Micronesica 25(2): 155–173, 1992

An Ecosystem Classification of Inland Waters for the Tropical Pacific Islands

DAN A. POLHEMUS

Applied Research Group, Bishop Museum.
P.O. Box 19000-A, Honolulu, HI. 96817

JOHN MACIOLEK

P.O. Box 7117, Mammoth Lakes, CA. 93546

JOHN FORD

USDI FWS Pacific Islands Office, 5302 Prince Kuhio Federal Building
P.O. Box 50167, Honolulu, HI. 96850

Abstract—Selected physical and chemical factors provide a method of classifying insular tropical Pacific inland waters into 18 classes and subclasses that are arranged graphically to show hierarchical interrelationships and utility in preliminary (e.g., map-based) inventories. Characteristic and distinguishing biota, primarily faunal groups, are added to the environmental scheme to complete the descriptions as ecosystems. Because on-site sampling is essential for biological and hydrochemical information, ecosystem examples are drawn principally from the Hawaiian Archipelago and New Guinea, areas which have had extensive ecological surveys, contain most island and ecosystem types, and represent the opposite extremes of geographical isolation and biotic composition in the region under consideration. Interfaces with marine and terrestrial systems are discussed, and conservation aspects are considered. To lessen ambiguity, relevant terminology is defined or qualified.

Introduction

There has long been a need for the development of a uniform and unambiguous classification system covering the terrestrial, marine and inland water ecosystems of the Pacific Basin. The inland waters ecosystem classification presented below is intended to address one aspect of this problem, and to apply primarily to the oceanic islands of the *insular tropical Pacific*, defined herein as including Micronesia, Polynesia (exclusive of New Zealand), and Melanesia, plus the southern Ryukyus and Bonins. Due to the geographical scope of the conference from which it originated, this classification is designed to apply provisionally to New Guinea as well, although this large island is in many ways a small con-

tinent and contains a diverse array of inland water ecosystems not generally seen on the other islands under discussion. This potential incongruity is mitigated to some degree by the fact that our classification is compatible with previous schemes based on continental ecosystems (see Cowardin et al. 1979), and general enough that it should be applicable in many continental settings, even though it was designed to apply most strictly to small oceanic islands.

Our intention has been to develop an inland waters classification system that has maximum utility for use in preliminary, map-based inventories that do not require extensive ground surveys. In defining ecosystem types we have focused primarily on physical and biotic characteristics relating to the aquatic systems themselves, without addressing the surrounding floral and faunal communities in any great detail. As a result, our classification is independent of the botanically-based classification of Pacific terrestrial ecosystems developed by Pearsall et al. (1992). These and subsequent authors may propose to further subdivide on botanical criteria ecosystems that we have treated as single units (e.g., lowland freshwater swamps).

The definitions and ecosystem descriptions presented herein draw heavily on the work of Maciolek (1977), who presented a similar classification of insular aquatic ecosystems for the Hawaiian Archipelago. In the present work Maciolek's basic classification scheme has been expanded and modified to take into account the entire range of inland water ecosystems occurring in the insular tropical Pacific, but many of Maciolek's physical ecosystem definitions still remain essentially unchanged. Diagnostic examples of flora and fauna associated with each ecosystem are drawn primarily from the Hawaiian Archipelago, which contains a wide spectrum of oceanic island types and has had the most intensive limnological study of any island group in the area under discussion, and from New Guinea, a continental island which represents the opposite extreme in terms of geographical isolation and biotic composition. Additional examples are given for other islands in the insular tropical Pacific in cases where this information is known, although in most cases biotic surveys are lacking or inadequate.

Terminology

Terminology presents a persistent problem in ecosystem classification schemes, since different authors have often employed the same ecological terms in different contexts (e.g., "habitat," "ecosystem"), and then discussed these terms without providing the necessary operational or pragmatic definitions.

The following definitions are used in the present classification of Pacific inland waters. The *aquatic ecosystem* is the principal coherent subunit of the aquatic biosphere, consisting of a watermass continuum with relatively sharp, delineable boundaries (ecotones), enclosing integral resident organisms and physiochemical features. Examples of common aquatic ecosystems are lakes, marshes, streams and estuaries. Two basic components of an ecosystem are the *biota* (biocoenosis), or totality of living matter, and the *environment*, which is here restricted to the nonliving (physiochemical) components of the ecosystem,

including spatial dimensions. *Habitat* is used strictly in an autecological sense to designate all ecosystem requirements of a species, including space. Habitats are thus not spatially exclusive subdivisions of an ecosystem, in contrast to divisions such as zones, strata, and reaches.

The various types of aquatic ecosystems recognized in the present classification are assigned to major divisions or *classes*, which generally correspond to the "ecological systems" of Cowardin et al. (1979). There are three exceptions to this rule: (1) the "marine" ecological system is excluded from the present classification, since it has been treated elsewhere (Maragos, in press), although comments are provided herein regarding estuaries, where the inland waters and marine classifications intermingle; (2) *anchialine*, a unique ecosystem class (discussed in greater detail below) is introduced; and (3) lotic is substituted for "riverine," the latter word being one which connotes large ecosystems of a specific type and is also etymologically aberrant in relation to the classical derivations of the other class names. "Lotic" fully covers the entire range of flowing water ecosystems recognized herein, including some not addressed by Cowardin et al. (1979).

An implicit assumption in the present classification is that ecosystem designations must be based on descriptions of both characteristic biota and environmental features. Ideally, ecosystem categories should be mutually exclusive, with each readily discernable based on observations and measurements that do not require a protracted amount of time to obtain. Criteria that we have used to distinguish ecosystem classes are hydrological regime, water depth, salinity, and characteristic major taxa of the biota (in general the fauna is more distinctive in this regard than is the flora). Ecosystem types are defined by criteria that include altitude, topography, water character (temperature, turbidity), cultural influences (environmental and biological), and the presence of individual genera or species. After reviewing the chemical data we have concluded that oxygen content and pH usually cannot be applied as descriptors at the ecosystem level (with certain exceptions; e.g., upland bogs). In many waters, particularly those of low ionic content and abundant flora, strong photosynthesis and respiration can diurnally change the levels of such characteristics significantly (pH sometimes more than two units). These criteria are defined further in Appendix A.

Ecosystem Classification: Overview

Eighteen types of inland aquatic ecosystems, occurring on diverse island types and at a wide range of elevations, are recognized in the present classification and presented in a hierarchical arrangement in Figure 1. These ecosystems are split into two major divisions, subterranean and surface, with the latter division further divided into two ecosystem classes, lotic and lentic. The defining features for these divisions and classes are provided in Appendix A.

The Lotic Ecosystem Class contains four types of flowing waters. *Perennial streams* form the largest (by area) and most widely distributed type of lotic ecosystem on the Pacific high islands. The recent Hawaii Stream Assessment (Wilcox

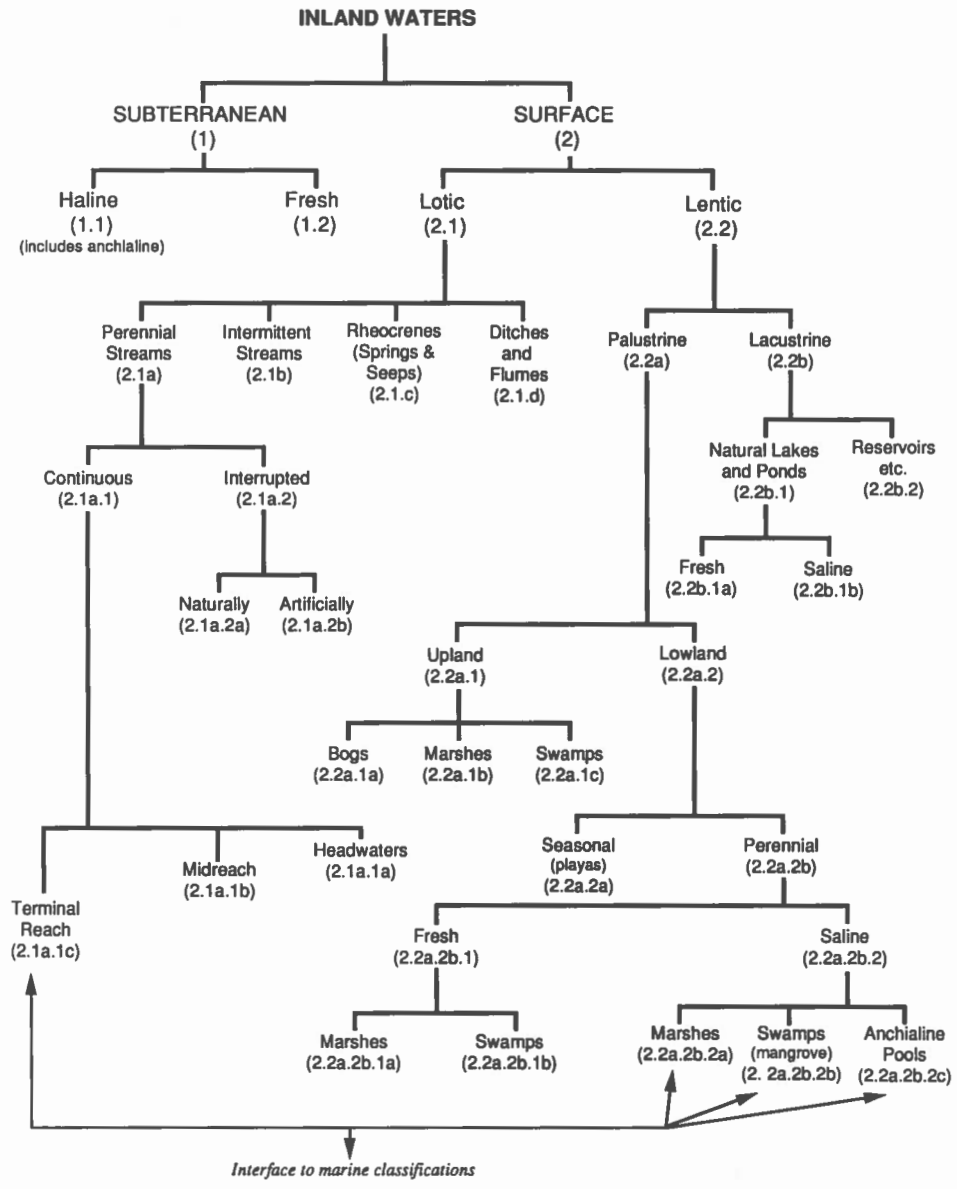

Figure 1. Classification of Pacific inland waters.

1990), for example, listed 376 streams of this type in the Hawaiian Islands alone. In Hawaii these streams are distinguished biologically by a mollusk and three diadromous gobies that live as adults in no other ecosystems. *Intermittent streams* differ environmentally from perennial streams in terms of flow regime, and biologically in lacking most diadromous fish species, but contain abundant small

invertebrates such as ostracods that are rare elsewhere. *Rheocrenes*, or flowing springs, are numerous, ubiquitous small seepages ("leaks" from elevated aquifers) without channels that provide habitat for aquatic snails and other invertebrates, particularly insects (e.g., veliid waterbugs, damselfly immatures). *Ditches and flumes* are artificial streams containing some native animals but generally dominated by introduced species. Some ditches were built by prehistoric Polynesians for taro irrigation, but most were constructed during the past century for irrigation of sugar cane and other crops, or to provide municipal water supplies. They occur on most high islands but for the most part have not been inventoried.

The Lentic Ecosystem Class contains two types of standing waters, lacustrine and palustrine. Natural lacustrine ecosystems are relatively uncommon in the insular tropical Pacific, although many artificial deepwater basins have been created by the construction of dams or by warfare (e.g., bomb craters). In Hawaii, for example, only four freshwater *natural lakes* are known, their presence limited by substratum permeability (Maciolek 1969). Each is distinctive in location, environmental features, and native invertebrate fauna. *Reservoirs* (impoundments) are the most abundant lacustrine ecosystem; more than 400 are shown on U.S. Geological Survey maps of the Hawaiian Islands alone. They are artificial ecosystems, not only in basin origin and structure but also in biota, which is dominated by introduced macrofauna. *Saline/haline lakes* also occur in the insular tropical Pacific as both high island shoreline features and as low island closed lagoons.

Palustrine ecosystems include wetlands at both high and low elevations, each with several types. Elevated wetlands, located in remote areas, are primarily natural systems in which native biota dominates. Low wetlands have been for the most part severely modified by man, although they still constitute a primary habit for many waterbirds. *Montane bogs* occur in limited sites on nearly all noncarbonate high islands in areas of stagnant ground water and are distinguished by strongly acidic water chemistry and impoverished invertebrate faunas. *Upland swamps and marshes* appear to be more productive than bogs and support a greater faunal diversity. Introduced biota predominates in most *freshwater lowland swamps and marshes*, a complex series of ecosystems ranging from flooded taro and rice fields to natural marsh basins and swamp forests. Both upland and lowland swamps and marshes form a graded series of ecosystems, and further study may indicate that they should be classified as a single ecosystem type. *Saline lowland wetlands* include shoreline salt marshes and mangrove swamps, as well as artificial ponds such as abandoned Hawaiian fishponds and recently constructed waterbird refuges. Salt-dependent pickleweed (*Batis maritima*) is a common emergent plant, while the fauna often includes introduced euryhaline fishes and invertebrates co-occurring with native snails and isopods. Present day aquaculture ponds can be fitted into either of the above types of lowland coastal palustrine ecosystems depending on their salinity.

An additional ecosystem type included under saline lowland wetlands is *anchialine pools*. The name (from Greek *anchialos*, "near the sea") was suggested by Holthuis (1973) to define "pools with no surface connection to the sea, con-

taining salt or brackish water, which fluctuates with the tides." The ecosystem definition should further note that the pools contain a distinctive biota, often including invertebrate species not found elsewhere. These pools appear to form most commonly in coastal lava fields, and are generally small, with the majority being less than 100 m^2 in area. Their surfaces are usually inland extensions of the oceanic water table, although mixohalinity, usually less than 10 percent, often results from dilution by seaward percolating groundwater. In Hawaii mat- and crust-forming algal communities occur in rocky pools, and widgeongrass (*Ruppia maritima*) is characteristic of sedimented basins. The fauna, which in Hawaii includes many endemic species, consists primarily of invertebrates of marine origin that have invaded through subterranean interstices (it is due to this subterranean connection that these pools are listed under both the surface and subterranean divisions of the present ecosystem classification). Characteristic taxa are snails, amphipods, and shrimps, with fishes being rare or absent.

Pacific Inland Water Ecosystems: Descriptive Features and Characteristic Biota

1. SUBTERRANEAN AQUATIC ECOSYSTEMS—Limnetic to haline underground inland waters, with or without discernable directional flow.

1.1. *Subterranean haline*—euhaline to mixohaline underground waters, primarily inland extensions of the oceanic water table that may or may not be diluted by limnetic groundwaters. Includes the subterranean component of anchialine pools (see subsequent discussion under Saline Lowland Wetlands).

1.2. *Subterranean fresh*—limnetic underground waters, primarily groundwaters percolating seaward along unidirectional altitudinal gradients. Includes the hyporheic zone of perennial streams. Biota largely unstudied.

2. SURFACE AQUATIC ECOSYSTEMS—Limnetic to haline above ground inland waters, with or without discernable directional flow.

2.1. *Lotic* (Riverine) *Ecosystems*—Limnetic surface waters flowing unidirectionally down altitudinal gradients.

2.1a. *Perennial Streams*—Waters draining land surfaces in discrete channels and flowing year-round. Turbidity low except during freshets; dissolved oxygen normally near saturation throughout watercourse. Flora mainly mosses, filamentous algae, and epilithic diatoms. Native macrofauna (fishes, shrimps, mollusks) on oceanic islands usually diadromous, with marine larval development. Prominent altitudinal zonation of environmental conditions and biota.

2.1a.1. *Continuous Perennial Streams*—Streams discharging continuously to the ocean in their natural state. Three divisions are recognized within this ecosystem:

2.1a.1a. *Headwater Reach*—Elevation >800 m or gradient >30%, or both. Substratum mainly bedrock. Water temperature <18 °C (usually 12–15°); conductivity < 50 μmhos (dissolved solids <40 mg/L); pH usually <5.5. Fauna in Hawaii dominated by insects, with fishes and crustaceans lacking. Characteristic fauna in New Guinea includes veliid waterbugs (*Rhagovelia*, *Microvelia*).

2.1a.1b. *Midreach*—Intermediate in environmental conditions between Headwater Reach and Terminal Reaches (see below). Substratum predominantly boulders, rocks and gravel. Distinguishing fauna in Hawaii includes endemic diadromous gobioid fishes (*Awaous stamineus*, *Lentipes concolor*, *Sicydium stimpsoni*), and native shrimps (*Atyoida bisulcata*), snails (*Neritina granosa*), insects (*Telmatogeton* and *Procanace* flies; *Hyposmocoma* moths; *Megalagrion* damselflies), and sponges (*Heteromyenia baileyi*). Representative introduced fauna in Hawaii includes tilapia, Chinese catfish, loach, poeciliid fishes (guppy, swordtail), various tadpoles, crayfish, Tahitian prawn, and caddisflies (*Cheumatopsyche pettiti*). Fauna on continental islands such as New Guinea diverse, including bagriid catfishes; baetid, leptophlebiid and prosopistomatid mayflies; hydropsychid caddisflies; protoneurid (*Notoneura*) and chlorocyphid (*Rhinocypha*) damselflies; libellulid dragonflies; dolichopodid and chironomid flies; gerrid (*Ptilomera*, *Tenagogonus*), veliid (*Rhagovelia*), and naucorid (*Sagocoris*, *Idiocarus*) water bugs.

2.1a.1c. *Terminal Reach*—Watercourse below sharp gradient that bars upstream migration of itinerant marine fishes. Elevation generally <50 m and gradient <5%. Substratum primarily rock, gravel and sediment. Water temperature >18 °C (generally 19–22°); conductivity >80 μmhos (mainly 100–150 μmhos); dissolved solids 60–100 mg/L; pH 6.5–7.8. Large lowland rivers in New Guinea (Fly, Sepik, Ramu) will fall within this division. Fauna in Hawaii includes euryhaline fishes and native prawns. Characteristic fauna in New Guinea includes baramundi, bagriid catfishes, palingeniid mayflies (*Plethogenesia*), and gerrid water bugs (*Rhagdotarsus*, *Limnogonus*).

Remarks: The above three divisions may each be further divided into two zones, erosional and depositional. Erosional zones include waterfalls, rapids, riffles, and other areas where there is a net loss of substrate or organic material due to the action of flowing water. Depositional zones include pools, the inner margins of stream bends, and other areas where such material is deposited. Since these two types of zones alternate and intergrade along the length of any given reach they are not considered ecosystems in the present classification but they are often important components of the habitats of individual taxa.

Perennial streams are common on nearly all noncarbonate high islands, with more than 360 identified in the Hawaiian Archipelago alone.

2.1a.2. *Interrupted Perennial Streams*—Streams flowing perennially in their upper reaches while discharging to the sea only a seasonal basis (e.g., Kawela Gulch on Molokai).

2.1a.2a. *Naturally Interrupted*—Streams with flow becoming subsurface in their middle or terminal reaches, although occasionally appearing as pools in areas of bedrock exposure. Fauna similar to that of continuous perennial streams, including diadromous gobioid fishes in Hawaii, but generally less diverse.

2.1a.2b. *Artificially Interrupted*—Streams partially or totally diverted for agricultural and domestic purposes. Generally accompanied by channel alteration which modifies or eliminates the native ecosystem character in many instances, particularly in urban areas. Many streams of this type in lowland areas are now dominated by introduced fauna.

2.1b. *Intermittent Streams*—Seasonally flowing waters draining land surfaces in discrete channels, with flowing water decreasing in volume to slow-exchanging pools prior to desiccation. Water quality variable. Characteristic biota appearing where water persists for at least a few weeks (usually as diminishing flow) includes filamentous algae, oligochaete worms, ostracod crustaceans, Coleoptera (Dytiscidae), and Heteroptera (Notonectidae). Diadromous fauna usually absent, but sometimes persisting in permanent lowland pools.

2.1c. *Rheocrenes*—"Flowing springs." Perennial seeps and springs flowing short distances over rock surfaces or in indistinct channels. Found typically as natural occurrences along coastal rock faces or banks of deeply incised streams (particularly adjacent to waterfalls), and artificially along road cuts. Variable water quality, sometimes iron-rich as evidenced by bacterial precipitation of ferric hydroxide. Two divisions are recognized: *thermal*, with average water temperature noticeably (at least 10 °C) above the mean annual temperature of the air at the same locality, and *non-thermal*, with water temperature near or below the mean annual air temperature. Characteristic non-thermal biota in Hawaii includes gelatinous (blue-green) algae, mosses, maidenhair fern, detritivorous leeches, immature Diptera and Odonata (*Megalagrion*), and lymnaeid snails (*Erinna*, *Pseudisidora*). Characteristic non-thermal biota in New Guinea includes veliid (*Microvelia*) and gelastocorid (*Nerthra*) waterbugs. Thermal rheocrenes support distinct algal communities, but in tropical regions appear to have poorer fauna than similar non-thermal ecosystems.

2.1d. *Ditches and Flumes*—Water flowing continuously in artificial channels. Environmental character and biota differ with location and degree of use. *Primary ditches/flumes* carry diverted stream water to reservoirs or other use areas. Generally high-quality water similar to that in stream at diversion point (most located at 100–500 m elevation, comparable to midreach stream water). Lack of shelter and slack water results in low faunal diversity; most prominent biotic elements in Hawaii are aquatic Diptera larvae and adults, snails, and occasionally atyid shrimps. Fishes generally scarce. *Secondary* (or effluent) *ditches* carry water from reservoirs, agricultural sites and use facilities. Moderate to low water quality, sometimes polysaprobic. Macrofauna, when present, consisting mainly of introduced fishes and hardy invertebrates. Mostly at elevations below 50 m.

2.2. *Lentic Ecosystems*—Standing or still waters, generally in definite basins.

2.2a. *Palustrine Ecosystems*—Lentic waters <2 m deep (usually <1 m). Sometimes in irregular or poorly defined basins.

2.2a.1. *Elevated Wetlands*—Natural limnetic water bodies located at elevations >100 m. Fauna in Hawaii predominantly native, but lacking fishes or shrimps.

2.2a.1a. *Upland Bogs*—Small bodies of acid, open water on flat elevated topography (usually 600–3000 m, but up to 4200 m on Mt. Wilhelm in New Guinea) in areas of high persistent rainfall (>500 cm year). Organic and hydromorphic soil substratum. Water clear, cool (<16 °C), very low in dissolved minerals (conductivity <30 μmhos), and yellow to brownish with humic solutes (pH <5.5). Bor-

dered by acidophilic flora (mosses, lichens, dwarf shrubs), including *Metrosideros* in Hawaii and *Agrostis, Gentiana, Brautelia, Gleichenia, Trochocarpa* and *Astelia* in New Guinea (for further discussion see Wade and McVean, 1969). Fauna low in abundance and diversity, consisting primarily of insects, particularly Odonata (Zygoptera), Coleoptera (Dytsicidae) and Diptera (Chironomidae, Dolichopodidae, Ephydridae). Exemplified on oceanic islands by Pepeopae Bog on Molokai, and on continental islands by the extensive bogs on Mt. Wilhelm and Mt. Giluwe in New Guinea.

2.a.1b. *Upland Marshes*—Perennial to seasonally intermittent non-forested wetlands in upland areas (100–1200 m) of moderate to high rainfall, but better drained than boglands. Water clear, sometimes yellowish, with low to moderate dissolved mineral content (conductivity 30–80 μmhos), and circumneutral (pH 5.5–7.5). Emergent aquatic plants (sedges and grasses) often abundant, including *Drosera, Gentiana, Utricularia, Brachyposium, Carex* and *Scirpus* in New Guinea. Fauna similar to that of bogs but more abundant and diverse.

2.2a.1c. *Upland swamps*—Perennial to seasonally intermittent forested wetlands in upland areas (100–1200 m) of moderate to high rainfall. Water non-acidic, with characteristics similar to those of upland marshes. Fauna diverse and often endemic, including Odonata (Zygoptera), Diptera (Dolichopodidae, Ephydridae), and Heteroptera (Veliidae). Examples include Alakai Swamp on Kauai and the summit plateau of Mt. Kaala on Oahu.

2.2a.2 *Lowland Wetlands*—Natural limnetic water bodies located at elevations $<$100 m. Includes altered or artificial shallow ecosystems located coastally or in valley flats (e.g., taro ponds, rice paddies). Fauna often dominated by introduced species; emergent flora predominant.

2.2a.2a. *Seasonal Lowland Wetlands* (playas)—Lentic waters occurring seasonally in shallow basins. Water warm (20–30 °C), generally mixohaline and poikilohaline (although evaporation may cause waters to become hyperhaline as drying progresses); pH 6.5–8.0. Characteristic biota in Hawaii includes primitive crustaceans (Conchostraca, Notostraca) and insects, primarily Diptera (Ephydridae). Ex-

amples include the playa "lake" on Niihau, and the seasonally dry basins formed between limestone anticlines east of Kaimana in western New Guinea. Also assignable here are the salt pans that border the back margins of mangrove estuaries along the southern New Guinea coast.

2.2a.2b. *Perennial Lowland Wetlands*

2.2a.2b.1. *Freshwater* (limnetic) *Lowland Wetlands*—Shallow, standing perennial limnetic waters in lowland areas (<100 m), in definite or indistinct basins not immediately adjacent to the coastline. Maintained by either stream, well, or ditch influent, or by exposure of the natural water table. Variable water quality, but salinity always <0.5‰ (conductivity 100–300 μmhos), pH 6.9–7.5. Includes broad assemblage of both natural basins, such as Kawainui Marsh on Oahu, and artificial basins, such as taro fields, waterbird refuges, and golf course ponds. Biota often dominated by introduced elements on oceanic islands.

2.2a.2b.1a. *Lowland Freshwater Marshes*—Perennial lowland wetlands lacking trees but with abundant emergent vegetation. Natural systems of this type exemplified by Kawainui Marsh on Oahu and the extensive trans-Fly wetlands of southern New Guinea; artificial systems numerous, often agricultural, dominated by monocultural taro or rice. Flora in Hawaii with sedges, bullrush, and California grass predominating in wild areas; *Colocasia esculenta* in taro fields. Fauna in Hawaii dominated by introduced elements, including crayfish, topminnows, tilapia, *Bufo* tadpoles, and *Ischnura* damselflies.

2.2a.2b.1b. *Lowland Freshwater Swamps*—Forested perennial lowland wetlands, water depth often fluctuating

on a seasonal basis due to influxes of limnetic water from perennial streams. This ecosystem category includes a range of botanically diverse coastal plain and riparian forested wetlands, including sago swamps, pandanus swamps and peat swamp forests, all of which are extensively represented on New Guinea and other continental islands. The latter forest type could potentially be segregated as a separate ecosystem on the basis of acidic water chemistry. Distinguishing flora in New Guinea includes *Metadina*, *Barringtonia*, sago (*Metroxylon sagu*), various *Pandanus* species (for list see Stone 1982), and *Campnosperma brevipetiolata* in very wet areas. In the Bismarcks and northern Solomons ecosystems of this type are florally characterized by *Terminalia brassii*. Also assignable here are the "freshwater mangrove" forests of New Guinea (well developed along the Sepik River) florally dominated by *Myristica*, *Callophyllum*, *Syzygium*, *Campnosperma*, *Palaquium*, *Intsia* and *Diospyros*, and similar riparian forests of *Sonneratia caseolaris* (for additional discussion see Johns 1982). Typical insect fauna in New Guinea includes protoneurid damselflies (*Notoneura*), libellulid dragonflies, and gerrid (*Limnometra*, *Rhagdotarsus*), veliid (*Microvelia*, *Strongylovelia*), hydrometrid (*Hydrometra*) and notonectid (*Anisops*, *Enithares*) water bugs.

2.2a.2b.2 *Saline* (mixohaline) *Lowland Wetlands*—Coastal wetlands with perennial, tidal, or seasonal water of variable salinity, often resulting

from intrusion of haline groundwater. Surface connection to ocean absent or rare. Water usually warm (20–30 °C), generally mixohaline and poikilohaline, pH 6.5–8.0. Flora in Hawaii includes blue-green algae, bullrushes, and sedges in low salinity waters, with pickleweed (*Batis maritima*) and mangrove in higher salinity situations. Fauna in Hawaii includes euryhaline fishes (tilapia, sailfin molly), and insects (hydrophilid Coloeptera, *Trichocorixa* water boatmen), *Ligia* isopods, *Melania* and *Assiminea* snails.

2.2a.2b.2a *Lowland Saline Marshes* (Salt Marshes)—Nonforested lowland saline wetlands dominated by emergent vegetation, most characteristically pickleweed (*Batis maritima*). Examples include Kanaha and Kealia ponds on Maui, man-made bird refuge ponds (West Loch, Oahu) and the coastal saline marshes of Babeldaob Island in Palau.

2.2a.2b.2b. *Lowland Saline Swamps* (Mangrove)—Forested lowland or riparian saline wetlands dominated by mangrove species. May or may not intergrade into true euhaline mangrove estuaries. Extensive development on oceanic islands west of the Tonga Trench, and on New Guinea and other continental islands, where areas subject to inundation by mixohaline waters support mixed floral assemblages of *Avicennia*, *Nypa*, *Rhizophora*, *Bruguiera* and *Sonneratia* (for further discussion see Johnstone & Frodin 1982). Typical insect fauna in New Guinea includes gerrid water bugs (*Stenobates*, *Rheumatometroides*).

2.2a.2b.2c. *Anchialine Pools*—Euhaline to mixohaline lentic waters occurring primarily in lava fields or elevated fossil reef rock. No surface connection with ocean, but tidal fluctuations evident. Occur singly or in groups with subterranean interconnections (see discussion under Subterranean Ecosystems). Surface level is inland extension of marine water table, with mixohaline water resulting from dilution of intruding ocean water with seaward-percolating groundwater. Homiohaline, but with sharp, stable, vertical salinity stratification evident in deep pools. Salinity of surface water usually 1–10‰, but occasionally approaching euhaline levels. Depth variable depending on tidal stage, with certain very shallow pools appearing only at high tide. Water usually clear, circumneutral, temperature 22–30 °C. Examples include coastal pools on Maui and Hawaii islands; Lake Kauhako on the Kalaupapa Peninsula of Molokai may also be assignable here.

Biota unique and distinctive, with some faunal species, particularly shrimps, not found elsewhere. Flora in Hawaii includes filamentous chlorophytes, mat and crust communities dominated by cyanophytes (*Lyngbya, Scytonema*), epilithic rhodopytes (*Hildenbrandia*), and widgeongrass (*Ruppia maritima*) where soft sediments occur. Fauna in Hawaii consists predominantly of shrimps (10 species), amphipods, and snails (*Melania, Assiminea, Theodoxus*), with fishes absent or rare. Endemic Hawaiian shrimps include a small (1 cm) red

atyid shrimp, *Halocaridina rubra* and unusual sightless hippolytid and procaridid shrimps, the latter only in water >10‰. Introduction of fishes degrades or eliminates this crustacean community, changing the ecosystem to a Saline Lowland Wetland type (see above).

2.2b. *Lacustrine Ecosystems*—Lentic water in definite basins with predominant open water and depth exceeding 2 m.

2.2b.1. *Natural Lakes and Ponds*

2.2b.1a. *Fresh* (limnetic) *waters.* Salinity <0.5‰. Individually distinctive in environmental character and biota. Native biota on oceanic islands generally limited to small invertebrates, with fishes and shrimps normally absent. Introduced fishes often present.

2.2b.1b. *Saline* (haline to mixohaline) *waters.* Salinity >0.5‰. Category not further subdivided. Includes single lacustrine ecosystems not classifiable elsewhere. Examples include Nomilo Pond, Kauai (6.2 ha; maximum depth 20 m) with marine algae, invertebrates and fishes; poikilohaline Laysan Lagoon, with fluctuating area and depth (maximum area 70 ha, maximum depth 5 m), harboring brine flies, *Artemia*, and amphipods. The "marine lakes" of Palau and Christmas Island are also assignable to this ecosystem category.

2.2b.2 *Reservoirs* and other artificial basins—Artificial water bodies constructed for irrigation and other socioeconomic purposes, or created by warfare (e.g., bomb craters). Generally not inhabited by native biota on oceanic islands. Environmental quality and biota vary with reservoir type.

Primary Storage Reservoirs—Primarily for agricultural and domestic water supply. Water bodies near source streams in remote upland sites. Relatively stable surface levels and good water quality. Some with submerged and floating water flora. Fauna in Hawaii often includes introduced crayfishes, sport fishes (especially largemouth bass, bluegill, and catfish), topminnows, tilapia, and insects.

Distributional Reservoirs—Water bodies mainly on agricultural lands or in populated areas, mostly for temporary water storage and

redistribution. Fluctuating surface levels. Water quality moderate to poor, usually turbid. Non-native fauna in Hawaii includes crayfish, tilapia, topminnows and tadpoles.

Effluent Reservoirs—Receiving waters for effluent ditches. Low quality water, very turbid, often anaerobic. Fauna consisting mainly of hardy invertebrates, including Odonata (Anisoptera, particularly *Pantala flavescens*), Coleoptera (Dytiscidae), and Diptera (Culicidae).

Interface to Marine Ecosystem Classifications

The inland water ecosystems described above intergrade into marine systems at several points, the most important being saline marshes and swamps, and the estuaries that form at the seaward ends of the terminal reaches of perennial streams (see Fig. 1). A classification of marine environments in the insular tropical Pacific prepared by Maragos (in press) addresses estuarine ecosystems, so these are not included in the above classification, but since they form a transitional environment exhibiting a combination of marine and inland water characteristics they are discussed briefly below.

The estuarine transition zone between limnetic and euhaline waters is primarily one in which mixohaline waters in delineable basins exhibit continuous or periodic surface connection to the ocean, allowing the entry of euryhaline marine fauna (this definition excludes waters inhabited by stenohaline marine inshore fauna such as corals, urchins, etc.). The level of the water surface exhibits tidal fluctuations, which may also produce strong inflows and outflows. Two basic types of estuaries conforming to this definition may be recognized:

1. *Natural Estuaries*—Waters in natural basins, ranging from limnetic to nearly euhaline. Pronounced stratification of halinity, temperature, and (usually) oxygen concentration. Diverse euryhaline fauna, which in Hawaii includes native neritid snails (*Theodoxus*), barnacles, palaemonid shrimps, introduced grapsid and portunid crabs, tilapia and topminnows. Two distinct subtypes of natural estuaries may be recognized based on freshwater inflows and diadromous fauna.

1.a. *True Estuaries* (drowned river and stream mouths)—Fed by limnetic water from perennial stream runoff. Inland extent determined by measurable tidal fluctuation and topography. Subtype extremes include *vertically stratified estuaries* with freshwater inflow volume low relative to basin volume (as seen at Huleia and Kilauea on Kauai) and *horizontally stratified estuaries* with relatively large freshwater inflow (Hanalei River on Kauai, Fly River Delta of New Guinea). Poikilohalinity in both types results from wide seasonal fluctuations in stream discharge. Estuaries of both types are often dominated by mangroves, particularly on continental islands, and serve as important migratory pathways for larval and juvenile diadromous animals.

1.b. *Estuarine Limnocrenes*—Nearshore basins with subterranean limnetic water sources (springs). Homiohaline, with biota similar to true estuaries but possessing submerged vascular plants and lacking transient diadromous stream fauna. Examples include Waiakea and Lokoaka Ponds, near Hilo on Hawaii Island.

2. *Developed Estuaries*—Estuarine systems constructed recently or prehistorically, or otherwise highly modified from their natural state. Mixohaline due to groundwater seepage or surface runoff. Water quality variable. Native biota similar to that found in natural estuaries (see above), but usually dominated by introduced plants (primarily mangroves in Hawaii) or animals (tilapia). Examples include walled Hawaiian fishponds, altered stream mouths (such as the Ala Wai Canal at Waikiki on Oahu, or Namo River estuary on Guam), and biologically modified systems (Heeia mangrove swamp and Pearl Harbor on Oahu).

Acknowledgements

This paper grew out of a meeting convened at the East-West Center on the University of Hawaii Manoa campus in March, 1991 by the South Pacific Regional Environmental Program (SPREP), the USDS Agency for International Development (AID), the U. S. Department of Interior Fish and Wildlife Service, the Environmental Policy Institute, The Nature Conservancy, and the World Wildlife Fund U. S. We wish to thank the above organizations, plus Dr. Jim Maragos and Samuel H. Pearsall of The Nature Conservancy for organizing the sessions in which this classification was developed. Additional thanks go to Dr. Lawrence Hamilton of the Environmental Policy Institute, East-West Center for coordinating local arrangements. The following persons reviewed prepublication drafts of this manuscript and offered helpful comments that greatly improved the final version: Dr. John T. Polhemus, University of Colorado Museum, Englewood, Colorado, USA; Dr. Scott E. Miller and Dr. Allen Allison, Bishop Museum; and two anonymous reviewers. The senior author's participation in this project was supported in part by grant BSR 9020442 from the National Science Foundation, Washington, D. C.

References

Cowardin, L. M., V. Carter, F. C. Golet & E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U. S. Dept. Interior, Fish and Wildlife Service, OBS-79/31. 103 pp.

Holthuis, L. 1973. Caridian shrimps found in land-locked salt water pools at four Indo-West Pacific localities (Sinai Peninsula, Funafuti Atoll, Maui and Hawaii islands), with description of one new genus and four new species. Zool. Verh., 128: 1–48.

Johns, R. J. 1982. Plant zonation. *In* J. L. Gressitt (ed.), Biogeography and Ecology of New Guinea, pp. 309–330. Dr. W. Junk, The Hague.

Johnstone, I. M. & D. G. Frodin. 1982. Mangroves of the Papuan subregion, *In* J. L. Gressitt (ed.), Biogeography and Ecology of New Guinea, pp. 513–528. Dr. W. Junk, The Hague.

Maciolek, J. A. 1969. Freshwater lakes in Hawaii. Verh. Int. Ver. Limnol., 17: 386–391.

Maciolek, J. A. 1977. Insular aquatic ecosystems: Hawaii. *In* Classification, Inventory and Analysis of Fish and Wildlife Habitat, pp. 103–120. U. S. Dept. Interior, Fish and Wildlife Service, OBS-78/76.

Margos, J. E. (in press). A marine ecosystem classification for the South Pacific region. Proc. 17th Pacific Science Congress, Honolulu (May, 1991). United Nations Environmental Program (UNEP), Nairobi.

Pearsall, S., J. E. Maragos, R. Thayman, E. Guinther, D. Polhemus, P. Holthus & P. Thomas. 1992. An ecosystem classification and criteria for biodiversity conservation in the tropical insular Pacific. Unpub. res. rep. prep. by The Nature Conservancy Pacific Region, Honolulu, for U. S. Agency for International Development (USAID) and South Pacific Regional Environmental Program (SPREP). 90 pp.

Stone, B. C. 1982. New Guinea Pandanaceae: first approach to ecology and phytogeography. *In* J. L. Gressitt (ed.), Biogeography and Ecology of New Guniea, pp. 401–436. Dr. W. Junk, The Hague.

Wade, L. K. & D. N. McVean. 1969. Mt. Wilhelm studies. I. The alpine and subalpine vegetation. Res. School of Pacific Studies, Dept. of Biology and Geomorphology Bio. Geo. Ser., BG/1. ANU Press, Canberra.

Wilcox, C. (ed.). 1990. Hawaii Stream Assessment. Draft August 1990. State of Hawaii, Dept. of Land and Natural Resources, Honolulu. 329 pp.

Received 14 Nov. 1991, revised 10 May 1992.

Appendix A: Definitions of Terms and Units

1. *Dimensions*

‰ = parts per thousand, a measure of salinity.
% gradient = relative slope measured as the unit of elevational change per 100 horizontal units (as in m/100 m).
μmhos = reciprocal megohms, a measure of water conductivity.
All distances, areas, volumes, etc. are given in metric units; temperatures are given in degrees Celsius.

2. *Water regime*

a. Lacustrine (lake-like) = deeper open standing waters occupying distinct basins; lakes and ponds.
b. Lentic (standing) = water not subject to direct gravitational movement, although internal currents may occur.
c. Limnocrene (spring pool) = a pond or pool having a noticeable, discrete, subterranean water source (cf. rheocrene)
d. Lotic (flowing) = water moving unidirectionally in response to substrate altitudinal (elevational) gradient. Excludes waters moving in response to wind currents, waves and tides.
e. Palustrine (marsh-like) = shallow standing water visually dominated by emergent vegetation such as mosses, sedges, rushes, trees, etc.
f. Rheocrene (flowing spring) = lotic water from a subterranean source but not in a well developed channel, and flowing in relatively low and constant volume.

3. *Dissolved Minerals*

   a. Qualitative aspects
      Haline (halinity) = brackish or salty water condition wherein dissolved ions are derived from seawater.
      Saline (salinity) = general term for water with noticeable salt content.
   b. Quantitative aspects
      Limnetic = freshwater, salt content <0.5 ‰.
      Mixohaline = brackish water, salt content 0.5–30 ‰.
      Euhaline = seawater, salt content 30–40 ‰.
      Hyperhaline = brine-like water, salt content >40 ‰.
   c. Concentration vs. time
      Homiohaline = salt concentration stable or fluctuating only over a narrow range.
      Poikilohaline = salt concentration fluctuating widely.

4. *Ecological qualifiers*

   a. Migration and movement
      1. Amphidromous—type of diadromous animal (see below) that migrates between fresh and marine waters but not for breeding (e.g. sicydiine gobies).
      2. Catadromous—type of diadromous animal that inhabits freshwater but breeds in the ocean (e.g. anguillid eels).
      3. Diadromous—broadly referring to animals (e.g. certain fishes) that obligately migrate between fresh and marine waters during their life cycle.
      4. Itinerant—refers to animals that may irregularly or opportunistically migrate between fresh and marine waters (e.g. haline marine fishes sometimes found in streams).
   b. Salt tolerance of biota
      1. Euryhaline/saline—occurs over a wide range of total dissolved solids.
      2. Stenohaline/saline—occurs in a narrower range of total dissolved solids.
   c. Substrate relationship
      1. Benthic—living on or in the bottom of a water body.
      2. Epigeal—living on or above the earth's surface.
      3. Hypogeal—living beneath the earth's surface (= subterranean).

5. *Geographical qualifiers*

   a. Oceanic island = island lying on oceanic crust and lacking any historical connection to a continental landmass. Geological composition carbonate or igneous (basaltic); metamorphic rocks lacking. Includes atolls, raised limestone islands, and islands formed along plate margin volcanic arcs and midplate hotspots.
   b. Continental island = island lying on continental crust, and often possessing previous connections to large continental landmasses. Geological composition variable, but often including metamorphic and andesitic igneous rocks. In the insular tropical Pacific as defined herein islands of this type include New Guinea and New Caledonia, and possibly portions of the Bismarcks, Solomons, and Fiji.