

Abstract.—The catch and effort of reef fisheries in seven areas of Belize and in six of south Jamaica were intensively surveyed to provide data for area-based surplus-production models (SPM) to manage these fisheries. Data were normalized to area of productive habitat. SPM's could not be defined for the Belizean or Jamaican data treated separately because the slopes of the relationships between catch per unit of effort and effort were nonsignificant and positive. This appeared to be due 1) to violations of the model's assumptions (catch composition was heterogeneous because fishermen target spawning aggregations and migratory fishes at particular sites) and 2) to possible differences in community composition among areas (the communities were not at equilibrium and productivity possibly differed among sites). Other assumptions had been violated by previous area-based SPM's so that the level of exploitation on the south Jamaican shelf has been seriously underestimated in recent decades. Although a SPM could be defined for the combined Jamaica-Belize data set, we conclude that these models should be used with caution in reef fisheries management because underlying assumptions are likely to be seriously violated. The surveys indicate, however, that levels of catch per unit of effort, catch, and effort in the south Jamaican reef fishery are significantly lower than those of 10 years ago. Depletion of a wide range of fish groups has apparently led to a decline in the equilibrium productivity of the fishery.

Catch and effort analysis of the reef fisheries of Jamaica and Belize

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Tropical coral reef fisheries are typically small scale but highly complex, artisanal multispecies fisheries. They are often overexploited (Munro, 1983; Koslow et al., 1988; Russ, 1991) but are rarely managed with conventional fishery methods (see Johannes [1978] on traditional management of reef fisheries). Conventional fishery models are not particularly suitable for complex, multispecies fisheries, and the requisite data, because of the highly decentralized landing and marketing systems typical of these fisheries, is often difficult to obtain. The regions supporting these fisheries often lack the technical and financial resources to manage them, and even if the resources were available, it is arguable whether these small-scale fisheries would justify the expenditure that such an exercise would require. However, although the overall yield of these fisheries is modest, they may provide an important source of employment, protein, and foreign exchange earnings for local economies.

In a pioneering study based on catch and effort data collected dur-

ing a single survey of landing sites that he grouped by coastal parishes, Munro (1978) developed a preliminary surplus production model (SPM) for Jamaican reef fisheries. His approach was attractive because data inputs and analytic requirements were modest, and the model provided long-term, albeit simple, guidance for optimal fishing levels.

However, the area-based SPM assumes that the fish assemblages, their habitats and productivity, and the fishery do not differ significantly among fishing areas; that the relationship between catch and effort is at equilibrium in each area; and that the fish stocks and effort are contained within the designated fishing areas (Caddy and Garcia, 1982; Nicholson and Hartsuijker, 1982). Nicholson and Hartsuijker (1982), in particular, pointed out the perils of violating the model's assumptions, but area-based SPM's for reef fisheries are being used increasingly to obtain first-order approximations of maximum sustainable yield based upon available catch and effort data (Aiken and Haughton, 1987; Haughton, 1988; Appel-

doorn and Meyers, in press). Area-based SPM's have not been developed further for management of reef fisheries, although more focussed studies have led to interesting results in freshwater systems (Marten, 1979).

Although both are within the Caribbean region, the reef fisheries of Belize and Jamaica contrast markedly. Belizean finfish stocks appear to be lightly to moderately exploited, an assessment not based on quantitative catch and effort data, which have never been systematically collected, but upon the continued availability of prime commercial species (snappers [Lutjanidae] and groupers [Serranidae]) that are the basis of an export-oriented fishery. This assessment is also based on the country's estimated low consumption of seafood; Belize has a sparse population (7.8 persons/km² totalling less than 200,000 persons) and has traditionally relied little on seafood. Conch (*Strombus gigas*) and lobster (*Panulirus argus*) are the main focus of Belizean commercial fisheries, followed by snapper and grouper, which are fished primarily for export.

In contrast, seafood is traditionally an important part of the Jamaican diet; the country is densely populated (216 persons/km² with a total population of 2,362,000), and its coastal fisheries have been heavily exploited for at least the past several decades (Aiken and Haughton, 1987). Since 1970, catch rates in the reef fisheries have markedly declined (Aiken and Haughton, 1987; Haughton, 1988), and the catch composition has shifted to commercially less valuable species (Koslow et al., 1988). Snappers, groupers, and large parrotfishes (Scaridae) that were abundant off Jamaica in the last century (Gosse, 1851) have virtually disappeared from most reef areas.

Our objective was to develop a SPM to manage the reef fisheries of Jamaica and Belize. To improve upon previous area-based SPM's, we carried out focussed surveys of catch and effort to better quantify the model in relation to some of its underlying assumptions. In particular, we assessed the productive area underlying each fishery by estimating the proportion of productive reef habitat in different parts of the shelf and by localizing the fishing grounds used, and we quantified annual fishing effort. By surveying reef fisheries in these two countries, we hoped to relate catch and effort over a range of exploitation rates and develop a broadly applicable SPM.

Methods

Field study

A two-phase survey was carried out in Belize and along the south coast of Jamaica (Fig. 1, A and B). First, a stratified systematic survey was carried out

to determine the numbers of fishermen by region, the types of vessels and gears in use, and the grounds fished, and to obtain general information on effort, catch, and seasonality in catch composition and abundance. Validated lists of fishing vessels in the two countries were obtained from the licensing registers of fisheries departments and from surveys of landing sites (20 active fishing beaches on the south coast of Jamaica and 10 cooperatives and markets in Belize). The lists were stratified by area and a sample from each area was systematically selected. A questionnaire was administered to the selected fishermen in Belize, but owing to difficulties in locating selected fishermen in Jamaica, a number of fishermen were chosen from those available on the fishing beaches.

Based on this survey, the fishing grounds were subdivided into seven areas in Belize and six in Jamaica. However, spawning aggregations fished in several of the areas in Belize accounted for a significant proportion of the fish landings and seemed likely to draw fish from nearby areas. In calculating the SPM, data from areas 4 and 5 (east and west Ambergris Cay) were pooled, as were data from areas 2, 3, and 7 (Fig. 1B).

In the second phase of the survey, six landing sites in Jamaica and five in Belize were visited to collect data on effort and landings over an annual cycle. Thus one site that was deemed representative was selected from each area, except in Belize City (Gallows Pt.) area, where two cooperatives were visited. Sites were visited every two weeks in Belize between July 1990 and August 1991 (except Placencia, which was sampled from March through August 1991) and in Jamaica from February through April and August through November 1991. Sites were monitored for the entire period during which fish were landed. As each vessel landed its catch, overall weights were recorded by family, and fishermen were interviewed to ascertain the gears used, the effort by gear-type, and the areas fished. In Jamaica, there were too many vessels at some sites to monitor all landings. In these instances, total effort and landings statistics for the site were estimated by the proportion of vessels actually surveyed: $X_T = X_i/F$, where X_T is the total landings or effort for a site on a particular day, X_i is the landings or effort recorded, and F is the proportion of vessels surveyed.

The effective area of the fishing grounds in each area was estimated. The total area of the shelf was estimated from charts both with a planimeter and by weight, whereby the shelf area was traced from a chart, cut out, weighed, and the weight related to that of a unit area (e.g. 10 km²). The extent of the actual fishing grounds was determined from interviews conducted during the surveys. In Belize, the

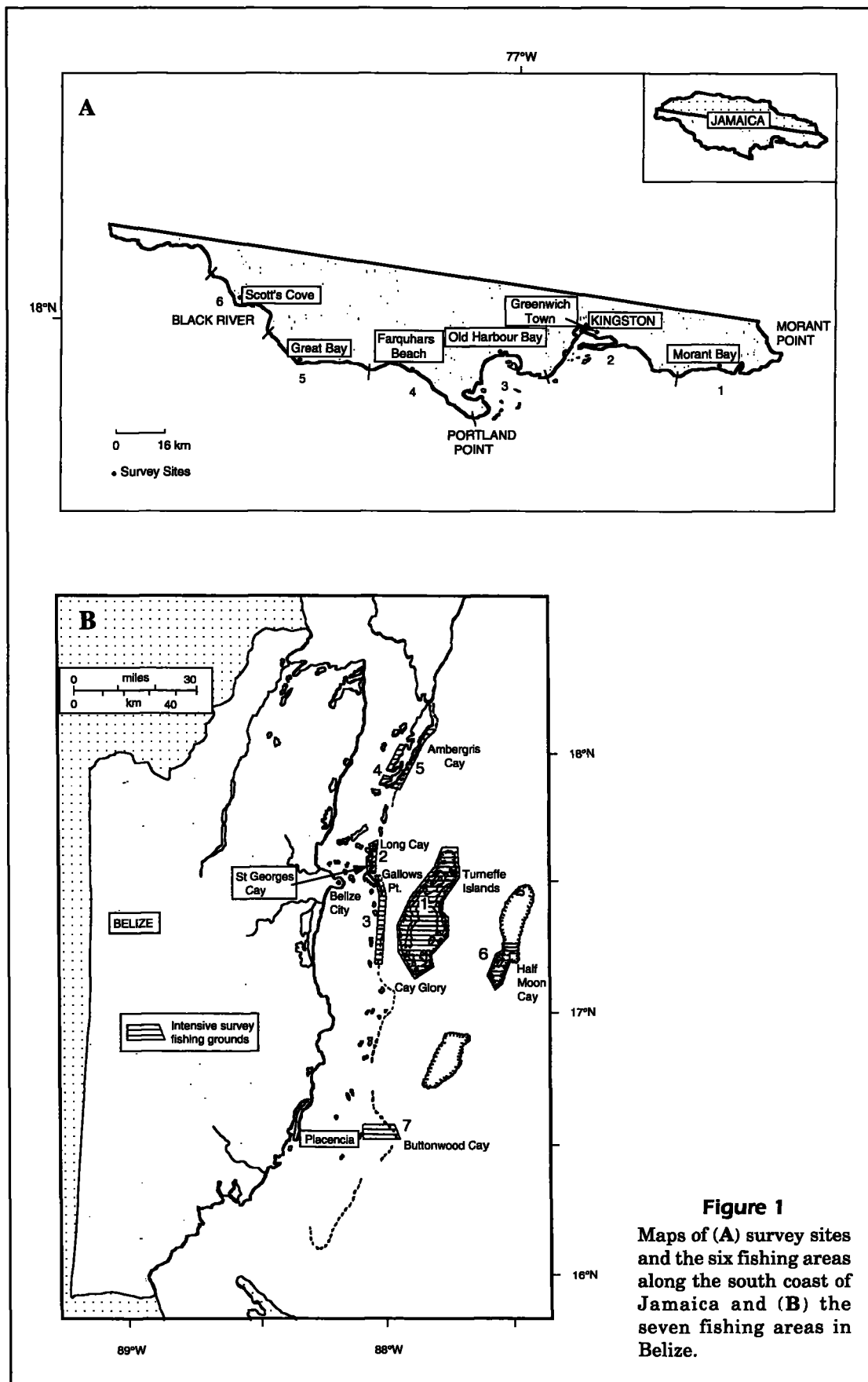


Figure 1
Maps of (A) survey sites and the six fishing areas along the south coast of Jamaica and (B) the seven fishing areas in Belize.

fishermen noted their fishing grounds on a chart in relation to the cays, and the fishing grounds were assumed to extend to the reef crest. The areas of these grounds were then measured with a planimeter.

In Jamaica, four line transects orthogonal to the shoreline from nearshore to the shelf edge were carried out in each of three areas: Old Harbour Bay, Farquhars Beach, and Great Bay (Fig. 1A). Transects within each area were approximately 2 nmi (=3.7 km) apart. The mean depth of the south Jamaican shelf is 20 m (Woodley and Robinson, 1977), and the dropoff is at about 50 m (Nicholson and Hartsuijker, 1982); observations of bottom type were made with a glass-bottomed viewing box deployed over the side of a small vessel. Observations were carried out at 4-km intervals of the dominant substrate material (i.e. sand, grass, coral, or mud). The proportion of shelf represented by each substrate type was estimated from the proportion of stations at which the particular substrate type was dominant. The results of these surveys were compared with historical surveys of the Jamaican shelf (Nicholson and Hartsuijker, 1982).

Data analysis

Catch and effort data were summed by area, gear type, and species group. Totals were standardized by proportions of the fishing year and of the population of fishermen surveyed. Fishing effort in a SPM must be expressed in a common unit. Hook-and-line effort (hook h/km²) was selected as the common unit of effort because our surveys indicated that it was the dominant fishing gear in Belize (in terms of incidence of use and yield obtained) and the most widely

used gear overall. Fishing effort from other gear types (i.e. bottom gill net, trap, weir, and spearing) was standardized to hook-and-line gear by using the weighted mean of the ratio of catch rates from the particular gear to the hook-and-line catch rate within each area. Effort was then summed within each area.

Catch and effort for each area were standardized per square kilometer of fishing ground. Log-transformation of the catch-per-unit-of-effort (CPUE) data (the Fox [1970] variant of the SPM) did not improve the fit, so it is not presented. However, the relationship between CPUE and effort (f) was highly nonlinear; therefore, the relationship is presented both without transformation and with effort data log-transformed, which linearized the relationship between CPUE and f .

Results

Catch and effort

Annual catch was estimated to be more than four-fold higher off the south coast of Jamaica (998 tonnes) than off the coast of Belize (240 tonnes) (Table 1). When landings were normalized to the area of productive fishing ground (Tables 1 and 2) (i.e. the portion of shelf estimated to be coral and sea grass), yield per unit of area from Jamaican waters (552 kg/km²) was 39% higher than off Belize (340 kg/km²). However, this difference was not statistically significant in a comparison of mean yield from the different fishing areas in the two countries (Kruskal-Wallis [KW] one-way ANOVA: $\chi^2=0.33$, $n=13$, $P>0.2$).

Table 1
Catch (Y) and fishing effort (f) data summary for sites in Belize and Jamaica. See Figure 1 for areas.

Country	Site	Area (A) (km ²)	Total Y (t)	Prime Y (t)	Total f (⁰⁰⁰ hook h)	Y/A (kg/km ²)	f/A (hook h/km ²)
Belize	1	312	30	26	22	97	71
	2	32	7	7	3	208	86
	3	47	31	24	34	655	720
	4	10	16	14	15	1,688	1,505
	5	33	8	4	9	250	275
	6	231	18	17	15	79	65
	7	44	130	126	52	2,929	1,172
Jamaica	1	46	55	8	286	1,197	6,209
	2	252	344	159	2,038	1,364	8,089
	3	607	265	51	1,303	437	2,147
	4	652	266	18	1,448	409	2,222
	5	115	37	4	265	319	2,307
	6	135	31	6	257	223	1,901
Totals	Belize	709	240	218	150	340	210
	Jamaica	1,807	998	246	5,597	552	3,098

Table 2

The shelf area of the south Jamaican shelf and the proportions represented by coral, seagrass, sand, and mud benthic habitat types. The regions are shown in Figure 1A.

Region	1	2	3	4	5	6	Total
Total shelf area (km ²)	127	331	797	1,390	316	372	3,333
Proportion of coral	0.32	0.48	0.48	0.22	0.32	0.32	0.33
Proportion of seagrass	0.05	0.28	0.28	0.25	0.05	0.05	0.21
Proportion of sand	0.32	0.15	0.15	0.34	0.32	0.32	0.27
Proportion of mud	0.32	0.09	0.09	0.19	0.32	0.32	0.19

The fishing effort and catch rates of the two countries differed considerably. The mean fishing effort per unit area on the Jamaican grounds was fifteenfold higher than off Belize: 3,098 hook h/km²-yr (equivalent to 527 trap hauls/km²) in Jamaica and 210 hook h/km²-yr in Belize (KW: $\chi^2=9.00$, $P<0.005$). However, catch rates were ninefold higher in Belize: 1.61 kg/hook h compared with 0.18 kg/hook h (equivalent to 1.06 kg/trap haul) in Jamaica (KW: $\chi^2=9.00$, $P<0.005$).

Catch composition

The composition of the fishery also was substantially different in the two countries (Fig. 2). Prime commercial fishes from the Lutjanidae (snappers) and Serranidae (groupers) dominated the Belizean fishery, representing 74% and 11% of the catch, respectively. In contrast, lutjanids represented 23% of the Jamaican catch and serranids only 2%. Of the landings in Jamaica, 62% were of low-value species, fishes in the families Scaridae, Sparidae, Labridae, Mullidae, Holocentridae, and Acanthuridae. Another 14% were haemulids, which composed only 2% of the catch in Belize. When the data were aggregated by area, the differences in catch composition between the countries were all significantly different (Table 3), as were the differences in actual catch for all groups except lutjanids. The catch of serranids was significantly higher in Belize and that of haemulids and 'other' fish was higher in Jamaica. When the data were examined on the basis of individual landings, the number of degrees of freedom was greatly increased. Differences were highly significant for all groups: landings of serranids and lutjanids were again higher in Belize; landings of haemulids and 'other' fishes were higher in Jamaica (Table 3).

Within each country, species composition also varied significantly among

fishing grounds (Fig. 2). Landings of the main species groups were approximately log-normally distributed among regions within each country, especially in Belize, where landings per unit of area generally varied among fishing grounds by two to three orders of magnitude. In Jamaica the differences were generally closer to two orders of magnitude. Thus in Belize, landings per unit of area of lutjanids were highest in areas 4 (west Ambergris Cay) and 7 (Placencia); of serranids in areas 3 and 4 (Gallows Point and west Ambergris Cay); and of haemulids in areas 3 and 5 (Gallows Pt. and east Ambergris Cay). Several of these areas were sites of major spawning aggregations (S. Auil, unpubl. data). The outer atolls, Halfmoon Cay and Turneffe (areas 1 and 6), did not appear to be intensively fished for finfish. In Jamaica, lutjanid and haemulid landings were higher in areas 1 and 2; serranid landings were higher in areas 2 and 3. The catches of low-valued fish were more evenly distributed.

Surplus production models

Because of the heterogeneity of the fishery, we examined catch-effort relationships for species groups, both individually and combined. The slopes of the relationships of CPUE with effort (f) were nonsignificant but were positive in sign for the Jamaican and Belizean reef fisheries considered separately (Table 4). When the data for the two countries were combined, the relationship between CPUE and f was negative (Table 4, Fig. 3A). A linear relationship, obtained after log-transforming the data on f , was due largely to the substantial difference in f and CPUE between the two countries (Fig. 3B). Based upon these relationships, MSY for the total reef fisheries was estimated to be 1,046 kg/km² of productive

Table 3

Results of Kruskal-Wallis one-way ANOVA to test for differences in catch composition between Jamaica and Belize for the data shown in Figure 2. (A) test for differences in proportion of catch by fish groups aggregated by area ($n=13$); (B): test for differences in landings of fish groups aggregated by area ($n=13$); (C): test for differences in landings by individual landing ($n=503$). The statistic shown is the χ^2 value. * $P\leq 0.05$; ** $P\leq 0.01$; *** $P\leq 0.001$. NS = not significant.

	Lutjanidae	Serranidae	Haemulidae	Other
A	7.37**	6.61*	4.00*	7.37**
B	2.47 NS	5.22*	4.00*	4.00*
C	19.42***	38.2***	52.6***	12.2***

habitat (sea grass+coral), with an annual fishing effort (f_{msy}) to obtain MSY of 3,497 hook h/km² (Fig. 4A). Current fishing effort in Jamaica and Belize (Table 2) is 89% and 6% of f_{opt} , respectively. MSY for the piscivorous fishes (e.g. Serranidae, Lutjanidae,

and Sphyraenidae) was estimated to be 638 kg/km² of productive habitat, which can be caught at f_{msy} = 2,200 hook h/km² (Table 4, Fig. 4B). To maximize catch of piscivorous fishes, present fishing effort in Jamaica and Belize is 141% and 10% of f_{msy} , respectively.

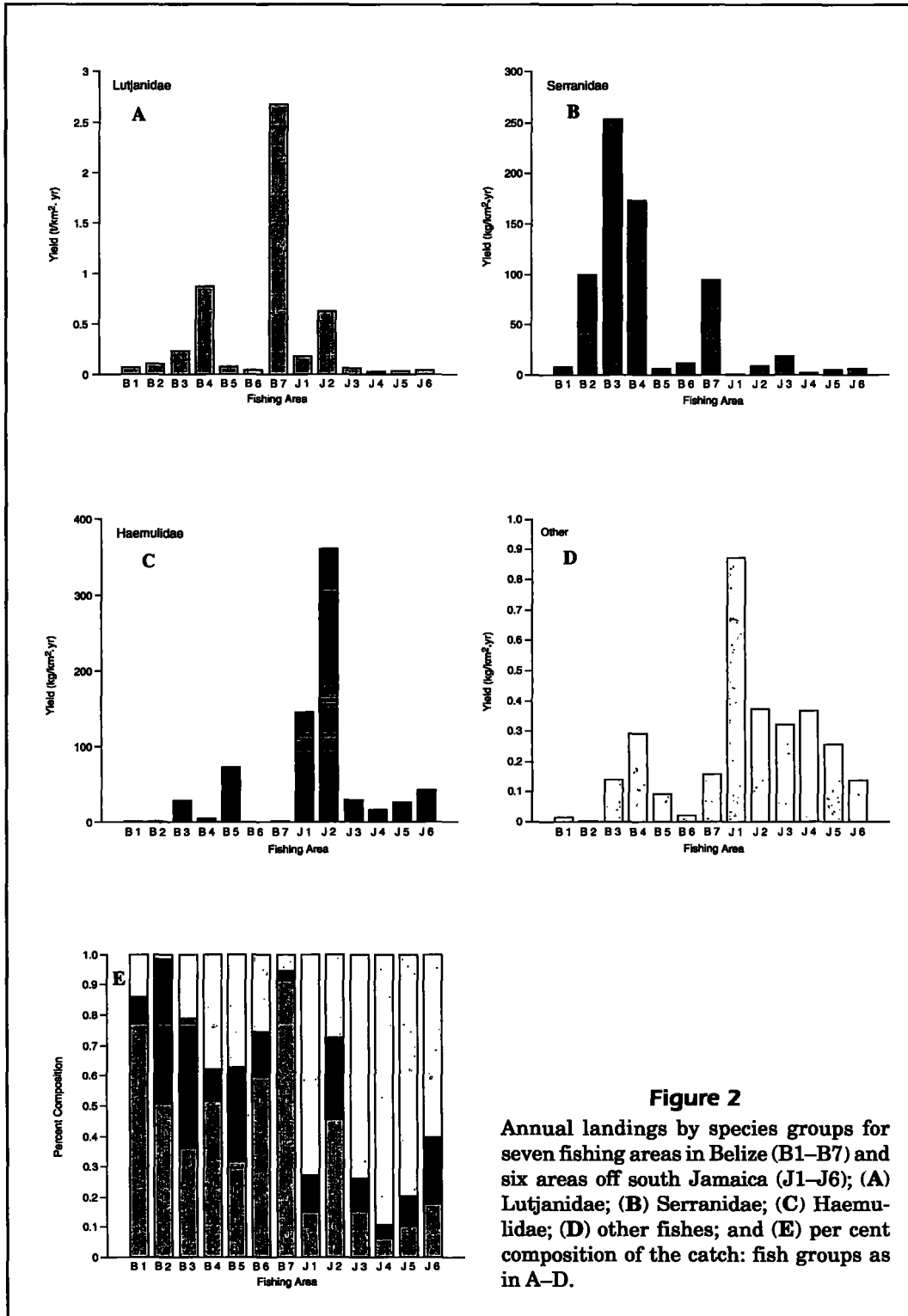
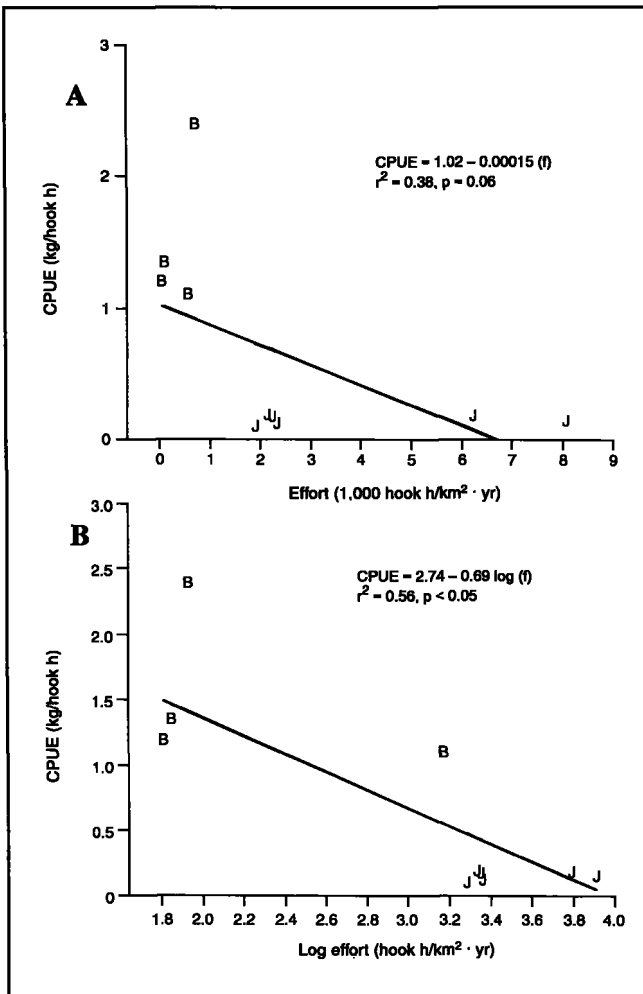


Figure 2
Annual landings by species groups for seven fishing areas in Belize (B1-B7) and six areas off south Jamaica (J1-J6); (A) Lutjanidae; (B) Serranidae; (C) Haemulidae; (D) other fishes; and (E) per cent composition of the catch: fish groups as in A-D.

Table 4

Surplus production model based upon Jamaica and Belize fishery data. Results of regressions between catch per unit of effort for all reef fish (Total CPUE) and prime commercial species (Prime CPUE) with fishing effort (f). Maximum sustainable yield (MSY) cannot be estimated for regression models for Belize and Jamaica data separately because the slopes are positive. Regression models for prime commercial species for Belize and Jamaica separately also had nonsignificant positive slopes and are not shown. R^2 =% variance explained; P =probability level; $f_{msy}=f$ at MSY.

Model	Area	R^2 (%)	P	Slope	Intercept	MSY (kg/km ²)	f_{msy} (hook h/km ²)
Total CPUE/ f	Belize	20	0.56	0.00048	1.21	—	—
Total CPUE/ f	Jamaica	3	0.79	$2.0 \cdot 10^{-6}$	0.17	—	—
Total CPUE/ f	Jamaica and Belize	38	0.06	$-1.5 \cdot 10^{-4}$	1.02	1,720	3,357
Prime CPUE/ f	Jamaica and Belize	39	0.07	$-1.4 \cdot 10^{-4}$	0.85	1,253	2,942
Total CPUE/Log(f)	Jamaica and Belize	56	0.02	-0.69	2.74	1,046	3,497
Prime CPUE/Log(f)	Jamaica and Belize	54	0.02	-0.67	2.52	638	2,200



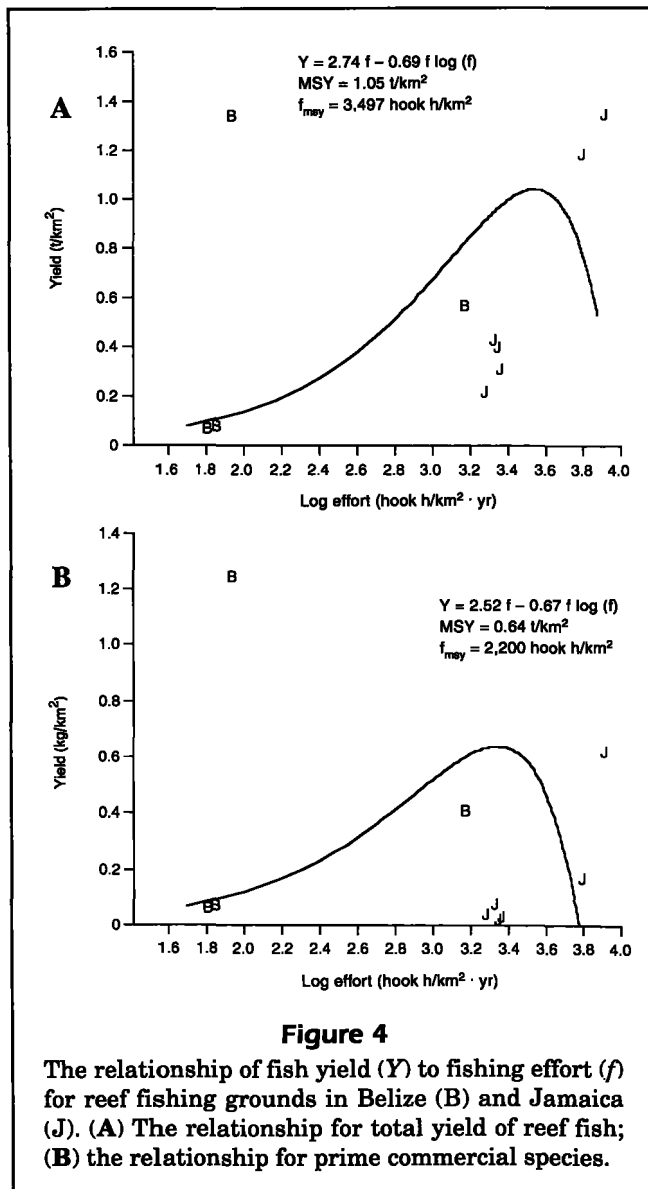
Discussion

Differences in catch composition between the two countries largely arose from the greater abundance of lutjanids and serranids in Belize. However, there may be several contributing factors. The Belizean fishery largely targets fishes for export, and only a narrow range of species, primarily lutjanids and serranids, are marketable overseas. In Jamaica, there is a large domestic market, in which a wide range of fishes may be sold. Furthermore, the predominant fishing gear in Belize is hook-and-line, which selectively catches piscivorous fishes, whereas the predominant gear in Jamaica is the Antillean fish trap, which catches a greater diversity of fishes. Less desirable species may be discarded in Belize, whereas in Jamaica, virtually all species are marketed locally. However, lutjanids and serranids are also considered prime commercial species in Jamaica, and local hook-and-line fisheries target lutjanids in particular. Thus if these groups were more abundant, they would represent a greater proportion of the catch. Historical records show that they were formerly caught in quantity by fish traps off south Jamaica (Gosse, 1851).

Figure 3

The fit of total catch of reef fish per unit of effort (CPUE) in relation to fishing effort (f) for fishing grounds in Belize (B) and Jamaica (J). (A) Fishing effort on an arithmetic scale; (B) fishing effort on a logarithmic scale.

Results of the SPM suggest that the Belize fishery is capable of further expansion in most areas but that Jamaican fishing areas are overfished. Current levels of effort in Belize seem to be only 10% of the levels that would maximize landings of prime commercial species. Landings are presently at about half of MSY for this group (Table 5). This is not surprising because many Belizean fishermen report that this fishery is virtually incidental to their lobster fishery. In Jamaica, on the other hand, present fishing effort is 41% above the level that would maximize the catch of prime commercial species, but effort is below the level predicted to maximize total fish landings. However, the low present catch of prime commercial species in Jamaica relative to their apparent potential (21% of MSY) is clearly due to the effects of overfishing rather than to under-exploitation.



The model's predictions must be regarded with caution, however, because of the poor fit of the SPM data. The relationships of CPUE and f within countries were nonsignificant but positive (Table 4). When the relationship between CPUE and f is non-negative, MSY cannot be estimated: the relationship of yield (Y) with effort (f) continues to increase rather than attain a maximum. Although a negative slope might be obtained if particular data points were removed, there was no objective basis for doing this. Thus, when data from Belize and Jamaica were pooled, the negative slope of the regression between CPUE and f was predominantly based upon the relationship between countries. This decreases the effective number of degrees of freedom and diminishes confidence in the estimate of MSY. The estimate may, therefore, serve to establish initial levels of MSY, but if time series of catch and effort are developed in the two countries, the present relationship is likely to be modified and should be reevaluated for each fishery and country as data allow.

The lack of significant relationships between CPUE and f within the Jamaican and Belizean reef fisheries may arise from several factors: heterogeneity of the fishery among areas; mixing of fish stocks between fishing areas or migration of fish into or out of these areas; and disequilibrium of the fisheries in the different areas. All of these factors appear to be present, although their relative importance is unclear.

Heterogeneity is apparent from the differences in composition of the catches within countries as well as between them. Heterogeneity was noted when landings were classified at familial or broader taxonomic groupings and likely is greater at the species level.

Movements of fishes among areas were noted particularly in the Belizean fishery, which is based upon a mix of targeted fishing on spawning aggregations and fishing on the nonspawning, more dispersed phase of the populations. CPUE may be expected to vary between these two phases of the fishery, thereby confounding the use of a spatially based surplus production model. Separation of these two phases of the fishery is difficult. CPUE is a function of both the degree of aggregation (or behavior) of the fish and of their abundance, which is presumably affected by total f . Therefore, data cannot be used from only one phase of the fishery. Furthermore, the catchability of a particular gear—and hence its impact per unit of f upon fishing mortality—presumably varies between the different phases of a fishery. It may therefore be necessary to standardize each gear type between different phases of the fishery, as well as to standardize among gears.

Jamaican, and perhaps Belizean, reef fisheries may be in a state of flux, which violates the model's as-

Table 5

Comparison of present levels of total and prime commercial fish yields (Y) and fishing effort (f) with maximum sustainable yield (MSY) (in tonnes) and f at MSY (f_{msy}) (in thousands of hook h) predicted by the surplus production model.

	Present fishery			Model			
	Total Y (t)	Prime Y (t)	f ($\times 1000$ hook h)	Total MSY (t)	Prime MSY (t)	Total f_{msy} ($\times 1000$ hook h)	Prime f_{msy} ($\times 1000$ hook h)
Belize	241	216	149	742	452	2,480	1,560
Jamaica	998	247	5,598	1,890	1,153	6,317	3,974

sumption of equilibrium. In Jamaica, one index of fishing effort, the number of fishing canoes, appears to have declined by 55% over the past decade. In a 1981 survey, 2,137 fishing canoes were recorded along the south coast (Haughton, 1988) but only 963 in the present study. (Because the fishery could be easily censused, the number of canoes on fishing beaches was the primary measure of fishing effort in most previous studies of Jamaican reef fisheries [Munro, 1978, 1983; Haughton, 1988]). Landings of fish from the south Jamaican shelf declined 82% during this decade from 5,475 metric tons (t) in 1981 (Haughton, 1988) to 998 t in 1991. The decline in landings and effort resulted in a 60% decline in CPUE from 2.56 to 1.04 t/canoe·yr. The decline in fishing effort may be a consequence of falling catch rates. The datum for CPUE in relation to f for 1991 does not fall along the line defined by the 1968–1981 data for the Jamaican fishery (Fig. 5), possibly because the fishery is not at equilibrium, that is, it has not recovered in response to recently reduced effort.

It may be expected that estimates of sustainable yield and effort obtained from the present survey would be significantly lower than previous estimates owing to reduced levels of CPUE, catch, and effort. Munro (1978) estimated that MSY for the Jamaican reef fisheries was 4.1 t/km² and that f_{msy} was 3.2 canoes/km² shelf area. These estimates were based primarily on data from the north coast, where the shelf is narrow and much of the substrate is coral, therefore they are probably comparable to our estimates based upon the coral and sea-grass fraction of the south Jamaican shelf. Munro's spatially based SPM used data from a 1968 fishery survey. Haughton (1988) developed an SPM for the Jamaica reef fishery based upon three fishery surveys of the north and south Jamaican shelves conducted between 1968 and 1981. Differences in the productivity per unit area of the north and south Jamaican shelf were not considered. Haughton estimated MSY for the south

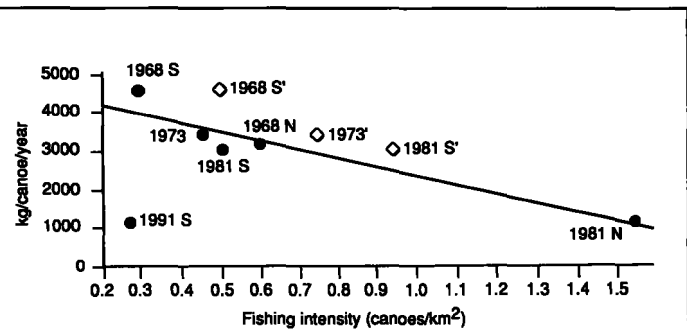


Figure 5

The relationship of catch per unit of effort for the Jamaican reef fisheries based upon data from 1968 to 1981 (from Haughton, 1988) and from the present study. Data are shown for reef fisheries off the north (N) and south (S) coasts of Jamaica. (') indicates data from the southern shelf that have been corrected for the proportion of reef and sea grass habitat. The regression line is based upon the original, uncorrected data from 1968 to 1981.

Jamaican fishery to be 2.2 t/km² of shelf with an f_{msy} of ~ 1 mechanized canoe/km². (The units of effort of the Munro and Haughton models are not entirely comparable because most canoes became mechanized after Munro's survey; Haughton standardized his effort data to the mechanized canoe.) If the data for the southern shelf in Haughton's model are normalized per unit of area of productive habitat ($\sim 50\%$ of the total shelf area), so that data from the north and south coast are comparable, the revised estimates of MSY and f_{opt} are 3.1 m/km² and 1.5 canoes/km² of productive habitat. However, there is no longer a significant relationship between CPUE and f (Fig. 5). Our estimate of MSY for the combined Jamaican and Belizean reef fisheries is 1.0 t/km² (Table 4). Based upon present effort in Jamaica being 89% of f_{opt} ($f=3,099$ hook h/km² [Table 2]; $f_{msy}=3,497$ hook h/km² [Table 4]), f_{msy} may be estimated to be approximately 0.6 canoes/km² of productive habitat; the present density of canoes is 963 canoes over a productive shelf

area of 1,807 km² or 0.5 canoes/km²). Thus, present estimates of MSY and f_{msy} are on the order of 20–30% of earlier estimates.

Declining levels of CPUE, catch, and effort in the south Jamaican fishery and lower estimates of sustainable yield and effort all indicate that the productivity of Jamaican reef fishes significantly declined because of overfishing. The species composition of the trap fishery in the 1800's appears to have been broadly similar to that off Belize today (Gosse, 1851). By 1968–71, when the first research surveys on the south Jamaican shelf were carried out, the catch was already dominated by relatively low-value fish: the Haemulidae, Scaridae, and Acanthuridae (Munro, 1983). By 1986, when these surveys were repeated, overall CPUE had declined 33%. Several families across a wide trophic range that represented the bulk of the catch in 1968–71 had declined by more than 50% (haemulids, small serranids, and acanthurids) or virtually disappeared (large serranids and large scarids) (Koslow et al., 1988). The Holocentridae and Pomacentridae were the only families that increased significantly. Thus large segments of the demersal fish community may be depleted on reefs overfished by traps. This is in contrast to reefs exploited by more selective gear, such as spears that target large piscivores, where a range of unfished or lightly fished species may increase because of reduced predation (Bohnsack, 1982).

Several factors in addition to overfishing may have contributed to the decline in productivity of Jamaican reefs. Pollution can be severe in the coastal zone (Goodbody, 1989). There has been extensive reef damage from hurricanes in recent decades. Reduced coral production is associated with coral bleaching and coral overgrowth by algae, which may be exacerbated by the decline in herbivorous fishes, as well as by eutrophication.

Previous estimates of sustainable yield from the south Jamaican shelf may have been biased upward. An important assumption of the SPM is that the fishery is at equilibrium, such that the reported catch and effort are sustainable. The progressive decline of the fishery indicates that previous yields were not sustainable; therefore, estimates of MSY based on those catch and effort data were likely inflated.

Despite the progressive decline of the reef fish fauna on the south Jamaican shelf over recent decades, fishery assessments based on area-based SPM's indicated that the region was underutilized or only moderately exploited until as late as 1981 (Munro, 1978; Haughton, 1988). These analyses seem to have been confounded by combining data from the northern and southern Jamaican shelves without normalizing for the ~50% lower density of productive

habitat on the southern shelf. The level of exploitation of the southern shelf relative to the northern shelf was therefore underestimated by ~50% (Fig. 5).

At present, the reef fishery on the south coast of Jamaica seems to be at the point of economic self-regulation (Gordon, 1954), such that effort has declined over the past decade owing to dramatically declining catch rates as a result of over fishing. In view of the general lack of opportunities in the Jamaican economy, an unmanaged reef fishery will remain heavily overfished and its productivity substantially reduced. Present landings from the southern shelf (0.5 t/km² of productive habitat) are approximately half the estimated potential MSY.

Our estimate of MSY (0.5 t/km² of shelf) is at the low end of estimates of maximum yield for reef fisheries in the Caribbean, which have generally ranged from 0.5 to 1.5 t/km² (Munro, 1983; FAO, 1985). Globally, estimates of sustainable yield from reef fisheries have ranged as high as 20 t/km², although these higher yields are generally from localized reefs rather than from entire shelf areas (Russ, 1991). Thus there may be a problem of standardization among studies.

In conclusion, we had only limited success in developing an area-based SPM for Jamaican and Belizean reef fisheries despite detailed surveys of catch and effort and estimation of the proportion of productive habitat in different areas. The difficulties seemed to be attributable to the nonequilibrium condition of the fisheries; the heterogeneous mix of species both within and between the two countries; the diversity of the fisheries that target a variety of spawning, sedentary, and possibly migratory animals; and to possible differences in productivity among sites. Thus the model's assumptions seem too restrictive to permit meaningful analysis of catch and effort data for such complex multispecies fisheries. Violation of the model's assumptions, particularly the nonequilibrium condition of the fishery, seems to have led to serious bias in previous analyses of sustainable yield and effort for the Jamaican fishery. More generally, these problems indicate that area-based multispecies SPM's should be used cautiously in guiding the future development of reef fisheries, unless the model's assumptions can be shown to be reasonably satisfied. Nonetheless, the changes in catch composition and the sharp declines in CPUE, yield, and estimated MSY in the Jamaican fishery over the past decade, despite declining fishing effort, are indicative of a severely overexploited fishery.

Acknowledgments

We thank the many people at the University of West Indies, the Belize Fisheries Unit, and the Jamaica

Fisheries Division who assisted with the project, particularly I. Goodbody, V. Gillett, A. Kong, and R. Mooyoung. We also thank R. Mahon and M. Haughton who provided useful discussions. The project was supported by a grant from the International Centre for Ocean Development of Canada (Project No. 870138). Earlier drafts of this paper were constructively reviewed by R. Johannes, T. Smith, J. Munro, and two anonymous reviewers. V. Mawson provided editorial advice.

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