Effect of a Change in Physical Structure and Cover on Fish and Fish Habitat

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by

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ABSTRACT AND RÉSUMÉ

Smokorowski, K.E., and Pratt, T.C. 2006. Effect of a change in physical structure and cover on fish and fish habitat. Can. Tech. Rep. Fish. Aquat. Sci. 2642 iv + 52 p.

As part of the Risk Management Framework being implemented in DFO's Habitat Management Program (HMP), a series of Pathways of Effects models have been developed to facilitate a more rapid and transparent assessment process. DFO Science Branch conducted literature reviews to validate key end-points (habitat impacts) resulting from development activities; this report covers the effects of a change in physical structure and cover on fish and fish habitat. Each year the HMP processes thousands of referrals proposing to alter the physical structure and cover of fish habitat. In the absence of clear quantitative guidelines linking the change in habitat to productive capacity, habitat mangers often use the change in habitat area as a basis for decisions. To assess the weight of scientific evidence in support of management decisions, we summarized both the observational and experimental fish-habitat literature. We found relatively strong and consistent correlational evidence linking fish and physical habitat features, yet inconsistent evidence in the experimental literature. On the whole, large decreases in structural habitat complexity are detrimental to fish diversity and can change species composition. Increases in structural complexity showed increases, decreases, or no measurable changes in species and/or communities. Decisions are most likely to affect individual species or community structure, and thus evaluating the extent of the effect on a biological basis depends on management objectives.

À l'occasion de la mise en œuvre du cadre de gestion du risque dans le cadre du Programme de gestion de l'habitat du MPO, une série de modèles de séquences des effets a été mise au point afin d'accélérer le processus d'évaluation et de rendre celui-ci plus transparent. Le Secteur des sciences du MPO a effectué des revues de la littérature afin de valider les principales conséquences (effets sur l'habitat) d'activités de développement. Le présent rapport porte sur les effets d'un changement de la structure physique et de la superficie sur le poisson et son habitat. Chaque année, des milliers de propositions de modification de la structure physique et de la superficie de l'habitat du poisson sont traitées dans le cadre du Programme de gestion de l'habitat. En l'absence de lignes directrices quantitatives claires reliant le changement de l'habitat à la capacité de production, les gestionnaires de l'habitat basent souvent leurs décisions sur le changement de la superficie de l'habitat. Pour évaluer le poids des preuves scientifiques à l'appui des décisions de gestion, nous présentons un résumé de la littérature sur les études et les observations relatives à l'habitat du poisson. Nous avons constaté une corrélation relativement forte et uniforme entre le poisson et les caractéristiques physiques de l'habitat, mais également des preuves contradictoires dans la littérature expérimentale. Dans l'ensemble, d'importantes baisses de la complexité de la structure de l'habitat ont des effets néfastes sur la diversité des poissons et peuvent entraîner des changements de la composition en espèces. Une hausse de la complexité sur le plan structurel donne lieu à une augmentation, à une baisse ou à aucun changement mesurable à l'échelle des espèces ou des communautés. Les décisions ont plus de chances d'avoir des conséquences sur certaines espèces ou sur la structure de communautés. Par conséquent, l'évaluation de l'ampleur des effets sur le plan biologique dépend des objectifs de gestion.

1. Background

Within Fisheries and Oceans Canada (DFO), the Habitat Management Program (HMP) is a key federal regulatory program with the mandate to conserve and protect fish habitat under Canada’s Fisheries Act. In 2004-2005, the Habitat Management Directorate implemented the Environmental Process Modernization Plan (EPMP) which is intended to provide more efficient and effective delivery of its habitat responsibilities, including improved predictability and timeliness in decision making regarding proposed developments. The EPMP is integral to the Government of Canada's "Smart Regulation" initiative by creating a more modern regulatory system that provides decisions in a more timely, efficient and effective manner. The key element in this ‘plan’ is the development and implementation of a science-based Risk Management Framework (RMF). This framework sets out a series of principles and practices used to evaluate development projects with the potential to affect fish habitat. The RMF is intended to ensure that project proposals (referrals) are evaluated in a consistent and transparent fashion and that Program resources can be re-allocated from the review of routine, low risk activities, to the review of projects with the greatest degree of risk to fish habitat.

A major underpinning of the Risk Management Framework is the development and validation of a series of Pathways of Effects (PoE) diagrams that describe the cause-effect linkages between a development activity and a habitat impact (see Jones et al. 1996; ‘hypothesis of effects’ diagrams). These diagrams are essentially a logical map (flow chart) that begin with a development activity, which leads to a series of qualitative changes in fish habitat (e.g. sediment increases, flow alterations, removal of riparian vegetation) which can be linked to changes in biological productivity (e.g.reduction in food availability, etc.- the effect). DFO’s habitat biologists and proponents are to use these PoEs to assess the potential effects from any given project. These PoE diagrams would also assist the proponents develop mitigation plans to avoid the negative effects of a given activity, where possible. To date the Habitat Management program has conceptually developed 21 PoE diagrams for land based (10) and in-water (11) activities.

The Habitat Management Program requested that Science Branch conduct a detailed scientific literature review to support and validate the cause-effect relationships within each Pathway of Effect. In reviewing the PoE diagrams it became apparent that there was considerable overlap in the cause-effect linkages between a variety of activities and the physical environmental (habitat) change, as the end point. For example, a change in sediment concentration is an end point in 14 PoE models. It was decided that Science Branch would therefore conduct the literature review and validation on the end points common to many of the PoEs. The initial focus was on four major endpoints that comprise 70% of all the linkages in the combined set of Pathway of Effects Diagrams, namely: (1) change in sediment concentrations, (2) change in habitat structure and cover, (3) change in water temperature, and (4) change in dissolved oxygen concentrations.

The literature review and validation were to consider the severity, reversibility, frequency, and duration of the effect. The reviews were also to document the fish species affected, the ecotype that the effect could be characterized for, and geographic extent of the documented relationships. The effects were to be characterized over multiple spatial and temporal scales, where possible, and were to consider individual effects, population level effects and habitat ‘function’, effects. The focus was on peer reviewed literature relevant in the Canadian context (literature from other countries was to be included if deemed relevant to species and ecotypes within Canada).

Three working papers/reports were developed, and subsequently presented at a DFO National Workshop Meeting to determine the scientific validity of the four reviewed endpoints. The participants, including both DFO scientists and academic researchers, conducted an impartial and objective scientific peer review of the working documents. The key conclusions (scientific information/advice) from this meeting have been documented in a Canadian Science Advisory Secretariat (CSAS) Proceedings report (DFO 2006). The working paper on change in habitat structure and cover is published as this report. A companion report on change in sediment concentrations has also been published (Robertson et al., 2006).

2. Introduction

One of the most consistent outcomes resulting from a development activity in aquatic ecosystems is a change in the available structure and cover. Because a physical effect is often the most simple to predict and to measure, it is also the effect upon which habitat biologists most frequently make decisions for compensation (e.g. creation of like-for-like habitat as close to the perturbation as possible, often in a ratio > 1 to allow for the expected reduced productivity of new habitat (Lange et al. 2001)). However, of all the potential effects on the productivity of aquatic ecosystems that could result from development activities (e.g. change in temperature, suspended sediment, nutrients), quantifying the effects of changes in structure and cover is the most elusive. This is possibly because the response of fish species to habitat change can depend on a number of factors including (but not limited to) geographic region, temperature, season, life stage, the presence or absence of other species and relative availability of habitat. Fish populations can also exhibit compensatory responses (e.g. changes in growth, fecundity, age-at-maturity and sex ratio) when stressed, making population-level changes difficult to detect. Compensation decisions are largely made on the basis of square meters of habitat, but whether or not they are effective in achieving no net loss of productive capacity is uncertain and often unmeasured.

It is nevertheless important that decisions continue to be made despite uncertainty, and that available information is summarized for efficient use by habitat biologists in their decision making efforts. Numerous habitat preference literature reviews exist, particularly for more valued species. Relatively strong, consistent evidence exists in the correlational literature that links fish with specific habitat features. In an attempt to strengthen observational evidence, researchers have manipulated fish habitat with the expectation that fish would respond in a predicable way, reflective of observed preferences. Experiments that manipulate physical structure and cover of fish habitat in a controlled, referenced, rigorous experimental design are rare, as are programs to quantitatively monitor results of management decisions. In this review we summarized observational literature available from searchable, published sources which can be applied in a Canadian context that correlate fish with various habitat features to demonstrate their relative value in support of productive capacity. In addition, we summarized knowledge from experiments which directly measured for a response to habitat change, to see if experimental testing supported correlational evidence linking fish to fish habitat.

3. Lotic (Streams/Rivers)

3.1.Morphology and Cover

3.1.1. Observational Evidence

3.1.1.1.Salmonids

A few summaries of the habitat requirements of western salmonids in streams were found including Bjornn and Rieser (1991) and Giannico (2000). Giannico (2000) described ideal coho spawning and nursery habitat as small, low grade coastal streams, with a large proportion of marginal areas, slow-flow, and relatively equal proportions of alternating riffles and pools. Using survey data from 119 coastal stream sites in B.C., Rosenfeld et al. (2000) found that cutthroat and coho densities were highest in very small streams (<5m) with low to intermediate gradients (Montgomery et al. 1999; Rosenfeld et al. 2000). Murphy et al. (1986) found a significant decline in cutthroat parr density with increasing stream size in Alaska.

Numerous studies have demonstrated that salmonid density or biomass (1+ coho, larger cutthroat, and bull trout) was highest in pools or deeper channel units relative to other lotic habitat types (Bustard and Narver 1975a; Glova, 1984; Bowlby and Roff, 1986; Murphy et al. 1986; Heggenes et al. 1991; Fausch and Northcote, 1992; Saffel and Scarnecchia 1995; Rosenfeld et al. 2000). Some habitat use studies state that pools or cooler tributaries are essential for rearing juvenile coho salmon (Stein et al. 1972; Bisson et al. 1988b; Bugert et al. 1991), and that they use instream structures, such as rocks and logs, as water current shelters to minimize the energy costs associated with maintaining position in the stream while feeding on drifting food (Mundie, 1969; Fausch 1993). In a survey of 1057 sites from 93 streams within 18 major drainages in the north-western U.S., Watson and Hillman (1997) found the highest relative densities of bull trout in stream areas with the deepest pools. It is believed that deeper pools provide more of the microhabitat features important to salmonids, such as cooler water temperatures, lower water velocities, cover and protection from predation.

Habitat preference or use can be dependent on age-class and the level of predation or competition. Observationally, age-0 cutthroat density was found to be lower in pools and highest in shallow habitats (Bustard and Narver 1975a; Glova 1984; Rosenfeld et al, 2000), yet in a habitat preference experiment in the absence of predation and competition, age-0 cutthroat preferred pools, and demonstrated increased growth rate in pools relative to riffles (Rosenfeld and Boss 2001). The same study found larger cutthroat trout grew in pools but observed negative growth rates in riffles; bioenergetics analysis demonstrated that food intake vs. swimming cost in riffles resulted in a negative net energy gain for larger trout in riffles. Energetically age-0 were not dependent on pools but larger trout were (Rosenfeld and Boss 2001). In a small stream in Oregon, Kruzic et al. (2001) found age-0 coho survival to be significantly lower in riffles (27%) vs. pools (67%) but that growth rate did not differ between habitat types. In a study of the distribution, growth and survival of fish species common to Washington streams in four depth and structure treatments, Lonzarich and Quinn (1995) found that shallow pools with the least structure were underutilized. Subsequent modelling determined that mortality (due to predation) in shallow, simple pools was 50% greater for water column dwelling fish than other treatments, but that mortality of benthic species was not affected, emphasizing the importance of a community level approach in studies.

Habitat preference or use can also be season dependent. Studies from the Pacific Northwest found that juvenile coho salmon prefer pool habitats during summer and off-channel areas (low velocity tributaries) and pools (alcoves and beaver ponds) with cover during winter to increase survival (Bustard and Narver 1975a; Peterson 1982; Tschaplinski and Hartman 1983; Swales et al. 1986; Nickelson et al. 1992a; Solazzi et al. 2000). Swales and Levings (1989) corroborated the winter use of off channel ponds by juvenile coho, but found that they could provide important refuge and rearing areas in summer as well. Bustard and Narver (1975a) found that depth occupied by coho and age 1+ steelhead was negatively correlated with water temperature below 8.5°C, a behaviour believed to reduce temperature and flow related stress. Some researchers have suggested that freshwater production of coho salmon is primarily controlled by the amount of available winter habitat (Mason, 1976; Hartman et al. 1996; Solazzi et al. 2000), and that creating off channel ponds or side channels could be an inexpensive technique to improve winter habitat (Hartman et al. 1996). In contrast, juvenile coho in Lake Superior tributaries were found to occupy main-channel pool habitat in winter, regardless of level of habitat complexity, possibly due to the less severe (flow, temperature) conditions encountered in the Great Lakes region relative to the Pacific Northwest (Ford and Lonzarich 2000; Healy and Lonzarich 2000).

Wintering coho, Dolly Varden and steelhead were found in pools with cover but not in pools, riffles, or glides without cover (Heifetz et al. 1986). Hillman et al. (1987) observed that age-0 chinook salmon associate with undercut banks in summer, move to faster, deeper water as they grew, and that 80% emigrated from study sites in winter. Those that remained used overhanging undercut banks with submerged sedges and grasses and where water velocities were less than 12 cm/s (Hillman et al. 1987). Heggenes et al. (1991) found that cutthroat preferred areas with overhead cover exceeding 40% local surface area, and that cover, velocity, and substrate use did not vary by season, but larger deeper pools were used less during winter than summer. However, cutthroat trout were retained at similar rates in pools with and without large woody debris in a California creek in all seasons but spring, but overall, substantial movement of trout was measured indicating management of populations should occur over large spatial scales (Harvey 1998). While coastal cutthroat use off-channel habitat extensively in winter (Bustard and Narver, 1975a; Peterson 1982; Cedarholm and Scarlett 1991), Swales and Levings (1989) found that steelhead do not move to off-channel habitat in winter. Availability of winter habitat can be a population bottleneck, for example, brook trout fry production was found to be extremely high in a southern Laurentian stream, though insufficient flows and a lack of deep pools resulted in extremely high winter fish mortality (Côté 1970, cited in Burgess 1985). It is important that seasonal habitat needs be considered in any habitat enhancement effort.

Studies have found that lateral habitats (characterized by slow, shallow-water, abundant detritus and benthic invertebrate assemblages of high density) are occupied by the fry of brook trout, rainbow trout and Atlantic salmon (Keenleyside 1962; Symons and Heland 1978), coho and chinook salmon (Lister and Genoe 1970; Everest and Chapman 1972) and cutthroat trout (Bustard and Narver 1975b; Moore and Gregory 1988a). In an artificial stream, larval grayling were found to prefer lateral habitat of specific slopes and depths depending on time of day, likely due to diurnal behavioural patterns (Sempeski et al. 1998).

From their survey of 118 streams, Stoneman and Jones (2000) developed models to predict habitat use and productive capacity of brook, brown and rainbow trout in southern Ontario streams. They found that generally, small substrate and plentiful cover favour brook trout; large substrate, riffles, and limited cover favour rainbow trout; and intermediate substrate, pools, and the presence of other trout favour brown trout. The results suggest that certain habitat attributes, most notably temperature, abundance of pools, substrate, and cover have a predictable effect on the biomass and species of trout found in southern Ontario streams. Their findings are consistent was an earlier, similar study by Bowlby and Roff (1986).

Studies of the habitat preference differences between brook charr and Atlantic salmon have generally found that brook char prefer deeper, slow flow habitats, whereas Atlantic salmon prefer shallower, higher velocity habitats (Gibson 1978; Gibson et al. 1993; Rodriguez 1995; reviews in Hearn 1987; Fausch 1998), and that they segregate spatially when occupying the same reach (Gibson et al. 1993; Rodriguez 1995). Similarly, in Newfoundland, brook trout and introduced rainbow trout were found to have different cover and velocity preferences similar to the separation of brook trout and Atlantic salmon (Cunjak and Green 1983). In Norway, brown trout and Atlantic salmon were also similarly separated spatially by velocity and depth (Heggenes and Saltveit 1990). In a study to determine local movement and habitat preference of brook charr and Atlantic salmon in eastern Quebec, the ranking of habitat quality for charr (pools ≥ glides > riffles) and salmon (riffles > glides > pools) was in agreement with other literature (Belanger and Rodriguez 2002). Gibson (1978) and Heggenes (1990) reported that juvenile Atlantic salmon and brook trout were often associated with cover, such as rubble, shade, floating foam or surface turbulence. Yet in a New Brunswick creek, Rimmer et al. (1983) found that juvenile Atlantic salmon occupied uncovered positions above the streambed in summer, only moving to shelter in the substrate in autumn; in both seasons, runs were preferred. Heggenes et al. (1990) found that assessments of habitat use of brown trout and Atlantic salmon depended on the method of assessment. Overhead or diving observations were most effective in slow areas without turbulence, whereas electrofishing was most effective in faster flow; effectiveness of method could alter reported habitat preferences (Heggenes et al. 1990).

In a snorkelling study of winter habitat use of age-0 Atlantic salmon and parr in Vermont, Whalen and Parrish (1999) determined that while the entire range of available depth was used, velocity use was restricted. Large instream cover that provided refuge from high velocity was hypothesized to be important to over winter survival (Whalen and Parrish 1999). Hiscock et al. (2002) found that winter habitat use was dependent on type of behaviour by juvenile Atlantic salmon in a Newfoundland river. Telemetry tracking of 10 juvenile salmon found that salmon in an active state (nocturnal only) used predominantly cobble-gravel substrates in higher velocity areas, whereas fish in an inactive state used predominantly cobble-boulder substrate (Hiscock et al. 2002). The principle variables influencing habitat use of Atlantic salmon are believed to be nose velocity in the summer (DeGraaf and Bain 1986, Morantz et al. 1987) and substrate size and water depth in autumn (Rimmer et al. 1984). Cunjak et al. (1998) reported that interannual variability in summer Atlantic salmon parr abundance was mainly explained by winter survival, which was strongly related to winter discharge (higher stream flow in winter leading to increased habitat availability under ice and greater survival).

3.1.1.2.Non-Salmonids

In an observational study of a low-gradient, prairie-margin stream with 14 adjacent pools in Oklahoma, Matthew et al. (1994) reported on the composition and consistency of fish assemblages. Correlation of species abundance indicated that generally many pools contained one of 2 assemblages: either high numbers of large Micropterus and large Lepomis, or many minnows and small sunfishes although there were some exceptions. Larger taxa were more consistent over time than smaller species in their distribution among pools, possibly because they have difficulty crossing shallow riffles separating pools, or their ability to prey upon or dominate small taxa. This also agrees with the known affinity of centrarchids for home pools, particularly in summer (Munther 1970; Berra and Gunning 1972). Other studies have found that pool availability is a key component of fish-habitat quality in warmwater streams (Schlosser 1987; Ebert et al. 1991 abstract only; Shields and Hoover 1991; Lobb and Orth 1991).

Sowa and Rabeni (1995) examined 23 sites on 19 streams in the Ozark border region of Missouri over 2 summers studying smallmouth and largemouth bass. They found most of the variability in density and biomass was explained by maximum summer temperature and percent pool area for both species. Smallmouth were negatively associated with temperature and pool area whereas largemouth were positively associated, suggesting that human activities have altered stream environments to favour largemouth bass. McClendon and Rabeni (1987) investigated relations between habitat variables and smallmouth bass and rock bass in multiple sites of a Missouri river. The variability in biomass (56%) and density (62%) of smallmouth bass was best associated with undercut banks and boulder substrate; the variability in biomass of rock bass was best associated with boulder substrate and vegetation (54%) and variability in density of rock bass with cobble and boulder substrate (49%). Other studies of habitat preference have shown that smallmouth bass prefer boulder and gravel substrates, logs, root wads, and undercut banks (Munther 1970; Probst et al. 1984; Todd and Rabeni 1989), and rock bass prefer root wads and logs (Probst et al 1984).

Many warmwater species are apparently positively affected by the presence of woody debris than in its absence (Talmage et al. 2002; Dolloff and Warren 2003). Quist and Guy (2001) found growth rates of some species (creek chub, green sunfish, not central stoneroller) significantly correlated with woody habitat availability in Kansas. Tillma et al. (1998) found that the area of root wad and undercut bank habitat explained over 60% of the variation in the relative abundance and biomass of spotted bass in Kansas streams. In Illinois streams, Putman et al. (1995) found that pools negatively affected channel catfish growth, but that the percent instream cover positively influenced channel catfish and small rock bass growth.

Nelson and Franzin (2000) studied habitat preference of 11 species in the Assiniboine River, Manitoba. Depth preferences were available (white sucker, golden redhorse, shorthead redhorse, silver redhorse, quillback, carp, goldeye, mooneye, walleye, sauger, and freshwater drum).

3.1.2. Experimental Addition

The role of channel morphology (width, depth, % pool, gradient) and cover in shaping fish community structure, distribution, and health has been the focus of many experimental research programs. Habitat features in lotic systems often are interdependent, confounding the isolation of any one factor when attempting to establish a cause and effect relationship between an activity altering physical habitat and a corresponding change in biota. For example, the placement of small dams formed from natural materials (e.g. large logs, rocks), generally have the compound effect of forming pools, increasing side channel habitat, and providing instream cover (Shetter et al. 1946; Burgess and Bider 1980; Crispin et al. 1993; Riley and Fausch 1995; House 1996; Cederholm et al. 1997; Reeves et al. 1997; Solazzi et al 2000; Collins et al. 2002; Zika and Peter 2002; Johnson et al. 2005). The role of woody debris has received significant attention since wood is the dominant pool forming mechanism in many small streams (Fausch and Northcote 1992; Ralph et al. 1994; Richmond and Fausch 1995; Rosenfeld et al. 2000), and has been shown to create deeper pools than those created by other mechanisms (Rosenfeld et al.

2000). While the addition of large woody debris to intermediate (Beechie and Sibley 1997) and low-gradient sand substrate streams can cause substantial pool formation, wood addition to high gradient streams dominated by large substrate can result in little change in habitat structure (Hilderbrand et al. 1997). Design specifications for a variety of instream channel structures intended to improve habitat of modified stream channels are available (Shields 1983), although reviews of the physical durability of structures have found high occurrence of damage or failure (House and Boehne 1986; Frissel and Nawa 1992; House 1996; Smokorowski et al. 1998). Because of interdependent and complex interactions resulting from alteration of physical habitat, in the following section we will not separate morphology and instream cover, but we will describe the biotic response to deliberate actions by resource managers or researchers.

3.1.2.1. Salmonids

Salmonid populations have been highly studied in regard to their stream habitat needs and response to placement of instream structures. Experimental design problems are frequent with a lack of reference sites, seasonal coverage, and narrow temporal scope (Roni et al. 2002). Of 29 instream habitat restoration projects, 12 of which demonstrated significant increases in juvenile salmonid abundance, only five were monitored beyond 5 years (House 1996; Cederholm et al. 1997; Reeves et al. 1997; Solazzi 2000). Ambiguity remains regarding the absolute nature of the change (redistribution of existing fish or increased production) or the sustainability of population response. A review of 13 projects designed to enhance instream structural cover (Smokorowski et al. 1998) found that only 2 measured fish production, and while both measured increases at the site of the enhancement, monitoring reference/reduced habitat reaches found a decrease in fish production which ultimately balanced the total production in the streams to no net change (Hunt 1974, 1976; Moore and Gregory 1988b).

Bayley (2002) reviewed 441 abstracts, 30 full papers, and 7 reviews on responses of salmonids to habitat change and concluded that due to poor experimental design, analysis flaws and biased density estimates, current monitoring programs of stream habitat restoration would either 1) fail to indicate an improvement at the watershed scale or 2) show improvement, but fail to demonstrate which and how habitat changes were responsible. Clear demonstration of cause-and-effect relationships at scales appropriate for populations will be elusive, even with well designed field experiments, and while using long-term, multi-stream studies to develop strong inference is feasible, no good examples were found (Bayley 2002). Similarly, Roni et al. (2002) conclude from their review of 93 papers that little is known about the effectiveness of most restoration techniques. Chapman (1995) examined instream habitat structural modifications in the Columbia River basin and concluded that failure to commit adequate money and time to monitoring programs has resulted in managers relying on faith, inference, and deduction to assume a biological benefit and to justify the continuation of the practice. Nonetheless, we decided to summarize results from specific studies to facilitate assessment of the utility of habitat enhancements, but caution should be employed when weighing the following specific results in management decisions.

Results from habitat improvement projects were varied and ranged from little or no response (Beschta et al. 1994, Chapman 1995), to increased biomass or abundance of some species at some life stages. An examination of 20 large woody habitat placement projects in western Washington and Oregon streams revealed significantly higher densities of juvenile coho salmon in treated reaches than in control reaches during summer and winter, and significantly higher densities of juvenile cutthroat trout and steelhead during winter (Roni and Quinn 2001).

The differences in seasonal response both within and among species appeared to be due to differences in species-specific seasonal habitat preferences. The addition of large woody material and the creation of alcoves (i.e. small ponds excavated adjacent to the stream channel) in Oregon streams increased juvenile coho salmon winter densities and overwinter survival, and increased numbers of summer juvenile coho and smolts, but there was no effect on steelhead (Solazzi et al. 2000). House (1996) found increased juvenile coho salmon densities, and Cederholm et al. (1997) reported a significant increase in coho smolt yield and increased abundance of juvenile coho in winter after placement of instream log structures in Oregon and Washington, respectively. Results for steelhead were less definitive, with age-0 showing some improvement at sites of enhancement, whereas age-1 steelhead showed no change in abundance before or after the study, among sites or seasons (Cederholm et al. 1997). Johnson et al. (2005) found an increase in juvenile coho and steelhead survival after wood addition in a 10-year study of Oregon streams (experimental vs. reference). Crispin et al. (1993) indicated that coho salmon spawner abundance in Elk Creek, Oregon, increased four-fold in the years following placement of instream structures, whereas spawner abundance elsewhere in the river basin remained the same or decreased during the study.

The creation of new off-channel ponds successfully increased winter survival of coho salmon (Cederholm and Scarlett 1991) but produced little response in Chinook salmon (Richards et al. 1992) or other salmonids. Yet, an experimental increase of 2.4 times the lateral habitat over control areas resulted in a 2.2 times greater density of age-0 cutthroat trout (Moore and Gregory1988b). Nickelson et al. (1992b) concluded that the development of off-channel habitat has the greatest potential to increase production of coho smolts in Oregon coastal streams. From their review, Roni et al. (2002) concluded that optimal depth, morphology and design of off-channel habitats are unknown. However, Peterson (1982) found higher survival in deeper ponds (78% in deep versus 28% in shallow ponds), but higher growth in shallow ponds (49% deep versus 94% in shallow). Lister and Finnigan (1997) suggested restricting pond area to 0.1 - 0.3 hectares, providing ample woody debris for cover and providing a variety of depths, among other citing and construction considerations.

The hypothesis that a variety of factors ultimately influence fish habitat selection was highlighted in studies of the response of B.C. juvenile coho salmon to experimental manipulations of food level and wood density in natural streams in summer (Giannico 2000), and to manipulations of wood density in artificially created side channels with differing winter temperature regimes (Giannico and Hinch 2003). In the former study, food level was the dominant factor in determining density of coho in pools and their response to density of woody debris. In the latter study, temperature was the dominant factor determining response to wood density: dense wood increased juvenile abundance and spring smolt output in colder surface-fed channels, whereas dense wood decreased spring smolt output in the relatively warmer groundwater-fed channels (Giannico and Hinch 2003).

The addition of smaller bushy woody material at 4 levels of complexity to an experimental stream failed to create pools, aggregate coho salon fry, or alter coho survival or growth over a 15 week observation period (Spalding et al. 1995). The addition of fine woody debris to a small Rocky mountain stream in Alberta did not alter depth or velocity, but did increase density and total biomass of rainbow trout fry (Culp et al. 1996). Because individual biomass and condition factors did not differ, the authors suggest that the structurally complex habitat provided refuge from predators but did not alter the net rate of individual energy gain. In experimental laboratory stream channels, increased habitat complexity providing visual isolation (large stones or plywood) significantly decreased the size of individual territories of rainbow trout, but did not alter population density or individual growth rates (Imre et al. 2002). Another experimental laboratory channel study involving sub-yearling coho salmon and/or steelhead trout, manipulated riparian cover, instream cover, a predator (adult brook trout) and evaluated habitat use and emigration. During the day, coho were higher in the water column mainly in pools, and steelhead were mainly in riffles; the presence of the other species and the presence of predators significantly increased emigration from the experimental units, although in sympatry, total density was greater (Bugert and Bjornn 1991). Fausch (1993) experimentally placed artificial habitat in a natural stream and found that coho showed a strong preference for velocity barriers regardless of level of cover, whereas steelhead gravitated towards habitat with or adjacent to overhead cover and the fastest velocity. More recently, Jones and Tonn (2004) measured increases in density and biomass of Arctic grayling at sites of enhanced structural habitat in an artificial stream channel (NWT), but failed to detect an improvement at the stream scale, and suggested that deficiencies existed at the catchment scale which prevented improvement in grayling production.

Shetter et al. (1946) found that the placement of current deflectors in a Michigan creek resulted in an increase in angler harvest of brook trout. Adding cover to a Montana creek resulted in a greater increase in biomass of rainbow and brook trout per inventory than control sections 2 years post-treatment (Boussu 1954). In a two-year study of a south Laurentian stream, Burgess and Bider (1980) added small rock and log dams, resulting in an increase of 208% and 179% of brook trout population and biomass respectively in the improved channel as well as an increase of 220% in crayfish biomass. Smaller increases were also observed in the control reach, and no differences in size-class distribution were observed (also summarized in Burgess 1985). Adding log and rock dams to a small PEI stream increased pools, removed silt, and increased abundance of both fingerlings and older brook trout post-treatment, but did not alter growth (Saunders and Smith 1962).

Over a 5 year period, Hartzler (1983) failed to show a significant increase in the abundance of brown trout after addition of wood in a stream with abundant existing cover. Growth rate of brown trout was found to be less negative in a complex experimental channel with woody debris than in a simple experimental stream channel without wood (Sundbaum and Naslund 1998). Observations of the fish behaviour demonstrated less aggression, swimming, and feeding activity in the complex channel with wood, possibly due to lower intraspecific competition (Sundbaum and Naslund 1998). After the addition of wood to a channelized stream in Western Europe, rainbow and brown trout biomass and abundance increased in the enhanced section in winter more so than summer (Zika and Peter 2002). Thorn et al. (1997) used case histories of experimental management of trout streams in Minnesota to develop a relationship between habitat quality and average sustainable biomass and fishing pressure for brook and brown trout, a table of recommended abundance of important habitat variables for brown trout, and a decision key for brown trout management that is dependent on land-use practices. While some have found that brown trout and rainbow trout show less consistent (marginal to negligible) responses to habitat development than brook trout (Hartzler 1983; Boreman 1974), Hunt (1988) determined that sympatric populations of brook and brown trout respond similarly, but allopatric brown trout respond more positively to habitat enhancement than brook trout.

After the addition of different sized artificial surface covers (1, 4, or 9 sq. ft. plywood) in a mountain creek, Butler and Hawthorne (1968) found an inverse relationship between activity and use of cover by trout, with the strongest preference for the largest cover. Rainbow trout were the most active and used cover least, brook trout were intermediate, and brown trout were the least active, highest users of cover (Butler and Hawthorne 1968). In a cover preference experiment in artificial stream channels in Michigan, brown trout preferred complex cover close to the stream bed (10 cm vs. 15 or 20 cm) (DeVore and White 1978). In a 2 year experiment in Idaho, chinook salmon demonstrated a strong affinity for overhead cover simulating undercut stream banks with both larger individuals and greater than 80% abundance and biomass found in covered sections vs. open sections (Brusven et al. 1986). In a southern Ontario creek, Cunjak and Power (1987) found that brook and brown trout preferred submerged cover vs. open or above-water cover during winter. In an artificial indoor plume experiment, brown trout were found to prefer the most cover in the winter, but velocity refuges in the summer (Vehanen et al. 2000). Adding floating cover to rearing tanks significantly increased the growth rate of Atlantic salmon, but had no effect on mortality or incidence of disease in salmon, nor on any parameter measured in brown or rainbow trout (Pickering et al. 1987).

In Eastern Canada, brook trout and Atlantic salmon often occur in sympatry, with juvenile salmon generally occupying riffles and brook trout occupying pools (Gibson et al. 1993). In an experiment intended to increase instream habitat complexity for all age-classes of brook trout, van Zyll de Jong et al. (1997) added v-dams, boulders and half-log covers to streams in Newfoundland and monitored the outcome for two years. The result was a redistribution of bed material, and increased variability in depth, velocity and instream cover, but while there was no significant change in brook trout densities except where pool habitat increased, juvenile Atlantic salmon abundance increased significantly at all treatment types. The addition of mid-channel (boulders, low head barriers), and stream bank (wing deflectors, undercut banks, overhead cover) habitat structures failed to improve habitat for Atlantic salmon parr as intended (i.e. to create plunge pools) at low flows (Mitchell et al. 1998). Mitchell et al. (1998) hypothesised that the habitat provided cover and protection from visual predators, and created a funnel effect of invertebrate drift, allowing increased efficiency when feeding and thus potentially higher specific growth rates (Fausch 1984; Metcalf 1986).

3.1.2.2. Non-Salmonids

Angermeier and Karr (1984) manipulated the abundance of woody debris in a small (3-5 m wide) Illinois stream dominated by cyprinids and centrarchids. A stream reach was divided along midchannel and debris was added to one side and removed from the other. They found that fish and benthic invertebrates were usually more abundant on the added debris side than on the cleared side. In further experiments comparing sections of the stream that were either altered (all woody debris removed), unaltered (control) and subsequently re-altered (altered sites which had artificial-debris structures installed after the debris removal), most large fish (+2) avoided reaches without debris whereas some smaller fish (such as johnny darter) preferred them (Angermeier and Karr 1984).

In a Mississippi warmwater stream restoration experiment, Shields et al. (1993, 1995) added habitat structures to a deeply incised sand-bed channel. While no major changes in channel characteristics resulted, the average depth of scour holes increased, pool habitat in the lower half of the study reach increased, median water depth at base flow increased, as did woody vegetation cover on one side of the channel (Shields et al. 1995). Fish numbers tripled, median fish size increased by 50% and the number of species increased from 14 – 19 (Shields et al. 1995). In a related study examining the effects of adding woody vegetation and stone structure to rehabilitate habitats degraded by erosion and channelization (5 years, 5 sites total), Shields et al. (1998) noted that rehabilitation increased pool habitat availability and made the treated sites physically more similar to the lightly degraded reference site. Fish species composition shifted away from small colonists (principally cyprinids and small centrarchids) toward larger centrarchids, catostomids and ictalurids. While at one rehabilitated site fish density and species richness increased, the other was stable (Shields et al. 1998). Other studies of similar channels have shown that grade-control weirs and spur dikes that created deep (>0.5m), low-velocity scour holes at base flow supported more fish species and larger fish than nearby channel habitats without similar structures (Cooper and Knight 1987, abstract only; Shields and Hoover 1991).

In Japan, an experimental channel simulating temporary lotic habitat was divided into complex and simple habitat and monitored for establishment of invertebrate and fish populations from the adjacent permanent stream (Katano et al. 1998). Chironomid larvae rapidly increased in the predator free environment, although the number and diversity of fish increased through time and was greater in the complex section than the simple section. By day 100, fish species richness and diversity were approaching the levels in the permanent streams, demonstrating the high value of temporary habitat as foraging sites for fish (Katano et al. 1998).

3.1.3. Experimental Removal

Between 1973 and 1981, Elliott (1986) assessed the biota in an Alaskan creek for response to effects of an experimental removal of all logging debris (removal 1976). Physical habitat changes included a reduction in wetted width, reduction in pools and increased water velocity. Macrobenthos density and invertebrate drift decreased 60-90% following debris removal but returned to pre-treatment levels one year post-treatment. Two years following treatment there was an 80% reduction in Dolly Varden abundance, which continued to fluctuate sharply the following 3 years, and a decrease in individual average growth. In a 3-year study of debris removal in an Alaskan creek, designed to minimize changes in channel structure (careful hand removal of small or unstable pieces), Dolloff (1986) found that numbers and production of larger coho and Dolly Varden were reduced in the cleared sections, but that density and production of age-0 coho were not consistently lower in cleaned vs. uncleaned sections of streams. A comparison of logged and unlogged sections of an Oregon creek found that the unlogged section contained more pools, spawning gravel, secondary channels, meanders, undercut banks and three times the coho salmon and trout fry relative to the logged section (House and Boehne 1986). However, after habitat modifications intended to mimic woody debris in the logged section, there was no significant difference in the salmonid biomass between sections. Beechie et al (1994) concluded that the loss of side-channel and distributary sloughs off the main-stem Skagit River, Washington, was the major factor limiting smolt production of coho salmon. Young-of-the-year cutthroat were virtually eliminated from stream sections with reduced area of lateral habitat (Moore and Gregory 1988b).

Channelization of streams in western Washington resulted in a reduction in habitat and biomass of salmonids (coho and cutthroat combined). Age-0 trout abundance, however, was not affected by channelization, possibly due to the lack of predators in the altered reaches (Chapman and Knudsen 1980). In a few less severely altered reaches, with low quantities of silt and sand and high quantities of periphyton, summer salmonid biomass was greater than in control reaches, possibly due to increased light input. Removing cover and undercut banks in Trout Creek, Montana resulted in a decrease of trout biomass per inventory while biomass increased in control areas (Boussu 1954). Removal of coarse woody debris in Japan rapidly decreased pool habitat and masu salmon populations in the affected reach (Abe and Nakamura 1999). The long-term reduction of large woody debris input rates by removal of riparian forest (Murphy and Koski 1989) would cause a loss of pool quality (Collins et al. 2002), and has the potential to seriously degrade rearing habitat for salmonids (Pess et al. 2002).

Hesse (1994) describes a reduction in the population density of catfish due at least in part to the removal of large woody debris (along with overharvest and reduced turbidity) in the Missouri river.

3.2. Substrate

3.2.1. Observational evidence

It has been shown that coho salmon and cutthroat trout typically prefer gravel to cobble sized substrate and are rarely observed in sand or other fine substrate (Moore and Gregory 1988a; Kondolf and Wolman 1993; Montgomery et al. 1999; Rosenfeld et al. 2000). Steelhead fry were most typically observed using rubble as cover when water temperatures were 7°C or less (Bustard and Narver 1975a). In a 2 year observational study, brown trout avoided areas with fine substrate, smaller brown trout were found to occupy shallow riffle areas with cobble substrate, whereas larger fish were found to prefer deeper areas with cobble/boulder substrate and abundant (> 50%) overhead cover (Heggenes 1988).

In Illinois streams, Putman et al. (1995) found that sand negatively affected largemouth bass growth, gravel negatively affected channel catfish and bluegill growth, but positively influenced largemouth bass growth, and that cobble negatively affected bluegill and smallmouth bass growth. Prairie river cyprinids (Western silvery minnows, flathead chubs) were most abundant over fine substrates and avoided gravel and large rocky substrate in order to avoid predators (Quist et al. 2004).

A comparison of natural prairie river substrates (generally clay and sand) vs. riprap (crushed limestone, 5-90 cm) or dyke sites (compacted clay with gravel) found significantly higher fish abundance at riprap and dyke sites (Watkinson et al. 2004). Pennington et al. (1983), Knudsen and Dilley (1987), Madejczyk et al (1998) and Bischoff and Wolter (2001) found some fish species had higher abundance on revetted or riprapped banks while others were higher on natural banks. Complex artificial substrates were found to have had little effect on overall fish or invertebrate community diversity, but altered community composition (Allan 1975; Madejczyk et al. 1998). A study of habitat use in the St. Clair River found that habitat enhancements were largely used by invasive species such as round gobies, tubenose gobies and zebra mussels; alewife, gizzard shad and white perch were relegated to open water, sandy habitat demonstrating a potential negative consequence of enhancement structures (Jude and DeBoe 1996).

Nelson and Franzin (2000) studied habitat preference of 11 species in the Assiniboine River, Manitoba, and report on substrate preferences (white sucker, golden redhorse, shorthead redhorse, silver redhorse, quillback, carp, goldeye, mooneye, walleye, sauger, and freshwater drum). The Eastern sand darter was found to be exclusively associated with sand substrate in the field (26 sites on a New York river), and in 90% of observations in an artificial stream with substrate choice, regardless of water velocity and depth (Daniels 1993).

In a study to determine summer habitat use and preference of Atlantic salmon in two types of Newfoundland rivers (fast vs. slow/deeper), substrate preference for both young of the year and parr salmon was gravel, though nose velocity was the principle variable that determined habitat use (deGraaf and Bain 1986). Habitat use and preference curves differed significantly between creek types and age class, implying the site-specific use and preference curves should be generated for use in habitat modelling (deGraaf and Bain 1986). Beland et al. (2004) found that juvenile Atlantic salmon in a river in Maine were predominantly located where cobble was either the dominant or sub-dominant substrate, but that suitable velocity and depth were the overriding habitat selection factors.

3.2.2. Experimental evidence

Many valued fish species use gravel for spawning, and therefore the restoration of spawning gravel has frequently been an objective of habitat enhancement projects where gravel is limiting (Roni et al. 2002). Placement of instream structures may trap gravel and improve spawning habitat. House (1996) reported an increase of 115% in salmon spawning habitat after placement of gabions in an Oregon creek, and found that 60% of steelheads and 56% of coho spawned within 5 m of structures (previously 18%). Gilbert (1978) found increases in the population densities of all age-classes of juvenile salmon following addition of large rocks (40-80 cm) to the substrate of the Big Tracadie River, NB. It was proposed that Atlantic salmon consistently placed most redds in added loose gravel limestone bars in an acidic brook because of the physical characteristics rather than the increased pH, although the latter may have enhanced survival (Lacroix 1996). Brown trout density increased at sites where islands of rocks and stones were added over uniform sand substrate in a channelized river in Norway, but the authors conclude it was likely due to redistribution of existing fish and not increased recruitment (Brittain et al. 1993). Adding cobble substrate to an Idaho river increased density (8 times) of age-0 chinook salmon at those sites in winter, but that by the following year when interstitial spaces were filled with fines, localized densities returned to pre-treatment levels (Hillman et al. 1987). Similarly, Greenberg and Stiles (1993) found that YOY of benthic stream fishes (*Cottus, Etheostoma, Percina*) colonized areas where cobble was added to deep habitat, but within 2 months those areas were covered by fine sediment. The addition of cobble-gravel spawning habitat increased use and area of egg deposition by walleye in a Lake Superior tributary, but there was no evidence to indicate total egg deposition increased (Geiling et al. 1996). An assessment of 43 other walleye habitat enhancement projects rarely demonstrated an increase in adult abundance (Geiling et al. 1996).

3.3.Aquatic Vegetation

3.3.1. Observational evidence

Aquatic vegetation is not a dominant habitat feature in most fluvial habitats, so little information is available as to its influence on aquatic biota in either an experimental or observational context. In a Montana Creek, rooted vegetation was used extensively as cover by smaller fishes, and floating rafts of broken vegetation that collect in quieter stream areas were used as cover by fish of all sizes (Boussu 1954). While juvenile Atlantic salmon prefer areas with cobble substrate without vegetation, in the absence of suitable cover provided by substrate (i.e. sand habitat), salmon were observed to use areas with moderate (but not dense) aquatic vegetation coverage (Beland et al. 2004). The authors hypothesized that rooted aquatic vegetation may provide enhanced protection from predators in the same manner as other forms of cover, but that dense vegetation may limit visibility and therefore feeding opportunities for this visual drift-feeder.

3.3.2. Experimental evidence

Dibble and Harrel (2000) used three species of shiners in a laboratory flume experiment that tested the use of macrophytes, vertical position in the water column, and water velocity when only conspecifics were present. They found that all species selected intermediate distances (30-60 cm) from macrophytes, but that vertical position within the water column was most important in determining differences among shiners (Dibble and Harrel 2000). By removing various portions of emergent macrophytes in an Alabama Creek, Fritz et al. (2004) found that removal of belowground structures led to streambed instability and a reduction in sedentary mussels but not mobile snails, whereas removal of aboveground stems led to increased periphyton biomass one year post treatment. After removal of macrophytes from riffles in a river in France, electrofishing demonstrated greater biomass and density of fish in vegetated habitats (significantly stone loach and European minnow), but that Atlantic salmon parr density was greater in unvegetated habitats with increased velocity (Roussel et al. 1998). Eklov and Greenberg (1998) experimentally manipulated vegetation density (adding artificial, undisturbed control, removal of natural) and examined distribution of juvenile sea trout (*Salmo trutta* – sea-run brown trout). They found that trout density was higher in artificial vegetation than in control areas, which had higher densities than areas of vegetation removal. They concluded that submerged macrophytes provide important cover for fish when other cover types were limited.

3.4. Riparian Vegetation

3.4.1. Observational evidence

The effect of the extent and coverage of riparian vegetation on streams has received empirical examination in a number of studies surveying aquatic biota post-logging activities. As with other habitat features, clear correlations between extent of riparian cover and/or buffer strips and aquatic productivity are elusive, with some studies demonstrating apparently contradictory results. In general, two schools of thought predominate: 1) riparian cover controls temperature, filters runoff, moderates the hydrograph, and provides significant input of terrestrial productivity, and 2) riparian cover provides excessive shade which reduces solar input and in situ primary productivity, with the accompanying trophic consequences. Literature providing evidence in both directions is summarized below.

Wesche et al. (1987) surveyed 27 sites on streams in Wyoming and found that, of the three cover types (overhead bank cover, rubble-boulder-aquatic vegetation, and deepwater), overhead bank cover explained the most variation in trout (brown, rainbow and brook trout) standing crop (positive relationship). Watson and Hillman's (1997) extensive survey of western streams found the greatest occurrence of bull trout in slow water habitat with undercut banks, large substrate, and trees and shrubs as the dominant riparian vegetation, but found lesser occurrence where overhanging vegetation and canopy were extensive. After studying 17 areas in Idaho, Nevada and Utah, Platts and Nelson (1989) suggest that a quality riparian canopy (to control summer water temperature) is critical for salmon production in interior streams. In a three year study of 20 streams in Norway (4 sites, 4 riparian categories), Johansen et al. (2005) determined that streams with high Atlantic salmon parr densities were those characterized by dense riparian vegetation providing terrestrial invertebrates, cover, food for benthic stream invertebrates, and cooler summer temperatures.

Overhanging vegetation has been shown to be important for the amount of terrestrial invertebrates entering streams (Wipfli 1997; Allan et al. 2003), which can be equal to or more common in trout and salmon stomachs than in the drift (Cada et al. 1987; Allan et al. 2003). Terrestrial invertebrate inputs and salmonid biomass in forested reaches were greater than in grassland reaches in a Japanese stream (Kawaguchi and Nakano 2001). In northern California, Newbold et al. (1980) found significantly lower diversity but higher density of total macroinvertebrates in unprotected streams than in control (unlogged) streams. Buffer strips were found to moderate the impact on diversity such that invertebrate communities in streams with wide buffers (≥ 30m) could not be distinguished from controls (Newbold et al. 1980).

On the other hand, dense riparian vegetation has often been associated with reduced flora and fauna relative to unshaded stream sections (Lyford and Gregory 1975; Newbold et al. 1980; Murphy and Hall 1981; Behmer and Hawkins 1986; Glova and Sagar 1994). In a brief survey of fish assemblages adjacent to river banks in Australia (3 sites, sampled 4 times in one year), grassy banks supported more fish species than banks with trees and shrubs, possibly due to a greater abundance of aquatic macrophytes in the more open, grass sites (Growns et al. 2003). Others have attributed this effect to the riparian trees affecting substrate distribution (reduced riparian vegetation can lead to increased fines) or inhibiting primary production (reduced canopy reduces shading) (Hawkins et al. 1983; Lester et al. 1994). Hawkins et al. (1983) clarify that while they found a significant negative correlation between fine substrate accumulation and abundance of invertebrates and vertebrates (salmonids, sculpins and salamanders), the reduction in shading increased abundance which masked the detrimental effects of fine sediment. They further cautioned however that if canopy removal resulted in additional effects (e.g. temperature change), any benefit of reduced shading may be lost (e.g. community structure shifts). Murphy and Hall (1981) and Murphy et al. (1981) found greater biomass, density and species richness of predators (salamanders, trout, sculpin and insects) in historically logged sections of streams in Oregon that were still open vs. old-growth sections, but emphasized that the increases were greatest where high gradient maintained coarser sediment. In addition, sections that were logged and shaded due to regrowth of the canopy had lower biomass of trout and fewer predator taxa than old-growth sites. A seasonal study of logging treatments along a stream in Alaska found that in the summer, clear-cut reaches held significantly greater numbers and larger juvenile steelhead than buffered or old-growth reaches (Johnson et al. 1986). However, by winter, density in clear-cut reaches decreased by 91% and increased by 100 and 400% in old-growth and buffered reaches respectively. Johnson et al. (1986) hypothesize that the change is due to larger trout requiring deeper areas with abundant cover to successfully overwinter. In Illinois streams, Putman et al. (1995) found that bluegill growth was negatively affected by riparian cover.

3.4.2. Experimental evidence

While many studies examining the importance of riparian vegetation to aquatic ecosystems involve assessing characteristics of streams in logged vs. unlogged reaches, few have directly manipulated overhead or riparian cover in a controlled experimental setting. In six small streams in southeast Alaska, various types of cover manipulated to assess the response of juvenile coho salmon and Dolly Varden (Bjornn et al. 1991). After removal of stream bank vegetation (3 m strips) at 6 sites (plus controls), there was no detectible change in standing crop after 18 days. There was also no significant change in salmonid abundance in a subsequent study of 30 sites (6 controls) which received addition of cover (riparian, woody debris, undercut banks, large boulders) after complete removal of existing cover (Bjornn et al. 1991). In an experimental assessment of the effect of different levels of irradiance on algae (12 streams, 4 treatments ranging from natural levels to saturation intensity of photosynthesis), Steinman and McIntire

(1987), found that the highest intensity treatment had a different assemblage and 25 times more biomass relative to the lowest, suggesting a direct influence of light intensity.

Many studies assessing the role of riparian vegetation did so in the context of assessing the effects of uncontrolled livestock grazing on lotic habitat productivity. A review by Rinne (1999) found that while the majority of studies of livestock grazing measured for an effect on riparian vegetation, few studies could directly and quantitatively link grazing to fish diversity, density or biomass. Rinne (1999) hypothesized this was largely due to poor experimental design and the indirect nature of the relationship. Platts and Rinne (1985) reviewed 16 studies which protected streams from grazing animals to improve riparian habitat and found that 11 reported an increase in fish populations and 4 which found no change. Excluding livestock grazing resulted in significant improvements in structure and composition of vegetation, channel geomorphology and densities of age-0 trout, but combined juvenile and adult salmonid abundance did not differ from unprotected sites. Kauffman et al. (2002) suggested recruitment bottlenecks or a home range beyond the scale of the study (Kauffman et al. 2002). In a review of three review papers (Kauffman and Krueger 1984, 64 papers; Platts 1991, 21 papers; Ohmart 1996, 30+ papers), Fitch and Adams (1998) conclude that inappropriate livestock management results in changes in the shape and quality of the channel morphology, increased water temperature, changes in the hydrograph, bank trampling and accelerated erosion, decreased vigour and biomass of vegetation, loss of some vegetation (esp. trees and shrubs), change in species composition and diversity, and decreases in fish and wildlife abundance and diversity. Hawkins (1998 – cited in Howell 2001) arrived at similar conclusions from his review of riparian grazing studies, and Belsky et al. (1999) concluded that while some studies showed no statistically significant effects, no studies they reviewed indicated positive effects of livestock grazing on riparian areas. Bank trampling and consumption of riparian vegetation by large wild ungulates (deer and elk) can produce similar effects on aquatic habitat (Myers and Swanson 1991).

After experimentally placing containers with varied substrates in the open, under willow trees or under artificial shade, willow trees sites were found to have significantly lower macroinvertebrate densities regardless of substrate type (Lester et al. 1996a). Because treatments were found not to affect periphyton production, it was hypothesized that a high level of chemical release by willow roots inhibits feeding and growth of invertebrates and vertebrates, as suggested by other studies (Rowell-Raheir 1984; Tahvanainen 1985 – cited in Lester et al. 1996a).

3.5. Forage Base

3.5.1. Observational evidence

Positive correlations have been found between trout biomass and biomass of benthic invertebrates (Murphy et al. 1981; Bowlby and Roff 1986; Imre et al. 2004). The highest densities of macroinvertbrates in lowland rivers in southeastern Australia are usually associated with stable substrata such as large woody debris and macrophytes (O'Connor 1991). In a Georgian stream, Benke et al. (1985) determined that invertebrate diversity, biomass and production were considerably higher on wood surfaces than in either sandy or muddy substrates. Wood supported 60% of total invertebrate biomass and 16% of production despite representing only 4% of available habitat surface. Approximately 78% of invertebrate drift originated from wood, and four of the eight major fish species (*Lepomis* species, pirate perch) obtained at least 60% of their prey biomass from wood (Benke et al. 1985).

In an examination of 30 sites in southern Ontario, suspended micro-community biomass (algae, bacteria and fungi as measured by ATP levels) was negatively correlated with trout biomass, an unexpected result based on models of trophic structure (Bowlby and Roff, 1986). The authors hypothesize that this may reflect the importance of groundwater to trout, because groundwater is relatively low in micro-organisms (Matthess 1982 cited in Bowlby and Roff 1986).

3.5.2. Experimental evidence

Because lower trophic levels form the basis of the aquatic food web, and ultimately fish production, the effect of habitat alterations on primary and secondary producers has also been extensively studied. Fish have been shown to have considerable flexibility in their diet, and can adapt to changes in available forage base, some examples of which are provided below. We avoided describing the literature that details species-specific or guild-specific responses to habitat change, instead focussing on the effect on total invertebrates (or fish forage). Not surprisingly, habitat modifications that were found to enhance site-specific fish abundance or biomass also had a positive effect on macroinvertebrates when examined.

Studies of the diet of stream-dwelling salmonids have shown they feed primarily on invertebrate drift (Keeley and Grant 1995; Keeley and Grant 1997), which is composed of both benthic and terrestrial invertebrates (Esteban and Marchetti 2004; Mookerji et al. 2004). Fish have considerable flexibility in their diet, and can adapt to changes in available forage base. Nakano et al. (1999 abstract only) conducted an experiment where they used greenhouse type covers to reduce input of terrestrial invertebrates into stream reaches. They found that fish diet shifted from terrestrial to benthic invertebrates, which resulted in increased periphyton biomass through depletion of herbivorous aquatic invertebrates. Mookerji et al. (2004) found that brook trout sympatric with Atlantic salmon fed primarily on terrestrial invertebrates in the drift whereas Atlantic salmon fed primarily on drifting aquatic invertebrates; allopatric brook trout shifted to consuming primarily drifting aquatic invertebrates. Reducing the abundance of drifting invertebrates resulted in juvenile Atlantic salmon foraging more frequently in the benthos, indicating an ability to compensate for reduced invertebrate drift (Nislow et al. 1998).

Adding boulders to a relatively straight channelled B.C. stream enhanced storage of particulate organic matter (550%) which produced an increase in total macroinvertebrate abundance (280%) to levels similar to the control reach within one year after treatment (Negishi and Richardson 2003). Increasing depositional habitat (via logs or artificially created leaf-packs) increased macroinvertebrate abundance (changing functional feeding groups) in both a North Carolina stream (Wallace et al. 1995) and in mid-Wales (Dobson et al. 1995), but not in a Finnish stream (Muotka and Laasonen 2002), likely because of the overriding importance of moss habitat in invertebrate productivity in those streams. Adding large wood to low-gradient streams created pools, did not change total invertebrate abundance, but did change the composition of invertebrate taxa (Hilderbrand et al. 1997). Lemly and Hilderbrand (2000) examined the influence of the addition of large wood, and subsequent creation of pools, on stream insect communities in a low-gradient stream in Virginia. All functional feeding groups were closely associated with either pools or riffles, and overall collector-gatherers were the most abundant group and inhabited pools almost three-to-one over riffles. The authors suggest that changes in habitat proportions due to instream structures may potentially reshape the overall trophic relations at larger spatial scales.

A study of invertebrates in a Louisiana coastal plain stream found that while species composition varied among wood, sand and gravel, the greatest number of macroinvertebrates were collected from gravel substrates, and that colonization was most dense on wood newly submerged over gravel habitat (Drury and Kelso 2000). Nilsen and Larimore (1973) describe the rapid and complex successional development of invertebrate communities following the introduction of logs to various habitats in an Illinois river. In New Zealand, forest harvesting practices on pine plantations result in large volumes of wood being deposited in spring-fed streams, and the usual management practice is to clear all logging slash (Collier and Bowman 2003). After only partially removing slash post-harvest to 3 wood density levels, they found minor and short-term (< 6 mo.) effects on water temperature, dissolved organic carbon, and nutrients; longer term (> 1 yr) effects were found on dissolved oxygen (decrease proportionate to wood volume); and ongoing (> 5 years) effects were found on substrate composition. Temporal changes in invertebrate communities through disturbance (changes proportional to disturbance) and recovery (most factors returning to pre-harvest within 5 years) were described (Collier and Bowman 2003).

Many experiments have demonstrated that complexity of habitat is important in determining density and diversity of aquatic macroinvertebrates. O'Connor (1991) demonstrated a significant positive relationship between species richness and surface complexity of wood, and suggested it was because complex surfaces contained more resources, although responses of individual taxa were complex and varied. Magoulick (1998) found that previous stream conditioning had a significant effect on taxa richness, and that soft wood had significantly greater densities of some taxa than firm wood. Following colonization of bricks with manipulated habitat structure (crossed design: large crevices, roughness, algae), Downes et al. (1998) found that each habitat element promoted increased invertebrate densities and species richness. In a study investigating the effect of fertilization, substrate type (bare rock, natural and artificial moss) and vertical position, Lee and Hershey (2000) determined that substrate type had an effect on only Ephemerella which had higher densities in complex (moss) habitat, regardless of the source of complexity (natural or artificial).

The role of predation in driving this apparent complexity-richness relationship was examined by Flecker and Allan (1984) when they quantified the invertebrate community colonizing substrate baskets providing 4 levels of complexity (refugia) and being open or closed to predation. They found that predation had little influence on diversity or abundance of invertebrates regardless of substrate type, even when refugia were limited, although the loose gravel consistently had greatest abundance. While other studies which have shown that predators more effectively capture prey when spatial refugia are scarce relative to complex substrate (Ware 1972; Brusven and Rose 1981), Flecker and Allan (1984) argue that there is little evidence demonstrating that predators regulate the composition of natural stream communities regardless of substrate type (Reice 1983 – cited in Flecker and Allan 1984).

The effect of physical disturbance and recolonization by macroinvertebrates was studied by Lake et al. (1989) in southern Australia whereby cobble/pebble substrate was artificially disturbed over a period of 20 days. They found that frequency of disturbance had no effect on species richness, density, or diversity, and that after 33 days, density in disturbed patches was similar to control patches. Harvey (1986) looked at the impact of dredging (before and after, 2 year study) and found that dredging significantly affected some insect taxa when the original cobble substrate was altered to sand and gravel, but that recovery was rapid.

4. Lentic (Lakes/ponds/reservoirs)

The utility of lakes as fish habitat depend on a variety of factors, including their glacial history, climate, morphometry, chemistry and productivity (Tonn and Magnuson 1982; Tonn 1990). Experimental evidence supporting the importance of physical habitat in maintaining aquatic productivity is surprisingly rare for lakes, especially given the high number of papers that use non-experimental (e.g. correlative) approaches to identifying fish habitat requirements. This is likely due to the high cost and low power of whole-system manipulations (Kelso et al. 2001). This section of the review will not attempt to document the specific habitat requirements of all lentic fishes, as such reviews have already been undertaken within DFO (e.g. Lane et al. 1996a, 1996b, 1996c, Bradbury et al. 1999; Langhorne et al. 2001; Richardson et al. 2001; Roberge et al. 2002). The review will highlight key correlational research and will focus on published experimental evidence of fish-habitat relationships.

4.1. Substrate

Lake substrate characteristics dictate the specific site-level habitat features of interest to habitat managers. Fluvial actions (e.g. erosion, transport and deposition processes) are the primary determinant of the distribution of substrate types, which in turn play a key role in structuring aquatic macrophyte (and ultimately fish) communities in Canadian lakes (Cyr 1998). Fetch, average wind speed and direction and shoreline gradient all affect the substrate composition and the limits of aquatic macrophyte distribution (Keddy 1982, 1983; Duarte and Kalff 1986; Wilson and Keddy 1986; Chambers 1987). Substrate includes habitats of varying levels of structural complexity, from featureless mud and sand flats to complex rock/rubble reefs. Structurally complex habitats provide refuge and enhanced foraging opportunities for small fishes (Hall and Werner 1977; Crowder and Cooper 1982; Savino and Stein 1982 – see the macrophytes section for a more thorough review). However, the role that substrate plays in lakes in mediating predator-prey interactions and increasing macroinvertebrate production, and ultimately fish production, has received little attention (Beauchamp et al. 1994). What is clear is that rocky substrates are critical spawning areas for a vast number of species. A high proportion of lake-dwelling fishes in Canada are lithophils (i.e. their spawning is associated with rock and gravel substrates), including members of the Acipenseridae, Clupeidae, Cottidae, Cyprinidae, Catostomidae, Centrarchidae, Percidae and Salmonidae families (reviews by Scott and Crossman 1973; Lane et al. 1996a, 1996b, 1996c; Bradbury et al. 1999; Langhorne et al. 2001; Richardson et al. 2001). Experimental evidence supporting the role of substrate as important fish habitat is limited, however.

4.1.1. Simple substrates, Observational evidence

Correlational evidence suggests that simple substrates (i.e. mud, sand) are generally of low value as fish habitat, and have the lowest fish abundance, richness and diversity of any habitat types (Keast et al. 1978; Randall et al. 1996; Brazner and Beals 1997; Weaver et al. 1997; Pratt and Smokorowski 2003), even in lakes without substantive aquatic macrophyte communities (Beauchamp et al. 1994). However, habitat utilization studies that have looked for diurnal patterns in fish habitat utilization have found that, while that overall use remains low, an increasing number of fishes use simple substrates in the evening (Emery 1973; Helfman 1981; Tabor and Wurtsbaugh 1991; Fischer and Eckmann 1997; Shoup et al. 2003; Lewin et al. 2004). Whole-lake losses of macrophytes, which resulted in large increases in simple substrate exposure, produced rapid shifts in fish communities, with losses of diversity, but no change in lake-wide biomass (Whitfield 1986; Bettoli et al. 1993). Experimental evidence supporting the role of open substrates as important fish habitat demonstrates the critical nature fish community dynamics play in fish habitat management (see role of biotic interactions section below).

4.1.2. Complex substrates, Observational evidence

It is hypothesised that non-vegetated complex substrates could play an important role, similar to the food production and cover role of macrophytes, in macrophyte-poor systems (Beauchamp et al. 1994). Correlational evidence suggests that complex substrates are characterized by having higher fish abundance, richness and diversity than simple substrate areas, but lower values than sites with submersed aquatic macrophytes (Keast et al. 1978; Weaver et al. 1997; Pratt and Smokorowski 2003). However, complex substrates possess a distinct, depauperate fish assemblage in north temperate lakes, which means that maintaining complex substrate habitats is likely important in maintaining lake-wide diversity (Weaver et al. 1997; Pratt and Smokorowski 2003). Complex substrates are believed to be critical for the successful spawning and nursery habitat of many lake-dwelling Canadian fish species (see reviews of Lane et al. 1996a, 1996b, 1996c; Bradbury et al. 1999; Langhorne et al. 2001; Richardson et al. 2001; Roberge et al. 2002).

4.1.3. Complex substrates, Experimental evidence

The experimental addition of complex substrate (i.e. reefs) into marine ecosystems has resulted in an intense debate as to what degree physical habitat structure is important in maintaining fish production (Bohnsack 1989; Polovina 1991; Pitcher and Seaman Jr. 2000). The question as to whether the addition of complex structure simply attracts fish, making them more vulnerable to exploitation, or provides refuge and area for the production of substrate-associated prey resources forms the core of what has been termed ‘the artificial reef attraction-production continuum’ (Lindberg 1997; Osenberg et al. 2002). The open nature of marine systems means that quantitative evidence is difficult to obtain, and thus there is limited experimental evidence to support either side of the debate. There is experimental evidence that complex substrates can increase larval and juvenile survival for invertebrates and fish (Hixon and Beets 1989; Butler and Herrnkind 1997), but different researchers reviewing studies performed to date have concluded that there is increased productivity (Peterson et al. 2003) or evidence for attraction only (Balgos 1995; Bohnsack 1989; Powers et al. 2003). Ultimately, there is likely not enough experimental evidence to properly evaluate the competing hypotheses in marine systems (Lindberg 1997; Pitcher and Seaman Jr. 2000; Osenberg et al. 2002).

There has been little effort expended in resolving the attraction-production debate in freshwater lakes, despite the addition of complex substrates in lake rehabilitation efforts for many decades (Hazzard 1937; Hubbs and Eschmeyer 1938; recent reviews by Smokorowski et al. 1998; Bolding et al. 2004) and the fact that it is easier to estimate fish production in lakes vs. marine systems. Smokorowski et al. (1998) noted that the vast majority of ‘successful’ habitat additions simply evaluated the physical habitat without quantifying any associated biological improvements. For example, man-made rock reefs have successfully been used as spawning substrate in lakes by fishes for decades (Martin 1955; Prevost 1956; Jude et al. 1981; Peck 1986; Marsden et al. 1995; Fitzsimons 1996; Benoit and Legault 2002), but effects on system-wide productivity have rarely been evaluated. A recent experiment demonstrated that the addition of complex substrate resulted in changes in the distribution of fishes, but no changes in fish biomass (Pratt et al., in press). Similarly, the experimental loss of complex substrates (by covering rocky spawning substrates with tarps) has resulted in lake trout simply utilizing new spawning areas (McAughey and Gunn 1995; Benoit and Legault 2002), with no apparent decrease in fish biomass or productivity (Gunn and Sein 2000). The results from these few studies suggest that the addition or loss of complex substrates will not alter system-wide fish biomass or productivity, though a greater number of whole-lake assessments are obviously needed.

4.2.Macrophytes

Aquatic macrophytes are a critical structural component and regulator in aquatic ecosystems. The within-lake distribution of macrophytes depends on light availability, sediment characteristics (including nutrient concentrations), and wind and wave energy (Nichols 1997). Thus, lake morphology, size and watershed characteristics are related to macrophyte distribution. At a broader spatial scale, among-lake macrophyte distribution is influenced by water chemistry, nutrient status and temperature (Nichols 1997). Aquatic macrophytes influence lake ecosystems in three main ways: through i) limnological effects (changes in the chemical and physical conditions of the water and sediments), ii) metabolic effects (nutrient cycling and the production and processing of organic matter, and iii) habitat effects (biotic interactions and community structure) (Carpenter and Lodge 1986; Dibble et al. 1996; Gaisith and Hoyer 1997; Chambers et al. 1999).

The majority of Canadian freshwater fish families rely on aquatic macrophytes for spawning, forage or refuge habitat. Fishes from many North American families, including Amiidae, Esocideae, Cyprinidae, Catostomidae, Cyrpinidontidae, Atherinidae, Umbridae, Centrarchidae and Percidae are phytophils or phytolithophils (obligatory or non-obligatory aquatic macrophyte spawners; reviews by Scott and Crossman 1973; Lane et al. 1996a, 1996b, 1996c; Bradbury et al. 1999; Langhorne et al. 2001; Richardson et al. 2001). Fishes from economically and ecologically important families, such as Esocidae, Cyprinidae, Centrarchidae and Percidae, utilize aquatic macrophytes at some point during their life history (Scott and Crossman 1973; Lane et al. 1996a, 1996b, 1996c). Many of the most ubiquitous Canadian species (northern pike, Casselman and Lewis 1996) are dependent upon aquatic macrophytes to complete their life cycle. Aquatic macrophytes are not usually an important direct food item for North American freshwater fishes, but aquatic macrophytes are consumed by epiphytic algae and macroinvertebrates that make up the base of the food chain.

A number of correlative investigations have identified the critical role of aquatic macrophytes in maintaining the overall habitat heterogeneity, or the collection of diverse microhabitats, in lakes. Among-lake heterogeneity is correlated with species richness (Tonn and Magnuson 1982, Eadie and Keast 1984); within lakes, aquatic macrophyte habitats with higher heterogeneity had greater species richness, diversity and abundance (Brazner and Magnuson 1994; Chick and McIvor 1994; Weaver et al. 1996, 1997; Pratt and Smokorowski 2003). Presumably, increasing heterogeneity results in more abundant and diverse fish communities as it benefits smaller fishes by i) altering the outcome of predator-prey interactions, ii) serving as critical refugia, iii) improving survival and recruitment, and iv) increasing growth rates (Dibble et al. 1996). There are four broad types of aquatic macrophytes: submersed (pondweeds, stoneworts, muskgrasses), emergent (reeds, bulrushes, cattails), floating-leaved (waterlilies,) and free-floating (duckweeds) (Nichols 1997). Submersed macrophytes likely contribute more to habitat heterogeneity than other macrophyte forms, and comprise the vast majority of fish habitat research performed on aquatic macrophytes to date.

4.2.1. Submersed macrophytes, Observational evidence

Non-experimental situations where vegetation was lost or removed demonstrate that fish communities can radically change without corresponding changes in system-wide biomass or productivity. For example, after the introduction of grass carp, which consumed all of the submersed aquatic vegetation that previously covered 40% of the substrate in a Texas reservoir, a number of phytophilic species disappeared and the fish community shifted and was dominated by planktivorous species (Bettoli et al. 1993). However, no obvious change in lake-wide biomass was apparent (Bettoli et al. 1993). Similarly, system-wide fish biomass and productivity did not change in an estuarine lake where submersed aquatic vegetation was lost due to excessive shading, despite significant changes in community composition and a decline in the number of fishes captured (Whitfield 1986). No changes in largemouth bass or bluegill abundance were detected in an uncontrolled vegetation removal study where 50% of the Eurasian watermilfoil wsas removed, though changes in growth were apparent for some year classes (Unmuth et al. 1999). In a review of over 100 Arkansas waterbodies where grass carp were stocked to remove vegetation, Bailey (1978) found no evidence for a loss of overall biomass though individual species biomass did fluctuate. Ware and Gasaway (1978) provide one example of apparent system-wide losses in biomass and species diversity with the introduction of grass carp to two small lakes.

Observational studies on largemouth bass, one of the species most commonly associated with submersed macrophytes, provide conflicting evidence on the importance of macrophytes in maintaining largemouth bass production in lakes. Many single-lake studies demonstrate that intermediate submersed macrophyte densities result in higher abundance and faster growth for largemouth bass (Miranda and Hubbard 1994; Miranda and Pugh 1997; Trebitz et al. 1997; Killgore et al. 1997), and Durocher et al. (1984) found a positive linear relationship with largemouth bass abundance and submersed macrophye cover in 30 Texas reservoirs. Conversely, Hoyer and Canfield (1996) found no relationship between submersed macrophyte coverage and adult largemouth bass abundance in a survey of 60 Florida lakes.

Observational fish habitat use and preference data from the few studies conducted in north temperate lakes provides evidence for the importance of submersed macrophytes for lake-dwelling fishes. Studies consistently find higher fish species richness, abundance and production in lake areas with submersed macrophytes in comparison to areas with simple or complex substrates (Keast et al. 1978; Randall et al. 1996; Weaver et al. 1997; Pratt and Smokorowski 2003). Overall, the observational and experimental evidence strongly suggest that submersed macrophytes play a critical role in determining community structure and maintaining rich and diverse fish fauna in lakes, but that submersed macrophytes do not influence system-wide fish biomass or productivity.

Within in the broad category of submersed macrophytes, individual species have different forms that likely affect their importance as fish habitat. For example, different submersed macrophyte species contain different macroinvertebrate densities and communities (Krecker 1939; Gerrish and Bristow 1979; Cyr and Downing 1988; Paterson 1993), and fish foraging success is significantly higher in submersed macrophytes with simple forms (Diehl 1988; Dionne and Folt 1991; Dibble and Harrel 1997). These results indicate that fish production likely depends on both the species composition and density of submersed aquatic macrophytes. As well, certain forms of submersed macrophtyes, e.g. muskgrass, provide year-round (as opposed to seasonal) refuge and foraging habitat (Caffrey 1993; Hargeby et al. 1994) and are preferred spawning (lake trout, Beauchamp et al. 1992; esocids, Dombeck et al. 1984 and Farrell and

Werner 1996) or feeding (age-0 walleye, Pratt and Fox 2001) habitat. Thus, managers need to value both species composition and density when considering development proposals regarding submersed macrophytes.

4.2.2. Submersed macrophytes, Experimental evidence

An intermediate level of submersed aquatic macrophytes is believed to be critical for maximizing fish productivity in lakes. In general, lakes with low submersed macrophyte densities are believed to have a limited food supply and as a result prey for fishes are scarce, while conversely foraging success can be physically hindered in lakes where macrophyte densities are too high. A number of laboratory and mesocosm experiments have demonstrated that high submersed macrophtye cover can reduce foraging success for benthivorous and piscivorous fishes (Crowder and Cooper 1982; Savino and Stein 1982; Rozas and Odum 1988; Gotceitas and Colgan 1989; Valley and Bremigan 2002a), and modelling exercises examining the trade offs between food production and foraging efficiency have indicated that an intermediate level of submersed aquatic macrophytes should maximize fish production (Wiley et al. 1984; Trebitz et al. 1997). It is therefore surprising that evidence supporting the importance of submersed macrophytes on fish production is rarely apparent when whole-system manipulations occur.

The experimental manipulation of aquatic macrophyte densities is one of the few areas where the role of physical habitat in maintaining fish productivity has been explicitly tested in lakes. Most experimental whole-lake submersed macrophyte removal studies have demonstrated only very minor or no changes in fish production. For example, Olson et al. (1998) found an increase in growth rates for juvenile bluegill in a whole-lake removal experiment of approximately 20% of littoral macrophytes, but no consistent increase in largemouth bass growth. The authors did not look for changes in abundance due to the manipulation because these changes were considered too difficult to detect (Carpenter et al. 1995). Pothoven et al. (1999) determined that there were only minor effects on the abundance and growth of bluegill and largemouth bass with a 50% reduction in submersed macrophytes. Significantly fewer age-0 bluegills were found in the treatment lakes, but no other changes in abundance were noted, while both bluegill and largemouth bass had significantly higher growth post-treatment in the removal lakes (Pothoven et al. 1999). Conversely, Valley and Bremigan (2002b) found no increase in largemouth bass growth in a whole-lake macrophyte removal experiment where Eurasian watermilfoil was selectively removed via a herbicide, and Radomski et al. (1995) found no change in fish (bluegill, largemouth bass, northern pike) abundance or growth with a 60% reduction in macrophytes in a single lake when compared with a control lake. These results indicate that hypotheses generated from small-scale experiments may not successfully scale up to the whole-lake level, as few of the expected effects of vegetation removal were realized in these experiments.

4.2.3. Emergent, floating-leaved and free-floating macrophytes

There is almost no observational evidence for the fish habitat value of floating-leaved and free-floating macrophytes (but see Bruno et al. 1990); in fact poor fish production and water quality has been attributed to excessive floating-leaved and free-floating macrophyte densities (Moore et al. 1994; Parr and Mason 2004).There is no experimental evidence supporting the importance of non-submersed macrophtyes as fish habitat, though many observational studies have found emergent macrophytes are important habitats for certain life stages in some species. Emergent macrophytes are utilized by nesting (Bruno et al. 1990; Pope and Willis 1997), spawning (Franklin and Smith 1963; Johnson and Moyle 1969), larval (Dewey and Jennings 1992; Cooperman and Markle 2004) and adult (Paukert and Willis 2002) fishes.

4.3. Shallow lakes

Unique biological and physical processes within shallow lakes affect the composition and abundance of submersed macrophytes, which ultimately affects the trophic state of the lake. Maintaining vegetative cover is critically important for sustaining fisheries in shallow productive lakes, where losses of submerged macrophytes (due to human or grazer disturbance) can result in a shift to a turbid, phytoplankton dominated system (the hypothesis of alternative stable states; Scheffer et al. 1993; Jeppesen et al. 1998; Stephen et al. 2004). Macrophytes harbour zooplankton and molluscs that graze the phytoplankton (Timms and Moss 1984; Bronmark 1985), and macrophytes restrict the availability of nitrogen in the water (Ozimek et al. 1990), all of which act to stabilize existing macrophyte (and ultimately fish) communities. These hypotheses have been challenged experimentally (mesocosms), primarily by European researchers (Scheffer et al. 1993; Stephen et al. 2004). The fine line between fish, zooplankton and submerged macrophyte dominated vs. a turbid phytoplankton dominated lake is one of the few examples of a threshold in aquatic ecology. Deeper lakes are inherently more resistant to alternating states due to the nutrient sink-source dynamics exhibited by stratified pelagic zones (Carpenter and Cottingham 1997; Ives et al. 2003).

4.4. Wood

Like substrate and aquatic macrophytes, the distribution of wood in lakes is a function of wave action, slope and wind (Cyr 1998; Mallory et al. 2000), but unlike other habitat types wood inputs into lakes take centuries to accumulate (Guyette and Cole 1999). Woody habitat is particularly sensitive to (and readily lost with) increasing human development (Christensen et al. 1996; Jennings et al. 2003), likely due to habitat changes at the lake / riparian zone interface (Schindler and Scheuerell 2002). Woody habitat supports similarly high macroinvertebrate densities as aquatic macrophytes (Bowen et al. 1998), and is has been experimentally tested as a refuge habitat for fish (Miranda and Hubbard 1994). One potentially important difference between most aquatic macrophytes and wood is that wood provides temporally stable structure (Guyette and Cole 1999). Reviews documenting the habitat requirements of various life history stages for Canadian lake-dwelling fishes only infrequently note wood as an important habitat (Lane et al. 1996a, 1996b, 1996c; Bradbury et al. 1999; Langhorne et al. 2001; Richardson et al. 2001), but the importance of woody habitat to fishes is possibly underestimated; this is evident as more researchers assess wood as a potential habitat (Barwick 2004; Lewin et al. 2004; Brind'Amour et al. 2005).

Wood has been added to lakes to improve fisheries for decades (Hazzard 1937; Rodeheffer 1939), and it has succeeded in attracting adult fish (Rodeheffer 1945; Wilbur 1978; Prince and Maughan 1979; Moring et al. 1989; Moring and Nicholson 1994) and improving angler catches. Given the large number examples of wood being used as a rehabilitation tool, it is surprising that lake-wide evaluations of changes in productivity with the addition or removal of woody habitat are absent, but this may be explained by the fact that managers rarely state increasing productivity as an objective when adding woody habitat (Tugend et al. 2002). Experiments have demonstrated that adding wood can improve spawning success and ultimately productivity for certain fish species (i.e. largemouth and smallmouth bass; Vogele and Rainwater 1975; Miranda and Hubbard 1994; Hoff 1991; Hunt and Annett 2002; Wills et al. 2004), but lake-wide assessments have either not been done or found no improvements in fish biomass or productivity (Bassett 1994, cited in Bolding et al. 2004).

4.5. Role of biotic interactions

It would be remiss to ignore the weight of scientific evidence that links two important biotic factors, predation and competition, as critical determinants of fish habitat use in lakes. The importance of these factors, in combination with critical abiotic parameters including physical habitat and physiological requirements in structuring aquatic ecosystems, has been the subject of much debate (e.g. reviews by Sih et al. 1985; Wellborn et al. 1996; Gurevitch et al. 2000; Jackson et al. 2001).

Observational evidence to support the effects of predators on fish habitat selection in north temperate (Brabrand and Faafeng 1993; Eklöv 1997; Hall and Rudstam 1999; MacRae and Jackson 2001; Pratt and Fox 2001; Byström et al. 2003), west coast (Rodewald and Foster 1998; Scheuerell and Schindler 2003; Cooperman and Markle 2004) and sub-arctic (Klemetsen et al. 2003; Kahilainen et al. 2004) lakes are common throughout the peer-reviewed literature. There are a number of experimental mesocosm (Werner et al. 1983; Gotceitas 1990; Tabor and Wurtsbaugh 1991; Diehl and Eklöv 1995) and whole-lake (He and Kitchell 1990; Landry et al. 1999; Biro et al. 2003) experiments that demonstrate flexible habitat use in the presence of predators. In the absence of predators, vulnerable fish used simple substrate or pelagic habitats which provided little or no refuge and where foraging opportunities where greater; when predators were introduced, habitats with little cover were consistently abandoned in favour of habitats with higher levels of structural complexity. In some studies, these habitat shifts resulted in reduced productivity due to slower growth rates in the small fishes due to increased intra- or inter-specific competition (Diehl and Eklöv 1995; Persson et al. 1999; Biro et al. 2003).

There are a number of observational studies that attribute competitive interactions to the spatial structuring of fishes in north temperate lakes (Gascon and Leggett 1977; Werner et al. 1977; Keast 1978; reviews by Ross 1986; Robinson and Wilson 1994; Jackson et al. 2001; Robinson and Parsons 2002). However, experimental evidence for the role of competition in determining fish habitat use is less prevalent, though a few small-scale experiments have demonstrated habitat shifts in lake-dwelling centrarchids and cyprinids with the introduction of competitors (Werner and Hall 1976; Marchetti 1999; Fischer 2000). The structuring role of biotic interactions means that the value of structurally complex habitats as fish habitat depends, to some degree, on the fish community composition, and that an understanding of what fishes are present is required to understand fish-habitat dynamics in a given lake.

4.6. Bottom-up influences on fish productivity

The above sections demonstrate that there is very little evidence to support the contention that fish productivity is influenced by structural habitat in lakes. That said, structural habitat does appear to be important in determining fish community structure, species richness and diversity in lentic systems. One parameter that does consistently affect fish production is lower trophic level productivity (reviews by Ryder et al. 1974; Lee and Jones 1991; Bachmann et al. 1996). Increasing nutrient loads results in increased fish production, though this increased production is often concurrent with reductions in fish species richness, diversity and the production of top piscivores (review by Larkin and Northcote 1969; Jeppesen et al. 2000).

4.6.1. Observational evidence

There are a number of papers that successfully correlate nutrient inputs (Moyle 1956; Vollenweider 1968; Hrbáček 1969; Hanson and Leggett 1982; Yurk and Ney 1989; Downing et al. 1990; Lee et al. 1991; Jeppesen et al. 2000), phytoplankton production (Smith and Swingle 1938; Sakomoto 1966; Melack 1976; Oglesby 1977; Bachmann et al. 1996), lake morphology (Rawson 1955; Northcote and Larkin 1956; Hayes 1957) and combinations of morphometric characteristics and nutrient status (Ryder 1965; Schindler 1971; Ryder et al. 1974; Olin et al. 2002) with fish production in lakes around the world. While there is strong evidence supporting the link between nutrient enrichment and productive fisheries, an increase in trophic state in lakes can negatively influence the quality of fisheries by altering thermal and oxygen regimes (reviews by Larkin and Northcote 1969; Lee et al. 1991), though this is not always the case in more temperate lakes (Bachmann et al. 1996). There are examples of a unimodal relationship with species richness and diversity and increasing nutrient loads across trophic levels (Stockner and Benson 1967; Jeppesen et al. 2000); presumably, the improvements in fish productivity are likely offset by a loss of macrophyte diversity at some level of increasing trophic state (Jeppesen et al. 2000). A number of authors have noted a decrease in the biomass of piscivores with increasing phosphorus levels (Persson et al. 1988; Bachmann et al. 1996; Jeppesen et al. 2000; Olin et al. 2002). Ultimately, a combination of nutrient inputs and lake morphology likely play a critical role in providing the basis for fish production and diversity in lake ecosystems, and a clear understanding of ecosystem goals are required to determine what habitat types are important in a given system.

4.6.2. Experimental evidence

There is overwhelming observational and experimental evidence linking trophic status and fish productivity. Pond fertilization to improve fish yield has a long history (Juday et al. 1938; Swingle and Smith 1939; Hasler and Einsele 1948), and total fish yield was highly correlated with gross photosynthesis in a mesocosm experiment with differing nutrient inputs (McConnell et al. 1977). Experiments that specifically aimed to increase fish production in oligotrophic lakes via whole-lake fertilization have clearly demonstrated increases in fish growth, biomass and production (LeBrasseur et al. 1978; Hyatt and Stockner 1985; Mills 1985; Mills and Chalanchuk 1987; Johnston et al. 1999; Bradford et al. 2000; Mazumder and Edmundson 2002). A recent review found that 11 of 13 sockeye salmon fertilization experiments resulted in an increase in sockeye smolt biomass (Hyatt et al. 2004). While there is almost always a response in fish yield when nutrient levels are experimentally altered, responses do depend on food web complexity which alters trophic dynamics and food web cycling (Carpenter et al. 1995; Hyatt et al. 2004).

5. Linking Physical Habitat and Productive Capacity

It is clear from this review that the linkage between physical habitat and productive capacity of aquatic ecosystems is complex. If any generalization can be made, it may be that the level of habitat complexity has a positive influence on diversity, and sometimes abundance, of aquatic biota, and that habitat can shape the fish community. The diversity of fishes response to change in physical habitat is attributable to a variety of factors which often beyond the control of the resource manager, and usually vary from case to case. Many critical reviews of habitat enhancement studies have been outlined throughout this paper, citing lack of pre-treatment data, lack of reference or control sites, small spatial and temporal scales, semi-quantitative measures, poor sampling techniques leading to poor data, or flawed analyses among others, as reasons to doubt or question reported results (Chapman 1995; Smokorowski et al. 1998; Rinne 1999; Bayley 2002; Roni et al. 2002). While overall we have demonstrated that linkages exist between fish community composition, abundance and/or biomass, and specific habitat features (and thus that certain habitat features should be maintained dependent on fishery management objectives), below we will outline more specifically ways in which we feel the relationship could be elucidated.

5.1. *Spatial and Temporal Scale*

From this review, we believe that the most significant factors contributing to the problem of trying to link physical habitat and productive capacity is a mismatch in the spatial and temporal scale over which functional relationships actually occur versus the scale of studies and experiments. The scale of studies can determine which habitat attributes are considered important, and may be misleading in terms of not focusing efforts where they will truly be most beneficial. Most studies occur at the scale of stream reach, sub-reach, or section of shoreline, whereas functional relationships occur at the watershed scale (both due to the movement of subject species and the influence of landscape management on aquatic habitat). For example, Feist et al. (2003) examined Chinook salmon redd densities at the stream reach scale and the watershed scale in the Salmon River, Idaho. They found that stream reach models had poor predictive power relative to watershed scale, and that redd density was most strongly correlated with climate, geology, wetlands and terrain. Restoration efforts should focus on conditions at the landscape or watershed scale when considering local reach scale habitat restorations. If the activity that caused the degradation of the watershed does not cease (i.e. passive restoration), the active restoration approaches will likely fail (White 1996; Kauffman et al. 1997).

The spatial scale mismatch is also frequently accompanied by a temporal scale mismatch. After restoration efforts are implemented the effects are often only monitored for fewer than 5 years. Because of the large interannual variability in abundance of fish, even if environmental conditions vary little, 10 years or more of monitoring is often required to detect a response to restoration (Platts and Nelson, 1988; Peterman 1990; Bisson et al 1992; Lester et al. 1996b; Bradford et al. 1997; Reeves et al 1997; Ham and Pearsons 2000; Bayley 2002). The physical modification itself may take a number of years to establish, particularly for example with riparian restoration efforts, which would extend the temporal scale of a biotic response to change. Most monitoring in fact has focussed on the physical response to restoration efforts, likely due to simplicity and cost, leaving the real measure of success, namely biota, unmeasured (Smokorowski et al. 1998; Roni et al. 2002). In addition, it is important to measure community response to change as opposed to individual species, since individuals and populations do not react in isolation of others. However, species-specific restoration efforts to achieve fisheries management objectives may be more easily attainable, given the relatively greater knowledge of habitat needs of individual, valued species. Yet, species-specific restoration efforts must consider all aspects of life history when different habitat requirements are associated with different life stages.

In fairness to the studies reviewed herein, it must be noted that the scale and intensity of an experimental design that may clarify habitat-biota relationships would almost always be beyond available resources. Collaboration of multiple researchers and resource management agencies may alleviate this constraint, however, it may also be beneficial to develop an experimental framework within which researchers can conduct complimentary whole system experiments over the long-term, and pool results to provide more clear answers to resource managers (Kelso et al. 2001).

5.2. Fish-Habitat Functional Responses

A third important consideration in understanding why the link between productive capacity and physical habitat remains elusive is that our appreciation of fish-habitat functional responses is limited (Rose 2000). It is unlikely that most fish population responses to habitat change would be linear, as fish populations routinely compensate for changes in morality by altering certain life history parameters (Becerra-Munoz et al. 1999). This makes fish populations inherently resistant to disturbance, and makes it difficult to detect the impact of habitat changes on fish populations. It is more likely that fish will exhibit threshold responses (Wang et al. 1997, Harding et al. 1998), and that habitat-induced changes will not be observed until significant losses in fish productivity are realized.

6. Conclusions

Given the enormous level of effort invested in observing fish in their physical habitat in both lentic and lotic waterbodies, and the resulting strong and relatively consistent correlational evidence linking the two, it was surprising that the review of experimental evidence did not yield a similar result. Yet habitat mangers are required to assess the extent to which a change in physical structure and cover of fish habitat will affect fish. To a great extent we can conclude that decisions made by habitat managers are consistent with the weight of scientific evidence presented herein. Overall, substantial decreases in structural habitat complexity are detrimental to fish diversity, simplify fish communities, and change species composition. The effects of increases in structural complexity are variable; with various studies showing increases, decreases, and no measurable changes in species and/or communities. Net changes in total fish biomass are not commonly recorded, but fish distribution and species composition can be changed. The scale of any effect is context, species and scale specific, and thus case-by-case reviews of proposed habitat alterations are required. Greater certainly could be placed on decisions where the weight of evidence is greater, for example, when highly studied salmonid species are involved. Decisions are most likely to alter individual species or community structure, and thus evaluating the extent of the effect would depend on fisheries management objectives and should be placed in a policy context.

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