

THE ECOLOGY OF TROPICAL ASIAN RIVERS AND STREAMS IN RELATION TO BIODIVERSITY CONSERVATION

David Dudgeon

*Department of Ecology & Biodiversity, The University of Hong Kong,
Hong Kong SAR, China; e-mail: dddudgeon@hkucc.hku.hk*

Key Words fishes, benthos, dams, pollution, freshwater

■ **Abstract** Tropical Asian rivers support a rich but incompletely known biota, including a host of fishes, a diverse array of benthic invertebrates, and an assemblage of mammals adapted to riverine wetlands. River ecology is dominated by flow seasonality imposed by monsoonal rains with profound consequences for fishes and zoobenthos. Information on life histories, feeding, and the trophic base of production of these animals is summarized. Widespread use of allochthonous foods by fishes and zoobenthos is apparent. Migration by fishes is often associated with breeding and results in seasonal occupation of different habitats. Riverine biodiversity is threatened by habitat degradation (pollution, deforestation of drainage basins), dams and flow regulation, as well as over-harvesting. Conservation efforts in tropical Asia are constrained by a variety of factors, including lack of ecological information, but the extent of public awareness and political commitment to environmental protection are likely determinants of the future of riverine biodiversity.

INTRODUCTION

Tropical Asia—the Oriental Region—has a rich flora and fauna yet, compared to the Neotropics and Africa, does not seem to invoke the same concern over biodiversity conservation. In addition, comparatively little ecological research undertaken in tropical Asia appears in the mainstream scientific literature. This is surprising. Asia is home to elephants, orangutan, gibbons and other primates (monkeys, tarsiers, and lorises), three of the world's five species of rhinos, buffalo and other wild cattle, bears, and tigers, lions, three species of leopards, and an assortment of smaller cats. Indonesia alone supports around 15% of the world's species, including more birds and flowering plants than the whole of Africa. This is megadiversity on a global scale! Of particular concern is the extent to which freshwater biodiversity in Asia has been neglected, especially that associated with rivers and streams. Hynes' (50) landmark treatise on the ecology of running waters

devotes hardly any space to tropical streams (and virtually none to Asian waters), indicating the state of knowledge of these habitats in the late 1960s. Subsequent reviews of limnology (i.e. the study of inland waters) in the tropics either focus mainly upon lakes (e.g. 5), or give scant coverage to Asia (57, 82), or both (71). The incompleteness of such reviews is not surprising when we consider the extent of the subject area encompassed by "tropical limnology." The freshwater fisheries literature likewise highlights Africa and the Neotropics (88a), and the major treatise on tropical fish ecology (60) contains relatively little about Asian rivers. This lacuna in our knowledge is due, in part, to a lack of primary research but is also a reflection of a scattered, highly fragmented literature, some of which is inaccessible. Important information may be published in obscure local or regional journals that frequently have limited distribution, or data appear only in reports (for government, private environmental consultants, and the like) and are never formally published. It is thus not surprising that Allan's (1) recent text on stream ecology matches Hynes (50) in the space devoted to the tropics.

Does this matter? Given time and effort, data accumulate and information gaps are filled. Gradually our knowledge of Asian rivers will be enriched. Unfortunately, we do not have the luxury of unlimited time for further studies. Asia is the most populous region of the planet, in terms of both absolute abundance (over 50% of the global human total) and density (in 13% of the world's land area). More people live in poverty in Asia than in Africa and Latin America combined. These facts contribute to a situation in which economic growth takes precedence over other considerations. "Development now, clean up later" has become the credo of most Asian governments, leading to environmental degradation and increasing demands on natural resources.

Anthropogenic modification of riverine habitats is not new. Several of the great rivers of Asia (e.g. the Ganges, Indus, and Yangtze) have been cradles of ancient civilizations. The Chinese hero-emperor Yu the Great, who reigned from 2205 to 2198 BC, was instrumental in building dams and dikes and channelizing rivers. Sustained and pervasive human impacts are thus typical of many Asian rivers and their drainage basins. None is pristine, and the extent of past and ongoing human impacts on riverine biodiversity cannot be assessed accurately because we know little of pre-impact conditions. Pollution from agricultural areas and non-point sources is largely uncontrolled, and domestic wastewater treatment is limited (41) such that (for example) almost all sewage entering the Ganges and the Yangtze (= Chang Jiang) is untreated. Many rivers in Southeast Asia are in such poor condition that fisheries have collapsed. Legislation concerning discharge of untreated industrial effluents has been enacted in several countries (e.g. Thailand, Indonesia, Malaysia) but is weakly enforced (41). Deforestation is another major conservation issue in Asia. It results in changed runoff patterns (typically making hydrographs more "flashy") and increased siltation of rivers. Around 2% of the remaining forest area is lost each year throughout tropical Asia, but local variation is considerable (13, 43a). In the Philippines, for example, only 5% of the land area remains under natural forest compared to about 35% for Southeast Asia as

a whole (13). In addition to deforestation, river flows are altered by dams, water extraction, and other river engineering works (36). Nevertheless, despite centuries of human impact in parts of Asia, large rivers such as the Mahakam, Kapuas, and Baram in Borneo retain a significant degree of ecological integrity. But even in these rivers, damaging fishing practices and over-harvest of fishes and turtles are causes of concern (16–18).

One conclusion to be drawn from these facts is that our opportunity to study the ecology of tropical Asian rivers is finite and, if we wish to preserve what remains of the biodiversity of these habitats, we must apply the ecological information we have now, notwithstanding its incompleteness. We should also decide what additional research is needed, and establish priorities so effort is put into studies that provide the information we need to underpin conservation and management strategies. This requires that we take stock. What do we know? What are the main threats to rivers and their biota? What do we need to know? How can we direct our research in order to generate the information we require? In this article I will address these questions, drawing upon and synthesizing information from a recent monograph on tropical Asian streams and rivers (33). The geographic scope is monsoonal Asia south of latitude 30°N (i.e. China north of the Yangtze is excluded), which corresponds to the Oriental Biogeographic Region, but many of my examples are from east Asia. For the sake of brevity, I have not cited primary sources for data which have been thoroughly reviewed elsewhere (33; see also 24, 25, 28, 29, 36–38, 41), although new research or noteworthy case studies and examples are referenced in full.

WHAT DO WE KNOW?

Riverine Biodiversity

Aquatic Biodiversity Asian freshwater habitats support an exceptionally rich biota. Indonesia, for instance, has 900 amphibian species, at least 1200 fishes (the final total may exceed 1700 species), and more dragonflies (>660 species) than any other country (13). The global proportion of riverine biodiversity in Asia is high. The region is, for example, home to three species of “true” river dolphins (i.e. dolphins that never enter the sea) of a global total of only five species: *Platanista gangetica* (in the Ganges and Brahmaputra), *Platanista minor* (in the Indus only), and *Lipotes vexillifer* (confined to the Yangtze, in which fewer than 200 individuals remain). All three are endangered by pollution, hunting, accidents with boat traffic, fisheries by catch, and population fragmentation by dams and barrages. Crocodylians (crocodiles, gharials, and one alligator) are well represented in tropical Asia, with eight of the global total of 23 species occurring in the region. All are endangered. Other herpetofauna are diverse also (6), and tropical Asia supports the world’s richest assemblage of freshwater turtles and terrapins (83).

Tropical Asia is home to the world's largest and one of the smallest lotic fishes (the Mekong giant catfish *Pangasias* (= *Pangasianodon*) *gigas* and the tiny cyprinid *Danioella translucida*). The regional fauna is diverse, and the Indochinese Peninsula has over 930 fish species in 87 families (56). Individual countries have diverse faunas: Thailand, for example, has over 500 species belonging to 49 families. China's rivers are home to 717 freshwater fish species in 33 families (58); a further 66 species spend part of their lives in rivers. Most of these Chinese fishes are Oriental in distribution: 586 of the 717 primary freshwater species occur in the Yangtze or farther south, and the tropical Zhujiang (or Pearl River, China's second largest river) supports 262 of them (59). Species totals for other Asian rivers are likewise impressive: 290 in the Kapuas River (Borneo), 245 in the Yangtze, 222 in the Chao Phraya (Thailand), 150 in the Salween River (Burma), 147 in the Mahakam River (Borneo), 141 in the Ganges (India), and 115 in the Baram River (Borneo) (56, 58, 66, 93). Despite evident richness, existing inventories of Asian fish biodiversity are far from complete, and the general picture is one of a rather poorly known fauna (93).

How does fish biodiversity in Asian rivers measure up in global terms? The Mekong is the largest river in Asia. Its basin (802,900 km²) contains more than 500 species (56), and perhaps as many as 1200 (73). That places it among the top three rivers in the world (after the Amazon and the Zaïre) in terms of fish species richness, although the Mekong ranks only 16th in the world in terms of length, and 15th in terms of discharge (28). If we consider richness of higher taxa, tropical Asia has more than 105 families of freshwater fishes compared to 74 in Africa and only 60 in South America. Moreover, the composition of these faunae is very different. Among 316 freshwater fish genera recorded from tropical Asia (56), the top three families are Cyprinidae (147 genera), Balitoridae (38 genera), and Sisoridae (19 genera). The Balitoridae (previously Homalopteridae) is an exclusively Oriental group of small benthic fishes, widespread in fast-flowing waters throughout the region. We know almost nothing about their ecology (21). Whereas cyprinids dominate in Asia, they are lacking in the Neotropics; Characidae is important in Africa and the Neotropics but does not occur in Asia, while Cichlidae—a major component of the fish fauna of Africa and America—is represented by only two species of *Etroplus* in Sri Lanka (although introduced African *Oreochromis* and *Tilapia* are now ubiquitous).

Invertebrate biodiversity in Asian rivers has not been studied thoroughly. The general composition of the benthos of large Asian rivers appears similar to that of such habitats the world over, and includes Tubificidae, Chironomidae (Chironominae), Gastropoda (Prosobranchia), and Bivalvia (50). However, a distinctive feature of rivers such as the Ganges, Zhujiang, and Chang Jiang is the regular occurrence of freshwater polychaetes. To this list can be added freshwater prawns (especially *Macrobrachium* spp.), which are circumtropical. Among meso- and macrocrustaceans, amphipods and isopods are scarce compared to their abundance in north-temperate habitats. Instead, Decapoda, comprising freshwater crabs, shrimps (Atyidae), and prawns (Palaemonidae), occupy

a pre-eminent position in tropical Asian rivers, and have penetrated fast-flowing upland streams.

Benthic community composition in smaller rivers matches Hynes' (50) assertion that "...one of the most striking features of the faunas of stony streams is their remarkable similarity the world over." That said, the lotic mollusc fauna of tropical Asia has some distinctive elements, such as the importance of thiarid (and sometimes neritid) gastropods and corbiculid bivalves. Among aquatic insects, the diversity of plecopteran families is low in tropical Asian streams. The order is typical of cooler, more northern latitudes, and is represented mainly by Perlidae (especially Neoperlinae) plus Nemouridae, Leuctridae, and Peltoperlidae. Odonata and Naucoridae (Hemiptera: Heteroptera) are conspicuous elements of the zoobenthos in many tropical Asian streams, and Lepidoptera (Pylalidae) may be diverse and abundant.

Although most invertebrate species are still undescribed, high diversity is displayed by certain taxa. For example, the Mekong contains endemic species-flocks of stenothyrid and pomatiopsid gastropods (more than 110 species), and a similar radiation has occurred in the Yangtze. Likewise, freshwater crabs are astonishingly diverse, comprising six families with more than 80 genera in Asia (67); at least 185 species occur in China, but many more can be expected (see 33). Schmid (78) estimated that India alone may support 4000 species of caddisfly (Trichoptera), with perhaps 50,000 species in the Oriental Region as a whole, and the single genus *Chimarra* (Philopotamidae) may contain 500 Southeast Asian species (61).

Mammalian Diversity in Riverine Wetlands A striking fact about tropical Asia is that many nominally terrestrial species of mammals are associated with riverine wetlands for part or all of the year (6, 36, 37). Many of these animals (some of them "charismatic megafauna") are listed as "vulnerable" or "endangered" by the IUCN (90a). Dudgeon (37) gave a full list of species, among them otters (*Lutra*, *Lutragale*, and *Aonyx*), otter civets (*Cynogale* spp.), and fishing cats (e.g. *Prionailurus planiceps* and *P. viverrinus*). The proboscis monkey (*Nasalis larvatus*) depends upon forested riverine wetlands and sleeps in tall trees along riverbanks. These monkeys have webbed fingers and toes to aid swimming. Other primates such as leaf monkeys (*Presbytis* spp.) and crab-eating macaques (*Macaca fascicularis*) are abundant in riparian forest, while swamp forest is key habitat for orangutans (*Pongo pygmaeus*) in central Kalimantan (Borneo). With around 100 individuals remaining in the wild, this is probably the rarest large mammal in the world (43). Malayan tapirs (*Tapirus indicus*) are riverine animals par excellence. They inhabit dense vegetation and swamp forest by day, but venture onto marshy grasslands or floodplains to feed at night. A tapir can remain submerged for long periods, breathing through its long snout. Other species of megafauna, including Asian elephants (*Elephas maximus*) and Javan rhinoceros (*Rhinoceros sondaicus*), are more wide-ranging, but use riverine wetlands during the dry season because of the availability of water and green forage.

One habitat of particular importance to some elements of the Asian megafauna are the seasonally inundated, grassy floodplains of large rivers. The Indian rhino (*Rhinoceros unicornis*)—which is rarer than either African species of rhino—is confined to such habitats, and formerly ranged along the Indus, Ganges, and Brahmaputra Rivers (43). The historical distribution of the Indian rhino indicates that, in the recent past, significant expanses of swampy grassland mixed with forest, covered floodplains in parts of Asia, providing habitat for a complex of large grazing animals including rhinos, deer, and water buffalo and other wild cattle. For example, Asian water deer (*Hydropotes inermis*) graze vegetation on periodically inundated alluvial soils; Père David's deer (*Elaphurus davidianus*) was restricted to wetlands along the Yangtze; Hog deer (*Axis porcinus*) occur on floodplains and marshy areas with tall grass; and Sambar deer (*Cervus unicolor*), which make opportunistic use of floodplains and riparian forest, often feed while wading. Species or subspecies of marshland deer [e.g. *Cervus (Ruvicervus) duvauceli*, *C. (R.) eldi*, *C. (R.) schomburgki*, and *E. davidianus*] are—or were—confined to particular river systems. These riverine species of *Cervus* are larger than congeneric species from drylands, a fact that may be related to the high productivity of floodplain grazing lands (44). Marshland deer (e.g. *C. (R.) eldi eldi* and *E. davidianus*) have splayed or unusually large hooves which are adapted to floodplain grasslands. Marshland deer are restricted to open floodplains. Their movement in forests and overhanging vegetation is limited due to their expansive antlers, which bear acutely angled tines or have radial branching.

Patterns and Processes

An Asian scientist—Sunder Lal Hora—contributed to the study of lotic ecology during the second quarter of the twentieth century. He highlighted the role of substratum and current as determinants of the distribution and morphology of fauna in Indian torrent streams (45–47). He was aware of the importance of human impacts on Indian rivers and drew attention to declining fish stocks (48). In 1973, 50 y after Hora's first publication, research in Malaysia established that invertebrates are abundant deep in the streambed, highlighting the importance of the hyporheic zone (10). Yet, despite an early start in tropical Asia, lotic ecology remains in its infancy. We have detailed information from rather few localities (e.g. Sungai Gombak in Peninsular Malaysia; Tai Po Kau Forest Stream in Hong Kong); quantitative data on the magnitude of primary and secondary production (benthos or fishes) are in very short supply. Apart from some in Hong Kong (e.g. 26, 30, 39, 41a), manipulative experiments have been undertaken rarely. The work of Benzie (8) on colonization mechanisms of zoobenthos is a notable exception, while Wikramanayake & Moyle (89) performed a novel translocation experiment to investigate resource partitioning among Sri Lankan stream fishes.

Seasonal and Spatial Dynamics of Aquatic Communities What is the ecological backdrop for biodiversity in tropical Asian rivers? Some of the greatest rivers in the world (ranked by magnitude of discharge) are located in the region: the Yangtze,

Brahmaputra, Ganges, Irrawaddy, Zhujiang, Mekong, and Indus. Natural lakes, apart from those associated with river floodplains, are of relatively minor importance, and are far exceeded in area by riverine swamps. The ecology of Asian rivers is profoundly influenced by monsoons, which create a characteristic pattern of seasonality: predictable periods of drought and water scarcity during the dry season alternate with intervals of increased discharge, when flood plains are inundated during the wet season. This has important implications for aquatic productivity, although our understanding of the effects of monsoons on all elements of the biota is far from complete. There are also implications for the ionic composition of river waters plus the transported organic and inorganic loads. In general, concentrations of major ions are inversely proportional to flow rate, and hence decline during the monsoon season. Elevations in nitrogen may occur during floods or in wet-season discharge, especially from densely settled catchments, and there is often a direct correlation between river discharge and the transport of inorganic suspended loads (for details, see 33).

Seasonal patterns in abundance of phytoplankton and zooplankton in large rivers are related to the monsoon, with a wet season low (due to washout, dilution, and turbidity) and a dry season high. Likewise, scouring of periphytic algae during wet-season spates reduces standing stocks, as in subtropical Australian streams (65). Declines in zoobenthos abundance might be expected during the wet season, at least in small streams, where spates associated with monsoonal rains and tropical storms could initiate catastrophic drift and washout. Data from Hong Kong suggest that the picture is far from simple; for example, hydropsychid caddisflies and heptageniid mayflies in one forest stream showed dry-season peaks in density and wet-season lows (31, 32), while polyvoltine calamoceratid caddisflies showed a boom and bust cycle as populations were depleted by spates but recovered when flow conditions stabilized (34). By contrast, in a second, smaller stream, the abundance and species richness of the benthos increased during the wet season (26). In the second stream, base-flow conditions during the dry season imposed a greater disturbance than periodic spates and high discharge during the wet season (see also 65). Evidently, there is inter-stream variation with respect to seasonal fluctuations in zoobenthos densities such that either the wet or the dry season may be the period of greater numbers. Arunachalam et al (2) recorded such variation at a smaller scale, noting that seasonal trends in invertebrate abundance differed among pools in a South Indian river.

While the seasonal dynamics of Asian rivers are driven by monsoons, we know little about the details of spatial or temporal dynamics of almost all elements of the aquatic biota. Studies that document changes in composition of the lotic flora and fauna from the headwaters to mouth are lacking entirely, although some components of the biota have been investigated. Where a sufficiently wide altitudinal range is considered, there are longitudinal changes in the composition of zoobenthos assemblages, diatoms, bryophytes, and fishes (e.g. 70). An important corollary of such longitudinal patterns is the concentration of diversity at lower altitudes. This has important conservation implications as human impacts on the landscape are greatest in the lowlands. Understanding of longitudinal zonation in (especially) large Asian rivers is confounded by the influence of pollution, so

it can be difficult to distinguish “natural” communities from those under anthropogenic influences. Local land use also affects the composition of the stream fauna and alters longitudinal zonation patterns. In his landmark monograph on Sungai Gombak (Peninsular Malaysia), Bishop (11) noted that clearance of riparian vegetation resulted in a marked decline in benthic invertebrate richness. More recent studies have also demonstrated the influence of riparian vegetation on community composition (22).

Zoobenthos: Life Histories, Trophic Relations, and Production While the seasonality of zoobenthos reflects, in part, washout and scouring during spates caused by monsoonal rains, the timing of life-cycle events influences population densities and community composition. The strategy of small polyvoltine insects, certain atyid shrimps, and some molluscs involves flexible, poorly synchronized life histories of the type that probably represents an adaptive response to streams with variable or unpredictable discharge. Periods of extended recruitment and multiple overlapping cohorts seem typical of many aquatic insects in which water temperatures remain above 15°C for most of the year (e.g. 92). Adult emergence prior to or at the start of the monsoon is common to a number of Hong Kong Odonata, Trichoptera, and Ephemeroptera. Such seasonality involves relatively large species. Compared to larger conspecifics, smaller larvae or eggs are less likely to be crushed or injured by the substratum movement during spates, and may be able to seek shelter deep in the hyporheic zone. Concordance of life histories among unrelated species from three insect orders lends support to the suggestion that timing of adult emergence (and subsequent oviposition) is an adaptive response to avoid spate-induced mortality of mature larvae during the peak of the summer monsoon, a degree of synchrony arising from physiological responses to increasing day length. Coincidence of reproduction with the monsoon—seen in some freshwater crabs and shrimps—could also reflect increased habitat availability (e.g. inundated floodplain) for hatchlings in large rivers swollen by monsoonal rains. The breeding habitats of these decapods in large rivers are similar to those of fishes (see below), and may involve migrations. Decapods in smaller streams tend to reproduce before the peak monsoon floods, and hatchlings are benthic forms resembling miniature adults. This life-cycle strategy avoids spate-induced washout of planktonic larvae. Molluscs also seem to have evolved strategies to cope with discharge seasonality: some pomatiopsid snails (e.g. *Neotricula*) in the Mekong River mate during the high-water period but oviposition does not occur until water levels have fallen. Other Mekong genera (e.g. *Paraprososthenia*) mate before the floods, but egg development is delayed so that recruitment takes place when low-flow conditions prevail (4).

Whether seasonal or longitudinal changes in zoobenthic community composition have implications for productivity is unclear. The River Continuum Concept (RCC; 85) makes predictions (albeit rather broad or approximate ones) about downstream changes in representation of functional feeding groups in response to changes in the food base (especially allochthonous inputs) in lotic habitats,

and can serve as an a template for comparing Asian running waters with those elsewhere. The functional organization of benthic communities in shaded streams in tropical Asia—which have high standing stocks of allochthonous detritus—does differ in a rather general way from that of communities in unshaded streams (23, 24; see also 91). However, the paucity of shredders (which comminute coarse detritus) in the upper course of some tropical Asian streams is a significant deviation from the RCC prediction that shredders and collectors should codominate in headwaters. Shredders comprise between 0.1 and 8.8% of the zoobenthos in Hong Kong streams (23, 38) and are scarce in leaf packs (41a). Even in primary rainforest streams in New Guinea, shredders do not exceed 2% of benthic populations (27, 91), and shredders were no more abundant in forested than unshaded streams in Nepal (70). If this under-representation of shredders is a general feature of tropical Asian rivers, it may reflect trophic flexibility and hence functional feeding-group misclassification, that is, the same taxon acting as a shredder or a collector of fine organic material under different circumstances. Alternatively (or in addition), a lack of shredders could reflect limited stream retentiveness for leaf litter (e.g. 69), an increased importance of microbes in litter breakdown in tropical streams (51), or higher investment in chemical defense by tropical leaves making them unpalatable to shredders (79). Leaf palatability (as influenced by toughness or tannin content) does affect the composition of invertebrate assemblages colonizing litter in Hong Kong streams, but most taxa are collector-gathers, not shredders (41a). Breakdown rates for the leaf species that have been studied are rapid, with complete disappearance of litter in less than three months (and within a month for some species). The paucity of shredders does not prevent litter breakdown, but the relative importance to this process of microbes, physical fragmentation, and high water temperatures has yet to be determined (51).

Our understanding of the functional organization of stream communities is based upon data on relative abundance of various feeding groups or, more rarely, absolute densities. Information on the biomass of benthos is limited, and data on periphyton primary production and invertebrate secondary production are fragmentary. Values seem to lie within the same order of magnitude as they do for temperate streams, but there can be considerable inter-annual variation in production by individual invertebrate taxa. For instance, rheophilic species were more abundant when stream discharge was above average in a Hong Kong stream (35). Despite considerable inter-year fluctuation (8 to 537%) in the production of individual species of eight species of filter-feeding caddisflies, total production by filter-feeders varied by only 1.8% between years. Thus, changes in the production of one or more filter-feeding species may be offset by alterations in others so that energy flow through the filter-feeder functional group remains rather constant. Likewise inter-annual variation in total production of heptageniid mayflies (8.6% for five species) was much less than that of individual species (28 to 674%). Generalizations about zoobenthos production in Asian streams must be qualified. Studies to date have focused mainly on larger species—most univoltine insects with rather synchronous growth and clear life-history patterns. However, most

invertebrate taxa exhibit asynchronous growth, with year-round emergence of adults, short life cycles, and polyvoltine life histories. Production estimates for these animals require in situ measurement of the growth of individuals maintained in cages (e.g. 7). Preliminary studies of this type in Asia indicate generation times of a month or less for some mayflies (M Salas, D Dudgeon, submitted for publication), which is similar to values from subtropical and tropical streams elsewhere (7, 53, 62). The turnover of zoobenthos in tropical Asian streams is thus higher than that of the univoltine insects for which we have production estimates, so the present data we have are derived from slow-growing, atypical species with rather low production.

The relatively low proportion of shredders in tropical Asian streams suggests that consumption of allochthonous organic matter is unlikely to make a major contribution to zoobenthos production, but other data imply that this supposition is incorrect. Food webs in streams and small rivers (11, 19, 20) involve widespread use of allochthonous foods by primary consumers, and a relatively high percentage of nominally predatory forms. Nevertheless, the contribution of autochthonous algal food should not be underestimated. A small-scale manipulative study in a Hong Kong stream showed that reductions in periphyton standing stocks led to declines in zoobenthos abundance—especially mayflies (39). Low standing stocks of algae in forest streams may be attributed to shading and nutrient limitation, but an alternative explanation is that periphyton biomass is limited by intense grazing pressure, in which case standing stocks will not give a reliable indication of the importance of algal food to primary consumers. Direct measurements of community metabolism (R) and primary production (P) would help resolve this matter. The only figures we have are from a single day in a Hong Kong stream: ($P/R = 0.17$), indicating heterotrophy in a shaded reach and 1.02 in an unshaded section (24). Data are needed from additional streams during different seasons.

Fishes: Life Histories, Trophic Relations, and Production Information on the ecology of fishes in tropical Asian rivers is considerably more comprehensive than that for invertebrates, but is nonetheless surprisingly meager. Standing stocks in small rivers seem to be somewhat lower than those reported for north-temperate streams with comparable water chemistry, but this generalization is based on few studies. Fish biomass is reduced markedly in acidic ($pH \leq 5.5$) blackwater streams draining peat swamp forest, although such waters may contain a diverse array of stenotopic species (54, 68). Fisheries yields from river floodplains may be high but are subject to substantial inter-annual variation according to the intensity of the monsoon, which drives flood pulses (i.e. the predictable advance and retraction of water over the floodplain). Generally, the result is higher yields during stronger monsoons (88a).

Many fishes show highly seasonal feeding activity, with alternating periods of resource scarcity during the dry season and resource glut during the wet season. A wide range of foods is exploited; allochthonous dietary items, such as terrestrial insects and fruits, are important and their use seems much greater than

has been reported for lotic fishes in temperate latitudes (33, 88a). Many Asian river fishes migrate within river systems. The migrations involve a significant upstream or lateral component, in addition to return or downstream movements. They are frequently, but not invariably, associated with breeding, and are timed to exploit allochthonous foods from inundated floodplains or riparian forests. Thus these are not only breeding migrations but represent migrations to superior living space. Most species that depend upon the floodplain for food and breeding sites show marked inter-annual variation in production (88a).

The Mekong River provides an example of the interaction between fish ecology and discharge. The timing of fish migrations differs somewhat according to species and among different parts of the Mekong Basin, but this complex situation is amenable to generalization (88a). Breeding migrations are made upstream during the wet season as water levels rise; downstream migrations occur when levels fall during the dry season. Planktivorous or piscivorous pelagic fishes (whitefishes) migrate a greater distance than do bottom-dwelling species (blackfishes). The latter feed on benthic organisms, and make shorter lateral movements between the main channel and floodplain or inundated forest than do the former. The fishes differ with respect to breeding habits also: many benthic species are multibrooded and practice parental care (mouthbrooding, bubble-nest building). In addition, these blackfishes can tolerate deoxygenation of stagnant floodplain waters because they have accessory breathing organs, whereas most pelagic whitefishes spawn only once per season and scatter their eggs. An intermediate, relatively species-poor assemblage of generalists (greyfishes) have both migratory and static/territorial behavioral components, enabling them to respond facultatively to changing flow conditions; they may thrive where the natural flood regime has been modified.

In smaller Asian rivers, most fishes synchronize breeding activity with the monsoon or flood season and, where there are two monsoonal floods each year (e.g. in south India, Sumatra and Sri Lanka), they may reproduce twice. There are a few exceptions to the general pattern of wet season spawning: some species of small *Barbus* breed throughout the year or during the dry inter-monsoon period, while spawning by the Taiwanese cyprinid *Zacco pachycephalus* takes place prior to the onset of monsoonal spates which reduce recruitment success (86). All generalizations must be qualified, because our knowledge of fish ecology in Asian rivers is extremely limited. Indeed, writing of the Mekong (a relatively well-known system), Roberts (74) states "...the entire field of fish reproductive biology, including timing and stimulus of reproductive migrations, time, place and requirements for spawning, physiological adaptations of eggs and larvae, and comparative reproductive biology of carps, catfishes, and other groups under natural conditions, is largely untouched..." p. 58.

What Are the Threats to Biodiversity?

Anthropogenic influences imperil the biodiversity of rivers and their associated wetlands at a variety of scales. The main threats are:

1. Deforestation and drainage-basin alteration that destroy or degrade instream and riparian habitat;
2. River regulation, including flow modification and impoundment by dams, water extraction for irrigation, etc;
3. Pollution;
4. Over-harvesting (mainly of fishes and reptiles).

The combined effects of these threats may be more damaging than the sum of each. A further threat—global climate change—will affect river discharge patterns and interact with threats 1 and 2 above to further impact riverine biota.

Deforestation and Drainage Basin Degradation While the fauna of tropical Asian rivers is adapted to seasonal flow fluctuations, unregulated rivers do not necessarily have natural discharge regimes. The consequences of drainage-basin misuse and deforestation are evident throughout the region, and include increased runoff, sedimentation, and flash floods (33). In particular, the effects of deforestation interact with seasonally variable river flows, increasing the frequency and intensity of flood flows with direct and profound consequences for human inhabitants of floodplains. In China, for example, devastating floods along the Yangtze in 1998 focused attention on the link between catchment conditions and runoff. Government blamed the floods on years of uncontrolled logging in upland catchments. Similar consequences of drainage-basin degradation led to a logging ban in Thailand after devastating floods in 1988 claimed several hundred lives.

The loss of forest cover in tropical Asia (estimates range from 0.9% to 2.1% per annum, but local variation is substantial) has important implications for river conservation since a significant proportion of the rich fish fauna of the region exploits allochthonous foods in inundated forests. For example, forest clearance around Le Grand Lac of Cambodia—a floodplain lake connected to the Mekong by the Tonlé Sap River—has led to declining fish catches through a combination of reduced food, erosion, and siltation (88a). Increased turbidity limits primary production, and results in lower fish populations. Forest clearance also threatens fishes confined to soft, acidic, blackwater streams that drain peat swamps. Many such fishes will become extinct (as has occurred already in parts of Malaysia and Indonesia) if logging and other degradation of their habitats continue (68).

Changes in habitat characteristics of drainage basins do not affect forests only; floodplains are also modified or degraded. Because marshland deer (see above) have a narrow reliance on grass as food and highly specific habitat preferences that preclude the use of drylands, they declined in numbers as floodplains were drained, settled, and converted to rice cultivation. During the 19th century, herds of them thrived along the major rivers of India and Thailand; ecologically equivalent species occurred in southern and central China until around 200 y ago (44). Père David's deer was exterminated on the Yangtze floodplain through a combination of habitat modification and hunting (although captive-bred animals have

re-established a population in a small part of the original range). Extinction of *Cervus (R.) schomburgki* in Thailand reflected, in part, possession of the most elaborate antlers of any marshland deer, restricting them to open floodplains and magnifying the risk from humans. Elimination of the Indian rhino over much of its range, the near extinction of wild water buffalo (*Bubalus arnee* [= *B. bubalis*]), and threats to other large grazers likewise reflect conversion of floodplains for agriculture (6, 37).

River Regulation and Dams Fishes and other elements of the lotic fauna are adapted to the floods that are typical of rivers in monsoonal Asia. Although there is some inter-annual variation in flood peaks, the flood-pulse is not a disturbance in the ecosystem. Instead, significant departures from the typical pattern of seasonal flow fluctuation can be regarded as disturbance. This sets the scene for conflict between the needs of humans and of riverine biota. The engineering response to flow seasonality is to capture and store water during flood times for use during the dry period, the benefits being amelioration of peak discharge (i.e. flood prevention) and a predictable water supply during the rest of the year. As many Asian rivers drain degraded and deforested catchments, the desire to limit peak flows by trapping flood waters behind huge dams is understandable. The conflict between human desires to limit or control flows and the requirements of the ecosystem for natural or semi-natural flows is heightened in Asia by high population densities that place severe constraints on the preservation of riverine biodiversity.

The recent trend in Asia has been toward more and bigger dams, culminating in the Three Gorges Scheme on the Yangtze—the largest dam in the world, which will impound Asia's largest river. Approximately 65% of large dams (≥ 15 m tall) are in Asia (63); China has almost half of these, including 10 major dams (> 150 m tall). India (second in Asia and fifth in world ranking) has more than 1100 large dams and 7 major dams. The Mekong has vast potential hydroelectricity-generating capacity and, in 1994, the Mekong Commission (an autonomous coordinating committee set up by three riparian states) identified 12 sites for dams (most with planned outputs $> 10,000$ MW) along the river mainstream in Laos, Thailand, and Cambodia. A predictable result of these dams is that natural flow variability—to which the fauna are adapted and upon which they depend—will be smoothed out. This averaging of flows is significant because ecological responses to environmental change may be non-linear: fish breeding migrations, for example, may not begin until flows have passed a critical threshold.

The consequences of the Mekong Dam array for individual taxa cannot be predicted with certainty. We know little about the zoobenthos of the Mekong but, for most species, the effects are unlikely to be positive. A possible exception is the pomatiopsid snail *Neotricula aperta*, which is a host of the human parasite *Schistosoma mekongi* (Trematoda: Schistosomatidae) and may be favored by modified flow regimes (4). Mainstream dams change the timing and extent of floodplain inundation and, in combination with altered flow and temperature regimes, may suppress fish breeding. They will obstruct the passage of long-distance whitefish

migrants, some of which cover 500–1000 km, including species forming the basis of Mekong wild-capture fisheries (36, 74–76). Dams will have their greatest impacts on species confined to the Mekong. Among them are *Pangasius gigas* and *P. krempfi* (Pangasiidae), the giant gouramy *Osphronemus exodon*, the carps *Probarbus labeamajor* and *Aptosyax grypus* (a 1.3 m-long, 30 kg predator), and the endangered freshwater herring *Tenualosa thibaudeaui*. Some of them could be driven to extinction by a single mainstream dam. The life history of *Pangasius* (= *Pangasianodon*) *gigas*—the 3 m-long Mekong giant catfish—and the routes taken during breeding migrations have yet to be elucidated. Other significant Mekong species are poorly known also: *Aptosyax grypus*, *Probarbus labeamajor*, and *Osphronemus exodon* were described by scientists within the last decade, yet all are fishes ≥ 10 kg in weight, with *P. labeamajor* attaining 70 kg!

Likely effects of dams on Mekong River fishes can be extrapolated also from changes in other large rivers. The more than 3000 dams that have been built along the course of the Zhujiang during the last 40 years have obstructed longitudinal migrations by *Clupanodon thrissa* (Clupeidae), and stocks of major carp species (including *Cirrhinus molitorella*) have fallen to levels that no longer sustain a viable fishery (59). Abundance of the Chinese sturgeon (*Acipenser sinensis*) has been greatly reduced, which has conservation implications because this fish is restricted to the Zhujiang and Yangtze. The anadromous clupeid *Tenualosa reevesii* has been eliminated from parts of the Zhujiang. Landings of *Tenualosa* (= *Hilsa*) *ilisha* likewise dwindled to almost nothing after completion of the Farakka Barrage on the Ganges (66).

The impacts of river regulation involve not only barriers to longitudinal migration but also limitations on lateral movements. Fisheries in the Jamuna River (Bangladesh) declined by over 50% when flood-control embankments reduced fish access to floodplains, and the major carp fishery of the Ganges practically disappeared after seasonal inundation of the floodplain was blocked (66). Other consequences of dams relate to the effects of thermal stratification (9). Water released from the hypolimnion is cool and oxygen-poor, and may even be anoxic and contain toxic hydrogen sulfide. This has predictable consequences for the downstream biota.

The detrimental effects of dams on river fish are often ignored because of the view that negative impacts are more than compensated for by fisheries in newly created impoundments (e.g. 12, 42). Most fishes adapted to the fluctuating discharge of a river will not thrive in a stagnant impoundment. High fisheries yields reported from Asian reservoirs depend on cage culture, stocking (usually of major carp), or introduction of exotic species (9). Such practices are accompanied by a loss of native biodiversity.

Pollution Water quality varies considerably through tropical Asia. However, most major rivers, as well as a host of minor streams, are grossly polluted, and some are among the most degraded in the world. Anti-pollution legislation is in place in some countries, but is weak and/or poorly enforced (41). Pollution from agriculture

and non-point sources is largely uncontrolled and, as cities and industries expand without adequate waste-treatment facilities, rivers receive increasing quantities of effluent. Many rivers are oxygen-poor for much of the year.

In parts of Peninsular Malaysia and Java, some rivers are so severely degraded that fisheries have collapsed. The situation is especially bad in China where, by 1995, some 80% of the 50,000 km of major rivers were too polluted to sustain fisheries (84a). Fish have been entirely eliminated from more than 5% of total river length in China. Fish kills (due to industrial waste water, pesticides, etc) occur frequently during the dry season when water flows are insufficient to dilute pollutants. Tributaries are more heavily contaminated than the main channels where dilution of pollutants is greater. Even in the Yangtze, which once produced 70% of China's freshwater catch, landings fell by more than half between 1954 and 1981, and they have declined ever since.

Things are no better in India. Fish kills are common in the Ganges, which ranks third in the region by flow volume and is probably the most polluted large Asian river. With approximately 400 million people in the catchment, human population density is high, and 600 km of the river course is grossly polluted by sewage, animal wastes, and industrial effluents. Most industries discharging into the river lack operational waste treatment plants, and some cities (e.g. the holy city of Varanasi) lack sewage treatment facilities entirely. Environmental degradation has continued despite the fact that the Ganges is viewed by Hindus as sacred, and pilgrimages to bathe in the cleansing river waters are an important religious practice. This contradiction epitomizes the challenges facing those wishing to protect Asian rivers.

Over-Harvesting Freshwater fishes and herpetofauna are widely harvested across the region for local and overseas consumption. The effects on wild populations of some reptiles have been significant. For example, all eight species of Asian crocodiles are endangered mainly because of hunting pressure. Huge numbers of river turtles are exported from Thailand and Indonesia to China, and there is concern for the long-term viability of some species in the wild (18). Amphibians (especially edible frogs) may also be threatened by over-harvesting, but causes of population decline in this group are complex and reliable data are wanting (6).

Information on fish harvest is more plentiful, albeit frustratingly incomplete. Asia accounts for 64% of the global total of inland fisheries landings (84a). China, India, Bangladesh, and Indonesia are the four most important inland fishery countries in the world, with Thailand ranking seventh (84a). Available figures do not separate yields of aquaculture-based fisheries and enhanced fisheries (in which stock is added to water bodies) from natural capture fisheries, nor do they distinguish reservoir from river fisheries. The dispersed and informal nature of many fisheries leads to under-reporting of landings, and subsistence fisheries are rarely reported. One thing is clear: high catches in Asia reflect heavy exploitation of virtually all freshwaters, and capture fisheries based on wild stocks appear to be at or exceeding the limits of sustainable yield.

The effects of overfishing first become manifest among large species (17). Thus, in east Sumatran rivers, the freshwater “shark” (*Wallago attu*: Siluridae), which can reach a length of 2 m, has been exterminated over part of its range. Populations of the 1-m long cyprinid *Probarbus jullieni* in Sungai Perak, Peninsular Malaysia, were devastated by capture of egg-bearing individuals during upstream migrations, and stocks collapsed when passage was blocked by the Chenderoh Dam (55). Reductions in *Probarbus jullieni*, *P. labeamajor* (which reaches 80 kg), *Catlocarpio siamensis* (120 kg, formerly the basis of an important fishery), and *Pangasius gigas* (300 kg) have occurred in Laos, Cambodia, and Thailand, apparently due to overfishing. *Pangasius gigas* was the basis of an important fishery in Cambodia because oil could be extracted from its fatty flesh. Population declines began decades ago, and stocks have collapsed in recent years so that the fish is now endangered (90a).

Dramatic declines in capture fisheries—such as a 40% reduction in landings by Laotian artisanal fishers between 1984 and 1992—may reflect the use of unsustainable fishing techniques such as explosives. Increased availability and use of synthetic chemicals, rather than natural poisons (such as rotenone extracted from plants), may be a contributing factor also (16). Motorboats and refrigeration technology allow the exploitation and marketing of previously inaccessible stocks. They contribute to overharvesting by reducing the extent of refuges in which stocks are not fished and from which recruits are derived. Unsustainable fishing practices, such as the use of ever-finer meshed nets and overfishing of spawning grounds, combined with the application of poisons, explosives, and electric shocking, have led to marked declines in major carp recruitment in the Zhujiang. In this instance, the damage of such fishing practices cannot be separated from the effects of dams and fish kills caused by pollution (59).

Combined Impacts The synergism of anthropogenic impacts on the aquatic biota is exemplified by the Acipenseriformes (sturgeons and paddlefish) of the Yangtze (88). Acipenseriformes and other large fishes are especially vulnerable to overfishing and other environmental hazards because the long maturation time limits rates of population recovery. Spawning migrations of the anadromous Chinese sturgeon (*Acipenser sinensis*) were blocked by the Gezhouba Dam (or Yangtze Low Dam); fish passes were not provided. Alteration in flow and sediment characteristics have reduced the spawning success downstream of the dam. The Gezhouba Dam fragmented populations of the endemic Yangtze sturgeon (*Acipenser dabryanus*). This potamodromous species undertakes breeding migrations along (but within) the Yangtze. It is now virtually extinct in downstream reaches because populations stranded below the dam cannot travel upstream to breed. Sedimentation (due largely to erosion from deforested uplands) has impacted the populations upstream of the dam. Completion of the Three Gorges High Dam on the Yangtze will bring additional environmental alterations that are likely to further endanger remaining sturgeons. Pollution from industrial and domestic sources has degraded habitat quality for sturgeons throughout the river, and overfishing has contributed

to declines of both species. The same combination of factors has led to the decline of the anadromous Chinese paddlefish (*Psephurus gladius*: Polydontidae) in the Yangtze. The Gezhouba Dam prevents access to upstream spawning sites, and this paddlefish (one of only two polydontids on the planet) is likely to become extinct.

Global climate change will affect river discharge patterns and may have other effects that are likely to impact riverine biota in tropical Asia (and elsewhere). The influence of water quantity on the life history of tropical fishes and other aquatic taxa seems to parallel the importance of temperature to fishes in temperate latitudes (36, 64). Possible scenarios of climate change include wetter wet seasons and drier dry seasons, with an increased frequency of extreme flow events. Because fish catches (and secondary production) from rivers are positively correlated with the extent of inundated floodplain, the increased frequency of extreme flow events will increase the variability of fisheries yields. In addition, lower flows during the dry season will concentrate pollution loads in many rivers. The combination of extreme flow events and the effects of deforestation of drainage basins on runoff can be anticipated to spur construction of even more dams and flood-control projects to the detriment of aquatic biodiversity.

What Do We Need To Know?

Existing conservation efforts are piecemeal and reactive—a result, at least in part, of a lack of awareness or interest in mitigation of anthropogenic impacts on rivers. Conservation must be proactive. Our ability to ameliorate or mitigate the effects of human activities is predicated upon an adequate understanding of river ecology. But information on the prevailing situation with respect to habitat integrity and biodiversity is rarely available. Even for fishes, which have direct relevance to human welfare, data on faunal composition are inadequate. Few countries have made systematic assessments of biodiversity. Some published catalogs are based on dated literature or old museum collections instead of recent surveys. Information on fish conservation status is thus unreliable, and extinctions may not be evident until long after they have occurred (72, 93).

The basic task of compiling species inventories is one priority for biodiversity conservation, but it should be accompanied by assessments of population size and long-term viability—especially for populations of wide-ranging species that are fragmented by dams. These tasks will require monitoring strategies, such as those developed by Humphrey et al (49) in tropical Australia, and formulation of indices of river health that can be applied to individual habitats. Study design and replication should unambiguously address the putative environmental impacts to the exclusion of confounding variables. Unfortunately, studies aimed at investigating the effects of pollutants in tropical Asian streams and rivers have failed to adopt appropriate, statistically rigorous designs (33) as advocated by Underwood (84), among others.

Detecting the onset of environmental degradation is problematic and may result in measures to reverse the situation being put in place only after population declines

and habitat degradation are irreversible. Subtle but important trends in species loss are generally not discernible early enough to permit appropriate remedial action. In the case of Asian river fishes, for example, we lack data on the extent of inter-annual variation in community composition although, like fish production, it may reflect the extent of floodplain inundation in large rivers (88a). The use of zoobenthos abundance data to assess anthropogenic impacts is unlikely to be feasible if natural variation is high. For example, in a Hong Kong stream in which inter-annual variation in the densities of 20 benthic insects was 238% (range 2–1001%), an annual population decrease of 30% might be undetectable!

Assessment of environmental impacts is an important part of the activities of many ecologists, but empirical studies of impacts need to be buttressed by process-oriented studies on the mechanisms underlying the changes caused by the impact. This requires identification of priorities about where knowledge of underlying mechanisms (or even identification of fundamental patterns) is needed. A model of river ecosystems that might allow us to make predictions about natural conditions (and hence recognize significant deviations from such states) would be of great value to environmental managers. Moreover, such a model might indicate the relative importance of contributions of allochthonous energy to aquatic consumers. Does the RCC have any utility in Asia? We cannot—and should not—ignore prevailing paradigms such as the RCC, but this model was derived from research in temperate North America where catchments are dominated by deciduous forest species and climatic factors impose fundamentally different regimes on aquatic biota and ecological processes. Not surprisingly, the functional organization of zoobenthic communities in Asian streams do not agree closely with the predictions of the RCC (38). However, it is not clear what kind of field data at what sampling scale would be required to determine which predictions of the RCC apply to Asian rivers. Quantification of longitudinal changes in the functional organization of benthic communities along several pristine Asian rivers is needed to develop a generally applicable model; a large-scale, multi-national study devoted to this objective would be valuable. Its usefulness could be increased if fish communities were included with measurements of the biomass (or better still, production) of various feeding groups, and if investigations were carried out so as to take account of extremes of flow in the dry and wet seasons. It will be essential to include the consequences of floodplain inundation in the model, since this was not incorporated in the original RCC. Among the obvious practical difficulties is finding several unimpacted rivers of a suitable size since no large, pristine rivers remain in Asia. Nevertheless, without such research, at least on sections of those rivers that have escaped the worst effects of human activities, we have no means of determining whether the RCC serves as anything other than a caricature of lotic ecosystems in Asia.

Two techniques used by ecologists in recent years that have yet to be applied in Asia would aid understanding of the trophic basis of production in rivers. Examination of the stable isotopic signature of consumers allows an assessment of the relative importance of allochthonous and autochthonous energy sources in

supporting secondary production. The ratios of stable carbon isotopes differ between terrestrial and aquatic plants; the stable isotope ratios of nitrogen also yield information about the trophic level of consumers. These methods have been used in tropical Australian rivers (14, 15). Preliminary results from Hong Kong streams have been surprising because they show that, despite low periphyton biomass and high detrital standing stocks, isotopic signatures indicate that mayfly larvae derive most of their assimilated energy from algae (M Salas, D Dudgeon, submitted for publication). Another technique that yields information about the importance of allochthonous and autochthonous energy sources involves the direct measurement of primary production and community respiration (and hence calculation of P/R ratios). When repeated several times over a year, annual production can be estimated. Workers in tropical Australia have deployed microcosms *in situ* to obtain habitat-specific measures of stream community metabolism (14, 15). Such measurements from tropical Asia could yield information that would be laborious to collect by other means and, because the RCC makes predictions about P/R ratios and the relative importance of various energy sources, could also be used to investigate the applicability of this model to Asian rivers.

Constraints and Challenges: Applying What We Know

Habitat destruction or degradation in and along Asian rivers is epidemic, with predictable consequences for resident and migratory species. How can the results of ecological research (including tests of the RCC) be applied to biodiversity preservation in such circumstances? Conservation of individual species will depend more on knowing the details of the natural history of the target organisms (although such data are generally lacking; 74) and less on a general understanding of ecosystem functioning. Conservation strategies must take account of the facts such as that Asian river fishes have complex life cycles and different habitat requirements at various stages of their life history, which means there are many routes of exposure to toxins, direct harvesting, and other detrimental influences. Data on habitat use must be collected on a case-by-case basis and used to develop species-based plans for *in situ* conservation. It can be hoped that strategies that are applicable to species of particular interest (such as the Mekong giant catfish) will protect other taxa that share the same habitat and have similar habits. However, there are few signs that relevant studies are being undertaken or even that there is much awareness of the need for such research (74, 75). For that reason, I (36, 37) have stressed the need to identify flagship species and keystone habitats that may help to increase public and government awareness of the existence of aquatic biodiversity. Effective habitat conservation will require forceful demonstrations of the benefits to be gained from the integrated use of floodplains, rivers, and riparian habitats as wetlands if we are to prevent their conversion to other uses. Promulgation of information on the value of these environments and their biota is the first step in this process.

Species that use distinct environments during different stages of their life histories (migratory fish for example) are at risk from elimination of crucial habitats

or erection of structures that impede movement. Fragmentation of resident populations also results from barriers, and may ultimately lead to species loss. If these statements are correct, why does maintenance of the free passage of fishes along rivers receive so little attention during the planning stages of many large dam projects? One reason may be that scientists are not good at applying what is already known about the consequences of human impacts. Is this because we need more data to underpin conservation strategies? Calls for time to do additional research such as those made in the previous section will come at the cost of further biodiversity loss.

We should apply what we already know (e.g. fragmentation of river dolphin populations increases their probability of extinction), and place less emphasis on what we do not know (e.g. how long will the fragmented populations persist before extinction? Does the RCC apply in Asia?). We must try to get the science right but must do so within the constraint of limited time and money for research versus rapid habitat degradation. The factors that limit research in tropical countries include a shortage of funds, which has consequences for laboratory facilities, equipment, computers, library resources, and so on. Access to the international scientific literature is problematic over much of Asia. Where English is not a native language, there are constraints on reading, reporting, and writing. In addition, there appears to be a failure of tropical ecologists to recognize the importance of disseminating their findings by publishing them in refereed, internationally reputable journals (90). This failure is often one of implementation, also. The integral value of tropical ecology is not always recognized in its own right, or as a contribution to global knowledge, and this makes it difficult for inexperienced researchers writing in a second language to get their work accepted for publication. Manuscripts dealing with tropical rivers seem generally to be perceived as interesting regional studies first and contributions to limnology second; studies of north-temperate waters are viewed in the opposite way (90). One solution to this "temperate hegemony" is for tropical scientists to recognize the significance of their work, relate it to a wider international perspective, and draw attention to it in their own publications. This is easier for me to write than for others to achieve; journal editors and reviewers have a role to play too.

All research efforts are in vain if the resulting knowledge is not translated into social and/or political action. This may be the greatest challenge facing conservation ecologists in Asia. Even if we provide policy-makers with the best ecological information, we cannot assume they will act upon it. For instance, we know that river fish migrate. Most dams in Asia lack fish passes, which can mitigate the impact of dams, or include inappropriate fish ladders, or do not allow for downstream post-breeding migrations of adults (except through the dam turbines). Conventional fish ladders (designed for salmonids) seem likely to have limited success because most Asian fishes do not jump, but fish passes have been effective on some impounded rivers in southern China (Jiangsu Province; 59). Other conservation strategies for Asian river fishes could include application of controlled flooding and drainage permitting adults to access spawning sites and

allowing the passage of water containing spawn and fry in a 'fish friendly' manner (80). Water allocation strategies that will maintain aquatic communities in river reaches downstream of dams (81) have yet to receive attention from water resource managers or funding agencies.

Non-scientific concerns are much greater obstacles to conservation in Asia than a paucity of data or uncertainty over the functioning of ecological systems. Institutional commitment to conservation over the long term is needed. Unfortunately, there is little pressure from the public to protect aquatic biodiversity, and scant evidence that biodiversity conservation or environmental protection are priorities of legislators. Non-government organizations promulgating conservation projects typically work within the political constraints set by governments; where these constraints include corruption and weak or inconsistent enforcement of legislation, conservation goals are compromised or unattainable. Aside from apathy and ignorance about aquatic biodiversity conservation, the major obstacle to conservation of remaining wildlands and rivers Asia is growing human populations. Tropical Asia is overpopulated, and many people are poor, landless, and crowded in burgeoning cities. All hope to improve their lives. The result will be per capita increases in resource use that will be accompanied by greater water consumption and further pollution, flow regulation, and habitat degradation. At the beginning of the third millennium, the prognosis for Asian rivers is grim.

Visit the Annual Reviews home page at www.AnnualReviews.org

LITERATURE CITED

1. Allan JD. 1995. *Stream Ecology*. London: Chapman & Hall. 388 pp.
2. Arunachalam M, Nair KCM, Vijverberg J, Kortmulder K, Suriyanaraynan H. 1991. Substrate selection and seasonal variation in densities of invertebrates in stream pools of a tropical river. *Hydrobiologia* 213:141–48
3. Deleted in proof
4. Attwood SW. 1995. A demographic analysis of *y-Neotricula aperta* (Gastropoda: Pomatiopsidae) populations in Thailand and southern Laos, in relation to the transmission of schistosomiasis. *J. Mollusc Stud.* 61:29–42
5. Beadle LC. 1981. *The Inland Waters of Tropical Africa: An Introduction to Tropical Limnology*. London: Longman. 475 pp.
6. Belsare DK. 1994. Inventory and status of vanishing wetland wildlife of Southeast Asia and an operational management plan for their conservation. In *Global Wetlands Old World and New*, ed. WJ Mitsch, pp. 841–56. Amsterdam: Elsevier
7. Benke AC, Jacobi DI. 1986. Growth rates of mayflies in a subtropical river and their implications for secondary production. *J. N. Am. Benthological Soc.* 5:107–14
8. Benzie JAH. 1984. The colonization mechanisms of stream benthos in a tropical river (Menik Ganga: Sri Lanka). *Hydrobiologia* 111:171–79
9. Bernacsek GM. 1997. *Large Dam Fisheries of the Lower Mekong Countries: Review and Assessment (MKG/R 97023, Vol. I)*. Bangkok: Mekong River Comm. 118 pp.
10. Bishop JE. 1973. Observations on the vertical distribution of the benthos in a Malaysian stream. *Freshw. Biol.* 3:147–56
11. Bishop JE. 1973. *Limnology of a Small*

- Malayan River Sungai Gombak*. The Hague: Dr W. Junk. 485 pp.
12. Biswas AK, El-Habr HN. 1993. Environment and water resources management: the need for a holistic approach. *Water Resour. Dev.* 9:117–25
 13. Braatz S, Davis G, Shen S, Rees C. 1992. Conserving biological diversity: a strategy for protected areas in the Asia-Pacific Region. *World Bank Tech. Pap.* 193:1–66
 14. Bunn SE, Davies PM, Kellaway DM. 1997. Contributions of sugar cane and invasive pasture grass to the aquatic food web of a tropical lowland stream. *Mar. Freshw. Resour.* 48:173–79
 15. Bunn SE, Davies PM, Mosisch TD. 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. *Freshw. Biol.* 41:333–45
 16. Caldecott J. 1996. *Designing Conservation Projects*. Cambridge, UK: Cambridge Univ. Press. 312 pp.
 17. Christensen MS. 1993. The artisanal fishery of the Mahakam River floodplain in East Kalimantan, Indonesia. III. Actual and estimated yields, and their relationship to water levels and management options. *J. Appl. Ichthyol.* 9:202–9
 18. Collins DE. 1999. Turtles in peril: the China crisis. *Vivarium* 10(4):6–9
 19. Costa HH. 1974. Limnology and fishery biology of the streams at Horton Plains, Sri Lanka (Ceylon). *Bull. Fish. Res. Stn, Sri Lanka (Ceylon)* 25:15–26
 20. Costa HH, Fernando ECM. 1967. The food and feeding relationships of the common meso- and macrofauna in the Maha Oya, a small mountainous stream at Peradeniya, Ceylon. *Ceylon J. Sci. (Biol. Sci.)* 7:74–90
 21. Dudgeon D. 1987. Niche specificities of four fish species (Homalopteridae, Cobitidae, Gobiidae) from a Hong Kong forest stream. *Arch. Hydrobiol.* 108:349–64
 22. Dudgeon D. 1988. The influence of riparian vegetation on macroinvertebrate community structure in four Hong Kong streams. *J. Zool. London* 216:609–27
 23. Dudgeon D. 1989. The influence of riparian vegetation on the functional organization of four Hong Kong stream communities. *Hydrobiologia* 179:183–94
 24. Dudgeon D. 1992. *Patterns and Processes in Stream Ecology: A Synoptic Review of Hong Kong Running Waters*. Stuttgart: Schweiz. Verlagsbuchhand. 147 pp.
 25. Dudgeon D. 1992. Endangered ecosystems: a review of the conservation status of tropical Asian rivers. *Hydrobiologia* 248:167–91
 26. Dudgeon D. 1993. The effects of spate-induced disturbance, predation and environmental complexity on macroinvertebrates in a tropical stream. *Freshw. Biol.* 30:189–97
 27. Dudgeon D. 1994. The influence of riparian vegetation on macroinvertebrate community structure and functional organization in six New Guinea streams. *Hydrobiologia* 294:65–85
 28. Dudgeon D. 1995. The ecology of rivers and streams in tropical Asia. In *Ecosystems of the World 22: River and Stream Ecosystems*, ed. CE Cushing, KW Cummins, GE Minshall, pp. 615–57. Amsterdam: Elsevier
 29. Dudgeon D. 1995. River regulation in southern China: ecological implications, conservation and environmental management. *Reg. Riv.: Res. Managage.* 11:35–54
 30. Dudgeon D. 1996. The influence of refugia on predation impacts in a Hong Kong stream. *Arch. Hydrobiol.* 138:145–59
 31. Dudgeon D. 1996. Life histories, secondary production and microdistribution of heptageniid mayflies (Ephemeroptera) in a tropical forest stream. *J. Zool. London* 240:341–61
 32. Dudgeon D. 1997. Life histories, secondary production and microdistribution of hydropsychid caddisflies (Trichoptera) in a tropical forest stream. *J. Zool. London* 243:191–210
 33. Dudgeon D. 1999. *Tropical Asian Streams: Zoobenthos, Ecology and Conservation*.

- Hong Kong: Hong Kong Univ. Press. 830 pp.
34. Dudgeon D. 1999. The population dynamics of three species of Calamoceratidae (Trichoptera) in a tropical forest stream. In *Proc. Int. Symp. Trichoptera, 9th*, ed. H Malicky, P Chantaramongkol, pp. 83–91. Chiang Mai, Thailand: Fac. Sci., Univ. Chiang Mai
 35. Dudgeon D. 1999. Patterns of variation in secondary production in a tropical stream. *Arch. Hydrobiol.* 144:271–81
 36. Dudgeon D. 2000. Going with the flow: large-scale hydrological alterations and the fate of riverine biodiversity in tropical Asia. *BioScience*. In press
 37. Dudgeon D. 2000. Riverine wetlands and biodiversity conservation in tropical Asia. In *Biodiversity in Wetlands: Assessment, Function and Conservation*, ed. B Gopal, WJ Junk, JA Davis. pp. 1–26. The Hague: Backhuys
 38. Dudgeon D, Bretschko G. 1995. Allochthonous inputs and land-water interactions in seasonal streams: tropical Asia and temperate Europe. In *Tropical Limnology, Past and Present*, ed. F Schiemer, pp. 161–79. The Hague: SPB Academic
 39. Dudgeon D, Chan IKK. 1993. An experimental study of the influence of periphytic algae on invertebrate abundance in a Hong Kong stream. *Freshw. Biol.* 27:53–63
 40. Deleted in proof
 41. Dudgeon D, Choowaew S, Ho SC. 2000. River conservation in Southeast Asia. In *Global Perspectives on River Conservation: Science, Policy and Practice*, ed. PJ Boon, GE Petts, BR Davies. pp. 279–308. Chichester, UK: Wiley-Intersci.
 - 41a. Dudgeon D, Wu KKY. 1999. Leaf litter in a tropical stream: food or substrate for macroinvertebrates? *Arch. Hydrobiol.* 146:65–82
 42. Economic and Social Commission for Asia and the Pacific. 1992. *Towards Environmentally Sound and Sustainable Development of Water Resources in Asia and the Pacific* (Water Res. Ser. No. 71). Bangkok: Econ. Soc. Commiss. Asia Pac. 214 pp.
 43. Foose TJ, van Strien N. 1997. *Asian Rhinos—Status Survey and Conservation Action Plan*. Cambridge, UK: World Conserv. Monit. Cent. 112 pp.
 - 43a. Fu CB, Kim JW, Zhao ZC. 1998. Preliminary assessment of impacts on global change in Asia. In *Asian Change in the Context of Global Climate Change*, ed. Galloway JN, Melillo JM, pp. 308–41. Cambridge, UK: Cambridge Univ. Press
 44. Giest V. 1998. *Deer of the World: Their Evolution, Behaviour and Ecology*. Mechanicsburg, PA: Stackpole. 421 pp.
 45. Hora SL. 1923. Observations of the fauna of certain torrential streams in the Khasi Hills. *Rec. Indian Mus.* 25:579–600
 46. Hora SL. 1930. Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. *Philos. Trans. R. Soc. London Ser. B* 218:171–282
 47. Hora SL. 1936. Nature of substratum as an important factor in the ecology of torrential fauna. *Proc. Nat. Inst. Sci. India* 2:45–47
 48. Hora SL. 1952. Major problems of the fisheries of India with suggestions for their solution. *J. Asiatic Soc. (Sci.)* 18:83–101
 49. Humphrey CL, Faith DP, Dostine PL. 1995. Baseline requirements for assessment of mining impact using biological monitoring. *Aust. J. Ecol.* 20:150–66
 50. Hynes HBN. 1970. *The Ecology of Running Waters*. Liverpool: Liverpool Univ. Press. 555 pp.
 51. Irons JG, Oswood MW, Stout RJ, Pringle CM. 1994. Latitudinal patterns in leaf litter breakdown: is temperature really important? *Freshw. Biol.* 32:401–11
 52. Deleted in proof
 53. Jackson JK, Sweeney BW. 1995. Egg and larval development times of 35 species of tropical stream insects from Costa Rica.

- J. N. Am. Benthological Soc.* 14:115–30
54. Johnson DS. 1967. Distributional patterns of Malayan freshwater fish. *Ecology* 48:722–30
 55. Khoo KH, Leong TS, Soon FL, Tan SP, Wong SY. 1987. Riverine fisheries in Malaysia. *Arch. Hydrobiol. Beih., Ergeb. Limnol.* 28:261–68
 56. Kottelat M. 1989. Zoogeography of the fishes from Indochinese inland waters with an annotated checklist. *Bull. Zool. Mus, Univ. Amst.* 12:1–56
 57. Lewis WM. 1987. Tropical limnology. *Annu. Rev. Ecol. Syst.* 18:159–84
 58. Li S. 1981. *Studies on Zoogeographical Divisions for Freshwater Fishes of China*. Beijing: Sci. Press. 292 pp. (In Chinese)
 59. Liao GZ, Lu KX, Xiao XZ. 1989. Fisheries resources of the Pearl River and their exploitation. *Can. Spec. Publ. Fish. Aquat. Sci.* 106:561–68
 60. Lowe-McConnell RH. 1987. *Ecological Studies of Tropical Fish Communities*. Cambridge, UK: Cambridge Univ. Press. 382 pp.
 61. Malicky H. 1989. Köcherfliegen (Trichoptera) von Sumatra und Nias: Die Gattungen *Chimarra* (Philopotamidae) und *Marilia* (Odontoceridae), mit Nachträgen zu *Rhyacophila* (Rhyacophilidae). *Mitt. Schweiz. Entomol. Ges.* 62:131–43
 62. Marchant R, Yule CM. 1996. A method for estimating larval life spans of aseasonal aquatic insects from streams on Bougainville Island, Papua New Guinea. *Freshw. Biol.* 35:101–7
 63. McCully P. 1996. *Silenced Rivers: The Ecology and Politics of Large Dams*. London: Zed Books. 350 pp.
 64. Meisner JD, Shuter BJ. 1992. Assessing potential effects of global climate change on tropical freshwater fishes. *GeoJournal* 28:21–27
 65. Mosisch TD, Bunn SE. 1997. Temporal patterns of rainforest stream epilithic algae in relation to flow-related disturbance. *Aquat. Bot.* 58:181–93
 66. Natarajan AV. 1989. Environmental impact of Ganga Basin development on gene-pool and fisheries of the Ganga River system. *Can. Spec. Publ. Fish. Aquat. Sci.* 106:545–60
 67. Ng PKL. 1988. *The Freshwater Crabs of Peninsular Malaysia and Singapore*. Singapore: Dep. Zool., Natl. Univ. Singap. 156 pp.
 68. Ng PKL, Tay JB, Lim KKP. 1994. Diversity and conservation of blackwater fishes in Peninsular Malaysia, particularly in the north Selangor peat swamp forest. *Hydrobiologia* 285:203–18
 69. Nolen JA, Pearson RG. 1993. Factors affecting litter processing by *Anisocentropus kirramus* (Trichoptera: Calamoceratidae) from an Australian tropical rainforest stream. *Freshw. Biol.* 29:469–79
 70. Ormerod SJ, Rundle SD, Wilkinson SM, Daly GP, Dale KM, Juttner I. 1994. Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. *Freshw. Biol.* 32:309–22
 71. Payne AI. 1986. *The Ecology of Tropical Lakes and Rivers*. Chichester, UK: Wiley-Intersci. 301 pp.
 72. Pethiyagoda R. 1994. Threats to the indigenous freshwater fishes of Sri Lanka and remarks on their conservation. *Hydrobiologia* 285:189–201
 73. Rainboth WJ. 1996. *Fishes of the Cambodian Mekong*. Rome: Food Agric. Organ. U. N. 265 pp.
 74. Roberts TR. 1993. Artisanal fisheries and fish ecology below the great waterfalls in the Mekong River in southern Laos. *Nat. Hist. Bull. Siam Soc.* 41:31–62
 75. Roberts TR. 1995. Mekong mainstream hydropower dams: run-of-the-river or ruin-of-the-river? *Nat. Hist. Bull. Siam Soc.* 43:9–19
 76. Roberts TR, Baird IG. 1995. Traditional fisheries and fish ecology on the Mekong River at Khone Waterfalls in southern Laos. *Nat. Hist. Bull. Siam Soc.* 43:219–62

77. Deleted in proof
78. Schmid F. 1984. Essai d'évaluation de la faune mondiale des Trichoptères. In *Proc. Int. Symp. Trichoptera, 4th*, ed. JC Morse, pp. 337. Clemson University, South Carolina, USA. The Hague: Dr W Junk (Abstr.)
79. Stout RJ. 1989. Effects of condensed tannins on leaf processing in mid-latitude and tropical streams: a theoretical approach. *Can. J. Fish. Aquat. Sci.* 46:1097–106
80. Sultana P, Thompson PM. 1997. Effects of flood control and drainage of fisheries in Bangladesh and the design of mitigating measures. *Reg. Riv.: Res. Manage.* 13:43–55
81. Sutton RJ, Miller WJ, Patti SJ. 1997. Application of the Instream Flow Incremental Methodology to a tropical river in Puerto Rico. *Rivers* 6:1–9
82. Talling JF, Lemoalle J. 1998. *Ecological Dynamics of Tropical Inland Waters*. Cambridge, UK: Cambridge Univ. Press. 451 pp.
83. Thirakhupt K, Van Dijk PP. 1994. Species diversity and conservation of turtles in western Thailand. *Nat. Hist. Bull. Siam Soc.* 42:207–59
84. Underwood AJ. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecol. Appl.* 4:3–15
- 84a. United Nations Food and Agricultural Organization. 1999. *Review of the State of World Fishery Resources: Inland Fisheries* *FAO Fish. Circ. No. 942*. Food and Agriculture Organization of the United Nations, Rome. 53 pp.
85. Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The River Continuum Concept. *Can. J. Fish. Aquat. Sci.* 37:130–37
86. Wang JT, Liu MC, Fang LS. 1995. The reproductive biology of an endemic cyprinid, *Zacco pachycephalus*, in Taiwan. *Environ. Biol. Fish.* 43:135–43
87. Deleted in proof
88. Wei Q, Ke F, Zhang J, Zhaung P, Luo J, et al. 1997. Biology, fisheries, and conservation of sturgeons and paddlefish in China. *Environ. Biol. Fish.* 48:241–55
- 88a. Welcomme RL. 1979. *Fisheries Ecology of Floodplain Rivers*. London: Longman. 317 pp.
89. Wikramanayake ED, Moyle PB. 1989. Ecological structure of tropical fish assemblages in wet-zone streams of Sri Lanka. *J. Zool. London* 218:503–26
90. Williams WD. 1994. Constraints to the conservation and management of tropical inland waters. *Mitt. Int. Ver. Limnol.* 24:357–63
- 90a. World Conservation Monitoring Centre. 1996. *1996 IUCN Red List of Threatened Animals*. Cambridge, UK: World Conserv. Monit. Cent. 228 pp.
91. Yule CM. 1996. Trophic relationships and food webs of the benthic invertebrate fauna of two aseasonal tropical streams on Bougainville Island, Papua New Guinea. *J. Trop. Ecol.* 12:517–34
92. Yule CM, Pearson RG. 1996. Aseasonality of benthic invertebrates in a tropical stream on Bougainville Island, Papua New Guinea. *Arch. Hydrobiol.* 137:95–117
93. Zakaria-Ismail M. 1994. Zoogeography and biodiversity of the freshwater fishes of Southeast Asia. *Hydrobiologia* 285: 41–8



CONTENTS

PREFACE: A Millennial View of Ecology and Systematics, and ARES at Age 30, <i>Richard F. Johnston</i>	1
THE KINSHIP THEORY OF GENOMIC IMPRINTING, <i>David Haig</i>	9
CENOZOIC MAMMALIAN HERBIVORES FROM THE AMERICAS: Reconstructing Ancient Diets and Terrestrial Communities, <i>Bruce J. MacFadden</i>	33
CONSERVATION ISSUES IN NEW ZEALAND, <i>John Craig, Sandra Anderson, Mick Clout, Bob Creese, Neil Mitchell, John Ogden, Mere Roberts, Graham Ussher</i>	61
THE EVOLUTION OF PREDATOR-PREY INTERACTIONS: Theory and Evidence, <i>Peter A. Abrams</i>	79
THE ECOLOGY AND PHYSIOLOGY OF VIVIPAROUS AND RECALCITRANT SEEDS, <i>Elizabeth Farnsworth</i>	107
INBREEDING DEPRESSION IN CONSERVATION BIOLOGY, <i>Philip W. Hedrick, Steven T. Kalinowski</i>	139
AFRICAN CICHLID FISHES: Model Systems for Evolutionary Biology, <i>Irv Kornfield, Peter F. Smith</i>	163
SHRUB INVASIONS OF NORTH AMERICAN SEMIARID GRASSLANDS, <i>O. W. Van Auken</i>	197
THE GRASSES: A Case Study in Macroevolution, <i>Elizabeth A. Kellogg</i>	217
THE ECOLOGY OF TROPICAL ASIAN RIVERS AND STREAMS IN RELATION TO BIODIVERSITY CONSERVATION, <i>David Dudgeon</i>	239
HARVESTER ANTS (POGONOMYRMEX SPP.): Their Community and Ecosystem Influences, <i>James A. MacMahon, John F. Mull, Thomas O. Crist</i>	265
ORIGINS, EVOLUTION, AND DIVERSIFICATION OF ZOOPLANKTON, <i>Susan Rigby, Clare V. Milsom</i>	293
EVOLUTIONARY PHYSIOLOGY, <i>Martin E. Feder, Albert F. Bennett, Raymond B. Huey</i>	315
MECHANISMS OF MAINTENANCE OF SPECIES DIVERSITY, <i>Peter Chesson</i>	343
TEMPORAL VARIATION IN FITNESS COMPONENTS AND POPULATION DYNAMICS OF LARGE HERBIVORES, <i>J.-M. Gaillard, M. Festa-Bianchet, N. G. Yoccoz, A. Loison, C. Toïgo</i>	367
IMPACTS OF AIRBORNE POLLUTANTS ON SOIL FAUNA, <i>Josef Rusek, Valin G. Marshall</i>	395

ECOLOGICAL RESILIENCE - IN THEORY AND APPLICATION, <i>Lance H. Gunderson</i>	425
QUASI-REPLICATION AND THE CONTRACT OF ERROR: Lessons from Sex Ratios, Heritabilities and Fluctuating Asymmetry, <i>A. Richard Palmer</i>	441
INVASION OF COASTAL MARINE COMMUNITIES IN NORTH AMERICA: Apparent Patterns, Processes, and , <i>Gregory M. Ruiz, Paul W. Fofonoff, James T. Carlton, Marjorie J. Wonham, Anson H. Hines</i>	481
DIVERSIFICATION OF RAINFOREST FAUNAS: An Integrated Molecular Approach, <i>C. Moritz, J. L. Patton, C. J. Schneider, T. B. Smith</i>	533
THE EVOLUTIONARY ECOLOGY OF TOLERANCE TO CONSUMER DAMAGE, <i>Kirk A. Stowe, Robert J. Marquis, Cris G. Hochwender, Ellen L. Simms</i>	565