Proc. 5th Indo-Pac. Fish Conf., Nouméa, 1997
Séret B. & J.-Y. Sire, eds
Paris: Soc. Fr. Ichtyol., 1999: 293-306

COMPARATIVE BIOGEOGRAPHY OF THE CHONDRICHTHYAN FAUNAS OF THE TROPICAL SOUTH-EAST INDIAN AND SOUTH-WEST PACIFIC OCEANS

by

Peter R. LAST (1) & Bernard SÉRET (2)

ABSTRACT. - The tropical Australasian region, which includes Australia, New Caledonia, New Guinea, and the eastern sector of the Indonesian Archipelago, breaches two major ocean basins. Its complex palaeohistory is strongly reflected in the size and structure of its chondrichthyan fauna where almost a third of the world's fauna (more than 300 species) occurs. The western (Indian Ocean) and eastern sectors (Pacific Ocean) each display surprisingly high levels of intraregional endemicity. Despite poorer sampling effort off Indonesia, diversity was found to be significantly greater in the Indian Ocean than in the Pacific reflecting a strong regional influence of the mega-diverse Indo-West Pacific biota. The strength of widely distributed Indian Ocean elements diminishes from west to east across the region but it is still relatively stronger off New Caledonia than the Pacific component reflecting the comparatively low biodiversity of the Pacific Plate. Tropical Australian subregions in both oceans are penetrated substantially by components from temperate areas to the south of which about half of the species are endemic to their respective oceans. Greatest biodiversity exists within demersal habitats with the continental slopes being slightly richer in species than the shelves adjacent. Slope habitats also exhibit higher levels of endemicity than shallow water habitats challenging the generality of the depth-dispersal paradigm. Recent French and Australian deepwater surveys of the region have provided new insights into the composition, structure and origins of this fauna.

RÉSUMÉ. - Biogéographie comparée des faunes chondrichtyennes tropicales de l'Océan Indien tropical du sud-est et de l'Océan Pacifique du sud-ouest..

La région tropicale australo-asiatique, qui comprend l'Australie, la Nouvelle-Calédonie, la Nouvelle-Guinée et la partie orientale de l'archipel indonésien, met en communication deux bassins océaniques importants. Son histoire géologique complexe se reflète dans la composition de la faune chondrichtyenne qui compte presque un tiers de la faune mondiale (plus de 300 espèces). Les parties occidentale (Océan Indien) et orientale (Océan Pacifique) ont chacune de surprenants taux d'endémicité qui apparaissent aux niveaux régional et sous-régional. Malgré le manque d'échantillonnage en Indonésie, la diversité s'avère significativement plus élevée dans la région indienne que dans la région pacifique; ceci est le résultat de l'influence de la région indo-ouest-pacifique à très forte diversité biotique. L'impact des éléments distribués largement dans l'Océan Indien diminue d'ouest en est dans toute la région, mais il est encore très marqué en Nouvelle-Calédonie et plus fort que l'impact des éléments pacifiques, traduisant en cela la relativement faible biodiversité de la "plaque Pacifique". Les sous-régions tropicales de part et d'autre de l'Australie sont notablement colonisées par des éléments provenant de zones tempérées; environ la moitié de ces éléments est constituée d'espèces endémiques de leur océan respectif. La plus grande biodiversité s'observe dans les habitats benthiques, les pentes continentales étant légèrement plus diversifiées que les plateaux adjacents. Les pentes montrent parfois des taux d'endémicité plus élevés que ceux des habitats moins profonds, contredisant ainsi

(1) CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tasmania 7001, AUSTRALIA. [Peter.Last@marine.csiro.au]

(2) Muséum national d'histoire naturelle, Laboratoire d'Ichtyologie générale et appliquée, Antenne ORSTOM, 43 rue Cuvier, 75231 Paris cedex 05, FRANCE.

l'hypothèse habituelle de la dispersion vers les profondeurs. Les récentes campagnes exploratoires effectuées par la France et l'Australie dans cette région ont apporté de nouvelles données et conceptions sur la composition, la structure et l'origine de cette faune.

Key-words. - Chondrichthyes, ISEW, SE Indian Ocean, ISEW, SW Pacific Ocean, Biogeography.

The tropical Australasian geographic region incorporates eastern Indonesia, Australia, New Guinea and New Caledonia, south to the tropic of Capricorn (Fig. 1). The following study is an investigation of the biogeographic patterns of the chondrichthyan fishes of this region based on a comparison of the faunas of its four major subregions: eastern Indonesia (including the western Arafura, Banda and Seram Seas); northwestern Australia; northeastern Australia (including the Great Barrier Reef and adjacent plateaus and slopes of the western Coral Sea); and New Caledonia (inshore islands and steep slopes of New Caledonia and Vanuatu, and the northern Norfolk Ridge). The westerly limits of this bioregion are defined by the Wallace line in the eastern Indian Ocean. Its easterly limits are the eastern Coral Sea in the south-west Pacific. It breaches two deep oceans basins, the Pacific and Indian Oceans, which are separated from each other by the shallow Arafura Sea, and the land masses of New Guinea and continental Australia. The region has an extremely complex plate tectonic history (Oosterzee, 1997) and the bathymetry and oceanography of the contemporary environment is equally complex. Its sea floor is heavily textured, its habitat diversity is high, and its marine fauna is one of the richest on earth with a high level of endemism.

The chondrichthyan fauna of the entire region is poorly documented, although those of the Australian subregions are best described (e.g., Whitley, 1940; Last and Stevens, 1994). Much of the fauna is undescribed and revisionary studies by the authors and several colleagues (i.e., Carvalho, Compagno, McEachran, Stehmann, Stevens, Yearsley) are in progress. Knowledge of its inshore communities are attributed largely to the efforts of 19th and early 20th C naturalists (e.g., Bleeker, 1852; Annandale, 1909) and collators (e.g., McCulloch, 1929; Fowler, 1941) whereas information on the deepwater component has been acquired more recently from trawl surveys, mostly in search of new fishery resources (e.g., Gloerfelt-Tarp and Kailola, 1984; Sainsbury *et al.*, 1985; Williams *et al.*, 1996). These include the cruises of the fishery research vessels «Bawal Putih 2», «Jurong», «Karubar» (eastern Indonesia), «Courageous», «Soela» and «Southern Surveyor» (northern Australia), and «Alis», «Capricorne», and «Vauban» (eastern Coral Sea), which within the last two decades, have variably surveyed continental shelves and slopes of the region to depths of about 1000 m. Much of the data from these cruises is yet to be published but initial studies of the deepwater communities have identified high levels of diversity and sibling speciation (Séret and Last, unpubl.)

The following study describes and assesses key structural features of this fauna such as its relative size, levels of endemism and faunal similarity, and identifies biogeographic patterns across the region. Preliminary hypotheses are proposed to explain the likely origin and derivation of this fauna.

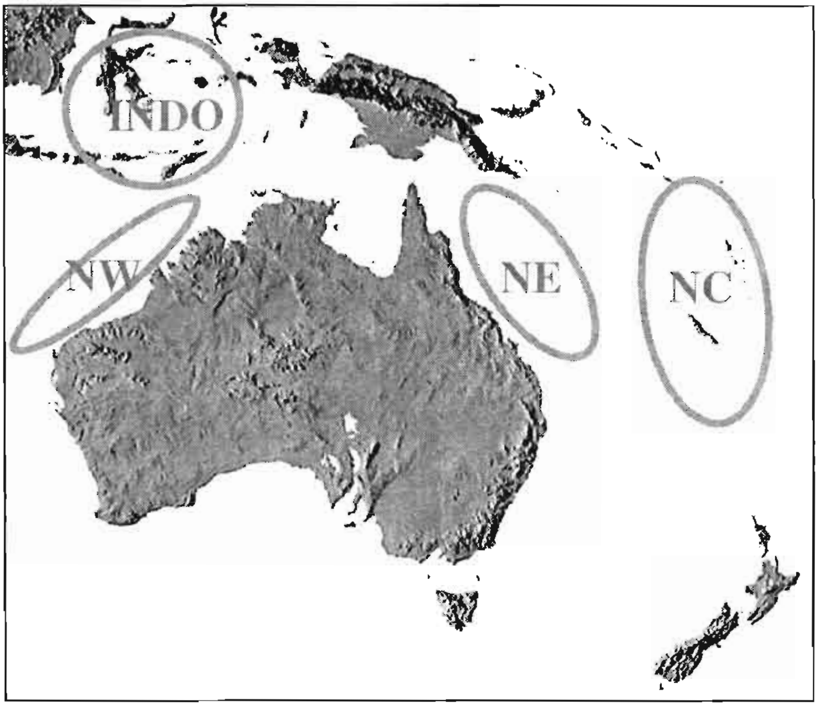

Fig. 1. - Australasian region. INDO: Indonesian subregion; NC: New Caledonian subregion; NE: northeastern Australian subregion; NW: northwestern Australian subregion.

METHODS

Species lists for each subregion were compiled from multiple sources including a large body of unpublished data held by the authors which is being summarised in a separate document (Séret and Last, in prep.). Species were classified into one of the distributional groups listed below based on information from the published literature (e.g., Chen, 1963; Masuda *et al.*, 1984; Monkolprasit, 1984; Compagno 1984, 1988; Compagno *et al.*, 1989) as well as several key regional references that are currently in press such as sharks of the South China Sea (Compagno, in press), rays of the South China Sea (Last and Compagno, in press), and FAO identification sheets to sharks and rays of the western Central Pacific (Compagno *et al.*, in press). The Australasian fauna consists of 5 primary biogeographic components and 23 secondary elements: 1. Subregional endemics (5 elements), endemic species confined to each of the four subregions or New Guinea; 2. Extraregional temperate component (2 elements), New Zealand species, or Australian temperate species that either have a primary distribution in the southwestern (Flindersian) or southeastern (Peronian) Australian Provinces, or have a widespread distribution around the southern coast (sensu Whitley, 1932; Thackway and Cresswell, 1997); 3. Australasian regional component (3 elements), Coral Sea species (Australian/New Caledonian endemics or species confined to the south-west Pacific), east Indian Ocean species (confined to eastern Indonesia and tropical Australia), and tropical Australasian species (species occurring only off tropical Australia or extending more broadly across

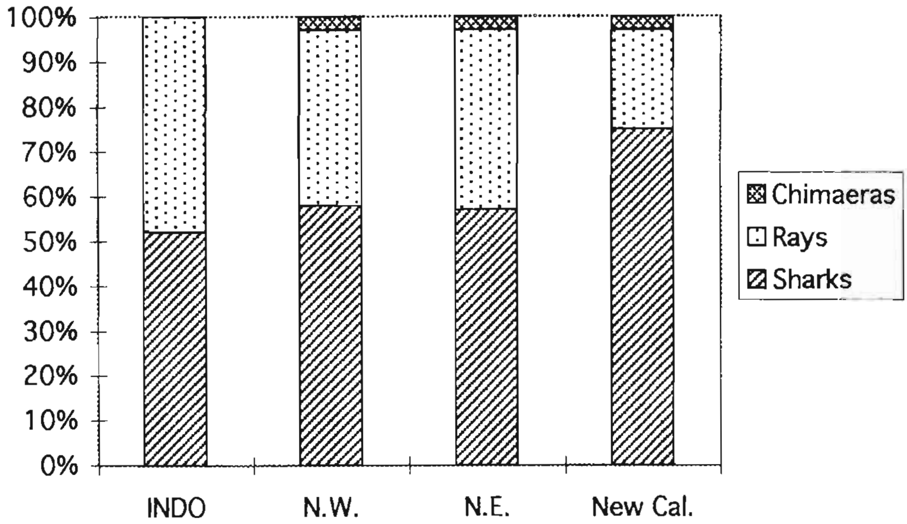

Fig. 2. - Proportional composition of primary chondrichthyan groups by region. INDO: Indonesian subregion; NC: New Caledonian subregion; NE: northeastern Australian subregion; NW: northwestern Australian subregion.

the Australasian region); 4. Indo-Pacific component (8 elements), widespread Pacific species, Indo-Malay endemics, Indo-NW Pacific species (Asian species not penetrating Australian seas or westward beyond the Indo-Malay Archipelago), Indian Ocean species (in the Indo-Malay Archipelago but not found off Australia or well into the North Pacific), western Indo-Australian species (wide-ranging in the Indian Ocean to Australia but with minimal penetration of the NW Pacific), northern Indo-Australian species (wide-ranging in the NW pacific to Australia but with minimal penetration of the Indian Ocean), widespread temperate Indo-Pacific species (distribution centred in band across temperate Indo-Pacific), and widespread tropical Indo-Pacific species (distributed widely across the tropical Indo-Pacific); 5. Ubiquitous component (5 elements), extremely wide-ranging species that have anti-tropical, circumtropical, and cosmopolitan distributions, or with species found in the Indo-Atlantic or Pacific-Atlantic basins. Intra-regional faunal similarity was investigated using Sorensen's coefficient (*sensu* Pielou, 1979).

RESULTS

The regional fauna

Size and structure

Some 313 or so chondrichthyan species, almost a third of the world's fauna, occur in this region. However, this figure is likely to be conservative. The taxonomy of some groups remains unresolved and the region has not been fully explored. We expect the number of species known from the region to increase significantly when remote areas, such as the slopes and basins of eastern Indonesia, have been surveyed and all available material has been examined. Nevertheless, current information is considered to be adequate to gain an understanding of the major faunal patterns within the region.

Of the faunas of the four subregions, the northwestern Australian assemblage (178 species) is the most species rich and the New Caledonian assemblage least diverse (92 species) (Fig. 2). The relative proportion of sharks, rays and chimaeras was identical in the two Australian subregions despite being in different oceans and differing slightly in species richness. Sharks are about 20% more diverse than rays off tropical Australia but exhibit an even greater relative dominance off New Caledonia (almost three-quarters of the species). The absence of several bottom-dwelling shark groups (e.g., hemiscylliids, heterodontids, squatinids or pristiophorids) and lower ray diversity of the New Caledonian subregion may be related to the lack of suitable habitat rather than patterns of evolution. In contrast, the numbers of sharks and rays in the eastern Indonesian subregion are about equal. Here the greater relative diversity of rays and benthic sharks may be due to higher inshore habitat diversity and more pronounced influence of the large Asian fish fauna. The absence of chimaeras in the eastern Indonesian assemblage is likely to reflect the inadequacy of deep sea survey coverage of the subregion.

The ordinal level structures of the eastern and western tropical Australian shark faunas are also extremely similar despite there being only 60% overlap in species composition (Table I). About half of shark species in the northwestern Australia, northeastern Australia and New Caledonian subregions belong to the order Carcharhiniformes, of which the whaler sharks (carcharhinids) are the dominant group. In the Indonesian subregion, almost three-quarters of the species belong to this order and a massive 43% of them are whaler sharks. Once again, fewer dogfishes in eastern Indonesia may be linked to the relative paucity of material from deepwater. In comparison, the continental slope chondrichthyans of New Caledonia are better known. Here, the dominance of dogfishes (33%) and the absence of the shark orders Pristiophoriformes, Squatiniformes, and Heterodontiformes and the ray order Pristiformes off New Caledonia may be habitat related.

The order Myliobatiformes, which includes the eagle and stingrays, is the dominant ray group throughout the region (Table II). Once again, the northwestern Australian and northeastern Australian assemblages are similar in their ordinal level structure but the greater relative importance of urolophids to dasyatids in the east is likely to be an example of ecological replacement. Stingrays are relatively more diverse in both western subregions (30-31% of Indian species versus 25-26% of Pacific species) whereas stinga-

Table I. - Proportional species richness of shark groups within each subregion.

Order	E. Indo. (%)	NW Aust. (%)	N.E. Aust. (%)	New Cal. (%)
Hexanchiformes	2	3	3	4
Squaliformes	8	21	17	33
Pristiophoriformes			1	
Squatiniformes		2	1	
Heterodontiformes	2	2	2	
Orectolobiformes	11	12	14	4
Lamniformes	6	9	8	9
Carcharhiniformes	71	51	53	49
Fam. Carcharhinidae	43	27	28	19
Fam. Scyliorhinidae	17	13	13	20
Other families	11	11	13	10
Total species	63	105	96	69

rees are relatively more diverse in the eastern subregions (13-21% of Pacific species versus 3-7% of Indian species). These observations are supported by their relative levels of abundance in catches (Last, unpubl. data). Of the other ray groups, skates were the next most diverse group comprising about a fifth of the ray species found off tropical Australia. Once again, smaller skate assemblages off New Caledonia are likely to be related to a paucity of sedimentary habitats and off eastern Indonesia to the lower levels of deepwater exploration. The proportion of shovelnose rays (10-12%) was remarkably similar across the region.

Faunal similarity

The species compositions in each of the subregions differs substantially from each other. Also, the relative levels of faunal overlap of the eastern Indonesian assemblage diminish from west to east (Table III). However, the nearby northwestern Australian assemblage is more similar in composition to the northeastern Australian assemblage (sharing about 62% of its species) rather than the eastern Indonesian assemblage (sharing about 43% of its species). Similarly, the northeastern Australian assemblage exhibited much greater relative overlap with the northwestern Australian assemblage than with the neighbouring New Caledonian assemblage. Relative similarity between the New Caledonian assemblage to the assemblages of the other subregions (19-22%) is due both to its uniqueness and its lower relative diversity. Only about half of the New Caledonian species were found off Australia. The strong similarity of the two Australian assemblages is due to the presence of a pronounced widespread Australian element in the fauna.

Biomic diversity

The representation of chondrichthyan diversity within primary aquatic ecosystem complexes (or biomes) is extremely similar off eastern and western Australia (Table IV).

Table II. - Proportional species richness of ray groups within each subregion.

Order	E. Indo. (%)	N.W. Aust. (%)	N.E. Aust. (%)	New cal. (%)
Pristiformes	8	7	6	
Rhinobatiformes	12	10	10	11
Torpediniformes	3	9	8	5
Rajiformes	17	21	21	16
Myliobatiformes	60	52	56	68
Fam. Dasyatidae	30	31	25	26
Fam. Urolophidae	3	7	13	21
Other families	27	13	17	21
Total species	60	67	63	19

Table III. - Sorensen's indices of faunal similarity between subregions.

Subregion	E. Indo.	N.W. Aust.	N.E. Aust.	New cal.
East Indonesia	1			
N.W. Australia	0,51	1		
N.E. Australia	0,42	0,64	1	
New Caledonia	0,31	0,33	0,38	1

The biomic structures of these subregions are more alike than structures observed within subregional pairs from the same ocean basin. Within those subregions having the greatest variety of inshore habitats (i.e., eastern Indonesia, northwestern Australia, northeastern Australia) the shelf assemblages (61-70% of species) were more species rich than those offshore. However, off New Caledonia most species live demersally on the continental slope with only 30% of species identified as belonging to a shelf assemblage. The freshwater/estuarine assemblage is absent in New Caledonia and tends to be small generally throughout the region (uniformly 2% elsewhere). Meso/bathypelagic communities of the eastern Indonesian subregion have not been well surveyed so this assemblage remains unknown.

Biogeographic patterns

Regional structure

Strong biogeographic patterns emerge from a comparison of the four subregions based on the relative influence of the 7 major distributional components (Table V). A half or slightly less of the Australian and New Caledonian chondrichthyans, but only about a quarter of those from the eastern Indonesian subregion, are confined to the Australasian region. Once again, the faunas of two Australian subregions were very similar to each other in structure and quite different from the subregions adjacent. Levels of intraregional endemism are reasonably high (12-18% in eastern Indonesian, northwestern Australian, and northeastern Australian subregions) and very high off New Caledonia (32%). Endemism is almost exclusively of demersal species (Table VI). It is most pronounced on

Table IV. - Proportional species richness for primary biomes within each subregion.

Biome	E. Indo. (%)	N.W. Aust. (%)	N.E. Aust. (%)	New Cal. (%)
Estuarine/freshwater	2	2	2	
Shelf-demersal	43	44	41	15
Shelf-pelagic	25	15	18	15
Slope-demersal	25	30	32	57
Epipelagic	5	5	6	8
Meso/bathypelagic		4	1	5
Total species	123	178	164	92

Table V. - Biogeographic structure of tropical Australasian chondrichthyans.

Component	E. Indo. (%)	N.W. Aust. (%)	N.E. Aust. (%)	New Cal. (%)
Subregional endemic	12	15	18	32
Extraregional temperate		12	15	3
East Indian Ocean	7	4		
Coral Sea			3	5
Tropical Australasian	2	14	14	2
Indo-Pacific	59	32	27	25
Ubiquitous	20	23	23	33
Total species	123	178	164	92

the continental slope (rather than inshore) in all subregions except northwestern Australia where more than 60% of the endemics are demersal shelf species.

The northern incursions of Australian temperates are significant along both Australian seaboards (12-15%) and differ markedly in species composition in each ocean. The bulk of these species are temperate endemics from either the south-east (Peronian) or the south-west (Flindersian) Australian faunal provinces that stray into adjacent tropical waters. The New Caledonian subregion is penetrated by a small temperate element from New Zealand but no Australian species. No Australian temperate chondrichthyans occur in the seas of the eastern Indonesian subregion. A small east Indian element (4-7%) was identified along with an equivalent small Coral Sea element (3-5%). A significant tropical Australian element (14% off each seaboard) is rudimentary within the eastern Indonesian and New Caledonian subregions (2%).

The two major groups of widespread elements include those species with an Indo-Pacific distribution and an assemblage of ubiquitous species. The eastern Indonesian fauna is dominated by a large assemblage (almost 60%) of species that also occur more widely throughout the Indo-Pacific. This element is also prominent in the other subregions but declines slightly from west to east. It is important to note that this element is more pronounced than any equivalent Pacific element which is consistent with a regional fauna whose primary origins are Indo-West Pacific based rather than derived in the Pacific Ocean. Most of the ubiquitous species were found across the region and these consisted of between a third and a fifth of the species in each subregion.

Indo-Pacific component

Careful examination of the substructure of the Indo-Pacific component provides insight to the likely biogeographic history of the region. The total number of Indo-Pacific species (including those with both Pacific and Indian Ocean distributions) also declines from west to east (Table VII). Similarly, the configuration of the Indo-Pacific components are remarkably similar off eastern and western Australia despite them being in different oceans. Also, the substructure off New Caledonia is more similar to Australian shores than to eastern Indonesia. It appears as if the Australian-New Caledonian region has been penetrated from the west by a strong but relatively uniform Indo-Pacific assemblage.

A large tropical Asian assemblage, consisting of species found only in the Indo-Malay Archipelago (3%), westward into the central Indian Ocean (26%), or northward to Japan (11%) penetrates eastern Indonesia but none of its species reaches further eastward to Australia or New Caledonia. The combined proportion of Indian Ocean based Indo-West Pacific species off eastern Indonesia is 44% versus 39% for those that extend into the north-west Pacific. Consequently, the faunal structure in the region to the east of Indone-

Table VI. - Distribution of subregional endemics in environments.

Environment	E. Indo.	N.W. Aust.	N.E. Aust.	New Cal.
Demersal	15 (100%)	26 (100%)	27 (93%)	28 (97%)
Shelf-demersal	2 (13%)	16 (62%)	7 (24%)	1 (3%)
Slope-demersal	13 (87%)	10 (38%)	22 (76%)	28 (97%)
Pelagic			2 (7%)	1 (3%)
Total species	15	26	29	29

sia is also likely to be dominated by Indian Ocean elements. Instead, these assemblages are dominated by Indo-West Pacific species (44-48%) that extend from the south-west Pacific to well north off south-east Asia but which do not penetrate far into the Indian Ocean. A much smaller suite of species (23%) extends from the south-west Pacific well into the Indian Ocean but not far into the north-west Pacific.

The relative strength of the widespread Indo-Pacific element increases within the region from west to east due to a decline in strength of more restricted Indo-Pacifics from west to east. However, the number of widespread Indo-Pacifics, varying between 10-14 species, is reasonably even across the region. In comparison, the widespread Pacific element is very small with 9% of the New Caledonian species, represented as trace elements (2-4%) off Australia, and absent from the eastern Indonesian subregion.

Ubiquitous component

The ubiquitous component, which consists of 25-41 species across the region, is dominated by cosmopolitan elements (comprised of 49-60% species) (Table VIII). Once again, these species are more closely linked to the Indian Ocean than to the Pacific Ocean. Only 3-8% of the ubiquitous Australian and New Caledonian species have a Pacific-

Table VII. - Biogeographic structure of the Indo-Pacific chondrichthyan components.

Element	E. Indo. (%)	N.W. Aust. (%)	N.E. Aust. (%)	New Cal. (%)
Widespread Pacific		4	2	9
Indo-West Pacific (to Indonesia)				
Indo-Malay endemic	3			
Indo-NW Pacific	11			
Indian Ocean	26			
Indo-West Pacific (to Australia)				
northern Indo-Australian	28	48	44	27
western Indo-Australian	18	23	23	9
Widespread Indo-Pacific				
temperate element	3	9	11	18
tropical element	11	16	20	37
Total species	71	56	44	23

Table VIII. - Biogeographic structure of the ubiquitous chondrichthyan components.

Element	E. Indo. (%)	N.W. Aust. (%)	N.E. Aust. (%)	New Cal. (%)
Indo-Atlantic	28	24	18	10
Pacific-Atlantic		5	8	3
Antitropical		2		7
Circumtropical	20	20	24	20
Cosmopolitan	52	49	50	60
Total species	25	41	38	30

Atlantic distribution whereas 10-18% of the Indo-Atlantic species occur in the Pacific subregions. Pacific-Atlantic species are absent from the eastern Indonesian subregion but 28% of its ubiquitous component is found throughout the Indo-Atlantic. The distribution of these Indo-Atlantic species follows the pattern exhibited by more restricted Indo-Pacifics in decreasing in richness from west to east across the region. The anti-tropical element is small to non-existent but the circumtropical element is well defined and consistent within all subregions (20-24%).

Faunal origins

Wilson and Allen (1987) have attempted to provide an explanation for the origin of Australia's fish fauna. The modern Indian and western Pacific Oceans are considered remnants of a once larger Tethys Sea (Oosterzee, 1997). A pan-tropical Tethyan fauna is thought to have dominated northern Australasian seas since the Tertiary. Some of these Indo-Pacific groups were able to radiate across the Tethyan Sea to colonise the broader region as well as the precursor of the Atlantic Ocean. These elements are evident within the chondrichthyan fauna as widespread components. The Tethyan fauna speciated greatly during the formation of shallow basins (i.e., Indo-Malay Archipelago) created by the partial separation of these oceans when the Australian shield impinged upon the Asian Plate. Most of the ancestral forms of the present fauna are presumed to have been derived before and during this period of fragmentation in the early Tertiary. Westward circulation between the Pacific and Indian Oceans is thought to have virtually ceased but biological dispersal into the Tethyan basins persisted providing the evolutionary ingredients for the modern marine megabiota, the richest of any region (Briggs, 1974). Chondrichthyan species diversity is significantly greater in the Indian Ocean than the Pacific despite poorer sampling efforts off Indonesia. Similarly, the influence of Indian Ocean elements in the Australasian region is substantially greater than that of Pacific elements.

The extant chondrichthyan fauna of the region is the product of several periods of faunal mixing and isolation. The deepwater fauna occurring along the most likely contemporary tropical dispersal route (i.e., along the northern coast of New Guinea) is almost unknown so we are unable to even speculate as to its affinities. Also, this pathway is likely to have changed greatly since the existence of a Tethyan Sea as islands to Australia's north are geological composites formed by plate tectonic rifts and collisions (Parenti, 1991). However, given that many extant species occur only in deepwater and cannot pass through the shallow aperture between northern Australia and New Guinea, this pathway is likely to be important for dispersal and is the most plausible corridor for the high proportion of north-west Pacific species occurring in the Coral Sea. Continuous deepwater around the southern coast of Australia links both ocean basins but the contemporary temperate fauna is strikingly different in composition to those of the north (Last and Stevens, 1994) and is unlikely to have been an important Quaternary pathway. Continental shelf chondrichthyans are likely to be less constrained in recent times by an east-west intraregional barrier. The shallow water components were able to coalesce with the opening of Torres Strait during the flooding of the shelf area between Australia and New Guinea in the Pleistocene (Wilson and Allen, 1987).

Some evidence exists to suggest that the regional was penetrated by elements from the Indian and north-west Pacific during separate events and at differing levels of impact. The absence off Australia of suites of Indian Ocean genera and species found off eastern Indonesia (e.g., *Chaenogaleus*, *Scoliodon*, and *Lamniopsis*) is suggestive of either a speciation event with a barrier between most of Australia and Indonesia, or of an Indian

Ocean origin with the new assemblage unable to subsequently disperse east across the region. Either way the southern pathway from the Indian Ocean appears to have been interrupted at some stage.

Similarly, the deep trenches and seas that separate parts of the Australasian region are likely to have acted as historical barriers that have affected the composition of the extant fauna. The high respective levels of intraregional endemism are indicative of lengthy isolation periods of at least some of these elements. Some benthic chondrichthyans (e.g., skates and stingarees), whose distributions are heavily constrained by depth related barriers (such as the deep ocean trenches and basins), are good biogeographic indicators. For example, islands of New Caledonia and New Zealand are partially connected across the deep south-west Pacific rim via the Norfolk Ridge. However, despite these submarine ridges acting as the likely pathways for the dispersal of several eurybathic teleost groups and some chondrichthyans (e.g., *Mustelus* and *Squalus*) no stingarees occur off New Zealand. Pavorajine skates species appear to have been isolated similarly in the Coral Sea.

Knowledge of the biogeographic structure and faunal origins within any region is only a good as the groups selected for its appraisal. When available, informative groups should be used to interpret biogeographic patterns rather than uninformative groups. The most informative groups tend to be genera or families that are medium to highly speciose and whose members mostly have restricted ranges. Small groups with predominantly wide-ranging species are typically less informative. Some sharks and rays, by the nature of their life history (e.g., low fecundity, narrow home range, short breeding period and poor juvenile dispersal) can be used as indictors to determine biogeographic patterns within realms. Possibly the most useful groups in this region include stingarees (*Urolophus* and *Trygonoptera*), stingrays (*Dasyatis* and *Himantura*) skates (*Anacanthobatus*, *Dipturus*, *Irolita* and *Pavoraja*), catsharks (*Asymbolus*, *Cephaloscyllium* and *Galeus*) and shovelnose rays (*Aptychotrema* and *Rhinobatos*). The family Urolophidae, which has mostly narrow-ranging species, occurs off both Australian coasts, New Caledonia, and along the northern New Guinea pathway to Japan. Based on centre of origin theory (Pielou, 1979) and the high level of speciation in the Australian region (28+ species versus only 1 species west of Australasia), it is most likely that the evolutionary pathway of this group extended from Australia rather than to it from the North Pacific. A similar argument probably can be applied to several other groups (e.g., *Pristiophorus*, orectolobids, *Cephaloscyllium*, and skates of the *Notoraja* complex).

An important feature of the Australian fauna is its structural similarity (based on the levels of representation of the three main chondrichthyan groups, their orders, their biomic structure, levels of endemism, and similarity to the more widely ranging Indo-Pacific fauna) despite sharing only about two-thirds of its species across oceans. These subfaunas are more similar to each other than they are to those of nearby regions in the same ocean. Interestingly, 11 genera (comprising 62% of the endemic species) of 30 regional endemic genera occur in both Australian subregions. The most diverse genera include *Squalus*, *Narcine*, *Pavoraja*, *Dipturus*, and *Urolophus*. The high level of sibling speciation across the region is indicative of one or more vicariance events, which based on the groups involved, may have occurred after the formation of barriers across both northern and southern Australian distributional pathways. The pathways would seem at least partially disjunct at their northern extremities as there seems to be limited spill over into adjacent subregions within the same ocean. In the south, vicariance speciation is thought to be due largely to rises and fall in sea level in the Pleistocene (Wilson and Allen, 1987). Species within some groups, such as *Trygonoptera*, *Aptychotrema*, and probably *Asymbolus* and *Pavoraja*, are likely to have arisen this way. These groups, which are most diverse in temperate seas, have unique sister species off either side of tropical Australia that are likely to have dispersed into these regions from the south. Similarly there are groups that are likely to be linked to a northern pathway (e.g., *Atelomycterus*, *Narcine*, *Insentiraja*, and *Anacanthobatis*). The association of the faunas of both ocean basins, presumably via a northern pathway in recent times is probably best demonstrated through the genus *Galeus*. Sibling species, *G. gracilis* (Indian Ocean) and *Galeus* sp. (Pacific Ocean) are so similar in morphology that the females are virtually indistinguishable. However, the external clasper morphologies of mature males differ so greatly from each other that they could be considered to be generically distinct.

The uniform infraregional structure of the contemporary Australian fauna at the supraspecific level means that similar ecomorphotypes will be represented off each region despite differences in the species mix. However, some differences in structure found in adjacent subregions may be attributed to habitat availability. New Caledonia is comparatively simple in habitat diversity inshore and this is reflected in the structure of its chondrichthyan fauna. Several soft-bottom groups are absent from this subregion. Conversely, the fauna of eastern Indonesia is relatively richer in soft-bottom elements found in southeast Asia. These habitats are particularly diverse across the Indo-Malay Archipelago. Wilson and Allen (1987) explained differences in the relative dominance of inshore continental to coral reef fishes between tropical oceans off Australia as an example. Continental fishes are dominant off northwestern Australia (where coral reef habitat is comparatively limited) and coral reef fishes are more diverse off eastern Australia (where coral reef habitats are more diverse).

In summary, the chondrichthyan fauna of the region is likely to be derived primarily of ancestral groups that evolved in the Indo-West Pacific but which are penetrated by derivatives of an older widespread Tethyan fauna and more recent post Gondwanan elements from temperate southern Australia. The influence of central and eastern Pacific elements is minimal. Habitat availability and diversity is a likely determinant of contemporary composition within the region. This research also highlights the need for exploration of remote zones such as the New Guinean slope and parts of Indonesia to obtain a better picture of the biodiversity of the region.

Acknowledgements. - The authors wish to thank the many field scientists and fishermen that have contributed survey material without which this study would not have been possible.

REFERENCES

ANNANDALE N., 1909. - Report on the fishes taken by the Bengal fisheries steamer «Golden Crown». Part 1: Batoidea. *Mem. Ind. Mus.*, 2: 1-60.

BLEEKER P., 1852. - Bijdrage tot de kennis der plagiostomen van den Indischen Archipel. *Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen*, 24: 1-92.

BRIGGS J.C., 1974. - Marine Zoogeography. 475 p. New York: McGraw-Hill.

CHEN J.T.F., 1963. - A review of the sharks of Taiwan. Dept. Biol. Coll. Sci., Tunghai Univ., *Biol. Bull.* (Ichthyol. Ser.), 19: 1-102.

COMPAGNO L.J.V., 1984. - FAO Species Catalogue. Vol. 4, Parts 1 & 2. Sharks of the World: An annotated and illustrated Catalogue of Shark Species known to Date. 655 p. *FAO Fish. Synopsis*, 125.

COMPAGNO L.J.V., 1988. - Sharks of the order Carcharhiniformes. 486 p. Princeton (New Jersey): Princeton Univ. Press.

COMPAGNO L.J.V., in press. - Review of the biodiversity of sharks and chimaeras in the region (South China Sea and adjacent areas). *In:* Proc. Int. Seminar and Workshop on Elasmobranch, Biodiversity, Conservation and Management, Sabah (Malaysia), July 1997 (Fowler S., ed.).

COMPAGNO L.J.V., EBERT D.A. & M.J. SMALE, 1989. - Guide to the Sharks and Rays of southern Africa. 160 p. Cape Town: Struik Publishers.

COMPAGNO L.J.V., LAST P., NIEM V. & M.R. de CARVALHO, in press. - FAO species sheets for sharks, batoids and chimaeroids of the West Central Pacific (FAO Area 71 and part of Areas 77 and 81), (Carpenter K. *et al.*, eds).

FOWLER H.W., 1941. - The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostariophysi obtained by United States Bureau of Fisheries Steamer Albatross in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Bull. U.S. Natl. Mus.*, (100)13: 1-879.

GARMAN S., 1913. - The Plagiostomia. *Mem. Mus. Comp. Zool. Harvard*, 36: 1-515.

GARRICK J.A.F., 1982. - Sharks of the genus *Carcharhinus*. Nat. Ocean. Atmosph. Adm. USA, *Tech. Rep. Nat. Mar. Fish. Serv. Circ.*, 445: 1-194.

GLOERFELT-TARP T. & P.J. KAILOLA, 1984. - Trawled Fishes of southern Indonesia and northwestern Australia. 406 p. Australian Development Assistance Bureau; Directorate General of Fisheries, Indonesia; German Agency for Technical Cooperation. Singapore: Tien Wah Press

HERRE A.W.C.T., 1953. - Check list of Philippine fishes. *U.S. Fish Wildl. Serv. Res. Rep.*, 20: 1-977.

LAST P.R. & L.J.V. COMPAGNO, in press. - Review of the biodiversity of rays in the region (South China Sea and adjacent areas). *In:* Proc. Int. Seminar and Workshop on Elasmobranch, Biodiversity, Conservation and Management, Sabah (Malaysia), July 1997 (Fowler S., ed.).

LAST P.R. & J.D. STEVENS, 1994. - Sharks and Rays of Australia. 513 p. Australia: CSIRO.

MASUDA H., AMAOKA K., ARAGA C., UYENO T. & T. YOSHINO (eds.), 1984. - The Fishes of the Japanese Archipelago. 437 p. Tokyo: Tokai Univ. Press.

McCULLOCH A.R., 1929–1930. - A check-list of the fishes recorded from Australia. *Mem. Austral. Mus.*: 1-534.

MONKOLPRASIT S., 1984. - The cartilaginous Fishes (Class Elasmobranchii) found in Thai Waters and adjacent Areas. 175 p. Bangkok (Thailand): Dept. Fish. Biol., Fac. Fish., Kasetsart Univ.

OOSTERZEE P.V. van, 1997. - Where Worlds Collide: The Wallace Line. 234 p. Kew: Reed.

PARENTI L.R., 1991. - Ocean basins and the biogeography of freshwater fishes. *Aust. Syst. Bot.*, 4: 137-149.

PIELOU E.C., 1979. - Biogeography. 351 p. Toronto: John Wiley & Sons, Inc.

SAINSBURY K.J., KAILOLA P.J. & G.G. LEYLAND, 1985. - Continental Shelf Fishes of northern and North–western Australia: An illustrated Guide. 375 p. Canberra: CSIRO Division of Fisheries Research; Clouston & Hall and Peter Pownall Fisheries Information Service.

SHEN S-C. (Chief Ed.), CHEN C.T., CHEN H.M., CHEN L.W., ESCHMEYER W.E., JOUNG S.J., LEE S.C., MOK H.K., SHAO K.T. & C.S. TZENG, 1995. - Fishes of Taiwan. 960 p.

TENG H-T., 1962. - Classification and distribution of the Chondrichthyes of Taiwan. PhD thesis, 304 p., Kyoto Univ., Ogawa Press, Maizuru. (In Japanese).

THACKWAY R. & I.D. CRESSWELL (eds), 1997. - Interim marine and coastal Regionalisation for Australia: an Ecosystem-based Classification for marine and coastal Environments, vers. 3.2. 120 p. Canberra: Environment Australia.

WHITLEY G.P., 1932. - Marine zoological regions of Australia. *Austral. Nat.*, 8: 166-167.

WHITLEY G.P., 1940. - The Fishes of Australia. Part I. The Sharks, Rays, Devilfish, and other primitive Fishes of Australia and New Zealand. Australian Zoological Handbook. 280 p. Sydney: Royal Zoological Society of New South Wales.

WILLIAMS A., LAST P.R., GOMON M.F. & J.R. PAXTON, 1996. - Species composition and checklist of the demersal ichthyofauna of the continental slope off Western Australia (20-35°S). *Rec. WA Mus.*, 18: 135-155.

WILSON B.R. & G.R. ALLEN, 1987. - Major components and distribution of marine fauna. *In:* Fauna of Australia. General Articles. Vol. 1A (Dyne G.R. & D.W. Walton, eds), pp. 43–68. Canberra: Australian Government Publishing Service.