# PROBABLE EFFECTS ON AQUATIC BIODIVERSITY AND ECOSYSTEM FUNCTION OF FOUR PROPOSED HYDROELECTRIC DAMS IN THE CHANGUINOLA/TERIBE WATERSHED, BOCAS DEL TORO, PANAMA, WITH EMPHASIS ON EFFECTS WITHIN THE LA AMISTAD WORLD HERITAGE SITE

Scientific Paper submitted to the World Heritage Committee providing additional information for the Petition to the World Heritage Committee Requesting Inclusion of Talamanca Range-La Amistad Reserves/La Amistad National Park on the List of World Heritage in Danger

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## INTRODUCTION

Four hydroelectric dams, with a combined generating capacity of 446 megawatts (mw), are currently planned for the Changuinola/Teribe watershed of Bocas del Toro Province, Panama (Cordero, et al. 2006); still other dams have been conceptualized or rumored in the watershed. The purpose of this paper is to outline the probable biological consequences of construction of the proposed (or other) dams in the watershed, with particular reference to the role of diadromous fish and invertebrates and effects on the Panamanian portion of the La Amistad International Peace Park and Biosphere Reserve (hereinafter referred to by its Spanish acronym, PILA), designated a World Heritage site by UNESCO. (See Map 1).

While the essence of this report is predictive, throughout it we will implicitly invoke the Precautionary Principle. Knowledge of the biology of the species and ecosystems involved is extremely limited, a factor which should incline all concerned to take a very conservative approach to any proposed major alterations to the landscape. We can be certain that the biological effects of the proposed dams would be severe; we cannot be certain just what they would be. To the degree that specific effects cannot be predicted, prevention or mitigation of some undesired effects becomes moot.

Three of the proposed dams, known respectively as CHAN-75 (El Gavilan), CHAN-140 (Cauchero) and CHAN-220, would be located on the mainstem of the Changuinola River. The other proposed dam, Bonyic, would be located on the Bonyic (or Bon) River, a tributary of the Teribe River, which is in turn the principal tributary of the Changuinola. (See Map 2). While all of the proposed dams, and their impounded reservoirs, would be located in the Palo Seco Forest Reserve, downstream of PILA, upstream biological effects of the dams and reservoirs would be profound and would be felt largely within PILA.

The total area of the Changuinola/Teribe watershed is 3,202 square kilometers (sq. km.), of which approximately half is located within PILA. The total watershed area above the proposed CHAN-75 and Bonyic dams is 1,493 sq. km., a large majority of which is in PILA, with the rest in Palo Seco. Within this area we estimate that there are over 700 miles (mi.) of permanently flowing streams. All of these streams, and the associated forested area, would be affected by the role of the dams as barriers to up and downstream movement of fish and other animals.

As we will show, based on experience in similar fluvial environments in Mesoamerica and the Caribbean, plus available information on the aquatic biology of the Changuinola/Teribe system and its fauna, probable upstream effects would be drastic, involving extirpation or severe reduction within PILA of populations of 8-11 species of migratory fish and several species of shrimps. Ecological consequences would be severe since these species comprise most of the most abundant and largest species, as well as species with unique ecological functions.

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In addition to the effects within PILA, the dams would cause alterations to aquatic and terrestrial ecosystems within the area of the 4 impoundments as well as to the Bonyic, Teribe and Changuinola Rivers and their tributaries downstream to and including the Changuinola estuary. Probable cultural and economic impacts on the Naso and Ngobe ethnias, who inhabit the Palo Seco area, should also be considered, as should the biological and economic effects on river and estuarine fisheries downstream of the dams. Non-biological effects will not be treated in this report; reference may be made to McLarney (2005), McLarney and Mafla (2006b) and Cordero, et al. (2006, 2007).

Effects within PILA are emphasized here because PILA is a UNESCO World Heritage site. The first justification for declaration of the Panamanian portion of PILA as a National Park was "to protect a significant sample of the biological diversity of one of the richest faunal and floral zones which still remains largely unaltered in the Republic of Panama" (Alvarado, 1989). It has been argued that if the biodiversity of a major portion of PILA were to be knowingly reduced, Panama would be failing to live up to its obligations to UNESCO, and that the World Heritage site status of PILA-Panama should be questioned. This is the subject of a petition submitted to the UNESCO World Heritage Committee on April 22, 2007 by the Center for Biological Diversity (CBD) (Thorson, et al. 2007. Petition to the World Heritage Committee Requesting Inclusion of Talamanca Range-La Amistad Reserves/La Amistad National Park on the List of World Heritage in Danger.) This paper provides a more detailed explication of biological information reviewed by the CBD in arriving at their position.

## DAMS AS BARRIERS, AND THE IMPORTANCE OF DIADROMY

Any obstruction placed in a flowing stream will function to some degree as a barrier to up and downstream movement by aquatic animals, and thus to some degree, will fragment the ecosystem. Even porous rock dams placed in small streams in order to temporarily impound water for uses such as irrigation or recreation may require fish and other animals to expend extra energy and expose them to predators. At the opposite extreme, high dams on major rivers can function as nearly absolute barriers, dividing the river into two isolated segments, separated not only by the dam, but by a third and extremely different environment in the form of a reservoir lake. The degree to which these effects may be mitigated is variable; here we will argue that in the specific case of the Changuinola/Teribe watershed, mitigation adequate to protect biodiversity within PILA is well-nigh impossible. This is especially true in the case of the CHAN dams; the barrier effect of 3 dams and reservoir lakes in sequence would likely negate even the slight possibility of long term survival of some diadromous species in the system were there only one dam and reservoir.

In defending this argument, we will need to introduce some very specific vocabulary anent the modes of movement of aquatic animals. Some fishes and many aquatic invertebrates are relatively sedentary; they tend to spend their entire lives within a fairly restricted area (though long involuntary movements may occur under conditions of extreme weather or as a consequence of anthropogenic disturbance). These animals are generally considered to be "non-migratory," though wandering by individuals or involuntary movement may play an important role in dispersal of populations.

Some forms of voluntary movement, even over long distances, are not properly referred to as "migratory." An example would be the opportunistic movements of some largely marine fishes up rivers in pursuit of prey. This accounts for the occasional capture of large marine fishes such as snooks (*Centropomus*) and jacks (*Caranx*) well inland on rivers such as the Changuinola and Teribe. This behavior is not strictly essential to the survival of these species; some populations exist without ever realizing this opportunity. "Migration" was best defined by Northcote (1979) as:

> "movement resulting in an alternation between two or more habitats (i.e. a movement away from one habitat followed by a return again), occurring with regular periodicity (usually seasonal or annual), but certainly within the life span of an individual and involving a large fraction of the breeding population. Movement at some stage of this cycle is *directed* rather than a random wandering or a passive drift, although these may form part, or one leg of a migration."

In other words, true migration is voluntary movement essential to the maintenance of species and populations. In fresh water fishes, true migration may be divided into two categories, as first defined by Myers (1949): *Potamadromy* refers to migrations carried out totally within fresh water. *Diadromy* is applied to those animals which are obliged to migrate between fresh and salt waters in order to complete their life cycle. There is no evidence of potamadromy in the Changuinola/Teribe watershed, although one of the commonest obligate fresh water species of the watershed (*Astyanax aeneus*) has been shown to be potamadromous in Guanacaste, Costa Rica (Lopez, 1978). However, we here identify (Table 1) 11-15 diadromous species in the watershed, of which 8 or 9 regularly reach the waters of PILA.

Some proportion of diadromous animals exists in most of the fresh waters of the world. However, diadromy is especially prevalent on islands and isthmuses, such as Mesoamerica, where river systems are necessarily short. In the case of Mesoamerica, including Bocas del Toro, the predominance of diadromous forms is also due to the periodic isolation, over geologic time, of the isthmus from the larger continental land masses of North and South America. As a consequence, diversity of "primary" fresh water fishes, defined by Myers (1966) and Miller (1966) as fishes strictly intolerant of salt water (stenohaline fishes), is low. "Apparently dispersal has been a slow process for the majority of the freshwater fishes due to their inability to travel by salt water or other means." (Bussing, 1998). As a consequence, euryhaline fishes (able to tolerate a wide range of salinities), most of them of marine origin, have had a competitive advantage, and Mesoamerican rivers contain an unusually large proportion of fishes which are not truly "fresh water" species, in the sense of Myers and Miller. (We here refer mainly to fishes; much of the same terminology and arguments apply to some crustaceans, and we will also refer to shrimps in developing our argument.)

Studies directed by us since 1999 in the Talamanca region of Costa Rica, bordering Bocas del Toro (McLarney and Mafla, 2006b) have resulted in a fairly complete list of the fresh water fish species of Talamanca. Of 43 species we have captured in fresh water (excluding species known only from estuaries), 20 move regularly between fresh and salt water and at least 14 exhibit true diadromous behavior. (McLarney and Mafla, 2006a) This information, supplemented by surveys conducted by Dr. Jorge Garcia of the University of Panama (personal communication, J. Garcia), information from the Smithsonian Tropical Research Institute database (STRI 2007), and informal reports by indigenous parataxonomists residing in the Changuinola/Teribe watershed (Mafla, et al., 2005) forms the basis for Table 1, which is a provisional list of the freshwater fishes of the Changuinola/Teribe watershed with what is known of their migratory behavior. (It is expected that this information will soon be updated by the results of a survey currently being conducted by a Smithsonian team in the Changuinola/Teribe watershed.) In Table 1 and the rest of this paper, we follow Myers (1949) and McDowall (1988) in dividing diadromy into 3 categories:

*Anadromous* fishes "pass the majority of their lives in the sea and migrate to fresh water to reproduce" (McDowall, 1988). The best known examples of anadromous fishes are the Pacific salmons (*Oncorhynchus*) which constitute a major commercial resource in North America and northern Asia. Although anadromy is by far the best known form of diadromy, it is little developed in the tropics. Most tropical anadromous fish, such as the pipefishes (Syngnathidae), do not ascend far above tidewater.

*Catadromous* fishes are the obverse of anadromous species; they "pass the majority of their lives in fresh water and migrate to the sea to reproduce." The best known examples are the freshwater eels (Anguillidae) of almost worldwide distribution, including Mesoamerica and Bocas del Toro.

*Amphidromous* fishes comprise a third and much less known category, although amphidromy is the dominant form of diadromy in the tropics and on many islands, and virtually the only form of diadromy known for crustaceans and molluscs. Amphidromy was first defined by Myers (1949) who used it to refer to nominally "fresh water" animals which are obliged to spend time in salt water outside of the reproductive period. It remained an obscure and often misunderstood category until McDowall (1987, 1988, 2007) published the definitive works on the subject.

The normal pattern of amphidromy begins with eggs laid in fresh water, sometimes after a downstream migration by the breeding adults. The newly hatched larvae are carried by the current to the sea where, after a developmental period of varying duration, they begin a long upstream migration as advanced larvae or juveniles, continuing to develop as they migrate.

A peculiar habit of some amphidromous animals is to migrate in mixed groups. Perhaps the best known manifestation of amphidromy is the "tismiche" of the Mesoamerican Caribbean (Gilbert and Kelso, 1971), in which large masses of larval and juvenile gobies (Gobiidae) and palaemonid shrimps, sometimes mixed with other groups and collectively called "titi," migrate upstream together.

All forms of migratory behavior, diadromous or otherwise, are subject to disruption when rivers are dammed. This may take various forms:

- Upstream migrants, even large, strong swimming fish, may be stymied by the physical barriers posed by dams, penstocks, and dewatered river reaches.
- Downstream migrants may be killed passing over drop structures or through turbines.
- Passive downstream migrants, such as many larval forms, depend on river currents, and may sink and perish in the slow moving to stagnant waters of reservoir lakes.
- Some actively swimming species depend on currents to orient themselves and may wander aimlessly, with consequent high mortality, in impoundments.
- Animals attempting to surmount barriers may be unduly exposed to predation, desiccation and other threats.

## EFFECTS OF DAMS ON DIADROMOUS ANIMALS IN MESOAMERICA AND THE CARIBBEAN.

In this section we will review literature to suggest the probable effects of large dams in the Changuinola/Teribe system, with emphasis on the area within PILA. There are no published studies on the effects of dams on diadromous animals in Mesoamerica. However, we can profit from experience in the larger West Indian Islands, where the rivers are similarly short, and where the mix of diadromous species is similar to that in Bocas del Toro.

- In Curacao, Dolphe and Ebrot (2003) implicated dams (along with water diversions) in the disappearance of diadromous fishes over much of the island.
- In Guadeloupe, Fievet (1999) and Fievet, et al. (2001a, 2001b) found total or near-total absence of diadromous fishes and shrimps in rivers upstream of dams.
- Perhaps the best test case is Puerto Rico. While in most of Latin America, pressure for construction of hydroelectric dams is only now reaching its peak, Puerto Rico, being part of the United States, is already saturated with hydroelectric dams (3 times more large dams per unit area than the continental United States, according to Greathouse, et al. 2006b). Holmquist, et al. (1998) found that all native fishes and shrimps were extirpated upstream of large (>15 m. high) dams with no spillway discharge in Puerto Rico and observed total or near-total absence of diadromous fishes and shrimps in rivers upstream of dams with spillways theoretically passable by fish and shrimp. Greathouse, et al. (2006a, 2006b) reviewed the situation in Puerto Rico and determined that dams with spillways "cause near, not complete, extirpation of upstream populations of migratory fauna." They estimated that "[l]arge dams eliminate or reduce access of migratory biota to 2,000 sq. km. of the island's watershed area or 22% of the island's land mass."
- Elsewhere, particularly strong negative effects of dams on diadromous fauna have been described for Japan (Miya and Hamano, 1998); Guam (Concepcion and Nelson, 1999); New Zealand (McDowall, 2000), Texas (Horne and Biesser, 1997) and the United States in general (Bowles, et al. 2000).

Taxa mentioned in these studies which also occur in Bocas del Toro include *Anguilla, Agonostomus, Joturus, Awaous, Sicydium, Gobiomorus* and palaemonid and atyid shrimps. Information on dam effects from Mesoamerica is largely anecdotal. Bussing (1998) cites personal communication (H. Arraya) to the effect that *Joturus pichardi* has disappeared from the tributaries of Lake Arenal, Costa Rica since it was dammed in 1980. Chris Lorion of the University of Idaho/CATIE reports the absence of this species from the Rio Reventazon at Turrialba, Costa Rica above the Angostura dam, whereas McLarney found it to be common there in 1968.

## PROBABLE EFFECTS OF DAMS IN THE CHANGUINOLA/TERIBE WATERSHED ON MIGRATORY AQUATIC FAUNA

Approximately 9 species of diadromous fish (pending the resolution of taxonomic disputes) in 6 families, plus representatives of 2 families of diadromous shrimp are known from the upper reaches of the Changuinola/Teribe watershed, including the waters of PILA. Here we summarize what is known about these animals relevant to their distribution and reproductive behavior and predict the consequences for them of construction of the proposed dams.

### Family Anguillidae (freshwater eels)

#### *Anguilla rostrata* (American eel, anguila del mar, pjokro in Naso or kru way in Ngobe)

The anguillid eels are distributed almost worldwide, and provide the best known examples of catadromous fishes. *A. rostrata* has an enormous range – extending from Greenland to some undetermined point in the Caribbean; it may be near the southern terminus of its range in Bocas del Toro. Due to its large size (up to 1.2 meters (m.) long), ample distribution, and commercial importance in North America, it is the exception among the diadromous fishes of Mesoamerica in that its life cycle is relatively well known. Although eels spend most of their lives in fresh water, sexual maturity is not achieved until they embark on a long journey from the rivers of the western hemisphere to the Sargasso Sea, off Africa, where they reproduce in waters 500 m. deep or more. (Some authorities believe that *A. rostrata* from Mesoamerica reproduce in the Caribbean; see Tesch, 1977.) Following the spawning act, the adults die.

Anguillid eels hatch as transparent, ribbon-like larvae ("glass eels" or leptocephali), and are carried by oceanic currents to the coast of the Americas, a journey which takes about a year. After some months in estuarine environments they become opaque, assume the form of small eels (elvers), and enter river mouths. The males remain small and do not venture far above the estuary, but the larger females venture far up rivers. Bussing (1998) reports *A. rostrata* at elevations to 20 m. "in stagnant waters or rivers of moderate current velocity." However, in Talamanca we have on several occasions captured eels in strong rapids, and at altitudes of up to 80 m. We have verifiable reports of *A. rostrata* from the Teribe and Bonyic rivers; in the Teribe watershed at least it is found well within PILA and has been reported from altitudes of up to 300 m. in the Bonyic.

As a largely nocturnal species, the American eel is relatively little known by the majority of the population in Panama and Costa Rica. However, it is common enough to be a minor source of food in the Teribe, where it is taken at night on hook and line. Eels have some ability to travel overland, and have been seen to scale or travel around dams on some occasions. Navigation in the still waters of reservoir lakes does not appear to present a problem. However, travel out of water is energetically costly and exposes the eels to predators. *A. rostrata* has become rare in inland North America, and was recently considered by the US Fish and Wildlife Service as a candidate for endangered listing (Bell, 2007). The main cause of reduction of eel populations is considered to be the proliferation of dams on the principal rivers of North America (Jenkins and Burkhead, 1993).

### Family Gobiesocidae (clingfishes)

#### *Gobiesox nudus* (clingfish, chupapiedra cabezon)

*G. nudus* is one of the few fresh water representatives of a principally marine family, and should not be confused with gobies of the genus *Sicydium*, also called "chupapiedras," which are much more common in Bocas del Toro. As with *Sicydium, G. nudus* has the pelvic fins modified into a thoracic sucking disc by means of which it clings to the rocky substrates where it is typically found.

The known range of *G. nudus* extends along the Atlantic coast from Honduras to Venezuela, where it is known from rivers between 25 and 580 m. in altitude (Bussing, 1998). In 7 years of intensive sampling we have never found a Gobiesocid in Talamanca, nor have we heard verbal reports of their existence. However, for some time we have received anecdotal reports of a chupapiedra cabezon in the Changuinola/Teribe watershed. This information was confirmed in 2007 with repeated sightings of a Gobiesocid, presumably *G. nudus* by qualified parataxonomists in the Teribe River, within and downstream of PILA (personal communication, M. Bonilla). So far we are not aware of any other sites, but it is likely that this small, secretive fish is more widely distributed.

There are no published studies of the reproduction of any of the freshwater *Gobiesox* species. However, given the family's marine affinities, and taking into account that adults have never been seen below 25 m. altitude, while larvae are unknown from the upper rivers, it is probable that *G. nudus* is amphidromous.

If *G. nudus* is in fact amphidromous, the eventual effect of dams could be considerable. At the present time, no dams are formally proposed for the Teribe River mainstem, so the only known population may be secure. However, if it exists in the Bonyic or Changuinola Rivers, upstream extirpation would be the likely effect of damming, since it is unlikely that eggs or recently hatched larvae could pass through reservoir lakes. Upstream migration by adults could also be precluded, since (unlike in the case of *Sicydium*) there are no reports of *Gobiesox* using the thoracic sucker to scale vertical surfaces.

## Family Haemulidae (grunts, roncadores)

***Pomadasys crocro*** **(burro grunt, Atlantic grunt, ronco; shyir in Naso or Bu in Ngobe)**

This large species (up to 355 mm. long) is important in artesanal fisheries in the Changuinola/Teribe watershed, where it inhabits all of the rivers and large creeks, in and out of PILA, up to an altitude of at least 250m.

There is nothing published on the reproduction of *P. crocro* or any other species of *Pomadasys.* Since the family Haemulidae is principally marine and *P. crocro* is found at sea level in estuaries but not in the open sea, and because no one has described the larvae, we conclude that *P. crocro* is probably amphidromous, though it could be catadromous. In either case a probable consequence of damming would be its disappearance from the upper watershed, including PILA.

## Family Mugilidae (mullets, lisas)

***Agonostomus monticola*** **(mountain mullet, sarten, lisa, tepemechin; dremkwo in Naso or kubia in Ngobe)**

*A. monticola* is by far the most abundant fish of edible size in the fresh waters of Bocas del Toro, and is thus of major importance in the diet of the inhabitants. It is more abundant in swift flowing rivers and creeks than in those of lower gradient, but it is found in every stream of the region up to the first natural barrier. Bussing (1998) cites *A. monticola* at up to 650 m. elevation in Costa Rica. It has appeared in 100% of the visual inventories made in the Changuinola/Teribe watershed. In PILA it is probably the second most abundant fish after *Sicydium*.

Surprisingly, for such a widely distributed (on both coasts from the southern United States to Venezuela and Colombia), abundant, visible and highly valued fish, there is not general agreement as to whether *A. monticola* is amphidromous or catadromous. Anderson (1957), who found pelagic *A. monticola* larvae off Florida, and Bussing (1998), based mainly on observations in Costa Rica, consider it catadromous. Phillip (1983) reported finding ripe and running females in the sea off Trinidad. However, Cruz (1987) who studied both species of diadromous mullets in Honduras, thought it might be amphidromous.

For whatever reason, McDowall (1998) in his text on diadromy did not include Phillip's observation, but cited Corujo-Flores (1980) to the effect that ripe adults have always been taken in fresh water. Loftus, et al. (1984), also cited by McDowall, went further and claimed that adults of any stage have never been taken in salt water, and reported "probable" spawning behavior in Puerto Rican rivers. Were *A. monticola* shown to be amphidromous it would be the first confirmed case of amphidromy in the Mugilidae; all those members of the family which have been studied are either catadromous or completely marine. Gilbert and Kelso (1971) and Gilbert (1978) attempted to summarize life history information on *A. monticola.*

In Costa Rica, at least (and probably in Panama), the situation is more complicated because according to Bussing (1998) "juvenile *Agonostomus* appear in different seasons of the year, which may indicate that *A. monticola* reproduces several times during the year or it may be that there is more than one species, each with a different reproductive period." Even if there is only one species of *Agonostomus* in Costa Rica and Panama, the great morphological variation and the irregular seasonality of its migrations suggest the possibility of different reproductive strategies, possibly including both catadromous and amphidromous populations.

Be it amphidromous, catadromous or both, *Agonostomus* is one of the few fish which appears in almost all samples and visual inventories from rivers, creeks and brooks in Bocas del Toro and Talamanca at all elevations below natural barriers. It would be vulnerable to extirpation above whatever dam – and the possibility of a range of reproductive behaviors within the species would make any effort to mitigate damage by providing passage for *Agonostomus* especially difficult.

***Joturus pichardi* (hogmullet, bocachica, bobo, cuyamel; ma in Naso or gwa kree in Ngobe)**

The bocachica, found from sea level up to at least 600 m. elevation, is at once the largest fresh water fish in upland Mesoamerica, and the preferred table fish. For this reason, among others, it has become scarce over much of its range (from Veracruz, Mexico to San Blas, Panama, plus Cuba, Hispaniola and Puerto Rico). There is general agreement that in Talamanca (where dams are not presently a factor) its abundance has declined greatly over the last 30 years.

Surprisingly, considering the growing population of Bocas del Toro and the high esteem in which *J. pichardi* is held as a food fish, it does not appear to be comparably rare there. During a visit to the upper Changuinola watershed in 2005, we found evidence of its apparent abundance in the form of great numbers of "tracks" (marks left on rocks where it scrapes the algae which form the major part of its diet). Based on all available anecdotal information from Costa Rica and other countries, it appears that the Changuinola/Teribe watershed is home to one of the strongest extant populations of *J. pichardi*, and is thus important to the long-term viability of the species. There, as elsewhere, it lives in or near the strongest rapids.

The gaps in our knowledge of the reproductive biology of this important species are enormous. As in the case of *Agonostomus monticola*, no one has observed the spawning act of *J. pichardi*. Darnell (1962) and Erdman (1984) considered that *J. pichardi* is catadromous, based on studies in Mexico and Puerto Rico, respectively. Cruz (1987) who dedicated several years to the study of this species in Honduras, opined that both *J. pichardi* and *Agonostomus monticola* are amphidromous, laying their eggs in rivers. (We have heard anecdotal reports of ripe females in both fresh and salt water.) Further, no one has collected larvae of *J. pichardi*, or juveniles less than 60 mm. long in fresh or salt water.

Our own observations, supported by anecdotal information from inhabitants of Talamanca and Bocas del Toro, show that *J. pichardi* is scarce or absent from rivers during the last months of the year, but that both adults and juveniles reappear from January on. We have also encountered segregation by size, with juveniles in creeks and the largest adults in the major rivers. This suggests that, in addition to an annual reproductive migration, they move from stream to stream during their life, as they grow.

We assume that *J. pichardi* would disappear from any river above a dam, including in PILA. There is precedent from Puerto Rico (Erdman, 1984), and strong anecdotal information (cited above) from the Arenal and Reventazon watersheds in Costa Rica, confirming lack of reproductive success above dams.

## Family Gobiidae (gobies, gobios)

***Awaous banana* (river goby, chuparena; lomdo in Naso or umana in Ngobe)**

The gobiid genus *Awaous* is almost universally distributed in tropical and subtropical regions. In many islands, such as Hawaii and the smaller West Indian islands, it is the only fish which inhabits some fresh water rivers and creeks. The only species of *Awaous* reported from Bocas del Toro, *A. banana,* is known from the entire Caribbean and southern Gulf of Mexico. It reaches 180 mm. in length, and is of minor importance as a food fish. It occupies a unique role in the ecosystem as the only fresh water fish which eats principally Chironomid larvae and other insects which it filters from sandy substrates (hence the common name "chuparena"). Although low in abundance at most sites, the population of *A. banana* is well distributed from near sea level up to at least 980 ft. altitude in PILA.

In spite of being well known on 4 continents and in many islands, much of the information on *Awaous* is conjectural. Yerger (1978) thought that *A. banana* spawned in the sea, but Bussing (1998) opines that "[t]hey probably reproduce near the sea and the larvae are swept into the sea where they develop in pelagic waters." If *A. banana* requires access to salt water to complete its life cycle, be it amphidromous or catadromous, it would probably disappear above the proposed dams; there is precedent for such a result in Puerto Rico.

***Sicydium* spp. (titi, chupapiedra; diogwo in Naso or malu in Ngobe)**

There is not agreement on the number of species of *Sicydium* in Bocas del Toro. Bussing (1996) divided *S. altum* into 2 species, designating the new species *Sicydium adelum*, but *S. adelum* is not recognized by all authorities. According to Bussing (1996, 1998) at lower elevations the 2 species nearly always occur together, but whereas *S. altum* is reported up to elevations of 1,200 m. in Costa Rica, *S. adelum* is known only to 90 m.

In the Changuinola/Teribe and neighboring watersheds, *Sicydium* is the most abundant fish wherever there is rocky substrate. Despite its small size (up to 140 mm.) it is so abundant in many rivers as to almost certainly comprise the majority of the fish biomass. It is nearly omnipresent, occurring in smaller numbers in rivers and creeks with lower gradients and finer substrate materials.

Thanks to its strong thoracic disk, *Sicydium* is capable of climbing vertical barriers such as waterfalls. (Another goby, *Lentipes concolor*, of Hawaii, is documented to have surmounted a set of waterfalls 300 m. high, with 100 m. vertical drops; England and Filbert, 1997). In Bocas del Toro and Talamanca, *Sicydium* is normally the only fish found above natural barriers where, along with diadromous shrimps, it is the principal consumer of benthic algae.

There are no published studies of the reproductive behavior of *S. altum* or *S. adelum*, but *Sicydium stimpsoni* of Hawaii and *Sicydium taeniurus* of Tahiti have been shown to be amphidromous. (Tomihama, 1972; Schultz, 1943). We know that the larvae of *S. altum/adelum* spend a developmental period in estuaries and that at certain times of year they migrate up the rivers of Talamanca in enormous numbers, many times moving together with larvae of shrimp and other fish. Apparently they are long-lived and continue growing as they migrate upstream. It is normal to encounter the largest individuals at the highest altitudes, with smaller individuals near the sea (and over fine substrates).

It is probable that *S. altum/adelum* could climb at least some dams, were the humidity adequate. However, it also appears that reservoir lakes constitute an insuperable obstacle for adults and juveniles ascending or descending. This conclusion is coherent with the natural absence, in Talamanca, of *Sicydium* in a few fluvial systems characterized by coastal lagoons with very little current. And it is sufficient to explain the disappearance of *Sicydium* above dams in Puerto Rico and Guadeloupe (Holmquist, et al., 1998; Benstead, et al., 1999; Fievet, 1999; Fievet, et al. 2001a, 2001b). Thus it is reasonable to suppose that *Sicydium* would disappear from river reaches above dams in PILA and Bocas del Toro in general. Although to the lay observer, the disappearance of large, edible fishes such as *Joturus pichardi* and *Agonostomus monticola* might be more alarming, the disappearance of *Sicydium* (along with the shrimps) might have the most profound ecological consequences. (See below.)

## Family Eleotridae (sleepers)

***Gobiomorus dormitor* (Bigmouth sleeper, mudfish, guavina, bocon; sekwo in Naso or njuduolo in Ngobe)**

This large predatory fish is more abundant in the lower watersheds, but has been reported in PILA up to at least 100 m. altitude. In general, larger specimens are found in the upper reaches, with juveniles largely confined to lower altitudes. *G. dormitor* is an excellent food fish, often targeted by local fishermen.

Nordlie (1981), Darnell (1962) and Gilbert and Kelso (1971) consider that *G. dormitor* is catadromous, reproducing in the lower reaches of estuaries. However, in some places it is capable of reproducing in fresh waters with little or no current. McKaye (1977) and McKaye, et al. (1979) reported on a population in an isolated crater lake in Nicaragua. Bacheler (2002) and Bacheler, et al. (2004) documented fresh water reproduction from Carite

Reservoir in Puerto Rico. However, *G. dormitor* has been extirpated from several rivers above dams in Puerto Rico, and did not occur in other reservoirs, including some on the same river as Carite.

The viable populations of *G. dormitor* in isolated lacustrine environments in Nicaragua and Puerto Rico suggest that, under certain conditions, it can maintain populations without access to salt water. One possible hypothesis is that there is a recessive gene for freshwater reproduction in *G. dormitor*. Statistically, the odds would appear to be against its persistence above any dams which might be constructed in the Changuinola/Teribe watershed.

## **Other migratory fish:**

The discussion in this section attempts to be conservative by including only known diadromous fishes which have been reported from PILA-Panama. Other diadromous species known from below the dam sites (Table 1) may eventually be reported from PILA. The most probable candidates are flatfishes (pez hoja or lenguado) of the families Paralichthyidae (*Citharichthys spilopterus*) and Achiridae (*Trinectes paulistanus*). Both species are known from the lower Changuinola/Teribe watershed and, based on occurrences from Costa Rica and the southeastern United States (Gilbert and Kelso, 1971;Bussing, 1998; Tucker, 1978; Gunter and Hall, 1963; Swingle, 1971). It would not be surprising to find occasional specimens within PILA in either mainstem river. Their small size and cryptic habits suggest that they may be more abundant than is appreciated. The life cycle of these fishes is not completely known, but eggs of both genera are known to be pelagic, which leads to a hypothesis of catadromy.

Mention should also be made here of at least two groups of marine fishes for which we have reliable reports from the Teribe River within PILA. Snooks or robalos (Centropomidae, *Centropomus undecimalis* and probably other *Centropomus* species) and jacks or jureles (Carangidae, *Caranx*) occasionally enter PILA, presumably in pursuit of food. Members of both families should probably be regarded as opportunist migrants in the Changuinola/Teribe watershed. River reaches located above the dam sites may be important occasional food sources for these euryhaline but primarily marine fish, both of which are much sought after as food by humans.

## **Shrimps:**

Of equal importance with the fish are 2 families of "freshwater" shrimps (Palaemonidae and Atyidae), all members of which are, so far as is known, amphidromous. Visual surveys have determined the presence of palaemonid and atyid shrimps at nearly 100% of sites in the Changuinola/Teribe watershed, in and out of PILA, and including tiny streams above natural barriers. The shrimps share several characteristics with the chupapiedras (*Sicydium* spp.)

- Together they form the greater part of the "tismiche," the mass upstream migration of larval fish and shrimp which is one of the most spectacular natural phenomena of the Mesoamerican Caribbean (Gilbert and Kelso, 1971), and a major food source for many organisms, occasionally including man.
- Both groups are capable of climbing vertical barriers, so they tend to be particularly prevalent above waterfalls.
- Both feed on benthic algae and, together with aquatic insects and a few other fishes, play a major trophic role in freshwater streams in Bocas del Toro. (See discussion below under "Secondary Effects of Species Extirpations")

Because they can surmount vertical barriers, there are instances of diadromous shrimps surviving above some dams. However, populations are always reduced in these situations, and the more common result is extirpation. (See references cited above under "Effects of Dams on Diadromous Animals in Mesoamerica and the Caribbean" for effects of dams on diadromous shrimps in various countries.) In the event of the construction of the Changuinola/Teribe dams, the best that could be hoped for would be a drastic reduction of shrimp numbers in the streams above them, and total extirpation of all or some forms would be a possibility.

## SUMMARY OF EFFECTS ON MIGRATORY AQUATIC FAUNA

To summarize the probable effects on diadromous fauna of construction of the proposed dams, we would expect all 11 migratory fish species known from PILA-Panama to be drastically reduced in numbers, and probably extirpated above the Chan-75 and Bonyic dams. (One possible exception would be *Gobiesox nudus*, which has only been documented from the upper Rio Teribe, where no dams are presently proposed. However, it is entirely possible that this small, cryptic benthic species also occurs in the Changuinola system or in the Rio Bonyic.) On a purely numerical basis, the loss of over 25% of freshwater species from such a large "protected" area would be catastrophic. However, the relevance of the potential losses is even greater when we consider that these species include most of both the most numerous and the largest bodied species.

In terms of total numbers *Sicydium* is undoubtedly the most abundant fish in the PILA waters of the Changuinola/Teribe watershed. Not only will it be found to be the most abundant fish at most multi-species sites, it is usually the only fish above natural barriers. Hard numbers are lacking, but it would not be surprising to learn that three quarters of all the individual fish above the proposed dam sites are *Sicydium*. At most sites, the second and third fish in terms of abundance will be the diadromous *Agonostomus monticola* and one of the non-diadromous "sardinas" (*Astyanax* and *Bryconamericus*). In a 2005 survey (Mafla, et al., 2005) over 75% of individual fish counted in a series of Changuinola and Teribe River tributaries within PILA were of diadromous species.

Based on numerical abundance alone, it is clear that the great majority of fish biomass in the watershed above the dam sites, and at most individual sites there, will be composed of diadromous forms. Biomass dominance is enhanced by the fact that most of the larger species are diadromous. Among primary freshwater fishes, only the catfish *Rhamdia guatemalensis* can compare in size with *Anguilla*, *Pomadasys*, *Agonostomus*, *Joturus*, *Awaous* and *Gobiomorus*. This fact is of course also of concern to human users of the fish resource.

Given the abundance and diversity of insect larvae and other small benthic macroinvertebrates in any healthy stream substrate, it is difficult to compare the abundance and biomass of the palaemonid and atyid shrimps to that of other aquatic invertebrates. But it is clear that they comprise the great majority of the larger bodied invertebrate taxa, and their numerical importance is visually apparent. Especially in high elevation streams above natural barriers, where predatory fish are lacking, shrimp and *Sicydium* gobies together must comprise a very high proportion of the animal biomass.

Based on numerical abundance and biomass contribution alone, the extirpation or near extirpation of palaemonid and atyid shrimps from a major portion of PILA would be equally as catastrophic as the effects predicted for the fishes if the proposed dams are constructed. The problem does not end there; alteration of species composition would produce significant secondary effects.

## SECONDARY EFFECTS OF SPECIES EXTIRPATIONS

Beyond "mere" loss of species diversity, the extirpations and near-extirpations likely to occur if the Changuinola/Teribe dams are built would set in motion a series of secondary ecosystem effects which can be predicted, albeit in very general terms. Chief among these would be the consequences of wholesale loss of primary consumers and detritivores (*Sicydium*, shrimps and other diadromous macroinvertebrates, plus some of the larger fish such as *Agonostomus* and *Joturus*). In the tropics, including Bocas del Toro, typically fish and shrimps are the main consumers of both allocthonous (leaf and fruit drop) and autocthonous (algae) vegetable matter, a role generally played by insects in temperate ecosystems. "When these fauna experience declines due to human activities such as dam building, there can be dramatic effects on primary producers and standing stocks of organic matter." (Greathouse and Compton, 2007).

Although these effects are insufficiently studied, examples abound. The diadromous goby *Sicydium salvini* was shown to reduce benthic sediment accumulation and algal biomass, with concomitant benefits to benthic insects in a Costa Rican stream (Barbee, 2002). Greathouse et al. (2006a) compared dammed and undammed rivers in Puerto Rico and showed that *Sicydium* and shrimps processed algae, benthic organic matter and fine sediments, potentially preventing algal “blooms” and buildups of organic matter in undammed rivers (Greathouse, et al. 2006b). Other papers demonstrating effects of diadromous shrimp in tropical streams on leaf litter processing, algal species composition and standing crop and accumulation of fine benthic matter are Pringle et al. 1993, Pringle and Blake, 1994; Pringle, 1996; Holmquist, et al., 1998; Benstead, et al., 2000; Crowl et al. 2001, and March et al. 2001 and 2002.

Indirect effects on non-diadromous fauna in PILA are harder to predict. Some species of fish and benthic insects will undoubtedly benefit, at least initially, from removal of predators or reduction of competition. But they may just as well suffer from loss of the “regulatory” function performed by diadromous fishes and shrimps. (For example, one can easily imagine the disappearance of many forms of benthic insects under the cover of an algal bloom.) A community lacking both aquatic top carnivores such as *Gobiomorus* and primary consumers such as *Sicydium* and diadromous shrimps will likely favor small “weedy” fish species such as *Poecilia gillii* which are typically among the dominant species in nutrient-rich, low gradient lowland streams but are numerically relatively unimportant in the low nutrient, high gradient streams typical of PILA.

Eventually some of the non-diadromous fish species may also disappear as streams with reduced biodiversity seek a new equilibrium. Over the very long run, fragmentation of the watershed can result in decline and disappearance of populations of non-migratory species isolated upstream of dams and reservoirs.

Equally probable, but even less predictable, are effects on the terrestrial ecosystems in which the streams of the Changuinola/Teribe watershed are embedded. Surely the loss of the most numerous and largest fish and shrimps will impact avian, reptilian, and mammalian predators (in some cases including *Homo sapiens*).

## ATTEMPTS AT MITIGATION OF DAM EFFECTS

The barrier effect of dams is most subject to mitigation where the species in question are large bodied, and where low species diversity is involved. The Pacific salmons provide the best example. There is comparatively little diversity of behavior among the 7 or so species and all are relatively large animals. In addition, the *Oncorhynchus* species are well studied, and their commercial importance justifies both further research on their behavior and investment in costly mitigation technologies. Even so, mitigation of dam effects on salmon migrations has had a spotty record (Orsborn, 1987), and in all cases, survival of migrants has been negatively impacted (National Research Council, 1996; Ferguson, et al. 2005; Williams, et al. 2005).

Successful mitigation of the barrier, habitat loss, and fragmentation effects of dams on diadromous animals in the tropics is much less likely for 3 reasons:

- The diversity of species and migratory behaviors far exceeds that in the salmon streams of North America and Asia. A successful mitigation strategy for one species might be totally ineffective, or even harmful, for another.
- For most tropical diadromous species, life histories are at best incompletely known, rendering mitigation efforts speculative at best. In the specific case of the Changuinola/Teribe watershed, with the possible exception of the catadromous *Anguilla rostrata*, we do not have a complete life history for any of the species of diadromous fish and shrimp. As an indicator of the state of knowledge, consider that Cruz (1987), after years of investigation, was reduced to postulating that prejuveniles of *Joturus pichardi* migrated upstream in the center of large rivers, close to the bottom, simply because this was the only place he was unable to sample.
- In the particular case of amphidromy, the dominant form of diadromy in Mesoamerica, the migratory stages are larvae and very young juveniles with limited locomotive capacity and which may be very sensitive to manipulation.

Few serious attempts at providing fish passage for tropical diadromous species have been made, but an effort was attempted in Guadeloupe, where amphidromous palaemonid shrimp of the genus *Macrobrachium* are commercially important. As described by Fievet (2000), the results were biologically marginal and economically inefficient.

Aquaculture as a mitigation strategy scarcely merits mention, but since it has been proposed in the discussion of the Bocas del Toro dams, it will be briefly discussed here. Aquaculture proposals bypass the biodiversity and ecosystem function issues with a species-oriented approach favoring animals of direct interest to human consumers – *Agonostomus monticola* and *Joturus pichardi* have been mentioned (Proyectos y Estudios Ambientales del Istmo (2004a, 2004b, 2004c; PLANETA Panama 2005). To propose aquaculture as a means of maintaining numbers of these or any of the other diadromous species mentioned here overlooks the inadequate to non-existent life history information on these species, discussed above.

Even with adequate biological information and the best of intentions, culture of most species is inherently difficult and expensive. Practical aquaculture, like other forms of animal husbandry, began with the search for that minority of species amenable to management in confinement. If aquaculture methods do not exist for a species as widely appreciated as *Joturus pichardi*, it is because their cultivation appears to be a poor economic proposition. For aquaculture to begin to contribute to the maintenance of biodiversity in PILA, it would require simultaneous multi-year research efforts on at least a dozen species. And even if successful, it could pose a threat to biodiversity from eventual replacement of wild genotypes with “domesticated” strains.

## EFFECTS OUTSIDE PILA

We are here focusing on effects within PILA, because the protected area is of direct interest to UNESCO. However, the fluvial system is best understood as a whole, from the headwaters to the sea. Therefore we include brief comments on probable biodiversity effects in two additional areas – the reservoirs behind the dams and the river systems downstream.

Each of the 4 dams would impound a reservoir of deep, low flowing to standing water, atypical for the region. Others (Cordero, et al. 2006, 2007) have focused on the ca. 22,000 hectares (ha.) of terrestrial habitat, principally tropical forest, which would be lost. We will focus exclusively on the aquatic habitat – the several km. of river which would be impounded to form artificial “lakes.”

We have already focused on the barrier effect of such reservoirs, in combination with dams, penstocks and dewatered downstream reaches, on migratory animals. To this must be added the loss of significant amounts of fluvial habitat within the reservoir. Reservoir lakes in tropical systems do not normally support robust populations of native (and/or exotic) fishes of high fishery value as occurs in other locations, notably the United States.

The low productivity of tropical reservoirs is partly a consequence of the fact that they do not mimic anything natural. Natural lakes are not a feature of most tropical environments, so there is no suite of native fishes waiting to take advantage of expanded habitat. While one cannot preclude an event like the unexpected adaptation of the normally riverine, potomadromous machaca (*Brycon guatemalensis*) to life in the artificially impounded Lake Arenal (Bussing, 1998), there is no doubt that reservoir lakes on the Changuinola and Bonyic rivers would be areas of low biodiversity, due to the loss not only of diadromous animals as described above, but also of non-diadromous species which require flowing water.

Another problem with most tropical reservoirs is that annual weather changes are not sufficiently pronounced to produce the “turnover” that characterizes most temperate zone lakes, both natural and artificial. This can result in permanent stratification, with large anoxic “dead” zones in the deeper waters. Any reservoir created in the Changuinola/Teribe watershed would likely become habitat for a few tolerant, omnivorous or detritivorous fishes such as *Astyanax aeneus* and *Poecilia gillii*, and would be both less diverse and less productive than the undammed river. The function of the reservoirs in the context of the river would be largely as travel corridors; and as we have seen even that function would not be available for many species.

The precise effects of impoundment on river reaches below the dams are impossible to predict without knowing design specifics for each of the dams. These have not been made public and are, we understand, in a state of flux. This section is therefore limited to a generalized discussion of the types of alterations observed below large dams. These impacts are generally thought of as being due to changes in 4 factors – flow regime, sediment transport, temperature, and water chemistry.

- Dams have the capacity to increase or decrease flow volume and velocity at any moment, but often the most important factor is changes in periodicity of flow, which can act as a cue for migratory and other behavior. Within limits of other management considerations, flow regime can be manipulated to the detriment or benefit of aquatic organisms. However, this implies that we understand the needs of the species living downstream of the dam.
- Every river has a natural sediment transport and deposition regime, to which its biota is adapted. Where human populations are high, land disturbance typically increases the rate of sediment transport. Dams and their associated reservoirs can sometimes compensate for this problem by serving as "traps" for excess sediment until their trapping capacity is used up. More typically, they alter the natural regime by altering the periodicity of sediment transport.
- Depending on design, dams may raise or lower temperature downstream. In extreme cases, this can completely alter the ecology of the river below. Many reservoir "tailwaters" in the southern United States now support only cold water fishes exotic to the region.
- Chemical alterations downstream can be due to processes such as decomposition of terrestrial vegetation in the reservoir, but more typically alterations of water chemistry come in the form of discharge of deoxygenated water from the bottom of the reservoir. In extreme cases, discharges for the purpose of generating electricity or regulating flood waters have killed fish for miles downstream and rendered significant stream reaches abiotic for months at a time.

Even absent the barrier effect of dams and reservoirs, these factors could all affect the diadromous fauna which are the focus of this paper. In addition, the reduction in biodiversity and biomass coming from and returning to the upper reaches would have profound effects on downstream ecosystems and fisheries. March et al. (1998) conservatively estimate the loss of 15.3 million shrimp larvae/day due to damming and water withdrawals in streams of the Caribbean National Forest, Puerto Rico.

To put this in a Mesoamerican context, consider the phenomenon of the tismiche – the periodic upstream migration of larval fishes and shrimp. This migration is typically followed by a suite of fresh water and marine predators (many of which are in turn the targets of human predators). With access denied to upstream habitat, the volume of the tismiche (and subsequent downstream migrations) would be reduced, with concomitant reductions in the amount of food available for predators – both river residents and opportunistic migrants. Thus anthropogenic impacts on the biodiversity of the upstream PILA would have a negative effect on ecosystems and human wellbeing downstream – exactly the opposite of the intent in creating an upland protected area.

## THE CORRIDOR CONCEPT

In recent years a great deal of attention has been given to the concept of biological corridors as an element in the solution to the problem of maintaining biological diversity and gene flow in an increasingly fragmented landscape. PILA is formally recognized as part of the Mesoamerican Biological Corridor, projected to extend along the entire spine of the Mesoamerican isthmus from Mexico to Colombia, with shorter corridors extending perpendicular to it along altitudinal gradients to sea level.

In most cases the most secure altitudinal corridors will be along rivers. While parallel terrestrial riparian corridors may be disrupted and waters may be polluted, all free flowing rivers in Mesoamerica serve to some degree as travel corridors for aquatic fauna unless they are physically blocked. Pollution can be cleaned up, and riparian areas can be revegetated. The most difficult problems to undo and, in the developing tropical countries, the most serious current threat to riverine corridor function is dam construction. As Freeman et al. (2003) point out "even when streams retain good physical integrity, they are likely to be biologically altered if they are isolated by structures that impede faunal movements. The growing evidence for effects on stream function of losing migratory fauna implies that these effects should be explicitly considered in decisions of whether or where to build dams. . . "

Freeman et al. (2003) go on to say that "For humans, the most obvious consequences are lost fisheries . . . However, other consequences may include: noxious algal blooms (e.g. with the loss of benthic algivores), reduced capacity to process and retain nutrients (e.g. with the loss of trophic pathways and productivity) and detrimental effects on riparian and wildlife populations."

In the case of the Rio Changuinola, it presently serves as a corridor connecting an upland World Heritage site (La Amistad International Park and Palo Seco), part of the Mesoamerican Biological Corridor, with the sea and two significant coastal protected areas, the San San – Pondsak Wetland (a Ramsar site) and Bastimentos National Park. Other World Heritage sites and Biosphere Reserves in the Mesoamerican region, for example Rio Platano in Honduras and the complex of Biosphere Reserves and protected areas around the Rio Usumacinta in Mexico and Guatemala, serve similar functions, and are also threatened by dam proposals. The case of the Bocas del Toro dams may provide an opportunity to evaluate the role of World Heritage site designation in protecting aspects of world heritage both within and outside designated World Heritage site boundaries.

## CONCLUSION

While acknowledging the great lack of information on the biology of aquatic organisms in general, and diadromous elements in particular in the region under discussion, we believe that sufficient information exists to justify a prediction of drastic reduction in biodiversity in and around the Panamanian portion of the La Amistad International Park and Biosphere Reserve (PILA) if projected dams are built on the Changuinola and Bonyic Rivers draining the park. The initial effects would be in the form of loss of multiple species upstream of the dams, followed by changes in ecosystem structure and function which could trigger further losses of biodiversity. We also predict less specific, but significant losses of ecosystem function and services in the impounded reaches between the dams and PILA and in river systems downstream of the dam sites.

The same lack of information which prevents us from making more precise predictions than those offered here should incline all actors to caution. We consider that the existing dam proposals are not in keeping with the first stated purpose for the establishment of PILA as cited earlier in this paper and are therefore not compatible with maintenance of World Heritage site status.

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**Table 1.** **Migratory and Non-migratory Fresh Water Fishes of the Changuinola/Teribe Watershed Bocas del Toro Province, Panama**

A. Diadromous and euryhaline migratory species

| Family | Species | Form of migratory behavior | References for diadromy | In PILA |
|---|---|---|---|---|
| Anguillidae | | | | |
| | *Anguilla rostrata* | Catadromous | Vladykov, 1964;<br>Tesch, 1977 | YES |
| Syngnathidae | | | | |
| | *Microphis brachyurus* | Anadromous | | No |
| Gobiesocidae | | | | |
| | *Gobiesox nudus* | Amphidromous? | | YES |
| Centropomidae | | | | |
| | *Centropomus undecimalis* | Opportunist migrant | | Occasional |
| | *Centropomus pectinatus* | Opportunist migrant | | ?? |
| Carangidae | | | | |
| | *Caranx* sp. | Opportunist migrant | | Occasional |
| Haemulidae | | | | |
| | *Pomadasys crocro* | Amphidromous? | | YES |
| Mugilidae | | | | |
| | *Agonostomus monticola* | Amphidromous and/or catadromous | Anderson, 1957;<br>Gilbert and Kelso,1971<br>Gilbert , 1978<br>Corujo-Flores, 1980;<br>Loftus, et al., 1984;<br>Cruz, 1987. | YES |
| | *Joturus pichardi* | Catadromous | Darnell, 1962;<br>Erdman, 1984;<br>Cruz, 1987. | YES |
| Gobiidae | | | | |
| | *Awaous banana* | Amphidromous | Yerger, 1978. | YES |
| | *Sicydium adelum* | Amphidromous | Bussing, 1996. | ?? |
| | *Sicydium altum* | Amphidromous | Gilbert and Kelso,1971 | YES |
| Eleotridae | | | | |
| | *Dormitator maculatus* | Catadromous? | McLane, 1955;<br>Darnell, 1962;<br>Winemiller and Ponwith, 1998. | No |
| | *Eleotris amblyopsis* | Amphidromous | Gilbert and Kelso, 1971<br>Nordlie, 1981 | No |
| | *Eleotris pisonis* | Amphidromous | Gilbert and Kelso, 1971<br>Nordlie, 1981 | No |
| | *Gobiomorus dormitor* | Catadromous or amphidromous | Darnell, 1962;<br>Kelso, 1965;<br>Nordlie, 1981 | YES |

| | | | | |
|---|---|---|---|---|
| | | | Winemiller and Ponwith, 1998. | |
| Paralichthyidae | | | | |
| | *Citharichthys spilopterus* | Catadromous? | | ?? |
| Achiridae | | | | |
| | *Trinectes paulistanus* | Catadromous? | | ?? |

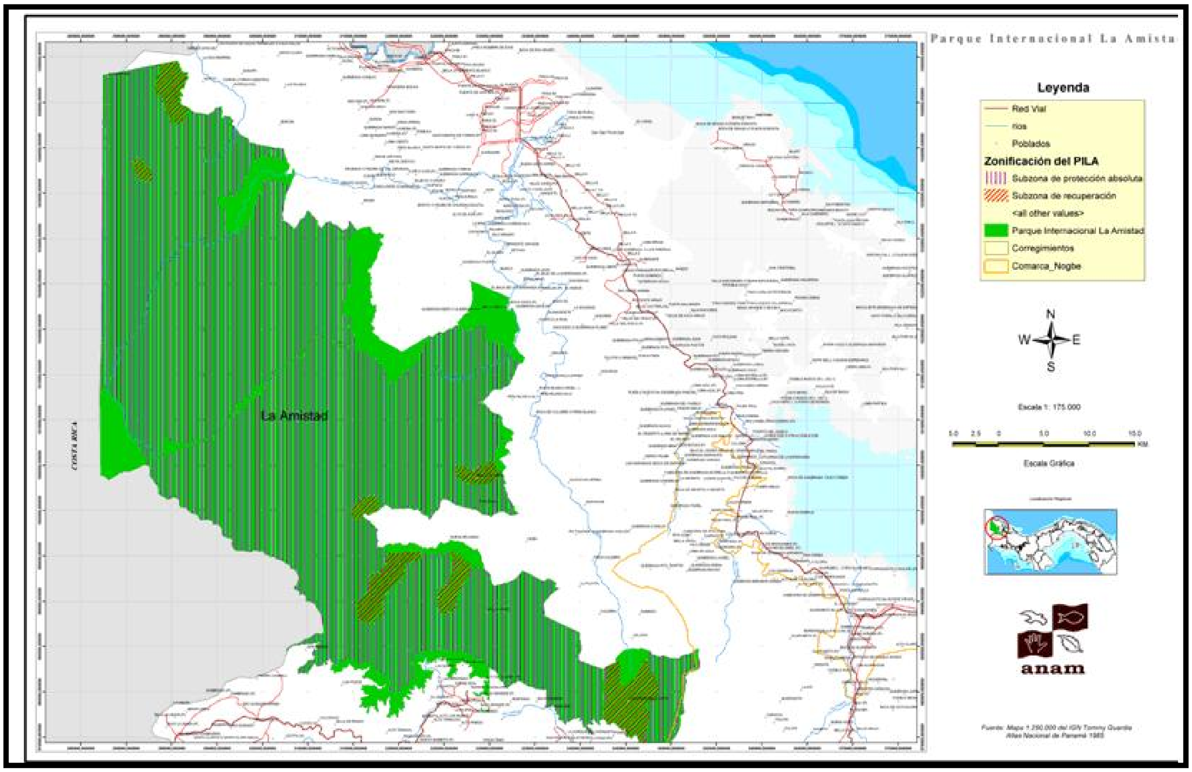
B. Primary fresh water species

| | | |
|---|---|---|
| Characidae | | |
| | *Astyanax aeneus* | YES |
| | *Astyanax orthodus* | YES |
| | *Bryconamericus ricae** | ?? |
| | *Bryconamericus scleroparius* | YES |
| | *Hyphessobrycon panamensis* | No |
| Rhamphichthyidae | | |
| | *Brachyhypopomus occidentalis* | YES |
| Pimelodidae | | |
| | *Rhamdia guatemalensis* | YES |
| Rivulidae | | |
| | *Rivulus birkhahni** | ?? |
| | *Rivulus isthmensis* | Probable |
| | *Rivulus wassmanni** | ?? |
| Poeciliidae | | |
| | *Alfaro cultratus* | No |
| | *Brachyraphis cascajalensis* | No |
| | *Phallichthys amates* | No |
| | *Phallichthys quadripunctatus* | No |
| | *Poecilia gillii* | YES |
| | *Priapichthys annectens* | No |
| Atherinidae | | |
| | *Atherinella chagresi* | No |
| Synbranchidae | | |
| | *Synbranchus marmoratus* | YES |
| Cichlidae | | |
| | *Archocentrus nigrofasciatus* | No |
| | *Astatheros bussingi* | YES |
| | *Astatheros rhytisma* | No |
| | *Parachromis loiselli* | No |

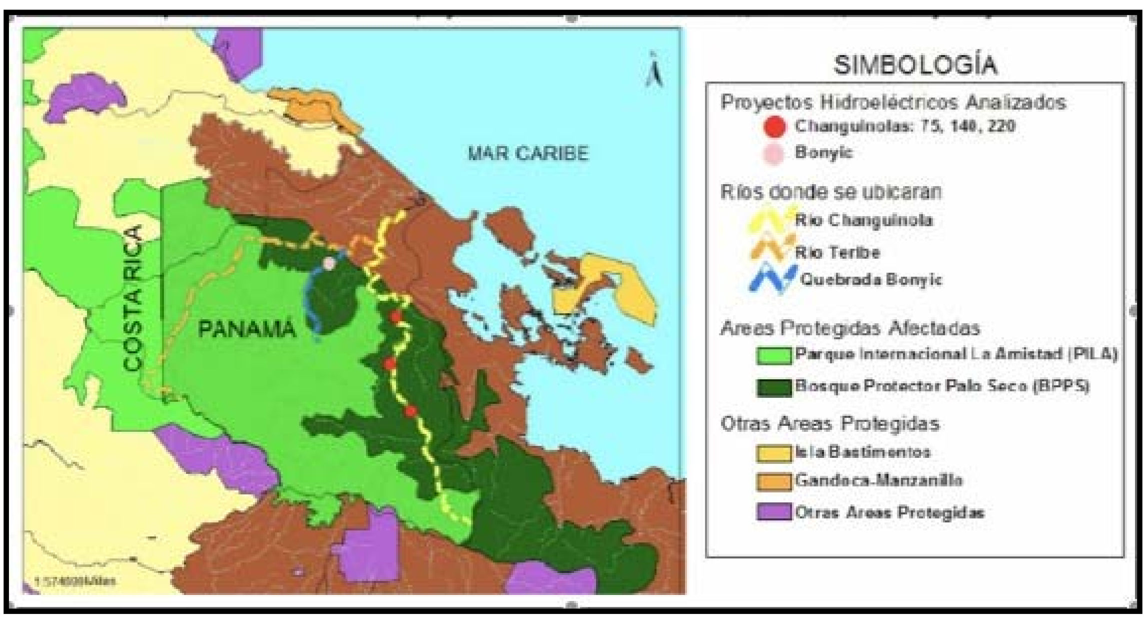
* Little known species listed in STRI (2007), but not verified by us.

## MAPS

**Map 1 –** La Amistad International Park




**Map 2 –** Location of the Dams on the Bonyic and Changuinola Rivers




Source: Cordero, S.; R. Montenegro; M. Mafla; I. Burgues and J. Reid. 2006. Analisis de costo beneficio de cuatro proyectos hidroeléctricos en la cuenca Changuinola-Teribe. Conservation Strategy Fund. 53 pp.