Principles for linking fish habitat to fisheries management and conservation

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A set of eight simple ecological and social principles is proposed that could enhance the understanding of what constitutes fish 'habitat' and, if implemented, could contribute to improved management and conservation strategies. The habitat principles are a small, inter-related sub-set that may be coupled with additional ones to formulate comprehensive guidelines for management and conservation strategies. It is proposed that: 1) habitat can be created by keystone species and interactions among species; 2) the productivity of aquatic and riparian habitat is interlinked by reciprocal exchanges of material; 3) the riparian zone is fish habitat; 4) fishless headwater streams are inseparable from fish-bearing rivers downstream; 5) habitats can be coupled – in rivers, lakes, estuaries and oceans, and in time; 6) habitats change over hours to centuries; 7) fish production is dynamic due to biocomplexity, in species and in habitats; 8) management and conservation strategies must evolve in response to present conditions, but especially to the anticipated future. It is contended that the long-term resilience of native fish communities in catchments shared by humans depends on incorporating these principles into management and conservation strategies. Further, traditional strategies poorly reflect the dynamic nature of habitat, the true extent of habitat, or the intrinsic complexity in societal perspectives. Forward-thinking fish management and conservation plans view habitat as more than water. They are multilayered, ranging from pools to catchments to ecoregions, and from hours to seasons to centuries. They embrace, as a fundamental premise, that habitat evolves through both natural and anthropogenic processes, and that patterns of change may be as important as other habitat attributes. © 2005 The Fisheries Society of the British Isles

Key words: conservation; ecological principles; fish habitat; management; strategies.

INTRODUCTION

The concept of habitat has a long and contentious history, deeply interwoven with the niche concept. At least some of the confusion about what constitutes habitat is that species and their habitats are inseparable, like a lock and key (Kolasa & Waltho, 1998). Without a lock, a key has no meaning. Likewise, without organisms, habitat has no meaning. Individuals within species essentially find, and sometimes shape, their habitat from the surrounding environment according to their life history needs and activities. Habitat has a particular structure (McCoy & Bell, 1991); vital resources are arranged in space and time

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according to changes in the physical environment and the changing life history requirements of species. The concept of habitat may also be extended to an entire community (Kolasa & Waltho, 1998). Thus, habitat varies over time and space and may be subdivided into many parts among species or aggregated over entire communities.

In a general sense, existing habitat used by organisms is the product of all the biophysical legacies and processes that have occurred over many scales of space and time. These will continue to change into the future, as they have in the past, in response to a host of environmental drivers. Concomitantly, management and conservation strategies are dynamic products of an environmental system interacting with a social system. They bear striking resemblance to the natural systems in which they are applied. Both systems have broad and often ill-defined borders. Both evolve in response to change. Management and conservation strategies evolve as knowledge, social traditions, perceptions, and belief systems change, as new experiences are accumulated, and as wisdom is developed.

Linking habitat to management and conservation is not trivial. Conventional wisdom suggests that preservation or restoration of 'habitat' underpins effective management and conservation of organisms. This implies that understanding, identifying, and protecting critical 'habitat' are the best avenues for success. Is this basic premise correct? Human-induced changes radically alter existing structural conditions as well as geological, hydrological and ecological processes shaping the future condition of habitats. Nevertheless, even in reasonably pristine systems, serious declines in fish populations or radical changes in communities and food web structure have occurred. How could this have happened? Likewise, even well-supported efforts to manage and conserve or restore degraded habitats can fail. Are some systems so fragile that even subtle alterations can have large-scale consequences? Alternatively, is the general understanding of 'habitat' incomplete?

These questions and issues are substantial challenges for all disciplines involved: science and management, conservation and policy. Several immediate challenges are clear, however. First, the issue of what constitutes 'habitat' needs to be carefully considered. Can its relevant scale and extent for an individual, a species and a community be truly understood? Second, an understanding of what constitutes habitat needs to be clearly and effectively communicated to those charged with managing and conserving natural resources. Can and will the scientific community do this, and are decision-makers willing to adopt a new paradigm and translate it into action? Third, approaches for effective learning in increasingly complex social systems need to be better matched to the level of change and biocomplexity encountered in natural systems. Are traditional approaches toward continued learning suitable for tomorrow's world?

In this paper the first of these challenges is addressed by proposing a set of principles that could contribute to a broader understanding of 'habitat' and to improved management and conservation. Several are general, and could be equally applied to terrestrial and aquatic systems. The examples are limited to fresh waters and their riparian areas, many from ecological systems with which we are most familiar: coastal rivers and salmon *Oncorhynchus* spp. fisheries in the temperate rainforests along the Pacific coast of North America (Naiman &

Bilby, 1998; Naiman *et al.*, 2000, 2005). The second and third challenges cannot be fully addressed in this essay. They are briefly revisited in the discussion, however, offering insights as to how they might be attained.

IDENTIFYING AND JUSTIFYING FISH HABITAT PRINCIPLES

In recent years there have been several successful attempts in identifying ecological and social principles to guide management of landscapes (Naiman *et al.*, 1998; Dale *et al.*, 2000), fisheries (Fausch *et al.*, 2002) and water (Stanford *et al.*, 1996; Jackson *et al.*, 2001; Bunn & Arthington, 2002; Bernhardt *et al.*, in press). Like habitat, ecological and social principles have both spatial and temporal dimensions. No attempt is made to provide an exhaustive list. Rather, those presented reflect the types of knowledge needing promulgation (Table I). The principles pertain to a broad array of system-level characteristics (*e.g.* composition, arrangement, fluxes, variability, complexity and directed learning) as well as to species, communities, food webs, stream types and physical connections (Michael, 1995; Dale *et al.*, 2000; Wiens, 2002). Collectively, they represent a broad perspective on what is probably needed to maintain robust fish communities over the long-term.

HABITAT CAN BE CREATED BY KEYSTONE SPECIES AND INTERACTIONS AMONG SPECIES

Certain animals, such as beaver *Castor canadensis* and predatory starfish *Pisaster ochraceus*, exert a disproportionately important influence on ecosystems in which they live, relative to their biomass. These are often termed keystone species (Paine, 1966). Although there is no universally accepted definition, certain requisite traits have been identified (Power *et al.*, 1996). Generally, they are native species that regulate, through their activities and abundances, the productivity, diversity or physical structure of their communities. Further, their influences extend beyond those organisms directly affected through trophic interactions. Implicit is that keystone species are exceptional in their importance relative to the rest of the community, that they have a unique functional role, and that their impacts on available resources are disproportionately large relative to their abundances. Loss of a keystone species changes ecosystem structure

TABLE I. Eight basic principles for effective management and conservation of aquatic and riparian habitat

1. Habitat can be created by keystone species and interactions among species
2. The productivity of aquatic and riparian habitat is interlinked by reciprocal exchangesof material
3. The riparian zone is fish habitat
4. Fishless headwater streams are inseparable from fish-bearing rivers downstream
5. Habitats can be coupled in rivers, lakes, estuaries and oceans, and in time
6. Habitats change over hours to centuries
7. Fish production is dynamic due to biocomplexity, in species and in habitats
8. Management and conservation strategies must evolve rapidly in response to present conditions, but especially the anticipated future

or functioning, often with adverse consequences for other native organisms. Thus, effective management strategies explicitly acknowledge and sustain both the abundance and activities of keystone species.

Most descriptions of the keystone phenomenon focus on single species, although it is understood that in many cases keystone effects arise through the interactions of two or more species (*e.g.* the 'keystone mutualist hypothesis', Christian, 2001, and facilitation, Bertness & Leonard, 1997; Mulder *et al.*, 2001). Positive interactions among different species appear to help maintain the structure and diversity of numerous biotic communities. Ecological complexity and community stability is thought by some to be more dependent on interspecific interactions than on the actions or abundances of any one species (Mills *et al.*, 1993; Lawton & Jones, 1995; Naiman & Rogers, 1997; Soulé *et al.*, 2003). Some keystone interactions involve species that migrate across ecosystem boundaries (Polis *et al.*, 1997). Animals that carry nutrients, energy or genetic material among otherwise separate habitats may exert a significant influence on the structure and dynamics of receiving habitats, even if they are extrinsic to those communities for most of their life histories.

One example of an interspecific, trans-boundary interaction of paramount importance is the transfer of nutrients from the Pacific Ocean to river and riparian ecosystems by Pacific salmon and by brown bear *Ursus arctos*. Pacific salmon have been described as keystone species in coastal ecosystems because of their importance as a food resource for vertebrate predators and scavengers (Willson & Halupka, 1995; Willson *et al.*, 1998). The interactions between species, including those that utilize Pacific salmon, collectively maintain the system structure and function for the long-term. The Pacific salmon–bear interaction has been described as a keystone process because of their synergistic role in transporting marine-derived nutrients to forest ecosystems in Alaska. Marine-derived nutrients can significantly influence the structure and growth of riparian vegetation (Helfield & Naiman, 2001, 2002; Bartz & Naiman, in press), especially nutrient-limited riparian spruce *Picea* spp.. Nitrogen (N) influx to riparian areas is enhanced in the presence of both Pacific salmon and brown bear, but not to the same extent by either species in isolation (Fig. 1; Helfield & Naiman, in press). The interactions of Pacific salmon and brown bear may provide up to a quarter of riparian N inputs, with the percentage varying according to Pacific salmon escapement, channel morphology and watershed vegetation. In any event, the added nutrients accelerate the growth of spruce so that trees become large enough to form log jams (when they fall into the river) more quickly than in the absence of the nutrients. Log jams enhance stream complexity and salmon rearing habitat throughout the Pacific temperate rain forest (Naiman *et al.*, 2002). Clearly, effective management strategies consider the biological components (*e.g.* species), but also the dynamics of their interactions because these may sustain the habitats of many species.

THE PRODUCTIVITY OF AQUATIC AND RIPARIAN HABITAT IS INTERLINKED BY RECIPROCAL EXCHANGES OF MATERIAL

Most materials underpinning food webs in streams originate from 'outside' the aquatic environment. Likewise, the aquatic environment may be an important resource for riparian organisms (Baxter *et al.*, 2004). Thus, effective fish
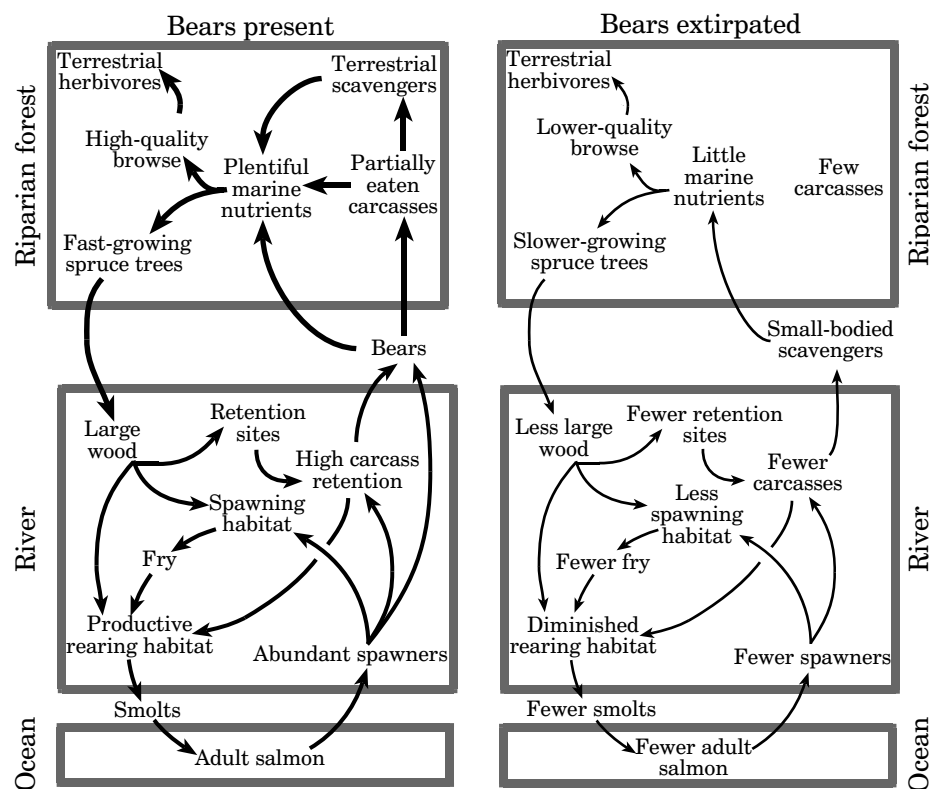
FIG. 1. The interaction between brown bear and Pacific salmon has profound effects on the cycling of marine-derived nutrients (MDN), with significant consequences for river and riparian ecosystems, and the long-term viability of the Pacific salmon population. Brown bears and other piscivores consume Pacific salmon, thereby spreading salmon-enriched wastes and partially-eaten Pacific salmon carcasses into the stream and the riparian forest. Terrestrial and aquatic insects colonizing the carcasses enhance decomposition and MDN diffusion. In the riparian forest MDN are taken up by vegetation, increasing foliar N content and growth rates. Large riparian trees, especially Sitka spruce, provide shade, bank stabilization, allochthonous organic matter and large woody debris (LWD), improving the quality of instream Pacific salmon habitat. LWD retains postspawn Pacific salmon carcasses in streams, further enhancing MDN availability. Increased foliar N content enhances palatability and nutrition of riparian plants, potentially altering patterns of browsing, which in turn affect patterns of riparian productivity and species composition. The net result is a positive feedback loop that, when the keystone interaction between brown bear and Pacific salmon is functional, ecosystem-scale productivity and biodiversity are significantly enhanced (modified from Helfield & Naiman, in press).

management and conservation strategies must consider the condition of the surrounding landscape and ensure connectivity between aquatic and riparian habitats (Wiens, 2002). Materials (*i.e.* carbon, plant-available nutrients, cations, sediments and woody debris) may originate from upstream, *via* precipitation, groundwater and allochthonous fluxes from surrounding vegetation, or from lateral channel migration (in the case of rivers). This principle is most easily demonstrated in rivers but also has strong implications for lakes (Pace *et al.*, 2004).

It is well established that terrestrial and aquatic systems are strongly linked (Naiman *et al.*, 2005). Only recently, however, have there been experimental

manipulations to elucidate pathways and quantify linkages. For example, sharp changes in the supply of wood and leaf litter to streams (*e.g.* by removal of riparian forests) causes significant changes in the abundance and biomass of macroinvertebrates (Wallace *et al.*, 1999). By reducing the allochthonous inputs of litter (by 94%) to a stream in western North Carolina, U.S.A., over 4 years (small woody debris was removed from the stream in the fourth year), Wallace *et al.* (1999) were able to decrease organic matter standing crop by 50% (from *c.* 2200 to 1100 g m^{-2}). This resulted in an 80% decrease in invertebrate abundance and biomass and a 78% decrease in total secondary production. Functional feeding groups responded differentially during the experiment; shedders, gatherers, total primary consumers and predators declined significantly, while scrapers and filterers did not.

Riparian arthropods are also important energy sources to stream secondary consumers, especially fishes (Cloe & Garman, 1996). Arthropods fall into streams from overhanging foliage. The flux of arthropods is proportional to their abundance in the canopy (Nakano & Murakami, 2001). In the per unit channel area, inputs are higher in smaller streams flowing beneath a closed riparian canopy. Substantial inputs, however, occur at the channel margins of larger streams and rivers. Once in the aquatic system, riparian arthropods are consumed by drift foraging fishes. In a northern Japanese stream, riparian arthropods accounted for 46% of the diet of rainbow trout *Oncorhynchus mykiss* (Walbaum), 51% for white-spotted charr *Salvelinus leucomaenis* (Pallas) and 57% for masu salmon *Oncorhynchus masou* (Brevoort). Terrestrial arthropods have also been found as a significant component of the stomach contents of redbreast sunfish *Lepomis auritus* (L.) and bluegill *Lepomis macrochirus* (Rafinesque) (Cloe & Garman, 1996). Consumption of terrestrial prey by aquatic consumers is viewed as an energy subsidy to aquatic food webs and the energy derived from riparian arthropods sometimes exceeds that available from aquatic arthropods.

These subsidies may also be reversed from the aquatic to riparian environment. Further, the magnitude of the subsidy can be dramatically altered by historic fisheries management, such as the introduction of exotic salmonids. For example, Baxter *et al.* (2004) found that the introduction of non-native trout (*O. mykiss*) resulted in a 65% decline in spider populations in the riparian forest. A large portion of the spiders' diet was comprised of emerging aquatic insects from the stream. Native white-spotted charr primarily consumed terrestrial insects falling into the stream from the riparian forest. In the presence of non-native rainbow trout, the white-spotted charr altered their foraging behaviour to consume grazing invertebrates, thereby releasing benthic algae from herbivory. Collectively, the white-spotted charr and rainbow trout reduced the amount of emerging invertebrates, and thus, restricted the food supply for riparian spiders.

THE RIPARIAN ZONE IS FISH HABITAT

As illustrated in the previous principle, riparian vegetation has strong and direct influences on fishes. Fishes, obviously, do not inhabit the riparian zone, except perhaps during overbank floods (Junk *et al.*, 1989). In spite of this, are the

linkages between riparian zones and fishes so strong that the riparian zone can be considered fish habitat? It is suggested that the consequences of inputs of food and large wood on stream structure and productivity are sufficiently strong to qualify the riparian zone as fish habitat.

The role of large wood debris (LWD) in shaping fish habitat in streams and along lakeshores is well known. The interplay between LWD, organic matter and sediments enhance the productivity of many organisms by creating resource-rich aquatic habitats. The LWD encourages retention of particulate organic material, where it can be processed and utilized by aquatic invertebrates (Bilby & Likens, 1980; Bilby, 1981). Likewise, in streams, LWD can slow the downstream transport of spawning substratum, which can benefit fish production (House & Boehne, 1986). Some fishes benefit from the energetically profitable habitat (Fausch, 1984) within backwater pools, side channels and eddies flanking marginal LWD 'jams' (Moore & Gregory, 1988). Pools created by LWD may contribute to fish productivity by providing refuge during climatic extremes, cover from predators, and encouraging habitat portioning among sympatric species (McMahon & Hartman, 1989; Reeves et al., 1997). Fishes and aquatic invertebrates often decline after LWD removal (Elliott, 1986; Fausch & Northcote, 1992) and increase (at least locally) in response to LWD additions (House & Boehne, 1986; Wallace et al., 1995; Cederholm et al., 1997; Roni & Quinn, 2001). These contrasting responses underscore the functional importance of LWD, which extends beyond the margins of riparian forests to streams. Increasingly, management strategies are now designed to protect existing sources of LWD and promote sustained future inputs of LWD in historically depleted streams.

As previously noted, riparian habitat is equally important in directly supplying food for stream fishes. Allan et al. (2003) observed substantial inputs of terrestrial invertebrates (i.e. 80 mg m^{-2} day^{-1}) in streams of south-east Alaska. Juvenile coho salmon Oncorhynchus kisutch (Walbaum) living in these streams relied upon these inputs for approximately half of their diet. Additional experimental evidence from Japan shows that withholding arthropod inputs from streams has consequences that reverberate through aquatic food webs and ultimately upset the basic composition of the stream community (Nakano et al., 1999). Dramatic consequences at the system-scale are apparent within weeks after blocking the influx of riparian arthropods, effectively removing arthropods from the diet of dolly varden Salvelinus malma (Walbaum). These fish, which are primarily drift foragers consuming riparian arthropods and drifting aquatic arthropods, shift to active foraging and significantly reduce the biomass of benthic aquatic herbivorous arthropods when denied riparian-derived insects [Fig. 2(a)]. The reduction in benthic herbivorous arthropods leads to a concomitant increase in periphyton biomass [Fig. 2(b)] and, like Baxter et al. (2004) found in the same stream, fundamentally shifts the stream's community structure and composition. Although the loss of riparian arthropods to stream ecosystems is minor compared to the energy flux in leaf litter, the shift in predator dynamics reverberates throughout the system, significantly impacting community-based functions. In effect, the riparian 'habitat' substantially influences the fish population and the stream community structure in a manner that is difficult to differentiate from in-stream habitat.
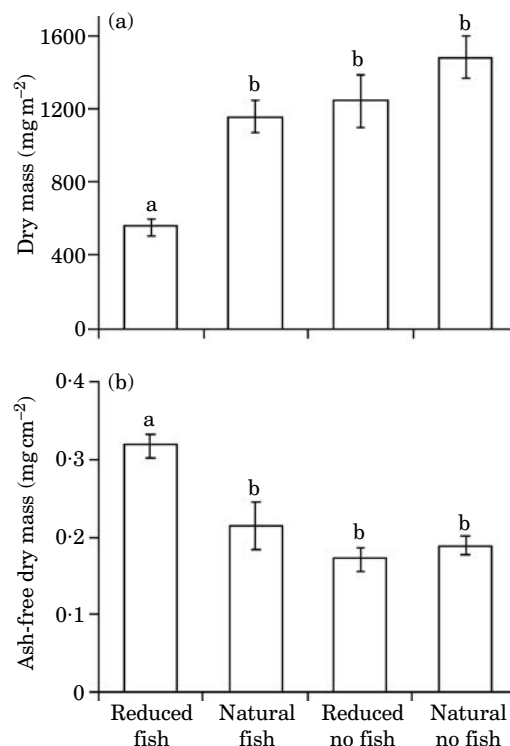
FIG. 2. Biomass (mean ± 1 S.E.) for (a) aquatic herbivorous arthropods and (b) periphyton for four experimental treatments: reduced riparian arthropod input with fish present, natural riparian arthropod input with fish present reduced riparian arthropod input with fish absent and natural riparian arthropod input with fish absent. Significant differences are indicated by the lower case letters above the bars (from Nakano *et al.*, 1999, with permission).

FISHLESS HEADWATER STREAMS ARE INSEPARABLE FROM FISH-BEARING RIVERS DOWNSTREAM

Much of the sediment, organic matter and water that shape habitat attributes in fish-bearing rivers originated in fishless streams. Headwater streams have an intimate relationship with terrestrial systems, and thus play an important role in controlling the impacts of land use activities on downstream aquatic resources and habitat (Lowe & Likens, 2005; Richardson *et al.*, 2005). These small streams occupy the headmost position in a drainage network, but are not necessarily at high elevation. Many do not contain fishes although they are frequently home to amphibians and other organisms with life cycles that have both aquatic and terrestrial stages. Many headwater streams may only be wetted on a seasonal basis. Even where fishes are absent, these streams are closely coupled to the adjacent hillslopes and riparian forest, and are particularly influential in regulating and processing inputs of energy, nutrients and organic matter. These inputs contribute material to downstream food webs and shape the structural characteristics of fish habitat in distant reaches. Thus, 'fishless' streams are fish habitat in much the same way as the riparian zone.

There is growing scientific recognition of the importance of headwater streams and their riparian zones as unique habitats and as sources (and controllers) of energy, water, sediment, nutrients and organic matter to downstream reaches (Meyer & Wallace, 2001; Gomi *et al.*, 2002; Wipfli & Gregovich, 2002). Yet, many jurisdictions stratify environmental protection primarily by stream size (Young, 2000; Blinn & Kilgore, 2001; Lee *et al.*, 2004). While most jurisdictions require the retention of riparian buffers along larger streams, prescriptions vary dramatically for riparian retention along smaller, usually non-fish-bearing, stream reaches. Some jurisdictions require buffers that extend up to, and sometimes upslope of, the perennial channel network and include intermittent streams (Blinn & Kilgore, 2001), while other jurisdictions do not require reserves along non-fish-bearing streams (unless they are a designated community water source) or even the smaller fish-bearing streams (*i.e.* those <1·5 m bankfull width). The diversity of riparian management standards has provoked increasing debate and highlighted the uncertainties in the current state of knowledge regarding headwater streams and the degree to which they must be insulated from human activity. Despite the scientific uncertainties, the sheer abundance and density of headwater streams, and their landscape position, emphasizes their interconnectedness with downstream fish habitat. Effective management strategies recognize and sustain material linkages between headwater streams and larger rivers, component parts of a single, interacting unit.

HABITATS CAN BE COUPLED IN RIVERS, LAKES, ESTUARIES, AND OCEANS, AND IN TIME

Nearly all aquatic organisms require different habitats to complete their life cycle. As previously discussed the creation and maintenance of discontinuous habitats is subsidized by fluxes of organisms, materials and nutrients, whether in rivers, lakes, estuaries or oceans (Polis *et al.*, 1997). For example, a lake may be regarded as a system of interacting habitats in the vertical, horizontal and temporal dimensions. Most lakes are typically small and there are generally high ratios of edge to volume and perimeter to area. This results in considerable potential for habitat coupling; no single habitat type may dominate. Coupling among various lake habitats is critical for maintaining processes that control overall ecosystem structures and functions, fluxes of organisms and nutrients between the benthos and water column, and movements of fishes from nearshore to pelagic zones (Lake *et al.*, 2000; Schindler & Scheuerell, 2002). Further, the riparian habitat of lakes is almost universally ignored in management and conservation; an oversight with severe implications for the long-term productivity and the ability to support freshwater biodiversity.

Individual fish or fish species follow distinct trajectories through space, but also in time, according to their life history. Thompson (1959) proposed that life histories dictate a chain of habitats arranged in a favourable distribution in both space and time. Mobrand *et al.* (1997) refined these ideas, and suggested that life histories can be defined in terms of co-ordinates in space and time. Considerable variability exists, but fishes evolve behaviours and life history characteristics that maximize fitness by ensuring they will be in the right place at the right time throughout their lifetime. These conditions may vary among rivers and lakes

(with concomitant differences in life history) and can also change over time in a given location. As the physical environment changes, it may cease to provide resources required by a particular species or life stage. The productivity of a fish over its life cycle is determined by the cumulative production in each life history stage. Thus, irregularities in the temporal distribution of favorable habitats, whether over a day, a season or a year, can have significant consequences for fish productivity. Effective management strategies recognize that species depend not only on the existence of suitable habitat, but on the availability of it in the right place at the right time.

HABITATS CHANGE OVER HOURS TO CENTURIES

Daily fluctuations in streamflow, temperature, shade and oxygen affect the distribution and quality of microhabitats. Fishes respond by selecting positions that balance demand for food with energetic costs, predation risk, and competition (Werner *et al.*, 1983; Fausch, 1984; Hubert *et al.*, 1994). Daily flow variability alters the hydraulics, volume, connectivity and spatial configuration of aquatic habitat (van der Nat *et al.*, 2003) with fishes responding to changes in stream hydraulics by actively selecting preferred microhabitats (Fausch, 1992; Shirvell, 1994; Heggenes, 2002). Diurnal patterns in temperature and photosynthesis cause fishes to seek areas with suitable thermal conditions and oxygen levels, particularly in isolated channels and pools (Labbe & Fausch, 2000). Fishes track the movement of shade patches across the streambed to reduce risk from UV radiation damage (Kelly & Bothwell, 2002) and predation.

The distribution and quality of fish habitat also shifts among seasons. Fishes move within systems to detect changing conditions and to select optimal locations (Gowan & Fausch, 2002). For example, increased turbidity during seasonal storms reduces foraging efficiency relative to clear summer low flows (Sweka & Hartman, 2003) and fishes alter their distribution and behaviour to compensate (Bisson & Bilby, 1982). Seasonal flood pulses allow fishes to leave the channel and exploit inundated floodplain habitats (Junk *et al.*, 1989), and fishes may seek refuge from winter floods in tributaries and floodplain sloughs, but re-emerge in spring (Tschaplinski & Hartman, 1983). Differences in the relative amount of autotrophic and heterotrophic production in summer and winter affect food, and thus, habitat quality. Deep pools may provide critical refuge from summer droughts and low winter temperatures (Cunjak & Power, 1986) but those lacking groundwater inputs may become lethal (Labbe & Fausch, 2000). In temperate regions riparian arthropod fluxes to streams are greater during warm months (Mason & MacDonald, 1982; Cloe & Garman, 1996). In tropical regions increased fluxes have been linked to the rainy season when high arthropod productivity coincides with frequent washing of riparian surfaces by floods and precipitation (Angermeier & Karr, 1983).

Fish habitat is clearly a shifting mosaic over years to decades, and perhaps even centuries, particularly in laterally unstable rivers (van der Nat *et al.*, 2003, J.J. Latterell J.S. Bechtold, R.J. Naiman, T.C. O'Keefe & R. van Pelt unpubl. data). Habitat changes at these intermediate scales are thought to have significant consequences on fish communities (Fausch *et al.*, 2002). Lateral instability and ongoing changes in substratum size or elevation of the streambed alters

habitat distribution, abundance, and quality among years within individual reaches (Fig. 3). The resource potential in a particular location may fluctuate dramatically over time, even in unimpaired rivers. Accordingly, some fish hedge their bets over time by developing variation in the duration of their life cycle, or
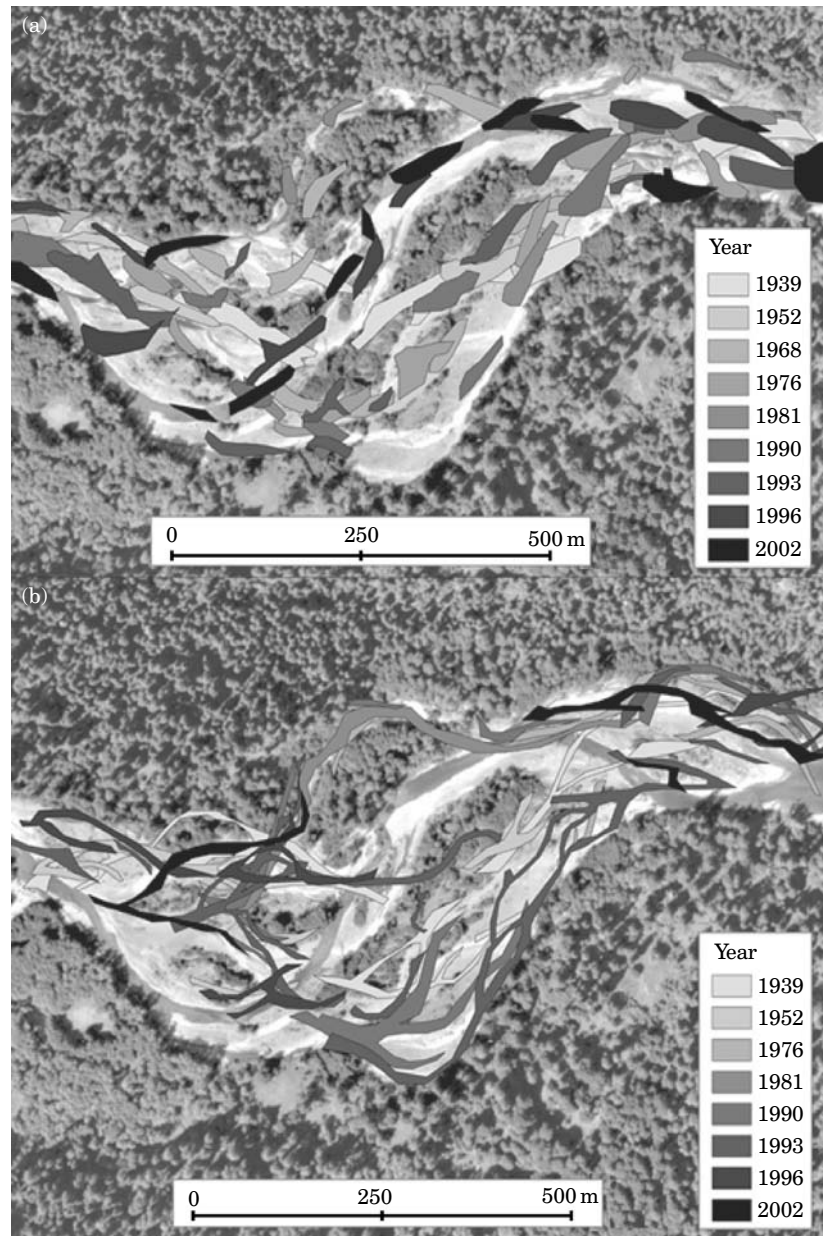

FIG. 3. Shifting habitat mosaics in the mainstem of the Queets River, Olympic National Park, Washington U.S.A. The position of (a) pools and (b) secondary channels are depicted over a time sequence from 1939 to 2002. Fish habitat is not static over space or time. Laterally unstable rivers work constantly to build, destroy and renew fish habitat.

reproduce in multiple years. Combined with short-term strategies for optimizing habitat use (Rosenfeld & Boss, 2001), these long-term strategies ensure fitness by increasing the probability that conditions will be suitable for at least 1 year of successful reproduction. The timing and location of salmonid spawning in rivers of the Pacific Northwest reflects, at least in part, patterns of variation in streambed mobility among channel types (Montgomery *et al.*, 1999). Over centuries or more, fluctuations in precipitation, sediment input rates, or even tectonic uplift may cause river valleys to alternate between erosional and depositional states. Thus, even the present distribution of channel types in a particular basin is unlikely to remain constant into the distant future. Effective management maintains flexibility and adaptability of populations in response to changing habitat conditions, and anticipates the potential consequences of management actions on future conditions.

FISH PRODUCTION IS DYNAMIC DUE TO BIOCOMPLEXITY – IN SPECIES AND IN HABITATS

The value of physically-based fish habitat is not constant over time; it changes with larger environmental conditions such as climate and land use. The 'same' habitat will be more or less productive as surrounding environmental conditions (or biotic communities; Schoenly & Cohen, 1991) change. While it is standard practice to consider uncertainty in estimates of future population abundance, the phenomenon of complex changes in future habitat conditions is rarely considered in management and conservation strategies.

The sockeye salmon *Oncorhynchus nerka* (Walbaum) fishery in Bristol Bay, Alaska, provides a good example of this principle (Hilborn *et al.*, 2003). This stock complex is an amalgamation of several hundred discrete spawning populations. The populations occur in lake systems that have virtually no human-mediated land use, and individual populations display diverse life history characteristics and local adaptations to variations in spawning and rearing habitats. These characteristics and adaptations include spawning phenology, egg and body size and body shape. This environmental and life history variability has enabled the stock complex to sustain its overall productivity despite major changes in climatic conditions affecting freshwater and marine environments during the last century. Different sub-populations with their inherent life history strategies that were minor producers during one climatic regime have dominated during others, despite little apparent change in habitat conditions. This can be seen in the variable number of recruits per spawner for different stocks over a 40 year period (Fig. 4). It appears that population-specific variability in response to climate fluctuations has been responsible for the resilience of the entire Bristol Bay sockeye salmon stock; thereby emphasizing that biocomplexity within fish stocks is critical for maintaining their resilience to change over a range of environmental conditions. This also implies that management and conservation strategies need to take larger and longer views than in the past, and that a range of strategies are needed to effectively address 'good' and 'bad' years in recruitment.

MANAGEMENT AND CONSERVATION STRATEGIES MUST EVOLVE RAPIDLY IN RESPONSE TO PRESENT CONDITIONS, BUT ESPECIALLY THE ANTICIPATED FUTURE

As societies change beliefs and perceptions, and acquire knowledge and experiences, approaches to management and conservation also change. This fact is pervasive in every academic department, management agency, and conservation organization addressing natural resources. In short, they adjust, often albeit slowly, to new information and to evolving beliefs and values. Perceptions may also lag behind advances in knowledge due to skepticism or lack of communication. They often reflect the legacy of historical events, both missteps and successes. The keys to staying on a sustainable course are learning: 1) how to continue learning in a changing world, 2) how to balance ecological principles with evolving social norms (Michael, 1995) and 3) how to adapt quickly to new knowledge and unexpected changes. Even though societal norms do change relatively quickly, people generally value (*i.e.* protect) only what they understand (Nassauer, 1997).

Holling, (1978) and Gunderson & Holling, (2002) have championed the socio-ecological process of adaptive change for nearly three decades. This process essentially entails treating management actions as experiments, and learning from them. It has been discussed and applied in a wide variety of situations with varying degrees of success (Biggs & Rogers, 2003). In a pragmatic world, however, it offers perhaps the best approach for learning, and for formulating better strategies, because effective monitoring and follow-up adjustments are core components (Fig. 5). The challenge for management and conservation is to see that all of components necessary for a successful application are in place for the long-term, as has been widely discussed with regard to terrestrial biodiversity and large charismatic animals (Western, 2000; Berkes *et al.*, 2002).
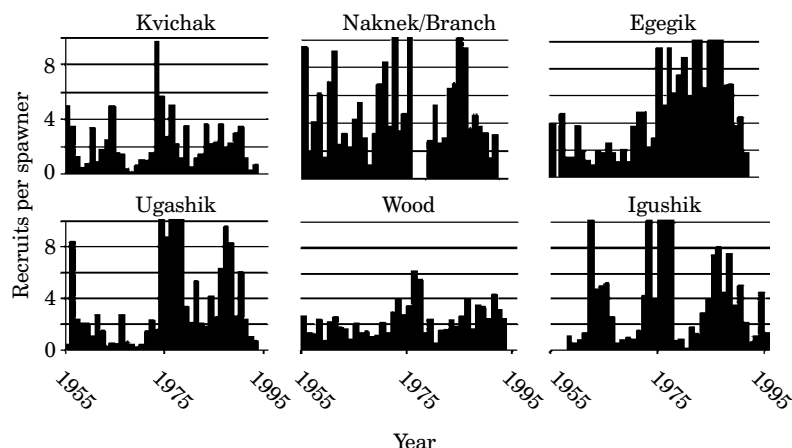

FIG. 4. Number of recruits per spawner for different Bristol Bay sockeye salmon stocks. Values >10 were truncated; the maximum was 27·4 for the Ugashik River in 1978 (from Hilborn *et al.*, 2003, with permission).
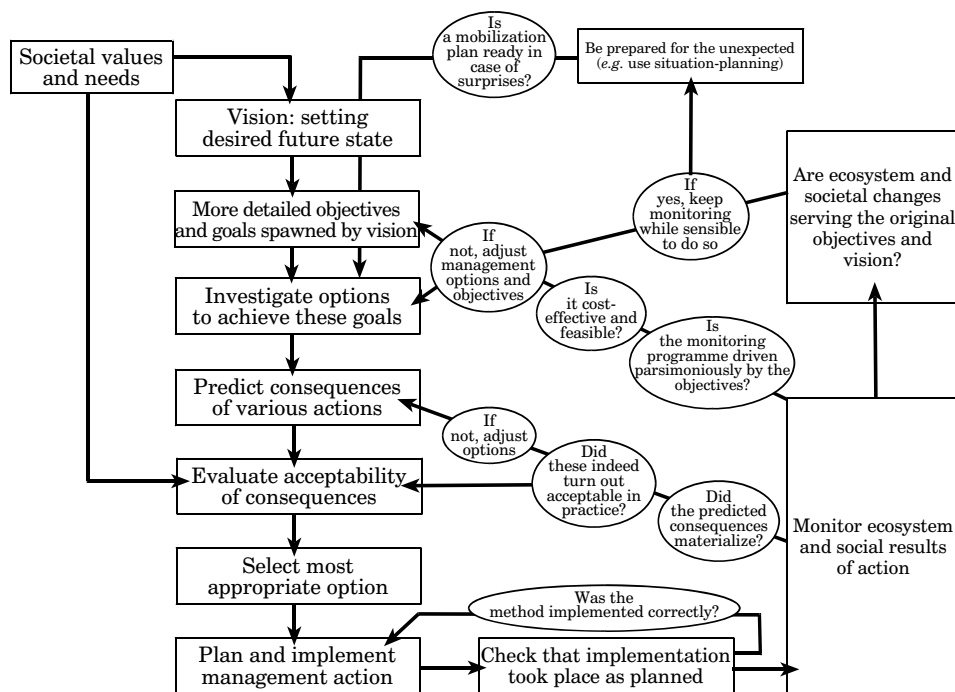
FIG. 5. Generalized version of an adaptive management system, emphasizing feedbacks between objectives, actions and monitoring (modified from Biggs & Rogers 2003).

An example of a successful evolution of management and conservation strategies can be found in Kruger National Park, South Africa (Biggs & Rogers, 2003). This approach evolved out of their 'Rivers Programme' of the 1990s. Kruger developed and implemented a unique version of adaptive ecosystem management (strategic adaptive management) built on recent developments in ecology and business management. For example, new paradigms in ecology stress complex adaptive systems and heterogeneity. Business management now emphasizes that organizations need to continually reinvent themselves through purposeful knowledge diffusion. Establishment of strategic adaptive management in Kruger was favoured by an interaction between certain catalysts and an existing legacy (F.J. Venter, R.J. Naiman, H.C. Biggs & D. Pienaar, unpubl. data). It differs from conventional adaptive management in having a stronger emphasis on the forward-looking component, attempting to operate in a proactive rather than reactive mode. It has a strong goal-setting component evidenced by a well-developed objectives hierarchy (Keeney, 1992) and strongly articulated monitoring endpoints (*i.e.* thresholds of potential concern). The objectives hierarchy and endpoints act as a nexus for connecting science, monitoring and management in an innovative and motivating way. In reality, this is an experiment in progress whose ultimate outcome depends on a number of factors (*e.g.* financial and political), the most important of which is the willingness of regional society to value nature.

CHALLENGES FOR MANAGEMENT AND CONSERVATION

The management and conservation communities, or the conservation management community, are facing several daunting challenges. The habitat principles presented here, are a small, interrelated subset that may be coupled with others to formulate comprehensive guidelines for fish management and conservation strategies. Basically, 1) terrestrial systems need to be embraced as part of fish habitat (and sometimes *vice versa*), 2) fish habitat evolves in both spatial and temporal dimensions, at a variety of relevant scales, 3) the life-histories of organisms have evolved and continue to evolve in response to habitat alterations and 4) successful management and conservation strategies plan for future habitat changes. The long-term resilience of fish communities in catchments shared or affected by humans probably depends on incorporating these principles into management and conservation strategies. Of course, the principles will evolve greater generality and accuracy as additional knowledge and wisdom are acquired about the habitat requirements of fishes and the systems supporting them. Clearly, traditional management concepts should be re-examined in light of the dynamic nature of habitat, the real extent of the habitat and the evolution of societal perspectives (Wiens, 2002).

Managing for change, especially future changes, is difficult. Yet, the notion of fixed habitat standards must become more flexible, especially since they dimly reflect, and are often not appropriate for, dynamic aquatic environments. Recognizing that aquatic environments are strongly interconnected and change not only spatially but over days, seasons and years provides a useful perspective for successful strategies. Ultimately, the outcomes will be the measures by which the strategies are judged; robust fish communities and the integrity of both ecological and social systems. There are four immediate challenges. Managers must explicitly plan for emerging conditions that will affect fisheries (*e.g.* climate change, population growth and surprises). Practical approaches for linking science and management that transcend cultural beliefs must be implemented. The public and decision-makers must be instructed (and be willing to learn) what is needed to sustain fish habitat for the long-term. The final challenge is to incorporate a philosophy that embraces variability (*e.g.* heterogeneity) in time and in space. These are not trivial challenges because they run counter to many traditions and beliefs, and firmly rooted protocols. Their resolution requires innovation and ingenuity. Nevertheless, they are challenges that can and must be met.

Forward-thinking fish management and conservation plans, and many aquatic scientists, view fish habitat as more than water. These plans are multilayered; ranging from pools to catchments to ecoregions, from hours to seasons to centuries. They embrace, as a fundamental premise, that habitat evolves through both natural and anthropogenic processes and that patterns of change may be equally important as any other habitat attribute. Yet most scientists and managers recognize that the most daunting obstacles to implementing new approaches are embedded in the social formulation and application of regulations, rather than a lack of scientific knowledge. How might the link between science, management and application be strengthened but also gain support from social leaders and the public? As one option, a well-articulated and

well-publicized report from respected international organizations may be an effective catalyst. It may be timely for the Fisheries Society of the British Isles and the American Fisheries Society to consider joining with the U.K. Royal Society and the U.S. National Academy of Sciences, and others, to collectively lead and support an effort to formulate a shared habitat vision and strategy for scientists, managers and society in the near-future.

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