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Appraisal of the selective properties of gill nets and implications for yield and value of the fisheries at the Itaipu Reservoir, Brazil–Paraguay

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Abstract

We studied the selective properties of gill net mesh-sizes used in the fisheries at the Itaipu Reservoir to assess the likelihood of growth and recruitment overfishing, and to explore modifications of current harvesting approaches and their effect on the fish stock and the value of the fishery. We used empirical growth estimates and gill net selectivity to model yield per recruit, size distributions, value per recruit, and spawner biomass per recruit under different natural mortalities, fishing mortalities, and gill net mesh-size restrictions. Our results suggest growth overfishing may be limiting fishery yield and commercial value. Increasing mesh-size (in most cases) and increasing fishing effort (in some cases) would lead to higher yields and commercial values. Nevertheless, such increases would further reduce the biomass of the spawning stock, and we could not predict whether such reductions would lead to recruitment overfishing, nor their effect on the interactions between the fishery species and the associated fish assemblage. However, we identify how fishing effort and mesh-size may be juggled to boost yield and commercial value without reducing current biomass of the spawning stock. Published by Elsevier Science B.V.

Keywords: Yield model; Gill nets; Reservoir; Overfishing; South America

1. Introduction

Beginning in the 1960s, chains of hydroelectric reservoirs were built along the principal tributaries and the mainstem Paraná River, encompassing parts of Argentina, Brazil, Paraguay, and Uruguay. Currently, there are over 130 major reservoirs (dam >10 m height), among them 28 are bigger than 10 000 ha, and four are located in the Paraná River main channel and range from 48 000 to 220 000 ha (Agostinho et al., 1995; Sugunan, 1997). Reservoir construction continues, with one mainstem 145 000 ha reservoir now partially impounded, and four others at various stages of construction (Calcagno, 1994). These reservoirs have brought economic development to the basin, but have substantially altered artisanal and commercial fisheries (Agostinho et al., 1994a). Whereas prior to impoundment these fisheries depended mainly on

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long-lines to capture large, long-distance migrators including catfishes and characids, they now depend mainly on gill nets to capture short-distance migrators or sedentary, small or medium size fish with lower commercial value (Agostinho et al., 1994a).

Fishery yields in reservoirs of the Paraná River average about 8 kg ha^{-1} ($N = 10$ reservoirs; Oldani, 1994; Agostinho et al., 1995) and are low relative to reservoirs in other parts of the world. Annual yield from commercial fisheries average near 100 kg ha^{-1} in African reservoirs (Marshall, 1984), 150 kg ha^{-1} in reservoirs of northeastern Brazil (Paiva et al., 1994), 120 kg ha^{-1} in Asian reservoirs (De Silva, 1987), and 13 kg ha^{-1} in recreational fisheries of the United States (Miranda, 1999). Various possible reasons have been suggested to account for low yields, including the absence of lacustrine-adapted species, long food chains, high number of predatory species, low primary production influenced by hydrological factors, and low fishing effort (Fernando and Holčik, 1982; Agostinho and Zalewski, 1995; Agostinho et al., 1995; Araújo-Lima et al., 1995; Petrere, 1996). The high yield in reservoirs of Africa, Asia, and northeast Brazil depends largely on the lacustrine-adapted tilapias (Cichlidae). Overharvest has not been seriously considered as a factor limiting fishery yield because fishing intensity (fishers km^{-2} $year^{-1}$) has been considered low: 0.2 in Upper Paraná, 3.2 in northeast Brazil, and 1.5 in Africa (Petrere, 1996).

Gill net fisheries provide the opportunity to regulate mesh-size and allocate exploitation to segments of fish stocks. Such rationing can be manipulated to balance welfare of the fish stock and societal profits. The purpose of this study was to consider the selective properties of gill net mesh-sizes used in the commercial fisheries at the Itaipu Reservoir to assess the likelihood of growth and recruitment overfishing, and to explore modifications of current harvesting approaches and their effect on the fish stock and the commercial value of the fishery.

2. Methods

2.1. Itaipu Reservoir

Itaipu (24°05′–25°33′S, 54°00′–54°37′W) is a 135 000 ha hydropower reservoir impounded in 1982 on the Paraná River along the Brazil–Paraguay border (Fig. 1). The reservoir has an average depth of 21 m and a maximum depth of 170 m. Retention time is about 40 days and discharge about 8200 m^3 s^{-1}. Total phosphorus concentrations average 22 mg m^{-3} and chlorophyll 3.6 mg m^{-3}, corresponding to trophic state indexes (Carlson, 1977) of 49 and 43, respectively, suggesting mesotrophic conditions. The reservoir is 150 km long and upstream has a 230 km long, free-flowing stretch of Paraná River.

Fig. 1. Location of 135 000 ha Itaipu Reservoir impounded on the Paraná River Basin along the Brazil–Paraguay border.

2.2. The fisheries

2.2.1. Yield

The fishery, consisting of about 91 500 fisher-days annually, exploits over 60 species that yield about 1560 tonnes and 11.6 kg ha^{-1}. Okada et al. (1996) modeled yield with 7 years of landings (1987–1993) and concluded that maximum sustainable total yield for all species was around 1600 tonnes, and optimum effort was 96 000 fisher-days. In 1993, effort was 120 817 (exceeded the optimum) and annual catch 1500 tonnes, showing some signs of possible overfishing (Okada et al., 1996; Agostinho et al., 1999a). Growth overfishing was identified for stocks of *Pter-*

odoras granulosus, *Paulicea luetkeni*, *Pseudoplatystoma corruscans*, and *Pinirampus pirinampu* (all migratory catfishes), and growth and recruitment overfishing for the stock of *Rhinelipis aspera* (an armored catfish) in as much as catches decreased by 70% and only small individuals were landed (Okada et al., 1996).

Among the over 60 species exploited, four account for nearly 75% of the yield (Agostinho et al., 1995; Okada et al., 1996). One of the four species, the siluriform *Pterodoras granulosus* (Doradidae), is harvested with long-lines. The other three species, the characiform *Prochilodus lineatus* (Prochilodontidae), the siluriform *Hypophthalmus edentatus* (Hypophthalmidae), and the perciform *Plagioscion squamosissimus* (Scianidae) are harvested with gill nets and are the focus of this study. *P. squamosissimus* (introduced from the Amazon Basin) and *H. edentatus* complete their life cycle within Itaipu Reservoir. *P. squamosissimus* is well adapted to lentic environments and in the Amazon Basin it is primarily a shrimp-eater, but in Itaipu Reservoir it exerts substantial predation on *H. edentatus*, an open-water zooplankton filterer that feeds mainly within surface waters (Agostinho et al., 1995). *P. lineatus* spawn in inflowing rivers, particularly the Paraná, where juveniles remain for about 2 years (until about 26 cm TL) in lentic areas of the floodplain, before migrating into the reservoir (Gomes and Agostinho, 1997). Within the reservoir this species feed primarily on organic matter accumulated in mud deposits and periphyton. Additional biological and fishery characteristics of the study species are summarized in Table 1.

2.2.2. *Fishery regulations*

The fishery is controlled by licensing, mesh-size, and season restrictions. In 1982 when the reservoir was impounded, the minimum mesh-size regulation was standard throughout the Upper Paraná River Basin (10 cm stretch), and fisheries were closed for the spawning season (November–February). As a result of research that began in the Itaipu Reservoir in 1986, the minimum mesh-size in the reservoir was decreased to 8 cm, and season restrictions were eliminated. Decreases in catch rates after the initial upsurge period (Agostinho et al., 1999b), and an abundance of

Table 1
Biological characteristics of the three main species in the gill net fishery at the Itaipu Reservoir

Characteristic	*Prochilodus lineatus*	*Plagioscion squamosissimus*	*Hypophthalmus edentatus*	Sources
Fishery contribution (%)	13.7	17.2	27.0	Agostinho et al. (1995)
Predominant feeding habit	Organic matter and periphyton	Carnivorous	Planktivorous	Agostinho et al. (1994a)
Growth curve parameters[a]				
L_∞ (cm)	80.5	47.6	56.0	Agostinho et al. (1995)
k	0.217	0.369	0.207	Ambrosio and Agostinho (unpublished data)
Length at maturity (L_{50}, cm)	26.7	22.8	27.4	Agostinho et al. (1995)
Weight–length parameters[b]				
a	0.0197	0.0164	0.0039	Agostinho (unpublished data)
b	3.087	3.076	3.130	
R^2	0.95	0.97	0.96	
Gill net retention parameters[d]				
a	8.88	5.81	6.84	Agostinho (unpublished data[c])
b_1	1.92	2.28	2.95	
b_2	10.52	13.42	8.96	
R^2	0.95	0.99	0.95	

[a] $L_t = L_4\ (1 - e^{-kt})$ where L_t = total length (cm) at year t.

[b] $W = aL^b$ where W = weight (g) at total length (cm) L; R^2 = coefficient of determination.

[c] Data were collected monthly throughout the reservoir during 1983–1989 with experimental gill nets.

[d] $L = a + b_1 m_i + b_2 d$ where m_i = quantitative variable representing mesh of the ith stretch size (cm), and d = dummy variable representing either the 10th (0) or 90th (1) percentile of lengths collected by m_i. This equation was derived from empirical data.

H. edentatus in the epipelagic zone, led to a reduction in mesh-size to 7 cm in 1989, with the limitation that this mesh could only be fished in the epipelagic zone (Agostinho et al., 1994a). Since then, meshes 7 and 8 cm are most commonly used to capture *P. squamosissimus* and *H. edentatus*, and 10, 12, 14, and 16 cm to capture *P. lineatus* (Agostinho et al., 1994a; Petrere, 1996). Gill nets used to capture these species are normally 100 m long, 2.2 m deep and constructed of monofilament nylon.

2.3. Modelling the fisheries

We used empirical growth estimates and the selective properties of gill nets to model yield per recruit, size distributions, commercial value per recruit, and spawner biomass per recruit under two natural mortality rates, various fishing mortalities, and four gill net mesh-size restrictions.

2.3.1. Yield per recruit

Jones' modification of the Beverton and Holt equilibrium yield model (Ricker, 1975) simulated yield per recruit (Y) as

$$Y = [(FN_1 e^{Fr} W_\infty)/k][H_1 - H_2],$$

where

F	instantaneous fishing mortality
N_1	number of individuals recruited to age 1
r	years elapsed between age 1 and when fish become susceptible to the gear
W_∞	average asymptotic weight of a fish
k	growth coefficient
H_1	$\beta(X_1,P,Q)/(1/((\Gamma(P) \times \Gamma(Q))/\Gamma(P+Q)))$
H_2	$\beta(X_2,P,Q)/(1/((\Gamma(P) \times \Gamma(Q))/\Gamma(P+Q)))$
β	probability from a beta distribution
Γ	complete gamma function (definite integral)
X_1	e^{-kr}
X_2	e^{-kl}
l	years elapsed between age 1 and when fish are no longer susceptible to the gear
P	Z/k
Z	instantaneous total mortality
Q	$b+1$
b	the exponent in the population weight–length relation
R	$N_1 e^{-Mr}$
M	instantaneous natural mortality

We arbitrarily set $N_1 = 1000$, but then adjusted this value by multiplying by the predicted representation (i.e., proportion) of the species at age 1 relative to the other two species. We predicted representation at age 1 by extrapolating from a catch curve described below. Values of L_∞ and k were derived from the available literature (Table 1). The value of W_∞ was estimated from L_∞ with empirically-derived weight–length equations (Table 1). We modeled the prevalent gill net mesh-sizes currently employed by commercial fishers in the Itaipu Reservoir, as well as smaller and larger mesh-size scenarios. Minimum and maximum lengths efficiently collected by the various mesh-sizes were estimated with equations derived empirically (Table 1). Values of r and l were estimated by solving the growth equation for the age at which fish recruited into the gear or were no longer susceptible to the gear, respectively. We assumed knife-edge recruitment; nevertheless, within the selection range of each set of meshes modeled we assumed a log-normal selection probability distribution (suggested by empirical data) used to adjust F. Simulations were conducted with M fixed arbitrarily at 0.2 (low) and 0.5 (high), and F ranging from 0 to 2; Z was computed as the sum of M and F. The chosen low and high values of M correspond to conditional natural mortality rates of 0.18 and 0.40, respectively (conditional natural mortality $= 1 - e^{-M} =$ fraction of the population that dies from causes other than fishing, if there were no fishing mortality; when fishing occurs, the actual natural mortality is reduced because both sources of mortality compete for the same fish, but conditional natural mortality remains unchanged; Ricker, 1975; pp. 9–11).

2.3.2. Size distribution

We separated the sizes of fish collected by each of the simulated mesh-size restrictions into the groups recognized by the commercial market. Small and large sizes are recognized for *P. lineatus* (threshold size = 2 kg) and *P. squamosissimus* (threshold = 0.8 kg), and a single size for *H. edentatus*. The proportions of large *P. lineatus* and *P. squamosissimus* in the catch were estimated with a continuous distribution as

$$P_{\text{large}} = \left\{ \begin{array}{ll} 0.5(L_l - L_{\text{th}})/(L_l - L_{\text{mean}}) & \text{if } L_{\text{mean}} \le L_{\text{th}} \\ 0.5 + 0.5(L_{\text{mean}} - L_{\text{th}})/(L_{\text{mean}} - L_r) & \text{if } L_{\text{mean}} > L_{\text{th}} \end{array} \right\},$$

where,

P_{large}	proportion of large fish in the catch
L_r	the length at which fish are recruited to the gear (from equation in Table 1)
L_l	the length at which fish are no longer susceptible to the gear (from equation in Table 1)
L_{mean}	mean length of fish captured by the gear
L_{th}	threshold length separating the small from large fish recognized by the commercial market

The yield of large (Y_{large}) and small (Y_{small}) fish was estimated as

$$Y_{\text{large}} = Y(P_{\text{large}}),$$
$$Y_{\text{small}} = Y(1 - P_{\text{large}}).$$

2.3.3. Commercial value per recruit

The commercial value of the catch was estimated as the yield of fish in each size group times its wholesale value. Fish harvested by fishers are bought by wholesalers who sell them to merchants. Agostinho et al. (1999a,b) estimated that the prices obtained by wholesalers were approximately US\$1.5 kg^{-1} for large *P. lineatus*, \$2 kg^{-1} for large *P. squamosissimus*, and \$0.9 kg^{-1} for small *P. lineatus* and *P. squamosissimus*, and all *H. edentatus*.

2.3.4. Spawner biomass per recruit

Alternative levels of harvest will influence spawner biomass and thereby could affect recruitment. Because the spawner–recruit relation was unknown, we estimated the stock biomass per recruit and used it as a benchmark for comparing alternative mesh-size regulations (Norris, 1991). With this information, comparisons of yield from different mesh-sizes can be limited to scenarios that produced the same spawner biomass per recruit.

Spawner biomass (B) was estimated as

$$B = \begin{Bmatrix} B_1 + B_2 + B_3 & \text{if } t_m < t_r \\ B_3 + B_4 & \text{if } t_m \geq t_r \end{Bmatrix}$$

where

B_1	$[(N_1 e^{Fm} W_\infty)/k][H_3 - H_1]$ for $F = 0$
B_2	$[(N_1 e^{Fr} W_\infty)/k][H_1 - H_2]$
B_3	$[(N_1 e^{Fl} W_\infty)/k][H_2]$ for $F = 0$ if $t > t_l$
B_4	$[(N_1 e^{Fm} W_\infty)/k][H_3 - H_2]$
H_3	$\beta(X_3,P,Q)/(1/((\Gamma(P) \times \Gamma(Q))/\Gamma(P + Q)))$
m	years elapsed between age 1 and when 50% of the fish become mature
t_m	time at maturity (Table 1)
t_r	time when fish become susceptible to the gear
t_l	time when fish are no longer susceptible to the gear
X_3	$= e^{-k(t_m - 1)}$

2.3.5. Empirical estimates of mortality

Estimates of Z for each of the three study species were made with empirical data on fish abundance collected with gangs of gill nets consisting of nets having 3, 4, 6, 8, 10, 12, 14 and 16 cm stretch mesh. These gill nets were fished throughout Itaipu Reservoir during 1984–1989. Age (t) was estimated from length (L) as

$$t = \log_e(1 - L/L_\infty)/k.$$

Age was regressed on $\log_e$ of catch of fish of age t. Regression was limited to the descending portion of the catch curve.

3. Results

Empirical estimates of annual Z averaged 1.29 (28% annual survival) for *H. edentatus*, 1.13 (32% survival) for *P. squamosissimus*, and 1.06 (35% survival) for *P. lineatus* (Fig. 2). The gill nets used to

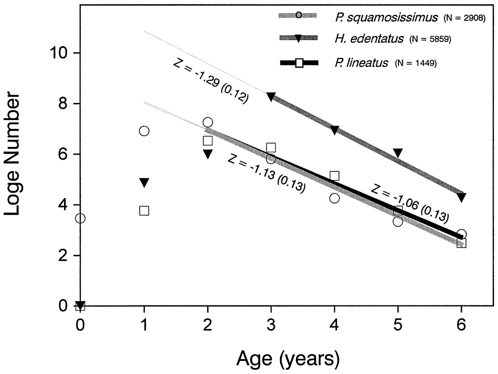

Fig. 2. Catch curves for the three study species. Regression lines (solid) were fit to the descending portions of the curves. The lines were extended (dashed lines) to extrapolate relative population density at age 1. Values in parentheses next to the Z values represent 1 S.E.

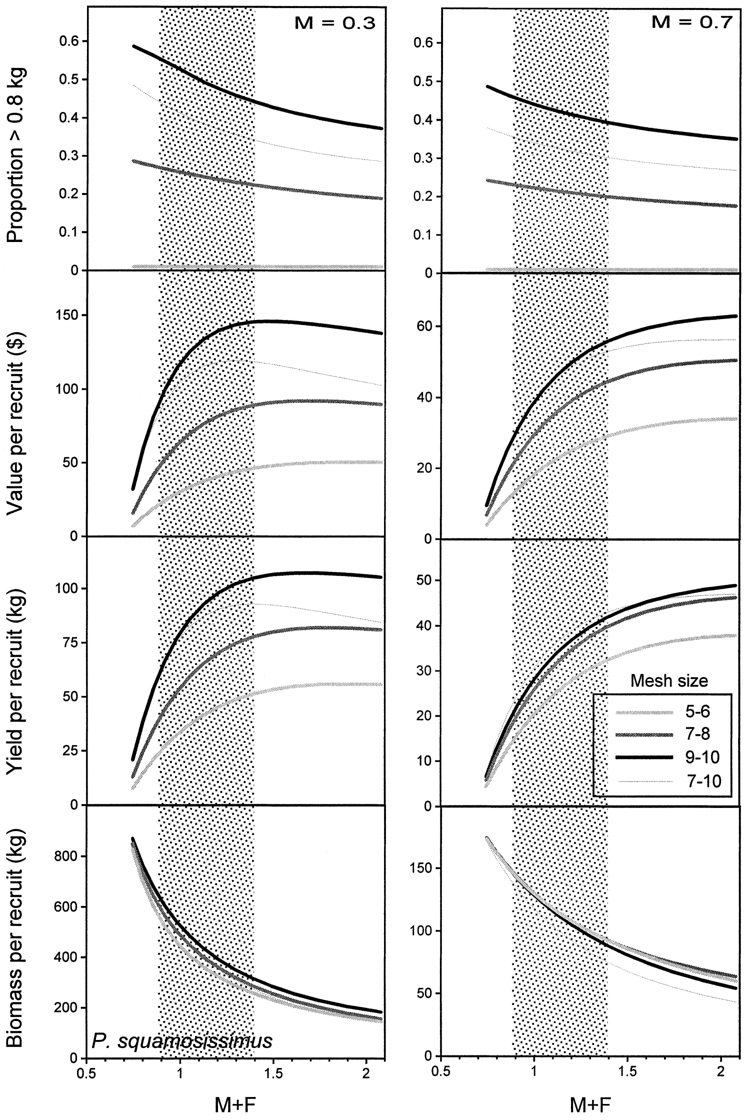

Fig. 3. Relations between $M + F(Z)$ and biomass per 60 recruits, yield per 60 recruits, commercial value, and the proportion of large fish in the catch of *Plagioscion squamosissimus* according to mesh-size (cm). Values were predicted with a Beverton and Holt equilibrium yield model. The shaded area represents two standard errors on each side of the mean Z from Fig. 2. We arbitrarily set the number of recruits to age $1 = 1000$, but adjusted this value by multiplying by the predicted representation of the species at age 1 (0.06, derived from Fig. 2) relative to the other two species.

collect fish samples were capable of retaining *P. squamosissimus* and *H. edentatus* as large as L_∞. However, the maximum length of *P. lineatus* that could be retained by the largest mesh-size was less than L_∞. Therefore, the samples used in this computation might have excluded the larger and older *P. lineatus*, resulting in an artificially steeper slope of regression, and thus inflated estimates of Z and N_1.

Yield, size, and commercial value of the principal species in the gill net fishery at the Itaipu Reservoir depended on rates of mortality and mesh-size (Figs. 3–5). Yield was inversely related to M and generally

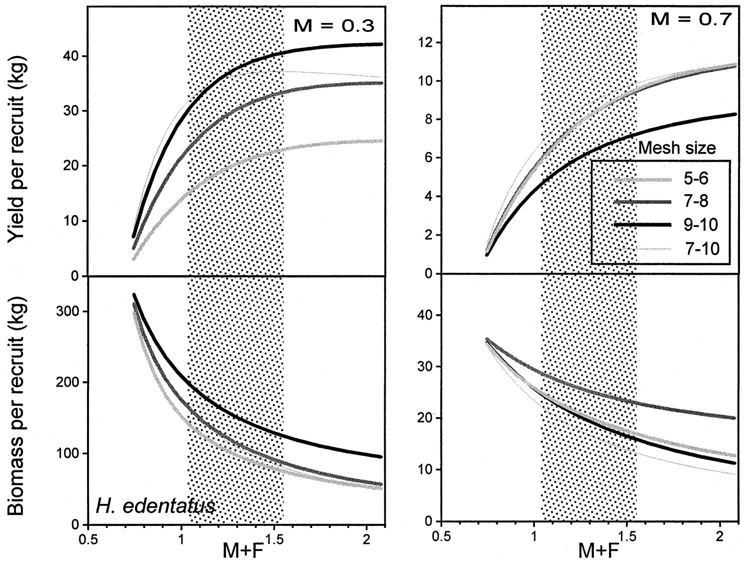

Fig. 4. Relations between $M + F(Z)$ and biomass per 890 recruits and yield per 890 recruits of *Hypophthalmus edentatus* according to mesh-size (cm). Values were predicted with a Beverton and Holt equilibrium yield model. The shaded area represents two standard errors on each side of the mean Z from Fig. 2. Size proportions were not provided because the market for this species recognizes only one size group; commercial values are 0.9 of yield values. We arbitrarily set the number of recruits to age 1 = 1000, but adjusted this value by multiplying by the predicted representation of the species at age 1 (0.89, derived from Fig. 2) relative to the other two species.

increased with expanding levels of F and either became asymptotic, or peaked at intermediate levels of fishing and then decreased. Size of fish harvested decreased with increments in M and F. Commercial value of the catch reflected trends in yield, but inequalities among mesh-sizes were accentuated by differences in sizes that commanded disparate commercial values. Average weight of fish harvested was directly related to mesh-size and inversely related to mortality rates, and for the scenarios considered the ranges were 0.17–0.92 kg for *P. squamosissimus* (Fig. 3), 0.08–0.38 kg for *H. edentatus* (Fig. 4), and 0.80–2.82 kg for *P. lineatus* (Fig. 5). *H. edentatus* manifested the highest potential yields and *H. edentatus* and *P. lineatus* commanded the highest commercial values.

Increasing length at recruitment through the use of progressively larger mesh consistently produced higher yields and commercial values when M was low (Figs. 3–5). When M was high, this trend changed for *H. edentatus* (Fig. 4). Moreover, when M was high yield appeared to be less responsive to changes in mesh-size (i.e., length at recruitment to the fishery). Increasing the sizes of fish targeted by the fishery through the use of nets with 7–10 cm meshes (or 13–18 cm) often produced results intermediate to those accomplished by using meshes 7–8 and 9–10 cm (or 13–15 and 16–18 cm). Also, increasing the range of sizes of fish targeted by using 7–10 or 13–18 cm mesh often resulted in yield and commercial value maxima or plateaus that occurred at lower F than when a narrower range of sizes were targeted.

Biomass of the spawning stock was lower at the higher M and decreased asymptotically with increments in F (Figs. 3–5). The effect of mesh-size on stock size was small at low F, but stock biomass became progressively more divergent among gill net mesh-sizes as F increased. For the low M, biomass of the spawning stock was consistently larger when harvest was deferred through the use of large meshes; for high M, only the spawning stock of *P. lineatus* could be enhanced by deferring harvest. Results also suggested that increasing mesh-size often allowed increased yield through increased F while keeping biomass of the spawning stock constant (Fig. 6). For instance, for *P. lineatus* and $M = 0.5$, at current $Z = 1.06$ and mesh-sizes 10–12 cm, biomass per

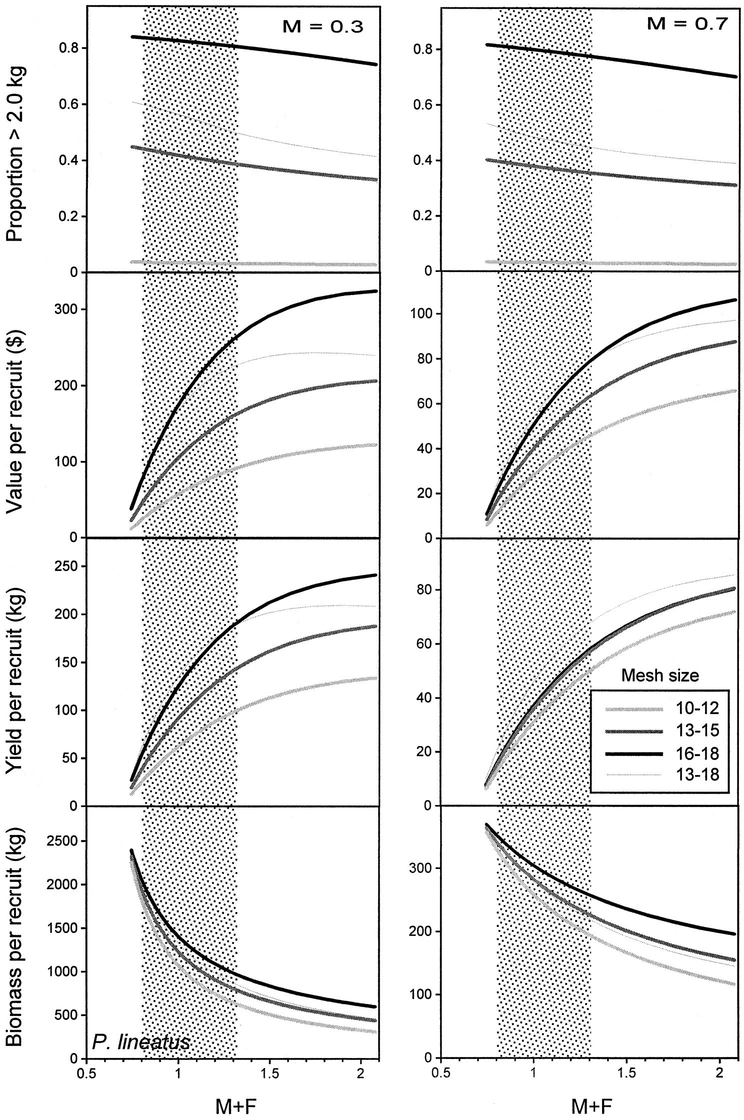

Fig. 5. Relations between $M + F(Z)$ and biomass per 50 recruits, yield per 50 recruits, commercial value, and the proportion of large fish in the catch of *Prochilodus lineatus* according to mesh-size (cm). Values were predicted with a Beverton and Holt equilibrium yield model. The shaded area represents two standard errors on each side of the mean Z from Fig. 2. We arbitrarily set the number of recruits to age 1 = 1000, but adjusted this value by multiplying by the predicted representation of the species at age 1 (0.05, derived from Fig. 2) relative to the other two species.

recruit is about 75 kg (solid horizontal line in Fig. 6), $F = 0.56$, and yield per recruit 14 kg. If mesh-size is increased to 13–15 or 16–18 cm, F may be increased to 0.78 or 1.18 to achieve yield per recruit of 21 or 27.5 kg, respectively, without changing stock biomass (Fig. 6).

4. Discussion

Our results suggest growth overfishing (fish harvested before they have achieved maximum yield per recruit; Gulland, 1988) may be limiting fishery yield and commercial value of *P. squamosissimus*, whether

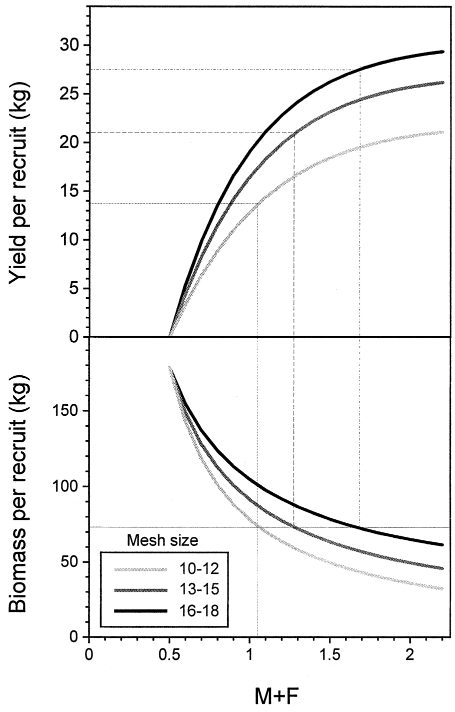

Fig. 6. Relations between $M + F(Z)$ and biomass per 50 recruits and yield per 50 recruits of *Prochilodus lineatus* at $M = 0.5$. At current $Z = 1.06$ and mesh-sizes 10–12 cm, biomass per recruit is about 75 kg (solid horizontal line), $F = 0.56$, and yield per recruit 14 kg. If mesh-size is increased to 13–15 or 16–18 cm, F may be increased to 0.78 or 1.18 to achieve yield per recruit of 21 or 27.5 kg, respectively, without changing stock biomass.

M is high or low, and *H. edentatus* if M is high. It was also apparent that increases in F could in some cases lead to increased fishery yield and value. Nevertheless, such increases in F would further reduce the biomass of the spawning stock, and we cannot predict whether such reductions would lead to recruitment overfishing (spawning stock reduced to a level that precludes adequate production of young fish, Gulland, 1988), nor their effect on the interactions between the study species and the associated fish assemblage. However, we can predict how F and mesh-size may be juggled to boost yield and commercial value without reducing biomass of the spawning stock. Below we explore the implications of manipulating mesh-size, consider the sustainability of yield and the limitations of our predictions, and conjecture whether harvesting strategies may be limiting fishery yield in the Itaipu Reservoir and the reservoirs of the Paraná Basin in general.

4.1. Implications of manipulating mesh-size

Our data allowed us to obtain estimates of total annual mortality, but did not allow us to separate fishing mortality from other causes of mortality. Separating Z into F and M is important because low versus high M values lead to different harvesting strategies. In general, when M is low, yield can be increased by delaying harvest, requiring use of large mesh-sizes and restraints on fishing effort; when M is high, fish may need to be harvested earlier, requiring use of small mesh-sizes and limited or no restraints on fishing effort. Nevertheless, without knowing M we can still draw some generalizations about appropriate mesh-sizes, and about whether increasing or decreasing F could lead to substantially different yields.

Meshes 7 and 8 cm account for nearly 85% of the gill nets used to target *P. squamosissimus* in the Itaipu Reservoir (Agostinho et al., 1994a). Our model indicated that this strategy resulted in growth overfishing. Greater yield and commercial value could be obtained from this species if a larger mesh-size was used (e.g., 9–10 cm scenario), or if the range of meshes currently used was expanded to include equal consideration of larger mesh-sizes (e.g., 7–10 cm scenario). Such mesh-size increases can also lead to increased biomass per recruit if M is low (Fig. 3). If M is high, biomass per recruit would be reduced slightly if mesh-sizes were shifted to 9–10 cm and considerably if shifted to 7–10 cm. The latter mesh-size scenario could be exercised if the management objective is to maintain a low biomass of *P. squamosissimus*, an introduced species that could potentially perturb the native fish assemblages (Agostinho and Julio, 1996).

Meshes 7 and 8 cm also account for nearly 85% of the gill nets used to target *H. edentatus* in Itaipu Reservoir (Agostinho et al., 1994a). Our model indicated that this strategy resulted in growth overfishing only if M was low. In this case, greater yield, commercial value, and biomass per recruit could be obtained from *H. edentatus* if the 9–10 or 7–10 cm mesh-sizes were used. If M was high, the 7–10 cm mesh scenario provided the highest yield and commercial value, but at the lowest biomass per recruit. The 7–8 cm mesh (current scenario) appeared to provide a compromise scenario by maintaining the highest biomass at a slightly reduced yield from the 7–10 cm scenario. Indeed, at the estimated Z of 1.29 the

7–8 cm mesh maintained a biomass per recruit of nearly 100 kg and a yield per recruit of over 30 kg; to maintain this biomass with the 7–10 cm mesh scenario, Z would need to be reduced to about 0.9 (F about 0.4) resulting in a lowering of yield to less than 30 kg.

P. squamosissimus and *H. edentatus* are captured with the same gear. It is apparent that the large mesh scenario would produce the highest commercial values if M was low for both species, or low for one species but not the other. However, if M was high for both species, mesh scenarios 7–8, 9–10, and 7–10 would produce similar commercial values, but the 7–8 scenario would retain the highest biomass per recruit. These two species appear to segregate vertically within the water column, with *H. edentatus* occupying the upper 5–10 m and *P. squamosissimus* inhabiting deeper water. Thus, if M were known to deviate substantially between these two species, different mesh-sizes may be used to target each species in different habitats and further optimize yield. Nevertheless, the effectiveness of this strategy may be restricted by *P. squamosissimus* which sometimes pursue and feed on schools of *H. edentatus* (Agostinho et al., 1994b).

Our model also indicated that higher commercial values and biomass per recruit may be obtained for *P. lineatus* if the mesh-sizes used in the fisheries are increased. This conclusion applied to the low or high natural mortalities modeled. Meshes 10, 11, and 12 account for about 40% of the gill nets used to target *P. lineatus*, mesh-size 14 cm 35%, and mesh-sizes 16 and 18 cm for less than 25%.

For all three species, a fishery with a broader range of meshes often produced yield and stock biomass intermediate to those obtained by a narrower range (e.g., 7–10 cm mesh versus 7–8 and 9–10 cm). The narrower range of meshes increases mortality in a constricted portion of the age structure, whereas the broader range spreads mortality over more age groups. Such different effects on age structures may influence the recruit-spawner relation, and how the species interact with the fish assemblage. Spreading mortality over a smaller portion of the population may produce age distributions that seem less natural, and gains in stock biomass associated with targeting a narrow portion of a stock may be nullified by an artificial age distribution. However, it is difficult to evaluate the significance of the differences in age structures rendered by different harvesting strategies without better knowledge of the factors influencing recruitment variability and community interactions.

4.2. Sustainability of yield estimates

The aim of commercial fisheries management should be to ensure sustainability while optimizing benefits. Yield is not sustainable when fish are harvested before they are allowed to spawn at least once, and when fishing greatly reduces population size. By comparing the length at which 50% of the fish become mature with the length at first capture we may obtain a rough idea of whether yield estimates are sustainable. We assumed that the stock is more likely to be sustained if the average length of fish in the harvest is larger than the average length at maturity. Thus, the average individual harvested has had a chance to spawn at least once. Based on estimates of length at maturity, growth, and gill net retention (Table 1) we estimate that 50% of *P. squamosissimus* spawn by age 1.8 whereas the minimum age retained by 5, 7, and 9 cm mesh are 1.2, 1.7, and 2.2 years. For *H. edentatus*, 50% spawn by age 3.3 whereas the minimum age retained by 5, 7, and 9 cm mesh are 2.4, 3.3, and 4.4 years. For *P. lineatus*, 50% spawn by age 1.9 whereas the minimum age retained by 10, 13, and 16 cm mesh are 2.0, 2.5, and 3.1 years. Thus, for *P. squamosissimus* and *H. edentatus*, high F with 5–6 cm mesh is probably unsustainable, whereas the 7–8 cm mesh scenario is marginal and risks recruitment overfishing given uncertainty and natural variability in the parameters. There appeared to be no such risks with *P. lineatus*. We do not know what constitutes an unsustainable high level of F, and such level would depend on M. However, we suspect that Z values greater than about 1.6 (about 80% annual mortality) are likely to limit sustainability (Patterson, 1992). Levels of Z for the study fisheries were lower than 1.6.

It is evident that small mesh-sizes and high fishing effort can lead to diminished economic benefits, reduced catch per effort, and the collapse of the fisheries for the current target species. However, even if the fisheries for the current species collapse, other species may be able to still sustain a fishery. In African lagoons overfishing led to a reorganization of the species assemblage, towards a few dominant species that were small in size and generally herbivorous (Laë, 1997). Whereas total yield did not decrease, fish biomass and catch per effort decreased. Thus, fishery yield remained relatively unchanged, but the economics of the fishery changed drastically (Laë, 1997).

4.3. Limitations of predictions

There is much uncertainty associated with predicting responses of fish populations with models. Firstly, there is uncertainty about the ability of the model to describe the biological and fishery system being modeled. By definition, models are abstractions of reality, and often fall short of accurately simulating reality. Also, the model we used provided a deterministic view, although we attempted partially to ameliorate this limitation by modeling various scenarios. Secondly, there is uncertainty about the parameters input into the model. These parameters were obtained empirically through field surveys afflicted by various limitations. Nevertheless, we believe many of the parameters were more realistic than the model itself. Despite these limitations, several generalizations could be made to diagnose the direction the fishery will take given major harvest modifications.

4.4. Are harvesting strategies limiting fishery yield?

The fisheries at the Itaipu Reservoir are not unlike those of other reservoirs in the basin. With few exceptions, the species common in the Itaipu fisheries are also common in other reservoirs (Agostinho et al., 1995). *P. squamosissimus* occurred in eight reservoirs examined in the Upper Paraná River, and its contribution to the total yield ranged 11–29% (Itaipu = 17). *P. lineatus* depends on lotic environments inflowing into the reservoir and occurred in seven of eight reservoirs, and its contribution to the total yield ranged 12–37% (Itaipu = 14). *H. edentatus* is important in the fisheries of the Itaipu Reservoir but not in any of the reservoirs upstream. This species is native to the middle and lower Paraná River and gained access to the Upper Paraná when Sete Quedas Falls, historically the upper boundary of the distribution of fish populations that occupied the Middle Paraná River, were flooded by the Itaipu Reservoir. When this flooding occurred, *H. edentatus* expanded beyond its original range, but access to the entire Upper Paraná Basin was limited by upstream dams.

Empirical estimates of Z suggested that overfishing, if it occurs, is not excessive. A similar conclusion was reached by Okada et al. (1996) who used a Schaeffer model to conclude that the fisheries (over 60 species included) in the Itaipu Reservoir were slightly overfished. Moreover, our results suggest that one or two of the study species may be experiencing growth overfishing, and increases in mesh-size would lead to increases in yield. Such increases could enhance yield, but probably could not double it. Thus, although harvesting strategies appear to be partially limiting fishery yield, other factors must also contribute to low yields in reservoirs of the Paraná River relative to those identified for reservoirs in northeastern Brazil, Africa, Asia, and North America.

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