EVOLUTION AND ZOOGEOGRAPHY OF

FRESHWATER ELASMOBRANCHS

WITH NOTES ON THEIR CONSERVATION

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Introduction

Freshwater elasmobranchs have been known for centuries but are not well known biologically. Their fishery management and conservation have received little study.

Salinity regimens used here are as follows:

Fresh water = salinity 0-10 ‰
Brackish = 11-32 ‰
Salt water = >‰

Following Compagno & Cook (1995a) freshwater elasmobranchs are divided into four habitat categories:

- Marginal (inshore marine, marginal in fresh water)
- Brackish Marginal (brackish to freshwater, marginal in rivers)
- Euryhaline (inshore marine, penetrating far up rivers into fresh water, far beyond tidal action; may breed in fresh water)
- Obligate Freshwater (occur only in fresh water)

Evolution

The earliest freshwater elasmobranchs were Xenacanthiformes, which arose in the upper Devonian (about 380 mya). Xenacanths appear to be the primitive sister taxon of the ctenacanths. Two families are recognized. *Orthacanthus*, from the Permian of Europe and North America, grew to a length of about 3 m. Xenacanths were widely distributed throughout what is now Europe, North America, and East Asia. This group persisted for nearly 200 million years, almost exclusively in freshwater habitats, until the end of the Triassic (about 215 mya).

In the Permian and Triassic, freshwater and brackish Hybodontiformes replaced the xenacanths. Hybodonts are derived protoselachians, sharing a common ancestor with xenacanths and ctenacanths. Six families are recognized. Hybodonts were widely distributed, found in freshwater and marine strata in what is now Europe, Spitzbergen, Greenland, North and South America, and southern Asia, and Australia. Freshwater hybodonts tended to be small. *Lissodus*, from the Permian of Africa (about 275 mya), was only 15 cm TL. Hybodonts persisted in freshwater habitats until the late Cretaceous (about 75 mya), surviving several million years longer than their marine relatives.

The earliest neoselachians to invade freshwater were probably the carcharhinoids, which arose during the late Jurassic (about 150 mya) in marine environments; it is not known when they first expanded to freshwater habitats. *Lamiopsis* is the primitive sister taxon to a clade formed by the euryhaline (*C. leucas* and *C. amboinensis*) + the euryhaline-obligate freshwater *Glyphis*.

Pristoids may have arisen as early as the late Cretaceous (about 100 mya), but the first undoubted pristid does not occur until the early Eocene (bout 57 mya). Pristids appear to have been euryhaline from their earliest appearance.

Myliobatoids arose in marine habitats of the late Cretaceous (about 100 mya). Some forms, e.g. *Heliobatis*, invaded fresh waters by the early Eocene (about 57 mya).

Potamotrygonids represent a monophyletic group derived from a Pacific *Urolophus*-like ancestor. Their common ancestor apparently became trapped in isolated freshwater habitats by orogenic events during the Paleocene-Miocene (65-23 mya). *Paratrygon* is the primitive sister taxon to the clade formed by

Plesiotrygon and *Potamotrygon*. The sister group to the potamotrygonids appears to be amphi-American *Himantura* (Thorson et al., 1983).

Diversity

Approximately 45 species of elasmobranch, in four families and ten genera, are found in fresh water far beyond tidal influences in rivers and estuaries; at least 48 additional elasmobranch species penetrate fresh water in estuaries or river mouths but are not found far from the sea. Diversity of freshwater elasmobranch is dominated by potamotrygonid and dasyatid stingrays, which together comprise almost half of freshwater elasmobranchs (Table 1). Extant obligate euryhaline and freshwater elasmobranchs comprise three relatively unspecialized ecomorphotypes (rajobenthic, pristobenthic, and littoral) and are largely restricted to tropical rivers and lakes. The low taxonomic, ecological, and morphological diversity of freshwater sharks and rays compared with freshwater bony fishes and marine cartilaginous fishes suggest that fresh water may be a marginal habitat for elasmobranchs.

Table 1: Summary of habitat distribution of freshwater elasmobranchs (Modified after and updated from Compagno & Cook 1995a)

1) MARGINAL SPECIES:	**Order Carcharhiniformes**
Order Hexanchiformes	Hound Sharks – Family Triakidae
Cow Sharks – Family Hexanchidae	*Mustelus* (2 species)
Notorynchus (1 species)	*Triakis* (1 species)
Order Squaliformes	Requiem Sharks – Family Carcharhinidae
Spiny Dogfishes – Family Squalidae	*Rhizoprionodon* (2 species)
Squalus (1 species)	*Scoliodon* (1 species)
Sleeper Sharks – Family Somniosidae	*Carcharhinus* (6 species)
Somniosus (1 species)	*Glyphis* (2 species)
Order Lamniformes	*Negaprion* (1 species)
Mackerel Sharks – Family Lamnidae	Hammerhead Sharks – Family Sphyrnidae
Carcharodon (1 species)	*Sphyrna* (2 species)
Lamna (1 species)	**Order Pristiformes**
Order Orectolobiformes	Sawfishes – Family Prisidae
Long-Tailed Carpet Sharks – Family Hemiscylliidae	*Pristis* (1 species)
Chiloscyllium (1 species)	**Order Rhiniformes**
	Wedgefishes – Family Rhinidae
	Rhynchobatus (1 species)

Table 1: (continued)

1) MARGINAL SPECIES (cont'd)**:** **Order Rhinobatiformes** Guitarfishes – Family Rhinobatidae *Rhinobatos* (2 species) **Order Myliobatiformes** Round Stingrays – Family Urolophidae *Urolophus* (1 species) Whiptail Stingrays – Family Dasyatidae *Dasyatis* (6 species) *Himantura* (2 species) (unidentified dasyatid, North Carolina) Butterfly Rays – Family Gymnuridae *Gymnura* (3 species) Eagle Rays – Family Myliobatidae *Aetobatus* (1 species) *Myliobatis* (2 species) Cownose Rays – Family Rhinopteridae *Rhinoptera* (2 species) **2) BRACKISH MARGINAL SPECIES** **Order Myliobatiformes** Whiptail Stingrays – Family Dasyatidae *Dasyatis* (1 species) *Himantura* (1 species)	**3) EURYHALINE SPECIES:** **Order Carcharhiniformes** Requiem Sharks – Family Carcharhinidae *Carcharhinus* (1 species) *Glyphis* (3 species) **Order Pristiformes** Sawfishes – Family Pristidae *Anoxypristis* (1 species) *Pristis* (5 species) **Order Myliobatiformes** Whiptail Stingrays – Family Dasyatidae *Dasyatis* (2 species) *Himantura* (2 species) *Pastinachus* (1 species) **4) OBLIGATE FRESHWATER SPECIES:** **Order Carcharhiniformes** Requiem Sharks – Family Carcharhinidae *Glyphis* (1 species) **Order Myliobatiformes** River Stingrays – Family Potamotrygonidae *Paratrygon* (1 species) *Plesiotrygon* (1 species) *Potamotrygon* (18 species) (undescribed potamotrygonid) Whiptail Stingrays – Family Dasyatidae *Dasyatis* (4 species) *Himantura* (4 species)

Taxonomic Problems

Taxonomic problems of fossil and extant freshwater elasmobranchs are summarized in Table 2.

Table 2: Taxonomic problems of fossil and extant freshwater elasmobranchs.

Taxon	**Problem(s)**
Antartilamna prisca	Does not appear to be a xenacanth
Aegyptobatis	Dubiously placed in Distobatidae
Asterocanthus eocaenus	Not a hybodont
Lissodus	Paraphyletic
Carcharhinus	Paraphyletic
Glyphis	3+ undescribed species
Pristidae	Systematics highly unsettled
Neotropical *Dasyatis*	Paraphyletic
Dasyatis ukpam	Does not appear to be a *Dasyatis*
Dasyatis sp. (China)	May be synonymous with *D. laosensis*
Himantura fluviatilis complex	3 species may be synonymous
Himantura krempfi	May be synonymous with *H. oxyrhyncha*
Potamotrygonidae	5+ undescribed species; many species inadequately defined; high degree of intraspecific polychromatism
Potamotrygon dumerilii and *P. humerosa*	Inadequately defined; lack material for proper characterization

Zoogeography

Some freshwater elasmobranchs occur in warm-temperate rivers such as the Mississippi River in the USA or the rivers of Natal in South Africa, but most occur in the tropics of both hemispheres.

The greatest diversity and endemism of freshwater elasmobranchs occurs in the Atlantic drainages of South America with its radiation of the Potamotrygonidae, but pockets of endemism and diversity also occur in West Africa and in Asia (from the Indian subcontinent eastward through Southeast Asia, southern China, Indonesia, New Guinea, the Philippines, and Australia). Freshwater elasmobranchs also occur in the Tigris River system of southern Iraq, from

several rivers in Africa, North America, southern Europe (Portugal), and rivers draining into the Mediterranean Sea.

Zoogeography of representative euryhaline and freshwater elasmobranch taxa (*C. leucas, Glyphis* spp., pristids, *Dasyatis*, *Himantura*, and potamotrygonids) are summarized in Figures 1-6. Selected records of euryhaline and freshwater elasmobranchs more than 200 km upriver from the sea are presented in Table 3.

Table 3: selected records of euryhaline and freshwater elasmobranchs >200 km upriver. Data from Compagno and Cook (1995a).

Species	**River**	**Distance from Sea (km)**
Carcharhinus leucas	Mississippi	3800
	Amazon	4200
	Zambezi	1120
Pristis perotteti	Amazon	1340
Dasyatis sabina	Mississippi	322
D. ukpam	Old Calabar	241
Himantura fluviatilis	Ganges	1600
H. uarnak	Trembeling	354

Threats

The tropical rivers and lakes where most freshwater elasmobranchs occur are mostly in developing countries with enormous, rapidly expanding human populations. Increasing levels of direct exploitation and modification or destruction of riverine and lacustrine ecosystems – especially where uncontrolled human population growth is occurring – threaten many freshwater elasmobranch stocks and obligate freshwater species with extinction (Compagno and Cook, 1995b). Threats to freshwater elasmobranchs are summarized in Table 4.

Table 4: Threats to freshwater elasmobranchs

Threat	Mechanism(s)	Status
Fisheries	Targeted and untargeted (bycatch) removal; reduction of prey base; ornamental trade	Increasing
Deforestation	Increased microclimate modification; damage to soil; water siltation; flooding	On-going
Damming Rivers	Cut off access to sea; extreme conditions in reservoirs	Increasing
Mining	Introduction of heavy metal pollutants (Pb, Cu, Hg) & radioactive isotopes (U) toxic to elasmobranchs and their prey	Increasing
Illegal Drug Manufacturing	Introduction of organic chemicals toxic to elasmobranchs and their prey	On-going
Warfare	Introduction of petrochemical compounds & herbicides toxic to elasmobranchs and their prey; habitat modification via blasting & mining (see above)	On-going

Conservation

Freshwater elasmobranchs at greatest risk of human impact are obligate freshwater species with limited geographical distributions (such as many dasyatid and potamotrygonid stingrays and possibly the Ganges Shark) or euryhaline species trapped by man-made barriers that prevent free transit to estuaries and the ocean. Euryhaline elasmobranchs may be less vulnerable than obligate freshwater species, but are generally confined to warm inshore marine environments exploited via low-technology, increasingly intensive artisanal and small-scale commercial fisheries as well as tourist sports fisheries, and coastal development/degradation. Certain euryhaline elasmobranchs (*Pristis microdon*, *P. perotteti*, *Pastinachus sephen*, and possibly *Himantura fluviatilis*) reproduce in fresh water and are affected by anthropogenic problems in these areas (Compagno and Cook, 1995c; Góes de Arûjo et al., 2003).

Economic and political issues affecting freshwater elasmobranch conservation are summarized in Table 5. Priorities for research and management of freshwater elasmobranchs include, 1) better monitoring of tropical freshwater populations, 2) encouragement of elasmobranch conservationists in tropical countries, 3) fostering studies of their systematics, life history and ecology, and 4) development of management protocols.

Table 5: Economic and political issues affecting freshwater elasmobranchs

- Poverty
  - Hunger
  - Disease
  - Inadequate education
- Political Instability
  - Civil strife
  - Regional or civil wars
  - Corruption
  - Ineffective governance
- Tourism Development
  - Sport angling
  - Anti-shark measures
- Exploitation of New & Underutilized Stocks
  - Targeted exploitation
    - Food
    - Leather
    - Liver oil
    - Pharmaceuticals
    - Ornamental trade
      - Curios
      - Aquarium specimens
  - Bycatch

References

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Góes de Arûjo, M.L., P. Charvet-Almeida, M.P. Almeida, and H. Pereira. 2003. Freshwater stingrays (Potamotrygonidae): status, conservation and management challenges. AC20. Inf. 8: 1-6.

Thorson, T.B., D.R. Brooks, and M.A. Mayes. 1983. The evolution of freshwater adaptation in stingrays. Nat. Geogr. Soc. Res. Rep., 15: 663-694.

Figure 1: Zoogeographic distribution of the euryhaline bull shark (*Carcharhinus leucas*)

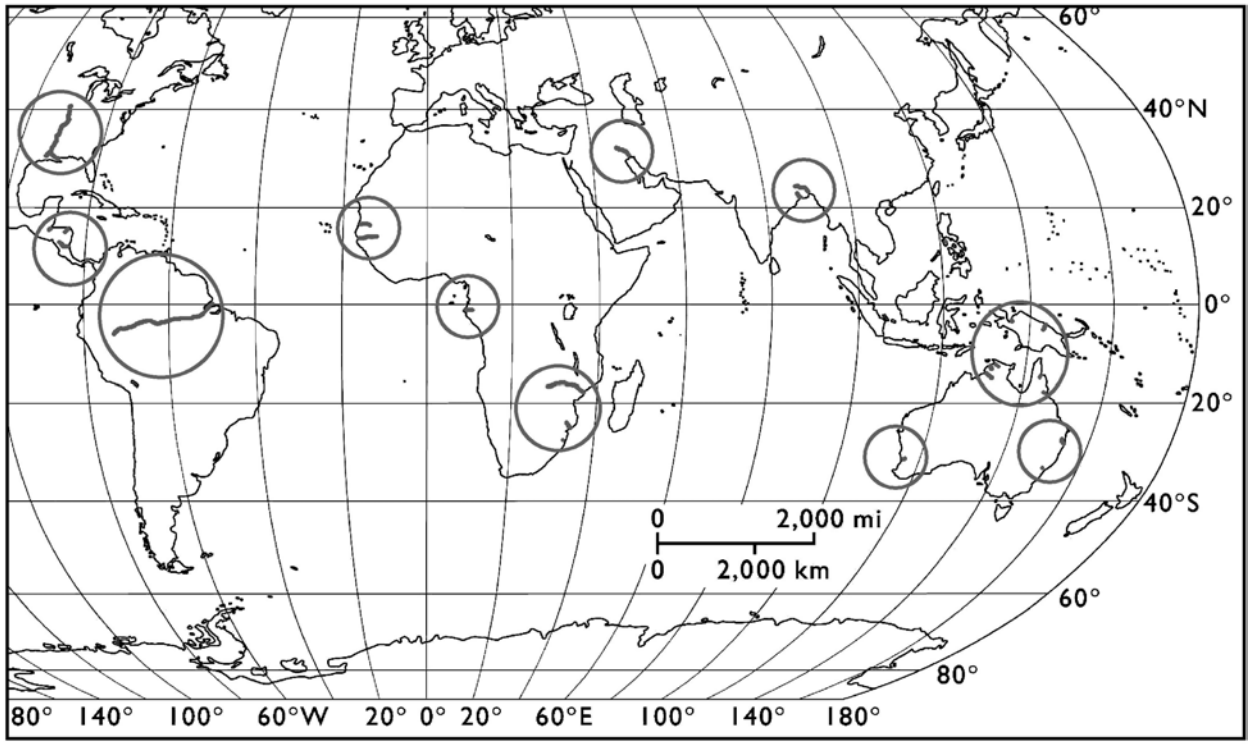

Figure 2: Zoogeographic distribution of the river sharks (*Glyphis* spp.)

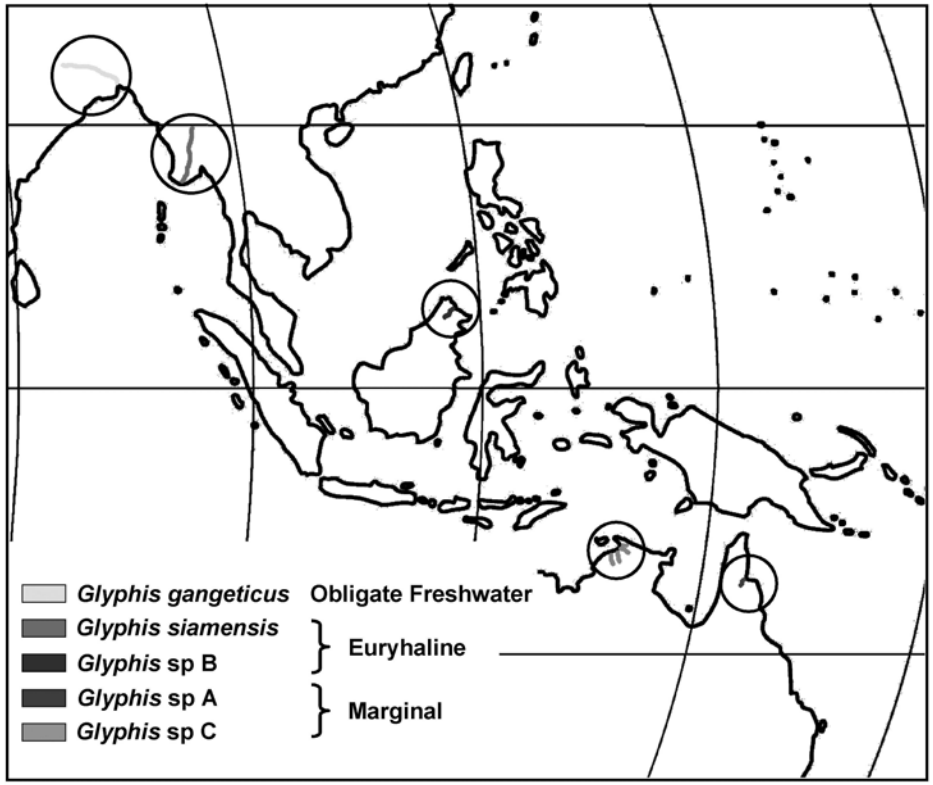

Figure 3: Zoogeographic distribution of the sawfishes (Pristidae)

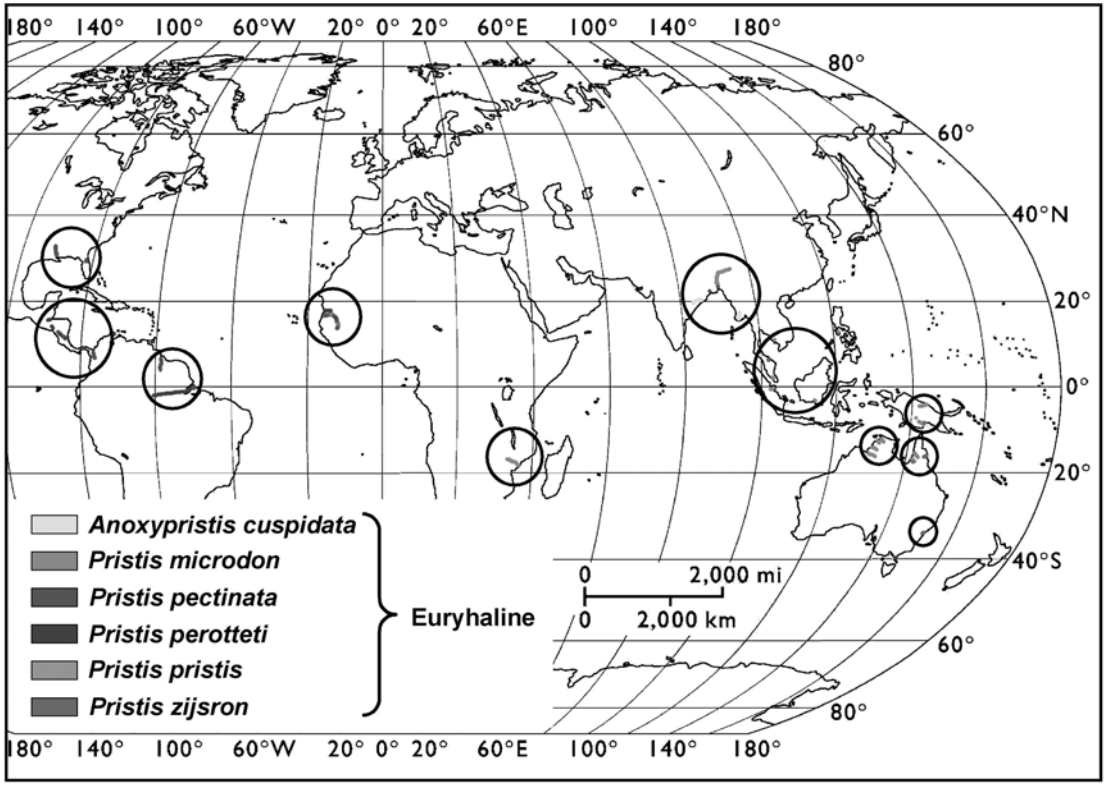

Figure 4: Zoogeographic distribution of fintail stingrays (*Dasyatis* spp.)

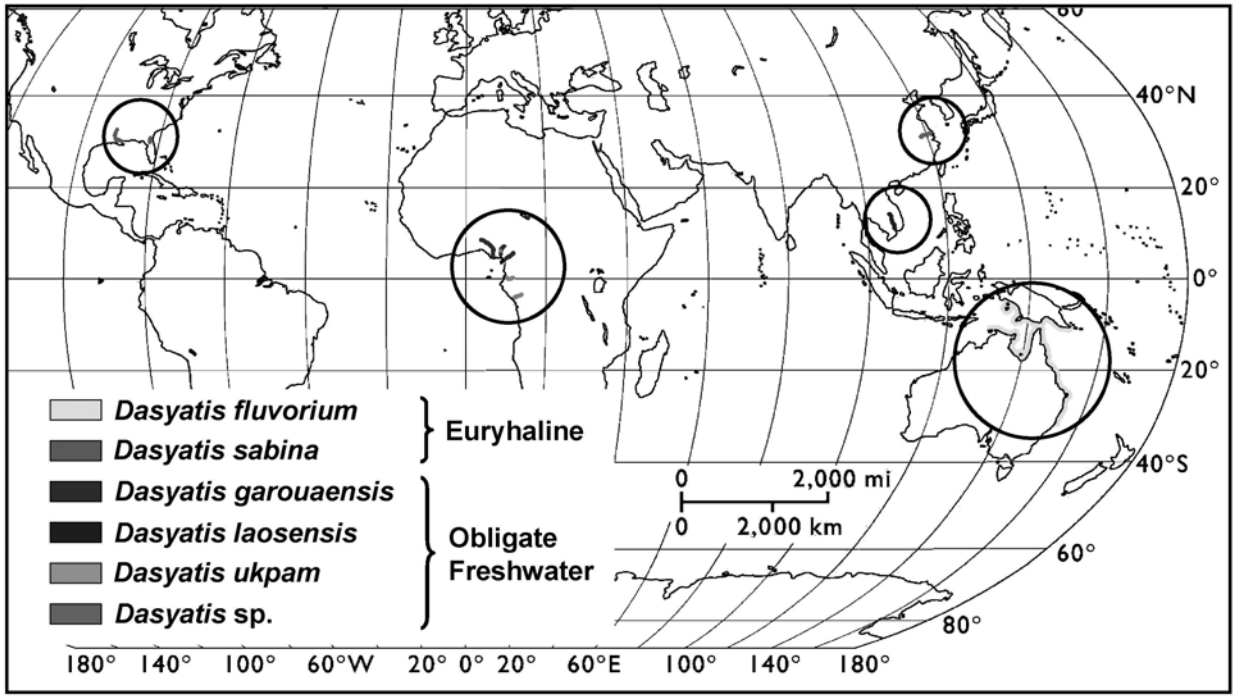

Figure 5: Zoogeographic distribution of the whip stingrays (*Himantura* spp.)

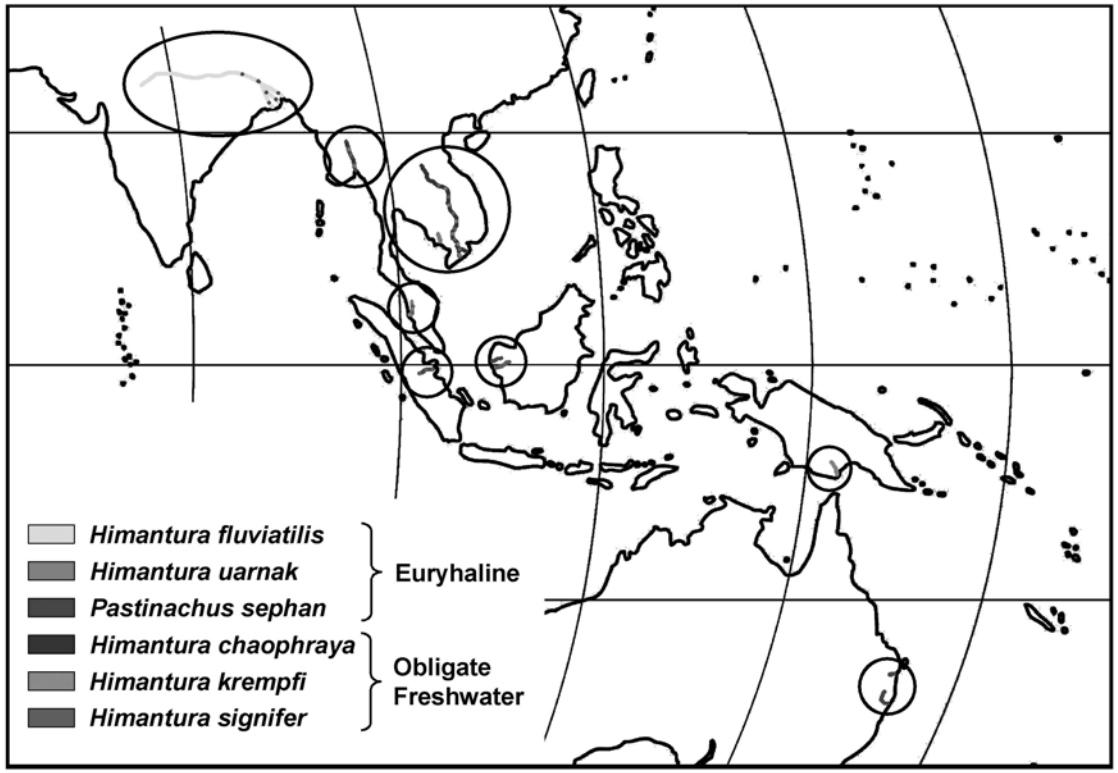

Figure 6: Zoogeographic distribution of the river stingrays (Potamotrygonidae)