The Rivers Handbook

HYDROLOGICAL AND ECOLOGICAL PRINCIPLES

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12: Riverine Fishes

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12.1 INTRODUCTION

This chapter puts the challenges of understanding and managing riverine fish and fisheries in an ecological and evolutionary context. An appreciation of the adaptations of fish and the reasons for characteristic assemblages will lead to a more strategic view of riverine fisheries management than the tactical ones often employed, such as maximizing the yield of a single species while ignoring environmental variation. We propose that most serious fisheries management problems result from actions that have changed the hydrological regime, habitats and/or fish fauna, thereby disrupting the long-term, dynamic patterns to which the indigenous fishes are adapted. This has resulted in the need for restoration in many systems. We discuss the options available to research and management agencies in the light of current limitations on our ability to sample fish quantitatively and our knowledge of their spatial and temporal dependence on their environment.

Apart from their aesthetic value, riverine fishes are important because they can be harvested for human consumption, caught for recreation, are useful as indicators of the well-being of the environment, or serve as appropriate subjects for testing principles of population or community ecology. Considerable knowledge has resulted from the independent pursuit of these interests. However, this knowledge is dwarfed by information of which we are ignorant, which includes many of the concepts and tools necessary to make inferences about fish populations or communities based on the few systems we can afford to study intensively.

In order that projects pursuing any of these interests are directed towards conservation or recovery of the natural system, have long-term economic viability, and have general application in fish resource management, we propose four requirements. First, the project must recognize (or investigate) the constraints imposed by the evolutionary adaptations (section 12.3) and interactions (section 12.5) of the taxa concerned. Second, the biases and variance of the sampling process must be known with sufficient accuracy (sections 12.4, 12.7; Chapter 13), and the long-term management costs of monitoring the resource with that accuracy must be included. Third, the investigator should be aware of the feasibility and cost of restoring a damaged system (section 12.6). Last, but not least, the project must be designed and reported to enable generalizations across systems on appropriate scales and classifications (sections 12.2, 12.7). Considering that many publications still account for few, if any, of these factors, there is much room for improvement.

12.2 CLASSIFICATIONS AND UNIFYING CONCEPTS FOR RIVERINE FISHES

There are about 8500 freshwater fish species (Lowe-McConnell 1987), most of which occur in rivers or connected floodplains. Current technology and resources (section 12.4) are probably insufficient to complete ecological studies by species and to predict population trends by stock before some of these species become extinct naturally. In view of the unnatural changes occurring in systems since the industrial revolution

and the subsequent human population explosion, it is clearly impossible to achieve a moderate level of predictive capability for each stock of each species of interest with respect to their exploitation or conservation.

Therefore, more studies must focus on comparisons among systems or their components, so that information from intensive, localized studies can be used to manage, conserve and restore fish populations and communities across many systems. This requires classifications of ecologically equivalent units that comprise functionally similar species and/or life stages so that generalizations can be tested. Classification of units, gradients of key variables within units, and the scale adopted depend on the problem and the information available. The pluralistic approach (Schoener 1986, 1987) emphasizes differences between ecological communities based on organismic and environmental axes. Elements of these axes, such as body size (section 12.3) and stream discharge values (section 12.2), may jointly indicate appropriate boundaries for working definitions of classification units. Inadequacies in data are common, and generalization can be more limited by appropriate survey information across systems than by results from localized studies.

Classifications at different spatial scales (sections 12.2–12.5) and unifying concepts within and across scales (section 12.6) are presented as heuristic tools to understand how fishes are organized in river systems within the hierarchy of spatial and temporal scales available.

Spatial and temporal scales and hierarchies

The spatial and temporal scales of environmental units available for studying river fishes are correlated (Fig. 12.1(a)). Unifying concepts and classifications of fish assemblages need to recognize this correlation as well as the hierarchical structure of these units, whose physical characteristics persist on scales of 10^5-10^6 to $10^{-1}-10^0$ years from landscapes to microhabitats, respectively (Frissell *et al* 1986), and are extended to evolutionary scales at the zoogeographical level in Fig. 12.1(a). Hierarchical scaling promotes the most effective solution of ecological problems (Allen & Starr 1982). The hierarchy implies

that the larger, more stable, environment imposes limits on the smaller, more variable, environmental units. Habitats, for example, can be classified within broader units, and thus lend themselves to statistically nested designs for the testing of differences in fish assemblages or other attributes.

Johnson (1980) suggested that resource selection by species follows a hierarchy from the zoogeographical range (first order), through microhabitat scales, with resource selection in each order being conditional on a lower order. Although we question his unidirectional dependence of selection (e.g. the home range can depend on the selection of habitat as well as vice versa) and the separation of feeding and habitat usage into different orders, it is important to understand resource selection in the context of spatial and temporal scales. Resource selection by a fish depends on a series of conditions: (1) ability to disperse among fluvial systems on a zoogeographical scale; (2) seasonal migrations of some species limited by basin extent, geomorphology and habitat availability; (3) home range limited by physicochemical factors (habitat distribution) on the reach or stream scale; and (4) activity under the constraints of biological interactions which include the probability of being killed, availability of prey and reproductive requirements at the microhabitat scale (Fig. 12.1(b)).

The time scales are complex, because those relating to persistence of environmental units (Fig. 12.1(a)) extend to evolutionary scales, and are two to three orders of magnitude greater (at similar spatial scales) than the ecological scales corresponding to the response times of individual fish (Fig. 12.1(b)). The formation of species assemblages depends on zoogeographical limits derived in evolutionary time scales (Fig. 12.1(a)), morphological and physiological preadaptations constraining distributional limits in ecological time scales (Fig. 12.1(b)), and interactions among species which fine-tune assemblage structure in ecological and evolutionary time scales. The following four subsections discuss the usefulness of classifying and predicting properties of fish and environments at decreasing spatial scales.

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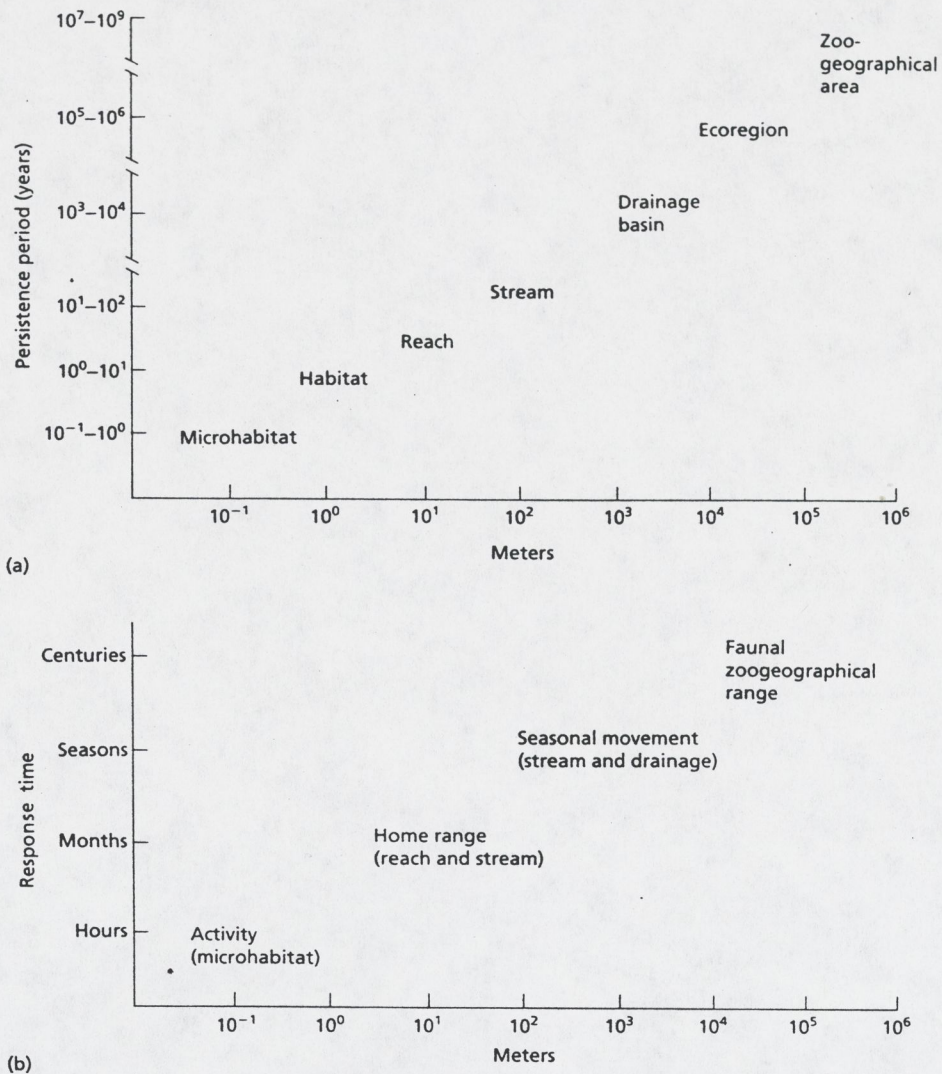the usefulness of
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Fig. 12.1 (a) Persistence period versus spatial scale of environmental units (after Frissell *et al* 1986). (b) Response time versus spatial scale of fish movements.

Zoogeographical scales

What can be learned from comparative zoogeography that is useful to the manager or the ecologist who is not concerned with historical reasons for current fish assemblages? Can one generalize among similar systems of different zoogeographical regions? Only with great care; for instance, physically similar drainage systems in Poland and Ontario, Canada differ in species richness and body-size distributions among species (Mahon 1984). In contrast, Moyle and Herbold (1987) found great similarity in assemblage structure among cold headwater streams of Europe and eastern and western North America, and found common structural features among the warm-water fishes of Europe and western North America. These patterns may have resulted from the degree

of similarity of conditions during Pleistocene glaciation events. In a comparison of external morphological measurements among stream fish assemblages from North and southern South America, Strauss (1987) found that correlations were high among North American zoogeographical areas and low between the two subcontinents, and reflected the phylogenetic constraints on morphology. To the extent that morphologies reflect ecological attributes, this evidence suggests that it is unwise to infer ecological similarities among assemblages that are distantly related phylogenetically. Likewise, evolutionary convergence of body form is not inevitable because there is not a unique morphological solution to a specific environment (Mayden 1987; Strauss 1987).

This phylogenetic limitation applies to comparisons of ecologies at the species level. At the opposite extreme of comparing gross energy transfers, such as fishery yield from a large proportion of the fish taxocene (section 12.4), similarities across zoogeographical areas reflect similarities in environment rather than in phylogenies.

Regional scales: ecoregions and hydrology

Ecoregional classifications such as those pioneered by Omernik (1987) and his co-workers (e.g. Larsen *et al* 1986; Hughes *et al* 1987; Whittier *et al* 1988; Hughes *et al* 1990) describe fish distributions at the landscape level by relating species presence to geomorphic/land-use patterns. Its use in anticipating where species may become endangered or in formulating broad management policies is not disputed, but in Wisconsin the classification was found to be fairly imprecise and fish assemblages were better classified by general habitat variables (Lyons 1989).
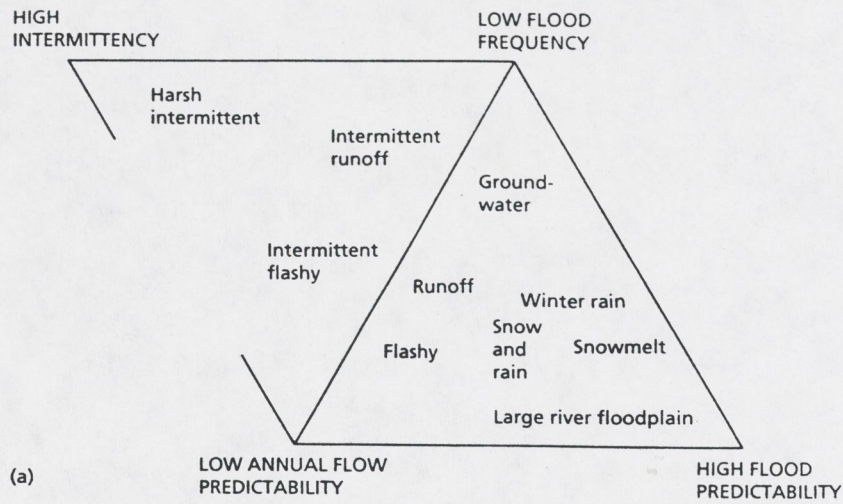
Ecoregions can divide basins and combine adjacent basins, resulting in a departure from the zoogeographical > basin > stream > habitat hierarchy of spatial units. Departing from this hierarchy and devising a network of scales is possible technically, but migratory fish can occupy two or more ecoregions. A classification that predicts and explains fish assemblages should have mechanistic links to finer scales; an ecoregional approach will not successfully predict or explain the presence of a migratory species which also depends on environments in adjoining ecoregions,

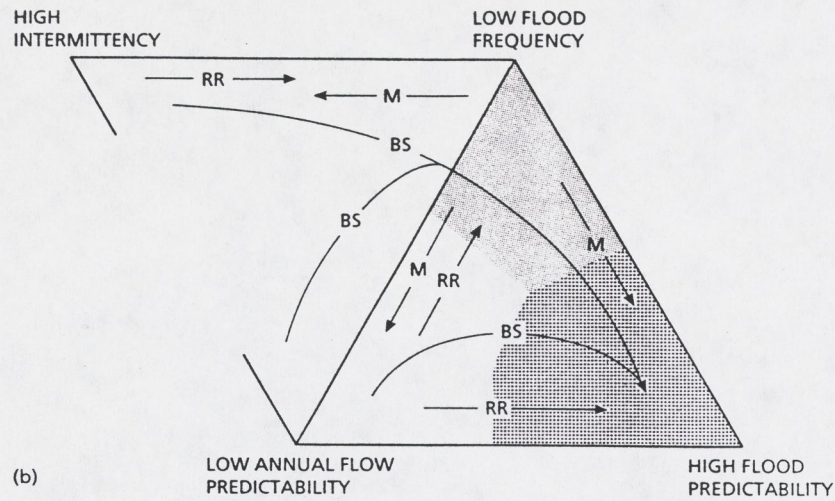including ocean habitats for anadromous species.

In addition, there is a cumulative effect of landscape that can also affect non-migratory fishes. A point in a stream downstream of an ecoregional boundary may reflect properties, such as hydrology, temperature and chemistry (e.g. Elwood *et al* 1983), that are controlled by the upstream ecoregion rather than by the ecoregion in which the point lies. Landscape elements from an ecoregional classification may be useful if they reflect environmental features affecting fish populations; the problem lies in assigning those elements within boundaries independently of watersheds and in implying that their effect is independent of their distance to the lotic area of interest (see Osborne & Wiley 1988 for an alternative approach).

Poff and Ward (1989) developed a regional classification of stream communities based upon variation in streamflow patterns of 78 streams across the USA. In Fig. 12.2(a) we have attempted to summarize the essential features of Poff and Ward's nine stream types plus large river-floodplains, in terms of four key hydrological attributes that are independent of spatial scale. Although this condensed representation assumes interdependence among four attributes and cannot represent all hydrological types precisely, these attributes were defined and positioned to account for Poff and Ward's significant correlations. Thus, data from most individual streams would occupy relatively small areas within the corresponding triangle. All types show some overlap with neighbors. Data for snowmelt, snow and rain, and winter rain showed considerable overlap (Poff & Ward 1989) and they, in turn, form a continuum with surrounding perennial types in the right triangle and with intermittent types in the left triangle (Fig. 12.2(a)). The left triangle is drawn incomplete because there is not a complementary relationship between intermittency and low annual flow variability, and examples do not exist along that axis.

Figure 12.2(b) shows some of the expected trends in fish population and community properties across different combinations of these hydrological attributes. In addition to these, Poff and Ward (1989) have suggested other plausible properties. Most published work has failed to put fish studies in an adequate hydrological frame-

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Fig. 12.2 (a) Stream types arranged according to approximate proportions of hydrological attributes (estimated partly from data in Poff & Ward 1989, Table 3). (b) Ecological attributes of fish species and assemblages corresponding to stream types in (a). Right-hand triangle in (a) and (b) includes all perennial stream types.

work, but there are exceptions. For instance, fish inhabiting streams subject to regular desiccation and flash floods were found to respond differently to streamflow changes than those restricted to small, clear creeks with permanent flow, resulting in different assemblages (Rohm *et al* 1987; Matthews 1988; Matthews *et al* 1988).

We believe that a hydrological approach, possibly in conjunction with different temperature regimes and landscape properties, may provide a

superior regional template for understanding community function, life-history patterns and making inferences than an ecoregional classification, because the hydrology is more directly associated with physical constraints on fish habitats while reflecting some geomorphological features of the basin. Also, one could monitor ecologically significant departures from the natural regime due to anthropomorphic disturbance.

Basin and reach scales: zonation

The basis of zonation is to find large gradients (generic sense) to which the fauna must respond. Zonation schemes have used stream order (Sheldon 1968; Lotrich 1973; Horwitz 1978), hydraulic stress and power (Statzner 1987), temperature (Gard & Flittner 1974), habitat heterogeneity (Gorman & Karr 1978; Gorman 1988) and physicochemical gradients (Echelle & Schnell 1976; Matthews & Styron 1981). Huet's (1947, 1959) longitudinal zonation used a combination of gradient and stream width in European rivers to relate reaches to fish communities characterized by individual species. This approach is more difficult to apply to rich faunal assemblages covering various climatic and geomorphic zones (Allen 1969), such as in North America and the tropics, but it can be useful when empirically derived for a particular area (e.g. Angermeier & Karr 1983; Moyle & Senanayake 1984; Matthews 1986b). However, longitudinal zonation does not explain how stream reaches influence assemblages, does not account for potadromy, and does not explain the distribution of fishes in rivers with significant floodplains.

Habitat and microhabitat scales

It is surprising that the distribution of habitat types within reaches has not received much attention because the measurement of riffle: pool ratios to characterize stream reaches is a cherished tradition. However, Bisson and his associates have refocused awareness on habitats as channel units (e.g. side-scour pools, step pools, riffles, glides), first by creating a typology based on hydrological features (Bisson et al 1982), followed by an examination of fish distributions among these habitats

(Bisson et al 1988). Building on this theme, Hicks (1990) found that the physical characteristics and distribution of habitats and faunal assemblages were different for sandstone versus basaltic drainages within the same ecoregion. Furthermore, habitats in sandstone drainages were more sensitive to changes in low summer discharge following logging than basaltic ones (Hicks et al 1991).

The Instream Flow Incremental Methodology (IFIM) is based primarily on microhabitat use patterns of fishes, e.g. current, depth and substrate (Bovee 1982). Some workers have claimed that IFIM shows promise for cold, headwater salmonid stream assemblages (Newcombe 1981; Moyle & Baltz 1985), where conditions and assemblages are quite consistent worldwide (Moyle & Herbold 1987), and for a few obligate warmwater stream fishes (Orth & Maughan 1982). IFIM does not work well when fishes do not have stereotyped behaviours on a limited spatial scale. Many stream fishes have extensive home ranges, select habitats at the channel unit level, or are relatively non-selective in microhabitat choice or are selective only under severe conditions (Angermeier 1987; Felley & Felley 1987; Ross et al 1987; Scarnecchia 1988). IFIM depends on fish biomass density being linearly related to the area of each available habitat type, which has been shown to be invalid (Mathur et al 1985; Conder & Annear 1987). In addition, IFIM does not work well when fishes are influenced by behavioural trade-offs such as risk avoidance or competitive spatial partitioning (Baltz et al 1982) (section 12.5). Finally, IFIM relates ephemeral, short-term behaviours to microhabitats, and such small-scale relationships will not necessarily maintain their predictive quality when extrapolated to larger scales (see Fig. 12.1(b)) that are more appropriate for management. The same general criticisms hold for the related Habitat Suitability Index (HSI) models (US Fish and Wildlife Service 1981; Terrell et al 1982).

River continuum and flood pulse concepts

Two unifying concepts, the river continuum (Vannote et al 1980) and the flood pulse (Junk et al 1989), provide ecological templates which can be used to compare and contrast fish com-

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(Fig. 12.3). Both concepts have the potential to
guide the derivation of sets of hypotheses to
identify dominant mechanisms, in particular
those operating between adjacent spatiotemporal
scales, and either should improve the derivation
of classifications at various scales to provide pre-
dictions useful for management in appropriate
systems.

Although both concepts are designed to work
up to a drainage basin scale, they are mutually
exclusive in low-gradient potamon reaches, be-
cause the flood pulse concept recognizes the
periodic nature of the interaction between the
flood pulse and the floodplain which influences
the adaptations of fish species. In contrast, the
phytoplankton-dominated description of low-
gradient reaches in the river continuum concept
has more in common with heavily regulated rivers
that have been denied access to floodplains, such
as the Thames (Mann *et al* 1970). Such rivers,
which are widespread in the temperate zone,

present a dilemma in formulating a unifying eco-
logical concept. Can we produce useful classifi-
cations of systems which are manipulated to the
extent that adaptive and coevolutionary features
of the fish species are no longer relevant, or do we
have to undertake detailed investigations in each
unique system?

The flood pulse concept has, at most, periph-
eral importance in the higher gradient rhithron,
where many of the longitudinal processes of the
continuum concept provide a more appropriate
description. However, the original continuum
concept needs to be adapted to, or excepted from,
the following: differences in upstream riparian
vegetation (Barmuta & Lake 1982; Wiley *et al*
1990), discontinuities (Statzner 1987; Naiman
et al 1988; Pringle *et al* 1988) and upstream
transport of nutrients and biomass through mi-
grations of temperate (Hall 1972; Li *et al* 1987)
and tropical fishes (Petrere 1985; Welcomme
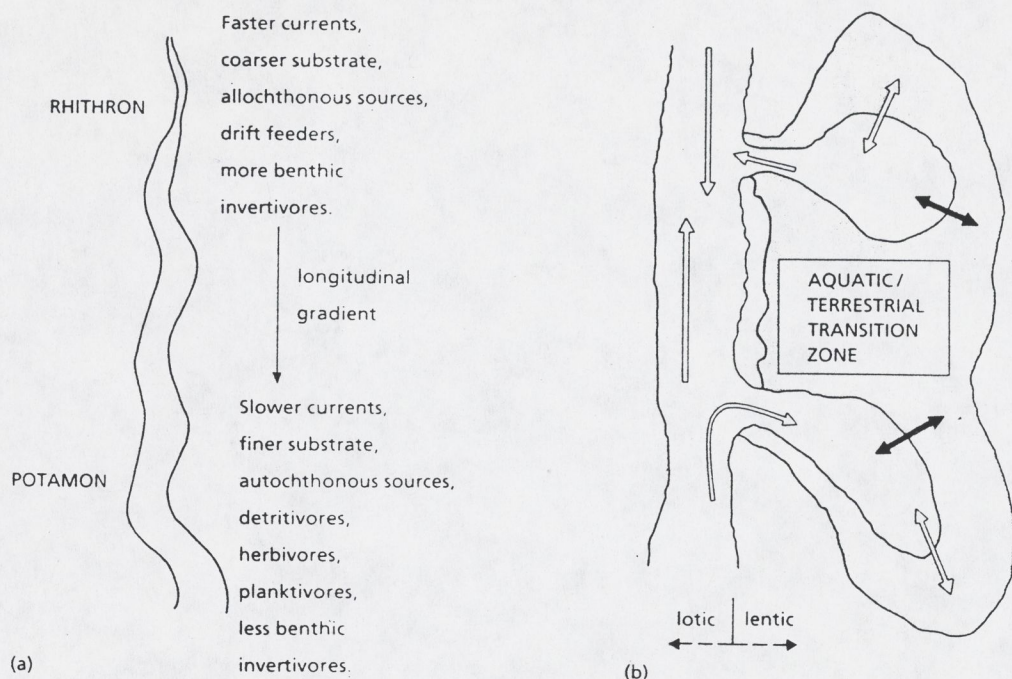1985).

In conclusion, the development of unifying con-

Fig. 12.3 Some contrasts between (a) the river continuum and (b) flood pulse concepts as applied to fishes. (⇨ 'white' fishes; ➤ 'black' fishes; arrows indicate migrations.)

cepts is still in its infancy and will remain so unless more studies and surveys follow guidelines such as those outlined in section 12.7. Nevertheless, the concepts are currently helpful in understanding life-history adaptations and in classifying functional groups to act as templates for testable hypotheses.

12.3 LIFE-HISTORY ADAPTATIONS

A Gleasonian view of fish species adaptations based on physiological and morphological responses to the environment is presented in this section. This is a complementary explanation of longitudinal zonation to that presented by (Horwitz 1978) with lateral effects of floodplains incorporated. We propose that, at least in the headwaters, constraints of habitat size, habitat variety (see also Gorman & Karr 1978) and hydraulic forces limit diversification of body form and limit resource partitioning according to the principle of limiting similarity (MacArthur & Levins 1967). We describe life-history adaptations to different classes of the environment in terms of body morphology and activity, P/B ratio and body size, trophic properties, reproductive strategies, and trade-offs and polymorphisms.

The rhithron and the potamon impose different requirements on fish life (Fig. 12.3). The classic, high-gradient rhithron is usually more restrictive: it is smaller, cooler, more highly oxygenated, and comprised primarily of fastwater habitats: rapids, riffles, cascades and step-pools. The low-gradient rhithron typical of surface-drained, low-lying areas is characterized by more variable temperature, oxygen and discharge (Wiley *et al* 1990). The potamon comprises habitats with a greater variety of size, depth and flow: large river channels and pools, braided stream channels, oxbows and sloughs, and habitats of the floodplain. The gradient is usually minimal, temperatures are higher, and some habitats become hypoxic. These features, and local variants, have a profound effect on the adaptations discussed below.

Morphology and activity

The attributes of rhithron fishes are more constrained by habitat size (Schlosser 1982) and hy-

draulic power and variability (Statzner 1987; Wiley *et al* 1990) than the fishes of the potamon. This is especially noticeable in terms of their size, shape and metabolism (Table 12.1). Smaller body size is not related just to the scale of available in-stream cover (Schlosser 1987); the demands for acceleration and agility in a turbulent environment also favour a smaller body mass (Webb & de Buffrénil 1990). A larger body increases speed, but at the expense of agility and manoeuvrability (Webb & de Buffrénil 1990).

Body shapes of non-benthic rhithron fishes should be closely distributed around an optimal fineness ratio (FR = ratio of body length to depth) of 4.5 (Webb 1975), in contrast to greater variation in the potamon. Scarnecchia (1988) found greater variation in FR for fish assemblages from reaches with complex flow than from those inhabiting fast, channelized reaches.

The greater muscular force needed for agility in fast currents of the rhithron suggests that those fishes should have higher metabolic rates than potamonic fishes of similar size. Clausen's (1936) initial evidence for this argument was flawed because allometric relationships were ignored. However, our survey of the metabolic literature suggests that Clausen's intuition may have been correct (Table 12.2). Haemoglobin of fishes inhabiting fast, cold stream reaches delivers greater amounts of oxygen to active tissues than in those fish found in typical potamonic habitats (Powers 1972; Cech *et al* 1979; Powers *et al* 1979). These generalizations apply to fishes swimming in the water column. Substrate-oriented fishes, including those that inhabit the hyporheos, have metabolic rates and morphologies reflecting low-flow and benthic environments (Facey & Grossman 1990).

P/B ratios and body size versus habitats

Even though metabolic expenditures are higher in the rhithron, fish communities in smaller streams tend to have higher P/B ratios (production/biomass or turnover rate on an annual basis; see section 12.4) than in larger streams (Lotrich 1973). We found a significant correlation between body size (as mean weight) and P/B ratios for 32 freshwater fish species ($r = -0.47$,

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Table 12.1 Typical distributions of fish attributes along the stream gradient

Attribute	Rhithron	Stream gradient	
		Intermediate	Potamon
Temperature guild	Stenotherms (high gradient) Eurytherms (temperate-continental, except springfed)	Mesotherms or eurytherms (temperate)	Eurytherms (temperate)
Metabolism	High standard metabolism		Low standard metabolism (except floodplain habitats)
Fineness ratio*	FR near 4.5 (optimal score)		FR variable
Oxygen-binding affinity or haemoglobin	Low (high gradient)		High
Fish size	Smaller		Variable
Life span	Relatively short		Greater longevity
P/B ratio (index of r_{max})	Relatively high		Relatively low (except floodplain habitats)
Reproductive guild (Balon 1975)	Lithophils and phytophils	Phytolithophils and psammophils and pelagophils	Lithopelagophils

* FR, fineness ratio (body length/depth).

$P < 0.01$), which confirms an earlier analysis of diverse groups (Banse & Mosher 1980) and recent analyses of cohorts within species (Boudreau & Dickie 1989).

Small body size is encountered in the rhithron in the form of small species and young of larger species which move upstream to spawn. Small body size is also dominant in seasonally inundated habitats in floodplains where high growth rates and production occur (Bayley 1983, 1988b; Junk et al 1989). Both environments have two significant factors in common: they are shallow and are subjected to flooding and dewatering to a much greater extent than the main channel of the potamon. The P/B ratio is strongly related to the intrinsic rate of increase, r_{max}, of the population. Small species and young stages of larger species with high r_{max} values and other r-traits (sensu Pianka 1970) are expected to dominate habitats in the rhithron (Hall 1972) and floodplains (Junk et al 1989). An exception to this may be small streams of unusual constancy of flow (groundwater type; see Fig. 12.2(a)). In the lotic component of the potamon, which is normally characterized by lower productivity, larger species with low P/B ratios and r_{max} values, and possibly species with relatively more K-traits (Pianka 1970), are expected to be relatively common, although large r-trait species whose young occupy the rhithron or floodplain may dominate.

Trophic adaptations

One morphological design often affects the rest of the body plan (Thompson 1942). Body size places limits on trophic specialization, life span, and reproductive capacity. Average food particle size is approximately 0.07 of fish length (L) (Kerr 1974), ranges up to 0.33 L for obligate piscivores (Popova 1978), but generally decreases as L increases (Webb & de Buffrénil 1990). Typical rhithron fishes are small and are primarily adapted to

Table 12.2 Standard metabolic rates of stenotherms and eurytherms among temperate fishes

Type	Fresh weight (g)	Temperature (°C)	Standard metabolic rate (mg kg^{-1}h^{-1})	Reference
Stenotherms				
Salmo trutta	100	9.5	73	Elliot (1979)
Oncorhynchus clarki	83–93	10	7	Dwyer & Kramer (1975)
		20	129	
Oncorhynchus mykiss	100	15	11	Rao (1968)
Oncorhynchus nerka	100	15	76	Brett (1965)
Salvelinus fontinalis	100	20	147	Beamish & Mookherjii (1964)
Eurytherms				
Gila attaria	100	18–20	42	Rajagopal & Kramer (1974)
Rhinichthys cataractae	100	18–22	40	Rajagopal & Kramer (1974)
Carassius auratus	87	20	50	Smit (1965)
Cyprinus carpio	100	10	16	Beamish & Mookherjii (1964)
		20	48	
Mylopharodon conocephalus	100	20	51	Alley (1977)
Catostomus catostomus	100	10	35	Beamish (1964)
		20	110	
Lepomis macrochirus	100	10	31	Wohlschlag & Juliano (1959)
		20	116	
Ictalurus nebulosus	100	10	20	Beamish (1964)
		20	66	

consume small aquatic and terrestrial invertebrates, especially terrestrial drift.

More diversification is possible in the potamon because greater habitat and food diversity confers advantages to large and small fishes (Welcomme 1985). A wide range of trophic adaptations results from the enormous productivity and variety of food in the tropical floodplain (Junk *et al* 1989). Seasonal changes result in oppportunistic behaviour. There are many generalists that consume invertebrates and plant matter of aquatic and terrestrial origin (Bayley 1988b).

Detritus and associated microflora appear to be the main repository of organic matter in river-floodplains. Subsequently many fishes have evolved to specialize on fine detritus (e.g. Bowen *et al* 1984). Such fish in the tropics start feeding on detritus when very small (Bayley 1988b) but become large (2–5 kg) compared with the small particle sizes they depend on.

The combination of seasonal food availability and low-water periods has resulted in many species building up large fat reserves to survive a season without feeding and to provide additional energy for migrations (Junk 1985). This applies to tropical and temperate rivers; the season of fasting for most species is the dry season in the tropics and the winter in the temperate zone (Cunjak & Power 1987; Cunjak *et al* 1987). Seasonal fluctuation in food supply demands that most fishes be flexible in food selection and/or energy storage within the limits of their size.

Reproductive strategies

Changes in substrates along the river continuum influence the mode of reproduction. Substrate size is much larger in high-gradient rhithron zones, corresponding to the greater hydraulic power in the steeper gradient (Richards 1982). Therefore, reproductive guilds (*sensu* Balon 1975) tend to be ordered from lithophils in high-gradient rhithron to lithopelagophils and psammophils in the potamon (see Table 12.1). Further generalization is possible by coupling Balon's reproductive guilds with Hokanson's (1977) concepts

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of temperature guilds. Hokanson (1977) recognized that physiological adaptations to seasonal temperatures affected patterns of growth, gonadal development and reproductive timing of temperate fishes (Table 12.3). In general, temperate fishes in the rhithron spawn primarily from the autumn to the spring, where oxygen conditions permit longer development or dormant periods, whereas most of the fishes remaining in the potamon spawn during the spring, summer or autumn months.

Large floodplains are still connected to rivers in many tropical regions and a few temperate ones, resulting in a full spectrum of lotic to lentic habitats and strong seasonal effects due to the flood pulse (Fig. 12.3) which may be independent of temperature. All spawning strategies seem to point towards giving as many young as possible access to the very productive, newly flooded, shallow areas created during the flood pulse (Junk *et al* 1989). However, the means to obtain this goal vary. The South-East Asian classification of 'black' fish and 'white' fish communities is a useful first-order differentiation of river-floodplain species (Welcomme 1985), and is partly based on reproductive strategy. Black fish prefer lentic habitats and undertake local migrations between floodplain habitats only in response to water level changes (Fig. 12.3). Many black fish species are multiple spawners and practice parental care. White fish undertake longitudinal migrations in the river, tend to be annual spawners influenced by the flood cycle, but also use the floodplain for feeding in nursery areas and, in some species, for spawning (Welcomme 1985; Junk *et al* 1989). Many white species are pelagophils, spawning in the main channel just before, or on the rise of, the flood pulse (de Godoy 1954;

Bayley 1973; Schwassmann 1978). This results in the eggs and larvae being dispersed widely over the floodplain during the flood pulse.

There are equivalents to this classification in temperate systems. For example, in North America the bluegill, *Lepomis macrochirus*, and the largemouth bass, *Micropterus salmoides*, are nestbuilding, floodplain lake species that correspond to black fish. The white basses, *Morone* spp., undergo longitudinal migrations when permitted and produce semibuoyant eggs in open water, and correspond to white fish.

Trade-offs in life-history strategies and polymorphism

Trade-offs in life histories and body designs are caused by conflicting selective pressures, particularly with reproductive strategies. Darwinian fitness of fishes is related to survival and fecundity, which are both size related (Calow 1985). The critical energy trade-off is between investment in gametes or in somatic tissues. Fish subjected to physically taxing spawning migrations tend to be semalparous and invest more energy in egg production; iteroparous fish do not exhaust body stores during the migration and tend to allocate energy to ensure post-spawning survival (Schaffer & Elson 1975; Glebe & Leggett 1981a, 1981b).

Iteroparous and semalparous life histories can occur in a single species; e.g. steelhead trout, *Oncorhynchus mykiss* (Ward & Slaney 1988); Atlantic salmon, *Salmo salar* (Schaffer & Elson 1975); and American shad, *Alosa sapidissima* (Glebe & Leggett 1981a, 1981b). A species possessing this polymorphic attribute is buffered against environmental uncertainty through increased specialization without losing fitness from con-

Table 12.3 Hokanson's (1977) temperature guilds for freshwater fishes in temperate zones

Guild	Optimal temperature (°C)	UILT (°C)	Gonadal growth phase	Spawning phenology
Stenotherm	20	<26	Summer (<20°C)	Autumn to spring (<15°C)
Mesotherm	0–28	<28–34	Autumn and winter (<28–34°C)	Spring (3–23°C)
Eurytherm	<28	<34	Increasing photoperiod (12°C)	Spring to autumn (15–32°C)

UILT, upper incipient lethal temperatures.

flicting gene recombinations. The species survives as a metapopulation, some populations of which are in the process of expanding their range and compensating for contractions by others in response to a changing environment.

Polymorphism may reflect adaptive responses to selective forces (Seghers 1974; Suzumoto *et al* 1977; Endler 1980; Taylor & McPhail 1985a, 1985b; Wade 1986), genetic drift (Allendorf & Phelps 1980) or a combination of both processes (Hatch 1990). Polymorphism can reflect fine tuning to local conditions (e.g. Zimmerman & Wooten 1981; Calhoun *et al* 1982; Matthews 1986b; Hulett 1991) or responses to large environmental gradients (Riddell & Leggett 1981; Riddell *et al* 1981; Schreck *et al* 1986; Hatch 1990). Some traits exhibit high degrees of heritability as demonstrated in breeding experiments focusing on the genetics of disease resistance (Wade 1986; Withler & Evelyn 1990). Polymorphism has been attributed to phenotypic plasticity responding to environmental change (Gee 1972; Stearns 1980; Metcalfe 1989).

Sedentary and anadromous phenotypes among salmonids have been attributed to phenotypic plasticity with arctic charr (Nordeng 1983) and to genetic differentiation with rainbow trout (Currens *et al* 1990). Various stocks exhibit polymorphic life-history traits, including migratory/sedentary tendencies among some white fishes of the river-floodplains (Welcomme 1985) and the diverse potamodromous life histories exhibited by Yellowstone cut-throat trout, *Oncorhynchus clarki bouvieri* (Varley & Gresswell 1988).

How should these stocks be managed? The most conservative, but recommended, approach is to assume that polymorphic traits are under genetic control and to adopt a policy that conserves the diversity of the metapopulation. This relates to problems with hatchery-reared fish.

Augmenting stocks from hatcheries

Hatchery fish account for the production of approximately 80% of the salmonids in the Columbia River. However, mitigation using current hatchery techniques will, at best, result in a pyrrhic victory. Although it is theoretically possible to manage hatcheries to conserve genetic

resources (Nyman & Ring 1989) and create conditions for heterozygous populations (Schreck *et al* 1986), much genetic diversity is lost through genetic drift and founder's effect (Allendorf & Phelps 1980; Ryman & Stahl 1980; Quattro & Vrijenhoek 1989) and a recent study has shown differences in selection between local hatchery and wild populations of chinook salmon (Hulett 1991). Hatchery-raised fishes tend to be more aggressive and dominate wild cohorts (Nickelson *et al* 1986; Noble 1991). The degree to which aggressive dominance is influenced by early exposure to hatchery conditions compared with genetic influences is still unknown. In any case, if hatcheries are to be used, genetic and environmental factors must be accounted for.

12.4 QUANTITATIVE MEASURES OF FISH POPULATIONS AND YIELD PREDICTION

Measures of the quantities by number or weight of fish in populations, guilds or communities is important for the management of fish for human exploitation and for the testing of effects of environmental change. Such changes can be caused by natural events (section 12.5) or human impacts (section 12.6). Details of the biases and variance associated with specific sampling methods are discussed in Chapter 13.

Rational exploitation for food or recreation requires prediction of the yield or the proportion of production that is available for human use on a sustained basis. In principle, this can be estimated through traditional dynamic pool models, from production estimates, or from comparative approaches. There are distinctions between the approaches to problems of exploitation and environmental change, but there are common practical limitations that will become apparent below.

Fish population dynamics

Fish population models (Schaefer 1954; Beverton & Holt 1957; Gulland 1969; Ricker 1975) have evolved to predict trends in intensive fisheries of significant value as measured by market economists, such as those exploiting offshore marine and anadromous populations. They explicitly or

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implicitly incorporate birth, death and growth rates on a given number of individuals. The simplest, the logistic or surplus-yield model (Schaefer 1954), requires the definition of a stock or viable population, yield estimates, and reliable indices of fishing mortality rate (fishing effort) and of population abundance (catch per unit effort) for a series of years. Typically, the most critical assumptions are that yield estimates be at equilibrium with the current exploitation rate, catch per unit effort be proportional to abundance density, and that the environment limiting the population is constant.
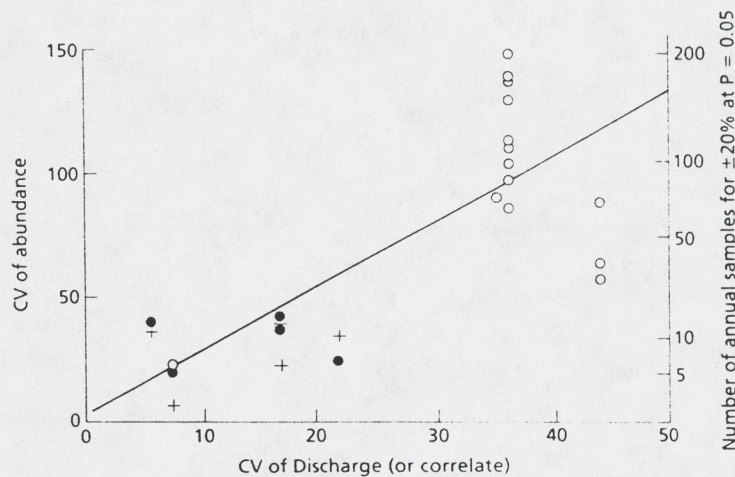
The yield-per-recruit model (Beverton & Holt 1957) requires knowledge of the age structure and natural mortality rate of the population in addition to the logistic model requirements. It provides an estimate of the fishing mortality rate that maximizes yield per fish recruited to the fishery. So far no models described have required population size estimates, but to estimate yield from the yield-per-recruit model the number of recruits obviously needs to be estimated each year (e.g. Pope 1972). Predicting recruits from abundance of parents has a good theoretical foundation (Ricker 1975), but with rare exceptions (Elliott 1985) these models are very noisy and have no predictive capability.

Can these models help us with river fisheries? They are sound theoretically, but their application is limited by the quality of data, the cost of obtaining data, and changes in the environment. Elliott's experience suggests that stream fish are more appropriate for the testing of population regulation mechanisms. More accurate estimates are possible in streams, although with more effort than most biologists realize (Bayley 1985), and fisheries in large rivers are generally more difficult to sample than benthic fish in many continental shelf environments. Fishery studies have tended to underrate environmental effects in all systems, but streams and smaller rivers are typically the most physically variable of them all.

A principal physical variable is discharge. Because fish recruitment and production are generally considered to be most affected by events in the first year of life, the variability of abundance of 0+ and 1+ fish was estimated from the literature (Table 12.4). Coefficients of variation of annual fish population measures were compared with those of annual discharge measures (Fig. 12.4). Despite the variety of streams, species, methods and lengths of stream sampled there is a clear dependence between year-to-year variability of population size and discharge. There are probably various mechanisms that connect discharge to population size, and critical periods of flow within systems may provide clues. Considering that for a given accuracy and time scale discharge is cheaper to measure than population size. It is disappointing that discharge is so often inadequately monitored.

Fig. 12.4 Coefficient of variation (CV) of autumn fish abundance versus CV of annual discharge or correlate (see Table 12.4 for further explanation of data and sources). Number of samples (= years) required for a precision of ±20% at $P = 0.05$, based on central limit theory applied to CV of abundance predicted by regression, is shown at right. (●, 0+ fish; +, 1+ fish; ○, mostly 0+ and 1+ fish.

Table 12.4 Coefficients of variation for fish abundances estimated near the end of the growing season and for discharges

Stream	Country	Years of study	Species	Mean dimensions of stream segment (m)		Age class	No. of years	% Coefficient of variation of annual	
				Length	Width			Abundance	Discharge
Black Brows Beck	UK	1967–83[1]	*Salmo trutta*	75	0.8	0+	17	24	26
			Salmo trutta	75	0.8	1+	16	34	26
Hunt Creek	USA	1949–62[2]	*Salvelinus fontinalis*	2816	5.6	0+	14	20	7.4
			Salvelinus fontinalis	2816	5.6	1+	14	6.3	7.4
Hunt Creek	USA	1968–86[3]	*Salvelinus fontinalis*	1610	4.0	0/1+	20	22	7.4
Laurence Creek	USA	1953–70[4]	*Salvelinus fontinalis*	5630	—	0+	18	39	5.5
			Salvelinus fontinalis	5630	—	1+	18	36	5.5
Shelligan Burn	UK	1966–75[5]	*Salmo trutta*	167	3.6	0+	10	41	17
			Salmo trutta	167	3.6	1+	10	22	17
			Salmo salar	167	3.6	0+	10	37	17
			Salmo salar	167	3.6	1+	10	39	17
Maquoketa River	USA	1978–82[6]	*Micropterus dolomieui*	3540	27.0	0/1+	5	90	35
Middle Fork Salt River	USA	1985–89[7]	*Lepomis cyanellus*	250	1.1	0/1+	5	86	36
			Pimephales promelas	250	1.1	0/1+	5	104	36
			Lepomis humilis	250	1.1	0/1+	5	113	36
			Notemigonus crysoleucas	250	1.1	0/1+	5	97	36
			Cyprinella lutrensis	250	1.1	0/1+	5	129	36

Titus Creek	USA	1985–89[7]	*Hybopsis dorsalis*	250	2.9	0/1+	5	148	36
			Lepomis cyanellus	250	2.9	0/1+	5	137	36
			Etheostoma nigrum	250	2.9	0/1+	5	139	36
			Semotilus atromaculatus	250	2.9	0/1+	5	138	36
			Pimephales promelas	250	2.9	0/1+	5	133	36
Jordan Creek	USA	1950–53[8]	*Pimephales notatus*	1450	6.7	0/1+	4	88	44
			Campostoma anomalum	1450	6.7	0/1+	4	63	44
			Ericymba buccata	1450	6.7	0/1+	4	57	44

[1] August/September abundance data from Elliott (1985); discharge estimate uses annual rainfall variation from June to August (Elliott 1984).

[2] September abundance data from McFadden *et al* (1967); CV of flow estimated from range of 21–27 cubic feet per second.

[3] Autumn abundance data of 2–4.9-inch fish in control stretch in Alexander and Hansen (1988), CV discharge assumed same as during previous period on Hunt Creek.

[4] September abundance data from R. Hunt, Wisconsin Department of Natural Resources, personal communication. Discharge CV estimated from 1961–6 data only.

[5] Autumn abundance data from Egglishaw and Shackley (1977); discharge estimate uses annual rainfall variation as a proxy.

[6] Autumn abundance data of fish <20 cm (mostly 0+ fish) from Paragamian (1987); discharge data May–September from Paragamian and Wiley (1987).

[7] Autumn abundance data of Smale and Rabeni (1990); the five most abundant species from each stream are shown; discharge estimate uses annual rainfall variation as a proxy.

[8] August abundance data from Larimore (1955); discharge estimate uses US Geological Survey data from River Vermillion downstream.

It is sobering to consider the number of samples, which in this case is years, required to obtain estimates of cohort sizes within ±20% of the mean with 95% confidence (see right ordinate, Fig. 12.4). Although in some cases the methods could be improved to reduce bias, reduction in measurement variance usually requires more sampling, which may itself influence the population in a small stream. The streams with lowest discharge variability (Table 12.4), situated in northern Michigan and Wisconsin, are fed by groundwater. The other examples of salmonid streams, although they are surface run-off, are unusually stable. In contrast, the examples of higher discharge variability, which happen to be surface run-off midwestern streams, show what to some would be an alarming variability, although the examples from Missouri include two drought years. While much of this variability might be explained by discharge or other factors within streams, this does not help prediction if next year's weather has to be predicted first. Thus, there is an important distinction between a *post-hoc* investigation, which for example tests the effect of an environmental change given a discharge pattern, and one that needs to predict the future trend of a population for management of a fishery. Problems of assessing effects of environmental change on salmonid populations have been assessed by Hall and Knight (1981).

Although high recruitment variability is not restricted to stream fish (Dennis *et al* 1985), the resources available to adequately sample stream fish, define each stock, and account for environmental change are quite inadequate to consider using traditional models on the majority of stream or river populations. An exception is the valuable sockeye salmon mixed-stock fishery of the River Fraser, Canada, but even with 34 years of spawner-recruit data, extreme harvest rate reductions on some stocks over two generations (8 years) were deemed necessary to give >50% chance of detecting an increase in spawner abundance (Collie *et al* 1990).

Fish production

Production is defined as the total addition of biomass or equivalent potential energy to a population, including that from individuals not surviving the time period concerned. Therefore, production can represent resources available for other trophic levels. The International Biological Program (IBP) prompted many biologists to undertake fish production studies since the 1960s. These efforts have been useful in providing first-order estimates of trophic efficiency and energy flow, but have limited utility for estimating the proportion of production available to humans or to predict changes in the community due to an environmental change. These limitations result as much from the lack of accuracy in methods as from the lack of appropriate comparisons among systems.

Unfortunately, many biologists have pursued fish production estimates, which are expensive endeavours, without a clear purpose. In addition, some bemoan the lack of production estimates for the first year of life, implying that only estimates for the whole population are useful. Sometimes the contrary is true. For instance, the production of exploited year-classes furnishes an upper limit to the yield potential. The production of a particular size-range of fish may better reflect the influence of a critical habitat type. The implication that the production of a fish population represents a single trophic level is usually false. Young fish can be trophically more similar to (or even consumed by) some invertebrates than older conspecifics. Designs for studies requiring knowledge of annual production of young fish should be aware that such estimates in streams may be as variable as those for 0+ abundance levels (Fig. 12.4) and be subject to similar biases, because both estimates depend on the same limited options for estimating abundance density (Bayley 1985). A similar argument applies to the use of bioenergetics to estimate production or yield.

It is useful to estimate the production of the whole fish taxocene to compare the broad, upper-trophic-level productivity of different systems whose fauna are dominated by fish (e.g. Table 6.14 in Welcomme 1985) or to estimate the primary production sources required to support the taxocene (Bayley 1989). This approach could be refined by stratifying the production along criteria of individual body size and trophic group (or guild within zoogeographical areas), but should prefer-

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ably include all significant fauna and not just fish. Conversely, comparing the production of fish populations at the species level or between species from different environments has no utility, unless differences in competitive or predatory environments and in population structure are accounted for. (For more discussion, see Chapter 17.)

Multispecies yields

The development and application of dynamic models, such as the surplus-yield model, to multispecies fisheries is in its infancy, and is severely limited by empirical data (Pauly & Murphy 1982). However, there is surprising consistency among yields of tropical river-floodplain fisheries (Welcomme 1985) that can largely be explained by fishing effort using a function related to the surplus-yield model (Bayley 1988a). This consistency across fisheries may be a result of common socioeconomic development of fishing communities in response to high species diversity (yields of species groups tend to be more stable than individual species), the dominance of native, coevolved fish fauna in tropical systems, and/or the relatively natural flood pulses and floodplain habitats in the tropics.

However, residual variability is significant, and the explanation of 74% of the variance in yield per unit floodplain area by fishing intensity (Bayley 1988a) should not hide the fact that the prediction of an individual system is still too imprecise for most management needs in individual river fisheries. Other factors at the comparative level, such as indices of system productivity or, at the individual system level, the hydrological regime in previous years (Welcomme 1985) should be explored to refine these 'top-down' approaches. However, the current models are adequate to alert politicians and economists of the current or potential animal protein yields that may be lost, and are currently being lost, by many basin development projects.

Summary

Three principal problems limit our ability to measure and predict fish populations: deriving

sampling methods of known accuracy (bias and precision), accounting for temporal and spatial variability, and accounting for environmental effects, particularly discharge (see Chapter 13). We consider age determination to be a secondary issue with most populations. Available models are not considered to be as limiting as good quality empirical data. Simulation models (e.g. DeAngelis *et al* 1991) can suggest plausible sets of mechanisms and driving forces, and reasons for the high variance found empirically. Such models indicate probable areas requiring better empirical data, which can be obtained to generate another cycle of improved simulations. In the absence of a large injection of empirical data, however, it is unlikely that simulation modelling will increase the accuracy of annual prediction that managers often require, even if such predictions are conditional on future weather patterns. More empirical data based on parallel time series of independent systems is one approach to developing more efficient syntheses and predictions (section 12.7).

12.5 COMMUNITY ECOLOGY AND MANAGEMENT

Fish resources have not traditionally been managed at the assemblage or ecosystem level. At best, we have monitored the welfare of a small fraction of the assemblage and concentrated management activities within the confines of the river channel. The difficulties of estimating populations (section 12.4), the need to account for environmental constraints and adaptations (section 12.3), and the effects of changes in single components on the assemblage (this section) all indicate the necessity to understand community- or assemblage-level processes at the habitat, stream and ecosystem levels, and to develop fisheries management approaches at those levels. But do we know enough to provide viable alternatives to current management methods?

Abiotic or biotic control in response to disturbance

Fisheries managers need to know the extent to which a change in one species affects the re-

sponses of the other species in the assemblage. If biotic interactions such as predation or competition are strong, one presumes that the loss or addition of a single species would change the structure of the remaining species of the assemblage. If a physical change, such as an environmental disturbance or intense exploitation, principally affected one species, would this result in more changes in the assemblage than would be expected from only the autecologies of the remaining species? If physical forces are highly dynamic, perhaps biotic factors do not have sufficiently short response times to intervene (Hutchinson 1961; Wiens 1984). These regulatory issues are at the heart of the controversy over whether abiotic or biotic effects govern assemblage structure of stream fishes (Moyle & Li 1979; Grossman *et al* 1982; Herbold 1984; Rahel *et al* 1984; Yant *et al* 1984; Grossman *et al* 1985).

Considerations of scale and generally acceptable definitions of terms (Schoener 1987) can increase the odds of solving this difficult problem. First, regional influences on hydrology (section 12.2; Fig. 12.2) should serve as the largest scale in which to assess the role of abiotic factors in structuring fish assemblages. Second, it is important to distinguish between contingency and magnitude as factors of disturbance (Colwell 1974). High flushing flows during normal periods of peak discharge, within typical bounds, do not disturb fauna coadapted to seasonal contingencies (Resh *et al* 1988). However, such flows during the base flow period can severely impact fauna. In systems with variable flood frequency and poor predictability, such as the prairie streams described by Matthews (1987), disturbances such as drought and flash floods are frequent events and when measured at small scales (habitat units and days) result in apparently randomly varying assemblages; but at larger scales (reaches and years) assemblages appear to be relatively stable (Ross *et al* 1985; Matthews 1986a; Matthews *et al* 1988). (Comparisons between scales should ensure that a difference is not an artefact of different measurement precision; for instance, a smaller standard error can result from a larger statistical unit associated with the larger scale.)

Intermittent disturbances such as floods of low predictability can act as resetting mechanisms

(Starrett 1951; Fisher 1983; Matthews 1986a) or mediate competitive and predatory interactions (Meffe 1984). Conversely, the lack of a flood in a river-floodplain where predictability is high (see Fig. 12.2(a)) comprises a disturbance because the fauna are adapted to a regular flood pulse (Junk *et al* 1989). Variable and stable assemblage components were observed following a severe drought over a 40-month period (Freeman *et al* 1988). Some fishes remained persistent, characterized by relatively stable populations, whereas others were less persistent and highly variable. The effect on the assemblage depended on timing, especially in relation to recruitment dynamics, frequency and magnitude of the event, and regional adaptation (Freeman *et al* 1988).

Predation and competition

Biological interactions are apparent at smaller spatial scales, such as at the stream reach or channel unit level. Studies indicating competition or predation suggest that assemblage structure may be controlled by non-random factors because observations of behavioural patterns, especially in experiments, appear to be predictable and repeatable.

In general, examples of competitive displacement from large sections of stream result from species introductions (Fausch & White 1981, 1986; Cunjak & Green 1983, 1984; Meffe 1984; Castleberry & Cech 1986; Fausch 1988). Competition among native assemblages generally evokes resource partitioning through selective and interactive segregation (Baker & Ross 1981; Baltz & Moyle 1984; Moyle & Senanayake 1984; Baltz *et al* 1987; Gorman 1987; Ross *et al* 1987; Wikramanayake & Moyle 1989; Wikramanayake 1990). For instance, the innate hierarchy of similar-sized salmonids in Cascadian streams is coho salmon > steelhead trout > cutthroat trout > chinook salmon in order of dominance (Li *et al* 1987). This social hierarchy has a direct effect on selection and use of microhabitats and habitat units among sympatric salmonids. Coho salmon force other salmonids to less desirable locations.

A comparison of stream sites with and without piscivores by Bowlby and Roff (1986) indicated that the biomass of non-piscivorous fish was

lower in the presence of piscivores. Piscivores can shape species composition, morphology, behaviour and size structure of their prey, as demonstrated when guppies of Trinidad were exposed to the piscivores *Rivulus harti, Crenicichla alta* and *Hoplias malabaricus* (Seghers 1974; Endler 1980). Predators can influence patterns of habitat use, activity budgets and foraging patterns of the prey through intimidation (Fraser & Cerri 1982; Gilliam & Fraser 1987).

Fish diseases and parasites

The effects of fish diseases on fish assemblage structure have been underestimated. Parasites can have more varied direct and indirect impacts on communities than predators (Holmes 1982; Holmes & Price 1986). Although spectacular epizootics have killed millions of fishes (Rohovec & Fryer 1979; Wurtsbaugh & Tapia 1988), the impacts of disease can be subtle. Patterns of abundance and distribution may appear to be governed by random physical processes when in fact a subset of species may be susceptible to a microparasite while others are not. As stated by Price *et al* (1986, p. 499) '... many interactions that appear to be between two species actually involve a third. Unless this is recognized, models will either fail to match field reality or will match it spuriously.'

Microparasitic infection has probably been a major selective force on fish assemblages of the Pacific Northwest (Li *et al* 1987). Subpopulations of steelhead trout, coho salmon and chinook salmon differ in genetic resistance to various microparasites (Suzumoto *et al* 1977; Winter *et al* 1979; Wade 1986). The degree of immunity reflects the historical distributions in space and time of the microparasite and host (Buchanan *et al* 1983). Microparasites, such as *Ceratomyxa shasta* and *Flexibacter columnaris*, can consequently act as zoogeographical barriers to specific populations. For instance, the epizootic of *F. columnaris* in the Columbia River during 1973 was responsible for the loss of approximately 80% of the spawning run of Snake River steelhead in eastern Oregon and Idaho (Becker & Fugihara 1978). Steelhead stocks that ascend early in the year in typically cold water, when columnaris

disease is neither prevalent nor virulent, were especially vulnerable. Columnaris disease became rampant when the Columbia River warmed early in the drought year of 1973, but not all size classes and species of fish were susceptible. In general, larger cypriniform fishes, a group which is tolerant of higher temperatures, were more immune (Becker & Fugihara 1978).

Monitoring changes in fish assemblages

It is well known that sufficient stress or 'press disturbance' on a community will reduce the number of species (species richness). We know that the number of species is related to the size of the basin (Welcomme 1985) and that this relationship changes among regions (Fausch *et al* 1984; Moyle & Herbold 1987) and continents (Welcomme 1985; Moyle & Herbold 1987). To the degree that species richness is predictable in natural systems, departures from the norm at a comparable scale can serve as an indicator of stress upon stream communities. However, even if non-native species are excluded and natural conditions are well defined, relative species richness is a crude measure of stress because it does not reflect different stress tolerances among species, is prone to measurement error because some species are always rare (Sheldon 1987) and suffers from measurement bias when gear selectivity cannot be corrected (Bayley *et al* 1989).

The Index of Biological Integrity (IBI) is an attempt to provide a more robust measure of stress or stream degradation than relative richness, diversity or methods using an indicator species (Karr 1981; Fausch *et al* 1984, 1990; Karr *et al* 1986, 1987), and has received wide publicity and use in the USA. The IBI is a sum of 12 metrics, each scored as odd numbers up to 5, that are estimated to represent the degree to which a particular stream locality is degraded from its natural state. The metrics, which are applied to fish that are not young-of-the-year, include species richness, proportions of trophic groups, total abundance, proportions of stress-tolerant species specific to the region concerned, abundance of all species, extent of hybridization and parasitism. Subsets of these metrics have varying degrees of correlation. Like relative species rich-

ness or diversity, the IBI is only as good as the information on the natural fish community for the reach being assessed; it is sensitive (to an unknown degree) to sampling bias; it does not relate directly to known ecological relationships among the species and with their environment; and it does not identify types of stress or disturbance. We are not suggesting that any single number could represent all these factors (multivariate approaches are called for) or that the pertinent ecological information is available (it usually is not). However, much information already exists that quantifies species/habitat relationships (sections 12.2 and 12.3). Although the IBI does not link species composition to physical characteristics, it could be modified to detect disruptions of longitudinal zonation patterns (Fausch *et al* 1984). If physical factors influence fish species distributions, then one should be able to infer 'habitat integrity' from species composition. Conversely, the IBI was insensitive to the environmental impacts of massive military exercises on a small prairie watershed (Bramblett & Fausch 1991), where hardy fishes are naturally subjected to flash floods and droughts, and whose presence and structure depend on their rate of colonization rather than habitat changes.

The IBI has definite limits and its assumptions should be carefully examined, as there are other more quantitative alternatives (Fausch *et al* 1990; Bramblett & Fausch 1991). However, the index is a laudable attempt to provide a yardstick for stream managers who have a good knowledge of local natural history (Karr *et al* 1986), but who lack cause-specific ecological information to identify the mechanism(s) and source(s) of degradation. Therefore, in common with any composite index composed of arbitrary elements, the IBI should be regarded as a useful management tool for preliminary diagnosis rather than as an index of ecological or heuristic value.

12.6 ANTHROPOGENIC DISTURBANCES, MITIGATION, AND RESTORATION

We have presented evidence that different species and life stages of fishes are adapted to particular components of the riverscape, and are sensitive to the spatial scales and dynamics in each system. Disruption of riverscape processes causes great damage. River fisheries management operates on the river channel, yet economic and social activities outside of the lotic habitat have profound cumulative impacts on fishes.

The effects of and recovery from disturbance are scale dependent with respect to fishes (see Fig. 12.1(b)) and environmental units (see Fig. 12.1(a)). Microhabitat units are more sensitive to anthropogenic disturbances but are also the quickest to recover. In contrast, damages to the river from the surrounding landscape may be measured in hundreds of years, if one takes into account geomorphic processes and key structural organisms. For example, it is estimated that at least 500 years are required to restore drainages of the Pacific Northwest where ancient forests of Douglas firs have been clearcut (Li *et al* 1987).

Major impacts on regional scales have occurred in the plains streams of Kansas and Missouri (Cross & Moss 1987; Pflieger & Grace 1987). The combination of dams, revetments and jetties created deeper, clearer, more channelized streams of high velocity. The native fishes are morphologically and behaviourally adapted to shallow, silty, highly braided rivers. This native fauna is disappearing and introduced species are becoming dominant. Further west, two-thirds of the fish species in the Colorado basin are introduced and 17 of 54 native species are threatened, endangered or extinct (Carlson & Muth 1989) owing to similar effects of mainstream dams. Dams impede the distribution of material and energy transfer through the drainage basin, obstruct spawning migrations (Bonetto *et al* 1989; Barthem *et al* 1991), inhibit reproduction by altering thermal regimes (Baxter 1977), alter faunal structure through habitat change (Bain *et al* 1988), are centers for disease transmission (Becker & Fugihara 1978) and create unstable fish assemblages (Gelwick & Matthews 1990). Impoundments in tropical river systems, where extant floodplains have demonstrated high fish yields (Welcomme 1985; Bayley 1991), can devastate fish production, in particular downstream where the flood pulse is affected (Bonetto *et al* 1989; Junk *et al* 1989).

The temptation is to mitigate for damage using

complicated, expensive, engineering solutions because these are politically attractive; but this has unpleasant consequences that are expensive in the long run. Gore (1985) correctly stated that river restoration should be equated to 'recovery enhancement' because it should accelerate the natural process of recovery. In general, the most cost-effective mitigation procedures mimic natural processes. Such procedures will also enable relatively painless restoration in the long term.

Mitigation to restore native fishes in the intermountain western USA will require burning and logging stands of newly invaded juniper (J. Sedell, personal communication, Forest Sciences Laboratory, Oregon State University). Native bunch grasses have virtually disappeared in just over a century. They did not coevolve with large grazing ungulates and declined when livestock was introduced. Exotic plants soon became established and artificial suppression of the natural fire cycle led to poorer water infiltration, greater siltation and runoff, and the massive invasion of junipers. Each mature juniper evapotranspirates 15−35 gallons (68−160 litres) of water daily, which resulted in many streams becoming ephemeral. Restoration of natural fire cycles will provide short-term mitigation, but full restoration of the watershed will require decades.

Habitat restoration has been very successful at reach, channel unit and microhabitat levels in the central USA (White & Brynildson 1967; Hunt 1976). However, the success of enhancement projects from Alaska and the Pacific Northwest has, with few exceptions (House & Boehne 1985, 1986), not been determined (Hall & Baker 1982). Blatant failures occurred when mitigation was attempted without a regional context; what succeeds in a low gradient stream in Wisconsin will not necessarily apply to high gradient streams along the Pacific coast. Recovery times of successful projects are only in terms of years at the reach scale. Hunt (1976) found maximum response to improvements of channel structures in 5 years.

Bayley (1991) has argued that the best short-term approach to restore the function of river-floodplains impacted by navigation impoundments is to control discharge to mimic the pattern of the natural hydrograph, providing that artificial levees are also removed. However, any extensive restoration of large rivers will require watershed restoration which reduces the drainage rate, and dam removal which will restore the natural downstream transport of sediment and permit the natural flood pulse and associated vegetation to return. This is not a restoration that is just in the interest of fish and other native biota, but will provide the most cost-effective flood control (see Belt 1977).

Mitigation using exotic fishes is a great temptation. However, it is one of the poorest tools because exotic fishes can cause more problems than solutions, and the treatment is irreversible. Exotic species have contributed to the defaunation of many areas, especially areas that are disturbed (e.g. Moyle *et al* 1986; Carlson & Muth 1989; Moyle & Williams 1990). Predation and competition have been implicated in many instances (Moyle *et al* 1986), but the role of fish diseases can be insidious. Transfers of exotic fish diseases are occurring at unprecedented rates (Ganzhorn *et al* in press) and coadapted (micro) parasite−host populations are more stable than novel ones. As in germ warfare, parasites carried by resistant hosts can enhance their invasion by infecting native competitors (Holmes 1982; Freeland 1983).

12.7 CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

We argue that in most parts of the world it is now more important to spend resources on the restoration and conservation of riverine environments than to promote and maximize exploitation of species of current interest. Exceptions are relatively pristine river-floodplains in some developing countries, where sustained food fisheries are a human necessity and are advisable to provide a defence against destructive river-basin development schemes (Bayley & Petrere 1989).

Given an environment to which they are adapted, riverine fish are remarkably persistent because of the intensity and frequency of natural disturbances in evolutionary time, such as extreme floods and droughts. Therefore, in the long term the cost of correcting mistakes in management of the exploitation process is negligible compared to that of correcting or compensa-

ting for the effects of permanent changes to the environment, such as dams, water extraction, floodplain habitat removal, chronic pollution or introduction of exotics.

Research on riverine fish is controlled to a large extent by cost which is governed by sampling limitations (Fig. 12.5). There is a high variance in population size (see Fig. 12.4) which may be accounted for only partly by measurement variance, so increased sampling intensity is not necessarily a solution. As is typical with all ecosystems, the population level is the noisiest, with many measures of individual organisms and communities increasing in stability on a comparable temporal scale (Fig. 12.5). Therefore, how can we obtain the information to understand the environmental requirements to which the fish have adapted, estimate an acceptable management protocol, and apply such findings to problems of conservation, restoration, or exploitation in other systems?

We believe that a co-ordinated approach that combines extensive, protracted, empirical data collection with experiments and modelling is required. The co-operation of fishery managers is important so that some experimental control over the exploitation process is achieved. However, fisheries managers have only limited control over most aspects of the environment, and the co-operation of agencies and the private sector that are associated with the hydrology, siltation, chemical loads and in-stream structures is essential. This degree of integration is rare because of the different philosophies and individuals involved, which results in educational and institutional divisions.

Long time-series are advocated as a partial solution to improved empirical data needs. Such series are important in assessing responses by fish to unpredictable disturbances or long-term effects such as global warming. However, when seeking 'natural experiments' from the data, confounding
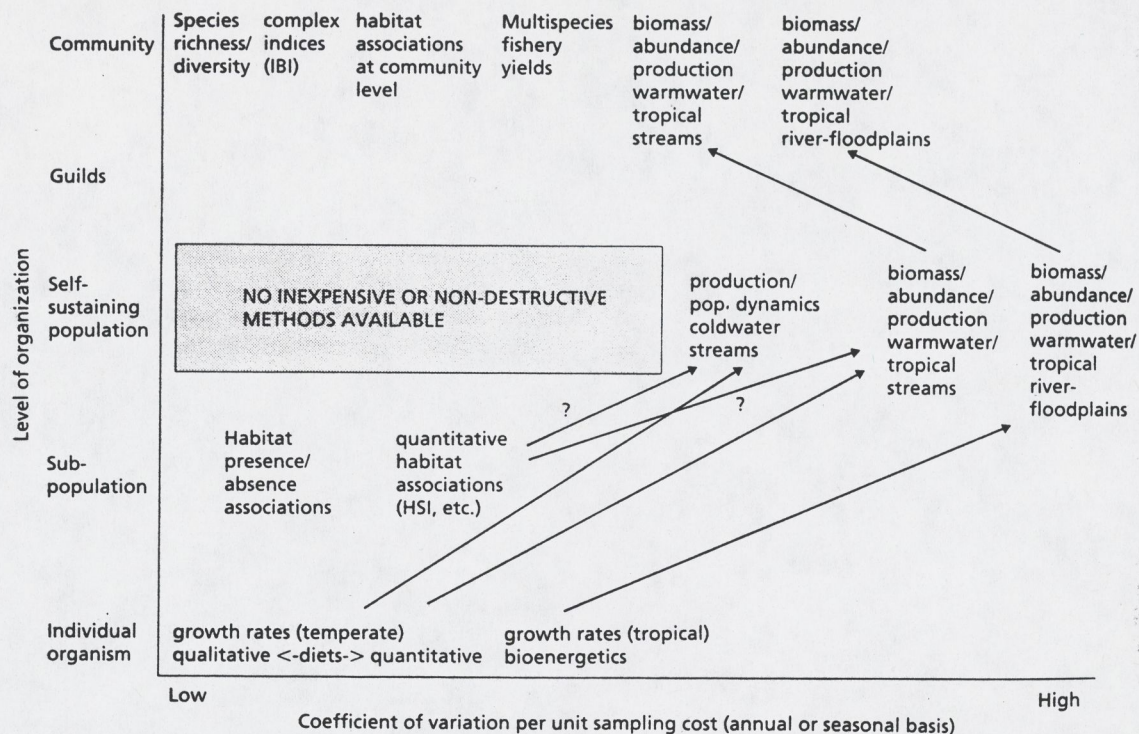

Fig. 12.5 Lotic fish investigations by level of organization versus adequate precision per unit cost. (Arrows indicate which higher level studies typically utilize information from a lower level.)

among time-correlated variables can produce too many alternative explanations. Concurrent time-series among 'ecologically comparable' systems (section 12.2) increases our ability to unravel time-correlated effects, such as when different climatic events affect fish in subsets of the systems being monitored. By ecologically comparable, we mean that the systems have comparable habitats and communities and have environments that are not drastically altered from important pristine conditions, particularly with respect to the hydrological regime. Comparisons among stressed systems are an alternative and are sometimes unavoidable, but the variety of stresses among systems may result in too many variables to control. In some river systems of developed countries this line of investigation will not be useful until some degree of restoration is attained.

Concurrent time-series of sufficient observation frequency and density will facilitate scale-dependent analyses of fish and habitat interactions that will permit more reliable inferences in other systems. One could obtain time-series by spending money on population estimates for a limited number of systems, or by spending a similar amount on community/guild/habitat/organism measures for a greater number of systems. In the majority of situations we advocate the latter approach, provided that every attempt is made to estimate fishery yield and effort. Such analyses should at least indicate the most economical paths towards the goal of restoration in many rivers and provide estimates of yield trends across sets of rivers.

Although extensive empirical data and natural experiments will narrow down the number of possible factors needed to improve prediction and understanding, the generality of results will be limited to those systems or very similar ones. Determination of dominant sets of mechanisms through experimentation and modelling within the context of a sound empirical database will broaden the application to more systems and reduce the future costs of empirical data collection. Reductionist approaches in the absence of preliminary analyses of empirical field data can result in the proposal of biologically plausible but ecologically insignificant mechanisms.

The cost and difficulty of analysing extensive field and experimental data have been reduced by improved computational facilities and methods. However, the cost of obtaining data has at least kept pace with inflation, and inadequate data have often been collected and published. If we are going to overcome the challenges of managing riverine fishes and their environment, researchers must strive for better quality data by investing more time to understand the sampling properties of their methods and to obtain the co-operation of managers and even the public to provide more extensive data. The ideal of cost-effective fishery management in rivers will not be achieved by a dependence on, or subjugation to, engineering approaches or byproducts, such as the development of unnatural hydrological regimes and attempts to utilize artificial habitats with hatchery-reared or exotic fishes.

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