>Myripristis jacobus</i>	1.8	<i>Panulirus argus</i>	1.7	<i>Lutjanus synagris</i>	2.1
<i>Haemulon melanurum</i>	1.7	<i>Lutjanus buccanella</i>	2.3	<i>Haemulon aurolineatum</i>	1.6	<i>Scarus taeniopterus</i>	1.7	<i>Balistes vetula</i>	2.0
<i>Gymnothorax funebris</i>	1.7	<i>Lactophrys triqueter</i>	2.2	<i>Sparisoma aurofrenatum</i>	1.6	<i>Haemulon plumieri</i>	1.7	<i>Carpilius corallinus</i>	1.8
<i>Mycteroperca interstitialis</i>	1.6	<i>Lutjanus vivanus</i>	2.1	<i>Balistes vetula</i>	1.5	<i>Lactophrys triqueter</i>	1.7	<i>Holacanthus tricolor</i>	1.6
<i>Octopusspp.</i>	1.5	<i>Epinephelus fulvus</i>	2.0	<i>Rhomboplites aurorubens</i>	1.5	<i>Lutjanus buccanella</i>	1.5	<i>Haemulon flavolineatum</i>	1.5
<i>Rypticus saponaceus</i>	1.5	<i>Balistes vetula</i>	1.9	<i>Rypticus saponaceus</i>	1.4	<i>Pomacanthus paru</i>	1.5	<i>Epinephelus guttatus</i>	1.4
<i>Lactophrys triqueter</i>	1.4	<i>Synodus intermedius</i>	1.7	<i>Lactophrys triqueter</i>	1.4	<i>Haemulon flavolineatum</i>	1.3	<i>Octopus spp.</i>	1.4
<i>Carpilius corallinus</i>	1.4	<i>Holocentrus ascensionis</i>	1.6	<i>Epinephelus guttatus</i>	1.2	<i>Holocentrus ascensionis</i>	1.3	<i>Lutjanus purpureus</i>	1.1
<i>Lutjanus mahogoni</i>	1.4	<i>Acanthurus chirurgus</i>	1.4	<i>Lactophrys polygonius</i>	1.1	<i>Holocentrus rufus</i>	1.3	<i>Sparisoma chrysopteryum</i>	1.1
<i>Epinephelus guttatus</i>	1.2	<i>Haemulon melanurum</i>	1.4			<i>Chaetodon sedentarius</i>	1.1	<i>Acanthurus coeruleus</i>	1.1
<i>Acanthurus chirurgus</i>	1.1	<i>Holocentrus spp.</i>	1.2					<i>Chaetodon striatus</i>	1.1
<i>Holocentrus spp.</i>	1.0	<i>Epinephelus cruentatus</i>	1.1					<i>Mithrax spinosissimus</i>	1.0
		<i>Lutjanus analis</i>	1.1					<i>Caranx ruber</i>	1.0
		<i>Epinephelus guttatus</i>	1.1						
		<i>Caranx lugubris</i>	1.1						
		<i>Haemulon plumieri</i>	1.0						

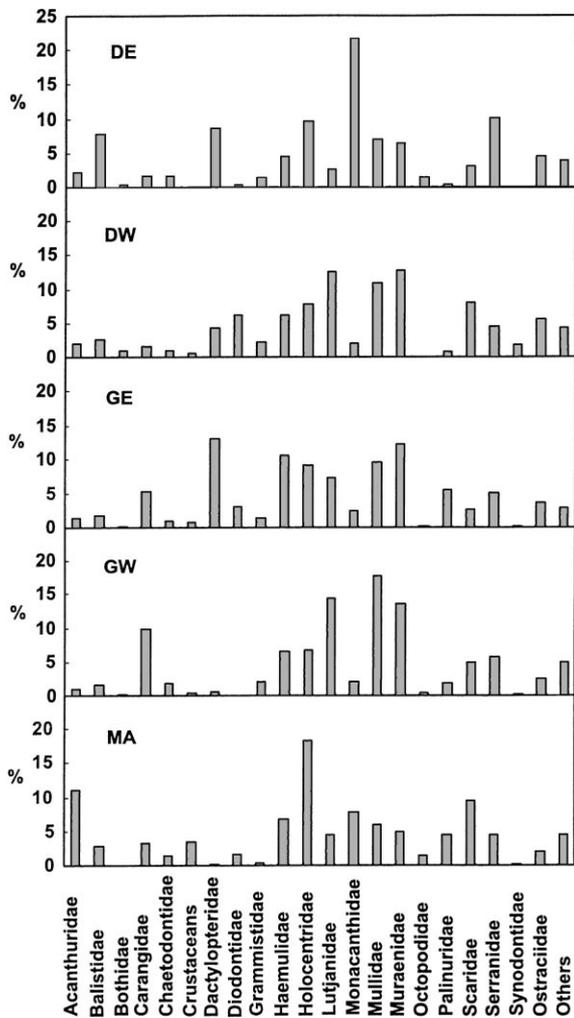


Fig. 3. Average relative catch composition by family.

by the pairwise comparisons: 93.3% of the tests involving DE and any of the other ones are highly significant.

In all sectors, predators of benthic invertebrates and of fishes account for a large part of the catch (36–50% in weight). No general tendency clearly appears among sectors when trophic categories are considered. Some high values may be related to ecosystem differences, as in the case of the abundance of herbivores (especially *Acanthurus bahianus*) in Martinique, where algal beds are important on the external reef slope (Adey and Burke, 1976; Laborel and Bouchon, 1986).

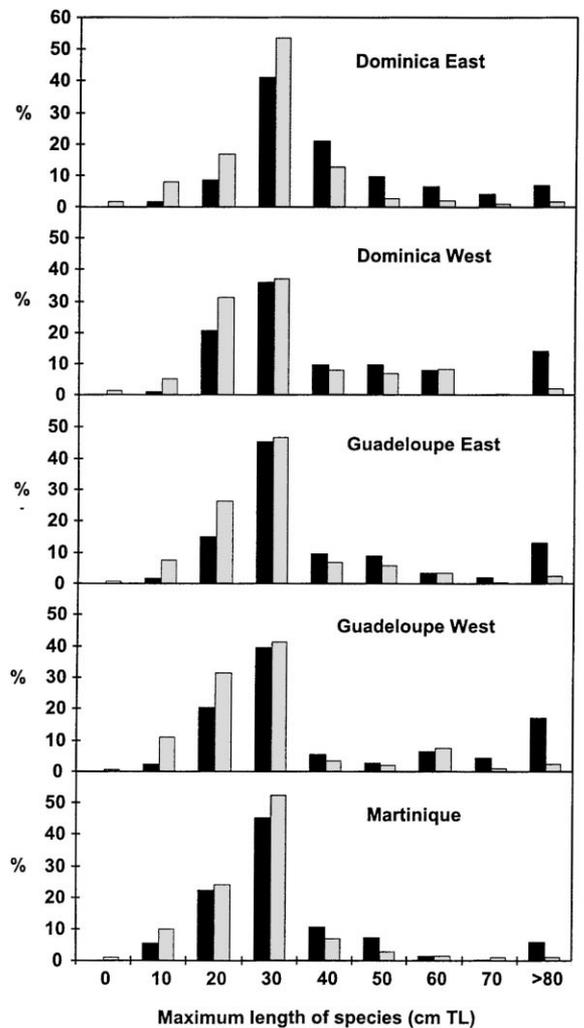


Fig. 4. Average relative catch composition by class of maximum species length, in weight (black bars) and in numbers (grey bars). Abscissa indicates the lower limit of the class (ex: 10 is for class 10–19 cm).

The distribution of numbers caught by classes of maximum length reached by the species (L_{max}) is very similar in all sectors (Fig. 4): the proportions steadily increase until the class 30–39 cm, then abruptly fall to less than 10%. In all sectors there is a low abundance, or even an absence, of the large piscivorous species (Serranidae, Carangidae, and Lutjanidae).

3.2.3. Average lengths

DE and MA are the most different sectors (highest values of SD), and the most extreme ones in this regard

Table 5
Summary of comparisons of average lengths among sectors

Sector	SD (%)	SD+ (%)	Number of comparisons
DE	66.0	98.5	68
GW	52.8	69.2	104
DW	52.4	58.1	43
GE	51.1	37.1	89
MA	66.3	11.8	118

(lowest and highest values of SD+): mean lengths are almost always greater in DE and lower in MA (Table 5), leading to the following ranking order: DE > GW > DW > GE > MA. In all sectors except DE the average length (most often between 20 and 25 cm) is much smaller than, and almost independent of, the size of the species, for L_{\max} ranging from 30 to 70 cm (Fig. 5). Sector DE shows a somewhat different pattern, with average lengths steadily increasing from 12 to 46 cm.

3.2.4. Overall size structure

The overall size structure (Fig. 6) shows in all sectors a main mode peaking between 15 and 25 cm, and one or two other modes made of very few species: Chaetodontidae and some Diodontidae (≈ 10 cm), *Dactylopterus volitans* (≈ 30 – 35 cm), *Aluterus* spp. (Monacanthidae) (≈ 40 – 45 cm), *Gymnothorax* spp. (Muraenidae) (≈ 70 – 80 cm). The main mode, made of the remaining species (Fig. 7), is made of 80–93% of the individuals and most of the species

diversity. It includes the families of major fisheries interest (Holocentridae, Haemulidae, Serranidae, Mullidae, Scaridae, Lutjanidae, Carangidae) which account for 55–76% of the total numbers and 39–66% of the total weight. Its ascending arm, which reflects the overall size selectivity of the fishery, is almost identical in both sectors of Guadeloupe and in DW, but is shifted left by about 2 cm in MA, and more progressive in slope in DE where the mode occurs at a much larger length. Its descending arm, which reflects both the succession of species of increasing maximal size and the mortality undergone in each species, shows in all sectors a relatively clear exponential trend.

3.2.5. Specific size structures

As far as selectivity is concerned, the main observation is that the ascending parts of the distributions are not always superimposed: there is often a gap of at least 1 cm, and several species have much larger differences among sectors. As mesh size was the same in all traps used for the survey, a density-dependent effect on selection probability is the most likely mechanism to explain such differences (Gobert, 1998). As far as mortality is concerned, the quantitative analyses of the descending parts of the distributions is limited to ratios of total mortality coefficients Z , by the amount and nature of available data. Z could be estimated with a good fit of the catch curve for six species with growth parameters available, yielding 17 ratio estimates (Table 6); for these species, Z is systematically lower in DE and generally higher in

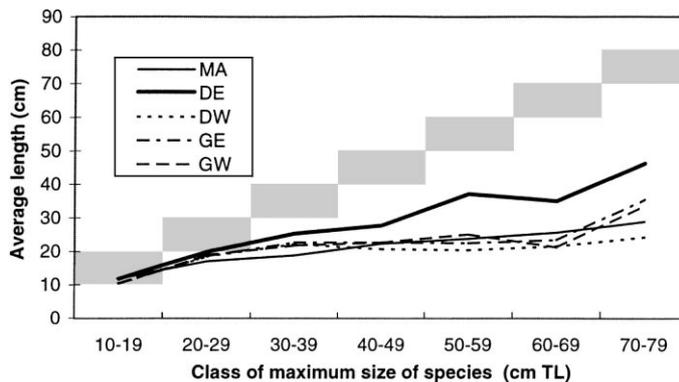


Fig. 5. Average individual length by class of maximum species length.

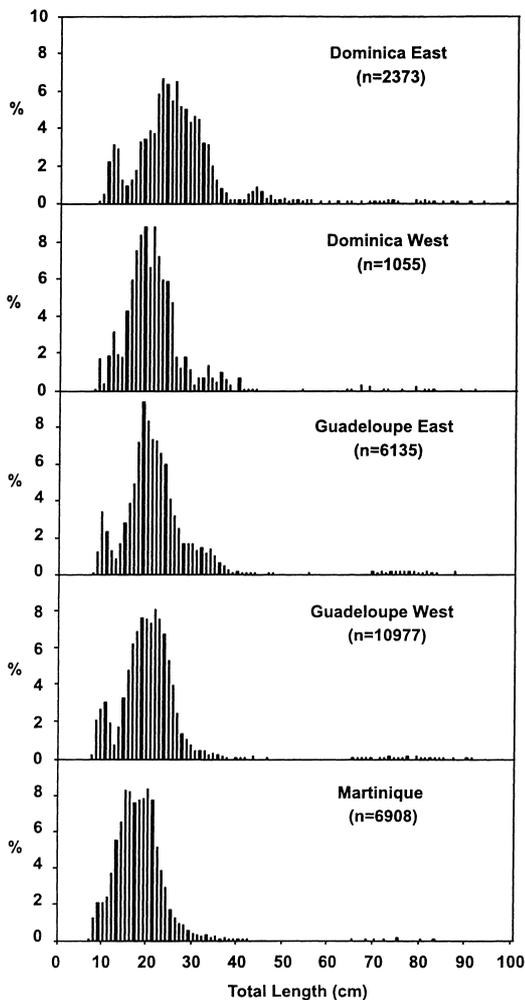


Fig. 6. Relative length frequency distribution of the whole fish catch.

MA and GE. The average Z-ratio could be estimated in satisfactory conditions (coefficient of variation of the ratio <10%) for six of the 10 species with unknown growth parameters and more than 100 fish measured in each of at least two sectors, also yielding 17 ratio estimates (Table 6). In summary, Z is always the lowest in sector DE, and is more often higher in MA than in GE and in GW (Table 7), thus leading to the following ranking of sectors: MA > GE > GW > DE.

3.3. Relation between cpue and fishing effort

The availability of measurements of fishing effort and standardized estimates of cpue makes it possible to study the quantitative relation between exploitation and status of stocks. As there is too much uncertainty on all variables (effort, landings, areas) at the scale of whole shelves, this approach was conducted at the scale of the sectors sampled during the fishery-independent survey. Among these five sectors, estimates of fishing effort span almost one order of magnitude (Table 8).

No clear tendency of decreasing cpue as effort increases appears on the five sector plot (Fig. 8a), owing to the wide dispersion of points in the lower range of efforts. However if sector DW is excluded from the data set, a negative linear relationship is highly significant for the other four points ($cpue = 1.012 - 0.0668 \times effort, R^2 = 0.879$). Although there is some indication that local conditions might have made trap poaching by fishermen easier in sector DW than in the other ones (cf. Section 4), it is not possible

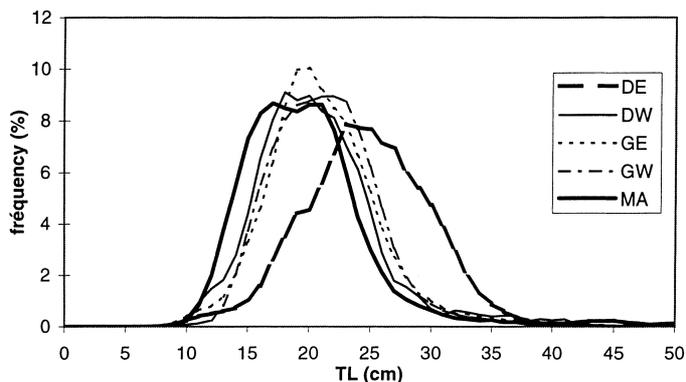


Fig. 7. Relative length frequency distribution of the main mode (moving average on three classes).

Table 6
Ratios of total mortality coefficients among sectors

Species	GE/DE	GW/DE	GW/GE	MA/DE	MA/GE	MA/GW
<i>Growth parameter estimates available</i>						
<i>E. fulvus</i>	2.07	1.20	0.58	1.40	0.68	1.16
<i>L. synagris</i>			1.02		1.10	1.08
<i>R. aurorubens</i>			0.80			
<i>H. plumieri</i>			0.63			
<i>M. martinicus</i>		2.60		2.78		1.07
<i>P. maculatus</i>			0.78		1.24	1.59
<i>Growth parameter estimates not available</i>						
<i>H. ascensionis</i>	1.84			4.74	2.57	
<i>H. rufus</i>			0.92		1.62	1.75
<i>M. jacobus</i>			1.61		1.39	0.98
<i>S. aurofrenatum</i>	1.50	1.41	0.95	1.23	0.83	0.87
<i>G. moringa</i>			0.68			
<i>R. saponaceus</i>			1.04			

Table 7
Number of comparisons of total mortality coefficients Z

Sector	DE	GW	GE	MA
Number of comparisons where Z is greater	0	8	12	14
Total number of comparisons	10	20	20	18
% of comparisons where Z is greater	0	40.0	60.0	77.8

Table 8
Fishing effort in the sectors sampled by the fishery-independent survey

Sector	Area (km ²)	Raw effort (×1000 td)	Relative effort (td/km ²)
Martinique	138.0	1040.4	7539
Dominica West	21.0	68.6	3265
Dominica East	18.7	17.1	919
Guadeloupe West	31.2	150.0	4806
Guadeloupe East	34.3	300.0	8746

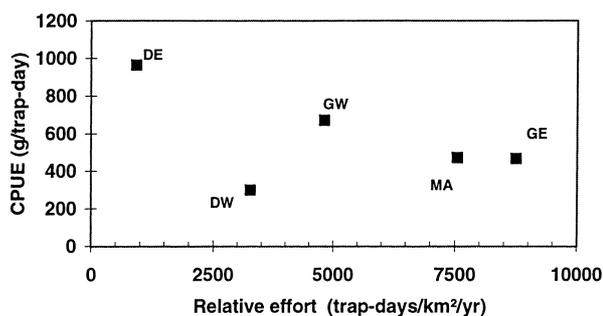


Fig. 8. Multispecies surplus production model applied to the Lesser Antilles data: (a) cpue-effort relationship; (b) catch-effort relationship.

to draw any firm conclusion on the relation between cpue and fishing effort.

4. Discussion

This work was an attempt to overcome some of the most usual shortcomings of comparative analysis of reef fisheries, which mainly stem from the difficulty of comparing catches of different gears and of quantifying fishing effort in small-scale multigear fisheries.

Data collection was hindered by many strong constraints, with consequences on the amount and quality

of data. Firstly, the cost and/or practical difficulties of conducting fishery-independent surveys in the local contexts seriously limited their ability to sample the resource. Thus the samples were collected over generally less than one year and their sizes are most often small, particularly as far as length–frequency distributions are concerned. Although many methods cannot be used properly in these conditions (for instance the estimation of growth parameters), the available information could be used as fully as possible within the limits of reliability through less rigorous methods (Z-ratio estimation) or analyses at a higher aggregation level (multispecies length–frequency distributions). Secondly, estimating fishing effort was faced with two main problems: standardizing fishing effort of different passive gears and, at least in Guadeloupe, estimating fishing activity from available statistical data. Nevertheless, if effort cannot be measured accurately, its order of magnitude can be considered as reliable and used as a raw indicator of fishing pressure.

The results confirm the general feeling that Martinique and Guadeloupe are presently much more heavily exploited than their neighbours, where fishing effort is 10–20 times lower. This high fishing pressure is related to socio-economic factors like human population size (about 400,000 in each island in 1997) and purchasing power of both fishermen and consumers (stemming from the status of French Overseas Department). Although lack of appropriate data, especially in Guadeloupe, precludes a reliable comparison of fishing pressure at the scale of whole islands, taking shelf areas into account when possible suggests that resources are globally subjected to about 10 times more fishing effort in Martinique than in Saint-Lucia or Dominica.

Exploring the relation between cpue and effort at the scale of sampled sectors did not yield conclusive results as the regression is not significant when all five sectors are used. Keeping or rejecting the outlier (DW) deserves some discussion, as it makes the fit shift from not to highly significant. In the first case (keeping the outlier), cpue and effort estimates are considered as reliable; it then means that ecological conditions on the leeward shelf of Dominica are different from those of neighbouring islands (and particularly of Guadeloupe), or that there is no statistical effort/cpue relation in the Lesser Antilles. In the latter case (rejecting the outlier), either effort or cpue are underestimated in sector DW. The most likely hypothesis in this case is that cpue estimates are biased as a result of hauling of survey traps by local fishermen, which could not have occurred significantly in the other sectors, where traps were either too heavy to be hauled manually (in Guadeloupe) or too difficult to access (in the windward sectors). It is noteworthy that the four-sector significant cpue-effort relation leads to a maximum relative yield on the order of 4 t/km²/yr, which is consistent with previous estimates for the Caribbean (Munro and Thompson, 1983; Arias-Gonzales et al., 1994). However, as neither keeping nor excluding the outlier DW cannot be justified on the basis of available information, no firm conclusion can be drawn from catch-effort analysis.

The resource reacts to exploitation along gradients which are generally consistent with fishing effort gradients. The effects of increasing fishing pressure can be summarized as a series of successive steps which were observed in the five sectors (Table 9). Most of these effects are not unexpected as they have been observed in many fisheries, but they had not been reported together from reef fisheries.

Table 9
Summary of the characteristics of the resource in the five sectors^a

	DE	DW	GE	MA	GW
Fishing effort	+	++	+++	+++	+++
Elimination of the largest species	X	X	X	X	X
Shrinking of the distribution of cpue	?	?	X	X	X
Relative importance of the small-sized species		X	X	X	X
Shrinking of the multispecies length-structure		X	X	X	X
Levelling off of total catch		?	X	X	X
Important modification of the selectivity function				X	

^a X denotes the occurrence of the observation and +, ++, +++ the levels of fishing effort (low, moderate, high).

The catches of the fishery-independent survey were found to be much more similar than might have been expected in view of the profound differences in fishing effort. In spite of the wide range of fishing effort, the most lightly and the most heavily exploited sectors do not show images of completely differently organized fish communities, but are rather separated by a weak and continuous gradient. Few studies dealt comprehensively with the changes in multispecies reef fish communities in response to fishing (Munro and Williams, 1985; Jennings and Lock, 1996). The pattern of species succession often referred to (shift from large, high-valued, predatory species towards small, herbivorous or planktivorous species of low market value; Munro and Williams, 1985; Jennings and Lock, 1996; Jennings and Polunin, 1996) is not found in all studies, but the decline and eventually the elimination of large species (large predators like Serranidae and Lutjanidae but also large herbivores) is a common observation. In the present case, these species have not been caught in any of the sectors although their former presence is testified both by scientific literature (Randall, 1983) and by the older fishermen (Gobert, 1996). This confirms that fishing affects the composition of an exploited reef fish community at relatively low exploitation rates (Koslow et al., 1988). The results of the present study suggest that, once these large species have been eliminated, the intensification of the fishery did not lead to another significant shift in the species composition, which remained dominated by medium-sized species feeding on benthic invertebrates, and that the subsequent evolution mainly affected the size structure by “pushing” it towards the selection interval.

The paradox of minor differences in fishery-independent survey catch composition and size structure under widely different fishing pressures suggests that in the Lesser Antilles the effects of increasing fishing effort on fish community could be to some extent moderated by conservative processes which are undetermined, but could possibly include decreasing catchability (through the behavior of fish towards passive fishing gears), external and at least partly common source of recruitment (Appeldoorn, 1987), compensatory density-dependent mechanisms involving growth and natural mortality. Although the generality of this conclusion is not certain, it has also been suggested that length–frequency data may provide

misleading impressions on reef fish species, at least for long-lived snappers (Williams et al., 1995).

The results of this comparative study somewhat contrast with the generally accepted diagnostic of severe overfishing for most reef fish stocks of the Antilles (Mahon, 1993), and especially of the two French islands; if this certainly applies to some individual species such as large predators, none of the global indicators described here shows unmistakable signs of extreme depletion of the resource as a whole, like strongly dwindling relative catches or a complete shift in species composition.

In a previous study of the Martinican fishery, the medium-sized fish species which could be analyzed through yield/recruit models were not found to be obviously growth overfished given the uncertainty on biological parameters (Gobert, 1991), whereas the lobster *Panulirus argus* was very clearly so (Gobert, 1994b). The present study was justified by the impossibility to generalize this conclusion from a few common species to the whole fish resource, or to replace it within a general picture of antillean reef fish stock exploitation. Its results confirm the previous findings and suggest that, within the observed range of exploitation levels, the reaction of stocks to increasing fishing pressure is not as severe as it might seem when fishing effort alone is considered. However the empirical nature of the study provides no light on possible mechanisms and confirms the need of a better biological and ecological knowledge, to improve the understanding of the dynamics of exploited reef fish communities.

In any case this apparently reassuring conclusion should not lead to an overly simplistic and optimistic short-term vision of Lesser Antilles reef fisheries, especially in the most heavily exploited islands. On the one hand, the notion of overfishing cannot be discussed in biological terms only; it seems clear that in the French islands the present level of effort corresponds to a production close to the maximum but exceeds by far the level of an economic optimum, whatever definition might be given to this notion. On the other hand, the analysis of effort and landings emphasizes the present production without considering the long-term preservation of the fishery potential; intensive exploitation can alter the productivity of the resource and the equilibrium of the ecosystem, through indirect effects such as habitat degradation

by mechanical action of the fishing gear or shifting of the species composition in favor of benthic invertebrates without marketing value. Finally, if an external source of recruitment contributes at least partially to sustain the production in the most exploited islands, the corresponding fisheries would be extremely sensitive to a decrease of this recruitment since their level of fishing effort would be far greater than what the real productivity of the local resource can tolerate. The possibility of this risk also reinforces the need to consider fisheries management at the regional scale.

Acknowledgements

Many people contributed to various aspects of this research programme, among whom G. Domalain, J.Y. Stanisière, J.P. Lamoureux, M. Louis, N. Diaz, S. George, W. Joseph, F. Narcisse, H. Guiste, A. Magloire, S. Coriette for the scientific work, and P. Gervain, G. Célimène and J. Adams for the work at sea. The programme was supported by the Chief Fisheries Officers of Dominica and of Saint-Lucia, and partly financed by the General Council of Martinique.

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