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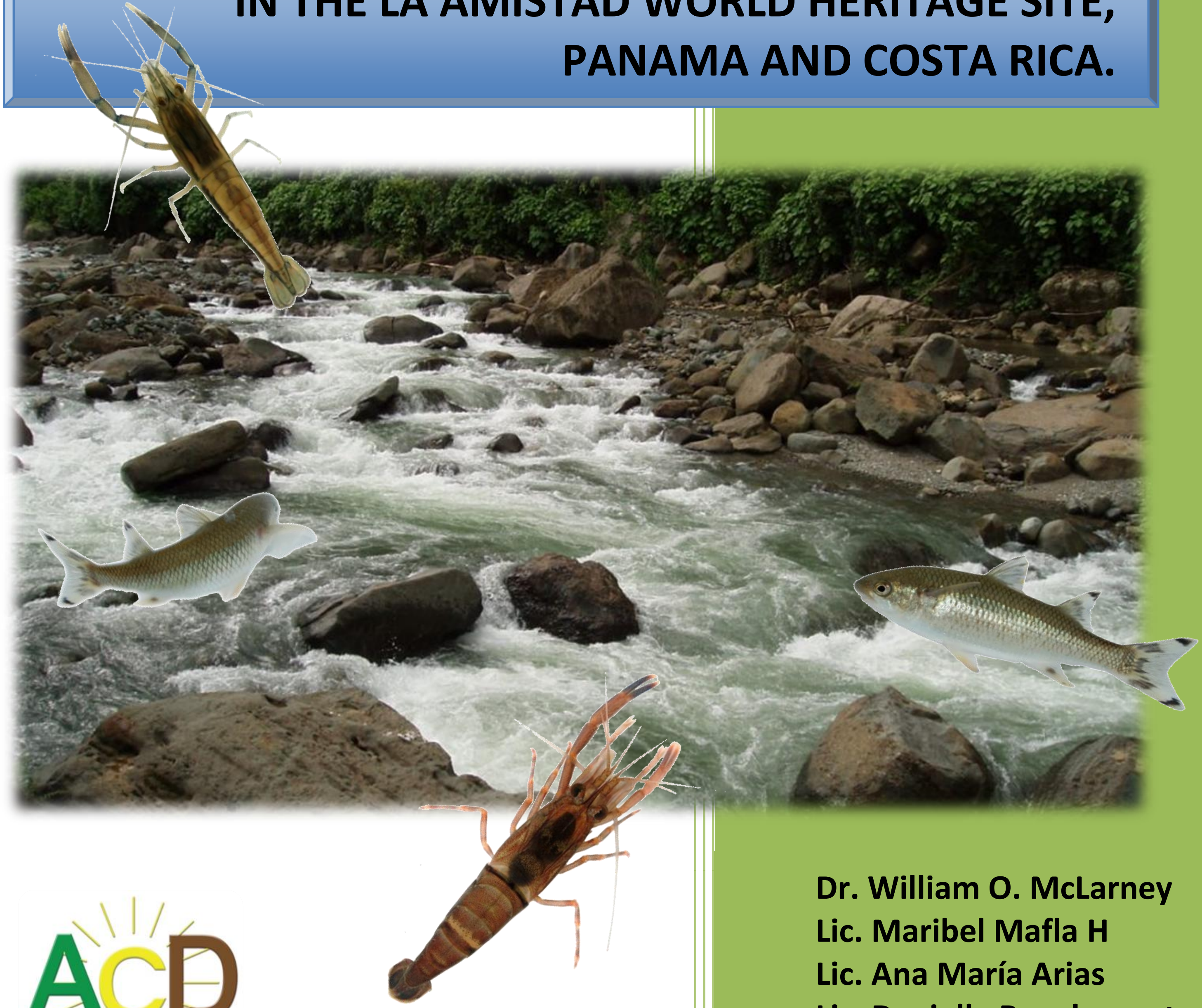
THE THREAT TO BIODIVERSITY AND ECOSYSTEM FUNCTION OF PROPOSED HYDROELECTRIC DAMS IN THE LA AMISTAD WORLD HERITAGE SITE, PANAMA AND COSTA RICA.



Dr. William O. McLarney
Lic. Maribel Mafla H
Lic. Ana María Arias
Lic. Danielle Bouchonnet

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THE THREAT TO BIODIVERSITY AND ECOSYSTEM FUNCTION IN THE LA AMISTAD WORLD HERITAGE SITE, PANAMA AND COSTA RICA, FROM PROPOSED HYDROELECTRIC DAMS

A follow-up to McLarney and Mafla (2007):

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

With consideration also of La Amistad/Costa Rica and the Pacific Slope of La Amistad.

Dr. William O. McLarney
Lic. Maribel Mafla H.
Lic. Ana Maria Arias
Lic. Danielle Bouchonnet

Programa de Biomonitoreo
Asociación ANAI

Contact Information:

Asociación ANAI (Costa Rica):
Apdo. 170-2070
Sabanilla de Montes de Oca
Costa Rica, C.A.
Phone: (506) 2224-3570
(506) 2756-8120
Fax: (506) 2253-7524
E-mail: mmafla@anaicr.org
anaital@racsa.co.cr

ANAI, Inc. (United States):
1120 Meadows Rd.
Franklin, North Carolina 28734
USA
Phone/fax: (828) 524-8369
E-mail: anaiinc@dnet.net

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EXECUTIVE SUMMARY

In this paper we expand and update our previous report "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", taking into account events occurring since that report was presented in February, 2008 and expanding coverage to include all of the La Amistad World Heritage Site watersheds in both countries and on both sides of the Continental Divide. This is necessary because it has become increasingly apparent that, chiefly as a consequence of dam proposals and in direct contravention of one of the stated purposes for declaring the La Amistad National Parks, all of the major watersheds within the World Heritage Site are threatened with multiple species extirpations and consequent secondary effects which stand to grossly alter the character of ecosystems within the Site and the surrounding protected areas and indigenous territories making up the La Amistad Biosphere Reserve. For the sake of convenience, in much of the discussion we divide the La Amistad region into 4 sectors – Costa Rica and Panama, Atlantic and Pacific slopes.

While this report focuses on biological events and predictions, we must take note of the numerous protests against dam plans and associated development which have occurred in all 4 sectors, based not only on environmental issues, but also reflecting valid socio-cultural, indigenous rights and local economic concerns. Of particular concern are open pit mining plans being developed in Bribri territory on the very periphery of the World Heritage Site on the Atlantic slope of Costa Rica, and which are perceived as related to nearby dam sites.

Results of several important biological investigations in the La Amistad area have been published since our last report. These include inventories of fish and macroinvertebrates carried out by University of Costa Rica biologists and sponsored by ICE in the Grande de Terraba River drainage on the Paciflc slope of Costa Rica, advances in Asociacion ANAI's continuing biomonitoring investigations on the Atlantic slope of that country, and an ongoing binational Darwin Initiative inventory focusing on the World Heritage Site, which has already reported numerous new country records and discovered 31 species of animals and plants new to science.

However, perhaps the most immediately significant new investigation is a series of inventories undertaken by the Smithsonian Tropical Research Institute (STRI) in the portion of the Changuinola River watershed which would be directly affected by the CHAN-75 and CHAN-140 dams. Along with important new species records, the STRI report confirms the ANAI biomonitoring team's assertion (based on monitoring in the Atlantic slope watersheds of Costa Rica and non-quantitative surveys in the Changuinola/Teribe watershed of Panama) of overwhelming dominance by diadromous migratory fish and shrimp in streams at middle and upper elevations on the Atlantic slope of the La Amistad area.

Unfortunately, the Executive Summary of the extremely long (total 1,081 pages) STRI report attempts to serve public relations functions by underplaying the significance of diadromy and glossing over problems and limitations which are acknowledged in the full text. This tendency is extended and exacerbated in the recently published mitigation proposal by the engineering firm AES Changuinola and the consulting firm MWH which does however constitute an important new bibliographic resource.

Descriptive sections of the present ANAI report place the rivers which arise within the La Amistad World Heritage Site in a geographic context of the ca. 10,000 sq. km. La Amistad Biosphere Reserve, and review the fish and macroinvertebrate taxa known from these watersheds, with emphasis on diadromous species known to occur within the World Heritage Site.

For each of the 4 sectors of the La Amistad area we analyze all publicly available information on proposed dams and relate it to the threat of species extirpation and related ecological consequences. For the Pacific slope of Panama, we note that all access by diadromous species to streams within the World Heritage Site is already blocked by existing or nearly completed dams, leading to a hypothesis of total or near-total species extirpation. On the Atlantic slope of Panama, the only significant change since 2007 is progress toward completion and closure of the CHAN-75 and Bonyic Dams. We report on proposals for 8 dams on the Atlantic slope of La Amistad/Costa Rica, and plans for one large and several smaller dams on the Pacific slope of that country. We conclude that if all presently proposed dams are constructed, 67% of the total watershed area of the La Amistad World Heritage Site will become inaccessible to diadromous and other upstream/downstream migratory fauna. As maps in this report suggest, similar figures could be derived for all of the upland protected areas and indigenous territories in the La Amistad region.

In the following discussion of the biological aspects of the dam threat, we will emphasize the Atlantic slope watersheds of both countries, for two reasons: 1) More than 90% of the World Heritage Site is located on that side of the Continental Divide and 2) Our knowledge of the biology of the Atlantic slope streams is much more detailed. With these limitations acknowledged, and recognizing also that the World Heritage Site and contiguous protected areas on the Pacific slope for the most part consist of a high altitude fringe, we must mention that, at the watershed level, the threat (and in Panama, losses to date) in Pacific slope watersheds is very comparable.

For the Atlantic slope we identify at least 16 diadromous species (8 fish and 8 shrimps) which will probably be extirpated from major portions of the World Heritage Site if existing dam plans are realized, and also discuss implications for potamodromous species (those which perform obligatory migrations entirely within fresh water) and others.

We argue that the ecological effects of predictable species extirpations will not be limited to a loss of biodiversity at the species level and that, in fact, secondary effects will be more significant. In addition to noting the implications of loss of species of seed dispersers and alteration of predator-prey relationships, we draw on a large, long term body of research from Puerto Rico (where rivers have a similar diadromous fish and shrimp fauna) and elsewhere to show how elimination of omnivores, herbivores and detritivores (categories which include all the shrimp and the most abundant fishes of the La Amistad region) affects sediment dynamics, breakdown of allochthonous vegetable matter, water and substrate chemistry, algal biomass and diversity and structure of the benthic macroinvertebrate assemblage. We apply the principles of the River Continuum Concept to show that loss of these “ecosystem engineers” would have profound negative effects on the fluvial systems of the La Amistad area within and downstream of the World Heritage Site, all the way to the estuaries.

A large body of experience at existing dams worldwide suggests that causes outside the World Heritage Site (dams) will have negative effects within the Site which will in turn contribute synergistically to effects occurring downstream. In addition to habitat loss in areas occupied by dam sites, reservoirs and downstream dewatered reaches, the effects of downstream alterations in flow rate and periodicity, sediment transport and deposition, temperature, and water chemistry will be exacerbated by biological impoverishment of the upper reaches of rivers.

In general, we take exception to government policies which permit and facilitate massive species extirpations and associated ecological impacts within a World Heritage Site, while noting that in this particular case the threat is to a nearly unique ecosystem. The faunal assemblage typical of high gradient streams in the La Amistad area, with high diversity in the lower reaches, coupled with dominance by *Sicydium* gobies and shrimps in the upper watersheds, occurs in only 3 other small areas in the Caribbean Basin. In large part because of the existence of the World Heritage Site and its surrounding complex of other protected areas, La Amistad represents our best chance to permanently protect this unique ecosystem.

The AES/MWH mitigation proposal for the CHAN-75 and CHAN-140 dams provides an opportunity to critique the concept of mitigation as it relates to this particular ecosystem. Beginning with the patently false assertion that the dams will occasion no alteration in downstream habitats and ecosystems, they propose as the best mitigation for upstream effects an aquaculture system which exists only conceptually and would be impossible to implement in a way compatible with dam construction schedules. While this mitigation proposal, like those previously presented in less developed form in the Environmental Impact Assessments for the Changuinola and Bonyic Dams, suggests a lack of willingness to sincerely address the problem of upstream species extirpations, the treatment of aquaculture and other options in it does serve to advance the discussion of mitigation alternatives and reinforces our conclusion: Based on all available information, we conclude that there is no possibility of significant mitigation for the ecological alterations which would result from completion of existing dam plans in the La Amistad region.

Recognizing that UNESCO, ANAM, MINAET and all others involved face clearly defined limits to their authority, we suggest that the threats facing the fluvial and other ecosystems of the La Amistad area cannot be dealt with solely through implementing policies within jurisdictional boundaries. The nature of the rivers of the La Amistad area, particularly their diadromous component, and their relation to terrestrial and marine environments, demands a watershed conservation approach, extending across all kinds of boundaries.

Our previous report to UNESCO was in support of a petition soliciting the declaration of La Amistad as a World Heritage Site in Danger; this has not yet occurred. In the interim it has become clear that the threat presented by proposed dams extends beyond the Changuinola/Teribe watershed in Panama. It is binational in nature and has the potential to grossly alter the natural character of the World Heritage Site and other areas on both sides of the Continental Divide.

At this point, in recognition of the greater severity of the threat, we recommend that the UNESCO World Heritage Committee reopen the discussion of possible listing of the binational La Amistad World Heritage Site as a World Heritage Site in Danger, in the context of considering all alternatives for the protection of its biodiversity. We would also strongly suggest to UNESCO, the two national governments and all other concerned parties that all discussions related to this threat take place in a context which recognizes the ultimate impossibility of protecting the biodiversity and ecosystem integrity of the La Amistad World Heritage Site without taking into account entire watersheds, from the Continental Divide to the sea.

RESUMEN EJECUTIVO

En este documento expandimos y actualizamos nuestro previo documento "Posibles efectos sobre la biodiversidad acuática y la función de ecosistemas de las cuatro represas hidroeléctricas propuestas en la cuenca hidrológica Changuinola/Teribe, Bocas del Toro, Panamá con énfasis en el Sitio de Patrimonio Mundial La Amistad", considerando los sucesos ocurridos desde que ese informe fuera presentado en febrero del 2008 y expandiendo el área de análisis a toda la región de Patrimonio Mundial en las cuencas de ambos países y a ambos lados de la división continental de aguas. Esto se hace necesario porque está llegando a ser obvio que mayormente como consecuencia de la propuesta de construcción de las represas, y contraviniendo directamente el propósito de la formación de La Amistad como parques nacionales, la mayor cantidad de cuencas en este Sitio de Patrimonio Mundial están siendo amenazadas con la extirpación de un gran número de especies y con consecuentes efectos secundarios que alterarán el carácter de sus ecosistemas, de las áreas protegidas y de territorios indígenas aledaños que en su conjunto forman la Reserva de la Biosfera de La Amistad. Para facilitar algunos aspectos del análisis, dividimos la región de La Amistad en 4 sectores - Costa Rica y Panamá, Vertientes Atlántica y Pacífica.

Mientras este informe se enfoca en sucesos y predicciones biológicas, debemos considerar también las numerosas protestas que se están llevando a cabo contra los planes de construcción de las represas y el desarrollo asociado a ellas en los 4 sectores; protestas basadas no sólo en aspectos de protección del medio ambiente sino también en la validez socio-cultural de los planes, y su impacto contra la economía local y los derechos de los indígenas. De particular preocupación son los planes mineros a tajo abierto que están siendo desarrollados en el territorio Bribri en la periferia misma del Sitio de Patrimonio Mundial sobre la vertiente atlántica de Costa Rica, que son percibidos como planes relacionados a la construcción de las represas.

Desde la presentación de nuestro último informe, se han publicado resultados de importantes investigaciones biológicas en el área de La Amistad. Éstos incluyen inventarios de peces y macroinvertebrados llevados a cabo por biólogos de la Universidad de Costa Rica con el apoyo de ICE en el drenaje del Río Grande de Terraba en la Vertiente Pacífica de Costa Rica; progresos en las investigaciones de monitoreo de la Asociación ANAI en la Vertiente Atlántica de ese país; y el inventario binacional de la Iniciativa Darwin que se enfoca en el Sitio de Patrimonio Mundial que viene reportando numerosos nuevos records y descubriendo 31 especies de plantas y animales nuevas para la ciencia.

Sin embargo, quizás la investigación más significante es una serie de inventarios llevados a cabo por el Instituto de Investigación Tropical Smithsonian (STRI) en la porción de la cuenca del Río Changuinola que puede ser directamente afectada por las represas CHAN-75 y CHAN-140. Además de registrar la existencia de nuevas especies, el informe de STRI confirma la afirmación del equipo de monitoreo de ANAI (basado en el monitoreo de las cuencas en la Vertiente Atlántica de Costa Rica y las encuestas no cuantitativas en la cuenca Changuinola/Teribe de Panamá) de la existencia de una abrumadora dominancia de peces y camarones diadromos (migratorios) en ríos y quebradas en elevaciones medias y altas de la Vertiente Atlántica del área de La Amistad.

Desafortunadamente, el resumen ejecutivo del extenso informe de STRI (con un total de 1,081 páginas) intenta cumplir más funciones de relaciones públicas al reducir la importancia de diadromia y al pasar por encima problemas y limitaciones que son reconocidos en el texto completo del informe. Esta tendencia es extendida y exacerbada en la propuesta de mitigación recientemente publicada por la firma de ingenieros AES Changuinola y la firma consultora MWH que constituye, sin embargo, un nuevo recurso bibliográfico importante.

Secciones descriptivas del presente informe de ANAI ubica los ríos que surgen en el Sitio de Patrimonio Mundial La Amistad en un contexto geográfico de cerca de 10,000 km^2 de la Reserva Biosfera

La Amistad, y revisa los taxones de peces y macroinvertebrados de esas cuencas con énfasis en especies diadromas que han sido identificadas en el Sitio de Patrimonio Mundial.

Para cada uno de los 4 sectores del área de La Amistad analizamos toda la información pública disponible sobre las propuestas de construcción de las represas y la conectamos con la amenaza de extirpación de especies y las consecuencias ecológicas relacionadas. Para la Vertiente Pacífica de Panamá, anotamos que todo el acceso de las especies diadromas a los ríos y quebradas dentro del Sitio de Patrimonio Mundial está actualmente bloqueado por las represas existentes o casi terminadas, lo que nos lleva a apoyar la hipótesis de extirpación total o casi total de las especies. En la Vertiente Atlántica de Panamá, el único cambio significativo desde 2007 es el progreso hacia la culminación de las represas CHAN-75 y Bonyic. Informamos sobre 8 de las represas propuestas en las cuencas de la Vertiente Atlántica de La Amistad/Costa Rica y sobre los planes existentes para construir una represa grande y varias represas pequeñas en la Vertiente Pacífica de ese país. Concluimos que si todas las actuales represas propuestas son construidas, 67% del total del área de las cuencas hidrológicas del Sitio de Patrimonio Mundial La Amistad llegará a ser inaccesible a diadromos y a otro tipo de fauna migratoria río arriba o río abajo. Como lo sugieren los mapas en este informe, porcentajes similares pueden ser estimados para todas las áreas protegidas y los territorios indígenas en la región de La Amistad.

En la discusión sobre los aspectos biológicos de la amenaza de las represas, enfatizaremos la situación de las cuencas en la Vertiente Atlántica en los dos países, por dos razones: 1) Más del 90% del Sitio de Patrimonio Mundial está ubicado a ese lado de la División Continental de aguas y 2) Nuestro conocimiento de la biología acuática de la Vertiente Atlántica es mucho más detallado. Con el reconocimiento de estas limitaciones y reconociendo también que el Sitio de Patrimonio Mundial y las áreas protegidas contiguas en la Vertiente Pacífica en su mayor parte consisten de una franja de gran altitud, mencionaremos que, al nivel de cuencas, la amenaza (y en Panamá las perdidas a la fecha) en las cuencas de la Vertiente Pacífica es muy comparable.

Para la Vertiente Atlántica identificamos al menos 16 especies diadromas (8 de peces y 8 de camarones) que probablemente serán extirpados de la mayor porción del Sitio de Patrimonio Mundial si los planes existentes de construcción de las represas son ejecutados, y también discutimos las implicancias para las especies potamodromos (animales obligados a migraciones largas en aguas dulce para completar su ciclo de vida) y otras especies.

Sostenemos que los efectos ecológicos de las predecibles extirpaciones de especies no estarán limitados a la pérdida de biodiversidad a nivel de las especies y que, de hecho, otros efectos secundarios serán aún más significativos. Además de considerar las implicancias de la pérdida de especies de dispersores de semillas y de la alteración de las relaciones de predadores-presas, nos basamos en una abundante información acumulada tras un largo periodo de investigación en Puerto Rico (donde los ríos tienen una fauna similar de peces y camarones diadromos) y en otros lugares para mostrar como la eliminación de omnívoros, herbívoros y detritívoros (categorías que incluyen todos los camarones y la mayor cantidad de peces de la región de La Amistad) afecta las dinámicas de sedimentación, descomposición de materia vegetal alóctona, la química del agua y los substratos, biomasa de algas y la estructura del ensamblaje de macroinvertebrados bentónicos. Aplicamos los principios del Concepto del Continuo del Río para mostrar que la pérdida de estos "ingenieros de ecosistemas" podría tener profundos efectos negativos en los sistemas fluviales del área de La Amistad, río abajo del Sitio de Patrimonio Mundial, y hasta los estuarios.

Una gran cantidad de experiencia acumulada en existentes represas a nivel mundial sugiere que las causas fuera del Sitio de Patrimonio Mundial (represas) tendrán efectos negativos dentro del Sitio lo que en su momento contribuirá sinergéticamente a efectos que ocurrirán río abajo. Además de la pérdida de hábitat en las áreas ocupadas por las represas, reservorios y trechos de desagüe, los efectos por la alteración del flujo de agua río abajo, en cantidad y periodicidad, transporte y deposición de sedimentos, temperatura y alteración química del agua, serán exacerbados por el empobrecimiento biológico de las áreas altas de los ríos.

En general, objetamos las políticas gubernamentales que facilitan y permiten la extirpación masiva de especies y sus impactos ecológicos asociados en el Sitio de Patrimonio Mundial, mientras observamos que en este caso particular la amenaza es a un ecosistema casi único. El ensamblaje de fauna típico de ríos de gradiente alta de La Amistad, con su gran diversidad en sus partes bajas, acompañada con la dominancia de gobios *Sicydium* y camarones en las cuencas altas, ocurre solamente en otras 3 áreas pequeñas en la región del Caribe. En gran parte por la existencia del Sitio de Patrimonio Mundial y su conexión a otras áreas protegidas aledañas, La Amistad representa nuestra mejor oportunidad para proteger permanentemente este ecosistema único.

La propuesta de mitigación AES/MWH por las represas CHAN-75 y CHAN -140 nos ofrece una oportunidad para criticar el concepto de mitigación en lo que se refiere a este ecosistema en particular. Empezando con la afirmación evidentemente falsa de que las represas no ocasionarán alteraciones al hábitat y ecosistemas río abajo, propone como la mejor mitigación para efectos aguas arriba un sistema de acuacultura que sólo existe conceptualmente y que sería imposible implementar de manera compatible con el programa de construcción de las represas. Mientras que esta propuesta de mitigación, al igual que las anteriormente presentadas en forma menos detallada en las Evaluaciones de Impacto Ambiental para las represas Changuinola y Bonyic, sugiere la falta de voluntad para enfrentar sinceramente el problema de extirpación de especies aguas arriba, la propuesta de acuacultura y otras opciones en ella sirven para adelantar la discusión sobre alternativas de mitigación, y refuerza nuestra conclusión: Basados en toda la información disponible, concluimos que no existe ninguna posibilidad de mitigación efectiva para contrarrestar las alteraciones ecológicas que resultarían de la ejecución de los planes existentes de construcción de las represas en la región de La Amistad.

Reconociendo que UNESCO, ANAM, MINAET y todas las demás organizaciones involucradas enfrentan limitaciones de autoridad, consideramos que las amenazas que confrontan los ecosistemas fluviales del área de La Amistad no pueden ser enfrentadas solamente con políticas dentro de los límites jurisdiccionales. La naturaleza de los ríos del área de La Amistad, particularmente su componente diadromo y su relación con ambientes terrestres y marinos, demanda un enfoque de conservación de cuencas que se extienda más allá de los límites y fronteras existentes.

Nuestro informe anterior a UNESCO fue escrito en apoyo a la petición de declaración de La Amistad como un Sitio de Patrimonio Mundial en peligro, la cual no ha sido promulgada aun. En este ínterin, ha llegado a ser evidente que la amenaza presentada por las represas propuestas se extiende más allá de la cuenca Changuinola/Teribe en Panamá. Es binacional por naturaleza y tiene el potencial de alterar tremendamente el carácter del Sitio de Patrimonio Mundial y de otras áreas en ambos lados de la División Continental de aguas.

En estas circunstancias, reconociendo la severidad de la amenaza, recomendamos que el Comité de Patrimonio Mundial de UNESCO reabra la discusión para la identificación del Sitio binacional de Patrimonio Mundial La Amistad como un Sitio de Patrimonio Mundial en Peligro, en el contexto de considerar todas las alternativas posibles para proteger su biodiversidad. También sugerimos enfáticamente a UNESCO, a los dos gobiernos nacionales y a las demás partes interesadas que toda discusión relacionada con esta amenaza se lleve a cabo en un contexto que reconozca la imposibilidad de proteger la biodiversidad y la integridad ecológica del Sitio de Patrimonio Mundial La Amistad con propuestas que no tomen en cuenta las cuencas en su totalidad, desde la División Continental de aguas hasta el mar.

INTRODUCTION

The present report expands and builds on our 2007 report, cited above, with 4 major differences:

1. It adds a summary of scientific investigations and publications, and a brief chronicle of other relevant events which have occurred since the 2007 report was prepared. In addition to the updating function, we use this as an opportunity to dispute misleading statements in the mitigation proposal for the CHAN-75 and CHAN-140 dams, recently published by proponents of the dams (AES and MWH, 2009).
2. The 2007 report was almost entirely focused on effects of dams in the Changuinola/Teribe watershed of the La Amistad World Heritage Site in Bocas del Toro Province, Panama. The present report expands the area of coverage, acknowledging and analyzing the threats implied by dams proposed for all of the La Amistad watersheds, in Panama and Costa Rica. We conclude that if all the dams for which details have been made public are completed, near or total extirpation of the diadromous fauna will occur over 67.1% of the La Amistad World Heritage Site. This clearly conflicts with one of the purposes for the creation of PILA, as articulated by Alvarado (1989) for the Panamanian La Amistad National Park "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".
3. We have had the opportunity to incorporate results from a more complete literature search, particularly with respect to documented effects of ecosystem alterations above high dams and reservoirs in the tropics. Beyond numerical loss of species level diversity, we point out that some of the species threatened are clearly strongly interactive "keystone" species, as initially defined by Paine (1969). We concur with Soule, et al. (2005) that "the disappearance of a strongly interactive species can lead to profound changes in ecosystem composition, structure and diversity" and that "A reasonable hypothesis is that ecosystems that have lost one or more strongly interactive species are destined to undergo profound degradation and simplification over time." This would be particularly unfortunate in the context of what we here identify as a unique assemblage of fish and shrimp inhabiting the Atlantic slope drainages of the La Amistad area.
4. We have also expanded our documentation of below-dam effects beyond what appeared in the previous report, to more forcefully make the case for treating the rivers of the La Amistad region as altitudinal biological corridors. We argue that, beyond the explicit commitment to preserve biodiversity, UNESCO, together with ANAM and SINAC, as stewards of the La Amistad International Peace Park, have an obligation to oppose measures which would reduce or eliminate corridor function in rivers arising in the World Heritage Site.

Our concerns for the La Amistad region echo those stated in global terms by Pringle (2001), who observed that "Increasingly, biological reserves throughout the world are threatened by cumulative alterations in hydrologic connectivity within the greater landscape. *Hydrologic connectivity* is used here in an ecological sense to refer to water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle."

She goes on to note that many "reserves" (among them the La Amistad World Heritage Site and the surrounding complex composing the La Amistad Biosphere Reserve) are concentrated in upper watersheds and, as such "may have intact physical habitat and certain important source populations of some native species, yet hydrologic disturbances in lower watersheds may cause extirpation of migratory species, cascading trophic effects, and genetic isolation . . . many reserves are in danger of becoming population 'sinks' for wildlife if we do not develop a more predictive understanding of how they are affected by hydrologic alterations that originate outside of their boundaries." The thrust of the present report is to begin to provide that "predictive understanding" as an aid to avoiding a chain of events similar to those which concern Soule, et al. (2005) and Pringle (2001).

In our previous report, following the introduction we devoted two pages to discussing:

- Generalized effects of dams as barriers to up and downstream movement of aquatic animals, particularly fish and shrimp, with emphasis on the generally underappreciated effects of dam/reservoir complexes on upstream river reaches.
- The particular significance of these effects in fluvial systems characterized by diverse and abundant diadromous animals, with emphasis on the Changuinola/Teribe watershed.
- Predictions re the effects of dams on the La Amistad rivers, drawing on experience in other parts of the world, particularly the West Indies.

This material is repeated in lightly edited form below, for those who may not have read McLarney and Mafla (2007). Many readers of the present document will not need to be convinced of the legitimacy of concern for the biotic health of the rivers of the La Amistad World Heritage Site if projected dam plans are realized. The arguments adduced in our earlier report and the analogies from experience in places like Puerto Rico and Guadeloupe are equally applicable to the watersheds of the Atlantic slope of La Amistad in Costa Rica, and in general terms to the Pacific slope watersheds of both countries as well. Some readers may wish to skip ahead to the succeeding sections which are made up of mostly newer material, including:

- Descriptions of the watersheds and biota which would be affected by the proliferation of dams in the watersheds which drain the La Amistad World Heritage Site.
- A review of related events in the La Amistad area since our last report, including recent publications.
- A more thoroughly developed section on secondary effects of species extirpations, including possible effects on neighboring ecosystems.
- Articulation of the unique character of the ecosystems represented by the Atlantic slope rivers of the La Amistad area.
- Presentation of the case for conservation of the rivers of La Amistad as altitudinal biological corridors, in and downstream of the World Heritage Site.
- Brief comments on mitigation methods for diadromous assemblages.
- Recommendations to UNESCO and other relevant agencies.

Our comments here reflect our concern for the La Amistad area as an irreplaceable repository of biodiversity, which is both our area of expertise and the principal reason for the declaration of a binational World Heritage Site. However, we would like to take this opportunity to emphasize that, insofar as the discussion is about the pros and cons of constructing hydro dams on the rivers of La Amistad, all involved need to be cognizant of a variety of related social justice and macro- vs. microeconomic issues. These important concerns have been and will continue to be raised by other individuals and organizations.

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 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 can function as nearly absolute barriers, dividing a 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 situation presented by the watersheds of the La Amistad World Heritage Site, mitigation adequate to protect biodiversity upstream of proposed dams is well-nigh impossible. This is especially true in the case of the Changuinola (Panama) and Telire (Costa Rica) watersheds which potentially face the effects of multiple dams in sequence, thus likely negating 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 presumably accounts for the documented occasional presence of large marine fishes such as snooks (*Centropomus*), jacks (*Caranx*), and most recently Gerreids (*Eugerres*) (Lasso, et al. 2008b and c) well inland on rivers of both slopes of La Amistad. This behavior, probably best described as “facultative wandering” (McDowall, 1988), 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): *Potamodromy* 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. Potamodromy is of major importance in very large rivers such as the Amazon, Mississippi or Mekong, but is relatively uncommon in the La Amistad region, where the best known examples are fishes of the characid genus *Brycon*, which are important elements of the fauna of the Pacific slope watersheds, but missing south of the Estrella River on the Atlantic. The possibility of undetected potamodromous behavior by smaller fishes exists. For example another characid, *Astyanax aeneus,* one of the commonest obligate fresh water fishes of all the La Amistad watersheds, has been shown to be potamodromous in Guanacaste, Costa Rica (Lopez, 1978). However, most of the emphasis here will be on diadromous fish and shrimps.

Some proportion of diadromous animals exists in most of the fresh waters of the world, even at locations far from the sea. An extreme example is provided by 5 species of catfishes which have been shown to spawn in headwater streams of the Amazon Basin and use the river's estuary as a nursery area (Borges Barthem, et al. 1991). However, diadromy is especially prevalent on islands and isthmuses, such as Mesoamerica, where river systems are necessarily short. In the case of Mesoamerica, including the La Amistad watersheds, 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 stenohaline fishes (fishes with a narrow range of salinity tolerance) strictly intolerant of salt water, 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 freshwater fishes best described as either "secondary" (largely restricted to fresh water but able to move through and survive in saline environments) or diadromous. (We here refer mainly to fishes; much of the same terminology and arguments apply to some crustaceans and molluscs, and we will also refer to shrimps in developing our argument.)

Studies directed by us since 1999 in the Sixaola/Telire and Estrella watersheds of Costa Rica and Panama, which drain the Atlantic slope of the La Amistad World Heritage Site (McLarney and Mafla, 2006b, 2008; McLarney, et al. 2009a), plus the more recent inventory efforts of a Smithsonian Tropical Research Institute (STRI) team (Lasso, et al. 2008b and c) and information compiled by indigenous parataxonomists residing in the Changuinola/Teribe watershed (Mafla, et al. 2005; McLarney and Mafla, 2008, 2009a) have resulted in a fairly complete list of the fresh water fish species of the Atlantic slope watersheds of the La Amistad area. Nearly half of a reported 40-odd fresh water species move regularly between fresh and salt water and at least 14 exhibit true diadromous behavior. (McLarney and Mafla, 2006b) This information, supplemented by other sources (Bussing, 1998; STRI, 2007; Goodyear, 1980; STRI, 2010, personal communication, Dr. Jorge Garcia, U. of Panama) forms the basis for the information on the Atlantic slope watersheds in Table 2.

The recent work of the STRI team in the upper Changuinola and of the ANAI team in the Sixaola/Telire and Estrella watersheds over several years provide an indication of the importance of diadromous fishes in the Atlantic slope watersheds of the La Amistad area:

Lasso, et al. (2008b) specify which of the species they collected in the Changuinola watershed above the CHAN-75 dam site are diadromous, but say nothing about their significance relative to the total fish assemblage. Using their raw data, we calculate that (summing all fish from all sites during both wet and dry season sampling) while only 7 of 15 species are unarguably diadromous (See discussions below about *Atherinella chagresi* and *Eugerres plumieri.*), 83.1% of a total sample of 3,724 individual fish and 82.4% of fish biomass were composed of diadromous species.

ANAI biomonitoring data from 16 fish samples at 11 sites on the PILA boundary in the Sixaola/Telire and Estrella watersheds during 2004-2009 show 13,234 of a total 18,691 fish captured

(70.8%) as belonging to 8 diadromous species. Proportions of diadromous fishes in individual collections ranged from 22.8 to 96.0%; in all but 5 instances diadromous fishes formed the majority of the sample.

Two principal factors contribute to the dominance by diadromous fish in both cases:

- At almost all sites, the single most numerous fishes, usually by a wide margin, are the diadromous *Sicydium* gobies.
- All of the other diadromous species are large-bodied fishes; the only non-diadromous fish which normally reach comparable sizes are the *Rhamdia* catfishes, which accounted for only 0.3% of individual fish in the Changuinola samples. The combination of "most numerous" and "largest" ensures dominance of biomass by diadromous species.

It may seem counterintuitive that the relative importance of diadromous fishes increases with altitude but, although every individual of a diadromous species must pass through the entire length of its home river below the World Heritage Site at least once, the greater total diversity of fish and/or scarcity of adults of diadromous species in downstream reaches is reflected in ANAI's survey data. We will take the most recent year of data collection (2009) as an example. In a total of 24 IBI samples from a wide diversity of streams in the Sixaola/Telire and Estrella watersheds downstream of the PILA boundary, we counted 13,302 fish of which 3,866 or 29.1% were of diadromous species (including *Eleotris* and *Microphis*, which have not been recorded from altitudes above 100 m.)

At the opposite extreme, above natural vertical barriers within the World Heritage Site we usually find *Sicydium* to be the only fish present. The same applies, in general to the shrimps – they are present at all sites, more abundant further upstream, and dominant above natural barriers. These numbers serve to underscore the particular importance of the World Heritage Site in preserving the diadromous component of the biota of the rivers of La Amistad.

Since 2008, we have accumulated some information on diadromous fishes and shrimps of the Pacific slope but, while we suppose that the dominance by *Sicydium* and shrimps represents the natural situation in high altitude rivers of that slope, we can cite no collection data in support of this assumption. Information on Pacific slope streams will be presented in following sections, as appropriate.

Diadromy may be separated into 3 categories, about which there is a certain amount of misunderstanding in the literature with respect to the category of amphidromy. The reader interested in this discussion is referred to McDowall (2004) and references therein. In Tables 2 and 3 and the rest of this paper, we follow the categories established by Myers (1949) and McDowall (1988):

- *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 the Atlantic slope watersheds of the La Amistad region.

- *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. Amphidromy was first defined by Myers (1949) who used it to refer to principally “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 (sometimes treated as a subset of catadromy) until McDowall (1987, 1988, 2004, 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. (In some cases, doubt about where this migration terminates blurs the line between amphidromy and catadromy.) The newly hatched larvae are carried by the current to the marine environment 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 types of fish and cructaceans 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.
- Free-floating sac fry of some amphidromous fishes and shrimps may die of starvation if they do not reach estuarine waters quickly enough; a reservoir lake may slow their progress and cause up to 100% mortality.
- Some actively swimming species depend on currents to orient themselves and may wander aimlessly, with consequent high mortality, in impoundments or be lured into flows associated with dam operations which have no outlet.
- Animals attempting to surmount barriers may be unduly exposed to fishing pressure, predation, desiccation and other threats.

EFFECTS OF DAMS ON DIADROMOUS ANIMALS IN MESOAMERICA AND THE CARIBBEAN

In this section we review literature to suggest the probable effects of dams, and especially large dams in the La Amistad region, with emphasis on the World Heritage Site. “Large” dams are here defined as those > 15 m. high (ICOLD, 1998; World Commission on Dams, 2000) a definition which applies to all but a few of the dams discussed here. The only published studies on the effects of dams on diadromous animals in Mesoamerica are those of Anderson, et al. (2006, 2007) referring to relatively small dams in the Sarapiqui watershed of north Atlantic Costa Rica. However, we can profit from experience in the larger West Indian Islands, where the rivers are similarly short, and where the mix of fish and shrimp species is similar to that of the Mesoamerican mainland, although with an even higher proportion of diadromous species.

In Curacao, Debrot (2002, 2003) implicated dams (along with associated water diversions) in the disappearance of diadromous fishes and shrimps 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.

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 a Commonwealth 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 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. Kwak, et al. (2007) in a survey of Puerto Rican streams, found no native fishes at any site upstream of a large reservoir.

Low head dams in Puerto Rico (much smaller than those proposed for the La Amistad area), did not always result in extirpation, but invariably caused severe reduction in numbers of diadromous Atyid and Palaemonid shrimps (Benstead, et al., 1999). 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.” However, presence of diadromous shrimps, or in one case a diadromous fish (*Gobiomorus dormitor*) above dams was usually linked to alternate migratory pathways, including leaks characteristic of older dams; successful reproduction of populations above dams was not demonstrated. They estimated that “Large dams eliminate or reduce access of migratory biota to 2000 sq. km. of the island’s watershed area or 22% of the island’s land mass.”

Outside the West Indies, particularly strong negative effects of dams on amphidromous fauna have been described for Japan (Han, et al. 2007; Katano, et al. 2006; Miya and Hamano, 1998), Brazil (Odinetz-Collart, 1996), Guam (Concepcion and Nelson, 1999), New Zealand (Joy and Death, 2007; McDowall, 2000), Australia (Gehrke, et al. 2002), Texas (Horne and Beisser, 1997) and the United States in general (Bowles, et al. 2000). Taxa mentioned in these studies which also occur in the La Amistad region include the fish genera *Anguilla, Agonostomus, Awaous, Sicydium,* and *Gobiomorus* plus palaemonid (*Macrobrachium*) and atyid (*Atya, Micratya* and *Potimirim*) shrimps.

Information on dam effects from Mesoamerica is largely anecdotal, although Anderson, et al. (2006, 2007) suggested that dams much smaller than those proposed for the La Amistad area negatively impacted fish diversity, including diadromous species, in the Sarapiqui watershed of northern Atlantic Costa Rica. 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 Reventazon River at Turrialba, Costa Rica, above the 35 m. high Angostura Dam, whereas McLarney (unpublished observations) found it to be common there prior to dam construction. Lorion's observation was confirmed in an unpublished student paper; Vormiere (2007) recorded *J. pichardi* and the related *Agonostomus monticola* up to the Angostura dam on the Reventazon, and up to the smaller, private Tuis Dam on the Tuis River, tributary to the Reventazon below the Angostura Dam, but was unable to find these species above either dam.

EVENTS SINCE 2008

1. Social, Political and Legal Events:

Much has happened relevant to discussion of proposed dams and conservation of biodiversity in the La Amistad World Heritage Site since the first UNESCO mission visit and presentation of our first report (McLarney and Mafla, 2007) in February, 2008. Others can, and we hope will do a more thorough job than we have in reporting and commenting on events in the social, political and legal spheres. However, some degree of summary is necessary to place the rest of the present document, including the news about scientific investigations which follows, in context. It will be convenient to frame this discussion in terms of 4 sectors comprising the "La Amistad area" – Panama and Costa Rica, Atlantic and Pacific slopes.

Panama-Atlantic slope: Our previous report focused almost exclusively on 4 dams proposed in the Changuinola/Teribe watershed, which drains most of the Atlantic slope of the Panamanian portion of PILA, and this remains the sector where the dam controversy is most heated. Construction is underway on two of the dams – CHAN-75 on the mainstem of the Changuinola River and Bonyic, on the Bon or Bonyic River, tributary to the Teribe River. These dams, and related indigenous and human rights issues, have been the subject of much discussion locally, in the press and in international venues. Thus far, questions raised by Panamanian and international conservation organizations, the indigenous Ngobe and Naso inhabitants of the affected area and international bodies from UNESCO to the Inter-American Commission on Human Rights have been largely ignored by the Panamanian government; the apparent response is to accelerate the pace of work on the CHAN-75 and Bonyic dams.

Panama-Pacific slope: The attention given to dams in Bocas del Toro Province has served as a stimulus to anti-dam efforts in adjacent Chiriqui Province, which contains the Pacific slope of the Panamanian portion of the World Heritage Site. Among the 4 sectors of the La Amistad area Chiriqui is unique in two respects: 1) It is the only sector which does not contain indigenous territories located directly downstream from the World Heritage Site, in the buffer zone of the La Amistad Biosphere Reserve. 2) It is the only sector with existing hydroelectric dams.

If we devote relatively little space to Chiriqui in this document, it is because it is the one sector where most of the damage is already done. Existing or nearly completed dams on the Chiriqui and Chiriqui Viejo Rivers effectively block all access by diadromous animals to the Pacific slope of PILA in Panama. Nevertheless, about 40 additional dams of varying size exist, are under construction or are proposed in Chiriqui Province. This activity, which also affects neighboring watersheds in Chiriqui which do not drain the World Heritage Site, has sparked protests including a press release from the Congress of Cattlemen and Producers of Chiriqui Province (Encuentro de Ganaderos y Productores, 2008), declaring solidarity with the Naso and Ngobe affected by dams proposed for the Atlantic slope, and rejecting " uncontrolled hydroelectric expansion in the absence of an Energy Policy based on technical parameters . . . which does not sacrifice our rivers."

An event which affected all sectors, but was particularly well attended by concerned parties from the Pacific slope of Panama, was the annual conference of REDLAR (The Latin American Anti-Dam Network), held at Boquete, in Chiriqui Province, in April, 2009, at which Bill McLarney and Maribel Mafla of ANAI, along with Hugo Sanchez of Fundacion Naso, presented on the importance of diadromy and the effect of dams on natural communities with a diadromous component.

Costa Rica-Pacific slope: At the time of the UNESCO mission visit, the government of Costa Rica was still proceeding with plans for the huge Boruca Dam project, on the Grande de Terraba River, which drains all of the World Heritage Site on the Pacific slope of Costa Rica. Controversy over this project was focused primarily on the displacement of human communities, including in several Indigenous Reserves (Bribri, Brunka, Cabecar, Naso and Ngobe ethnias) and associated economic issues, and did not refer to the La Amistad National Park.

Since then, the project has been scaled down in size, and is now called the Diquis project. This has not satisfied all land tenure concerns, and protest continues. From the point of view of La Amistad and diadromy, the Diquis dam proposal, combined with several smaller private dam projects, is no different from the larger Boruca Dam. Granted that the area of the World Heritage Site affected would be small and located at altitudes above 900 m., a significant portion of the watershed at lower elevations within the indigenous reserves and the La Amistad Biosphere Reserve would be affected, and we feel that the arguments presented below re corridor function and the River Continuum Concept obtain in the Grande de Terraba watershed.

Costa Rica-Atlantic slope: As of February, 2008 this was the sector where there was the least discussion of dam-related issues. However, this has changed since ANAI obtained and circulated details of plans from ICE (the Costa Rican Electrical Institute) for 6 hydroelectric dams to be located in the Talamanca Bribri, Talamanca Cabecar and Telire Indigenous Reserves on 4 of the 5 rivers which form the Sixaola, and which would affect all of the World Heritage Site in the Sixaola/Telire watershed in Costa Rica (plus a small portion in Panama) (ICE, 2001). We have also documented plans for a private hydroelectric dam planned for the upper Estrella River, in the Tayni Indigenous Reserve, which would affect 100% of the World Heritage Site in that watershed (Fernandez Marin, 2009; Machore Levy, 2009; Rivera Mesen, 2008).

Public awareness of the Sixaola/Telire watershed dams coincided with the revelation of applications for three open pit mining concessions (based on possible deposits of silver, copper, nickel, gold, molybdenum, chrome and zinc) in the area. The Uren and Yuani projects (essentially one project, but divided into two properties for legal reasons) in the Uren River watershed and the Dueri project, located in the Coen River watershed, all within the Talamanca Bribri Indigenous Reserve, would together occupy 60,000 hectares. Both project areas border directly on the La Amistad World Heritage Site.

The original applications for mining concessions, which are still pending, were made in the name of ADITIBRI (the governing body of the Bribri tribe), apparently without the knowledge of the Bribri rank and file; the ensuing controversy led to the deposition of the president of ADITIBRI. The proximity of the mining concession sites to some of the proposed dam sites in the Sixaola/Telire watershed has not escaped notice. (MINAE, 2008 a, b; MINAET, 2009 a, b, c).

The events reported here, plus publicity about events in Panama and informal exchanges with Panamanian indigenous groups concerned with dam proposals have placed dams and related social and environmental issues in the forefront of concerns in the canton of Talamanca at this time.

Perhaps the most significant dam-related development in the Atlantic slope indigenous communities of both countries since 2008 has been a shift of attitude re the World Heritage Site ("el Parque") among the Ngobe, Naso, Bribri and Cabecar indigenous communities. Traditionally, while there has not generally been overt hostility to the protected areas of La Amistad, and land invasions have been sporadic and opportunistic, the attitude among the indigenous inhabitants of the La Amistad area has been that el Parque is not intended for them but apparently for the ill-defined benefit of people from outside the area. It is seen by them as territory where they are legally denied use, and they lack a clear perception as to the intended utility of protecting such a vast area.

However, as the dam controversies have evolved, protected area advocates and biodiversity conservationists on the one hand and indigenous communities on the other have perceived common cause. The World Heritage Site has increasingly become seen as a source of benefits which accrue to the indigenous communities located downstream. This is perhaps a fragile coalition, which could dissolve if the dam issues are resolved one way or another. However, insertion of the diadromy issue into the larger discussion has served a vital environmental education function. The indigenous communities are increasingly able to see beyond the convenience represented by coalitions of activists not all of whom necessarily share all the same interests, and to perceive the protections afforded the National Parks as a service which benefits them, independently of any controversies which may exist.

In our opinion, this constitutes a window of opportunity for UNESCO, the natural resources agencies of both countries and the conservation community in general. If we are successful in preserving the integrity of the rivers of La Amistad, with their diadromous fauna intact, we will have won permanent support for the concept of National Parks and World Heritage Sites and reduced the threat to these protected areas from inappropriate use or invasion by their indigenous neighbors. If we fail, the probability of locally generated problems increases for the future.

2. <u>Biological Investigations</u>:

As in the case of the social, political and legal developments reported above, most of the aquatic biological investigations carried out in the La Amistad watersheds during 2008-2009 are best reported by geographic sector. There is still no significant ecological research being carried out in the La Amistad area, but there have been several contributions to our knowledge of species distributions in and downstream of the World Heritage Site. Here we will present broad outlines of the work carried out, with some of the principal conclusions. For detailed information on species distributions and ecological interactions, see other sections of this report.

<u>Panama</u>: We are not aware of any new biological information which has been generated from the Pacific slope of La Amistad/Panama, with the possible exception of some records from the Darwin Initiative expeditions (described separately below). However, some of the most significant inventory information gathered during 2008-2009 was the result of an expedition mounted by the Smithsonian Tropical Research Institute (STRI) in the Changuinola watershed on the Atlantic slope. There Lasso, et al. (2008a, 2008b, 2008c) inventoried fish and aquatic macroinvertebrates including shrimp, as well as a large suite of terrestrial plants and animals in the area which would be directly affected by the CHAN-75 and CHAN-140 dams. The results take up 1,081 pages, spread over 3 volumes (one of which, here designated as Lasso, et al. 2008c, is a 49 page Executive Summary.) Before going on to describe the contents of the STRI report, it is necessary to note that there are serious differences between the Executive Summary and Vol. 2 of the text, which apparently reflect a desire to use the Executive Summary as a public relations document. To cite two examples:

- The Executive Summary plays up the fact that electrofishing (the principal fish survey method used) is a nondestructive method which permits the return of captured animals unharmed to the water. This is true, but the report notes that all fish and shrimp collected were preserved for the STRI collection, a practice which was not well understood or received by the local populace and, in the given instance, obviates the advantages described.

- The Executive Summary states that the STRI team had the "full cooperation" of the local people. However, in the full text Lasso, et al. (2008b) offer an apologetic note re not being able to sample at all planned sites because "in some areas the communities resisted our presence due to the tension and distrust provoked by the various development projects in the area."

The treatment of diadromy is a more serious problem, both in the main text and in the Executive Summary. Lasso, et al. (2008 b) properly attribute diadromy to the shrimps in general and to 8 species of fish (including *Atherinella chagresi*, which according to all other sources we have found, is restricted to fresh water), but always qualify it with statements such as "this classification is based on references consulted for these species in other watersheds and not on data collected in this study where for none of the species has salinity tolerance been tested." This is disingenuous, among other reasons because it confounds salinity tolerance with migratory behavior, but is unfortunately typical of an unwillingness, throughout the report, to treat diadromy as an issue related to dam construction and operation. And nowhere in the report, despite the presence of 40 tables and charts in the fish section alone, is there any indication of the relative importance of diadromy in quantitative terms. (The proportions of species numbers, individual abundance and biomass for diadromous fishes cited above appear nowhere in the STRI report, but are calculated by us from their raw data.)

With these limitations acknowledged, and allowing for relatively small sample sizes, the STRI report is a valuable contribution to our knowledge of the biology of the Changuinola watershed above the confluence of the Teribe River. Of particular value is the first listing of which we are aware of the diadromous shrimp fauna of the upper Changuinola watershed. As for the fish sample, it produced one totally unprecedented record (*Eugerres plumieri*, generally considered to be a marine species). STRI's total of 17 fish species surpasses the list compiled by ANAI personnel and ANAI-trained parataxonomists, (14 species in roughly the same reach of the Changuinola, and 15 species in a similar reach of the Teribe) (Mafla, et al. 2005; McLarney and Mafla, 2006b) and because they were able to use capture-based methods they have also provided valuable data on habitat use and size distribution within that portion of the Changuinola which would be directly affected by the CHAN-75 and CHAN-140 dams.

While Lasso, et al. (2008b) cite statistical tests (accumulation curves) in support of the assertion that their fish inventories approach completeness, we do not share their confidence. We would note that the total of 3794 fish collected by the STRI team in 33 samples is extremely low compared to results recorded by the ANAI Biomonitoring Program in more than 300 samples during a 9 year period in the neighboring Sixaola/Telire watershed. Excepting a few very small high altitude streams with extremely low fish density, all of our individual samples are in the range of 200-2,000 individuals, with a normal range of 600-800 (McLarney and Mafla, 2006a, 2008; McLarney, et al. 2009a, 2009b).

Since the ANAI team has never been able to sample with electrofishing gear in the Changuinola/Teribe watershed we cannot exclude the possibility of extremely low total fish numbers in the Changuinola watershed upstream of the CHAN-75 site. However, the species records of the two teams (STRI and ANAI-trained parataxonomists) suggest that neither team can claim to have exhausted the species list for the upper Changuinola watershed. On the one hand, Lasso, et al. (2008) recorded *Gobiesox nudus*, which the ANAI team found in the Teribe watershed, but not above the mouth of the Teribe in the Changuinola watershed. On the other hand, the ANAI team recorded two primary fresh water species (*Astyanax orthodus* and *Archocentrus nigrofasciatus*) from the upper Changuinola/Teribe watershed which the STRI team failed to find. Based on ANAI's surveys in the Yorkin watershed within PILA, we would consider that yet another obligate freshwater species, *Rivulus isthmensis*, probably inhabits the Changuinola watershed within the World Heritage site, though only a small minority of our records for this wetland species are from free-flowing streams. And our data show 5 additional fresh water species from lower elevations within the World Heritage Site in the adjacent Sixaola/Telire watershed.

Perhaps the most significant difference between the STRI and ANAI experiences in terms of the dam controversy is our records of the catadromous American eel (*Anguilla rostrata*) from the Teribe. (Mafla, et al. 2005) (We also have unconfirmable verbal reports of *A. rostrata* in the Changuinola above the Teribe in past years.) While *A. rostrata* has no official listed status in Panama or any other country, the species is in worldwide decline, it has been proposed as a candidate for protection in the United States (see species accounts below) and is certainly a species of concern in terms of global biodiversity conservation. Taken together, the STRI and ANAI results suggest the need for further fish inventory work in the upper Changuinola watershed.

Mention should also be made of the discovery by the STRI team of several plant and animal species which may be new to science. (Lasso, et al. 2008a, 2008b). While none of the new species are aquatic, we second the conclusion of Lasso, et al. (2008c): "The results of this study reveal that we are just beginning to understand the biodiversity of the Bocas del Toro region. It is extraordinary that in this short inventory, which has covered less than 4% of the Changuinola River watershed and much less than 1% of all the forests in the province of Bocas del Toro, four species of epiphytes have been found which are probably new to science, as well as two new amphibian species and one unidentified snake species."

The STRI reports served as the basis for publication in May, 2009 of a 171 page document (AES and MWH, 2009) suggesting mitigation methods to reduce damage to populations of some of the diadromous species of the upper Changuinola watershed from construction of the 3 dams presently proposed for the Changuinola mainstem. This report (which was not circulated until December, 2009) includes copious bibliographic references for all of the fish species and 2 of the shrimps encountered by Lasso, et al. (2008b). In this respect it will form an invaluable reference for all concerned with the aquatic biota of the Atlantic slope of the La Amistad area for many years to come.

AES and MWH (2009) represents an advance over the STRI reports in that it acknowledges that, although as Lasso, et al. (2008b and c) note, biological investigations on fish and shrimps of the Changuinola/Teribe watershed beyond the level of species inventory are almost completely lacking, it is reasonable to assume that several of the fish species and all of the shrimps collected are diadromous in the Changuinola. This reveals doubts about the existence of diadromous behavior in the Changuinola watershed expressed in the STRI reports (Lasso, et al. 2008b and c) to be a specious concern. From that admission AES and MWH (2009) draw the logical and correct conclusion that any plans to build dams on the Changuinola imply an obligation to take specific measures to protect the diadromous fauna. While it is gratifying to see unanimity of scientific opinion on this point, the proposal advanced fails to convince in terms of the mitigation strategies suggested.

- AES and MWH (2009) fail to take account of the possibility of additional diadromous species in the watershed. In view of the extensive bibliographic research carried out, the failure to cite ANAI reports (Mafla, et al. 2005; McLarney, et al. 2006b, 2008) re records of the catadromous *Anguilla rostrata* in the Changuinola/Teribe watershed is puzzling.

- Mitigation measures are proposed for only 3 fish and 2 shrimp species, out of a total of 8 fish species recognized in the report as diadromous and 5 diadromous shrimps identified by Lasso, et al. (2008b). Since rarity of individual species is often cited in support of conservation measures, their justification of the omission of 5 diadromous fish species on the basis of their relatively low abundance in the STRI samples is questionable.

- The possibility that the CHAN-75 dam would have any effect on diadromous and other species in the river downstream is simply dismissed. This flies in the face of copious research in other watersheds throughout the world (a small sample of which is cited further on in this report) which shows that large dams always occasion significant alterations of the biotic community downstream.

- The strategies proposed utterly fail to take into account the importance of maintaining the River Continuum and biological corridor function of the Changuinola River. No reference is made to the large body of research (cited elsewhere in this report) suggesting that the free movement of diadromous fauna between estuary and headwaters is essential to maintenance of biotic integrity and ecosystem function over the complete altitudinal range of riverine systems, in this case including portions within the World Heritage Site. Rather, mitigation is treated as a species level concern, independently of its ecological context.

- Virtually no reference is made to the importance of the La Amistad National Park, Biosphere Reserve or World Heritage Site, suggesting a desire to address species level concerns while avoiding protected areas issues.

- The mitigation measures proposed rely almost exclusively on aquaculture methods which, especially for the 3 fish species discussed (and to a lesser extent for the shrimps) have yet to be developed. Statements such as this one for *Agonostomus monticola*: “Sera necesario desarrollar anticipademente los protocolos tecnicos que permitan la reproducción en cautiverio para esta especie.” (It will be necessary beforehand to develop technical protocols which permit the reproduction in captivity of this species.) not only overlook the difficulty (or even impossibility) of developing such methods, they are completely unrealistic in terms of planning. Based on worldwide experience in development of aquaculture methods for new species, implementation of the above suggestion could imply multi-year delays in completion of the CHAN-75 project.

- The report contains optimistic absurdities such as the “possibility” that *Sicydium* spp. larvae could adapt to the lotic conditions of reservoirs on the Changuinola, using them as a substitute for estuarine habitat. While there is no relevant research on either of the two *Sicydium* species which may occur in the upper Changuinola (*S. altum* and possibly *S. adelum*), research on other *Sicydium* species and related amphidromous gobies in both the Caribbean and the Indo-Pacific has consistently shown that prolonged exposure to fresh

> water retards development and causes mortality of larvae (Bell and Brown, 1994; Keith, 2002 and 2003; Lindstrom and Brown, 1994).

The general impression left by AES and NWH (2009), the valuable bibliographic content notwithstanding, is of a belated and hurried effort (as evidenced by frequent misspellings) to deal with an unanticipated issue (protection of diadromous species in a larger context of biodiversity conservation) and a failure to reconcile this need with the goal of constructing hydroelectric dams on the Changuinola River. Considering that the authors of the report (No individual authors are listed or acknowledged.) are the company chiefly responsible for construction of dams on the Changuinola (AES) and the consulting firm (MWH) hired as liaison between AES and the responsible environmental authorities (ANAM), it is not surprising that the thrust of the intellectual effort is toward justifying dam construction, and not conserving the biotic resources of the Changuinola River watershed and the protected areas within it.

Costa Rica – Pacific slope: ICE has responded to concerns over the Boruca/Diquis dam project by sponsoring three valuable investigations of aquatic fauna in the Grande de Terraba watershed. Results (reported in greater detail elsewhere in this document) provide the first organized listing of fish and shrimp fauna for this watershed.

Rojas and Rodriguez (2008) sampled fish at 4 stations along the Grande de Terraba at altitudes of 15-145 m., reporting 36 species, representing 26 genera and 14 families. Excluding 11 marine species which enter rivers as facultative wanderers, 4 of these species are definitely diadromous and 2 others are probably so. Interestingly, all 6 probable diadromous species, plus 6 of the marine facultative wanderers, were found at an altitude of 145 m., the highest elevation sampled, corresponding to the level of the proposed Diquis Dam. It is thus highly probable that extirpations of diadromous fish would occur in the Grande de Terraba watershed below the World Heritage Site, if not within it. The same would apply to the potamodromous *Brycon behreae*, also found up to at least 145 m.

The abundance of diadromous fishes in the Grande de Terraba was extremely low; the 6 probable diadromous species together accounted for only 2.0% of a small total sample of 984 fish. The low total abundance of fish may reflect a barrier to diadromous fish posed by the highly polluted lower reaches of the Grande de Terraba where it passes through a major concentration of pineapple plantations; 4 of the 6 probable diadromous species were found only at the highest site. However, the potamodromous *B. behreae* was by far the most abundant species, found at all sites.

Results of a more intensive inventory of the diadromous shrimps of the Grande de Terraba watershed directed by Dr. Ingo Wehrtmann of the University of Costa Rica were recently published (Lara, 2009). The UCR team visited 65 sites in the watershed from sea level to 1075 m., finding 9 species of Palaemonids and 4 species of Atyids. Of these species 4 are documented from altitudes higher than that of the proposed Diquis Dam. Lara (2009) also represents a first contribution to an understanding of the ecology and habitat preferences of some of these species in Costa Rica.

ICE also supported a study of benthic macroinvertebrates, directed by Dr. Monika Springer of the U. of Costa Rica, in the Grande de Terraba watershed (Umana-Villalobos and Springer, 2006). Results demonstrate intact benthic assemblages at their highest altitude sites, nearest the World Heritage Site and generally good conditions overall, but with significantly reduced diversity and dominance by pollution-tolerant forms at the lowest site sampled (in the town of Palmar Norte).

Costa Rica – Atlantic slope: The ANAI biomonitoring team continue to be the principal investigators in this area. During 2008 - 2009 we have continued to emphasize ecological monitoring and inventory work on streams in and near the World Heritage Site, principally in the Yorkin, Coen and Uren watersheds of the Sixaola/Telire system. One consequence of this work (McLarney, et al. 2009a, 2009b) is that we are much more confident than we were in 2008 in reporting species occurrences from within the World Heritage Site.

Beginning in 2009, under the terms of a contract with the U.S. Fish and Wildlife Service, Division of International Conservation, we have placed particular emphasis on the Uren watershed as the most threatened component of the larger Sixaola/Telire system due to the combination of proposed hydroelectric dams and two solicitations for open pit mining concessions in the watershed (McLarney, et al. 2010). A final report on this work will be available in June, 2010.

Three important results of our work during 2008-2009 are:

- Confirmation of the presence of 4 species of diadromous fish, plus both families of diadromous shrimp, at elevations of nearly 400 m. in the Uren watershed, with *Sicydium* and shrimps up to at least 469 m. – the highest altitude at which we have worked in Talamanca.
- A preliminary catalog of the diadromous shrimps of the Sixaola/Telire and Estrella watersheds, which will culminate in a simple laminated guide to the species of the region (Asociación ANAI, in prep.)
- Accelerated training of indigenous parataxonomists and development of Community Biomonitoring Groups in key watersheds, which will enable us to more rapidly develop our knowledge of the presence and distribution of diadromous fishes and shrimps in the Atlantic slope watersheds of La Amistad/Costa Rica.

Darwin Initiative: One other major investigative effort, with implications for all 4 sectors of the World Heritage Site, should be mentioned. In 2006, the Darwin Initiative of the United Kingdom, with collaboration from the Museum of Natural History of London, INBIO, ANAM, SINAC (the protected areas system of Costa Rica), and 4 universities (Panama, Costa Rica, Autonomous of Chiriqui and Oxford), launched a project entitled "Herramientas Basicas para el Manejo del PILA" (Basic Tools for the Management of the La Amistad International Park). It aims to provide access to maps and other data for use by governments and all others concerned with the biodiversity of the La Amistad World Heritage Site.

The Darwin Initiative La Amistad Expedition is scheduled to continue through 2011. Early efforts have concentrated on mapping and systematic biological inventory, with emphasis on 4 groups deemed most likely to yield new discoveries (vascular plants, reptiles, amphibians and scarab beetles). The project has issued 3 reports, beginning in 2007 (Monro, et al. 2007, 2008, 2009). Among the most noteworthy results to date are the discovery of 12 vascular plants, 15 reptiles, 3 amphibians and 1 scarab beetle new to science. The project has also identified a large number of species endemic to Panama and/or Costa Rica, including 79 species endemic to the La Amistad World Heritage Site.

None of the new species are aquatic, nor does the Darwin Initiative plan investigations focused on aquatic environments. However, the project is important to all concerned with biodiversity in La

Amistad because it draws attention to the enormous conservation value of Central America's largest protected area and the extremely limited nature of our knowledge of its biodiversity.

While the potential for new discoveries in the aquatic environment of La Amistad is relatively limited, it would be opportune to complement the Darwin Initiative efforts with systematic evaluation of aquatic biodiversity in the World Heritage Site. The greatest opportunity might be in the area of benthic macroinvertebrates, principally insects, but the increasing availability of molecular genetic methods in taxonomic studies strengthens our belief that fish should also be considered. Three genera would seem to be of particular interest:

- *Rivulus*, a highly diverse genus (132 species according to Froese and Pauly, 2009), is represented in Costa Rica by 5 species on the Pacific slope, but only one on the Atlantic slope (*R. isthmensis*) (Bussing, 1998) reported from within the World Heritage Site (McLarney, et al. 2009b). Three of the Pacific species are narrowly endemic (Bussing, 1980), with *R. uroflammeus* known only from the two principal Pacific La Amistad drainages (Grande de Terraba and Chiriqui Viejo), while *R. glaucus* is known only from the watershed of the General River, a tributary of the Grande de Terraba in Costa Rica (Bussing, 1998). We suggest that the general inaccessibility of the Talamanca region may have limited collection of *Rivulus* on the Atlantic slope of La Amistad, and that prospects for new discoveries there are considerable. The STRI database (STRI, 2010) lists 4 additional species, *R. birkhahni, R. kuelpmanni, R. rubripuncatus* and *R. wassmanni* for Bocas del Toro Province, with *R. rubripunctatus* reported from the Sixaola watershed and *R. wassmanni* from the Changuinola.

- *Bryconamericus*: A recent revision of *Bryconamericus* (Roman-Valencia, 2000, 2002) erected the new species *B. gonzalezi*, and Lasso, et al. (2008b) have so identified their specimens from the upper Changuinola watershed. The locality designations in Roman-Valencia (2002) leave us somewhat doubtful as to distribution of this species and *B. scleroparius*, to which we have so far referred all *Bryconamericus* specimens, but it seems highly likely that both species occur in the Atlantic slope La Amistad watersheds. Froese, and Pauly (2009) lists an additional species, *B. ricae,* for various sites in Costa Rica, including one in the La Amistad drainages (Sepeque River in the Sixaola/Telire watershed) and STRI (2007) lists this species for the Changuinola watershed, but it is mentioned in neither Bussing (1998) nor Roman-Valencia (2002).

- *Rhamdia*: The *Rhamdia* catfishes are notoriously challenging taxonomically Silfvergrip (1996), reduced a total list of over 100 species to 11, of which 2 are definitely found in the La Amistad watersheds, though there is still discussion over which specific names should apply to them. The possibility exists that application of molecular genetic methods to *Rhamdia* might partially reverse the work of Silfvergrip (1996) in simplifying the genus, with the possibility of new species for the La Amistad watersheds.

THE LA AMISTAD AREA AND ITS WATERSHEDS

THE LA AMISTAD AREA

The term “La Amistad” is variously applied, according to the category of protected area under discussion. The binational **La Amistad World Heritage Site** is considered to consist of two contiguous National Parks, both called “La Amistad”, which extend for a linear distance of 140 km. along the spine of the Continental Divide at elevations from approximately 1,800 to 3,549 m. (Cerro Kamuk), connecting two iconic National Parks, Chirripo in Costa Rica in the west with Volcan Baru in the east in Panama, and protecting a combined total of over 4,000 sq. km. In 1982 the two parks together were named the La Amistad International Peace Park, commonly referred to by the Spanish acronym “PILA” (Parque Internacional La Amistad). In 1983 the Panamanian portion was added to the Costa Rican portion, already designated a World Heritage Site, to form the unitary La Amistad World Heritage Site. Since 1982 UNESCO has also designated a larger area around and including PILA as a Biosphere Reserve. The La Amistad Biosphere Reserve is generally considered to include a buffer zone which encompasses the following additional areas:

- Other national protected areas contiguous to PILA: Palo Seco and La Fortuna Forest Reserves and Volcan Baru National Park in Panama plus Chirripo, Barbilla and Tapanti – Macizo de la Muerte National Parks, the Hitoy-Cerere Biological Reserve, Las Tablas and Pacuare Protection Zones, Rio Macho Forest Reserve and Robert and Catherine Wilson Botanical Garden in Costa Rica. The Volcan Baru and Chirripo National Parks are of particular importance since they bracket La Amistad along the continental divide and contain the highest peaks in each country (Volcan Baru, at 3,475 m. in Panama and Mt. Chirripo, at 3,819 m. in Costa Rica).

- Four coastal/marine protected areas - Bastimentos National Park and the San San/Pondsak Wetland of International Importance in Panama and the Gandoca/Manzanillo Wildlife Refuge and Cahuita National Park in Costa Rica: All four are physically disjunct from the La Amistad parks, but San San/Pondsak and Gandoca/Manzanillo (both UNESCO-designated Ramsar Sites) are contiguous to each other. They protect the lower reaches and estuaries of the two principal rivers draining La Amistad (the binational Sixaola River and the Changuinola River in Panama), and will be directly affected by any change in upstream hydrology or biology. Bastimentos and Cahuita are primarily marine parks which may provide estuarine, inshore and coral reef habitat for fish and shrimp which also utilize the rivers of La Amistad.

- Recognized and unrecognized indigenous territories. In Costa Rica, these include 4 “Indigenous Reserves” belonging to the Bribri ethnia (Talamanca Bribri, Cabagra, Salitre and Kekoldi) and 8 Cabecar reserves (Talamanca Cabecar, Telire, Tayni, Pacuare, Alto Chirripo, Bajo Chirripo, China Kicha and Ujarras) all of which are duly recognized. In Panama part of the semi-autonomous Ngobe-Bugle Comarca lies within the designated Biosphere Reserve, as do 3 territories inhabited solely by indigenous groups, but as yet unrecognized by the Panamanian government – the Ngobe-Bugle “annex” along the Rio Changuinola, traditional

> Naso territory along the Rio Teribe and a Bribri territory along the Rio Yorkin contiguous with the Talamanca Bribri Indigenous Reserve in Costa Rica. (These latter 3 areas are largely coterminous with the Palo Seco Forest Reserve.)

If the areas of 4 formally protected areas in Panama and 9 in Costa Rica contiguous to the La Amistad World Heritage Site are added to the World Heritage Site, the additional area of protected forest in the La Amistad region comes to about 1,600 sq. km. in Panama and 3,450 sq. km. in Costa Rica. With a total area of over 9,000 sq. km. the La Amistad block is easily the largest block of protected forest in Mesoamerica. For some purposes to this may be added about 400 sq. km. in the 4 coastal protected areas (both countries combined), and nearly 3,000 sq. km. of recognized indigenous territories in Costa Rica. Figure 1 is a map of the greater La Amistad area showing the relationship of these various jurisdictions to the World Heritage Site.

While the La Amistad World Heritage Site straddles the continental divide over its entire length, in both countries the vast majority of the area included in the two La Amistad National Parks is located on the Atlantic slope, comprising the upper watersheds, down to elevations of 90-100 m., of the Changuinola, Sixaola and Estrella Rivers, plus minor portions of the extreme upper watersheds of the Banano and Chirripo Rivers (the latter forming part of the larger Matina River watershed). On the Pacific slope in both countries the park boundary occurs at much higher elevations (900 - 3,000 m.), and the La Amistad Parks protect only extreme headwater areas of the watersheds of the Grande de Terraba River in Costa Rica and the Chiriqui Viejo River (plus a tiny portion of the Chiriqui River watershed) in Panama. Table 1 shows the total watershed area, and the area within the World Heritage Site for each of these rivers in both countries, along with the areas which stand to be affected by proposed dams in each watershed.

Please note that the information presented above is based on maps and data some of which are contradictory, erroneous or unavailable in official form. (For example, we have seen the watershed area for the Estrella River cited at from 717 to 1,002 sq. km. in various publications.) We do not pretend to precision in Table 1, but we do believe it serves a useful purpose in putting the material which follows in context. Any errors are the responsibility of the authors of this report and not of the many individuals and institutions who have collaborated in its preparation.

FLUVIAL SYSTEMS OF LA AMISTAD, WITH COMMENTS ON PLANNED DAMS

In this section we will discuss the watersheds of the 4 sectors of the La Amistad area (Panama and Costa Rica, Atlantic and Pacific), including what is known about dam plans for each. Table 1 displays some of this information in tabular form. Figures 2-6 are maps of the region showing the location of most of the proposed dams and outlining their areas of upstream influence (in gray). Figure 7 is a simplified, black and white map of the entire area designed to dramatize the potential impact of proposed dams on upstream watersheds.

Atlantic slope – Panama:

Changuinola/Teribe watershed (Figure 2): Our first report to UNESCO (McLarney and Mafla, 2007) dealt primarily with 4 controversial dams in the Changuinola/Teribe watershed which comprises 90 % of this sector, located in the Panamanian Province of Bocas del Toro. (The small portion of the Sixaola/Telire watershed in Panama will be discussed below, under Atlantic slope – Costa Rica.) We prefer to speak of the Changuinola/Teribe watershed, rather than simply “Changuinola” because the principal tributary of the Changuinola River, the Teribe River is so large, accounting for 28% of the total Changuinola watershed.

The Changuinola watershed begins on the Continental Divide, which is also the division between Bocas del Toro and Chiriqui Provinces. While the extreme headwaters and most of the tributaries above the Teribe arise within the World Heritage Site, much of the main channel (67 km.) lies outside the World Heritage Site, but within the Palo Seco Forest Reserve, established in 1983. Prior to that date much of this area was inhabited by members of the Ngobe ethnia, who continue to promote its annexation to the Ngobe/Bugle Comarca.

The Teribe joins the Changuinola at El Silencio, about 115 km. above the Caribbean. Similarly to the case of the Changuinola, much of the main channel above El Silencio (82 km.) lies outside PILA and within Palo Seco. This narrow strip forms part of the ancestral homelands of the Naso (Teribe) ethnia who, like the Ngobe along the Changuinola mainstem, have long advocated the establishment of a Naso Comarca centered around this area. (It is probable that this strip, and the analogous area in Ngobe territory along the Changuinola, were excluded from the La Amistad National Park, not in deference to the indigenous communities, but rather to avoid the controversy which would inevitably arise from any proposal to build a dam in a national park.) Although the Teribe arises in Panama, within the World Heritage Site it loops briefly into Costa Rica. This relatively small area (255 sq. km.) comprises the entirety of the Changuinola/Teribe watershed in Costa Rica.

Below El Silencio, the Changuinola flows through the Changuinola Valley, dominated by banana plantations, with its urban center of Changuinola, and then bisects the San San/Pondsak Wetland, which forms part of the La Amistad Biosphere Reserve. Despite serious agricultural and urban-related pollution issues, the lower reaches of the Changuinola and its extensive lateral system of lagoons and canals comprise an important fishery area.

At present, 4 dams are formally proposed in the Changuinola/Teribe watershed, with two under construction; others are rumored. Three of these dams, called CHAN-75, CHAN-140 and CHAN-220 (with the numbers standing for the distance above the sea in km.) are planned for the mainstem of the Changuinola River in Ngobe territory, while the fourth dam, Bonyic, is sited on the Bon (sometimes referred to as Bonyic) River, tributary to the Teribe River in Naso territory. CHAN-75 and Bonyic are under construction, despite continuing protest from the indigenous inhabitants of the area and national and international conservation organizations (Thorson, et al. 2007, McLarney, 2005; McLarney and Mafla, 2006a; Cultural Survival, 2008; Anaya, 2009). None of the Environmental Impact Assessments for the Changuinola or Bonyic dams (PLANETA Panama, 2005; Proyectos y Estudios Ambientales del Istmo, 2004a, b and c) deal seriously with diadromy and related biodiversity issues.

Figure 2 does not show the CHAN-220 dam, for which we were unable to find geographic coordinates. Even if CHAN-140 and CHAN-220 are never constructed and no dams are ever built on the mainstem of the Teribe, closure of CHAN-75 would severely compromise the biological corridor function of the Changuinola River, and cause extirpation or near-extirpation of diadromous fauna in over half of the Panamanian portion of the World Heritage Site. (This figure holds even without taking into account similar losses which have occurred or are expected on the Pacific slope of La Amistad in Panama; see below).

The only portions of the greater Changuinola watershed within the World Heritage Site which would not be closed off by dams would be the Teribe River watershed (minus the tributary Bon or Bonyic subwatershed) and the small Boca Chica Creek watershed, tributary to the Changuinola downstream of the CHAN-75 site. The latter area, being one of the few areas above CHAN-75 with relatively flat land and alluvial soil, is in the process of being colonized – a predictable effect of beginning dam construction on the middle reaches of the Changuinola.

In terms of total watershed area or area within PILA which would be affected, the Bonyic Dam is comparatively insignificant. However, it would destroy a river of extraordinary scenic beauty and great importance to Naso culture. The reservoir behind Bonyic Dam would extend to within 60 m. of the World Heritage Site boundary.

In this report we deal mainly with those dams for which we have been able to review some form of official documentation. This is not to be interpreted as the totality of dams which exist conceptually in the La Amistad watersheds. This is particularly important in the case of the Teribe. In 2000, a Panamanian government website (ETESA, 2000), in addition to the 3 Changuinola dams and Bonyic, listed “prefactibility” studies for no less than 5 dams on the Teribe mainstem, plus one on the Culubre River, the next major tributary to the Changuinola above the CHAN-75 site.

One scheme which has been unofficially discussed has one of the Teribe dams diverting waters through a penstock into the neighboring low gradient San San River. This plan would have severe impacts both on the San San Lagoon area in the San San/Pondsak Wetland (part of the La Amistad Biosphere Reserve), and also on two Naso communities along the San San, already embattled in a land dispute with neighboring cattle interests, with the government of Panama supporting the latter (Mayhew and Jordan, 2010).

Costa Rica’s small portion of the Teribe watershed, although located entirely within the World Heritage Site, is not exempt. A 1979 ICE review of the hydropower potential of the Sixaola/Telire watershed (ICE, 1979) notes “the possible utilization of waters of the upper watershed of the Teribe River, in Costa Rica, which could be passed into the Sixaola watershed,” but concludes that in order to take optimum advantage of the hydropower resource, it would be better to think in terms of a binational project.

<u>Atlantic slope – Costa Rica</u>:

Sixaola/Telire watershed (Figure 3): The majority of this watershed is located in the canton of Talamanca, Costa Rica, with 23.5% in Panama. Its most unique characteristic is the broad (up to 10 km. wide) alluvial Talamanca Valley, which forms just above where the Sixaola River formally ends, at the mouth of the Yorkin River. The Yorkin watershed is home to the only Bribri population in Panama; like their Naso and Ngobe neighbors, they have long and so far unsuccessfully sought for their traditional lands (estimated at 370 sq. km.) to be recognized as a Comarca by the Panamanian government.

Above the Yorkin, the Sixaola divides into 4 major rivers, the largest being the Telire. The Telire, Coen and Lari watersheds are all located entirely within Costa Rica, while a small headwater portion of the Uren watershed, along with the majority of the Yorkin, is in Panama.

Below the Yorkin, the Sixaola forms the boundary between Costa Rica and Panama for 70 km., passing by the lower portion of the Talamanca Bribri Indigenous Reserve and large areas of agro-industrial banana plantations in both countries. The extreme lower end of the Sixaola separates two Ramsar wetlands – the San San/Pondsak Wetland of International Importance in Panama and the Gandoca/Manzanillo Wildlife Refuge in Costa Rica. Unlike the Changuinola, the Sixaola does not have an extensive lagoon system at its mouth, and its fishery significance is very local. However periodic flooding from the Sixaola plays an important role in the hydrology of the Gandoca Lagoon, one of the key elements of the Gandoca/Manzanillo Refuge. The same is true to some extent of the San San Lagoon on the opposite side of the river, although a dike along much of the Panamanian bank of the Sixaola reduces the frequency and volume of natural flooding in the San San area.

In the past ICE (the government-owned Costa Rican electrical power authority) has proposed up to 16 hydro dams in the Telire watershed above the mouth of the Yorkin (ICE, 1979). As of 2001, the Durika and Broi-Matama (Telire River), Bugu (Coen River) and Uren (Sukut River, Uren watershed) projects are off the table, at least in part because they would be located within the La Amistad National Park. (ICE, 2001). The same applies to projects referred to as Sku, Betsu, Uri, Dika, Kivut and Ourut, for which locations beyond "Parque Nacional La Amistad" are not specified in documents we have been able to access. However, in 2007 the Minister of the Environment suggested in a newspaper interview that ICE might propose changes to the law which would permit development of energy resources in the National Parks in the future (Dobles, 2007). In fact, a certain precedent exists in the form of a micro hydroelectric dam on the Genio River in Isla del Coco National Park (Rojas M., no date), which is also a UNESCO World Heritage Site.

Six of the original 16 dams are currently considered viable projects, including Talamanca, Telire and Nakeagre on the Telire River, Coen and Cabecar on the Coen River and Lari on the river of the same name. All are located within the Talamanca Bribri, Talamanca Cabecar or Telire (Cabecar) Indigenous Reserves. The scope of the original plans for the Talamanca and Lari dams has been reduced to avoid direct impacts to the La Amistad National Park, as was done for the Telire dam project in relation to the Hitoy-Cerere Biological Reserve (although current plans still call for a tunnel under part of Hitoy/Cerere). However, all of the plans would impact upstream watersheds within the World Heritage Site.

The most worrisome of the dams from a biodiversity conservation point of view is also by far the largest. The Talamanca Dam, sited at only 80 m. above sea level, would create a reservoir of 37,000 ha. by flooding the entire Talamanca Valley, formed by the braided and interconnected channels of the Telire, Coen, Lari and Uren Rivers. It would destroy the communities of Boca Uren, Tsuidi, Katsi, Amubri, Cachabri, Tsoki, Bajo Coen, Coroma, Sepeque, Shiroles and Suretka, thus displacing over half of the population of the Talamanca Bribri Reserve (which is in turn the largest concentration of indigenous people in Costa Rica). The map (Figure 3) shows the area of the proposed Talamanca Reservoir, along with the approximate location of the Bribri communities which would be flooded.

The Talamanca Reservoir would also destroy the most important agricultural area in the indigenous territories of Talamanca. Most of the plantains consumed in Costa Rica are grown in the canton of Talamanca, and the Talamanca Valley has for many years been the single most important producing area. In recent years the Talamanca Valley has also assumed great importance as a source of cocoa and bananas for the organic market.

From a biodiversity point of view, the Talamanca Dam would completely eliminate access by diadromous animals to the entirety of the Uren, Lari and Coen watersheds in and out of PILA, plus all but the lower 3 km. of the Telire River. As Figure 3 and Table 1 show, the only portion of the World Heritage Site in the Sixaola/Telire watershed which would not be directly affected would be the Yorkin watershed. Since all of the World Heritage Site in the Yorkin waershed is located in Panama, the Talamanca Dam would thus close access by diadromous animals to 100% of PILA in the Sixaola watershed of Costa Rica. The large area and roughly circular shape of the Talamanca Reservoir would make it particularly effective as a barrier to movement by species adapted to fluvial habitats.

The other 5 projects would all be located above the Talamanca Dam at relatively high elevations (280-630 m.) and, while they would cause further fragmentation of the Telire, Coen and Lari watersheds, they would not add anything to the total watershed area cut off by the larger dam. In this respect, they could be considered potentially less damaging. However, given that (as opposed to the Talamanca Dam site, located near the highway which serves communities located along the Telire) they would be difficult and expensive to access, it seems likely that they would form a less attractive option without the counterpart of the larger Talamanca Dam project.

As opposed to the situation in the Changuinola/Teribe watershed, so far as we know, no investment beyond initial planning has been made in any of the dams proposed for the Sixaola/Telire watershed. However, in the long run, in terms of the area and river mileage potentially affected, we consider the Sixaola/Telire watershed to be even more severely threatened than the neighboring Changuinola/Teribe; the potential is for extirpation of diadromous forms in 77% of the watershed.

Estrella watershed (Figure 4): Beginning in 2009, a private corporation (Santuario Indigena, S.A.) began to enter into negotiations with representatives of the Community Development Association of the Tayni (Cabecar) Indigenous Reserve, which occupies the buffer zone of the La Amistad Biosphere Reserve immediately downstream from the PILA boundary in the Estrella valley, about the possibility of exploiting hydropower resources in the Tayni Reserve (Fernandez Marin, 2009). Figure 4 shows the location of a projected dam on the Estrella River. The legitimacy of this proposal has been disputed by environmental groups based in the Estrella Valley (Machore Levy, 2009) and also by the Costa Rican Attorney General's office (Rivera Mesen, 2009). If built, any such dam would eliminate access by diadromous fish and shrimps to 100% of the Estrella watershed within the World Heritage Site (gray area on map).

Banano watershed (Figure 4): A single dam proposed for the Banano River, below the PILA boundary but within the Rio Banano Protected Zone, would close 79% of the 24 sq. km. headwater area of the Banano River watershed within the World Heritage Site to access by diadromous fauna. (Note the distinction between the Banano River and the Bananito River, which is bracketed by the Estrella and Banano watersheds, but which has no drainage area within PILA.)

Matina watershed (Figure 3): This large watershed is represented in PILA only by a small headwater area (58 sq. km.) of the tributary Chirripo River system, adjacent to Chirripo National Park. While another Matina system tributary, the Pacuare River, has for some years been the locus of great controversy over dams proposed by ICE, we know of no dam plans for the Chirripo watershed nor for the portion of the Matina watershed below the mouth of the Chirripo. This high altitude area (lowest point 1,700 m.) may not have any streams habitable by diadromous animals. (Since the great majority of the Matina watershed and all tributaries with proposed dams, is located outside PILA, this watershed is not included in our overall calculations of affected watershed areas in Table 1 and elsewhere.)

Pacific slope – Costa Rica:

Grande de Terraba Watershed (Figure 5): Damming has long been a controversial topic in the Grande de Terraba watershed (the largest watershed in Costa Rica, and the only one draining the Pacific slope of La Amistad/Costa Rica), not because of potential effects on the World Heritage Site, but owing to social issues, including displacement of indigenous and non-indigenous communities. Castro (2004) cites 26 dam projects – 17 private and 9 public – in this watershed, but we have collected information only for those on the lowermost reaches of streams flowing out of the World Heritage Site. This includes one major ICE project, initially known as the Boruca Dam, and 6 private hydropower initiatives on tributaries which join the Grande de Terraba River downstream of the ICE project site.

In its original form, first proposed in the 1970's, the Boruca Dam, to be located on the mainstem of the Grande de Terraba River, was designed to provide power for a bauxite mining project which ultimately failed to materialize. The largest public works project in the history of Costa Rica, it would have created the largest reservoir lake in Central America behind a dam 230-260 m. high, inundating 260 sq. km., including the entire Rey Curre Indigenous Reserve (Brunka ethnia) along with portions of 3 other indigenous reserves (Brunka, Teribe and Guaymi ethnias) and private lands in the General Valley. This dam, if built, would have eliminated all access by diadromous animals to the entirety of the World Heritage Site on the Pacific slope of Costa Rica.

In its more recent versions, the Boruca project has been a centerpiece of the present Costa Rican government's energy policy, aimed at doubling the country's hydroelectric capacity within 10 years. The current smaller but still controversial version is known as the Diquis Dam. Located on the General River, which joins with the Coto Brus River to form the Grande de Terraba, it would be 179 m. high and flood 60 sq. km., still including part of Rey Curre and other indigenous reserves, while displacing about 1,100 people.

As Table 1 shows, the affected area within PILA in the General watershed would be relatively small and concentrated at altitudes above 2,000 m. However, note that more than a third of the whole Grande de Terraba watershed in and out of Protected Areas and Indigenous Reserves would be affected (gray area in Figure 5), including 100% of the watershed within Chirripo National Park and roughly half of 3 contiguous indigenous reserves bordering the World Heritage Site.

The Diquis Project would not directly affect up and downstream movement of animals in the Coto Brus subwatershed, which accounts for almost a third of the Grande de Terraba watershed in and out of the World Heritage Site. However, 6 of 10 smaller, private dams planned for tributaries to the Coto Brus would block access to nearly a quarter of the area of PILA in that watershed, at altitudes as low as 900 m.

Overall, with construction of the Diquis Dam and as few as two of the dams planned for the Coto Brus watershed, 55.8% of the total Grande de Terraba watershed would be closed to access by migratory aquatic animals. Altered flow downstream would also affect the Terraba-Sierpe Ramsar Wetland, located where the Terraba reaches the Pacific, with consequent impacts on diadromous animals migrating through or using that area as nursery grounds.

While, as noted above, from an aquatic biodiversity conservation standpoint, the portion of the World Heritage Site lying on the Pacific Slope in Costa Rica is relatively less important than its Atlantic slope counterpart by virtue of its small size and uniformly high altitude, it is also true that we have virtually no knowledge of the headwater streams in that area.

Pacific slope – Panama:

Chiriqui Viejo, Piedras/Chico and Chiriqui watersheds (Figure 6): These three watersheds, which reach the Pacific within a straight line distance of less than 50 km. from each other, are best understood as a unit. An interactive map posted on ANAM's website to promote their "Clean Development Mechanism" shows 42 existing or proposed dams among the 3 watersheds (ANAM, 2009). While these dams are smaller than most others described here, most if not all would be large enough to block upstream movement of migratory fish.

Of the three watersheds, the Chiriqui Viejo, with 68 sq. km. in the World Heritage Site, is the most important in terms of this discussion. The map (Figure 6) shows only the lowermost dam (Burica) on the Chiriqui Viejo; individual treatment of 13 dam sites in the watershed is beyond the scope of this paper. As the gray area on the map indicates, access by diadromous fauna to the World Heritage Site in this watershed is or shortly will be totally eliminated. Another effect, once the Bajo de Minas and Baitun dams (with water rights owned by the Mexican investor Carlos Slim) are completed, will be the total destruction of Panama's premier whitewater rafting river - a touristic and recreational resource of great importance to Chiriqui Province.

The Chiriqui Viejo and Chiriqui watersheds are separated by the Chico River watershed, which has no watershed area within the World Heritage Site, although the Piedras River, tributary to the Chico, drains part of the Volcan Baru National Park, a component of the La Amistad Biosphere Reserve. A total of 11 dams are planned for this watershed. Access by diadromous fauna to the Volcan Baru Park stands to be totally eliminated, since the majority of the park lies within the Chiriqui Viejo watershed.

The Chiriqui River has only a tiny area (17 sq. km.) within the World Heritage Site, and it, along with neighboring portions of the La Fortuna Forest Reserve (also part of the La Amistad Biosphere Reserve) has been inaccessible to diadromous fauna since well before the controversies provoked by the Changuinola/Teribe dams on the Atlantic slope began. This is the consequence of dams constructed earlier on the mainstem of the Chiriqui River (total of 19 existing or proposed dams in the watershed as a whole). The map (Figure 6) shows only the lowermost dam.

Among the 4 quadrants of the La Amistad region, the Pacific slope in Panama, which happens to be the quadrant with the most present economic importance for tourism, is currently the most drastically affected in terms of aquatic biodiversity. It is highly probable that within a short time after this report is completed, 100% of the diadromous fauna in the Pacific slope watersheds of the World Heritage Site in Panama will have been extirpated by dams. This serves as a warning, but is particularly unfortunate because we are only belatedly realizing that the fish fauna of this area is very different from that of the other 3 quadrants. (See discussion below.)

Conclusion:

In terms of damage/threat to aquatic biodiversity, maintenance of diadromous fauna and river corridor function, we may rank the 4 quadrants of the La Amistad World Heritage Site as follows, from most to least impacted:

- Pacific slope – Panama: Almost certainly a total loss within the World Heritage Site and in major portions of the watersheds outside it, based on dams existing and in late stages of construction.
- Pacific slope – Costa Rica: Its future depends on the status of one major project (the Boruca/Diquis Dam), completion of which seems likely, and 6 smaller private initiatives. The result of completion of these projects would be a 37% loss within the small World Heritage Site area and extensive damage to a major portion of the downstream watershed, including portions of several indigenous reserves.
- Atlantic slope – Panama: Two dams presently under construction would cause extirpation of diadromous fauna within the World Heritage Site in the upper Changuinola watershed, plus the much smaller Bon watershed, with similar damage in the Palo Seco Forest Reserve and two indigenous territories. Eventual emergence of dam plans elsewhere in this quadrant, particularly on the Teribe River, cannot be ruled out.
- Atlantic slope – Costa Rica: Based on existing dam plans the potential exists for total extirpation of diadromous fauna in nearly 100% of this area. However dam plans are not nearly as advanced here, and this quadrant may represent the best opportunity to preserve biodiversity and riverine corridor function in and downstream of the La Amistad World Heritage Site.

If all the proposed dams identified in this report were to be completed, the only areas within the La Amistad World Heritage Site in Panama which would still be accessible to diadromous fish and shrimp would be in the Atlantic slope Yorkin and Teribe watersheds (excepting the Bon subwatershed, tributary to the Teribe). In Costa Rica, all that would remain on the Atlantic would be in a small high altitude portion of the Banano watershed, the Chirripo watershed above 1,700 m., and some small portions of the Grande de Terraba watershed on the Pacific slope. Overall, within the World Heritage Site, this amounts to a 67% reduction in watershed area accessible to marine migrants compared to natural levels and a 55% reduction in the La Amistad watersheds as a whole. The black and white map, Figure 7, dramatizes this effect by showing the portion of the binational World Heritage Site where species extirpations would occur in black. Note that a decision to construct even a single dam on the Teribe River mainstem would eliminate the entirety of the large white area separating the two major black areas, resulting in loss of access by diadromous animals to 75-80% of the area.

Given the inadequacy of available maps in the upper watersheds it is impossible to say exactly how many stream miles would be affected. However we previously calculated that the CHAN-75 and Bonyic dams together would block access by diadromous animals to some 700 miles (1127 km.) of perennial streams (McLarney and Mafla, 2007). Extrapolating on the basis of watershed area, this leads to a conclusion of 4,000 km. of perennial streams affected, with well over half that length located within the World Heritage Site.

Damage within other protected areas, indigenous reserves and some privately owned lands would be significant in both countries. It is not inconceivable that these effects, combined with downstream impacts from the dams, could cause complete extirpation of some diadromous species in the entire binational La Amistad area.

THE AQUATIC FAUNA OF LA AMISTAD

FISH

Introduction and Overview:

The work of the Asociación ANAI Stream Biomonitoring Program in the Sixaola/Telire and Estrella watersheds (including the Panamanian portion of the Sixaola/Telire) has led to a virtually complete list of fresh water and diadromous fish and macroinvertebrates (excluding primarily estuarine species which have never appeared in our freshwater samples); see Table 2. (In our usage "fresh water" excludes those species known only from estuaries; the category "estuarine" in the tables connotes species associated with estuaries and the lower reaches of rivers.) We have identified 46 species of fresh water fish (15 of them considered to be diadromous) reported for these two river systems draining the World Heritage Site; this includes all of the species indicated for these watersheds by Bussing (1998). Of these 46 we have confirmed the presence of 24 species (7 of them diadromous) within, or immediately downstream of the La Amistad National Park (Asociación ANAI, 2007; McLarney and Mafla, 2006b, 2008; McLarney, et al. 2009a, 2009b). (Some of our sampling sites are located precisely at the PILA boundary; absent the existence of physical barriers at the boundary it is to be presumed that fish found in these locations also inhabit significant stream reaches within PILA.)

Our list of freshwater fishes from the Changuinola/Teribe watershed of Panama is derived from a variety of sources, including the early survey work of Goodyear, et al. (1980) sporadic investigations by the University of Panama (personal communication, Dr. Jorge Garcia), the work in 2006-2008 of 5 Naso and Ngobe parataxonomists trained by the ANAI team (Asociación ANAI, 2007; Mafla, et al. 2005; McLarney and Mafla, 2007, 2008) and information from the Smithsonian Tropical Research Institute (STRI) website (STRI, 2010), supplemented by their 2008 inventory work on the Changuinola mainstem and tributaries above the CHAN-75 dam site (Lasso, et al. 2008 a, b and c). Based on synthesis of this data, we count 42 species of freshwater fish, including 13 diadromous species for the watershed as a whole. Of these, 25 are found above the CHAN-75 dam site, thus effectively within PILA; 19 species, including 8 diadromous species, have been confirmed from within the World Heritage Site boundaries in the Changuinola/Teribe watershed. (These numbers should not be taken to be exact, since they reflect certain taxonomic inconsistencies among the authorities cited.)

Detailed fish collection records for the Banano River watershed are not available, but the ichthyofauna of this river should be very similar to that for the Estrella. Fish diversity, if any, in the portion of the Matina/Chirripo watershed in PILA, located at above 1700 m. would almost certainly be low and comprised primarily of diadromous species.

In general, the fish species lists for the 3 main Atlantic watersheds (Table 1) are very similar, but 3 differences are worthy of mention:

- The Changuinola/Teribe watershed list includes one additional diadromous species, due to documentation of the presence of *Gobiesox nudus*. Although *G. nudus'* range extends from Honduras to Venezuela, it has not been collected from the greater Talamanca region of Costa Rica.
- The machaca (*Brycon guatemalensis*), native to most Atlantic drainages from Guatemala to western Panama is, for unknown reasons, absent from the watersheds between the Estrella

and the region east of Almirante in Panama. However it is a prominent member of the fauna of the Estrella River watershed, where it is an important food fish. While stenohaline and confined to fresh water, it is highly potamodromous (migratory within fresh water), and would likely be severely impacted by dams on the Rio Estrella or its tributaries.

- The alert reader will notice differences between the two country lists for the non-diadromous genera *Bryconamericus, Poecilia, Rivulus, Rhamdia, Amphilophus* and *Astatheros.* These differences, which will be further discussed in the text when appropriate, are nomenclatural and/or result from recent taxonomic "splitting", and do not reflect significant differences in diversity.

On the Pacific slope, we were not able to obtain fish diversity information for the Chiriqui Viejo watershed. It is not safe to assume what one might conclude from looking at the map - that the native fish fauna of this watershed is similar to that of the neighboring Grande de Terraba watershed in Costa Rica. Briceño and Martinez (1986) offer a list of 36 species for the nearby Chiriqui River, of which only 2 coastal species appear in the inventory of 33 species for the Grande de Terraba cited below (Rojas and Rodriguez, 2008). Even allowing for some confusion due to nomenclature and the inclusion in the Chiriqui survey of a large number of essentially marine species, this is a remarkable difference for two rivers separated by a straight line distance of 119 km. In this regard, it should be noted that while Bussing (1976) assigned the Grande de Terraba and Coto River watersheds, representing the southern extreme of the Costa Rican Pacific, to the Chiapas/Nicaraguan Ichthic Province, the dividing line between that province and the Isthmian Province follows the national boundary with Panama.

In any event, it should be assumed that diversity, particularly of diadromous fish, in the Chiriqui Viejo watershed (and thus effectively in the entire Pacific slope area of the World Heritage Site in Panama) has been irreversibly reduced through damming of the mainstem downstream of the World Heritage Site. A further threat to native biodiversity in the headwater area of this watershed is the introduction of the exotic rainbow trout (*Oncorhynchus mykiss*). What we have only belatedly realized is that this critically imperiled fauna may have been unique among the La Amistad drainages.

Our list of species for the Grande de Terraba watershed (Table 3) is drawn partially from examination of the range maps in Bussing (1998) supplemented by one recent study (Rojas and Rodriguez, 2008). Given that only high altitude areas in the headwaters of Pacific slope watersheds are included in the World Heritage Site, the proportion of these species which actually inhabit PILA should be much lower than for the Atlantic slope, and could approach zero. The species most likely to occur are the diadromous *Sicydium salvini* (based on its ability to surmount natural vertical barriers) and the non-diadromous *Rivulus uroflammeus,* already known from altitudes of up to 1,100 m. in the watershed (Bussing, 1998).

In the pages which follow, we emphasize diadromous species documented from within or very close to the World Heritage Site as those species within UNESCO's purview which are most vulnerable to severe population reduction and probable extirpation above future dams in the watersheds draining PILA. We base our determinations of diadromy for the most part on the Global Registry of Migratory Species (GROMS, 2009), supplemented by our own observations in the La Amistad area. We also discuss two potamodromous species which might also be adversely affected by dams. This material updates the treatment of individual species in McLarney and Mafla (2007). We give detailed treatment to species found on the Atlantic slope, and more cursory treatment to Pacific slope fish.

ATLANTIC SLOPE SPECIES:

Family Anguillidae (freshwater eels)

Anguilla rostrata (American eel, anguila del mar)

The anguillid eels are distributed almost worldwide (although none are known from the eastern Pacific, including the Pacific slope of Mesoamerica), 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 Talamanca and Bocas del Toro. Due to its large size (up to 1.2 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 American 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. (Vladykov, 1964). (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 may journey far up rivers. Bussing (1998) reports *A. rostrata* at elevations to 20 m. "in stagnant waters or rivers of moderate current velocity". However, in the Sixaola/Telire watershed we have on several occasions captured eels in strong rapids, and at altitudes of up to 80 m. (McLarney and Mafla, 2006b, 2008; McLarney, et al. 2009a, 2009b). We have verifiable reports of *A. rostrata* from the Teribe and Bon 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 Bon (Mafla, et al. 2005; McLarney and Mafla, 2007).

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. They may also use subterranean channels, as evidenced by their existence in karstic sinkholes in Yucatan, Mexico (personal communication, J.J. Schmitter-Soto). 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 severity of any impact to *A. rostrata* from dams in Talamanca and Bocas del Toro would depend on the significance, as yet unknown, of the females' upstream journeys. However in North America, the main cause of reduction of eel populations is considered to be the proliferation of dams on the principal rivers (Jenkins and Burkhead, 1993).

Family Atherinidae (silversides, pejerreyes)

Atherinella chagresi (sardina plateada)

We have seen no evidence of diadromy in this species, and Bussing (1998) treats it as an exclusively fresh water fish. The majority of species in the Atherinidae are marine; on the Costa Rican Caribbean slope and elsewhere the family is represented by species which live in lowland streams and others which inhabit the littoral zone, so it is surprising not to encounter a diadromous species. This observation is echoed by McDowall (1988) “Atherinids are well known for their euryhalinity and it is surprising that various forms of diadromy are not well reported for the family . . . As strictly defined, diadromy does not seem to occur in any atherinid.”

We include *Atherinella chagresi* in this section because it was treated as a diadromous species by AES and MWH (2009) and because, athough Bussing (1998) cites a maximum altitude of 60 m., both the ANAI and STRI teams have encountered it in the Changuinola mainstem at locations above the CHAN-75 dam site and we have taken it within PILA in the Sixaola/Telire watershed (Lasso, et al. 2008b; McLarney and Mafla, 2006b; McLarney, et al. 2009 b). Thus if *A. chagresi* were diadromous, construction of proposed dams would threaten it with extirpations within the World Heritage Site in both countries.

AES and MWH (2009) cite Zaret and Paine (1973) in support of apparent amphidromous behavior by *A. chagresi* in the vicinity of the Panama Canal, but also mention the long term existence of a reproducing population above the dam forming Lake Gatun in the same area. However, we note that Lake Gatun, as part of the Panama Canal system, is porous to marine species so, even were *A. chagresi* well documented as diadromous, its presence there can scarcely be cited as proof of adaptation. In terms of the discussion of which this report forms part, *A. chagresi* is perhaps most useful as a reminder of how little we really know of the life histories of the fresh water fishes of Mesoamerica.

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” and much more common and widely distributed in the La Amistad watersheds. 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 9 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). Subsequently the STRI Inventory of the Changuinola mainstem above the CHAN-75 damsite demonstrated its presence in the Changuinola watershed above the Teribe (Lasso, et al. 2008b). 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 not unreasonable to posit that *G. nudus* is amphidromous, and it was so considered in the STRI inventory.

Bussing (1998) casts some doubt on amphidromy by pointing out that "if it has to descend to the sea, this small fish that inhabits even the tributaries of Lake Arenal, would have a very long migration to achieve this end." However, AES and MWH (2009) err in citing this comment to support successful adaptation to impounded watersheds, since Lake Arenal was a natural lake before it was impounded to form a larger "lake", which should properly be known as the Arenal Reservoir. All records for *G. nudus* in the Arenal watershed above Lake Arenal appear to date from prior to impoundment of Arenal Reservoir in 1973 (personal communication, W. Bussing). While it is not known if *G. nudus* persists in the upper Arenal watershed, other diadromous fishes, notably *Joturus pichardi,* have disappeared since the dam was built.

If *G. nudus* is in fact amphidromous, the eventual effect of dams could be considerable. In addition to blocking downstream movement by larval fish, upstream migration by adults could also be precluded, since (unlike in the case of *Sicydium* and some other gobies) there are no reports of *Gobiesox* using the thoracic sucker to scale vertical surfaces.

Family Gerreidae

Eugerres plumieri (estrombal, mojarra prieta)

This species is included on the basis of the capture of 2 specimens by the STRI inventory expedition in the mainstem of the Changuinola River above the CHAN-75 dam site (Lasso, et al. 2008b) at an altitude of over 100 m. Bussing (1998) mentions records of the capture of this species in the San Juan River at elevations of up to 31 m. However, while we find *E. plumieri* to be common in estuarine habitats in Talamanca, we have never taken it in 9 years of intensive fresh water sampling in the region.

The occasional occurrence of marine top carnivores (notably *Centropomus* and *Caranx* in the Atlantic watersheds of La Amistad) is well documented; the general assumption is that they are not obligate migrants, but rather opportunistic hunters wandering beyond their normal range in pursuit of prey. The same could apply in the case of the invertivorous *E. plumieri*. We include this species here because we are unable to confirm either this behavior or possible diadromy and as an example of how much we have yet to learn about the biology of the rivers of La Amistad.

Family Haemulidae (grunts, roncadores)

Pomadasys crocro (burro grunt, Atlantic grunt, ronco, roncador)

This large species (up to 355 mm. long) is important in artesanal fisheries in all of the Atlantic watersheds of the World Heritage Site, where it inhabits streams of all sizes, in and out of PILA, up to an altitude of at least 250 m. (Mafla, et al. 2005). Cervigon (1993) reports capture of this species at a depth of 120 m. in the Caribbean off Venezuela but, while it is common in estuaries in Talamanca, we have never observed it in a marine habitat.

There is nothing published on the reproduction of *P. crocro* or any other species of *Pomadasys.* Since the family Haemulidae is principally marine, while *P. crocro* is found chiefly in rivers and estuaries, and because no one has described the larvae, we accept its listing as amphidromous in the Global Registry of Migratory Species (GROMS, 2009), but it could be catadromous. In either case a probable consequence of damming would be its disappearance from the upper watershed, including in PILA.

Castro-Aguirre, et al. (1999) report the existence of a landlocked population in a reservoir lake (Miguel Aleman or El Temascal) in Veracruz, Mexico. However, one of the authors of that text affirms that *P. crocro* does not usually adapt in this way in Mexico (personal communication J.J. Schmitter-Soto). The conservative stance is to continue to assume that *P. crocro* is an obligate diadrome in Talamanca and Bocas del Toro.

Family Mugilidae (mullets, lisas)

Agonostomus monticola **(mountain mullet, sarten, lisa, tepemechin, mechin)**

A. monticola is by far the most abundant fish of edible size in the fresh waters of Talamanca and 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, and Cruz (1987) found it in small tributaries at up to 1,500 m. in Honduras. It has appeared in 100% of the visual inventories made in the Changuinola/Teribe watershed, and in nearly every fish sample carried out by the ANAI Biomonitoring Team in the Sixaola/Telire and Estrella watersheds (McLarney and Mafla, 2006b; 2008a; McLarney, et al. 2009a, 2009b). It has also been reported from the Grande de Terraba (Rojas and Rodriguez, 2008) and Chiriqui (Briceño and Martinez, 1986) watersheds, making it the only diadromous fish present in streams draining both slopes of the World Heritage Site. On the Atlantic slope, 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, considered it catadromous, as did Aiken (1998), Bussing (1998), Erdman (1972, 1976), and Thomson (1978), based on observations in Jamaica, Costa Rica, Puerto Rico and Florida, respectively. Phillip (1983) reported finding ripe and running females in the sea off Trinidad, which would support the argument for catadromy. Cruz (1987) who studied both species of diadromous mullets in Honduras, thought *A. monticola* might be either catadromous or amphidromous.

For whatever reason, McDowall (1998) in his text on diadromy and a later publication on amphidromy (McDowall, 2007) 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 well studied are either catadromous or completely marine. (However, see the following account for *Joturus pichardi*.) 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." However, Phillip (1983) detected a "single, distinct reproductive season" in Trinidad. 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, as suggested by Marcy, et al. (2005).

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, penetrating to the uppermost headwaters (as also observed by Cruz, 1987 in Honduras and Kenny, 1995 in Trinidad). 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)**

The bobo or bocachica, found from sea level up to at least 600 m. elevation (Bussing, 1998), 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 (on the Atlantic slope from Veracruz, Mexico to San Blas, Panama, plus Cuba, Hispaniola and Puerto Rico). There is general agreement that, while *J. pichardi* may still be found in most streams of the Estrella and Sixaola/Telire watersheds (where dams are not presently a factor) in Talamanca 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, Panama 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), Diaz-Vesga (2007) and Erdman (1984) considered that *J. pichardi* is probably catadromous, based on studies in Mexico, Colombia 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. However, he subsequently found ripe female *J. pichardi* in Honduran estuaries. Recently Villalobos and Molina (no date) found ripe females in the Sarapiqui River, Costa Rica in October of 2005, but were unable to find them from November on, supporting the popular concept of an annual migration by adult *J. pichardi* to the lower reaches of rivers and/or estuaries. Any attempt to draw conclusions is clouded by the fact that 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 (McLarney, et al. 2009b). This suggests that, in addition to an annual reproductive migration, they move from stream to stream during their life, as they grow.

Information on dam effects from Mesoamerica is largely anecdotal. Anderson, et al. (2006) associated a small dam on the Puerto Viejo River in north central Costa Rica with the disminution of *J. pichardi* in that river. 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 1973, and suggests that similar effects may occur on other dammed rivers in Costa Rica. Chris Lorion of the University of Idaho/CATIE (personal communication) and Vormiere (2007?) both report the absence of this species from the Reventazon River watershed above the Angostura dam, whereas McLarney (unpublished observations) found it to be common there in 1968. However, there is documented precedent for the disappearance of this species above dams from Puerto Rico (Erdman, 1984; Kwak, et al. 2007). We assume that *J. pichardi* would disappear from any river above a dam, including in the World Heritage Site.

Family Gobiidae (gobies, gobios)

Awaous banana **(river goby, chuparena)**

The gobiid genus *Awaous* is almost universally distributed in tropical and subtropical regions; *Awaous transandeanus* (the Pacific geminate species of *A. banana*) inhabits Pacific slope streams of Mesoamerica from Costa Rica to Peru (Bussing, 1998) and may ascend into the La Amistad World Heritage Site in tributaries of the Grande de Terraba and/or Chiriqui Viejo rivers.

On many islands, such as Hawaii and the smaller West Indian islands, *Awaous* spp. are the only fish which inhabit some fresh water rivers and creeks. *A. banana*, universally distributed in the rivers of Talamanca and Bocas del Toro, 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. Although low in abundance at most sites, the population of *A. banana* is well distributed from near sea level up to nearly 500 m. altitude within the World Heritage Site (Mafla, et al. 2005; McLarney and Mafla, 2006b; McLarney, et al. 2009b).

As noted by Keith (2003), while the Gobiidae are “the most diverse family of freshwater fish, their biological cycle and the parameters and evolutionary processes that lead to such diversity are poorly understood.” In the case of the genus *Awaous,* in spite of being well known on 4 continents and in many islands, much of the available information is conjectural. Yerger (1978) thought that *A. banana* spawned in the sea, which would make it catadromous, but Bussing (1998) posits amphidromy, opining that “They probably reproduce near the sea and the larvae are swept into the sea where they develop in pelagic waters.”

The best studied species of *Awaous* (*A. guamensis* of the western Pacific islands) is amphidromous. Ego (1956) and Kido and Heacock (1992), cited in Keith (2003), have shown that “the adult fish normally migrate downstream to the spawning grounds, which are situated in general in the first shallow rapids encountered upstream from the river mouth". Individual young fish may spend over 4 weeks in estuaries.

Be it amphidromous or catadromous, if *A. banana* requires access to salt water to complete its life cycle it would probably disappear above the proposed dams; there is precedent in Puerto Rico (Holmquist, et al. 1998; Kwak, et al. 2007).

***Sicydium* spp. (titi, chupapiedra)**

There is not agreement on the number of species of *Sicydium* which ascend streams draining into the Gulf of Mexico and the Caribbean. Bussing (1996), reviewing Brockmann (1965) thought it probable that *Sicydium antillarum* of the northern coast of South America was synonymous with *Sicydium altum*, but reserved the latter name for the Costa Rican population. At the same time he divided *S. altum* into 2 species, designating the new species *Sicydium adelum*. However *S. adelum* is not recognized by all authorities. Lasso, et al (2008b) refer all *Sicydium* captured in their inventory work in the Changuinola watershed to *S. altum.* According to Bussing (1996, 1998) at lower elevations the 2 species nearly always occur together, but whereas *S. altum* is reported at elevations of up to 1200 m. in Costa Rica, *S. adelum* is known only to 90 m. This leaves open the possibility that *S. altum* occurs at altitudes below the level of the CHAN-75 dam site (ca. 100 m.) in the Changuinola/Teribe watershed, but not within the World Heritage Site. In discussing the Atlantic slope watersheds draining the La Amistad World Heritage Site we will refer simply to *Sicydium*.

While there is some doubt about the taxonomic identity of *Sicydium* on the Pacific slope of Mesoamerica (Brockmann, 1965), it is probably safe to assign any individuals from the La Amistad Pacific watersheds (Grande de Terraba, Chiriqui Viejo and Chiriqui Rivers) to *Sicydium salvini*.

In the Changuinola/Teribe, Sixaola/Telire and Estrella watersheds, *Sicydium* is the most abundant fish wherever there is rocky substrate. Despite its small size (up to 140 mm.) it is often dominant in terms of number of individuals and biomass. Lasso, et al. (2008b) found *Sicydium* to comprise 62.5% of their total fish collections (comprising a total of 15 species) in the Changuinola watershed above the CHAN-75 dam site during the dry season; it contributed from 39 to 77% of biomass in individual samples. Our dry season investigations in the Sixaola/Telire and Estrella watersheds (McLarney and Mafla, 2006b, 2008; McLarney, et al. 2009a, 2009b), show that proportional abundance increases with altitude and gradient. Even in some moderately diverse samples (6-12 species), *Sicydium* comprises 75-95% of individual fish. Naso and Ngobe parataxonomists trained by ANAI arrived at similar visual estimates for several sites on the mainstem and tributaries of the Changuinola and Teribe Rivers (Mafla, et al. 2005; McLarney and Mafla, 2006). Overall *Sicydium* is nearly omnipresent, occurring in smaller numbers in rivers and creeks with lower gradients and finer substrate materials.

Thanks to their strong thoracic disk, *Sicydium* gobies in general are considered to be "able to scale any gradient over which water flows" (Covich, 1988). (Another sicydiine goby, *Lentipes concolor*, of Hawaii, is documented to regularly surmount a set of waterfalls 300 m. high, with 100 m. vertical drops; Englund and Filbert, 1997). In Bocas del Toro and Talamanca, *Sicydium* is normally the only fish found above natural barriers such as waterfalls 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 antillarum* and *S. punctatum* of Dominica (Bell and Brown, 1995; Keith, 2003), *S. plumieri* of Puerto Rico (Erdman, 1961, 1986), *S. stimpsoni* of Hawaii (Tomihama, 1972) and *S. taeniurus* of Tahiti (Schulz, 1943) have been shown to be amphidromous, and most authorities share the assumption with McDowall (1988) that all sicydiine gobies are diadromous.

We know that the larvae of *S. altum/adelum* (known locally as "titi") 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 of the proposed dams, were the humidity adequate. However, it also appears that reservoir lakes could constitute an insuperable obstacle for adults and postlarvae ascending and almost certainly for newly hatched individuals descending. The latter argument is supported by the assertion of Balon and Bruton (1994) that for free embryos of amphidromous fishes the time taken to descend to their estuarine feeding site is critical. Research in Japan on *Rhinogobius* gobies (Moriyama, et al. 1997; Tsukamoto, 1991), and one non-gobiine amphidromous fish (*Plecoglossus altivelis*) (Iguchi and Mizuno, 1998) demonstrates that the survival of drifting embryos is inversely related to the time of transit (as determined by distance from the sea and current velocity). Lyons (2005) related the presence/absence of *Sicydium* gobies in Mexico and Central America to the length and velocity of rivers; in slow moving rivers traversing wide coastal plains, *Sicydium* are rare or absent.

These conclusions are coherent with the natural absence, in Talamanca, of *Sicydium* in a few fluvial systems characterized by coastal lagoons with very little current (McLarney and Mafla, 2006b, 2008; McLarney, et al. 2009a, 2009b). And it is sufficient to explain the disappearance of *Sicydium* above dams in Puerto Rico and Guadeloupe (Benstead, et al. 1999; Fievet, 1999; Fievet, et al. 2001a, 2001b; Holmquist, et al. 1998; Kwak, et al. 2007). Thus it is reasonable to suppose that alteration of flow regimes by large dams in the PILA watersheds would cause *Sicydium* to disappear from upstream river reaches. 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) could have the most profound ecological consequences. (See sections on shrimps, and secondary effects of species extirpations, below.)

Family Eleotridae (sleepers)

Gobiomorus dormitor (Bigmouth sleeper, mudfish, guavina, bocon)

This large predatory fish is more abundant in the lower watersheds, but has been reported in the World Heritage Site up to at least 100 m. altitude (McLarney, et al. 2008, 2009), and to at least 543 m. in Puerto Rico. (Bacheler, et al. 2004) (The similar *Gobiomorus maculatus* of the Pacific slope is known from the Chiriqui and Grande de Terraba watersheds but probably does not ascend to the higher elevations where PILA begins on that slope.) In general, larger specimens of *G. dormitor* 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.

While amphidromous behavior cannot be ruled out, Nordlie (1981) and Gilbert and Kelso (1971) consider that *G. dormitor* is catadromous, reproducing in the lower reaches of estuaries. Darnell (1962) thought that *G. dormitor* was normally catadromous, but under some circumstances capable of reproducing in fresh water, as did Greenfield and Thomerson (1997). Three authors have reported on putatively landlocked populations:

- McKaye (1977) and McKaye, et al. (1979) reported on a population in Lake Jiloa, an isolated crater lake in Nicaragua, where apparent reproductive behavior was observed. However, the suggestion has been made that the Lake Jiloa *Gobiomorus* are genetically distinct from diadromous *G. dormitor* (personal communication, P. Esselman).
- Bacheler (2002) and Bacheler, et al. (2004) reported a landlocked population in Carite Reservoir in Puerto Rico. However, no young-of-the-year *Gobiomorus* were taken, and it has been questioned whether the Carite population is actually reproducing in fresh water (Neal, et al. 2001 and 2004; Greathouse, et al. 2006b) *G. dormitor* has been extirpated from several rivers above dams in Puerto Rico (Kwak, et al. 2007), and does not occur in other Puerto Rican reservoirs, including some on the same river as Carite.
- Castro-Aguirre, et al. (In Press) mention the occurrence of *G. dormitor* in Miguel Aleman (El Temascal) Reservoir, Veracruz, Mexico, along with two other species of normally diadromous fish (*Pomadasys crocro* and *Dormitator maculatus*). We are not aware of any reason to doubt that these are truly landlocked populations.

On the basis of 1 to 3 occurrences at widely separated locations, the future establishment of viable fresh water populations of *G. dormitor* in the La Amistad region cannot be ruled out. But even if the Nicaraguan and/or Puerto Rican populations are ultimately verified as landlocked, naturally reproducing *G. dormitor*, the infrequency of the occurrence suggests that unknown but very special conditions in the habitat or the genetic makeup of the isolated population are involved. Statistically, the odds would appear to be against its persistence above any dams which might be constructed in the La Amistad watersheds.

OTHER FISHES OF CONCERN:

Emphasis here is on those species deemed most likely to be negatively impacted by the construction of dams in the watersheds draining the World Heritage Site – namely those diadromous or possibly diadromous species which are known from within the PILA boundaries on the Atlantic slope, where there is a greater mileage of larger streams within the park and also a greater knowledge of the fish fauna. There are 5 other categories of fish which merit mention:

- Potamodromous species:

Potamodromy was defined by Myers (1949) as referring to those obligate fresh water species which must undertake considerable migrations within fresh water in order to complete their life cycle. Such behavior is of course fully as susceptible to disruption by anthropogenic barriers such as dams as is any form of diadromy. Little mention was made of potamodromy in our previous report (McLarney and Mafla, 2007) because it dealt exclusively with the Changuinola/Teribe watershed, where there are no confirmed potamodromous species. However, the potamodromous machaca, *Brycon guatemalensis* is an important element in the fish assemblage of the Estrella River watershed in Costa Rica (McLarney and Mafla 2006b, 2008; McLarney, et al. 2009a, 2009b), where it is an important food resource, and its potamodromous congener *Brycon behreae* occurs in the Grande de Terraba watershed draining the Pacific slope of the World Heritage site, while *B. striatulus* is reported from the Chiriqui River (Briceño and Martinez, 1986). Rojas and Rodriguez (2008) found *B. behreae* to comprise over half of individual fish and fish biomass in limited sampling at 4 stations on the Grande de Terraba River.

It must be noted that *B. guatemalensis* inhabits the lakes of Nicaragua, from which it moves into tributaries to spawn, and has survived, and even thrived, in the impounded Lake Arenal in Costa Rica. But survival of *Brycon* spp. above or below dams in the La Amistad area should not be assumed.

Potamodromous behavior has also been observed for at least two other genera known from the World Heritage Site: *Astyanax aeneus* performs a massive annual upstream migration in Guanacaste (Lopez, 1978), though this may be triggered more by water levels than by reproductive behavior. The hepapterid catfish *Rhamdia nicaraguensis* (which may or may not occur in the La Amistad area; the taxonomy of *Rhamdia* is cloudy) was described by Alfaro (1935) as making long mass spawning migrations in the Meseta Central of Costa Rica. The point here is that, in the absence of studies of these fish in the La Amistad area, we cannot rule out potamodromous movements of *A. aeneus* and other characins, the two *Rhamdia* species known from PILA, or other species of the La Amistad area.

- Cryptic diadromous species:

Tables 2 and 3 list several diadromous species known from the watersheds of the World Heritage Site, but not reported from within PILA. In most cases, these are species of low altitude, low gradient streams which we would not expect to see above 100 m. However, allowances must be made for two small, cryptic flatfishes (pez hoja or lenguado) of the families Paralichthyidae (*Citharichthys spilopterus*) and Achiridae (*Trinectes paulistanus*), which spend most of their time hidden in sandy substrates, and are among the most difficult of fishes to detect or capture. 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.

Both species are known from the lower reaches of the Atlantic slope watersheds of PILA and, based on occurences from Costa Rica and the southeastern United States (Bussing, 1998; Gilbert and Kelso, 1971; Gunter and Hall, 1963; Swingle, 1971; Tucker, 1978) it would not be surprising to find occasional specimens of these species or their congeners within PILA in sandy reaches of the largest rivers, particularly the Changuinola.

On the Pacific slope, Rojas and Rodriguez (2008) found *Trinectes fonsecensis* at altitudes of up to 55 m. in the Grande de Terraba River, but did not report any Paralichthyid flatfishes. However, Alpirez (1985) reported *Citharichthys gilberti* from an altitude of 640 m. in the Pacuar River, tributary to the General River, (Grande de Terraba Watershed) upstream of the Diquis Dam site. *Achirus mazatlanus* and *Achirus lineatus* have been reported from the lower reaches of the Chiriqui River (Briceño and Martinez, 1986) and could be present in the Chiriqui Viejo.

- Euryhaline facultative wanderers:

Eugerres plumieri, first recorded from the inland waters of the World Heritage Site by the STRI inventory team (Lasso, et al. 2008b) may properly fall in this group, but is here described with the diadromous species. Other representatives of this group are principally large top carnivores normally found in the inshore oceans and estuaries, but which occasionally undertake long upstream voyages, presumably in the pursuit of prey. The Teribe River is known locally for the particular frequency of these occurrences, but euryhaline facultative wanderers may occur in any accessible stream. The most frequent and conspicuous fishes of this group are the snooks (*Centropomus* spp.), but we also have reliable reports of jacks (*Caranx* spp.) from the Teribe River near the PILA boundary.

While facultative wandering is clearly not essential to the maintenance of populations of these fishes in Talamanca and Bocas del Toro, it may contribute to the total size of their populations and the growth of individuals. Construction of dams on the rivers below the PILA boundary could result in the elimination of 2-5 species in these two genera from the faunal list for the World Heritage Site.

- "New" species:

Recent advances in taxonomic methods have led to the splitting of at least one species from the La Amistad watersheds. Since 2001, in our work in the Sixaola/Telire and Changuinola/Teribe watersheds, we have routinely assigned all individuals of the distinctive characid genus *Bryconamericus* to the widely distributed *B. scleroparius*. However we have become aware that Roman-Valencia (2000, 2002), has described a new and superficially similar species, *Bryconamericus gonzalezi* (written as *gonzalezoi* in Roman-Valencia, 2002) which appears to be endemic to eastern Atlantic Panama (Bocas del Toro Province), including the Changuinola/Teribe watershed, plus the Sixaola watershed of Costa Rica. As nearly as we can determine from published data, the ranges of the two species overlap, so that it is highly probable that some of our *"B. scleroparius"* from the lower Sixaola watershed are actually *B. gonzalezi*. In Panama, Roman-Valencia (2002) lists both species from "Rio Bongie", which we presume is the Bonyic (Bon) River, tributary to the Teribe.

Similar changes may eventually occur with some of the taxonomically challenging genera represented within the World Heritage Site, such as *Rivulus* and *Rhamdia*. In the event that such changes occur and contribute to the erection of species with limited distributions, the threat of loss of species viability through fragmentation, or disruption of possible potamodromous behavior by anthropogenic barriers such as dams would be more serious than hitherto supposed.

- Pacific slope diadromous species:

Occurrences on the Pacific slope of several of the diadromous genera, and one of the species found in the Atlantic slope La Amistad watersheds are mentioned above. While because the PILA Boundary does not extend much below an elevation of 900 m. on that slope there is less potential for Pacific diadromous species to enter the World Heritage site, their presence cannot be ruled out, and susceptibility to extirpation above dams but below the protected areas is a concern. This ichthyofauna is much less studied. Rojas and Rodriguez (2008) report 7 fish species from the Grande de Terraba for which diadromy is known or may be surmised. If we take the Chiriqui River as a surrogate for the Chiriqui Viejo (See discussion above) we count 10 such species from waters draining the Pacific slope of the World Heritage Site in Panama (Briceño and Martinez, 1986). Based on known behavior and altitudinal records from other watersheds, the diadromous species most likely to be found in the headwater streams of the Pacific slope of PILA include one species known from the Atlantic slope (*Agonostomus monticola*) and 4 congeners of Atlantic slope species (*Pomadasys bayanus, Pomadasys panamensis, Awaous transandeanus* and *Sicydium salvini*).

MACROINVERTEBRATES

BENTHOS:

The macroinvertebrate fauna of the La Amistad watersheds has been relatively little studied. The most complete collections are those made by the ANAI Stream Biomonitoring Program during the period 2000-2009 in the Estrella and Sixaola/Telire watersheds (McLarney and Mafla, 2006b, 2008 and McLarney, et al. 2009a, 2009b), using conventional benthic macroinvertebrate sampling methods, supplemented by a smaller number of collections made from the Changuinola/Teribe watershed by parataxonomists associated with the ANAI program. During this period, the ANAI team has identified 17 orders and 108 families in the two watersheds. Much more cursory investigations in the Changuinola/Teribe watershed yielded a count of 12 orders and 40 families. Most of these collections have been made outside PILA, at elevations of 0-200 m., so it is likely that some of the taxa collected do not occur within the World Heritage Site.

Other relevant work on the Atlantic slope includes collections made by the STRI team (Lasso, et al. 2008b) in the Changuinola River and some of its tributaries above the CHAN-75 dam site (13 orders, 55 families and 94 genera), and the earlier studies of Flowers (1991) who collected representatives of 75 insect taxa, many of them unidentified, belonging to 9 orders, in the lower Teribe watershed.

On the Pacific slope the most relevant work is that of Umana-Villalobos and Springer (2006) who monitored 14 sites in the Grande de Terraba watershed, at altitudes of 18-1320 m., of which 6 were located upstream of the Diquis Dam site. While we have not been able to obtain taxa counts from this study results for the BMWP-CR Biotic Index suggest taxa diversity comparable to that of the Estrella, Sixaola/Telire and Changuinola/Teribe watersheds of the Atlantic slope at high altitude sites near the World Heritage Site boundary, grading to significantly reduced diversity, with dominance by tolerant forms at the lowest altitude station sampled.

The best reference for the Panamanian Pacific slope is Flowers (1991). Although, based on earlier observations (Flowers, 1979, 1981), he documented virtual elimination of the benthic fauna of the upper Chiriqui River in the area flooded by the Fortuna Dam, streams tributary to the Fortuna Reservoir in the Fortuna Forest Reserve yielded 101 insect taxa, representing 9 orders.

In addition to making the first major benthic collections from the Teribe and Chiriqui watersheds, Flowers (1991) collected from two neighboring areas in western Panama (the Guabo River watershed in the Palo Seco Forest Reserve and a series of lowland streams draining to the Chiriqui Lagoon between Chiriqui Grande and Almirante). Perhaps the most interesting result of his work is the great variability among four contiguous watershed areas; "nearly 45% of the taxa were found in only one of the drainage areas." This suggests that the benthic fauna of the La Amistad area may be unusually vulnerable to extirpations from limited, local impacts.

Predictably, the great majority of all aquatic macroinvertebrate taxa which have been identified from the La Amistad area are insects, which do not exhibit diadromous behavior. This does not mean that this component of biodiversity in the World Heritage Site and its watersheds would not be affected by downstream dams. There are 3 areas of concern:

- Without a doubt, the composition of the benthic macroinvertebrate assemblage would be drastically altered and its diversity reduced within the confines of reservoir lakes created by dams in the La Amistad watersheds. While the total area affected would be relatively small, as Lasso, et al. (2008b) point out it is probable that the greatest diversity of benthic macroinvertebrates occurs at the middle elevations where most large dams are proposed. Thus the possibility exists of localized extirpations of narrowly endemic species.

- The structure of benthic macroinvertebrate assemblages in the river mainstems for varying distances downstream of dams would inevitably be altered. (See discussion of downstream effects of dams, below.)
- The least obvious, but possibly most important effect would be the alteration of benthic macroinvertebrate species composition resulting from the extirpation of diadromous shrimp and fish with which benthic fauna interact. Among the studies which have elucidated the effects of diadromous species of benthic grazers, both shrimp and fish, on benthic macroinvertebrates in Central America and the West Indies are those of Barbee (2002, 2004); Greathouse, et al. (2006); March, et al. (2001, 2002) and Pringle and Hamazaki (1997, 1998). The importance of such interactions in maintaining biodiversity is discussed below in the section on secondary effects of species extirpations.

It is particularly difficult to assess or predict the threat from dams to insect diversity due to two interrelated factors – the enormous taxonomic diversity of this group and our limited knowledge of that diversity in most tropical areas, including La Amistad. In the case of insects there is a very real risk of eliminating species before we know they exist.

The situation is somewhat less complex with respect to some of the major non insect groups of aquatic macroinvertebrates. Within this grouping the most relevant animals in terms of dam effects are the shrimps. With the possible exception of crab and snail species which may exist in the lower reaches of the major rivers draining PILA, the only macroinvertebrates in the La Amistad region which exhibit diadromous behavior are shrimps of the families Atyidae and Palaemonidae, discussed immediately below. As we will show in following sections, in addition to their importance as numerical contributors to biodiversity in the World Heritage site, the shrimps are especially important as “keystone” species which interact with other animals and with the physical environment in ways which are critical to maintaining ecological integrity in the upper reaches of the La Amistad watersheds.

SHRIMPS:

Overview:

If the threat to benthic macroinvertebates represented by proposed dams is little understood and difficult to quantify, in the case of the Atyid and Palaemonid shrimps (not normally considered as "benthic" despite the life habits of the Atyidae) it is clearly severe. Although Holthuis (1952) suggested that some species of *Macrobrachium* are capable of completing their life cycles entirely within fresh water, so far as is known all of the "fresh water" shrimp of Mesoamerica are diadromous (principally amphidromous, though the possibility of catadromy exists). As we will show in other sections of this report:

1. Experience in other areas suggests that populations of diadromous shrimps would be drastically reduced and probably extirpated above dams, including within the World Heritage Site.
2. The contribution of diadromous shrimps to biomass in tropical streams is underappreciated. As Bright (1982) pointed out, in some tropical streams shrimp may even account for the majority of secondary production. This is most often the case on islands or above natural vertical barriers, where fish are undiverse or even lacking.
3. Apart from their contribution to secondary production and to biodiversity at the species level, the diadromous shrimps play keystone roles in the fluvial ecosystems of the La Amistad area. Pringle (1996) and Pringle et al. (1999) compare their role to that of large terrestrial "megaherbivores" (e.g the bison of North America or the mixed herds of large grass-eating mammals of the African plains) defined by Owen-Smith (1992), pointing out that in headwater streams they are among the largest bodied animals and "functionally behave as 'megaomnivores' . . . with respect to their impact on single- and multicelled algal vegetation, organic and inorganic material, and associated nutrients." Their loss could be ecologically catastrophic.

Here we will attempt to recount what is known about the Atyid and Palaemonid shrimps of the La Amistad watersheds, beginning with the admission that they are little studied and poorly known. This is due in part to the fact that shrimp are the "orphans" of fluvial ecology, generally ignored in biomonitoring studies, whether these focus on fish or benthic macroinvertebrates.

The only study of which we are aware which attempted to inventory fresh water shrimp in streams of the Atlantic slope of the La Amistad area is the STRI inventory of the Changuinola River and its tributaries above the CHAN-75 dam site. There Lasso, et al. (2008b) found 5 species of diadromous shrimp. The great majority of their samples (97 % of individuals) were made up of 3 species, the Palaemonids *Macrobrachium heterochirus* and an unidentified *Macrobachium* sp., plus the Atyid *Atya scabra.* Two additional species, *Macrobrachium carcinus* (Palaemonidae) and *Potimirim* sp. (Atyidae), were present but extremely rare.

In the case of the ANAI stream biomonitoring program, we have routinely recorded the presence or absence of Atyid and Palaemonid shrimps in our fish and macroinvertebrate samples (McLarney and Mafla, 2006b; 2008, McLarney, et al. 2009a, 2009b), as have the Naso and Ngobe parataxonomists who have carried out visual surveys in the Changuinola/Teribe watershed in and downstream of the World Heritage Site (Mafla, et al. 2005; McLarney and Mafla, 2006b, 2008). In the great majority of cases, both groups have recorded the presence, and often high abundance, of members of both families. However, only in 2009 did we begin to pay attention to the shrimp in our samples at the levels of genus and species, leading to publication of a laminated field guide to the diadromous shrimps of Talamanca (Asociación ANAI, in prep.).

In 2009, we made selective collections of large adult shrimp from 12 of a total 29 fish sampling sites (2 in the Estrella watershed and 9 in the Sixaola/Telire, plus 1 site in the Hone Creek watershed, which does not drain PILA). These individuals were identified to species with the assistance of Yorlandy Gutierrez of the U. of Costa Rica. Based on this survey, we identify 4 species of diadromous shrimp (*Atya scabra, Macrobrachium carcinus, Macrobrachium heterochirus* and *Macrobrachium olfersi*) as definitely inhabiting the watersheds of the Atlantic slope watersheds draining the World Heritage site. According to Gutierrez (personal communication), the following additional species should be present: *Macrobrachium acanthurus* (largely limited to sites near the coast, where we did not collect) and two small Atyids (*Micratya poeyi* and *Potimirim glabra*) which were probably overlooked in our preliminary samples.

Until recently there have been no studies of diadromous shrimps in streams draining the Pacific slope of La Amistad. However, between 2006 and 2008, ICE commissioned a study of these animals in the Rio Grande de Terraba watershed, with samples taken from sea level up to an altitude of 1075 m. (Lara, 2009). This study revealed the presence of 10 species of Palaemonidae and 4 species of Atyidae. Of these, 4 Palaemonids and 2 Atyids were found at altitudes near or above the level of the proposed Diquis dam on the General River, tributary to the Grande de Terraba. The highest recorded shrimp occurrence was for *Macrobrachium digueti*, found at up to 765 m.

Following are brief comments on native Atyid and Palaemonid shrimp species which occur or may occur in the watersheds draining the Atlantic and Pacific slopes of the World Heritage Site, based principally on the STRI, ANAI and ICE surveys plus the work of Cedeño-Obregon (1986), who reviewed specimens in the National Museum of Costa Rica and provided the following list of species of diadromous shrimp from Costa Rica. It should be noted that, for unknown reasons, Cedeño-Obregon concentrated on the larger shrimps, and makes no mention of the 3 genera of small Atyids (*Jonga, Micratya* and *Potimirim*):

- Atlantic slope only: *Macrobrachium acanthurus, Macrobrachium heterochirus, Macrobrachium olfersi, Macrobrachium carcinus* and *Macrobrachium crenulatum* (Palaemonids)
- Both slopes: *Atya scabra, Atya crassa* and *Atya innocous* (Atyids)
- Pacific slope only: *Palaemon gracilis*, *Macrobrachium panamense, Macrobrachium tenellum, Macrobrachium digueti, Macrobrachium occidentale, Macrobrachium hancocki* and *Macrobrachium americanum* (Palaemonids)

Supplementary sources include a variety of publications and records gleaned from the Internet (cited under the individual species accounts) plus Page et al. (2008), who offered a list of Atyid species which "should" be present on the Atlantic slope of Central America (not necessarily Costa Rica or Panama), and which included 3 species not already mentioned - *Potimirim mexicana, Potimirim potimirim* and *Jonga serrei*, the latter listed as "uncommon".

For each species we discuss, within limitations posed by available information, the probability that it occurs within the World Heritage Site. We consider that any Atlantic slope species which has been documented at elevations of > 100 m. (which includes all the sites monitored by the STRI team) has a good chance of being found in PILA. We also include notes on habitat preference, reasoning that a preference for high gradient, rocky streams makes it more likely that a diadromous species will penetrate to higher elevations.

ATYIDAE – ATLANTIC SLOPE:

Atya inocous (basket shrimp) has been reported from one low elevation site in the La Amistad watersheds - the Sixaola River at California, within the San San/Pondsak Ramsar Wetland (Panama) (Global Biodiversity Information Facility, 2009). *A. inocous* is a generalist which inhabits swift, rocky streams as well as low gradient coastal rivers (Felgenhauer and Abele, 1983; Fievet, 1999; Fryer, 1977). It has been reported at elevations of up to 800 m. in Guadeloupe (Fievet, 1999; Fievet, et al. 2001a; Fryer, 1977) and at over 1,000 m. in the Bayano River, Panama before closure of the Bayano Dam (Felgenhauer and Abele, 1983). It is one of the diadromous species reported as strongly affected by dams in Puerto Rico (Holmquist, et al. 1998).

Atya scabra (camacuto shrimp or burra) is probably the most widely distributed Atyid, inhabiting both the Atlantic and Pacific Oceans. In fresh water, it is characteristic of the fastest rapids in rocky streams and is found to the very headwaters of small streams (Darnell, 1956; Fryer, 1977; Fievet, et al. 2001b; Sanchez Palacios, et al. 2007). It is known to altitudes of at least 150 m. in Guadeloupe (Fievet, 1999; Fievet, et al. 2001a) and 800 m. in the Caribbean drainages of Colombia (Escobar, 1979). In the La Amistad region, *A. scabra* is documented from above the CHAN-75 dam site in Panama (Lasso, et al. 2008b), from within the World Heritage Site in the Sixaola/Telire watershed of both countries at altitudes of up to 182 m. and in at least some swift streams of the Estrella watershed (ANAI, unpublished data).

Jonga serrei: While Page, et al. (2008) indicated that *J. serrei* should be present on the Atlantic coast of Central America, we have not been able to locate any records. Fievet (1999) found it to be a species of sluggish waters in Guadeloupe, where it does not normally ascend to beyond 20 m. altitude. Thus, although it may be present in the Atlantic drainages of the La Amistad area, it likely would not be directly affected by dam closures.

Micratya poeyi (burrita), described by Fryer (1977) as “a miniature *Atya”,* occurs in Talamanca, according to Gutierrez (personal communication) but so far we have only found it near the coast in the Hone Creek watershed, which does not drain La Amistad. It is characteristic of small, fast streams (Fievet, 1999; Fryer, 1977) and has been reported at altitudes of up to 250 m. in Guadeloupe (Fievet, 1999; Fievet, et al. 2001a). Both Fievet (1999, 2000) in Guadeloupe and Holmquist, et al. (1998) in Puerto Rico report *M. poeyi* as a species impacted by damming.

Potimirim glabra, Potimirim mexicana, and *Potimirim potimirim*: The three species of *Potimirim* possibly found in the Atlantic slope La Amistad watersheds are discussed together because it is more frequent to encounter “*Potimirim* sp.” in the literature than references to particular species. So far the only documentation for a *Potimirim* sp. in the La Amistad watersheds is that of Lasso, et al. (2008b) for several individuals of an unidentified species from the Changuinola watershed above the CHAN-75 dam site. *P. glabra* is reported by Fievet (1999) to prefer medium to fast flowing water over rocky substrates in Guadeloupe, and Lasso, et al. (2008b) found *Potimirim* sp. only in the main channel of the Changuinola River, but Abele and Blum (1977) considered it a habitat generalist, found in both flowing and stagnant waters in the Perlas archipelago of Panama (Pacific Ocean). Fievet (1999) and Fievet, et al. (2001a) found *P. glabra* at altitudes of up to 250 m. and *P. potimirim* at up to 100 m. in Guadeloupe. Holmquist, et al. (1998) found *P. glabra* and *P. mexicana* to be strongly impacted by dams in Puerto Rico.

Cedeño Obregon (1986) reported one additional Atyid species, *Atya crassa,* from the Atlantic slope of Costa Rica, but we have been unable to find any records, in or out of the La Amistad drainages.

PALAEMONIDAE – ATLANTIC SLOPE:

Macrobrachium acanthurus (river shrimp or cinnamon river shrimp) occurs in Talamanca, according to Gutierrez (personal communication) and has been documented by the ANAI team in the Hone Creek watershed, but so far not from the La Amistad watersheds. This may be due to its being apparently restricted to the lower reaches of streams, near the sea. Fievet (1999) did not report it above 5 m. altitude. Gamba (1982) found *M. acanthurus* at considerable distances from the sea in Venezuela, but never at altitudes above 20 m. Similarly, in Nuevo Leon, Mexico Almaraz and Campos (1996) found this species at distances of up to 360 km. above the coast, but not at high altitudes. *M. acanthurus* has been reported from Bocas del Toro Province (San Pedro River) (Global Biodiversity Information Facility, 2009), but not from the La Amistad watersheds.

Macrobrachium carcinus (big claw river shrimp or langostino) is the largest fresh water shrimp of the Central American Caribbean and is frequently consumed by natives of the region. It has been documented for all 3 of the principal watersheds draining the Atlantic slope of the World Heritage Site (Estrella, Sixaola/Telire and Changuinola/Teribe), including within PILA in the Sixaola/Telire watershed of both Costa Rica and Panama (ANAI, unpublished data) at altitudes of up to 182 m., and above the CHAN-75 dam site in Panama (Lasso, et al. 2008b). It has been documented to altitudes above 600 m. in Guadeloupe (Fievet, 1999; Fievet, et al. 2001a). Bowles, et al. (2000) have documented *M. carcinus* at distances of up to 320 km. from the sea in Texas, and consider that it has considerable ability to climb the dams of “small top-release reservoirs, particularly those that are cracked and leaking,” but it cannot successfully negotiate bottom-release reservoirs of the type normally built today.

Macrobrachium crenulatum has been documented from 3 sites in drainages located east of the Changuinola River in Bocas del Toro Province (Global Biodiversity Information Facility, 2009), but has so far not been reported from Costa Rica or from the La Amistad drainages of Panama. Fievet (1999) reports it from altitudes of up to 200 m. in Guadeloupe, where it inhabits pools and shallow, rocky areas.

Macrobrachium heterochirus (banded shrimp or cascade river prawn) has been reported from the Sixaola/Telire watershed in Costa Rica and Panama, including sites within the World Heritage site (ANAI, unpublished data) at up to 182 m., and from the Changuinola watershed above the CHAN-75 dam site (Lasso, et al. 2008b), where it was the most abundant shrimp in the STRI team’s samples. It had previously been reported from 3 sites in the Changuinola/Teribe watershed below the CHAN-75 dam site. It seems to prefer high gradients, with the upper limit on its distribution imposed by its inability to withstand streams which dry up during drought periods (Hunte, 1978). It has been reported to altitudes of 450 m. in Guadeloupe (Fievet, 1999), 470 m. in Venezuela (Abele and Kim, 1989; Gamba, 1982), and 535 m. in Vera Cruz, Mexico (Mejia-Ortiz, et al. 2001). AES and MWH (2009) cite its presence in Gatun

Lake, Panama as evidence of its adaptability to adapt to impounded conditions; however as part of the Panama Canal system Gatun Lake is very porous to marine migrants, and this assertion should be discounted.

Macrobrachium olfersi (popeye shrimp or bristled river shrimp) has been reported from the mainstem of the Changuinola River and 3 of its tributaries below the CHAN-75 dam site (Global Biodiversity Information Facility, 2009), but so far not from above that point, near the PILA boundary. However, the ANAI biomonitoring team (unpublished data) has found it in rocky streams of both the Estrella watershed of Costa Rica and the binational Sixaola/Telire watershed to elevations of nearly 100 m. While we have not yet documented it from the World Heritage site, we do have records from just a few km. below the PILA boundary in the Tscui River (Costa Rica) and the Dacle River (Panama). Gamba (1982) reported *M. olfersi* at altitudes of up to 140 m. in Venezuela.

Numerous individuals of an unidentified *Macrobrachium* sp. reported from the Changuinola watershed above the CHAN-75 dam site (Lasso, et al. 2008b) probably belong to one of the species discussed above. (Identification of juvenile and small adult Palaemonid shrimp can be difficult to impossible.)

Based on the available information we consider that on the Atlantic slope within the World Heritage Site the Palaemonids *Macrobrachium carcinus* and *Macrobrachium heterochirus*, possibly plus *Macrobrachium crenulatum* and *Macrobrachium olfersi* are threatened by dam construction. The comparable list for the Atyids includes *Atya inocous, Atya scabra, Micratya poeyi* and at least 2 of the 3 *Potimirim* spp.

ATYIDAE – PACIFIC SLOPE:

Lara (2009) lists the following species for the Grande de Terraba watershed, with the maximum altitude to which each has been found:

Atya inocous – 65 m.
Atya margaritacea – 465 m.
Atya scabra – 65 m.
Potimirim glabra – 135 m.

Lara found all of the Atyid species to be associated to some degree with rocky substrates, and found none to be abundant. Among the Atyids, he distinguished *A. inocous* as preferring high quality water. (We note that Hobbs and Hart, 1982, cited by Lara, 2009, consider *A. margaritacea* to be a synonym of *A. scabra.* However, we follow Lara in treating the two species as distinct.) Page, et al. (2008) also lists *Atya crassa* as present on the Central American Pacific coast, but we have been unable to find any reference to this species in the La Amistad area.

PALAEMONIDAE – PACIFIC SLOPE:

Lara (2009) lists the following native *Macrobrachium* species from the Grande de Terraba watershed, with the maximum altitude to which each has been found:

Macrobrachium americanum – 550 m.
Macrobrachium digueti – 765 m.

Macrobrachium hancocki – 110 m.
Macrobrachium occidentale – 625 m.
Macrobrachium panamense – 125 m.
Macrobrachium rathbunae – 85 m.
Macrobrachium tenellum – 135 m.

Macrobrachium americanum (Cauque river prawn) and *Macrobrachium hancocki* have each been documented from 2 sites in the Chiriqui Viejo watershed, which drains the Panamanian portion of the Pacific slope of the World Heritage site (Global Biodiversity Information Facility, 2009). Lara (2009) associated *M. rathbunae* and *M. tenellum* with muddy and sandy substrates, *M. digueti* with roots and submerged vegetation and the other *Macrobrachium* species with rocky substrates. He associated *M. hancocki* with good quality water.

The list is completed by the native *Palaemon gracilis* and *Palaemon hancocki*, plus *Macrobrachium rosenbergi,* native to the Indo-Pacific, and introduced to Costa Rica for aquaculture purposes (Howell, 1985). All three of these species seem to be confined to the coast (Lara, 2009); if this is the case, they would not be directly affected by dam closures.

SUMMARY:

Probable effects within the World Heritage site of dams on diadromous shrimps are likely to be more severe on the Atlantic slope, due to geographic reasons dictating a probable higher diversity of shrimp species within PILA on the Atlantic slope. (Here we will make the convenient, but not necessarily correct assumption that no shrimp species in addition to those discussed here will be discovered in the La Amistad watersheds.)

The probable number of diadromous shrimp species in the La Amistad Atlantic slope watersheds is 12, including 7 Atyids and 5 Palaemonids, but could be as few as 9, pending secure documentation of *Jonga serrei* and proper identification of up to 3 *Potimirim* spp. Of these, 4 have been securely documented within the World Heritage site, and another 4 are highly probable based on documentation from near the PILA boundary and known altitudinal distribution from other locales. Again pending identification of *Potimirim* spp., the total number of diadromous shrimp species inhabiting the Atlantic slope sector of the World Heritage Site, and thus facing at least drastic population decline, and probable extirpations, within and below the PILA boundary is 8 to 10. (Two species, *Jonga serrei* and *Macrobrachium acanthurus* are likely confined to low altitudes and would thus not be directly affected by dam closures.)

We discuss 14 native species of diadromous shrimps (4 Atyids and 10 Palaemonids) documented from the Grande de Terraba watershed which drains the Pacific slope of PILA in Costa Rica. Only 2 of these are documented from the watersheds draining PILA on the Pacific slope of Panama, but most or all may be present there. Of the 14 Pacific slope species, 7 (*M. americanum, M. digueti, M. occidentale, M. panamense, M. tenellum, A. margaritacea* and *P. glabra*) are documented from above the Diquis dam site on the General River, where they would probably face local extirpation if the dam is constructed. All of these species except *M. panamense* and *M. tenellum* were also documented for the Coto Brus watershed (Lara, 2009).

SECONDARY EFFECTS OF SPECIES EXTIRPATIONS OR DRASTIC POPULATION DECLINES ABOVE DAMS

The most obvious biological effect of damming the rivers of the La Amistad area downstream of the World Heritage Site boundaries, and the one which most clearly contravenes the conservation purposes for which the two La Amistad National Parks were established, would be simple numerical loss of biodiversity. As we have shown above, on the Atlantic slope alone at least 8 species of fish and 8 species of diadromous shrimps are severely threatened with multiple extirpation events in the Changuinola, Telire, Estrella and Banano watersheds. On the Pacific slope an unknown number of fish and shrimp species were presumably extirpated from the Chiriqui Viejo (and possibly Chiriqui) watershed by dam construction undertaken before scientists, conservationists and local residents began to question the propriety of damming rivers downstream of a World Heritage Site. A similar number of species are threatened in the Grande de Terraba watershed below, and possibly within the La Amistad National Park. While taken by itself the loss of these creatures, and the high proportion of total animal biomass they represent in a significant portion (potentially the great majority) of the World Heritage site would be catastrophic, it is fundamental to the science of ecology that "everything is connected" – which in this case implies that the consequences of multiple species extirpations cannot be considered in isolation. Although the nature and extent of these effects cannot be predicted with precision, and there are no relevant studies from the La Amistad watersheds themselves, we have sufficient information from other areas to predict the general outlines of expected, and even more drastic, change with confidence.

Predator – prey relationships:

With regard to top carnivores (principally fishes, including *Anguilla rostrata, Pomadasys crocro,* and *Gobiomorus dormitor*) the immediate, "top-down" effects of extirpations are easy to predict – proliferation of prey species, notably those smaller fishes which presently (with the exception of the *Bryconamericus* characins) appear to make up a small portion of fish numbers and biomass in PILA. Removal of *A. rostrata, P. crocro* and *G. dormitor* from the system might be partially compensated in this respect were it to facilitate increased piscivory by the few relatively large non-diadromous fishes present in PILA (principally the *Rhamdia* catfishes, but possibly also including *Astatheros bussingi*). Even absent this compensatory effect, the overall impact of predator removal in PILA would probably be minor compared to well known phenomena for other parts of the world (for example, the selective harvest of predatory fishes for human use, for the simple reason that the abundance of top carnivores in streams of the La Amistad area located at altitudes of over 100 m. is relatively low).

Frugivores:

Before moving on to a consideration of omnivores and herbivores, one special case merits consideration:

The potamodromous machaca (*Brycon guatemalensis*) is known on the Atlantic slope of the La Amistad region only from those watersheds north of Cahuita National Park (in the present context, Estrella, Banano and Matina/Chirripo). Its lesser-known congener *Brycon behreae* inhabits the Pacific slope watersheds of La Amistad. Both species, but especially *B. guatemalensis*, are known to be frugivores as adults (Bussing, 1998). The research of Horn (1977) and Banack, et al. (2002) in the Sarapiqui watershed of northern Atlantic Costa Rica showed that *B. guatemalensis* played a critical role in the dispersal of tree seeds, particularly *Ficus* figs, upstream and downstream of their point of origin. Horn calculated "an estimate of more than half a billion fig seeds dispersed per year by the machaca population along a 6 km. stretch of the Rio Puerto Viejo." Similar results were reported by Rey, et al. (2009) for *Brycon hilarii,* which was found to be responsible for 50% of seed dispersal for 8 tree species along a river in western Brazil. Thus the possible extirpation of *B. guatemalensis* above dams in the Estrella watershed could result in alterations to terrestrial forest ecosystems in a little studied portion of the World Heritage Site.

Omnivores, herbivores and detritivores:

General considerations:

Because in the tropics fish and shrimps are typically the main consumers of both allocthonous (leaf and fruit drop) and autocthonous (algae) vegetable matter, a role generally played by insects in temperate ecosystems, the most far-reaching effects of extirpation or drastic reduction in populations of diadromous animals in the World Heritage site would be those resulting from loss of members of the often overlapping categiores of omnivores, herbivores and detritivores, including *Agonostomus monticola, Joturus pichardi, Sicydium* spp. and possibly *Gobiesox nudus* among the fishes, plus all of the shrimps. (All of the Atyids are clearly detritivores; while many of the Palaemonids function opportunistically as carnivores, they are best considered as omnivores.)

Were this suite of fish and shrimp to be extirpated above dams in the La Amistad area, the most immediately perceived effect would be the absence of the Mugilid fishes *A. monticola* and *J. pichardi*, both large, easily observed species highly valued locally as food fish. However, the loss of the *Sicydium* gobies and the shrimps would be more far-reaching, for the simple reason that these animals inhabit high altitude streams above natural barriers (waterfalls) where even the Mugilids, prodigious leapers naturally adapted to life in torrential streams, have not penetrated. Thus, in terms of watershed area occupied, they are by far the dominant relatively large bodied aquatic animals in the La Amistad region.

Below we will describe the results of investigations which elucidate the functional roles of herbivorous and detritivorous fish and shrimps in stream ecosystems similar to those of the La Amistad area, and outline the probable effects of elimination of such animals from portions of the La Amistad watershed, especially within the World Heritage site. Part of our general thesis was stated succinctly by Greathouse and Compton (2007): "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." To which we would add that research cited here (Barbee, 2002; Greathouse, et al. 2006a; March, et al. 2001, 2002 and Pringle and Hamazaki, 1997, 1998) has only begun to scratch the surface of effects on associated aquatic and terrestrial fauna.

Effects in high altitude streams:

The discussion which follows will focus on effects which, in the La Amistad area, would likely be most profound in areas above natural barriers (waterfalls) closed to migration by diadromous animals other than *Sicydium* and shrimps, which can climb vertical faces. On the Atlantic slope, such barriers may be found at elevations from below the lowest altitudes in the World Heritage site (ca. 90 m.) to over 1500 m. in some watersheds. On the Pacific slope much of the World Heritage Site in Costa Rica lies above such natural barriers; the lowest altitudes along the La Amistad National Park boundary are at around 900 m. Discussion of natural barriers related to the corresponding area in Panama is moot, since anthropogenic barriers have likely eliminated any diadromous fauna there.

While the presence of diadromous shrimp and fish is well documented for the Grande de Terraba watershed below 900 m, including in three indigenous reserves, the question might be raised as to whether any diadromous animals ascend to within the World Heritage Site on the Costa Rican Pacific slope. The fact is that we don't know, and published literature, supplemented by our own observations, yields fragmentary knowledge:

- The maximum altitude so far reported for a diadromous shrimp on the Pacific slope of the La Amistad area is 765 m., for the Palaemonid *Macrobrachium digueti* in the Grande de Terraba watershed. (Lara, 2009). However, Lara (personal communication) considers that shrimps may eventually be found at higher elevations.
- *Atya inocous,* known from both slopes of the La Amistad area, was recorded above 1,000 m. in the Rio Bayano, Panama prior to closure of the Bayano Dam (Felgenhauer and Abele, 1983).
- Parataxonomists associated with ANAI report observing *Sicydium* and other diadromous fishes in abundance at elevations of around 400-500 m. in the Rio Uren watershed of Costa Rica (personal communication, M. Bonilla). Bussing (1998) reports *Sicydium altum* from altitudes to at least 1,180 m. in other parts of Costa Rica.
- The *Awaous* gobies do not appear to have climbing abilities comparable to *Sicydium,* and *A. banana* of the Atlantic slope of the La Amistad area and *A. transandeanus* of the Pacific slope are reported only up to 300 and 120 m. respectively (Bussing, 1998). However, *A. staminius* is reported from altitudes of > 500 m. in Hawaii (Ego, 1956). Ego's record is from a site only 13 km. from the ocean, suggesting that *A. staminium* is capable of moving upstream over extremely high gradients, with probable vertical barriers. Thus we reserve the possibility that *A. transandeanus* may eventually be found in Pacific slope waters of the World Heritage Site.
- Bussing (1998) reports *Agonostomus monticola* from altitudes of up to 650 m. in other parts of Costa Rica.
- The highest reported altitude for a fish in Costa Rica pertains to a non-diadromous species, *Rivulus isthmensis,* which has been reported from 1,500 m. in other parts of the country (Bussing, 1998). (Since this species, found throughout the Atlantic slope watersheds of La Amistad, with various congeners on the Pacific slope, is also found at sea level, and is known to disperse through river systems during storm events, fragmentation of its range by dams may be a threat.)

The point of citing all these figures is to emphasize that we cannot predict the maximum altitudinal occurrence of any of those species capable of surmounting vertical barriers. For obvious and understandable reasons, few biological inventories have been carried out in the high altitude fluvial systems of the La Amistad World Heritage site and surrounding areas. Until data are available from high altitude sites above barriers, it is prudent to think in terms of access in assessing dam threats on either slope; any large dam on a river mainstem (and many small dams) will preclude access by diadromous animals to the entire upstream watershed.

While diadromous and non-diadromous omnivores, herbivores and detritivores undoubtedly have important roles to play in the function of fluvial ecosystems at all altitudes, they play keystone roles in the fish-poor systems of swift, high altitude streams. The role of Atyid shrimps is particularly important at such sites, where predatory fish are generally absent and their other potentially significant aquatic predators, the omnivorous Palaemonid shrimps, occur in reduced numbers. While the citations which follow will draw on a variety of taxa across a range of altitudes the emphasis, in terms of the work cited, but also in terms of its implications for the La Amistad World Heritage site, will be on high altitudes and those animals (shrimps and *Sicydium* gobies) which are clearly capable of surmounting natural vertical barriers.

In very general terms, the effects of benthic omnivores, herbivores and detritivores in streams can be grouped in 5 categories. Such animals may act on 1) sediment dynamics, 2) breakdown of allocthonous vegetable matter, 3) water and substrate chemistry, 4) algal biomass and diversity and 5) structure of the benthic macroinvertebrate assemblage. Each of these categories will be discussed separately below. Since none of the relevant research has been done in the La Amistad watersheds, and very little in Mesoamerica, most of the phenomena reported will be from other areas, in particular Puerto Rico, where stream fish and shrimp assemblages are very similar with the notable exception that all native "fresh water" fish in Puerto Rico are diadromous. Research in temperate zone streams has sometimes contradicted most of the conclusions presented here (Feminella and Hawkins, 1995; Steinman, 1996). However, it is widely held that the dynamics of tropical streams, which tend to be dominated by omnivores, are very different in regard to processing of allochthonous organic and inorganic materials. Therefore, we will discuss only work carried out in the tropics.

1. Sediment dynamics: Among the earliest work showing a causal relation between benthic animals and sediment dynamics was that of Power (1984, 1990), who showed that the herbivorous loricariid catfish *Ancistrus spinosus* intentionally cleared sediment from portions of stream substrates in western Panama. Flecker (1996) found "highly significant increases" in accumulation of sediment in streams of the Venezuelan Andean foothills when the herbivorous characoid fish *Prochilodus mariae* was excluded. Barbee (2002) working on a small river in west-central Costa Rica, found that density of *Sicydium salvini* was "negatively correlated with silt in both riffles and pools". She acknowledged that this could simply reflect avoidance of sedimented habitat, but hypothesized that it demonstrated that "grazers" reduce silt levels. Greathouse (personal communication, cited in Greathouse and Pringle, 2005) noted that in a stream in Puerto Rico, below a waterfall where predatory fishes reduced populations of *Sicydium plumieri* "thick layers of fines occur on rocks in pools" whereas "rocks in pools above the waterfall are clean".

The first published work suggesting that shrimps also affect sediment dynamics was that of Pringle and her associates in Puerto Rico. Pringle, et al. (1992) noted that "When tiles incubated in shrimp exclosures for 2 wks were place outside of cages, atyid shrimp removed 100% of the sediment cover within a 30 min. observation period." Subsequently, Pringle and Blake (1994) found that "Shrimp exclusion experiments experienced slow and steady accumulation of sediments under base flow conditions and a large stepwise increase in sediment weight following a storm. No measurable sediment accrued in the presence of natural densities of shrimp under base flow conditions. Shrimp rapidly removed sediments that accrued during the storm". Other researchers in Puerto Rico (Crowl, et al. 2001; Greathouse and Pringle, 2005; March, et al. 2002; and Pringle, 2005) verified their experimental conclusions.

Subsequently, Greathouse, et al. (2006a, 2006c) determined that in the same Puerto Rican streams, under natural conditions sediment deposition was greater in pools above dams where diadromous animals had been extirpated and that while “at sites without large dams, floods can result in temporary deposition of fine materials” that shrimp were able “to remove these materials in less than a day after return to base flow” whereas natural processes in the absence of shrimp took much longer.

However, in a stream located on an island off southern Brazil, Silveira and Moulton (2000), Silveira (2002) and Moulton, et al. (2004) concluded that “Shrimps (*Macrobrachium olfersi* and *Potimirim glabra*) by themselves apparently do not remove . . . sediments in our system.” Moulton, et al. (2004) attributed this surprising result to their selection of shallow riffle habitats for their experiments, whereas previous experimental studies had been carried out in deeper water, mostly pools, where natural sediment accumulation in the absence of animal life would be greater. Without suggesting any causative mechanism, we would also note that while the Brazilian studies were carried out at near sea level, all of the other studies cited here (with the exception of the work of Barbee, 2002, located at 50 m. altitude) were carried out at relatively high elevations, more nearly corresponding to conditions in the portions of the La Amistad watersheds potentially impacted by dams.

Benthic fishes and Palaemonid shrimps both disturb sediments, intentionally or otherwise, and so affect rates of sediment deposition. However, Atyid shrimps are adapted to burrow within gravelly substrates, and are thus presumably much more effective bioturbators (Pringle, et al. 1992), whose burrowing activity can result not only in resuspending surface sediments, but in flushing fine materials from the interstices of the streambed. Extirpation of diadromous fish and shrimps from the upper reaches of streams in the La Amistad area would effectively remove most of the bioturbators, resulting in greater retention of accumulated sediments at high altitudes, with unpredictable but significant effects on sedimentation patterns, channel dynamics and biotic interactions both within and downstream of the World Heritage Site.

2. <u>Breakdown of allochthonous vegetable matter</u>: This is the area where the real and supposed differences between the dynamics of tropical streams and their more thoroughly studied temperate counterparts are most often cited. Bass (2003a), citing Bass (2003b), Dudgeon and Wu (1999), Ramirez and Pringle (1998), and Turner (2003), summarized the prevalent view “that the breakdown of leaf litter, facilitated by shredders in temperate streams, must be brought about largely by microbes in tropical streams”. Irons et al. (1994) rationalized this on the basis that “the constant high temperatures of the tropics encouraged leaf litter decay through increased and continuous microbial activity”. This view is supported by the relative scarcity of benthic insects, and the typically smaller size of individual insects, in tropical streams. However, it perhaps fails to take into account the condition of high altitude streams, such as many of those in the La Amistad World Heritage Site, where large shredders (Atyid shrimps) may be among the dominant benthic life forms.

Crowl, et al. (2001) acknowledged the paucity of studies of “the role and importance of detrital processing in tropical latitudes”, citing Dudgeon (1982) and Gessner and Schwoerbel (1989) in support of the notion that “microbial processing is rapid in tropical streams due to high ambient temperatures, potentially resulting in a less important role for macroinvertebrates such as insects and shrimp”. However, they also prefaced their own work with the shrimps *Atya lanipes* and *Xiphocharis elongata* in a Puerto Rican stream by noting the lack of experimental data on shredders in tropical streams.

The experimental work of Crowl, et al. (2001) and March, et al. (2001) in Puerto Rico, established the importance of shrimps, both shredders (Atyidae) and scraper/filterers (Xiphocarididae and Palaemonidae) in accelerating leaf decay rates in high altitude tropical streams. Rosemond, et al. (1998), working at lower elevations in northern Atlantic Costa Rica, expanded the list of macroconsumers to include fish, noting that "in tropical streams, macroconsumers may plan an analogous role to insect shredders in many temperate streams by accelerating decay rates of leaves". Crowl, et al. (2001), Greathouse and Pringle (2005), and Pringle, et al. (1999) concurred that shrimps affect leaf decomposition rates.

Greathouse and Pringle (2005) attempted to synthesize viewpoints like those just cited by applying the River Continuum Concept (Vannote, et al. 1980) (RCC) to Puerto Rican streams. They noted that the RCC predicts that "the proportion of total macroinvertebrate biomass attributable to shredders decreases downstream because of a decline in availability of coarse particulate organic matter", and found this prediction applicable to their streams.

If we consider these observations in the context of the La Amistad area, they turn out to be largely applicable. At lower elevations, coarse particulate matter may be relatively scarce and abundance of shredders is low to moderate. The scarcity of coarse particulate matter appears to be to a considerable degree due to the abundance of shrimp, particularly shredders (Atyidae) above natural barriers where shrimp predators are largely absent. Thus we can predict that the extirpation of diadromous shrimps from the streams of the La Amistad area would have drastic ecosystem effects through altering the dynamics of processing of forest-derived materials at all elevations, both in and downstream of the World Heritage Site.

3. Water and substrate chemistry: Most of the chemistry determinations associated with the studies reviewed here have been peripheral, or have had to do with chlorophyll-a, discussion of which properly belongs in the next section on algae. However, a few studies have looked at carbon and nitrogen chemistry in situations with and without shrimp.

Crowl, et al. (2001) determined that in a Puerto Rican stream dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) increased significantly in pools where shrimp (*Atya lanipes* and *Xiphocaris elongata*) were present, as compared to pools where shrimp were artificially excluded. DOC concentrations in pools with shrimp exceeded those in pools without shrimp by factors of as much as 1.7. Similarly, Greathouse, et al. (2006c) reported significant reductions in carbon and nitrogen in Puerto Rican stream substrates with Atyid, Palaemonid and Xiphocarid shrimps present, as compared to sites where shrimp were excluded.

Pringle, et al. (1999), also in Puerto Rico, showed that "Ten-fold more organic material and five-fold more nitrogen accrued in shrimp (Atyidae and Xiphocarididae) exclosures than in controls. By reducing the quantity of fine particulate organic material and associated nitrogen in benthic environments, omnivorous shrimps potentially affect the supply of this important resource to other trophic levels." However, Greathouse, et al. (2006a) were unable to demonstrate a pattern for the C: N ratio in pools in dammed vs. undammed streams.

Lack of convincing C: N data notwithstanding, these results together show that Atyid and Xiphocarid shrimps reduce concentrations of organic carbon and nitrogen in small areas (exclosure experiments), thus making it available over a wider area (pool experiments). They may thus be expected to have a positive effect on the productivity of upland tropical streams, such as those found in the La Amistad World Heritage Site.

4. Algal biomass and diversity: Both shrimps and fishes have been widely shown to affect algal assemblages in diverse tropical streams. Moulton, et al. (2004), Silveira and Moulton (2002) and Silveira (2000) showed that chlorophyll-a decreased with shrimp (*Macrobrachium olfersi* and *Potamirim glabra*) inclusion in their experiments on a small stream situated on an island off southern Brazil, even though at this site the shrimp-sediment relationship confounded expectations. Souza (2000) working at an upstream site on the same stream, showed that *P. glabra* had strong negative effects on periphyton growth.

Multiple experiments in Puerto Rican streams show shrimp effects on algal biomass and species composition (Crowl, et al. 2001, Greathouse and Pringle, 2005; Pringle, et al. 1999). The best summary of the results of this work is that of March, et al. (2002) who compared high and low altitude exclusion experiments. At a high altitude site exclusion of shrimps (principally *Atya spp.* and *Xiphocara elongata*) increased chlorophyll-a and algal biovolume. Under these conditions the algal assemblage was dominated by filamentous green algae. Similar effects were not observed at a low altitude site, but this was attributed to abundance of competitors in the form of snails.

These experimental approaches are complemented by the observations of Greathouse (personal communication, cited in Greathouse, Pringle and McDowell, 2006) in natural situations. She reported that "pools above large dams had high levels of epilithic algae", whereas downstream pools did not. Taken together, these experimental and field studies suggest the particular importance of shrimp in managing algal assemblages above natural barriers in the La Amistad watersheds, where other algivores (snails and fish other than *Sicydium*) are likely to be absent.

With regard to algae, fish play as important a regulatory role as shrimps. One of the first papers to report on fish/algae relationships in a tropical stream was that of Power (1984) who described how the Loricariid catfish *Ancistrus spinosus* determined the location and abundance of benthic algae in a central Panamanian stream. Barbee (2002) demonstrated a similar relationship for *Sicydium salvini* which "tracked and depressed their algal resources, so that algal biomass was evenly distributed on the stream bed regardless of light availability or grazer density". However, she also concluded that in the west-central Costa Rican stream where she worked an insect (*Protoptila*, a caddisfly) was perhaps more important. (But see the following section re the *Sicydium/Protoptila* relationship.) Greathouse and Pringle (2005) concluded that "grazing by the high abundance of algivorous gobies (*Sycidium plumieri*) in the middle reaches of Rio Mameyes (Puerto Rico) is an important factor in maintaining low standing stocks of chlorophyll-a".

Algivorous fish have the same effect as shrimps on the composition of the algal assemblage: Flecker (1996) showed that the herbivorous characoid fish *Prochilodus mariae* reduced abundance of diatoms and facilitated the growth of nitrogen-fixing cyanobacteria in streams of the Andean foothills of Venezuela. Pringle and Hamazaki (1997, 1998) studied a diverse assemblage of fishes in a river in northern Atlantic Costa Rica and concluded that "Fishes influence the stability of algal assemblages by maintaining the dominance of the blue-green alga *Lyngbya*, which is relatively resistant to scouring during high discharge. In the absence of fishes, algal assemblages are dominated by easily erodible diatom communities, which undergo dramatic fluctuations in response to high discharge."

Certainly *Sicydium* spp. are important in determining the nature of algal assemblages in streams of the La Amistad watersheds, as are at least two other diadromous herbivore/omnivore fishes, *Agonostomus monticola* and *Joturus pichardi,* in streams below vertical barriers. While we lack quantitative observations on algivory in the La Amistad area, the enormous abundance of *Sicydium* at many sites, and the frequency of "scrapes" observed on rocks in the upper Changuinola River, reflecting the abundance of *J. pichardi*, speak to high significance. Doubtless the roles described above for algivorous fishes in Venezuela, Puerto Rico and northern Atlantic Costa Rica apply in and downstream of the La Amistad World Heritage Site.

5. Structure of the benthic macroinvertebrate assemblage: The relation of diadromous shrimp and fish to benthic macroinvertebrate diversity and abundance is extremely complex. Several of the diadromous fishes of the La Amistad area are carnivorous and may consume large quantities of aquatic insects. The omnivorous Palaemonid shrimps also feed on benthic insects, as do the two diadromous Mugilid fish of the region (*Agonostomus monticola* and *Joturus pichardi*), which may ingest insects intentionally and/or incidentally in the process of scraping algae off rocks. However, the relationship of predatory/omnivorous fish and Palaemonid shrimps to benthic macroinvertebrate assemblages cannot be described simply in terms of predator/prey dynamics, nor can any general statements about effects on benthos be made. The best which can be done is to describe various relevant findings in Costa Rica and Puerto Rico.

Apparently contradictory findings abound: Pringle and Hamazaki (1997) who conducted exclosure experiments in a northern Atlantic Costa Rican river with a diversity of fishes and shrimps, reported that "Fishes significantly reduced numbers of larval Chironomidae (Diptera) and total insects." But later the same two authors (Pringle and Hamazaki, 1998), working on the same river, concluded that "Fishes shifted . . . benthic insect communities toward chironomids, while shrimps had no significant effect on community composition". Rosemond, et al. (1998) carried out exclusion experiments on the same stream at the same time and found that "Exclusion of macroconsumers resulted in significantly higher densities of small invertebrates inhabiting leaf packs. Most of these were collector-gatherers, none were shredders," which suggests competition between aquatic insects and Atyid shrimps.

In Puerto Rico, March, et al. (2001) reported that exclusion of Atyid, Palaemonid and Xiphocarid shrimps at high and low altitude experimental sites resulted in significantly less and more insect biomass, respectively. However, a year later, two of the same authors published a paper (March, et al. 2002) concluding that, at a high altitude site "Excluding shrimps did not significantly affect total insect biomass but significantly decreased mobile baetid mayflies (Ephemeroptera: Baetidae) and increased sessile chironomids (Diptera: Chironomidae)." No effect was reported at a low altitude site. Subsequently, Greathouse, et al. (2006a) clarified this somewhat by focusing on high gradient Puerto Rican streams above and below dams, where they found that "Nine of 11 common non-decapod invertebrate taxa in pools showed significant, or marginally significant, differences in biomass between dammed (lacking diadromous macroconsumers) and undammed (with shrimp and *Sicydium*) sites".

Perhaps the most novel finding was the apparently symbiotic relationship between *Sicydium salvini* and a Glossosomatid caddisfly in a stream in west central Costa Rica suggested by Barbee (2002). She hypothesized that "gobies facilitate *Protoptila* access to algal resources, or the quality of algal resources, possibly through the removal of fine benthic silt."

Attempting to apply this to macroconsumer effects on the diverse aquatic insect fauna of the La Amistad region leads to only very general predictions. Certainly the two groups interact, and in the high gradient streams typical of the World Heritage Site, we would expect that eliminating the macroconsumer group would result in significant change in the abundance and diversity of non-decapod invertebrates. With or without damming, there is clearly a need for research into macroconsumer/benthos interactions in the La Amistad area, in and out of the World Heritage Site.

Conclusion: Flecker (1996), in describing his work with the herbivorous fish *Prochilodus mariae* in Venezuela, borrowed the concept of "ecosystem engineering" as originally defined by Jones, et al. (1994) to describe the contribution of migratory benthic detritivores to stream ecology. The aptness of this description has been borne out by multiple subsequent studies in the natural laboratory that is Puerto Rico.

Most of the studies reported here to suggest possible effects of extirpation of diadromous fishes and shrimps in waters of the World Heritage site are controlled experiments based on use of exclosures or enclosures. However, Greathouse, et al. (2006a, 2006c) were eventually able to verify many of the experimental results from Puerto Rico through direct observations and measurements on dammed and undammed streams, taking advantage of the fact that dams and reservoirs have resulted in the extirpation of diadromous shrimp and *Sicydium* populations from many, but not all free-flowing streams in Puerto Rico (Holmquist, et al. 1998, Kwak, et al. 2007), creating a series of "natural experiments". Their findings confirm the earlier statement of Greathouse and Pringle (2005), based on in-stream experimental work, that diadromous shrimps "have dramatic effects on algal biomass and species composition, quantity and quality of benthic organic matter, quantity of epilithic fine sediments, leaf decomposition rates, and abundance and mass of benthic invertebrates."

The field studies of Greathouse, et al. (2006c) showed that "Compared to pools in high gradient streams with no large dams, pool epilithon above dams had 9 times more algal biomass, 20 times more fine benthic organic matter (FPOM), 65 times more fine benthic inorganic matter (FPIM), 28 times more carbon, 19 times more nitrogen and 4 times more non-decapod invertebrate biomass." Dammed/undammed comparisions were less dramatic in riffles on high gradient streams and on low-gradient streams, but similar patterns obtained. In the authors' words "These results match previous stream experiments".

Previously, Greathouse and Pringle (2005) had demonstrated that the River Continuum Concept (Vannote, et al. 1980) or RCC, commonly employed to elucidate longitudinal changes in biotic conditions along temperate streams "generally applies to running waters on tropical islands". Specifically, "tropical insular and coastal streams across the Caribbean, Latin America, the Pacific Islands and Asia have abundances of snails and algivorous gobies at low and mid elevations and high shrimp abundance above waterfalls that block upstream migration of predatory fishes", as demonstrated by Hunte (1978) for Jamaica, Lyons and Schneider (1990) for the Osa Peninsula of Costa Rica and Craig (2003) for Polynesia (among others). In general, based on our observations, the RCC would seem to apply to the Atlantic slope streams of La Amistad (and probably the Pacific slope streams as well).

UNIQUE CHARACTER OF LA AMISTAD FLUVIAL ECOSYSTEMS AND THEIR RELATION TO OTHER ECOSYSTEMS

Importance of high altitude streams:

Both the "Eco-engineering" and "River Continuum" concepts referred to in the preceding section are relevant to discussion of known and possible links of fluvial ecosystems in La Amistad to other ecosystems in and out of the World Heritage Site. However, first we would like to make the case for the unique character of the fluvial ecosystems of the Atlantic slope of the La Amistad World Heritage. The amount of information available does not allow us to so much as form an opinion about the ecosystems of the Pacific slope, beyond noting that the fish assemblage of the Chiriqui and Chiriqui Viejo watersheds downstream of the World Heritage site in Panama appears to be substantially different from that of the neighboring Grande de Terraba system which drains the Pacific slope of La Amistad in Costa Rica. It is probable that migratory fauna within the World Heritage Site on the Pacific slope of Panama have already been extirpated; so it is likely that we will never be able to offer an opinion on the particular qualities of the upper reaches of the rivers there.

As we begin to attempt to describe the unique qualities of the rivers of La Amistad in Bocas del Toro and Talamanca, we find we must take exception to the dismissive attitude apparent in some of the statements in the AES/MWH mitigation document (AES and MWH, 2009), which appear to us to reflect the viewpoint of persons committed to dam construction, rather than an objective assessment of what is known and not known about the ecosystems in question.

We will begin with the misleading statements "Uno de los resultados mas sorprendentes del estudio de bioversidad realizada en el rio Changuinola por el STRI fue la escasa presencia de peces y camarones en ese tramo del rio." (One of the most surprising results of the biodiversity study carried out by STRI in the Changuinola River was the small numbers of fish and shrimp in this reach of the river.) and "Se reportaron menos especies (17) que la esperada (42) " (Fewer species were reported (17) than expected (42)). In this case, the "expected" number apparently refers to the number of species found by prior investigators in the Changuinola below the CHAN-75 dam site. (STRI, 2010; Goodyear, et al. 1980) Inspection of the results obtained by ANAI-trained Ngobe parataxonomists in the same reach of the Changuinola would have revealed a similar number of fish species (15), which is also similar to results from the neighboring Teribe and Sixaola/Telire watersheds (Mafla, et al. 2005, McLarney and Mafla, 2006b).

In the same report, the unnamed authors cite 8 different references showing that the widely recognized general pattern of diminishing fish diversity as one ascends watersheds and streams become smaller applies in the Neotropics. This suggests – we assume incorrectly, and perhaps unintentionally – that Lasso, et al. (2008b and c), who provide the basis for the AES/MWH argument, carried out literature research only after completing their field research. In any event, the results of the STRI team inventory are in no way surprising to anyone familiar with the rivers of the Atlantic slope of La Amistad.

The relatively low total numbers of fish and shrimp reported in Lasso, et al. (2008b) are to a degree surprising, but say little about the "importance" of stream ecosystems in the La Amistad area above 100 m. elevation. One of the most common misunderstandings about biodiversity is that sites with greater biodiversity as expressed in taxa counts, or with greater apparent productivity, are per se "more important" than less diverse or productive sites. This is a seductive argument, but leads rapidly to the fallacy that the tropics are more important than the temperate zones or the arctic, that the rivers of the Amazon Basin are more important than those of Mesoamerica or, in this case the implication that the (largely unprotected) lower reaches of rivers such as the Changuinola are somehow more important than the upper reaches in PILA.

It is well known that if we use risk of extirpation/extinction as a criterion for prioritizing biodiversity conservation efforts, many of the priority taxa will be those with restricted ranges, often found in small, relatively undiverse ecosystems, which are themselves at risk of destruction by virtue of their small size. In addition, to dismiss the importance of small, high altitude rivers ignores the River Continuum Concept (Vannote, et al. 1980, Greathouse and Pringle, 2005), by offhandedly dismissing the possibility that restricting access to high altitude areas could significantly impact downstream river reaches. This leads AES and MWH (2009) to a further irrelevant statement:

"Por este motivo, no existen razones técnicas objetivas que permitan sostener que los peces y camarones de la cuenca alta del río Changuinola pudieran constituirse en el único soporte trófico (ni el más importante) del ecosistema terrestre que contiene al río Changuinola en la zona del PILA. La biomasa de peces y camarones en la cuenca alta se presume como extremadamente baja para sustentar la biomasa de tan importante ecosistema terrestre." (Thus there is no objective technical justification supporting the statement that the fish and shrimp of the upper Changuinola River could constitute the only trophic support (nor the most important) for the terrestrial ecosystem containing the Changuinola River in the area of PILA. We presume that the biomass of fish and shrimps in the upper watershed is extremely low to sustain the biomass of this important terrestrial ecosystem.)

Apart from the fact that this assertion seems to make the value judgement that the terrestrial ecosystems of the World Heritage Site are "important" and the aquatic systems not so, it appears to be refuting a statement that, to our knowledge, has never been made. Certainly our previous report (McLarney and Mafla, 2007) summarizing the ecosystem-based arguments against dam construction in the Changuinola/Teribe watershed does not claim that the river is "the only trophic support" for the forests of PILA. We will reaffirm that, independent of taxa counts and biomass determinations, aquatic systems in the La Amistad area at altitudes of > 100 m. are important in maintaining the overall biological integrity of the La Amistad region, within and outside protected areas.

Before going on to describe the unique character of the river systems of Talamanca and Bocas del Toro and then to suggest possible negative impacts of dam construction on biodiversity and ecosystem health in La Amistad beyond directly affected river reaches, we would like to comment on one more predictive statement which appears in AES and MWH (2009): "se presume que la biomasa de peces y camarones en la cuenca alta del rio Changuinola es mucho menor a la reportada para la zona de proyecto." (It is assumed that the biomass of fish and shrimp in the upper Changuinola River watershed is much less than that reported for the project area.) Here "project area" refers to the reach of the Changuinola and some of its tributaries located roughly between 100 and 200 m. altitude, surveyed by Lasso, et al. (2008 a, b and c). We are in cautious agreement with the authors of the mitigation proposal up to a certain point. There is no lack of local and worldwide precedent for assuming that the diversity of fish, and to a lesser extent, shrimp will decline at higher altitudes in watersheds such as the Changuinola. This decline may be abrupt above natural barriers to fish movement. To the extent that the animals excluded by barriers (fish) tend to be the largest-bodied members of the fluvial fauna, the effect on total animal biomass may be negative. However, no data exist to support extrapolation from this reasonable assumption to a prediction that total animal biomass will continue to decline as altitude increases. Objective discussion of the possibilities requires that the following factors be taken into account:

- The single most important contributors to fish biomass in the STRI inventory area (Lasso, et al. 2008b) were the “chupapiedras” (*Sicydium*) – precisely the only fish capable of surmounting natural barriers such as waterfalls. It would not be surprising if the density of *Sicydium* gobies were higher in high altitude stream reaches where aquatic predators are absent.
- The same argument holds for the shrimps.
- AES and MWH (2009) say nothing about macroinvertebrates other than shrimp in this context. While insects as individuals can be viewed as having negligible biomass, they can collectively be of great importance. There is no *a priori* reason to assume lesser abundance of larval insects and other small benthic macroinvertebrates at higher altitudes, and the absence of predatory fish suggests the possibility of relatively greater abundance.

In the following sections we will take these factors into account, along with the unarguable reality that detailed knowledge of high altitude fluvial systems in the La Amistad region is severely limited.

Uniqueness of La Amistad fluvial ecosystems:

Rivers draining into the Caribbean and southern Gulf of Mexico – from Puerto Rico to Mexico to Venezuela – have in common a preponderance of diadromous fauna, with the fish genera *Anguilla*, *Agonostomus*, *Gobiomorus*, and *Sicydium* and the shrimps *Atya* and *Macrobrachium* universally distributed. On the islands of the Caribbean, primary and secondary fresh water fishes are few, with a preponderance of endemics with severely limited distributions. The extreme case is represented by Puerto Rico, which has no native purely freshwater species (Lee, et al. 1983). As compared to the islands, mainland rivers exhibit much greater diversity due to the presence of a substantial coterie of primary and secondary fresh water fishes.

The rivers of the Caribbean coast of Mesoamerica and northwestern South America thus share a fish fauna comprised of a mix of purely freshwater species derived from both South and North American elements with diadromous species found throughout the Caribbean. The shrimp fauna is similar but somewhat less diverse due to the absence of the family Xiphocarididae on the mainland.

Among the coastal drainages extending from east-central Mexico to western Venezuela, four relatively small areas stand out as having a similar and distinctive ichthyofauna (Lyons, 2005; Silva-Melo and Acero, 1990). They are:

- A small area between the cities of Tuxpan and San Andres Tuxtla in Veracruz, Mexico.
- North-central Honduras between the city of Puerto Cortes and the mouth of the Rio Platano.
- The Talamanca/Bocas del Toro region of Costa Rica and Panama.
- Streams draining the Sierra Nevada de Santa Marta in Colombia.

What these areas have in common ichthyologically is an unusually, and often spectacularly high abundance of *Sicydium* gobies in their frequent swift-flowing, rocky river reaches. While numerous other diadromous fish and shrimps are fairly evenly distributed along the entire coast, *Sicydium* spp. are scarce or lacking in watersheds outside these areas. What unites these areas geographically is high relief in close proximity to the sea, where the presence of coastal mountain ranges gives rise to relatively short, swift, high gradient rivers. Ten years of inventory work in the Sixaola/Telire and Estrella watersheds (McLarney and Mafla, 2006b, 2008; McLarney, et al. 2009a, 2009b) permit us to describe the general distribution of large-bodied aquatic fauna in one of these areas (Talamanca/Bocas del Toro) as follows:

- During periodic migrations of post-larvae of *Sicydium altum/adelum*, together with other diadromous fishes and shrimps, the lower river reaches crossing the narrow coastal plain may be numerically dominated by small individuals of diadromous forms. At other times, primary and secondary freshwater fishes are more common, but usually with an admixture of large individuals of diadromous forms and facultative, mostly predatory, marine wanderers. The latter group may be present as a consequence of their pursuit of migratory diadromous post-larvae.
- As one ascends the watersheds, or wherever there are high gradient reaches with rocky substrates, the proportional abundance of diadromous taxa, especially *Sicydium* increases, while some strictly fresh water species begin to drop out of the biota. Both numerical dominance and average size of *Sicydium* increase with altitude. In streams above 100 m. altitude, while species diversity may still be relatively high, *Sicydium* may account for 90% or more of individual fish in samples.
- Above the natural barriers frequently created by waterfalls, most fish species are excluded, giving rise to a biota in which the only large-bodied forms may be *Sicydium* and shrimps, both of which can climb moist vertical surfaces. Under these circumstances, with aquatic predators and most competitors excluded, *Sicydium* may reach extraordinary levels of abundance.

The pattern described above (greater proportion of “marine” forms as distance from the sea increases) is perhaps counterintuitive. Certainly the typical situation (including in the La Amistad watersheds) is that the number of diadromous species decreases with altitude and distance from the sea, as described for streams of the Panama Canal watershed (Consorcio TLBG / UP / STRI, 2009) and elsewhere (Angermeier and Karr, 1983; Horwitz, 1978; Welcomme, 1985). But as we have already seen in the discussion of the results of the STRI inventory in the middle Changuinola watershed (Lasso, et al. 2008b), this relationship does not necessarily apply in terms of proportional abundance of species, individuals or biomass.

As we have noted above, free embryos of Sicydiine gobies need to reach their estuarine nursery areas rapidly or risk dying of starvation (Moriyama, et al. 1997; Tsukamoto, 1991). Lyons (2005) points out that this need is not met in the majority of the Atlantic coastal area between Mexico and Colombia, where the typical geography includes a broad coastal plain, traversed by slow, meandering rivers. As research in Puerto Rico shows (Holmquist, et al. 1998; Greathouse, et al. 2006b, 2006c) the same mortality effect may result from inserting a stretch of slow-flowing water, in the form of a dam impoundment, into an otherwise swift-flowing river.

Similar constraints apply to shrimp; although postlarvae and adults of some species may be more able than *Sicydium* gobies to take advantage of short windows of opportunity to climb dams under favorable flow conditions, delays in reaching the estuary can be critical. Lewis and Ward (1965) and Choudhury (1971) have shown that larvae of *Macrobrachium carcinus* (and likely other amphidromous shrimps) die after just a few days in fresh water. Diadromous shrimps are everywhere severely reduced and often extirpated above dams. To give an idea of the numerical importance of blockage of shrimp migrations, consider the findings of March, et al. (1998). They compared passive downstream transport of larval shrimp in dammed and undammed rivers of the Caribbean National Forest in Puerto Rico. Even though the low dams (< 15 m. high) characteristic of this area are somewhat porous to shrimp, they estimated the loss of shrimp larvae to dams and associated water withdrawals at 15.3 million individuals/day.

In following sections we will point out how the unique *Sicydium*/shrimp assemblage in the high altitude rivers of the La Amistad region may affect terrestrial ecosystems and its role in maintaining intact River Continua regionally. Here we would like to point that while similar associations (but with arguably different *Sicydium* species) exist in 3 other widely separated areas along the Gulf of Mexico and Caribbean coast, the largest such area is that comprised by Talamanca and Bocas del Toro. Moreover, because of the existence of a complex of protected areas centering around the La Amistad World Heritage Site, it is the one with the best long-term prospects for preserving this unique assemblage and ecosystem.

<u>Terrestrial systems within the World Heritage Site</u>:

This section will necessarily be largely speculative but, given the extreme importance of the La Amistad World Heritage Site as the core of the largest block of forested land and concentration of protected areas in Mesoamerica, and the acknowledged extremely high biodiversity of that area, it can scarcely be omitted from any discussion about management of the rivers which flow through it. The importance of the terrestrial ecosystems of La Amistad is accented by recent discoveries of new species by the STRI team (Lasso, et al. 2008a) and by the ongoing work of the Darwin Initiative team (Monro, et al. 2007, 2008, 2009). We are sure that all involved would acknowledge that these discoveries represent the proverbial tip of the iceberg, and that much more remains to be learned. Application of the Precautionary Principle, then, would strongly suggest the inadvisability of actions which could eliminate elements of biodiversity through local extirpation, or even species extinction, before we are aware of their existence.

We will concede that, insofar as aquatic species are concerned, the likelihood of discovering new species is low (though it cannot be precluded, particularly with respect to the insect fauna), with the possibility of new diadromous species particularly low. However, as we have pointed out above, the aquatic faunal assemblage structure of high altitude streams in the La Amistad drainages is both unique and threatened. Further, we will assert that, contrary to the position implied by AES and MWH (2009), the streams which drain the La Amistad World Heritage Site have an integral relationship to the terrestrial ecosystems through which they flow, whether or not we have progressed very far toward defining this relationship.

Let us start with the assumption that the 3 principal components of the aquatic fauna at high elevations in the World Heritage Site, and especially above natural barriers to upstream movement, are fish (especially *Sicydium* gobies), Atyid and Palaemonid shrimps, and benthic macroinvertebrates, with aquatic larvae of insects which are terrestrial as adults dominating the latter group. We can then ask what might happen were two of the three principal components (diadromous *Sicydium* and shrimp) removed.

We have already seen that, even though the diadromous fish and shrimp found above barriers are not always quantitatively significant predators on benthic macroinvertebrates, their elimination can cause major changes in the composition of the benthic macroinvertebrate assemblage. A commonly reported result of exclusion of grazers such as *Sicydium* and Atyid shrimps is a shift from active, mobile forms to sessile forms, especially Chironomidae (March, et al. 2002; Pringle and Hamazaki, 1998).

The best known benthic macroinvertebrate assemblage for the La Amistad area is that of the Changuinola watershed upstream of the CHAN-75 dam site. Of 11,865 non-decapod aquatic invertebrates collected by the STRI team (Lasso, et al. 2008b) in that area 10,364 (87.3%) were larvae of insects belonging to orders which without exception transform into flying adults. (This does not take into account 3,130 individuals of the order Coleoptera, many of which metamorphose into flying adults, while others are aquatic throughout their life.) Effectively then, around 90% of the non-decapod "aquatic" macroinvertebrates in the middle Changuinola watershed could equally well be described as "terrestrial."

Of the >10,000 insects in the samples which were destined to emerge as flying adults, only 313 (2.6% of the total macroinvertebrate sample) belonged to the order Diptera, which includes the Chironomidae. Clearly if, as a consequence of extirpation of diadromous fish and shrimp, the benthic macroinvertebrate fauna of the river, presently dominated by Ephemeroptera, Coleoptera and Trichoptera (78.8% of the total sample) were to shift toward dominance by Chironomidae (a not uncommon condition in heavily sedimented rivers, but not expected in the typically "clean" rivers of the La Amistad area) it would represent an enormous change in both the terrestrial and aquatic fauna, over and above the loss of fish and shrimp species.

We can only guess what other consequences might follow, but consider this: Adult chironomids are normally much smaller than those of most of the taxa representing the other 9 insect orders found. As flying adults they often exhibit unique behavior, forming swarms rather than flying about as individuals. Among the groups of insectivorous animals inhabiting the World Heritage Site are birds, bats, reptiles and other insects (notably the aquatic Odonata). What might be the effect on these predators of a drastic shift in prey size and behavior? Clearly we are confronting the possibility of effects up to and including endemic species extirpation which are not only unintended, but which might go unperceived.

Possibilities are suggested by the work of Chan, et al. (2008) in tropical forests of Hong Kong. They found the seasonality of aquatic insect abundance to match that of insectivorous forest-interior bird species. Given that these bird species are morphologically adapted to exploit larger, solitary and less mobile prey, changes to stream bed composition leading to fewer large insects and highly mobile swarms of smaller ones could cause reduced availability of preferred prey, leading to alterations in the bird assemblage.

Downstream effects of natural barriers:

It is virtually certain that the existence of large numbers of adult *Sicydium* gobies in reaches of the World Heritage Site rivers above natural barriers, where they face greatly reduced predation pressure and competition for resources, contributes to the unusual abundance of *Sicydium* in river reaches below barriers, in and out of the World Heritage site. The same may apply to Atyid and Palaemonid shrimps.

While scientific studies are lacking it is also highly probable that downstream drift of *Sicydium* and shrimp eggs and larvae and periodic upstream mass migrations of postlarvae of both ("titi") are of major importance in maintaining populations of aquatic predators, including high value, economically important food fish, in the lower reaches of the La Amistad rivers. It should be noted that in the past the titi migration formed the basis for a subsistence fishery in Talamanca. Economically important fisheries based on the postlarvae of *Sicydium* spp. or other amphidromous gobies, first documented for Dominica by Atwood (1791) have had historical importance in many countries and persist in some tropical island river systems. Such fisheries have been documented for the West Indies in general (Clark, 1905), Jamaica (Aiken, 1985, 1988), Dominica (Bell, 1994), Puerto Rico (Erdman, 1961, 1984), Guadeloupe (Fievet and LeGuennec, 1998), Hawaii (Titcomb, 1977; Ego, 1956), the Phillipines (Taylor, 1919; Montilla, 1931; Blanco and Villadolid, 1939; Acosta, 1952, Manacop, 1953, Blanco, 1956), Reunion (Aboussouan, 1969), Madagascar and Mauritius (Catala, 1982), New Zealand (McDowall, 2004), Tasmania (Fulton, 1984) and north Atlantic Costa Rica (Gilbert and Kelso, 1971). Bell (1994) summarized many of these fisheries and documents their decline or disappearance in most localities.

To give an idea of the potential magnitude, in terms of biomass, of movements along river corridors by larval and post-larval diadromous fish and shrimp in the La Amistad area, we cite two examples from Puerto Rico:

- Erdman (1961) observed upstream migrations of *Sicydium plumieri* in the Añasco River, which on the average took two days to pass an observation point. Based on point counts and measurement of the 2 migrating columns (typically one on each side of the river) a single migration was estimated to consist of about 90 million individuals.
- March, et al. (1998) estimated numbers of downstream migrant shrimp larvae in undammed streams of the Caribbean National Forest and used those calculations to arrive at an estimated figure of 15.3 million shrimp larvae/day lost in dammed rivers in the same area.

The River Continuum Concept (Vannote, et al. 1980; Greathouse and Pringle, 2005) predicts that all biological activity in the upper reaches of a watershed will have an effect downstream. In the particular unique case of high elevation streams above anthropogenic barriers, we have cited studies demonstrating local effects of elimination of diadromous fauna on the composition of the benthic macroinvertebrate assemblage, sediment accumulation, processing of allochthonous matter, water and substrate chemistry and algal assemblage composition. (See references in section on secondary effects.) We need not enter into a speculative discussion of how these effects might play out to assert that they have physical and biological consequences downstream which would be replicated in the event that La Amistad streams are dammed.

<u>On site and downstream effects of dam/reservoir complexes</u>:

<u>Overview and reservoir effects</u>:

Here we must begin by taking vigorous exception to the following statement in AES and MWH (2009):

"Es necesario destacar que aguas abajo del sitio de presa de Changuinola I ninguno de estos grupos será afectado por la obra ya que tanto los peces como los camarones encontrarán todos los biotopos necesarios para completar su ciclo de vida, ya sea en agua dulce o en el mar." (It is necessary to point out that downstream of the Changuinola I dam none of these groups will be affected by the work because both fish and shrimp will encounter all the biotopes necessary to complete their life cycle, be it in fresh water or in the sea.)

This may be an accurate reflection of what the authors wish were true, but it is entirely incorrect, and reflects a failure to review the abundant literature on downstream effects of high dams. (An excellent overview is provided by Ahearn, et al. 2005.) The truth is nearly diametrically opposed, and may be stated as follows: For a considerable distance below any dam, including Changuinola I (= CHAN-75) all forms of aquatic life, as well as some terrestrial species and systems, will be profoundly affected and in many cases, threatened. Some of the effects on downstream trophic structure are described by Cortes, et al. (1998), Petts, et al. (1993), Ward and Stanford, (1979) and Webb and Walling, (1993).

To this must be added 1) inevitable short term impacts occurring during dam construction and 2) the substantial effects above the dam resulting from the conversion of a reach of free flowing river (lotic environment) to the lentic environment of a reservoir lake. Many of these dam site effects are summarized in Collier, et al. (1996) and McCully (1996).

We are not aware of any comparably egregious examples of wishful thinking related to other dams proposed for the La Amistad area, but there is a natural tendency on the part of dam proponents to minimize the negative environmental impacts of dam projects and/or to overestimate the capability to mitigate these effects (See following section on mitigation.) An honest cost-benefit assessment of any dam proposal must acknowledge some degree of negative environmental impact to the affected river system, both up and downstream of the dam site.

So far as we know none of the dams or reservoirs presently existing or proposed for the waterways draining the two La Amistad National Parks are within the parks (although the reservoir created by the Bonyic Dam is projected to reach to within 60 m. of PILA). Thus technically the dams, reservoirs and downstream river reaches are not the responsibility of the two countries' National Park Services or of UNESCO. However, we would argue that just as the entities responsible for promoting or permitting dam construction on the rivers downstream of the World Heritage Site have a responsibility to maintain biodiversity upstream, within the parks, so do the national and international agencies involved in park management bear responsibility for delivering the benefits of conserving the protected area to the river and its users downstream of the World Heritage Site.

Here we apply the River Continuum Concept (Vannote, 1980; Greathouse and Pringle, 2005) to elucidate that argument. If effects of human activities downstream of the World Heritage Site threaten major and not altogether predictable ecosystem damage within the Site, including loss of specific portions of the biodiversity the area was established to protect, then it should be the responsibility of ANAM, MINAET and UNESCO to attempt to prevent foreseeable damage. In the specific cases of the Changuinola/Teribe, Sixaola/Telire and Grande de Terraba watersheds draining the La Amistad World

Heritage Site the concept of "offsite" responsibility is reinforced by the existence of, respectively, the San San/Pondsak Wetland (Panama) and the Gandoca/Manzanillo National Wildlife Refuge and Terraba-Sierpe mangrove wetland (Costa Rica) – all of them UNESCO-designated Ramsar wetlands – dependent not only on the quality of water received from the World Heritage Site and other protected and unprotected areas upstream, but on maintenance of the biotic continuum along the entire length of their respective rivers.

The economic, social, cultural and environmental effects of converting a reach of free flowing river to a reservoir "lake" are many, and not limited to the aquatic habitat. Most of these effects, which were discussed at some length in McLarney and Mafla (2007) and which are the subject of an abundant literature need not be repeated here. (The reader interested in local effects such as greenhouse gas generation and enhancement of human disease vectors, as well as cumulative global scale effects of dams and reservoirs, is referred to Rosenberg, et al. 2000, and other articles in a special issue of BioScience devoted to hydrological alterations.) Suffice to say that between a dam and the high pool level of its reservoir the principal biological effects of impoundment are the replacement of an area of fluvial and riparian terrestrial habitat with an artificial habitat and the introduction (in conjunction with the dam and any dewatered reaches which may exist downstream) of a discontinuity in the natural function of the river as an altitudinal biological corridor. The first effect (loss of fluvial habitat) is proportionally more severe in the tropics, since lakes are not a natural feature of most tropical areas, and there are few native animals preadapted to take advantage of the altered habitat.

Downstream effects:

Effects downstream of dams would seem to merit more discussion here. Some of those effects may be due to fragmentation of populations. Independently of any need to migrate, any time a population is divided into two or more segments, all segments will be more vulnerable than the original population. This was demonstrated by DeMarona and Albert (1999), who documented reductions in species diversity and changes in relative abundance both up and downstream of a dam constructed in 1994 on the Sinnemary River, French Guiana – a river with a low incidence of diadromy. Downstream effects of fragmentation may be exacerbated by density-dependent effects due to the tendency of fish to accumulate below barriers. This can lead to greater susceptibility to disease (Moring, 1993; Welcomme, 1985), and predators (Barlow and Bock, 1984; Elson, 1962; Feldham and Maclean, 1996; Kennedy and Greer, 1988), including humans (Aass and Kraabol, 1999; Harris, 1984).

The nature of other downstream dam effects is to a large degree site-specific, depending on both the physical and biological condition of the undammed river and the design of the particular dam. Even were final plans for all the proposed La Amistad dams available for inspection, our expertise does not permit in-depth comment and the sheer number and diversity of dams proposed would render the task of analyzing problems dam by dam impractical in this context. We can offer some general information:

Most downstream biological effects of dams can be described under 5 categories – dewatering, alteration of flow, sediment transport or temperature regimes and changes in water chemistry. In the case of single dams these effects may be categorized as "local", but where multiple dams are proposed, whether in sequence (as on the Changuinola River), or dispersed throughout a watershed (as in Talamanca), we must consider effects at the landscape level (Poff and Hart, 2002). Below we will discuss each of these categories and attempt to place them in the context of the La Amistad area at both local and landscape levels.

Dewatering occurs when, for engineering reasons, electrical generating facilities need to be located some distance downstream of the dam. In such cases it is often convenient to pass a large portion of the impounded river's volume through a "penstock" of up to several kilometers length, leaving a parallel reach of natural river bed dry or with greatly reduced flow. In addition to the loss of yet another section of fluvial habitat, such diversions serve to magnify the barrier effect of the dam. A number of the dams proposed for the La Amistad area incorporate this feature. Anderson, et al. (2006) suggested that one of the long term consequences of dewatering by small dams on the Puerto Viejo River in north central Costa Rica will be impacts on "species with more complex reproduction requirements" leading to a river "increasingly dominated by opportunistic type, colonizing fish species."

Flow rate alteration capability is built into all large dams. Most dams have the capacity to increase or decrease flow volume and velocity at any moment, for purposes of electricity generation or water level control. This same capability can be used to ensure a certain minimal flow deemed to be necessary for the maintenance of desired biological condition downstream. This is the basis for the relatively new concept of "environmental flows" (Richter, et al. 2006; Richter and Thomas, 2007). Within limits, dams can also be made to mimic natural changes in periodicity of flow, which can be crucial as cues for migratory and other behavior. However, in practice even when environmental flow plans exist they may not be consistently implemented, especially if they conflict with uses for which dams are designed (in the case of all the La Amistad area dams, electrical power generation).

Even in the absence of changes in flow rate, alteration of current patterns by dams can have negative effects on downstream biota. For example Fievet and LeGuennec (1998), in Guadeloupe, document the attraction of great numbers of migratory postlarval *Sicydium* gobies to canals leading to a hydroelectric facility, but which do not provide access to the river above the dam.

While we were able to find no published studies showing effects of flow rate alteration by dams on downstream biota in tropical streams, an example from Vermont and Massachusetts, USA, illustrates the potential: Bain, et al. (1987) studied fish community structure in two naturally similar Connecticut River tributaries, one regulated by dams and the other undammed. They found that "An abundant (>90% of all fish) and diverse (nine species) group of small fish species and size classes were restricted to microhabitat that was characterized as shallow in depth, slow in current velocity, and concentrated along stream margins. This group of fish was reduced in abundance in the regulated river and absent at the study site with the greatest flow fluctuation." Zdankus, et al. (2007) provides an example of how flow alterations act on the following category of effects, sediment transport.

Sediment transport: 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 locally by serving as "traps" for excess sediment until their trapping capacity is used up. On a global scale, impacts on downstream river reaches and inshore marine environments resulting from dams depriving rivers of natural sediment loads are of greater concern. Some of the consequences are summarized by Williams and Wolman (1994) and Vorosmarty, et al. (2003).

Altered sediment transport regimes downstream of dams can affect not only riverine species, but are also documented to occasion loss of floodplains with associated wetland and terrestrial biomes. In addition to physical damage to riparian areas, riparian vegetation may be altered. For example Nilsson and Berggren (2000) suggest that the diversity of riparian plant communities in Europe has been reduced through interruption of transport of waterborne seeds by multiple dams. More generalized treatments of this type of effects are provided by Magilligan, et al. (2003), Shafroth, et al. (2001) and Tockner and Stanford (2002).

Damage to river deltas on the fresh water/estuary interface may also occur (Rosenberg, et al. 1997) as a consequence of sediment starvation, as has been documented (Meade, 1995) for the Mississippi River Delta in the Gulf of Mexico. Effects on estuaries have been summarized by Olsen, et al. (2006). "Starvation" of ocean beaches is another possible far downstream effect, documented for California rivers by authors from Grant (1938) to Willis and Griggs (2003).

In virtually all cases, dam managers will prefer to manage sediment in a way which prolongs the useful life of the dam and reservoir; this may or may not be optimal in terms of maintaining natural conditions downstream. In tropical rivers such as those of the La Amistad area the effect on sediment transport regimes of bioturbation by diadromous shrimps, and the possible downstream consequences of their extirpation above dams (Cowl, et al. 2001; Greathouse and Pringle, 2005; Greathouse, et al. 2006c; March, et al. 2002; Pringle, et al. 1992; Pringle and Blake, 1994; Pringle, et al. 1999) is a factor which has largely been ignored.

Temperature regimes downstream are nearly always altered by dams; depending on design, they may raise or lower water temperatures downstream. When lentic habitats are inserted into the natural continuum of a river they function as solar water heaters. Where dams discharge surface water, as do many small dams, this can result in elevated temperatures downstream. Most modern large dams, presumably including those contemplated for the La Amistad region, are designed to discharge at or near the bottom under normal flow conditions (hypolimnetic dams), so that some of the sediments which normally occur behind dams are continually flushed. This typically results in lowered river temperature downstream.

Either outcome (heating or cooling) can significantly alter the ecology of the river below; here we will focus on the consequences of temperature depression, which would appear to be of more concern in our area. Extreme examples are presented by many reservoir "tailwaters" in the southern United States which now support only cold water fishes exotic to the region (Brooker, 1981; Krause, et al. 2005; Olden, 2004). A combination of sediment sequestering and temperature impacts occurs in the Colorado River of the southwestern US, where a suite of regional endemics, some of them officially listed as Endangered, are threatened by the conversion of a naturally warm, turbid river to a cold, clear one downstream of major dams (Clarkson and Childs, 2000; Minckley and Deacon, 1991). A similar effect has been observed on the commercially valuable Murray Cod (*Macullochella peelii*) in rivers of Australia (Todd, et al. 2005). A spectacular example of wholesale alteration of an ecosystem by downstream temperature alteration is described by Lehmkmuhl (1974), for the Saskatchewan River in Canada, where a hypolimnetic dam reduced a benthic insect assemblage comprising 12 orders, 30 families and 75 species, to one composed of a single family (Chironomidae). Other examples of downstream temperature effects on biota are provided by Ward and Stanford (1979) and Webb and Walling (1993).

Depending on many factors, negative effects of temperature change have been documented at distances of over 40 km. downstream of hypolimnetic dams (Ward, 1985). In the extreme case of the Glen Canyon Dam on the Colorado River, USA, Stevens, et al. (1997) calculated a distance of 939 km. for full recovery (in practice prevented by other dam/reservoir complexes downstream).

An excellent recent review of downstream thermal effects by dams is offered by Olden and Naiman (2010) who note that "Despite the global scope of thermal alteration by dams, the prevention or mitigation of thermal degradation has not entered the conversation when environmental flows are discussed." Certainly this is currently the case in Panama and Costa Rica.

Changes in water chemistry inevitably occur in reservoir lakes, and are passed on downstream. Especially below new dams, chemical alterations, including methylation of toxic mercury (Fearnside, 2001; Kelly, et al. 1997; Verdon, et al. 1991) can be due to processes such as decomposition of terrestrial vegetation in the reservoir, which may also alter nutrient cycling processes (Pringle, 1997; Rosenberg, et al. 1997). 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 (Caufield, 1985; Goldman, 1979). Deoxygenation could be a serious concern for the native fauna of the turbulent rivers of the La Amistad region, some species of which are adapted to continuous near-saturation levels of dissolved oxygen. Other changes in downstream water chemistry may be provoked by alteration of natural flow cycles. The classic example is that of Ahearn, et al. (2005) who compared two adjacent rivers in California (the Mokelumne with 10 dams, and the undammed Cosumnes) and found dramatic differences in metabolism of nitrogen, phosphorus and silicon (as well as differences in flow periodicity, sediment transport and temperature).

Even absent the barrier effect of dams and reservoirs, the factors just described have the potential to affect both diadromous and non-diadromous fauna downstream, setting off a chain of effects extending from the estuary and the beaches to the headwaters. While compensation for some effects is possible, it is unrealistic to expect that any large dam will not have profound effects on the River Continuum. In the case of multiple dams within a watershed, we agree with the conclusion of Anderson, et al. (2007), based on research in the Sarapiqui watershed of north central Costa Rica that "There is a need for consideration of the basin-scale ecological consequences of hydropower development." This discussion will be continued in the following section on mitigation.

MITIGATION

The following section is an expanded version of our earlier discussion of mitigation for proposed dams in the Changuinola/Teribe watershed (McLarney and Mafla, 2007), and reaches the same conclusion: that no satisfactory environmental mitigation is possible for proposed large dams. When the scale is expanded to include proposed dams on other watersheds which together could impact as much as 67% of the World Heritage Site, the effect is to reinforce that conclusion.

Fish passage strategies:

The barrier effect of dams as they affect diadromous fauna 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 the North American portion of their range they normally do not share streams with other diadromous taxa. 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 through facilitation of migration around dams and reservoirs has had a spotty record (Francfort, et al. 1994; Orsborn, 1987; Petts, 1984). In all cases, survival of migrants has been negatively impacted (National Research Council, 1996; Ferguson, et al. 2005; Williams, et al. 2005). Helfman (2007) provides an excellent overview of the roles of lack of adequate life history information, poor design, shoddy construction, neglect, and prioritization of public relations over actual conservation goals in the history of dam-related fish passage structures designed for Pacific salmons and other fishes.

Successful use of fish passage strategies to mitigate 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 the North Pacific. 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 La Amistad region, with the possible exception of the catadromous *Anguilla rostrata* on the Atlantic slope*,* for not one of the species of diadromous fish and shrimp discussed here do we have a complete life history. 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 principal migratory stages are larvae and very young juveniles with little to no 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 made in Guadeloupe, where amphidromous palaemonid shrimp of the genus *Macrobrachium* are commercially important. One difficulty facing the project was the different climbing regimens displayed by the 3 shrimp species concerned. A design which was ultimately partially successful for *Xiphocaris elongata* (a non-commercial Atyid) and *Macrobrachium faustinum* did not facilitate passage by another small Atyid, *Micratya poeyi* (Fievet, 1999). As described by Fievet (2000) the results were biologically marginal and economically inefficient.

To our knowledge, the only apparently successful application of fish passage technology to mitigation of dam effects in the tropics occurs on Cocos Island, located in the Pacific Ocean off Costa Rica. There Rojas (no date), observed successful use of a "paso ecologico" (ecological passage) structure at an ICE hydroelectric facility on the Genio River by 5 species of diadromous fish including two members of a genus restricted in the La Amistad area to elevations below that of proposed dams (*Eleotris picta* and *Eleotris tubularis*), two endemic congeners of species of concern in our context (*Gobiesox fulvus* and *Sicydium cocoensis*) and one species found throughout the La Amistad area (*Agonostomus monticola*), plus an unidentified *Macrobrachium* shrimp. Adults of all 6 species (representing the total known diadromous fauna of the island) were observed to pass upstream through a "fish ladder" type structure in the center of the dam. However, the value of this facility and study "evidencia de que la planificación y ejecución de este tipo de obras permite el desarrollo de infraestructuras en armonia con el entorno ecologico" (evidence that planning and execution of this type of work pemits the development of infrastructure in harmony with the surrounding ecology) is overstated.

The utility of the information provided by Rojas (no date) in any discussion of mitigation methods for dam effects in the La Amistad area is virtually nil for two reasons:

- The study spanned a period starting before the initiation of dam construction in 2002, and terminating in 2005. While during this period the numbers of fish and shrimp passing the dam site remained steady or increased, there is at yet no proof that demersal eggs and larvae are successfully passing downstream to the estuary. Thus the sustainability of the structure as a conservation strategy has yet to be determined.
- The crest of the ICE dam on the Rio Genio is at the normal water surface level, so results are not comparable even with most of what are by generally accepted standards (World Commission on Dams, 2000) "small" dams (<15 m. high), let alone with the large dams planned for the La Amistad area.

The efficacy of measuring success of fish passage facilities by quantifying upstream passage by adults is further thrown into doubt by studies in Brazil, where fish passage facilities are mandatory on new dams. In that country, efforts to facilitate migration by potamodromous fish were tentatively qualified as successful for some species. However, in some cases what at first blush appeared to be successful fish-passage facilities proved to function as traps, enticing fish away from adequate reproductive habitat below dams and into unsuitable habitat above them (Pelecice and Agostinho, 2008). Based on a survey of fish passage facilities at dams throughout Brazil, and allowing for some provisional successes, Agostinho, et al. (2002) considered that the particular reproductive strategies employed by neotropical fishes "make fish passages in most situations an inadequate instrument for preservational management." Species diversity seems to be part of the bottleneck; at none of the specific dam sites detailed by Agostinho, et al. (2002) did more than 44% of species known from the river immediately below the dam ascend fish passage facilities.

We concur with the general assessment of Ledec and Quintero (2003): "Fish passage facilities (fish ladders, elevators or trap-and-truck operations). . . are usually of limited effectiveness for various reasons (including the difficulty of ensuring safe downriver passage for many adults and fry)." We also agree with the conclusion of AES and MWH (2009) that "la construcción de un canal de desove no es una medida de mitigación adecuada para el proyecto Changuinola". (The construction of a fish passage facility is not an adequate means of mitigation for the Changuinola project.)

Artificial rearing of migratory species:

Aquaculture as a mitigation strategy scarcely merits mention, but since it was proposed in the Environmental Impact Assessments for the Bocas del Toro dams (Proyectos y Estudios Ambientales del Istmo, 2004a, 2004b, 2004c; PLANETA Panama, 2005), and forms the centerpiece of the recent mitigation proposal for the Changuinola mainstem dams (AES and MWH, 2009) it will be briefly discussed here.

The aquaculture proposals floated in the EIA's 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* were discussed, virtually to the exclusion of other species. AES and MWH (2009) avoid that particular distortion and prioritize the diadromous species they considered, based on abundance, to be most important (*Agonostomus monticola, Joturus pichardi, Sicydium altum, Macrobrachium heterochirus* and *Atya scabra*), with "less important" species to be left for later study at the hydrobiological stations they propose to establish. However, 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.

It should be noted that establishment of aquaculture facilities to mitigate damage done by dams is a particularly attractive strategy when the real goal is public relations. A poignant example is provided by the Elwha Dam on the Elwha River in Washington, USA. When this dam was constructed in 1913 it incorporated no fish passage facilities, in direct violation of state law. To "mitigate", a fish hatchery was constructed at the dam, with the goal of supplying artificially reproduced salmon for stocking elsewhere. In 1922 the hatchery was written off as a failure and closed; the dam remains (Montgomery, 2003). (Beginning in 2012, some degree of mitigation may be achieved when the Elwha Dam becomes the world's largest dam removal project to date.) (Wunderlich, et al. 1994).

The gap between aspirations and reality in the aquaculture field is illustrated by AES and MWH's (2009) citation, in reference to *Agonostomus monticola* and *Joturus pichardi,* of work at a hydrobiological station at an ICE hydroelectric facility in Costa Rica (variously cited in their report as Piedras Blancas or Penas Blancas) as a "valuable antecedent" and opportunity for collaboration. However, our own investigations in ICE (personal communication, J.R. Rojas) revealed that work on these two species at Penas Blancas (the correct name) has yet to begin.

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 species as widely appreciated as *Joturus pichardi*, it is because their cultivation so far appears to be a poor economic proposition. For aquaculture to begin to contribute to the maintenance of biodiversity in PILA 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.

The "landlocking" phenomenon:

For most species diadromy appears to be obligate behavior; one of the factors determining success for most diadromous species is a range of salinities at different life stages. However, in some cases natural or artificially induced (through introductions) landlocking occurs, with a naturally diadromous species able to complete its life cycle by substituting a large body of fresh water for the estuarine or marine component. This occurs most frequently with anadromous salmonid species giving rise, for example, to the natural landlocked populations of Atlantic salmon (*Salmo salar*) in the northeastern United States and eastern Canada, or to the successful introduction of various species of Pacific salmon (*Oncorhynchus*) in the North American Great Lakes. McDowall (1988) notes that in some families of fishes "non-diadromous species have evolved and become distinct species that are reproductively isolated from either former or still-existing diadromous species."

This gives rise to speculation about the possibilities of serendipitous landlocking as a form of "accidental mitigation". For example AES and MWH (2009) raise the possibility that *Sicydium* could utilize reservoir lakes on the Changuinola mainstem as substitutes for the normal estuarine nursery environment. While this may technically not be "impossible", the absence of any documented such occurrence among the 16 recognized members of a pantropical genus eliminates this possibility from serious consideration in any discussion of the environmental and biodiversity issues raised by dam proposals in the La Amistad watersheds.

Four other cases of putative landlocking are raised by AES and MWH (2009):

- They cite Castro-Aguirre, et al. (1999) as reporting the existence of a landlocked reproducing population of *Pomadasys crocro* in a reservoir lake (Miguel Aleman or El Temascal) in Mexico, located well inland and not far from the Continental Divide. Castro-Aguirre, et al. (In Press) add two species to this list, reporting on apparent landlocked populations in the same reservoir of two additional diadromous species – *Gobiomorus dormitor* and *Dormitator maculatus*. The latter occurrence is unusual, since *D. maculatus* is generally considered a coastal species, not known from above 12 m. in Costa Rica (Bussing, 1998).
- As discussed above, there are reports of landlocked populations of *Gobiomorus dormitor* in a natural lake in Nicaragua (McKaye, 1977; McKaye, et al. 1979) and a reservoir lake in Puerto Rico (Bacheler, 2002; Bacheler, et al. 2004). For different reasons we suggest that neither population constitutes definitive proof of the existence of a self-sustaining non-diadromous population of *G. dormitor.* But the more compelling information is the documented disappearance of *G. dormitor* above a much larger number of high dams in Puerto Rico (Holmquist, et al. 1998; Kwak, et al. 2007).
- AES and MWH (2009) interpret Bussing's (1998) mention of *Gobiesox nudus* from streams tributary to "Lake Arenal" in Costa Rica as evidence for successful landlocking. They were presumably unaware that Lake Arenal was originally a natural lake which was impounded

in 1973 by a power dam to form a larger body of water, Arenal Reservoir. So far as we can determine all of the records referred to by Bussing date to before impoundment.

- The least compelling argument advanced by AES and MWH (2009) is that the presence of self-sustaining populations of two diadromous shrimps (*Atya scabra* and *Macrobrachium heterochirus*) and one possibly diadromous fish (*Atherinella chagresi*) in Gatun Lake, Panama is evidence of successful adaptations to an entirely fresh water life cycle. Gatun Lake forms part of the Panama Canal, which is ecologically notorious for having facilitated the passage of marine organisms between the Atlantic and Pacific Oceans. It thus presents multiple opportunities for intentional or unintentional movement of the species in question and others. "Isolated" populations in Gatun Lake cannot legitimately be adduced as evidence of successful landlocking.

The doubts expressed above notwithstanding, it is not possible to assert that successful landlocking of one or more of the diadromous species of the La Amistad Region in a new reservoir lake could not occur. In the event of such an occurrence landlocking might function serendipitously as mitigation for some portion of the species in question. However, given the number of diadromous species involved and the number of proposed dam/reservoir complexes, this possibility does not merit serious inclusion in the debate about possible mitigation strategies.

Furthermore, even were it possible to establish a complete range of diadromous species in an isolated habitat fragment above some future reservoir, this would do nothing to address the River Continuum issues raised above. The contribution to downstream and estuarine ecosystems by the "eco-engineering" activity of herbivorous fish and shrimps in headwater areas and the biomass of larval forms descending from these areas would still be largely eliminated by the combined effects of the dam and reservoir.

Downstream mitigation:

Mitigation of environmental impacts on fish and other animals downstream of dams is a subject which has attracted some attention in recent years. Many countries, including Costa Rica and Panama, legally mandate dam design and management to maintain "environmental flows" downstream. Since the principal focus of this paper is on conservation of biodiversity within the La Amistad World Heritage Site and maintenance of connectivity and corridor function in the rivers of the area, our treatment of mitigation of direct downstream environmental effects will be brief. We will note that environmental flows are calculated as a minimum percentage of "normal" flow which must be maintained. While this is certainly a step in the right direction, it falls far short of managing to prevent the multiple potential downstream impacts mentioned in the preceding section. Regulations which fail to take into account the particular needs of species inhabiting the regulated river reach may pass the test of "good intentions", but should not be interpreted as guaranteeing protection of biodiversity.

Mitigation at the regional scale:

All of the discussion here has been about site- or river-based mitigation. Some of the participants in the larger discussion have opened the theme of "regional scale" mitigation (personal communication, J. Opperman, The Nature Conservancy). In practice, this would involve "sacrificing" some of the rivers of the La Amistad area in turn for guarantees of protection of corridor function and a range of habitats adequate for all diadromous and potamodromous species on other rivers. This concept is at most a “better than nothing’ concept with three obvious defects:

1. The great diversity of actors, including both governmental and private sectors in both countries, would tend toward an unwieldy process which could seriously limit conservationists’ ability to find partners both willing and able to contribute to watershed preservation schemes.
2. One of the four quadrants of the La Amistad area (Panama – Pacific slope) is already to a large degree “off the table” by virtue of the existence of dams which close all World Heritage Site watersheds in that quadrant to upstream migrants.
3. A regional-scale mitigation proposal would perhaps be more attractive were there other major threats to the maintenance of diadromy and corridor function in the La Amistad World Heritage Site and its downstream watersheds. However, on the Atlantic slope, which comprises most of the area of concern, watersheds at altitudes above proposed dams already enjoy fairly good to excellent protection from on-site anthropogenic stresses, thanks to their location within PILA and other protected areas. In this context, the “swapping off” of particular watershed areas would not seem an attractive bargain, even if other alternatives are not available.

Conclusion:

Effective mitigation of environmental problems caused by damming rivers requires that a number of conditions be met:

- Implementation of mitigation measures must be technically feasible, based on present knowledge: In the particular case presented by the rivers, and especially the diverse biota, of the La Amistad region it would be far from feasible to meet this condition even were the multiple research projects necessary to approach the condition already funded and underway.
- Incorporation of mitigation strategies must be economically feasible during both the construction and operational phases of the dam. At best, meeting this condition will normally require a lengthy process of negotiation, since the purpose of building a dam is not to enhance natural values. Dam builders and operators are motivated principally by the purpose of the particular dam (in the La Amistad context, generation of electrical power) and the desire to realize a profit. Modifications to achieve other goals are usually seen as distractions and added cost items which contribute nothing to achievement of primary goals.
- There should be a willingness on the part of those involved in dam operation to “play by the rules.” If the slightest doubt exists (and it usually does), full implementation of a mitigation strategy will require the availability of a dedicated, knowledgeable and capable regulatory force.

- If mitigation is to be more than pro forma, there must also be a provision for long term monitoring to determine whether mitigation goals are being met, and to detect any problems which may call for changes in dam management.

In general, we agree with the assessment of a World Bank Working Paper entitled "Good Dams and Bad Dams" – "In the real world of limited budgets, tight construction timetables, conflicting priorities and weak implementing agencies, the ideal mitigation measures are often not carried out, even if properly planned" and "because mitigation measures are often not fully implemented, and are sometimes inherently inadequate, the single most important environmental mitigation measure for a new hydroelectric project is good site selection, to ensure that the proposed dam will be largely benign in the first place." (Ledec and Quintero, 2003).

Relating this specifically to migratory fish and shrimp, Freeman, et al. (2003) assert that "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."

It seems to us that Ledec and Quintero (2003), Freeman, et al. (2003) and most others who have attempted to analyze the environmental effects of damming rivers at global or regional scales project an unwarranted confidence in the willingness/ability of national governments at the highest levels to prioritize biodiversity and other environmental concerns in planning for infrastructure projects such as dams. In the specific cases of Costa Rica and Panama, while within the national governments, and especially within those agencies charged with natural resource conservations, there is no great lack of awareness of the kinds of concerns expressed here, to all appearances the only goal driving dam planning is to maximize development of each country's energy potential. Within that single criterion the factors influencing site selection appear to be economic potential, projected energy contribution and feasibility of construction. Preservation of stream functions, biodiversity conservation and other environmental factors (along with sociocultural issues) enter as a subset of the feasibility concern – i.e. they become important to the extent that other actors raise objections or undertake actions which can lead to delays or unanticipated costs or which reflect poorly on the international conservation image of the countries. This situation is exemplified by the belated appearance of a totally inadequate mitigation proposal for the CHAN-75 dam (AES and MWH, 2009), over a year after construction began, and apparently at least partly in response to environmental concerns raised by environmental and indigenous rights advocates. The obvious reality that the mitigation measures proposed are untested and could not possibly be set in place until years after scheduled dam closure impugns the seriousness of the whole mitigation endeavor.

Based on long term familiarity with the biotic resources to be impacted, plus considerable knowledge of specific dam plans in the Changuinola/Teribe and Sixaola/Telire watersheds, we consider that the dams proposed for the rivers draining the La Amistad World Heritage Site in general are unacceptable at the level of site selection. Thus no adequate mitigation is possible.

RECOMMENDATIONS

Our previous report (McLarney and Mafla, 2007) was prepared for presentation with and in support of a petition to UNESCO to place La Amistad on the official list of World Heritage Sites in Danger (Thorson, et al. 2007). This step has not been taken, and at this time we do not wish to make a firm recommendation that UNESCO do so. Neither do we wish to discourage such a step; we are simply not in a position to suggest which steps might be most effective in arresting what we see as very serious threats to the biodiversity and ecological integrity which the two National Parks comprising the La Amistad World Heritage Site were established to protect (Alvarado, 1989).

We would note that the threat has become more serious with the disclosure of multiple dam plans on the Atlantic slope of the La Amistad area in Costa Rica (complemented by our own greater awareness of pre-existing similar problems on the Pacific slope of both countries). While the 2008 UNESCO mission necessarily involved the governments of both countries, and some problems in Costa Rica's La Amistad National Park were identified, the burden of criticism and ensuing recommendations fell much more heavily on the country (Panama) where a clear and direct threat to biodiversity was identified in the form of hydroelectric dam proposals in the Changuinola/Teribe watershed.

At this time, the scope of the threat is equal in the two countries, though more immediate in Panama. As we have shown in this report, the potential damage at this time is not just to parts of one of the major watersheds draining PILA (the Changuinola/Teribe), with probable multiple species extirpations in over half of that watershed within the World Heritage Site, but to two thirds of the two combined national parks, including large portions of all major watersheds, with similar damage in the other protected areas and indigenous territories forming the La Amistad Biosphere Reserve. We recommend that, in the light of this information on the increased dimension of the threat, the question of designating La Amistad as a World Heritage Site in Danger, along with all alternatives, be considered as though this were a new issue.

In considering the complex situation presented by the La Amistad area, we acknowledge two facts stated in Pringle (2001). Referring to the frequent declaration of Protected Areas in upper watersheds, she stated that:

- "Governments often protect such areas because of a combination of poor agricultural potential, scenic value or protection of human water supplies. Ecological and wildlife values are often a secondary benefit." We would note that, as cited above, in the specific case of La Amistad there is a clearly articulated commitment to "ecological and wildlife values".

- ". . . protection and management of hydrologic connectivity have not been given the attention that they deserve by either conservation biologists or resource managers."

To which we would add that conservationists and resource managers no longer have the luxury of defining "the resource" within administrative borders. We cannot fully protect the diadromous species of the La Amistad World Heritage Site, the biodiversity of which they form part, or the ecosystem within which they function by acting solely within the boundaries of the World Heritage Site or a larger cluster of Protected Areas. We suggest that UNESCO is in an excellent position to provide leadership toward implementation of a broader concept of protecting biodiversity in the La Amistad Area, taking full account of hydrologic connectivity.

Our fundamental recommendation is that, for the purpose of maintaining the outstanding biodiversity of the >9,000 sq. km. area of which the binational La Amistad World Heritage Site forms the core, hydrologic connectivity needs to preserved, and large dams should not be built on the rivers draining the area. While one may or may not agree with one of the founders of the Costa Rican National Parks System, Mario Boza, that “International environmental standards should be set by a United Nations environmental organization that is empowered to infringe upon the sovereignty of individual states in environmental matters” (Boza, 1993) one must recognize that UNESCO cannot order the implementation of such a recommendation. We therefore respectfully request the UNESCO World Heritage Committee to carry out whatever actions will, in your judgement, best move the governments of Costa Rica and Panama, along with other actors, toward the realization of our recommendation.

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The Spanish version of the Executive Summary was translated by Elena Carlson. Former ANAI intern Diego Rivera will be responsible for preparing a Spanish version of the complete document, for publication later this year.

The impetus for an expanded version of our original report to UNESCO came from Osvaldo Jordan, and his willingness to help throughout the process was an indispensable asset.

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TABLE 1. La Amistad World Heritage Site Watersheds, with Areas Above Proposed Dams.

				Areas above dam affected:			
Watershed/Country:	**Total Area (sq. km.):**	**Area in PILA (sq. km.):**	**Lowermost Dam:**	**Total (sq. km.):**	**%**	**in PILA (sq. km.):**	**%**
Atlantic slope							
Changuinola/Teribe	3,445	2,069		1,587	46.1	1,066	51.5
Panama	3,190	1,814	CHAN-75 (Gavilan)*	1,443	45.2	990	54.6
			Bonyic*	144	100.0	76	100.0
Costa Rica	255	255	No Dams	—	—	—	0.0
Sixaola/Telire	2,752	1,396	Talamanca	2,123	77.1	1,282	91.8
Panama	647	207	No Dams	94	14.5	94	45.4
Costa Rica	2,105	1,189	Talamanca	2,029	96.4	1,189	100.0
Estrella, Costa Rica	717	180	Estrella	308	43.0	180	100.0
Banano, Costa Rica	202	24	Banano	30	14.7	19	79.2
Matina, Costa Rica	1,428	58	No Dams	—	—	0	0.0
Pacific slope							
Chiriqui, Panama	1,925	17	Los Añiles **	782	40.6	17	100.0
Chiriqui Viejo, Panama	1,339	68	Burica*	760	56.8	68	100.0
Grande de Terraba, Costa Rica	4,897	255		2,733	55.8	95	37.3
General River	3,294	14	Diquis	2,394	72.7	14	100.0
Coto Brus River	1,603	241	6 small dams on tributaries	339	21.1	81	33.6
TOTALS:***							
La Amistad watershed	15,277			8,323	54.5		
World Heritage Site (PILA)		4,067				2,727	67.1
Panama	7,101	2,106		3,070	43.4	1,169	55.5
Costa Rica	8,176	1,903		5,264	64.4	1,483	77.9

* Under construction

** Constructed and operational

***(Do not include Rio Matina watershed, with 4% of its total watershed in PILA, and several dams in the watershed which do not directly affect PILA)

TABLE 2. Fresh Water Fishes of the La Amistad Watersheds (Atlantic Slope)

	Watershed:					
Species:	**Changuinola/ Teribe:**	**Sixaola/ Telire:**	**Estrella:**	**In PILA:**	**Type of diadromy:**	**Comments:**
1. Known diadromous species						
Anguilla rostrata	X	X	X	X	Catadromy	Sensitive species
Microphis lineatus	X	X			Anadromy	
Pseudophallus mindii			X		Anadromy	
Agonostomus monticola	X	X	X	X	Amphidromy?	Important food fish
Joturus pichardi	X	X	X	X	Catadromy?	Important food fish
Awaous banana	X	X	X	X	Amphidromy	
Sicydium adelum/altum	X	X	X	X	Amphidromy	Single dominant species in PILA
Dormitator maculatus	X	X			Catadromy?	
Eleotris amblyopsis/pisonis	X	X	X		Catadromy	
Gobiomorus dormitor	X	X	X	X	Catadromy	Important food fish
2. Possible/probable diadromous species						
Atherinella chagresi	X	X	X	X	Amphidromy?	
Gobiesox nudus	X			X	Probable amphidromy	
Eugerres plumieri	X				???	Probable marine wanderer
Pomadasys crocro	X	X	X	X	Probable amphidromy	Important food fish
Citharichthys spilopterus		X			Catadromy?	Possible in PILA
Trinectes paulistanus			X		Catadromy?	
3. Non-diadromous species						
Myrophis punctatus	X					Principally estuarine
Astyanax aeneus	X	X	X	X	(Possible potamodromy)	
Astyanax orthodus	X	X		X		

Brycon guatemalensis			X		(Potamodromy)	Important food fish
Bryconamericus gonzalezi	X	X		X		
Bryconamericus scleroparius	X	X	X	X		
Hyphessobrycon panamensis	X	X				
Brachyhypopomus occidentalis	X	X				
Gymnotus cylindricus		X	X			
Rhamdia guatemalensis	X	X	X	X	(Possible potamodromy)	
Rhamdia laticauda/rogersi	X	X	X	X	(Possible potamodromy)	
Rivulus spp.	X	X	X	X		
Alfaro cultratus	X	X	X	X		
Brachyraphis cascajalensis/parismina	X	X				
Phallichthys amates	X	X	X	X		
Phallichthys quadripunctatus	X	X				
Poecilia gillii	X	X	X	X		
Priapichthys annectens	X	X	X	X		
Synbranchus marmoratus	X	X	X			
Centropomus pectinatus	X	X	X			Marine wanderer
Centropomus undecimalis	X	X	X	X		Marine wanderer
Caranx sp.	X			X		Marine wanderer
Amphilophus (Astatheros) bussingi	X	X	X	X		
Amphilophus (Astatheros) rhytisma	X	X	X			
Archocentrus myrnae		X	X	X		
Archocentrus nigrofasciatus	X	X	X			
Archocentrus spilurus	X					
Oreochromis spp.	X	X	X			Exotic
Parachromis loiselli	X	X	X			
Parachromis managuense			X			Exotic
Vieja maculicauda			X			Principally estuarine
Mugil curema			X			Marine wanderer
Gobionellus fasciatus	X					Principally estuarine

TABLE 3. Fresh Water Fishes of the La Amistad Watersheds (Pacific slope)

	Watershed:			
Species:	**Grande de Terraba:**	**Chiriqui Viejo/ Chiriqui:**	**Possible in PILA:**	**Comments:**
1. Probable/possible diadromous species				
Pseudophallus starksii		X		Anadromous
Haemulopsis leuciscus		X		
Pomadasys bayanus	X		X	Probably amphidromous
Agonostomus monticola	X	X	X	Amphidromous
Awaous transandeanus	X	X	X	Amphidromous
Sicydium salvini	X	X	X	Amphidromous
Hemieleotris latifasciatus	X	X		Catadromous?
Dormitator latifrons	X			Catadromous?
Eleotris picta	X	X		Amphidromous?
Gobiomorus maculatus	X	X		Catadromous
Trinectes fonsecensis	X			Amphidromous?
2. Non-diadromous species				
Astyanax aeneus	X	X	X	Possibly potamodromous
Cheirodon dialepturus		X		
Pterobrycon myrnae	X			
Brycon behreae	X	X		Potamodromous
Bryconamericus terrabensis	X		X	
Hyphessobrycon savagei	X			
Pseudocheirodon terrabae	X			
Roeboides ilseae	X			
Piabucina boruca	X		X	
Arias seemani	X	X		Primarily estuarine
Cathorops steindachneri		X		Primarily estuarine
Cathorops tuyra		X		Primarily estuarine
Nannorhamdia lineata	X		X	Possibly potamodromous
Rhamdia guatemalensis	X	X		Possibly potamodromous

Rhamdia laticauda/rogersi	X	X	X	Possibly potamodromous
Pimelodella chagresi	X	X		Possibly potamodromous
Trichomycterus striatus	X	X		
Hypostomus panamensis	X	X		
Oncorhynchus mykiss		X	X	Exotic
Rivulus hildebrandi	X	X		
Rivulus uroflammeus	X	X	X	
Rivulus glaucus	X			
Brachyraphis episcopi		X		
Brachyraphis rhabdophora	X			
Brachyraphis terrabensis	X	X	X	
Poecilia gillii	X	X	X	
Poecilia mexicana	X			Questionable identity
Poeciliopsis elongata	X			
Poeciliopsis paucimaculata	X		X	
Poeciliopsis retropinna	X	X	X	
Poeciliopsis turrubarensis		X		
Priapichthys panamensis	X	X		
Synbranchus marmoratus	X	X		
Centropomus nigrescens	X			Marine wanderer
Centropomus viridens	X			Marine wanderer
Caranx caballus	X			Marine wanderer
Caranx caninus	X			Marine wanderer
Lutjanus jordani	X			Marine wanderer
Lutjanus novemfasciatus	X			Marine wanderer
Eucinostomus currani	X			Principally estuarine
Eugerres brevimanus	X			Principally estuarine
Astatheros altifrons	X			
Astatheros diquis	X			
Archocentrus sajica	X			
Theraps sieboldii	X	X		
Oreochromis niloticus	X			Exotic
Mugil curema	X			Principally estuarine


La Amistad World Heritage Site and Protected Natural Areas
N
W
E
S
Nairi Awari Indigenous Reserve
Barbilla National Park
Bajo Chirripó Indigenous Reserve
Limoncito Wildlife Refuge
Banano Buffer Zone
Alto Chirripó Indigenous Reserve
Tayni Indigenous Reserve
Cahuita National Park
Río Macho Forest Reserve
Tapantí National Park
Hitoy Cerere Biological Reserve
Telire Indigenous Reserve
Cabecar Indigenous Reserve
Kekoldi Indigenous Reserve
Gandoca-Manzanillo Wildlife Refuge
San San-Pondsak
Bribri Indigenous Reserve
Chirripó National Park
La Amistad World Heritage Site
Ujarrás Indigenous Reserve
Isla Bastimentos National Park
Salitre Indigenous Reserve
Cabagra Indigenous Reserve
Palo Seco
Térraba Indigenous Reserve
Boruca Indigenous Reserve
Las Tablas Buffer Zone
Rey Curré Indigenous Reserve
86°0'0"W
84°0'0"W
82°0'0"W
80°0'0"W
78°0'0"W
12°0'0"N
10°0'0"N
8°0'0"N
Coto Brus Indigenous Reserve
Volcán Barú National Park
Lagunas del Volcán Wetland
Fortuna Forest Reserve
Ngobe-Bugle Indigenous Reserve
Scale 1:1,100,000
0
12.5
25
50
75
100
km

Figure 1

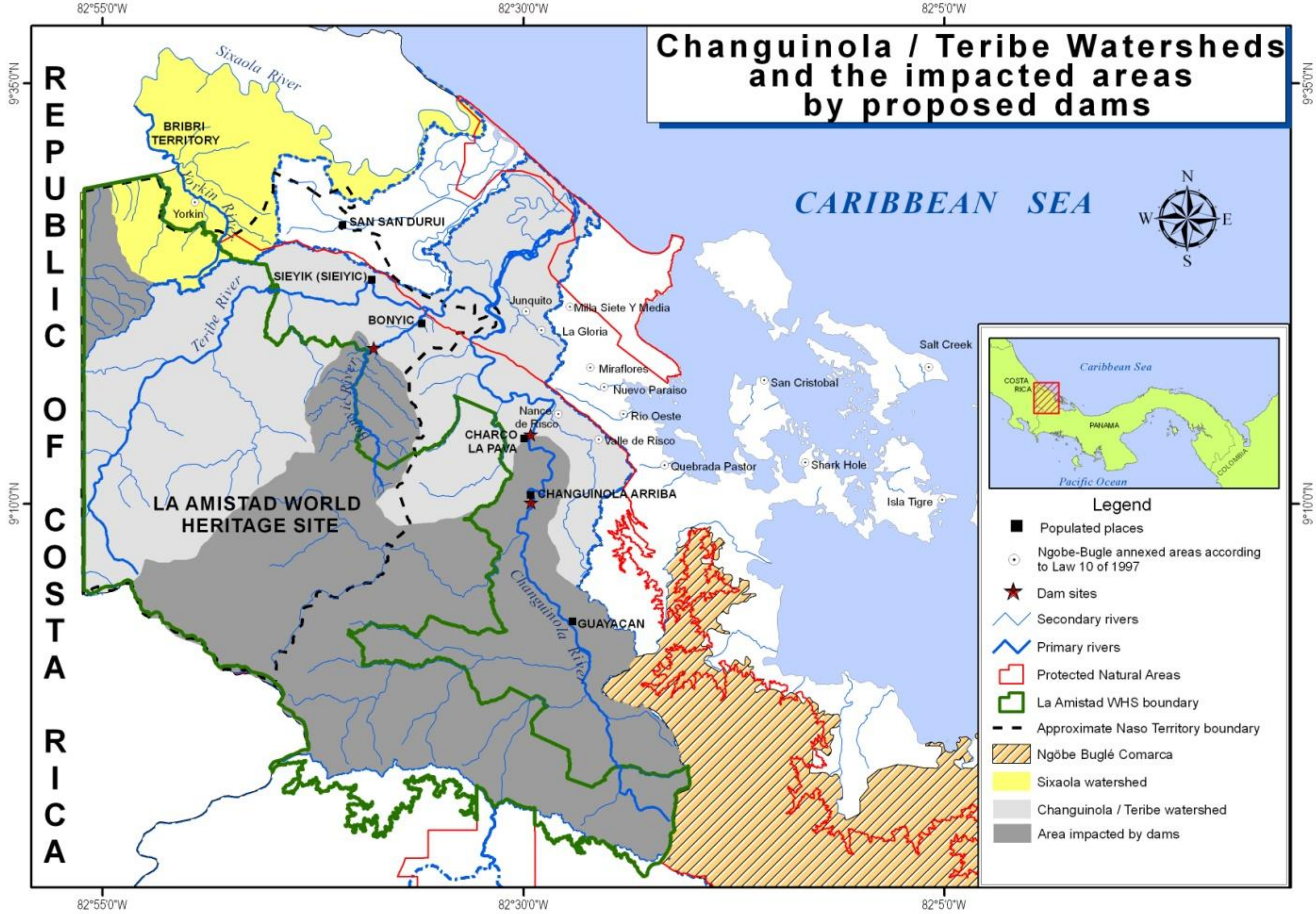

Changuinola / Teribe Watersheds and the impacted areas by proposed dams
82°55'0"W
82°30'0"W
82°5'0"W
9°35'0"N
9°10'0"N
REPUBLIC OF COSTA RICA
CARIBBEAN SEA
N
S
E
W
Sixaola River
BRIBRI TERRITORY
Yorkin
Yorkin River
SAN SAN DURUI
SIEYIK (SIEIYIC)
BONYIC
Teribe River
Junquito
Milla Siete Y Media
La Gloria
Miraflores
Nuevo Paraiso
Rio Oeste
Nance de Risco
Valle de Risco
CHARCO LA PAVA
Quebrada Pastor
CHANGUINOLA ARRIBA
LA AMISTAD WORLD HERITAGE SITE
Changuinola River
GUAYACAN
San Cristobal
Shark Hole
Salt Creek
Isla Tigre
Caribbean Sea
COSTA RICA
PANAMA
COLOMBIA
Pacific Ocean
Legend
Populated places
Ngobe-Bugle annexed areas according to Law 10 of 1997
Dam sites
Secondary rivers
Primary rivers
Protected Natural Areas
La Amistad WHS boundary
Approximate Naso Territory boundary
Ngöbe Buglé Comarca
Sixaola watershed
Changuinola / Teribe watershed
Area impacted by dams

Figure 2

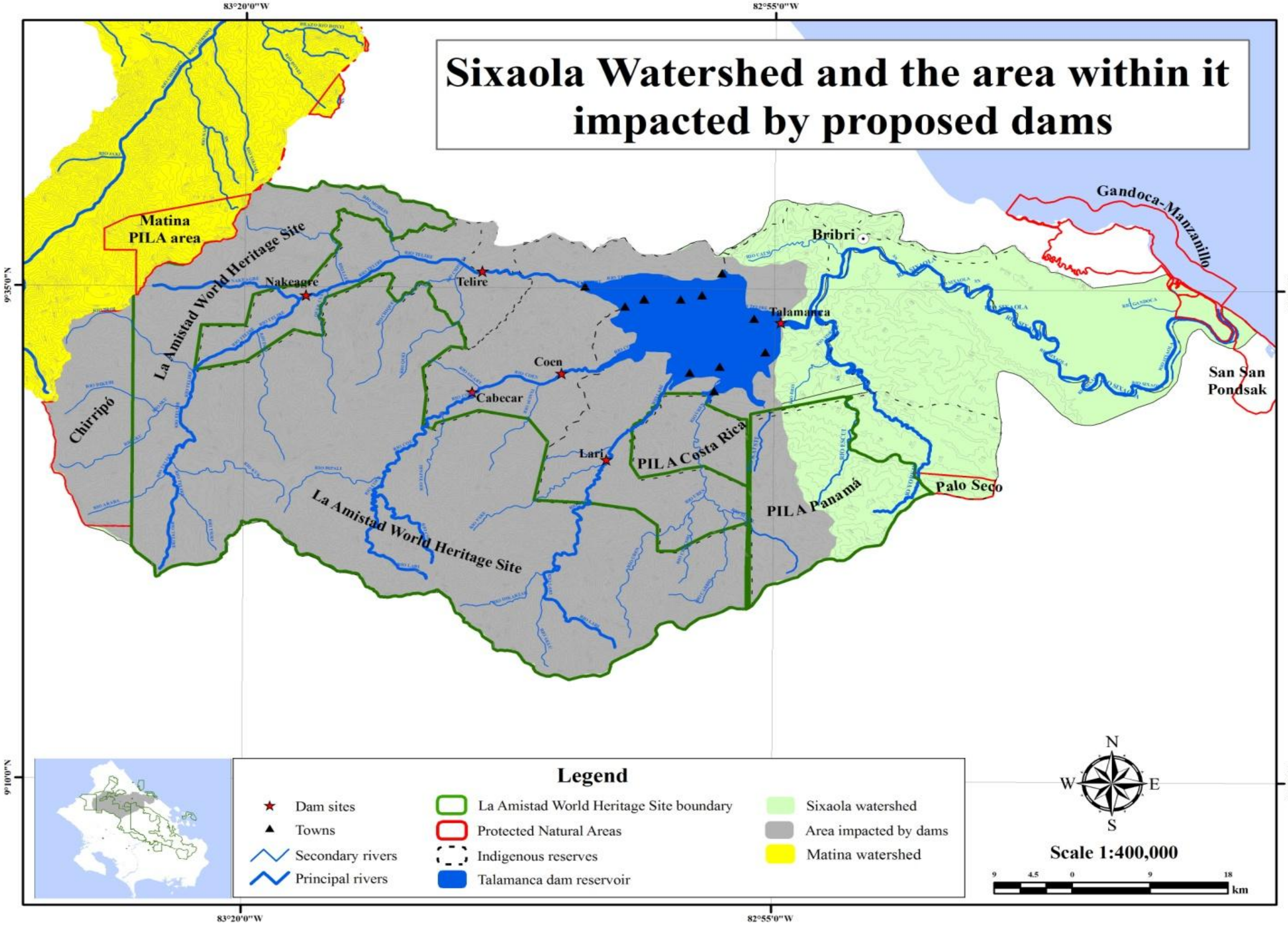

Sixaola Watershed and the area within it impacted by proposed dams
83°20'0"W
82°55'0"W
9°35'0"N
9°10'0"N
Matina PILA area
La Amistad World Heritage Site
Nakeagre
Telire
Coen
Cabecar
Lari
Talamanca
Bribri
Gandoca-Manzanillo
San San Pondsak
Palo Seco
PILA Costa Rica
PILA Panamá
Chirripó
La Amistad World Heritage Site
Legend
Dam sites
Towns
Secondary rivers
Principal rivers
La Amistad World Heritage Site boundary
Protected Natural Areas
Indigenous reserves
Talamanca dam reservoir
Sixaola watershed
Area impacted by dams
Matina watershed
N
S
E
W
Scale 1:400,000
9
4.5
0
9
18
km

Figure 3

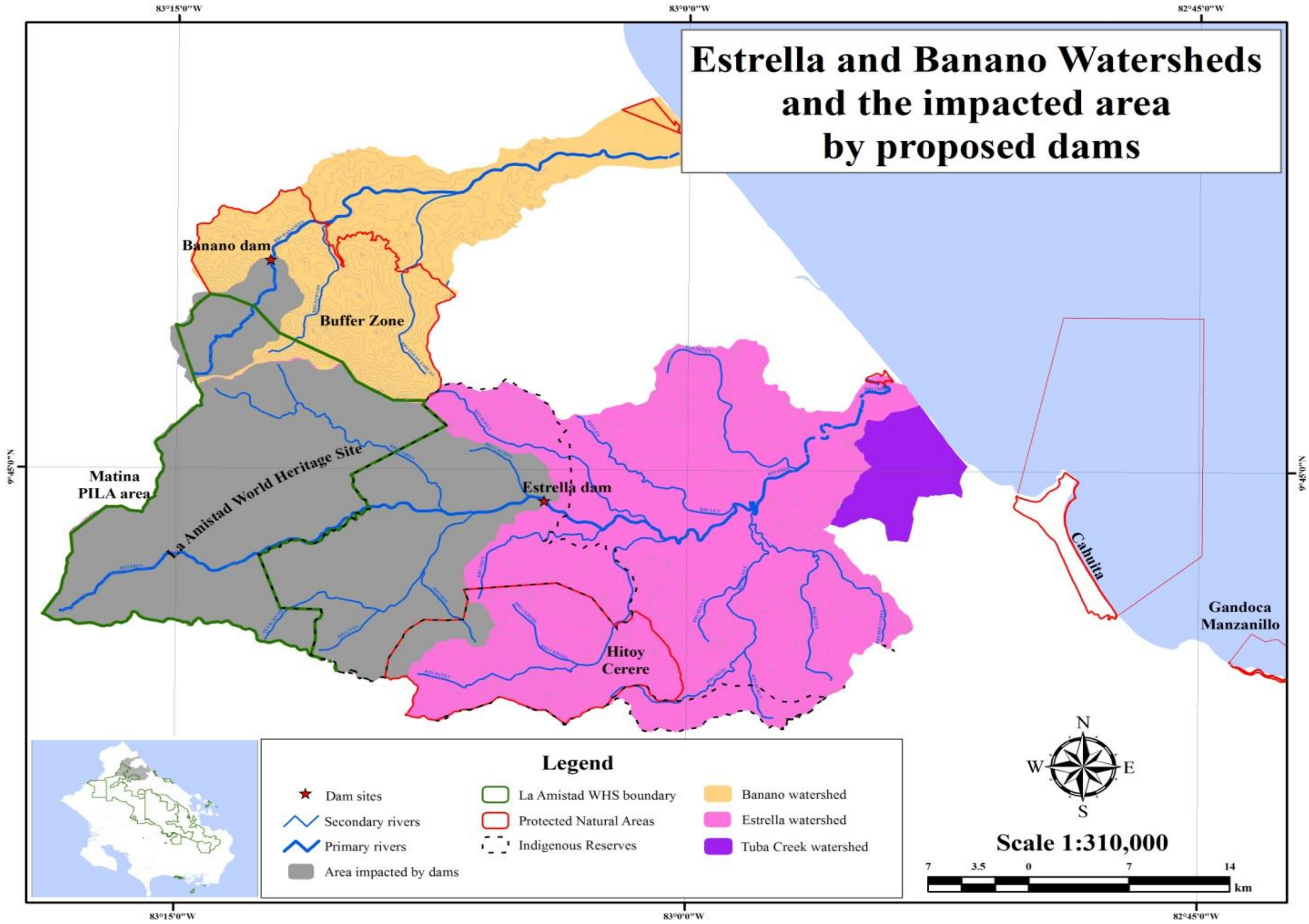
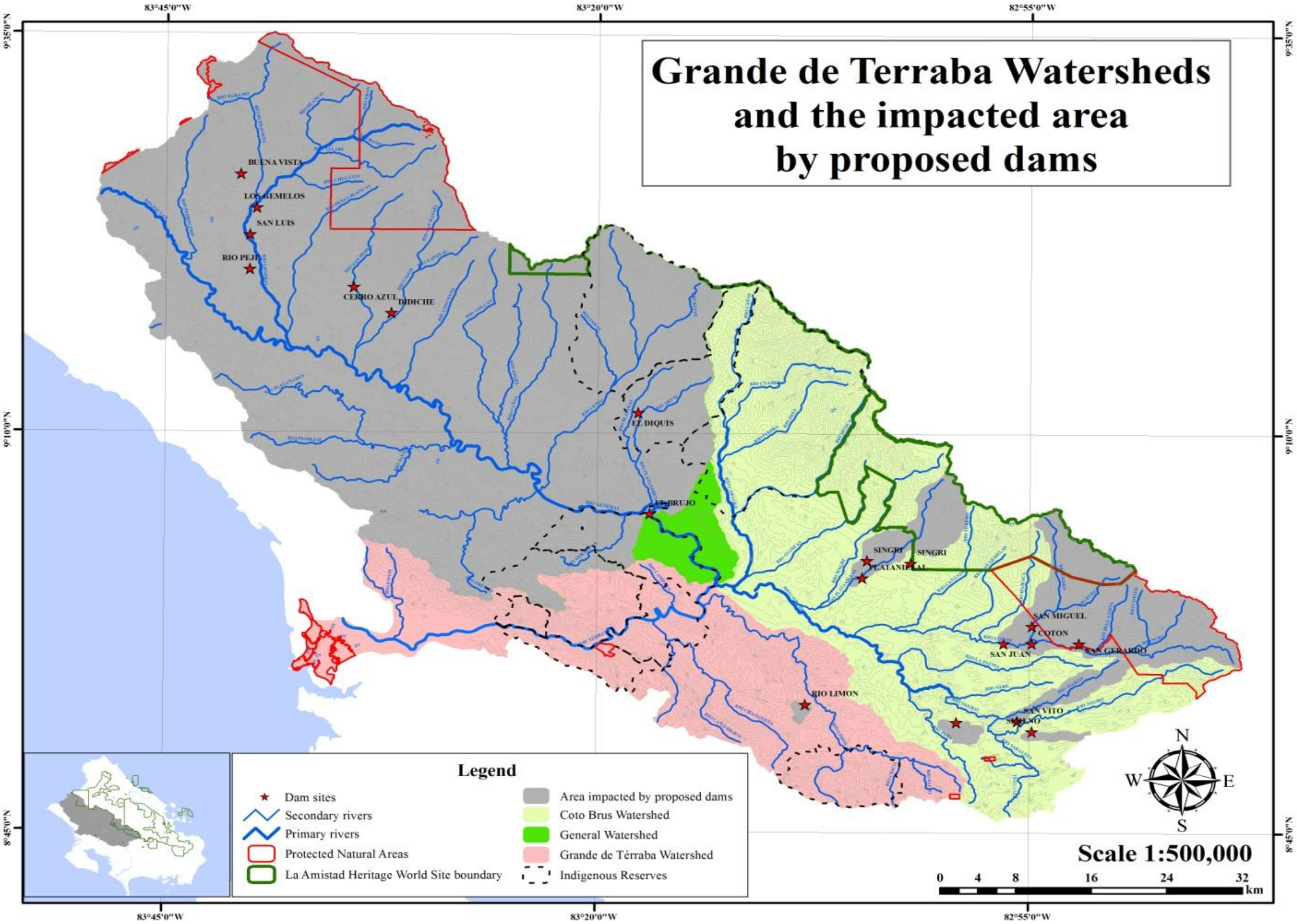

Estrella and Banano Watersheds and the impacted area by proposed dams
83°15'0"W
83°0'0"W
82°45'0"W
9°45'0"N
Banano dam
Buffer Zone
Matina PILA area
La Amistad World Heritage Site
Estrella dam
Hitoy Cerere
Cahuita
Gandoca Manzanillo
Legend
Dam sites
Secondary rivers
Primary rivers
Area impacted by dams
La Amistad WHS boundary
Protected Natural Areas
Indigenous Reserves
Banano watershed
Estrella watershed
Tuba Creek watershed
N
W
E
S
Scale 1:310,000
7
3.5
0
7
14
km

Figure 4



Grande de Terraba Watersheds and the impacted area by proposed dams
83°45'0"W
83°20'0"W
82°55'0"W
9°35'0"N
9°10'0"N
8°45'0"N
BUENA VISTA
LOS GEMELOS
SAN LUIS
RIO PEJE
CERRO AZUL
DIDICHE
EL DIQUIS
EL BRUJO
SINGRI
SINGRI
PLATANILLAL
SAN MIGUEL
COTON
SAN JUAN
SAN GERARDO
RIO LIMON
SAN VITO
Legend
★ Dam sites
Secondary rivers
Primary rivers
Protected Natural Areas
La Amistad Heritage World Site boundary
Area impacted by proposed dams
Coto Brus Watershed
General Watershed
Grande de Térraba Watershed
Indigenous Reserves
N
S
E
W
Scale 1:500,000
0 4 8 16 24 32 km

Figure 5

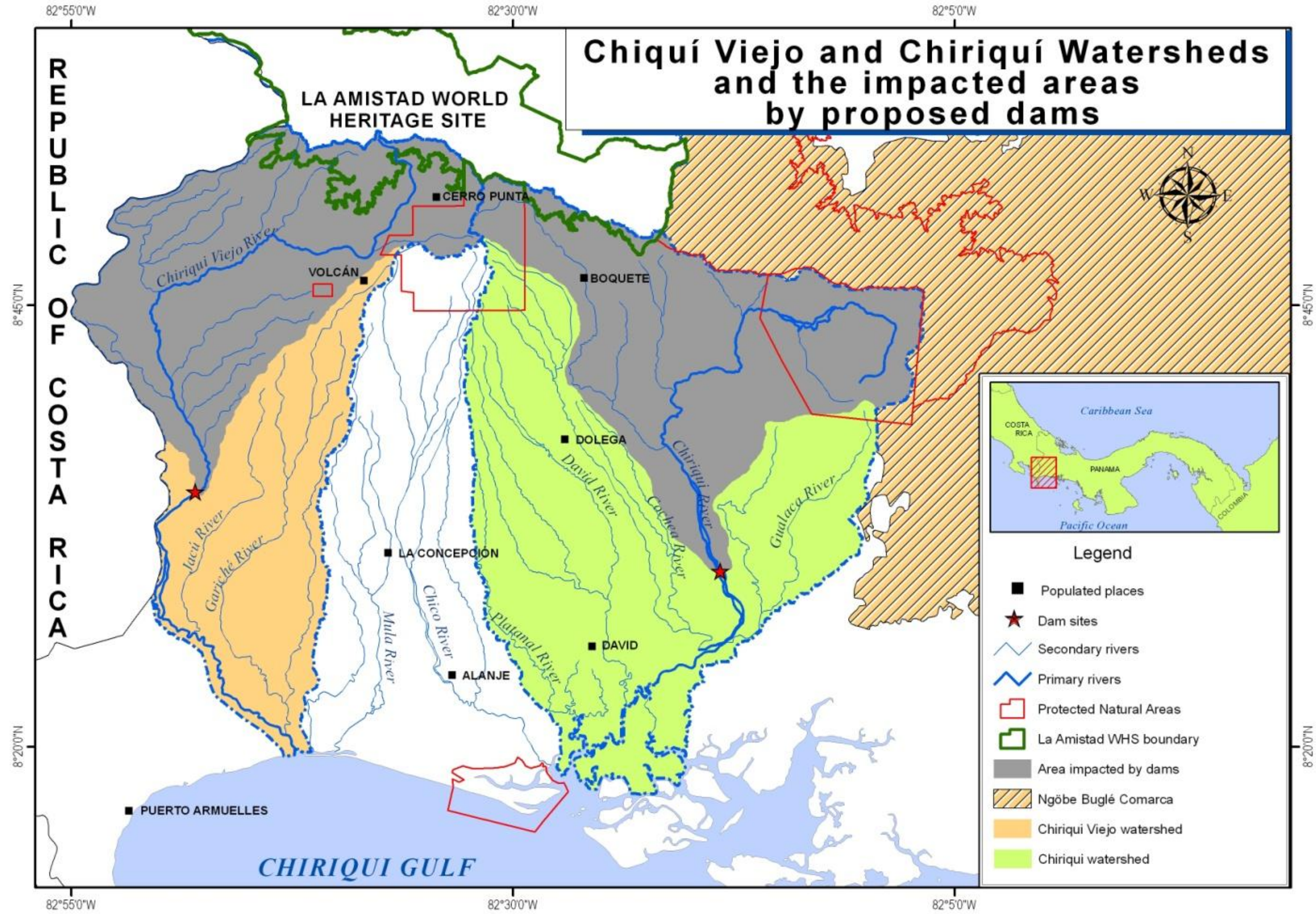

Chiquí Viejo and Chiriquí Watersheds and the impacted areas by proposed dams
82°55'0"W
82°30'0"W
82°5'0"W
8°45'0"N
8°20'0"N
REPUBLIC OF COSTA RICA
LA AMISTAD WORLD HERITAGE SITE
CERRO PUNTA
VOLCÁN
BOQUETE
DOLEGA
LA CONCEPCION
ALANJE
DAVID
PUERTO ARMUELLES
CHIRIQUI GULF
Chiriqui Viejo River
Jacú River
Gariché River
Mula River
Chico River
Platanal River
David River
Cochea River
Chiriqui River
Gualaca River
N
S
E
W
Caribbean Sea
COSTA RICA
PANAMA
Pacific Ocean
COLOMBIA
Legend
Populated places
Dam sites
Secondary rivers
Primary rivers
Protected Natural Areas
La Amistad WHS boundary
Area impacted by dams
Ngöbe Buglé Comarca
Chiriqui Viejo watershed
Chiriqui watershed

Figure 6

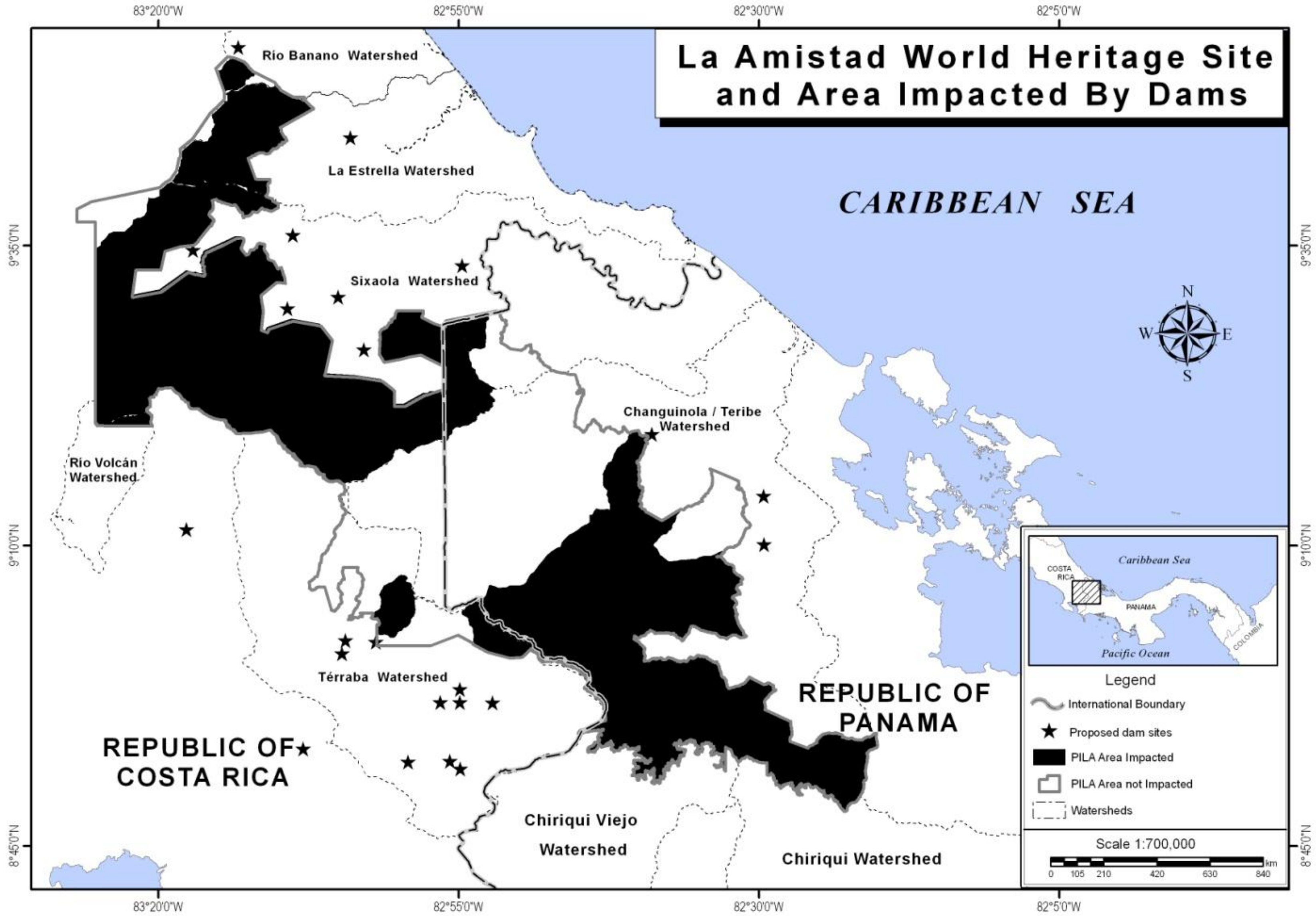

La Amistad World Heritage Site and Area Impacted By Dams
CARIBBEAN SEA
Rio Banano Watershed
La Estrella Watershed
Sixaola Watershed
Changuinola / Teribe Watershed
Río Volcán Watershed
Térraba Watershed
REPUBLIC OF COSTA RICA
REPUBLIC OF PANAMA
Chiriqui Viejo Watershed
Chiriqui Watershed
N
S
E
W
Caribbean Sea
COSTA RICA
PANAMA
COLOMBIA
Pacific Ocean
Legend
International Boundary
Proposed dam sites
PILA Area Impacted
PILA Area not Impacted
Watersheds
Scale 1:700,000
0
105
210
420
630
840
km
83°20'0"W
82°55'0"W
82°30'0"W
82°5'0"W
9°35'0"N
9°10'0"N
8°45'0"N

Figure 7

Asociación ANAI, Apartado 170-2070 Sabanilla de Montes de Oca, Costa Rica.
Tel (506) 22243570 Fax (506) 22537524