Catchability estimates and their application to the red grouper (*Epinephelus morio*) fishery of the Campeche Bank, Mexico

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Abstract.–We applied a length-based additive catchability model that accounts for several sources of variation, namely time (i.e. years, months), density-dependence effects, and different fishing fleets. The model is based on 1) a transition matrix and 2) population length-structured data expressed as catch per unit of effort. Other sources of variation were estimated as anomalies from the average pattern and incorporated as additions to the slope of the catchability-at-length equation. The catchability model was applied to the red grouper (*Epinephelus morio*) fishery of the north continental shelf of Yucatan, a demersal fish resource exploited by three different fleets. A sigmoidal shape catchability-at-length function was fitted on the basis of grouper population biology and behavior, particularly reproductive aggregation. Catchability of immature fish was constant but increased with size for adult fish, especially during the reproductive season. Time- and density-dependent catchability responded to reproductive behavior and the allocation of fishing effort. When differences between fleets were incorporated, catchability differences emerged. The catchability model has the ability to identify the main properties of the fish resource and fishery that affect the relation between fishing effort and population abundance; it may therefore be helpful as an alternative stock assessment tool.

Manuscript accepted 19 November 1998.
Fish. Bull. 97:746–757 (1999).

Catchability has been considered in fisheries science as a parameter in the catch equation that relates fishing effort to population abundance:

$$C = qsEN, \tag{1}$$

where C = catch in numbers;
q = catchability;
s = probability of gear selection;
E = fishing effort; and
N = the stock size in numbers.

From this relation it is easy to understand the key role of q. Because s and E are controlled by man, changes in population abundance will be reflected in catch through q. Although classically considered a constant, q represents different sources of variation affecting stock size. Most of the existing catchability models deal with only one source of variation related to schooling of fish (e.g. MacCall, 1976; Csirke, 1988, 1989), although a few of them also consider environmental factors (Table 1).

Investigations on catchability have developed mainly in two directions (Arreguín-Sánchez, 1996): 1) those related to measuring and increasing gear efficiency, and 2) those that use catchability as a parameter to relate fishing effort to fishing mortality and population abundance for stock assessment and management purposes. The aim of this contribution is to apply a catchability model that accounts for several sources of variation related to fishing and to population processes, as proposed by Arreguín-Sánchez (1996).

The red grouper (*Epinephelus morio*) stock over the Campeche Bank is one of the largest in the world, distributed on a continental shelf of more than 100,000 km^2. As with many serranids, the red grouper stock over the Campeche Bank, Gulf of Mexico, aggregates for reproduction, a fact that is well documented in the literature (Arreguín-Sánchez et al., 1996). While they aggregate, these fish are highly vulnerable to fishing; therefore this fish behavior is a key aspect for management of the resource. Three fleets target this fish species: two from Mexico (an artisanal and a midsize fleet); and a third from Cuba. These fleets do not completely overlap in respect to their fishing grounds, and their catch structure, efficiency, and the fishing mortality that they cause to the stock are different. Our contribution is aimed to estimate catchability for the red grouper fishery.

Table 1

Catchability models in literature accounting for more than one source of variation.

Catchability model	Comments	Reference
$q_t = q_0\, exp^{-ri}$ $r_1 = \alpha_1\,(t)$ $r_2 = \alpha_2\,E(t)$	t=time, E= fishing effort	Quinn (1987)
$q = 0.085\ N^{-0.384}$ $q = 0.287\ N^{-0.278}$	Haddock, George's Bank N = population abundance $Area$ = population habitat	Grecco and Overholtz (1990)
$q = 0.095\ N^{-0.787}$ $q = 0.003\ Area^{-0.747}$	Cod gill net, Atlantic B=Stock biomass $Area$ = population habitat	Rose and Legget (1991)
$q = q_1 \dfrac{T/q_2}{1+q_3 B_t}$	Peruvian anchoveta. q_1 = base fraction of the stock size per unit of effort (when stock size is low); B = biomass; T = temperature; q_2 and q_3 are constants	Hilborn and Walters (1992)
$q(\ell, t, E, F) = f(\text{size})$	ℓ = length, t = time, E = fishing effort; f = fleets	Arreguín-Sánchez (1996)

Materials and methods

We assume that catchability 1) is length dependent; 2) depends on fish behavior; 3) and is density dependent. For fishing effort, we also assume that 1) these assumptions can be valid for individual fishing fleets, such that we can explicitly consider the individual contribution of the several fleets participating in the fishing process and 2) that units of effort have static properties, that is to say, a consistent fishing power over time.

Length-dependent catchability

The catchability coefficient must be estimated for each length class in a given time, $q(\ell,t)$. A convenient form to represent the transformation of one length-frequency distribution (representing the structure of the stock) into another is by means of a transition matrix (Shepherd, 1987; Caswell, 1988), so that

$$N(\ell,t+1) = A(\ell,k)\,N(\ell,t), \qquad (2)$$

where k and ℓ = successive length intervals;
$N(\ell,t)$ = is the stock size in numbers at time t; and
A = the transition matrix that depends on growth and mortality.

Although these processes occur concurrently, Shepherd (1987) assumed that they can be separated as the product of two terms:

$$A(\ell,k) = G(\ell,k)\,S(k),$$

where G = the effect of growth in absence of mortality; and
S = the effect of mortality (survival) and also of selection of the sampling gear.

Matrix $G(\ell,k)$ can be easily estimated by following the criteria defined by Shepherd (1987) to assign growth probabilities to each length class. The elements of $S(k)$can be defined in terms of mortality as

$$S(k) = e^{-Z(k)t} = e^{-[M+q(k,t)s(k)E(t)]},$$

where $S(k)$ represents the values of the elements in the main diagonal of the survivorship matrix (other elements are zero; see Caswell, 1988); $Z(k)t$ is the instantaneous rate of total mortality for the k^{th} length group at time t; M is the instantaneous rate of natural mortality (assumed constant); $s(k)$ is the probability of gear selection for length k; and $E(t)$ is the fishing effort at time t (which is assumed nontargeted to specific sizes within a range of sizes captured by the gear). Then fishing mortality is given as $F(k,t) = q(k,t)\,s(k)E(t)$.

Equation 2 can therefore be represented as

$$N(\ell,t+1) = \sum_k G(\ell,k)e^{-[M+q(k,t)s(k)E(t)]}N(k,t). \qquad (3)$$

If $N(\ell t{+}1)$, $N(k,t)$ and $G(\ell,k)$ are known, as well as M, $s(k)$, and $E(t)$, then $q(k,t)$ can be estimated. Equation 2 can then be solved iteratively for $q(k,t)$ by using an algorithm to minimize differences between observed and calculated values of $N(\ell,t+1)$.

Once $q(k,t)$ values are obtained, the catchability pattern with length can be observed and a tendency quantified. Although a catchability-at-length model may be empirically determined, its interpretation must be made by considering the population biology and behavior of the fish. On an annual basis, the model is represented by the function

$$q(\ell)\alpha\beta(\ell)\cdot\ell \tag{4}$$

whose slope $\beta(\ell)$ represents the rate of change of catchability with length for a given year. If several years are considered for a stable period of the fishery, then a general function can be estimated where the slope of the length-based catchability pattern in Equation 4 can be expressed by $\beta(\ell,\bullet)$, where the symbol • represents the average stock level over a range of years in which it can be reasonably assumed to be stable.

Time-dependent catchability

Gulland (1983) expanded the scope of the catchability coefficient to a structured population as expressed in the following equation:

$$C(\ell,\Delta t)=q(\ell,\Delta t)s(\ell)E(\Delta t)N(\ell,\Delta t). \tag{5}$$

This represents the capture of fish of various sizes (ℓ) during a time period Dt. Taking the mean stock size ($\overline{N}$), and rewriting Equation 5 in terms of catch per unit of fishing effort, U, we obtain

$$U(\ell,\bullet)=q(\ell,\bullet)\overline{N}(\ell),$$

with $$U(\ell,\bullet)=C(\ell,\Delta t)/s(\ell)E(\Delta t)$$

and then

$$\begin{aligned}\mathrm{Ln}\big[U(\ell,t)/U(\ell,\bullet)\big]&=\mathrm{Ln}\Big[q(\ell,t)\overline{N}(\ell)\big/q(\ell,\bullet)\overline{N}(\ell)\Big]\\&=\mathrm{Ln}\big[q(\ell,t)/q(\ell,\bullet)\big].\end{aligned} \tag{6}$$

This can be interpreted as the departure or anomaly in catchability at time t with respect to the average for a given length class. Arreguín-Sánchez (1996) suggested that this ratio is a linear function of size, represented by the midlength class as

$$\mathrm{Ln}\big[q(\ell,t)/q(\ell,\bullet)\big]=\alpha(t)+\beta(t)\ell, \tag{7}$$

where

$$\beta(t)=\mathrm{Ln}\big[q(\ell+1,t)/q(\ell,t)\big]-\mathrm{Ln}\big[q(\ell+1,\bullet)/q(\ell,\bullet)\big].$$

The intercept $\alpha(t)$ in Equation 7 can be interpreted as the relative vulnerability of small fish, and also as an index of the relative abundance of recruits. The slope $\beta(t)$ expresses the rate of change of catchability-at-length with respect to the average, or in other words, the departure (anomaly) from the average catchability pattern with length.

Once $\beta(\ell,\bullet)$ is estimated from Equation 4, the value of $\beta(t)$ can be added to $\beta(\ell,\bullet)$ to obtain the corresponding catchability values for a given time period.

Amount of fishing and density-dependent catchability

The relation between population size and catchability has been most studied in pelagic clupeoid fish (Murphy, 1966; MacCall, 1976; Csirke, 1988, 1989; Pitcher, 1996), where catchability is inversely related to stock size. Thus a density-dependent effect can be approached by considering the population as a whole, and the function

$$\overline{q}\,w(t)=f\{N(t)\} \tag{8}$$

can be fitted, where $\overline{q}\,w(t)$ is the weighted value of q at time t, with U at time t as a weighting factor. An analogous approach is proposed for each length class. For a stable period of time, we can assume that the amount of fishing, or the total fishing effort E, is one of the main sources of variation of the population density and the structure of the exploited stock. A change in both of these population characteristics will be reflected in the $\beta(t)$ coefficient. With Equations 1 and 8, it is possible to relate changes in $q(\ell,t)$ as a function of coefficient $\beta(t)$:

$$\beta(t)\alpha\,\beta(E)\cdot\ell, \tag{9}$$

where a constant natural mortality rate is assumed for all length classes over time.

Because $\beta(t)$ represents the departure of the catchability pattern with length at time t, Equation 9 measures the effect of the amount of fishing on the anomaly, and it is represented by the slope $\beta(E)$. The magnitude and sign of $\beta(E)$ will provide information about changes in stock density. A negative sign means that for a low level of fishing, q will increase with fish length.

Catchability differences between fleets

Following the same rationale as that in Equation 7, differences in q between fleets as a function of length can be estimated. If q and h represent two different fishing fleets, Equation 6 can now be expressed as

$$\mathrm{Ln}\big[U(g,\ell,t)/U(h,\ell,t)\big]=\mathrm{Ln}\big[q(g,\ell,t)/q(h,\ell,t)\big] \tag{10}$$

and

$$\mathrm{Ln}\left[q(g,\ell,t)/q(h,\ell,t)\right]=\alpha(f)+\beta(f)\cdot\ell, \qquad (11)$$

where f indexes fishing fleets.

In this case, the intercept $\alpha(f)$ is the relative difference in catchability between fleets for the smallest fish. The slope $\beta(f)$ reflects the difference in fishing performance measured as the anomaly in catchability of the fleet g with respect to the fleet h.

The additive catchability model

The deterministic model that incorporates the processes discussed can now be set out. It relies on the changes of the slope $\beta(\ell, \bullet)$, representing the catchability-at-length pattern, by the addition of the slopes of the partial effects described by Equations 7, 9, and 11. The slope of the catchability model, with the form defined by Equation 4, is represented by

$$\beta(\ell,t,E,f)=\beta(\ell,\bullet)+\beta(t)+\beta(E)+\beta(f). \qquad (12)$$

The value of $\beta(\ell, t, E, f)$ represents the slope of the catchability-at-length function without restriction to equilibrium, which has been compensated by the addition of the term $\beta(t)$, where t refers to any appropriate unit of time.

The red grouper (*Epinephelus morio*) fishery in the Campeche Bank, Mexico

The red grouper on the North continental shelf of Yucatan is exploited by three fleets: an artisanal and a mid-size fleet from Mexico, and a large-scale fleet from Cuba. These fleets overlap in respect to their fishing grounds (Moreno et al.[1]): Mexican fleets overlap in a range of 60% to 70%; the midsize fleet from Mexico and large-scale fleet from Cuban, around 60%; and the artisanal and Cuban fleets, between 12% and 16%. This overlap in fishing grounds means that each fleet causes fishing mortality on different sizes of the stock and thus necessitates that the fleets be considered separately for stock assessment purposes.

The artisanal fleet of Mexico is composed of vessels of approximately 9 m long, operating from the coast to 20 m depth, and catching mainly juvenile and preadult fish. The midsize fleet uses 15-m vessels operating at depths of 10 to 80 m, and catch comprises both juvenile and adult fish, according to the season. The Cuban fleet fishes mainly with 27-m vessels, operates between 20 and 90 m depth, and catches adult fish. Both Mexican fleets have free access and move seasonally in the area following changes in fish density (i.e. with reproductive aggregation). The Cuban fleet has a catch quota of 3900 t of demersal fish, of which more than 80% is red grouper. This fleet remains in the central and eastern region of the continental shelf of Yucatan most of the time.

Differences related to gear, fishing effort, and fishing strategies among fleets are described in Moreno (1980), Burgos (1987), and Fuentes (1987) for the midsize fleet; Sáenz et al. (1987), Salazar (1988), and Solana-Sansores and Arreguín-Sánchez (1991) for the artisanal fleet; Valdés and Padrón (1980) for the Cuban fleet; and Seijo (1986), González-Cano et al. (1993), and Arreguín-Sánchez et al. (1996) for the three fleets. In this paper we used standardized fishing days as the unit of fishing effort.

For the catchability model, available data for the red grouper fishery are summarized in Table 2. Detailed information is derived from the midsize fleet, which harvests around 70% of the total annual yield. Other fleets share the remaining 30% more or less equally. Because the midsize fleet also catches a size range that overlaps the other two, this fleet is the start of our analysis. Later, we will incorporate the other fleets into the catchability model.

To solve Equation 3, we assumed that individual growth follows the von Bertalanffy equation with values of L_∞ = 87 cm total length (TL) and K = 0.12/year (Arreguín-Sánchez[2]), and the natural mortality coefficient M = 0.3/year (Doi et al., 1981; Contreras et al., 1994).

The selection factor for each length class $s(\ell)$, representing a probability term directly affecting the abundance of length classes in the catch, was set to be $s(\ell) = 1$. For simplicity, red grouper fishery gears were assumed nonselective (hook-and-line and hand lines with different sizes and baits).

Annual catch-per-unit-of-effort(U)-at-length data for the period 1973 to 1987 for the midsize fleet was used. The iterative procedure described for Equation 3 was applied to each pair of yearly data to obtain initial values of catchability per length class and year. Catchability values for each length class $q(\ell, y)$ were used to fit the trend with length (Fig. 1) and to describe variability of $q(\ell,\bullet)$. The solution for Equation 3 does not require a previous knowledge of recruits at $U(\ell, t)$ and $U(\ell, t+1)$, and it was solved for

[1] Moreno, V., F. Arreguín-Sánchez, M. Contreras, and R. Burgos. 1991. Analysis of usage patterns in shared stocks: the red grouper fishery from the continental shelf of Yucatan, Mexico. Proc. 44th Ann. Sess. Gulf and Caribb. Fish. Inst., 18 p. [Mimeo.]

[2] Arreguín-Sánchez, F. 1996. Length-based growth estimation for the red grouper (*Epinephelus morio*) in the North continental shelf of Yucatan, Mexico. Centr. Interdiscip. Cienc. Mar., México, 19 p. [Manuscript.]

Table 2

Summary of the data used in this paper for the red grouper fishery on the north continental shelf of Yucatan, Mexico. Fleets operate with long lines of different sizes (artisanal also uses hook-and-line). Fishing effort was standardized as fishing days (see Arreguín-Sánchez et al., 1996)

Fleet	Annual catch-at-length	Monthly catch-at-length	Sampling design	Site of landing
Artisanal[1]	1987	1987	three stages (port, vessels, baskets)	Ports along the coast of Yucatan, Mexico
Midsize[2]	1975 to 1987 (except for 1986)	1975 to 1987 (except for 1986)	two stages (day/vessel and commercial size)	Port of Progreso, Mexico
Cuban fleet[2]	1975 to 1987		two stages (vessels and commercial size).	Port of La Havana, Cuba

[1] Source: Centro de Investigación y de Estudios Avanzados del IPN, Yucatan, Mexico.
[2] Source: Instituto Nacional de la Pesca. Centro Regional de Investigación. Pesquera de Yucalpetén, Yucatan, Mexico.

n–1 or *n*–2 catchability values, with differences in *n* caused by the absence of recruitment estimates. Because we fitted the general tendency as a catchability-at-length pattern, one or two missing points will not affect the estimates.

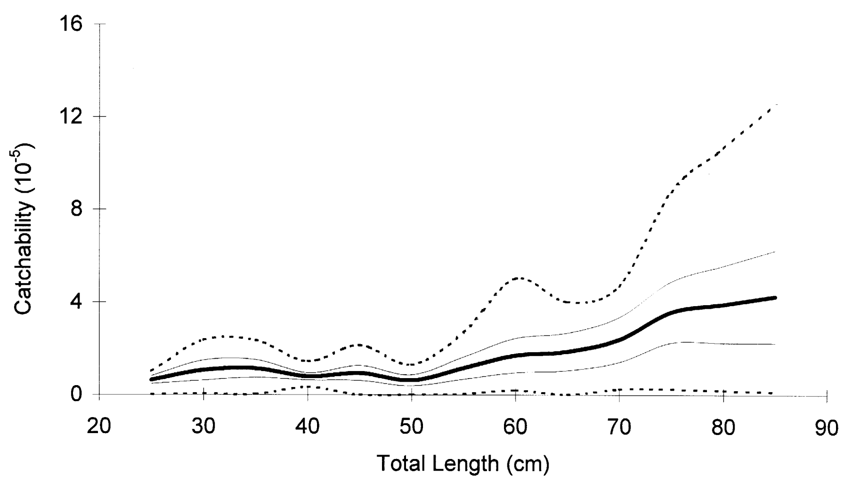

Figure 1

Catchability-at-length pattern for the Mexican midsize fleet of the red grouper fishery estimated with Equation 3. The bold line indicates average values over the period from 1973 to 1987; thin lines denote one standard deviation, dashed lines represent absolute minimum and maximum values.

Results

Length-dependent catchability

The fitting process required some consideration of population behavior because trend could be adjusted to an exponential or sigmoidal function. We decided on a sigmoidal form because of reproductive behavior. During reproductive aggregation, adult fish (>50 cm TL) form groups with a sex ratio (females: males) close to 6:1, comprising individuals of around the same size, but without any apparent size segregation between groups. This is well known by fishermen, and has been described by Moe (1969), Shapiro (1987), and Mexicano-Cíntora (1990). In terms of fishing, adults within a specific area have the same probability of catch. In the catchability-at-length trajectory, we think this reproductive behavior can be well represented by an asymptotic trend of catchability for large fish.

The variation in catchability of young fish, as expressed by one standard deviation (Fig. 1) was similar for lengths between 20 to 50 cm and increased sharply after first maturity (at 50 cm TL, as defined by Mexicano-Cíntora, 1990).

The generalized catchability-at-length equation fitted for the red grouper was

$$q(\ell,\bullet)=\frac{0.00004256}{1+e^{-(3.896+0.0064\cdot\ell)}} \qquad (13)$$

with the standard error (SE) of the ordinate SEα = 0.773, and SE$_\beta$ = 0.012 for the slope; R^2 = 0.728 (df=10).

Time-dependent catchability

Time variation of catchability was analyzed considering both annual and monthly catch-structured data. From Equation 7, parameters $\alpha(y)$ and $\beta(y)$ were estimated by regressing

$$\mathrm{Ln}[U(\ell,t)/U(\ell,\bullet)]$$

with length (Fig. 2). Table 3 shows values of the constants for both midsize Mexican and Cuban fleets for annual data.

On a monthly basis, the same computations were developed for the mid-size fleet. Departures represented in parameters $\alpha(m)$ and $\beta(m)$ were estimated in a similar way to those in Equation 7, but considering annual catch-structured data. Seasonal changes in vulnerability occurred: q increased in winter (December to February) in synchrony with the reproductive aggregation (Fig. 3). Catchability was lower in autumn, when the population is dispersed along the continental shelf and the vulnerability of young fish in coastal waters increases.

Catchability differences between fleets

Following Equation 11, differences between fleets were evaluated by comparing annual data for the Cuban fleet with those of the midsize fleet for the period 1975 to 1987. Mexican mid-size and artisanal fleets were compared on a monthly basis for 1987. Parameters for $\alpha(f)$ and $\beta(f)$ were obtained (Tables 4 and 5). Positive values of $\beta(f)$ indicate that relative catchability for small fish is higher for the midsize fleet than for the Cuban fleet; and lower for large fish. This scheme represents differences in fishing areas between fleets. The negative value $\beta(f)$ for in 1982 suggests fleets changed their usual behavior. Similar interpretation can be made for monthly data between the artisanal and midsize fleets.

Figure 3 shows the tendency of

$$\mathrm{Ln}[U(\text{mid-scale},\ell,t)/U(\text{Cuban},\ell,t)]$$

with length. An inflection point is observed just at the length at first maturity (i.e. 50 cm LT). Positive values indicate that q is higher in small (immature) fish for the midsize fleet than for the Cuban fleet, whereas q is equal in both fleets for mature fish. For the tendency of

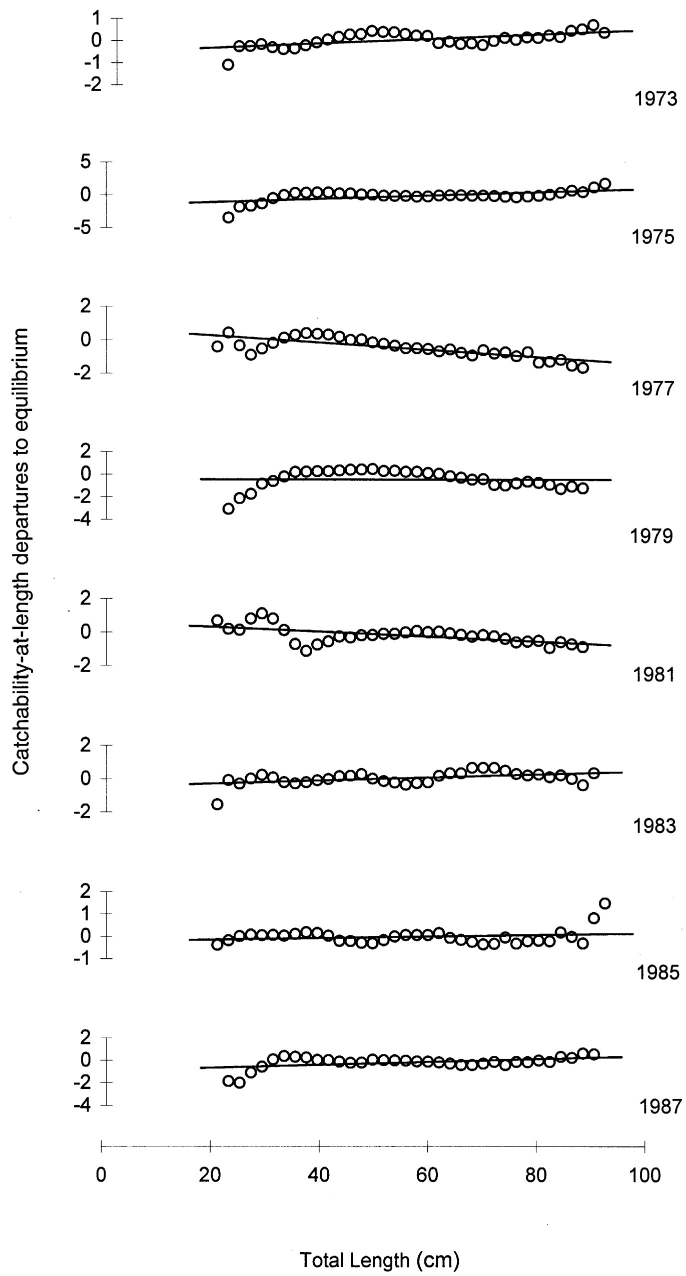

Figure 2

Annual tendencies of the ratio $\mathrm{Ln}[U(\ell,t)/U(\ell,\bullet)]$ with length for the Mexican midsize fleet of the red grouper fishery representing departure of catchability-at-length pattern with respect to equilibrium, as expressed in Equation 6.

$$\mathrm{Ln}[U(\text{artisanal},\ell,t)/U(\text{mid-scale},\ell,t)]$$

with length, catchability of immature fish was higher for the artisanal than for the midsize fleet, and again equal for adult fish up to 65 cm TL. For fish larger than 65 cm, q was higher in the midsize fleet.

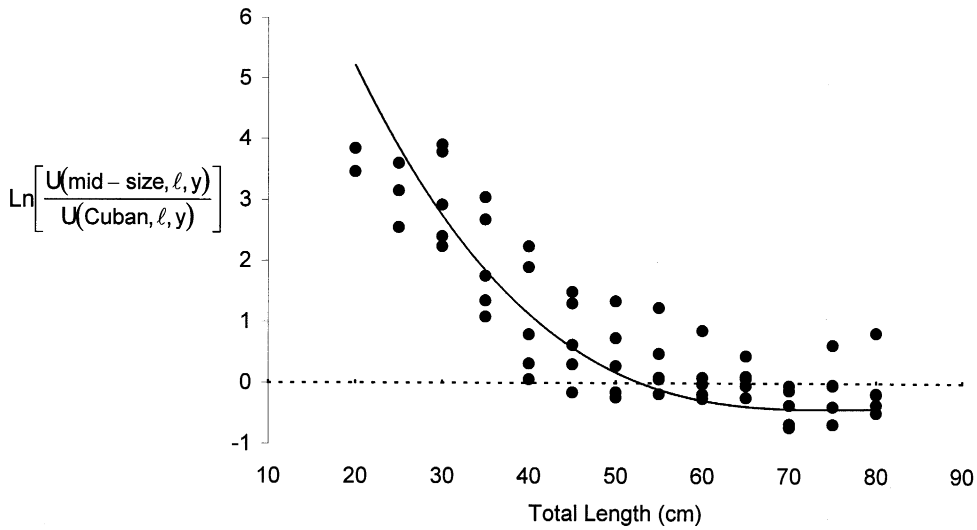

Figure 3

Trend in catchability-at-length differences, between Mexican midsize and Cuban fleets for the period 1975 to 1979, as expressed by Equation 11. Positive values indicate higher vulnerability for immature fish for the midsize fleet than for the Cuban fleet. Vulnerability of adult fish to both fleets is equal.

Table 3

Parameters of Equation 7 for the Mexican midsize and Cuban fleets for the red grouper fishery. $\alpha(y)$ expresses relative vulnerability of recruits each year and $\beta(y)$ departure of catchability trend with length, both with respect to equilibrium. (*P<0.05; **P<0.01).

Year	$\alpha(y)$ midsize	$\beta(y)$ midsize	R^2	$\alpha(y)$ Cuban	$\beta(y)$ Cuban	R^2
1973	–0.509	0.010	0.405*			
1974	0.508	–0.013	0.664*			
1975	0.511	–0.010	0.487**	–1.494	–0.018	0.602*
1976	0.953	–0.025	0.610**	0.865	–0.006	0.507**
1977	0.683	–0.022	0.600**	0.767	0.024	0.624*
1978	1.045	–0.024	0.686**	0.416	0.047	0.496*
1979	0.941	–0.021	0.757*	–1.396	0.033	0.771**
1980	–0.612	0.015	0.614**	–2.925	–0.043	0.544**
1981	0.476	–0.013	0.643**	–2.147	–0.026	0.622*
1982	0.487	–0.012	0.396*	1.923	–0.021	0.483**
1983	–0.401	0.009	0.371*	1.448	0.020	0.701**
1984	0.175	–0.005	0.446**	0.828	0.079	0.513**
1985	0.135	–0.004	0.432*	–1.126	0.026	0.661**
1986	–1.064	0.023	0.739*	–4.889	0.079	0.596**
1987	–0.915	0.013	0.581*	–1.250	0.026	0.470**

Amount of fishing and density-dependent catchability

As in Equation 9, values of $\beta(y)$ from Table 3 were fitted against fishing effort at time t. Figure 4 shows the tendency for both the midsize and Cuban fleets. For the midsize fleet, the model gives the following values for the parameters: $\alpha(E) = 0.1252$, $\beta(E) = 4.8 \cdot 10^{-6}$; $R^2 = 0.74$. Although the tendency for the Cuban fleet was also negative, the observed variability was higher, and at least two probable tendencies were empirically identified (Fig. 4B), both of them as a consequence of changes in the catch quota assigned to the Cuban fleet. For further computations, the density-dependent effect was assumed to be similar for both fleets because of the absence of more detailed information to support quantitative analysis. This assumption is reasonable because both fleets average more than 60% overlap in a year, but almost 100% during reproductive aggregation.

Because of the evident differences in behavior between juvenile and reproductive fish, the density-dependent effect of the amount of fishing was also applied within each length class, as in Equation 9. Parameters of the model are given in Table 6. Variation of the slope $\beta(E)$ with length class is shown in Figure 5. Once again, immature fish behaved differently from adults. The density-dependent effects for immature fish were constant, whereas the same effect increased with size for sizes >50 cm TL. It is clear that the density-dependent effect during aggregation promotes a greater catchability, and because the older adult fish tend to remain longer in deeper waters (Shapiro, 1987), the density-dependent effect will increase with size (age).

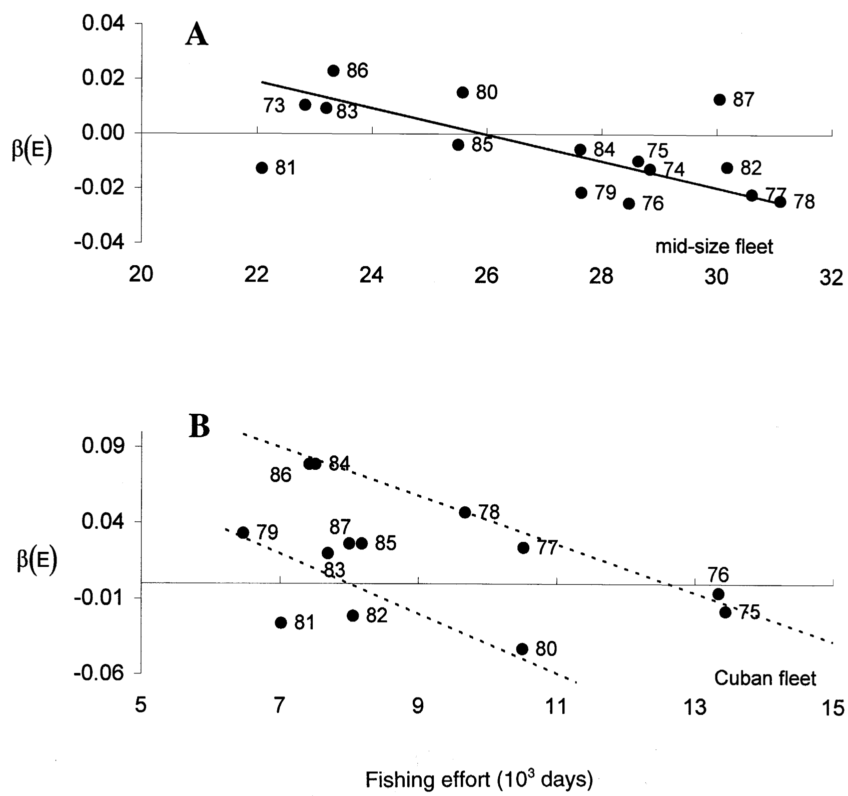

Figure 4

Estimation of density-dependent effects on catchability-at-length pattern for (**A**) the Mexican midsize fleet and (**B**) Cuban fleet of the red grouper fishery (Eq. 11). General trends suggest density-dependent effects by fleets are of the same magnitude (see text for interpretation).

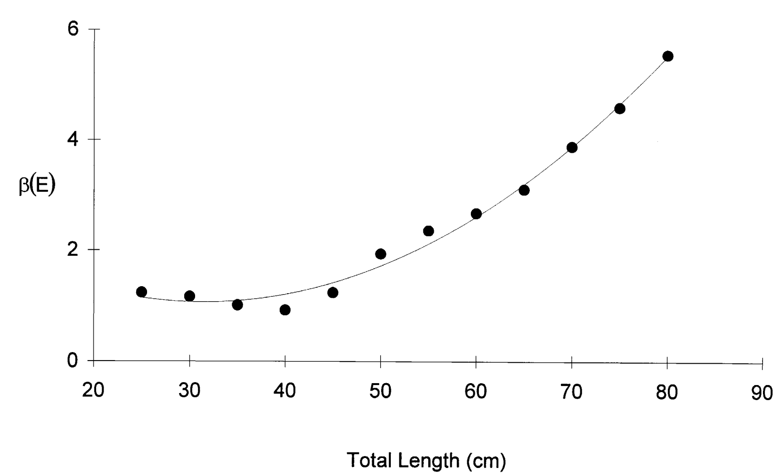

Figure 5

Trend in density-dependent effects on q within each length class with size.

The additive catchability model for the red grouper fishery

Once several sources of variation were estimated, a model (Eq. 12) was obtained by adding partial effects to the slope of Equation 13, as follows:

$$q(\ell,t,f,E)=\frac{0.00004256}{1+e^{-\{3.896+\beta(\ell,[y,m],f,E)\ell\}}},$$

where

Table 4

Estimates of parameters for Equation 11 describing departure of catchability coefficient with length for the Cuban fleet with respect to the Mexican midsize fleet for the red grouper fishery (*$P<0.05$; **$P<0.01$).

Year	$\alpha(f)$	$\beta(f)$	R^2	n
1975	–4.474	0.052	0.636**	14
1976	–2.956	0.047	0.613*	13
1977	–3.590	0.058	0.807**	14
1978	–3.904	0.065	0.822*	12
1979	–5.186	0.076	0.795*	11
1980	–4.713	0.055	0.736*	12
1981	–6.476	0.097	0.708*	13
1982	0.323	–0.020	0.711**	9
1983	–4.527	0.051	0.713*	10
1984	–3.936	0.059	0.561**	11
1985	–3.847	0.050	0.848**	13
1986	–6.149	0.070	0.873*	13
1987	–3.942	0.055	0.606*	11

$$\beta(\ell, y, m, f, E) = \beta(\ell, \bullet) + \left[\beta(y), \beta(m)\right] + \beta(f) + \beta(E),$$

where i indexes fleet, and each constant takes the corresponding value, depending on the specific length class (ℓ), time, year (y) or month (m), fleet (f), and the specific density-dependent effect (E).

Discussion

The catchability model incorporates several sources of variation, such as individual size, time variations, and density-dependent effects, for which we assumed fishing effort is the most important variable affecting fish density, and the participation of several fishing fleets which differ in gear, catching power, and effort allocation.

The additive-catchability model, as applied to the red grouper, performed well and allows us to identify some aspects of fish behavior that influence catchability. For example, reproductive aggregation increases vulnerability of fish. Of particular importance are the relative constancy of catchability and its variance for immature individuals, and the increasing vulnerability of adult fish with size, especially during reproductive aggregation. This is related to the reproductive behavior of the population. Young fish remain close to the coast, with east–west seasonal displacements, whereas adults move across the continental shelf and aggregate during winter for reproduction. This means that juveniles and adults respond differently to fleets. The model also identified the differential accessibility of specific size ranges to different fleets. This is important because, in a fully exploited fish resource such as the red grouper, controls on fishing mortality must enhance survival of spawners and recruits. Figure 6 summarizes the relation between fishing effort, maturity, and seasonal changes in catchability for the red grouper fishery. During reproductive aggregation, identified by the maturity index, vulnerability increases and vessels spend less fishing effort to obtain a given level of yields. After reproduction, groupers disperse along the continental shelf and fleets must increase fish-

Table 5

Estimates of parameters for Equation 11 describing departure of catchability coefficient with length for the midsize fleet with respect to the artisanal fleet, both from Mexico (*$P<0.05$; **$P<0.01$).

Month	$\alpha(f)$	$\beta(f)$	R^2	n
January	2.953	–0.071	0.576*	23
February	2.654	–0.083	0.701**	22
March	4.180	–0.107	0.719*	24
April	7.904	–0.230	0.965**	14
May	2.524	–0.064	0.769*	28
June	1.295	–0.032	0.483*	31
July	1.426	–0.041	0.720*	28
August	–1.589	0.041	0.562**	16

Table 6

Estimates of parameters for Equation 9 representing density-dependent effects within each length class (n=13, df=11; *$P<0.05$; **$P<0.01$).

Total length (cm)	$\alpha(E)$ 10^{-8}	Standard error $\alpha(E)10^{-7}$	β(E) 10^{-8}	Standard error $\beta(E)10^{-9}$	R^2
25	3.76	1.211	1.238	1.282	0.89**
30	31.05	3.356	1.164	3.471	0.50**
35	54.72	3.276	1.013	2.905	0.52**
40	48.32	1.574	0.926	2.013	0.66*
45	26.39	1.147	1.237	2.718	0.65*
50	3.68	1.091	1.936	2.426	0.85*
55	–0.31	1.123	2.360	2.974	0.85*
60	0.62	1.144	2.678	2.857	0.89*
65	1.56	1.316	3.198	1.892	0.96**
70	–1.17	1.388	3.886	2.593	0.95**
75	–2.83	1.510	4.589	2.621	0.96**
80	0.43	0.743	5,549	3.282	0.96*

ing intensity because vulnerability of fish will decrease.

For the density-dependent catchability, the model describes fish behavior reasonably well. The red grouper is a gregarious and territorial fish. Stock density is reflected straightforwardly in yields. If fish densities decrease, q will decrease, and vice versa. This response to the amount of fishing is reflected by the model.

For the catchability model, note that although a transition matrix is very helpful for the estimation process, the form of the catchability-at-length function must be interpreted with good understanding of the biology of the exploited fish resource and of the fishery. Fish biology probably is the most important aspect because the effect of other sources of variation are added to the slope of this function.

The resulting catchability model can be easily incorporated into estimations of fishing mortality and population size; i.e. for the midsize fleet at time t, fishing mortality can be expressed by

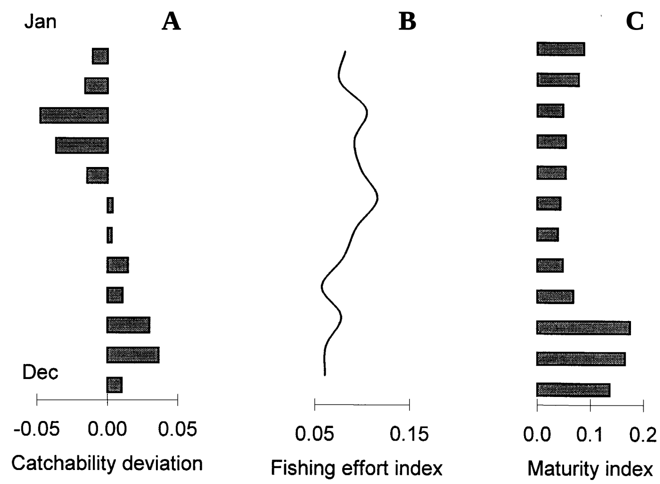

Figure 6

Schematic representation of the main q features of the red grouper fishery on the Campeche Bank: (**A**) seasonal catchability variation represented as departure of the annual average; (**B**) fishing effort index, represented as a monthly proportion of the year; (**C**) maturity index, reflecting diameter of oocytes.

$$F(\ell, t, \text{midsize}, E) = q(\ell, t, \text{midsize}, E) \cdot E(t, \text{midsize}). \quad (14)$$

For the population size, the participation of the three fleets can be incorporated,

$$N\left(\ell, t, \sum_{i=1}^{3} f_i, E\right) = \frac{F\left(\ell, t, \sum_{i=1}^{3} f_i, E\right) C\left(\ell, t, \sum_{i=1}^{3} f_i\right)}{F\left(\ell, t, \sum_{i=1}^{3} f_i, E\right)\left[1 - e^{-\left\{M + F\left(\ell, t, \sum_{i=1}^{3} f_i, E\right)\right\}}\right]}. \quad (15)$$

Despite the potential use of the catchability coefficient in some stock assessment models (i.e. age-based virtual population analysis, VPA, Pope, 1972; and length-based VPA, Jones 1981, 1984; Gulland[3]), Equations 14 and 15 suggest an alternative stock assessment tool, based on length-composition data.

A detailed description of catchability through the additive model reflecting fish behavior and fishery practices could be very useful for management purposes when it is incorporated into assessment models such as the above. Currently the red grouper fishery is subjected to heavy fishing where the main problems are intensive fishing of juveniles and the high vulnerability of adults. Because the additive catchability model describes these processes and incorporates all fleets, results can strongly aid management decisions based on a differential control of fishing mortality within the stock structure and between fleets.

Even when the model can describe the study well, we observed some critical aspects during application. The first is that we must know red grouper behavior sufficiently well to decide the form of the catchability-at-length relation (Eq. 4). Statistical criteria (i.e. a correlation coefficient) are not sufficient. A wrong interpretation of this could mean a disaster for the fishery. A second and similar aspect can occur for density-dependent catchability. The third aspect is the significance of sources of variation. Because the catchability model is based on the addition of the slopes of each particular variable and relation (i.e. with length, time, etc.), we must test that these slopes are significantly different from zero (see Equations 4, 7, 9, and 11), and if they are not different, the source of variation tested does not help to explain changes in q.

The fourth aspect involves the number of parameters to be estimated, which usually is taken as proportional to the complexity of the model computations, and inversely related to applicability. For the present case, the number of parameters in the model is $n + 2$, where n is the number of sources of varia-

[3] Gulland, J. A. 1965. Estimation of mortality rates. Annex to rep. Arctic Fish. Working Group. ICES Council Meeting (CM), 1965, paper 3, 9 p.

tion to be considered. However, the number of constants to be estimated strongly increases with the length of the time-series of data as $3(m \bullet y \bullet f) + 2(\ell) + 2$, with m = number of months, y = number of years, f = number of fleets, and ℓ = number of length classes. For example, in our study case, with $y = 13$, $f = 2$, and $\ell = 12$, the number of constants to be estimated will be 104. We think these are a lot of parameters; however, they are easily estimated because all of them are obtained by regression or by an analogous technique.

Acknowledgments

Some of the initial ideas developed in this paper were inspired by the late John A. Gulland, while F. A.-S. was at the Renewable Resources Assessment Group, London, in 1989. We want to dedicate this contribution to his memory. Our gratitude is also extended to S. Rodríguez, L. Capurro, and D. Pauly for their support and valuable comments on an early draft. We also thank three anonymous referees for their valuable comments. The first author was funded by the National Polytechnic Institute through COFAA, EDD and DEPI. Lastly, we thank Ellis Glazier, CIBNOR, who edited the English-language text.

Literature cited

Arreguín-Sánchez, F.
1996. Catchability: a key parameter for fish stock assessment. Rev. Fish Biol. Fish. 6:1–22

Arreguín-Sánchez, F., M. Contreras, V. Moreno, R. Burgos, and R. Valdés.
1996. Population dynamics and stock assessment of the red grouper (*Epinephelus morio*) fishery on Campeche Bank, Mexico. *In* F. Arreguín-Sánchez, J. L. Munro, and D. Pauly (eds.), Biology of tropical groupers and snappers. ICLARM Conf. Proc. 48:202–217.

Burgos, R.
1987. Operaciones y rendimientos de la flota pesquera mayor de Yucatán durante 1985. Ph.D. diss., Contr. Invest. Pesq. Cent. Reg. Invest. Pesq. Yucalpetén, Inst. Nal. Pesca, México.

Caswell, H.
1988. Approaching size and age in matrix population models. *In* E. Ebenman and L. Persson (eds.), Size-structured populations, 85–105 p. Springer-Verlag, Berlin, Heidelberg.

Contreras, M., F. Arreguín-Sánchez, J.A. Sánchez, V. Moreno and M.A. Cabrera.
1994. Mortality and population size of the red grouper (*Epinephelus morio*) fishery from the Campeche Bank, Mexico. Proc. 43th Ann. Sess. Gulf Caribb. Fish. Inst., 393–401 p.

Csirke, J.
1988. Small shoaling pelagic fish stocks. *In* J. A. Gulland (ed.), Fish population dynamics, 2nd ed., p. 271–302. John Wiley and Sons, London.

1989. Changes in the catchability coefficient in the Peruvian anchoveta (*Engraulis ringens*) fishery. *In* D. Pauly, P. Muck, J. Mendo, and I. Tsukayama (eds.), The Peruvian upwelling ecosystem: dynamics and interactions, 207–219 p. ICLARM Conf. Proc. 18. IMARPE-Perú, GTZ-Germany, ICLARM-Philippines.

Doi, T., D. Mendizabal, and M. Contreras.
1981. Análisis preliminar de la población de mero *Epinephelus morio* (Valenciennes) en el Banco de Campeche. Ciencia Pesquera, Inst. Nal. Pesca., México. 1(1): 1–16.

Fuentes, D.
1987. La pesquería de mero en el Banco de Campeche. Mem. VII Congr. Nal. Oceanogr. Ensenada, Mexico 1:361–374.

González-Cano, J., F. Arreguín-Sánchez, M. Conteras, V. Moreno, R. Burgos, C. Zetina, and V. Ríos.
1993. Diagnóstico del estado de la pesquería de mero (*Epinephelus morio*) en el Banco de Campeche. Informe del Grupo de Trabajo sobre el Recurso Mero. Inst. Nal. Pesca. México, 47 p.

Grecco, V., and W. J. Overholtz.
1990. Causes of density-dependent catchability for George's Bank haddock *Melanogrammus aegelfinus*. Can. J. Fish. Aquat. Sci. 47:385–394.

Gulland, J. A.
1983. Fish stock assessment: a manual for basic methods. John Wiley and Sons, New York, NY, 223 p.

Hilborn, R., and C. J . Walters.
1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York, NY, 570 p.

Jones, R.
1981. The use of length composition data in fish stock assessment (with notes on VPA and cohort analysis). FAO Fish. Circ. 734, 55 p.
1984. Assessing the effect of changes in exploited pattern using length composition data. FAO Fish. Tech. Pap. 256, 118 p.

MacCall, A. D.
1976. Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse seine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 18:136–148.

Mexicano-Cíntora, G.
1990. Análisis preliminar de algunos aspectos reproductivos del mero (*Epinephelus morio*) de las costas de Yucatán. Rep. Esp. Acad. Centr. Invest. Est. Avanz. Inst. Politéc. Nal., Mérida, México, 42 p.

Moe, M. A.
1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Fla. Dep. Nat. Res. Prof. Ser. 10, 95 p.

Moreno, V.
1980. La pesquería de mero (*Epinephelus morio*) en el Estado de Yucatán. Ph.D. diss. Univ. Autón. Edo. Morelos, México, 63 p.

Murphy, G.
1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci. 34:1–84

Pitcher, T. J.
1996. The impact of fish behavior on pelagic fish and fisheries. Scientia Marina 59(3-4):295–306.

Pope, J. G.
1972. An investigation of accuracy of Virtual Population Analysis. Int. Comm. NW Atl. Fish. Res. Bull. 9:65–74

Quinn, T. J.
1987. Standardization of catch per unit effort for short-term trends in catchability. Nat. Res. Model. 1:279–296.

Rose, G. A., and W. C. Legget.
1991. Effects of biomass-range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). Can. J. Fish. aquat. Sci. 48: 843–848.

Sáenz, M., F. Mendoza, and J. C. Pisté.
1987. Diagnosis de la pesquería artesanal del Estado de Yucatán. Contr. Invest. Pesq. Cent. Reg. Invest. Pesq. Yucalpetén, Inst. Nal. Pesca, México. Dcto. Téc. No. 5:1–18.

Salazar, A. R.
1988. Contribución al conocimiento de la pesquería de mero (*Epinephelus morio*) de la flota menor de las costas de Yucatán. Tesis Lic. Esc. Nal. Ens. Prof. Iztacala, Univ. Nal. Autón. México, México, 81 p.

Seijo, J. C.
1986. Comprehensive simulation model of a tropical demersal fishery: red grouper (*Epinephelus morio*) of the Yucatan continental shelf. Ph.D. diss., Michigan State Univ. city, MI, 210 p.

Shapiro, D. Y.
1987. Reproduction in groupers. *In* J. J. Polovina and S. Ralston. (eds.), Tropical snappers and groupers: biology and fisheries management, 295–328 p. Westview Press, London.

Shepherd, J. G.
1987. Towards a method for short-term forecasting of catch rates based on length compositions. *In* D. Pauly and G. R. Morgan, (eds.), Length-based methods in fisheries research. ICLARM, Manila; and KISR, Kuwait. ICLARM Conf. Proc. 14:167–176.

Solana-Sansores, R., and F. Arreguín-Sánchez.
1991. Diseño de muestreo probabilístico para la pesquería artesanal de mero (*Epinephelus morio*) del Estado de Yucatán, México. Ciencias Marinas 17(1):51–72.

Valdés, E., and G. Padrón.
1980. Pesquerías de palangre. Revista Cubana de Investigaciones Pesqueras. 5(2):38–52.