

Effects of River Impoundment on Ecosystem Services of Large Tropical Rivers: Embodied Energy and Market Value of Artisanal Fisheries

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Abstract: *Applying the ecosystem services concept to conservation initiatives or in managing ecosystem services requires understanding how environmental impacts affect the ecology of key species or functional groups providing the services. We examined effects of river impoundments, one of the leading threats to freshwater biodiversity, on an important ecosystem service provided by large tropical rivers (i.e., artisanal fisheries). The societal and economic importance of this ecosystem service in developing countries may provide leverage to advance conservation agendas where future impoundments are being considered. We assessed impoundment effects on the energetic costs of fisheries production (embodied energy) and commercial market value of the artisanal fishery of the Paraná River, Brazil, before and after formation of Itaipu Reservoir. High-value migratory species that dominated the fishery before the impoundment was built constituted a minor component of the contemporary fishery that is based heavily on reservoir-adapted introduced species. Cascading effects of river impoundment resulted in a mismatch between embodied energy and market value: energetic costs of fisheries production increased, whereas market value decreased. This was partially attributable to changes in species functional composition but also strongly linked to species identities that affected market value as a result of consumer preferences even when species were functionally similar. Similar trends are expected in other large tropical rivers following impoundment. In addition to identifying consequences of a common anthropogenic impact on an important ecosystem service, our assessment provides insight into the sustainability of fisheries production in tropical rivers and priorities for regional biodiversity conservation.*

Keywords: ecological economics, ecosystem services, energy, food webs, Itaipu Reservoir, sustainability, trophic position, Upper Paraná River

Efectos de las Represas en Ríos Tropicales sobre los Servicios del Ecosistema: Energía Virtual y Valor de Mercado de las Pesquerías Artesanales

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Resumen: *La aplicación del concepto de servicios del ecosistema a iniciativas de conservación o al manejo de servicios del ecosistema requiere del entendimiento del efecto de los impactos ambientales sobre la ecología de especies clave o grupos funcionales que proporcionan los servicios. Examinamos los efectos de los reservorios en ríos, una de las principales amenazas a la biodiversidad dulceacuícola, sobre un importante servicio del ecosistema proporcionado por ríos tropicales (i.e., pesquerías artesanales). La importancia social y económica de este servicio del ecosistema en países en desarrollo puede proporcionar impulso para avanzar en las agendas de conservación donde se están considerando represas en el futuro. Evaluamos los efectos de las represas sobre los costos energéticos de la producción de pesquerías (energía virtual) y el valor de mercado comercial de la pesquería artesanal del Río Paraná, Brasil, antes y después de la formación de la Represa Itaipu. Las especies migratorias de alto valor que dominaban la pesquería antes de que se construyera la represa constituían un componente menor de la pesquería contemporánea que se basa fundamentalmente en especies introducidas adaptadas a la represa. Los efectos en cascada de la represa resultaron en una incompatibilidad entre la energía virtual y el valor de mercado: los costos energéticos de la producción de pesquerías incrementaron mientras que el valor de mercado decrecía. Esto se debió parcialmente a cambios en la composición funcional de especies, pero también estuvo ligado estrechamente a las identidades de las especies que afectaron el valor de mercado como un resultado de las preferencias de los consumidores aun cuando las especies eran similares funcionalmente. Se esperan tendencias similares en otros ríos tropicales después de la construcción de represas. Adicionalmente a la identificación de consecuencias de un impacto antropogénico común sobre un importante servicio del ecosistema, nuestra evaluación ofrece una visión reveladora de la sustentabilidad de la producción de pesquerías en ríos tropicales y permite priorizar la conservación de la biodiversidad regional.*

Palabras Clave: Alto Paraná, economía ecológica, energía, posición trófica, redes tróficas, servicios del ecosistema, Represa Itaipu, sustentabilidad

Introduction

Natural ecosystems provide numerous services that are the life-support systems of our planet (Daily 1997). Ecosystems can be considered renewable natural capital in that they may be renewed using a portion of the original stock and solar energy (Costanza & Daly 1992). This renewable natural capital produces a flow of natural income that may be harvested as ecosystem goods (e.g., fisheries harvest) and yields a flow of ecosystem services (e.g., nutrient cycling, climate regulation) when left in place. These ecosystem goods and services contribute directly and indirectly to human welfare, representing a significant component of our global economic value (Costanza et al. 1997; Holmlund & Hammer 1999; Balmford et al. 2002).

Production of manufactured capital (e.g., buildings) and human capital (e.g., knowledge and culture) requires reorganization of energy bound in renewable and nonrenewable natural capital (Costanza & Daly 1992). Because many ecosystem services are not captured by commercial markets or are not quantified in comparable terms with economic services, they are generally undervalued in decisions regarding the use of natural capital (Costanza & Daly 1992; Farber et al. 2006). This undervaluation threatens sustainability and frustrates conservation efforts. To help remedy this shortcoming, numerous methods of valuing ecosystem services relative to other forms of capital have been developed, and valuing ecosystem goods and services is a burgeoning conservation and manage-

ment tool (e.g., Costanza et al. 1998; Farber et al. 2002; Turner et al. 2003).

The ecosystem services concept has direct and timely applications to conservation of biodiversity in freshwater ecosystems (e.g. Postel & Carpenter 1997; Wilson & Carpenter 1999). Freshwater biodiversity has declined at a rate outpacing both terrestrial and marine biodiversity (Sala et al. 2000; Jenkins 2003), and future human water needs in a changing climate are likely to exacerbate this trend (Palmer et al. 2008). One of the primary threats to freshwater biodiversity worldwide is river impoundment and modification of natural hydrologic regimes (Nilsson et al. 2005; Dudgeon et al. 2006). Impoundment affects species composition and community structure due to ecosystem fragmentation, extirpation of native species dependent on lotic conditions, and modification of patterns of energy flow and trophic structure (Allan & Flecker 1993; Hoeinghaus et al. 2007, 2008). In addition, hydrologic modification facilitates invasions by non-native species (Havel et al. 2005; Johnson et al. 2008), which are in turn implicated as primary threats to native biodiversity in freshwaters (Sala et al. 2000; Agostinho et al. 2005b; Dudgeon et al. 2006).

Alterations to species composition or community structure, such as those that follow river impoundment, may disrupt the ability of the ecosystem to provide goods and services (e.g., Bunker et al. 2005; Larsen et al. 2005). One important ecosystem service provided by large tropical rivers is fisheries production (Postel & Carpenter 1997; Holmlund & Hammer 1999). In developing tropical

countries, freshwater fisheries may provide the majority of dietary protein consumed by rural and urban communities and offer an economic opportunity of last resort for millions of low-income families in rural areas (Allan et al. 2005). Understanding impacts of river impoundment on this important ecosystem service may facilitate conservation initiatives in developing countries in tropical latitudes, where development of large impoundments continues to threaten rich biological diversity (Dudgeon 2000; Pringle et al. 2000; Agostinho et al. 2005b).

We examined effects of river impoundment on artisanal fisheries harvest of a large tropical river system. We analyzed long-term data on artisanal fisheries landings and fishing effort and on trophic characteristics and market value of the fishery of the Upper Paraná River, Brazil, before and after formation of Itaipu Reservoir. Specifically, we asked how impoundment has affected relative species abundances, including native and non-native species, in fisheries landings over the last three decades; how direct and indirect energetic costs of fisheries production (embodied energy) have responded to impoundment; and how changes in species composition and abundance affected the relative market value of fisheries landings. Our combination of approaches allowed us to compare trends in energetic costs of fisheries with market value, identify the key functional group in the provisioning of this ecosystem service, and assess cascading effects of river impoundment on sustainability of fisheries production. In addition to applications to conservation initiatives where impoundments are currently being considered, our findings allow us to discuss implications of alternative management strategies on regional biodiversity and social conditions of fishers of this tropical river basin and others already affected by impoundments.

Methods

Regional Description and Fishery Characteristics

The Paraná River is the second-longest river in South America (4695 km), tenth-largest river in the world based on discharge, and fourth-largest in drainage area (2.8×10^6 km²). The Upper Paraná River includes approximately the upper third of the Paraná River basin and lies almost completely within Brazilian territory, draining 891,000 km² or 10.5% of Brazil's area. Notable features of this basin are the highest human population density in Brazil (54,640,000 inhabitants; 32% of total Brazilian population), several industrialized centers, intensive agriculture, ranching, and numerous reservoirs (Agostinho et al. 2007). Itaipu Reservoir on the Brazil-Paraguay border is the third largest reservoir in the basin (surface area of 1,350 km², basin area of 820,000 km²). Its average depth is 22 m, reaching 170 m near the dam, and average hydraulic retention is 40 days. A 230-km floodplain

stretch, representing the last free-flowing section of the Upper Paraná River, is located upstream from the reservoir and serves as nursery habitat for many migratory fish species during the flood season, although upstream impoundments have altered flood intensity and duration. The functioning of the Upper Paraná River floodplain is critical for maintenance of regional biodiversity; more than 3000 species occur in the floodplain, including 170 fish species, 298 bird species, 712 species of aquatic and terrestrial plants, 59 species of amphibians and reptiles, and 60 mammal species (Thomaz et al. 2004).

The artisanal fishery in this region dates to the 1960s, when agricultural mechanization led many newly unemployed people to fishing as a profession. During this same decade, the first two professional fishing associations were created, and improved infrastructure (e.g., roads) facilitated development of the commercial fishery. Itaipu Reservoir began filling in October 1982 and pushed still more people, especially small landowners in the affected area, to this activity in 1985 when fishing was formally allowed in the newly filled reservoir. The artisanal fishery plays an important social and economic role for a large number of fishers, who generally have limited legal employment alternatives in this border region, where illicit activities such as smuggling, drug trafficking, and transportation of stolen vehicles are commonplace (Okada et al. 2005).

Valuation of Ecosystem Services, Data Compilation, and Analyses

Numerous methods of valuing ecosystem services relative to other forms of capital have been developed. One such valuation method is the energetic value of capital, specifically the total amount of energy used directly and indirectly in the production of that capital (Costanza 1980; Odum 1988; Odum & Odum 2000). The combined direct plus indirect energy required to produce an ecosystem good or service is its embodied energy (Costanza 1980), which is fundamentally equivalent to the *emergy* concept (Odum 1988). Embodied energy is a useful metric for ecosystem goods such as fisheries harvest because trends in embodied energy and yield may also provide insight into resource sustainability.

Food webs describe the flow of energy through complex trophic structures of biological systems and provide an appropriate ecological framework for investigating some aspects of ecosystem goods and services (Kremen 2005). Because energetic assimilation efficiency is around 10% (Humphreys 1979), a consumer feeding at trophic level four, all else being equal, is approximately 10 times more energetically costly to produce than a consumer of the same biomass feeding at trophic level three, and 100 times more costly than a primary consumer (trophic level two). Therefore, comparisons of species trophic positions depict relative efficiency of production (e.g.,

Table 1. Commercial classification of fish species captured in artisanal fisheries of the Upper Paraná River basin, Brazil.^a

Class ^b	Description
I	“pescado de primeira”—large fishes with high-quality flesh traditionally consumed in the region, especially a few long-distance migratory species (e.g., <i>Pseudoplatystoma corruscans</i> , <i>Salminus brasiliensis</i>)
II	medium to large species with high fat content “carne remosa” (e.g., <i>Zungaro zungaro</i> , <i>Pinirampus pinirampu</i>); smaller individuals of class I species; largest individuals of introduced species not historically accepted in the market (e.g., <i>Cichla</i> sp., <i>Plagioscion squamosissimus</i>) are occasionally sold in this category
III	larger “cascudo” (armored catfishes) and armado <i>Pterodoros granulosus</i> (after processing of filets began in 1987), which have high palatability yet have consumer restrictions because of their appearance (even when filleted); large individuals of <i>Prochilodus lineatus</i> ; most individuals of <i>P. pinirampu</i>
IV	majority of captures—small to medium-sized individuals of various species sold together as “misto” (mixed); includes almost all <i>P. squamosissimus</i> and three of the other top species in the postimpoundment commercial catch (<i>Hypophthalmus edentatus</i> , <i>Hoplias malabaricus</i> , <i>Pimelodus maculatus</i>); individuals <30 cm of species sold in higher classes
Other	many species of small size that are generally discarded, fed to domestic animals, or used as bait; medium to large species with many bones (e.g., <i>Raphiodon vulpinus</i>) and culturally unaccepted species such as piranhas (<i>Serrasalmus</i> spp.) and stingrays (<i>Potamotrygon motoro</i>); some sold as class IV after being filleted or donated to low-income households during certain times of year associated with religious observations (e.g., Lent)

^aModified from Agostinho et al. (2005a).

^bMarket values by unit biomass are highest for fishes in class I and decrease with increasing class number.

Pinnegar et al. 2002). We used trophic positions of species captured in the artisanal fishery as an index of energy *directly* assimilated in the biological production process. Species were classified into trophic groups based on dominant dietary items in stomach contents in Hahn et al. (2004), and classifications were assigned an estimated trophic position of 4 for piscivores, 3 for invertivores and omnivores, and 2 for primary consumers (e.g., algivores, herbivores, detritivores). A composite trophic position for the fishery as a whole for each year was calculated as the relative proportion of trophic groups by weight in the landings.

Unlike fundamental ecosystem services provided by fish populations (e.g., cycling and transport of nutrients, regulation of carbon fluxes from water to atmosphere; Holmlund & Hammer 1999), fisheries provide an ecosystem good that requires additional energy associated with harvesting before it can be used by humans. The total amount of energy associated with harvesting (e.g., energy bound in the fisher’s labor, boat, fuel, materials, knowledge) is the *indirect* energetic cost of fisheries. This indirect cost of harvest is extremely difficult to estimate. Nevertheless, the relationship between fishing effort (fisher days) and yield (tons), specifically the amount of time invested per ton yield, may be used to provide a suitable surrogate for energy expended to harvest a given biomass of fish (similar to analyses in Glaser and Diele [2004]). Therefore, we examined trends in effort per yield of the artisanal fishery over time as an index of indirect energetic costs associated with harvest.

Demand-derived ecosystem services (goods) such as fisheries are directly appreciated in human market economies (i.e., a direct link exists between ecosystem service and commercial value), allowing for comparisons of energetic cost (embodied energy) and market value

without estimating some alternative dollar value based on replacement or willingness-to-pay estimates (Groot et al. 2002). Comparisons among methods of valuing ecosystem services, such as between energetic value and market value as in our study, may be especially informative (e.g., Costanza 1980; Cleveland et al. 1984). To estimate market value, we separated species into locally used commercial classes (Table 1) that are based on quality of flesh, fish size, and traditional acceptance in the market. Although actual prices may change over time, these general market classifications remained consistent throughout the period and provide a stable index for our analyses. Class I was given a value of 5, and each lower commercial class decreased by 1 to a minimum value of 1 for the “other” class. We calculated the relative proportion of fisheries landings by weight in each class and generated a composite value for each year.

Although long-term data on annual fisheries landings are available for Itaipu Reservoir after it filled (Agostinho et al. 2005a; Okada et al. 2005), data from this stretch of the Upper Paraná River before impoundment are limited. We compared energetic costs of production and harvest and commercial market value for years with sufficient data: 1977 (5 years before impoundment) and the period from 1987 to 2005. Fishing effort was only available for the period following dam closure (1987–present); however, it is known that fishery start-up and operational costs were less prior to impoundment (Agostinho et al. 2005a). Surveys were suspended in 1994 and 1999, so no data are available for these 2 years. We have no reason to believe that species harvested or relative biomasses were significantly different in 1977 than other years prior to impoundment. The same primary fisheries species were consistently sought prior to impoundment (Agostinho et al. 2005a), and any variation in relative abundances of target species for that year would affect our



Figure 1. Dominant species by biomass in artisanal fishery landings of the Upper Paraná River before and after impoundment of Itaipu Reservoir. Dominant species prior to impoundment: (a) jaú, *Zungaro zungaro*, (b) dourado, *Salminus brasiliensis*, (c) pacu, *Piaractus mesopotamicus*, (d) pintado, *Pseudoplatystoma corruscans*. Dominant species following impoundment: (e) armado, *Pterodorus granulosus*, (f) curimba, *Prochilodus lineatus*, (g) perna-de-moça, *Hypophthalmus edentatus*, (h) curvina, *Plagioscion squamosissimus*. Photographs by E.K.O., except *P. granulosus*, which is by D.J.H.

comparisons of embodied energy and market value before and after impoundment in a minor way because differences in trophic positions and especially market values were much greater between periods than within (see Results).

Results

Artisanal fisheries of the Paraná River changed dramatically over the last 30 years, including changes to the species composition and fishery strategies over

time (Figs. 1 & 2). In 1977, 5 years prior to closure of Itaipu Reservoir, over 90% of landings were composed of eight large, migratory species (Fig. 2). Five of the eight species occupy high trophic positions (piscivores) and accounted for approximately 55% of the landings (Fig. 2): jaú (*Zungaro zungaro*), dourado (*Salminus brasiliensis*), pintado (*Pseudoplatystoma corruscans*), cacharra (*P. fasciatum*), and barbado (*Pinirampus pirinampu*). The remaining three large migratory species (approximately 35% of landings) feed low in the food web: pacu (*Piaractus mesopotamicus*, approximately 20% of landings) consumes plants, fruits, and insects;

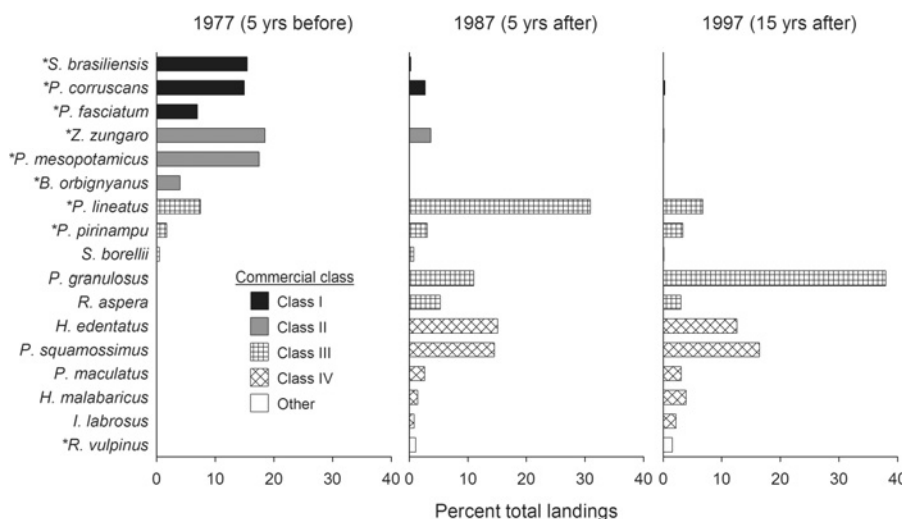


Figure 2. Decadal trends in the dominant species in artisanal fishery landings of the Upper Paraná River before and after impoundment. Years shown are 5 years before and 5 and 15 years after impoundment of Itaipu Reservoir in 1982. Species are coded according to their commercial classification (see Table 1). Species with an asterisk (*) attain lengths > 60 cm.

curimba (*Prochilodus lineatus*, approximately 10%) grazes detritus and attached algae; piracanjuba (*Brycon orbignyianus*, 5%) feeds on fruits and a minor fraction of insects.

By 1987 (5 years following impoundment), lentic conditions of the reservoir and the typical pulse of production during the first few years following impoundment (the so-called trophic upsurge) resulted in large fishery yields of curimba, perna-de-moça (*Hypophthalmus edentatus*), curvina (*Plagioscion squamosissimus*), and armado (*Pterodorus granulosus*) (Fig. 2). Curimba and perna-de-moça both feed at low trophic positions (detritivorous and planktivorous, respectively), whereas curvina and armado feed higher in the food web (piscivorous and omnivorous, respectively). By 1997 the relative yield of curimba had fallen back to preimpoundment levels, whereas curvina and especially armado increased greatly as they came to dominate the lentic and semilentic areas of the reservoir (Fig. 2). With reduced importance of curimba and perna-de-moça, the fishery became dominated by species with higher trophic positions.

On the basis of a 10% efficiency of energy assimilation, these higher trophic position species are 10–100 times more energetically costly to produce per unit biomass than species in lower trophic positions, such as curimba, that dominated the fishery during early stages of reservoir development. Changes in trophic composition following impoundment resulted in an initial decrease in direct energetic cost of fisheries production, followed by a rapid rise to preimpoundment levels by 1995 and thereafter fluctuating around that level (Fig. 3a). It is worth noting, however, that different species were responsible for the high direct energetic costs observed in 1977 and 1997; most migratory piscivores that were staples in the preimpoundment period disappeared from landings after the construction of Itaipu Dam (Fig. 2).

Total fisheries yield of Itaipu Reservoir followed a strong declining trend over the last two decades, with the yield in 2004 representing approximately half that of 1987 (Fig. 4a). Although annual yields dropped consistently following reservoir formation, this was not the result of reduced fishing effort. Total fishing effort almost doubled over the same period, increasing rapidly from 1987 to 1993 then stabilizing around 110,000 fisher-days per year (Fig. 4b). Consequently, the effort required to harvest 1 t of fish increased more than three-fold during the two decades following impoundment, from 40 fisher days in 1987 to 120 fisher days in 2005 (Fig. 3b). Low indirect energetic costs of artisanal fisheries production exhibited a strongly increasing trend during the postimpoundment period, with no indication of abating. Over the last few decades following impoundment, the Itaipu fishery experienced both negative growth (greatly diminished yield) and, perhaps more important, negative development (increased embodied energy per unit biomass harvested).

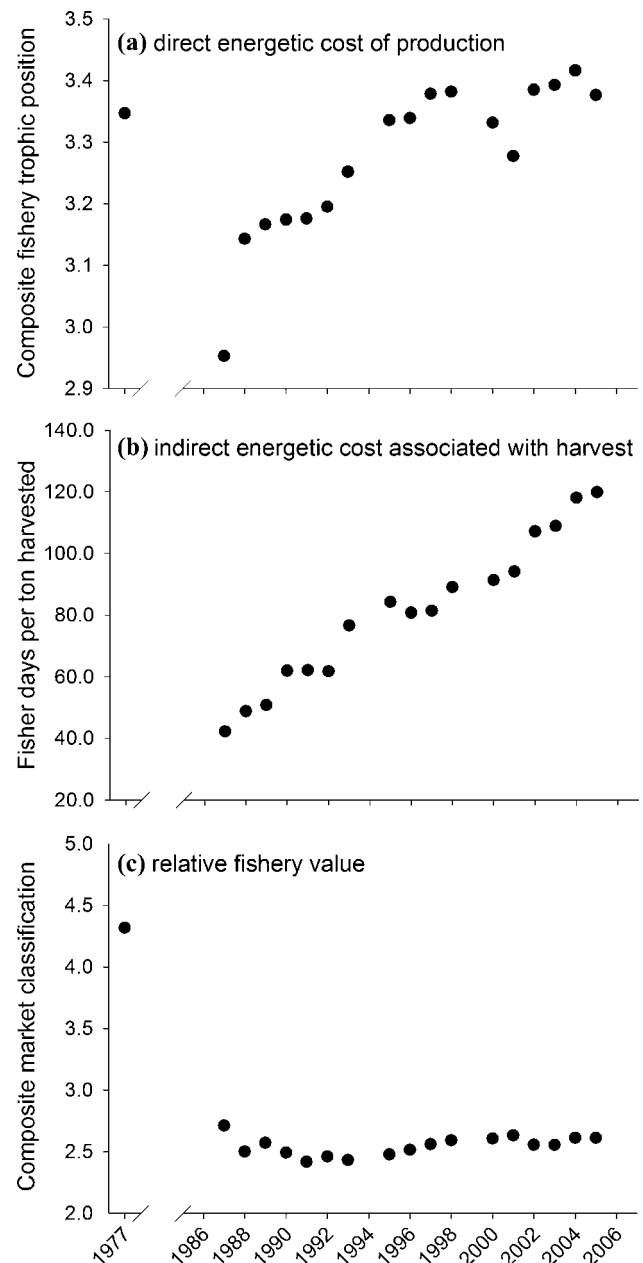


Figure 3. Annual trends in relative (a) direct energetic cost of production (composite trophic position), (b) indirect cost of harvest (effort per yield), and (c) market value of landings of the artisanal fishery of the Paraná River 5 years prior to impoundment (1977) and following formation of Itaipu Reservoir (1987–2005). Although indirect costs could not be estimated for 1977 in a manner similar to the other time periods, start-up and operational costs were comparatively lower following impoundment (Agostinho et al. 2005a).

In 1977, 5 years prior to impoundment, all species important in the artisanal fishery were native and the top four species (jaú, pacu, dourado, and pintado; Fig. 1), which represented approximately 75% of the landings

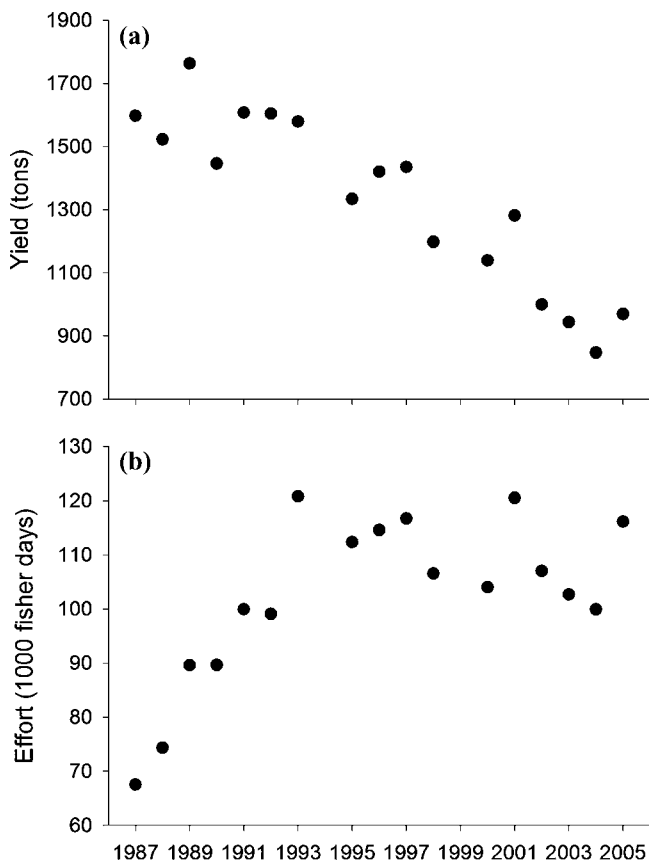


Figure 4. Annual trends in (a) yield and (b) effort of the artisanal fishery of Itaipu Reservoir from 1987 to 2005.

(Fig. 2), were all sold in regional markets in the highest commercial classes (class I or II; Table 1). By 1987, 5 years following impoundment, high-value species that dominated the fishery in 1977 contributed a combined 5% to fisheries landings (Fig. 2). The four dominant species in 1987 (curimba, perna-de-moça, curvina, and armado; Fig. 1) all had relatively low market values (Table 1), either because of lower-quality flesh or because they had not been consumed historically in the region (as in the case of curvina and armado, both non-native). As described earlier, large changes in the relative proportions of landings occurred between 1987 and 1997 (Fig. 2); however, the relative commercial value of the fishery re-

mained low because the two dominant species in 1997 were both low-value species in the commercial market, and high-value species remained rare or absent (Table 1; Fig. 2). Following river impoundment, the market value of the fishery dropped greatly and remained low over the subsequent 2 decades (Fig. 3c).

Discussion

Applying the concept of ecosystem services to aid conservation of biodiversity and naturally functioning ecosystems requires understanding how environmental impacts affect the ecology of key species or functional groups providing the services (Kremen 2005; Farber et al. 2006). To date, only a handful of ecosystem services have been investigated in this manner (Kremen & Ostfeld 2005). We examined effects of river impoundment, one of the leading threats to freshwater biodiversity, on an important ecosystem service provided by large tropical rivers (i.e., fisheries harvest). Although impoundments supply alternative services (e.g., hydropower), the societal and economic importance of fisheries in developing countries may provide the necessary leverage to advance conservation agendas where future impoundments are being considered. Furthermore, the importance of this ecosystem service in tropical latitudes coincides with diverse and often endemic native faunas, such as in our study region.

River impoundment greatly affected direct and indirect energetic costs of artisanal fisheries production and harvest and market value of the Upper Paraná River fishery (Table 2; Fig. 3). The artisanal fishery prior to impoundment was characterized by relatively high trophic position species and low harvest costs, which suggests a comparatively moderate embodied energy of this ecosystem good. The species harvested were well appreciated in the market and commanded relatively high prices. Although reservoir impoundment initially decreased direct energetic costs of fisheries production, market value of the fishery also decreased greatly. Over time impoundment resulted in a progressively widening mismatch between embodied energy and market value: the contemporary high embodied-energy fishery yields low commercial value.

Table 2. Qualitative comparison of market value and relative embodied energy of the Paraná River fishery before and after closure of Itaipu Reservoir in 1982.

	1977 (5 years before)	1987 (5 years after)	1997 (15 years after)
Market value	high	low	low
Embodied energy*	medium	low-medium	very high
direct cost	high	low	high
indirect cost	low	medium	high

*Embodied energy is separated into the direct energetic cost of production and the indirect cost associated with harvesting (see Fig. 3).

Mismatched trends in embodied energy and market value following impoundment appear to be driven by two different mechanisms. Shifts in direct and indirect components of embodied energy of the fishery generally reflect stage of reservoir ecosystem development. Early stages of reservoir ecosystem development increased ecological efficiency of fisheries production as low trophic-position species (especially algivorous/detritivorous curimba) responded positively to the initial pulse of terrestrial vegetation decomposition and aquatic production that typically occur during this phase (Agostinho et al. 1999). Also contributing to increased ecological efficiency were declines in the relative contributions of higher trophic-position migratory species. Over the next decade, fisheries landings became dominated by omnivorous armado and piscivorous curvina, reflecting a large decrease in ecological efficiency of fisheries production compared with earlier stages of reservoir development. The relative effort necessary to harvest the same biomass of fish also increased greatly over time, representing increased indirect energetic costs. As a result, embodied energy of the Itaipu fishery increased markedly and steadily with time following impoundment.

Although also greatly affected by impoundment, market value of the fisheries landings depended on species identities and consumer customs and preferences rather than stage of reservoir development. Just as in other river basins worldwide (e.g., Reynolds et al. 2005), populations of migratory species were greatly affected by river impoundment, whereas non-native species thrived in the new reservoir (Agostinho et al. 2004c; Pelicice & Agostinho 2008, 2009). Several dominant species in postimpoundment fishery landings are non-native, including species introduced from the Amazon Basin such as curvina. Armado and perna-de-moça, along with more than 20 other species, colonized the Upper Paraná River basin following inundation of Sete Quedas waterfalls (a former biogeographic barrier) on filling of Itaipu Reservoir (Agostinho et al. 2004a). Although some non-native species are of comparable palatability, they have lower market values due to consumer preferences for native species traditionally consumed in the region. This observation highlights the importance of species identities in addition to functional role in ecosystem services: two species may be comparable in provisioning of ecosystem goods or services (e.g., embodied energy in our analyses), but cultural preferences may ultimately dictate the value assigned in the commercial market and have cascading effects on economic well-being and resource sustainability. Because of cultural preferences, native long-distance migratory species, such as dourado and pintado, are fundamental components affecting the quality (i.e., market value) of this ecosystem service.

The observed trends for this fishery as a result of impoundment are likely representative of other im-

pounded tropical river systems and are likely to occur in other tropical basins if impounded. Naturally functioning large tropical rivers experience predictable seasonal flooding over large areas, resulting in a pulse of primary production that drives ecosystem dynamics (Junk et al. 1989). Long-distance migratory species are a conspicuous component of tropical fish faunas that have evolved reproductive strategies to maximize fitness in response to this predictable large-scale environmental variation (Winemiller & Jepsen 1998). By coinciding reproduction with floodplain inundation, juveniles benefit from the pulse of production and refuge habitats within the floodplain, thus maximizing growth and recruitment. These species also serve as important vectors of production into nutrient-poor habitats (e.g., blackwater rivers, reservoirs) as migrating young-of-the-year are consumed by resident piscivores, including some important fisheries species (Winemiller & Jepsen 2004; Hoeinghaus et al. 2006). Long-distance migratory species are imperiled in the Upper Paraná River basin and in many other large tropical river basins, primarily as a result of impoundments (e.g., Agostinho et al. 2003, 2005b; Dudgeon et al. 2006). In impounded tropical rivers, the same climatic conditions that create the flood pulse in natural systems often result in decreased production owing to increased discharge and lower water residence time in reservoirs, constraining fisheries production of resident reservoir species (Gomes et al. 2001). By reducing flood intensity and duration, disrupting migration routes, and limiting productivity, impoundments severely affect the ability of large tropical rivers to provision artisanal fisheries.

In the Upper Paraná basin several different management strategies have been attempted to improve sustainability of the artisanal fishery and social conditions of families dependent on this resource. These strategies include stocking programs and construction of fish ladders throughout the basin in an attempt to rebound stocks of high-value native migratory species, and introduction of non-native species adapted for reservoir conditions to increase fisheries yield. These actions have not worked or may have made the situation worse (Agostinho et al. 2004b, 2007). The current fishery is dominated by non-native species that complete their entire life-cycle within the reservoir but are energetically inefficient and have low market values. Native migratory species may facilitate fishery sustainability by linking reservoir food webs with production sources across broader spatial scales tied to seasonal pulses of production (Winemiller 2004). Management actions (i.e., stocking programs, fish ladders) specifically targeting these high-value native species have failed. For example, fish ladders upstream of the Upper Paraná floodplain may be ecological traps as migratory species ascending ladders arrive in a series of reservoirs without suitable habitat for juvenile development and recruitment, whereas suitable habitats are available below the dams (Pelicice & Agostinho 2008).

In addition to aiding biodiversity conservation initiatives where reservoirs are being considered, our findings have management applications for basins already affected by impoundments. Native migratory species are critically important to artisanal fisheries in tropical river systems (in terms of market value and ecological sustainability) and may also serve as umbrella species for conserving biodiversity (Agostinho et al. 2005b). As in many other tropical rivers (Dudgeon et al. 2006), the primary threat to biodiversity in the remaining free-flowing reaches of the Upper Paraná River is reduced flood intensity and duration caused by upstream impoundments (Thomaz et al. 2004). Recruitment and condition of native migratory fishes are also strongly correlated with these factors (Gomes & Agostinho 1997). In impounded rivers, water releases from upstream reservoirs should be managed to achieve key hydrologic characteristics of the natural flood pulse, thereby supporting spawning, growth, and recruitment of native migratory species, as well as ecosystem functioning for conservation of biodiversity in general (Richter et al. 1997; Arthington et al. 2004; Welcomme & Halls 2004). In this way management actions aimed at improving socioeconomic conditions of local fishers would also help conserve biodiversity and ecosystem function.

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