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Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems – a review and meta-analysis

K.E. Smokorowski and T.C. Pratt

Abstract: Aquatic resource managers are continually faced with construction or site development proposals which, if allowed to proceed, would ultimately alter the physical structure and cover of fish habitat. In the absence of clear quantitative guidelines linking the change in habitat to fish, resource managers 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 freshwater fish-habitat literature. We then extracted data from experimental studies (where possible) for inclusion in a meta-analysis, to provide a more rigorous assessment of the published results of experimental habitat manipulations. We found relatively strong and consistent correlational evidence linking fish and physical habitat features, yet inconsistent evidence when narratively reviewing the experimental literature. On the whole, 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. The majority of our meta-analyses resulted in supporting a direct link between habitat and fish abundance or biomass, with fish biomass responding most strongly to habitat change. Habitat alterations 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.

Key words: fish habitat, experiments, management, meta-analysis.

Résumé : Les aménagistes des ressources aquatiques sont continuellement confrontés à des propositions de constructions et de sites de développement, lesquelles, si elles sont autorisées, vont ultimement altérer la structure physique et la couverture des habitat des poissons. En absence de références quantitatives claires, liant le changement de l'habitat au poisson, les aménagistes des ressources utilisent souvent le changement de l'aire de l'habitat comme base de décisions. Afin d'évaluer le poids des preuves scientifiques supportant les décisions d'aménagement, les auteurs résument la littérature portant sur des observations aussi bien que des expérimentations. Ils ont ainsi relevé les données d'études expérimentales (lorsque possible) pour les inclure dans une méta-analyse, afin de produire une évaluation plus objective des résultats publiés sur les manipulations expérimentales d'habitats. Ils ont trouvé une preuve corrélationnelle forte et congrue reliant le poisson aux caractéristiques physiques de l'habitat, avec cependant une évidence incongrue lors d'une revue textuelle de la littérature expérimentale. Dans l'ensemble, des diminutions de la complexité de la structure des habitats sont néfastes à la diversité des poissons et peuvent changer la composition en espèces. Des augmentations de la complexité des structures montrent des augmentations, des diminutions ou aucun changement dans la composition en espèces ou dans les communautés. La majorité des résultats des méta-analyses conduites par les auteurs supportent un lien direct entre l'habitat et l'abondance ou la biomasse des poissons, la biomasse des poissons réagissant le plus fortement au changement de l'habitat. Les modifications d'habitat sont plus susceptibles d'affecter les espèces individuelles ou la structure des communautés, et ainsi, l'évaluation de l'importance des effets sur une base biologique dépend des objectifs d'aménagement.

Mots-clés : habitat des poissons, expériences, aménagement, méta-analyse.

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Introduction

The importance of strong fish habitat governance as a prerequisite for healthy fisheries is becoming globally recognized. For example, Canada (Policy for the Management of Fish Habitat, which prohibits any activity resulting in a "harmful alteration, disruption or destruction of the productive capacity of fish habitat"), the United States of America (Sustainable Fisheries Act, which recognizes "essential fish habitat" for marine species), and New Zealand (Fisheries Act, which identifies the importance of "habitat of particular significance for fisheries management") have developed legislative frameworks to support the link between healthy fish habitat and sustainable fisheries. 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 via enforcing provisions of the federal *Fisheries Act*. Across Canada thousands of proposals for development affecting fish habitat are proc-

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essed annually, some of which receive an authorization to alter fish habitat. Since the goal of the Policy for the Management of Fish Habitat (DFO 1986) is to achieve "no net loss" of the productive capacity of fish habitat, the first step is to try to mitigate an activity to prevent the loss, failing which, the loss must be compensated for by creating habitat elsewhere.

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 resource managers most frequently make decisions. 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 on biota 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 metres of habitat, but whether or not they are effective in achieving no net loss of productive capacity is uncertain and rarely measured.

It is nevertheless important that management decisions continue to be made despite uncertainty, and that available information is summarized for efficient use by resource managers in their decision making efforts. Correlational evidence linking fish with various habitat features (preferences for velocity, depth, complexity of structure, etc.) abounds and will not be thoroughly reviewed here. 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. However, 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 literature available from published sources that can be applied in a primarily Canadian context that describe experiments that directly measured responses to habitat change, to see if experimental testing supported correlational evidence linking fish to physical habitat. We then proceeded to take the analyses a step further by extracting data from experimental studies (where possible) for inclusion in a meta-analysis, to provide a more independent assessment of the published results of experimental habitat manipulations.

Meta-analysis approach

Meta-analysis, defined as the quantitative synthesis, analysis, and summary of a collection of studies, has been used extensively in medical and social sciences, and has been increasingly applied in ecological problems in more recent years (Osenberg et al. 1999). Due to inconsistent results from the experimental literature on the effects of a change in physical structure and cover on fish, there is no single study that defines and moulds ecological theory on the importance of physical habitat to fishes. Narrative literature reviews are criticized for being largely qualitative and subjective. Meta-analysis has the potential to apply rigorous quantitative analysis to more traditional literature reviews by generating a common "effect size" across disparate studies and then applying further analysis to these estimates (Arnqvist and Wooster 1995). Meta-analysis has also been criticized for a number of reasons, with the most significant being that (1) results can differ depending on the literature included in the analysis (though often only studies with significant results are even available through the published literature) and (2) the choice of the effect size metric, which is influenced by the question posed, can affect results and interpretation (Englund et al. 1999).

In our case our question was explicit: Does altering the availability or type of physical structure and cover in aquatic habitat relate directly to changes in fish abundance or biomass. We examined all papers that presented experimental results from direct habitat manipulations and extracted data that could be used in a meta-analysis (Table 1). We required the ability to extract a mean and standard deviation (abundance and (or) biomass) from both an experimental and reference site with either both pre- and post-manipulation data or just post-manipulation data. The scale of the data was noted to be either at multiple sites within a stream or lake (site scale) or between reference and experimental systems (stream or lake scale). Data were extracted from tables or estimated from figures. If multiple sites or time periods were presented without error, then error was calculated by averaging across sites or times (pre vs. post separately). If mean numbers were presented with error then we used propagation of error rules to generate one standard deviation. The vast majority of experimental studies addressed in the narrative review did not provide a measure of error, did not use a reference system(s), or examined a less common parameter (i.e., growth, diet composition) and could not be used in our analyses. Overall, 7 of 12 lentic and 14 of 28 lotic studies classified as experimental and discussed in our narrative review were excluded from our meta-analysis.

Meta-analysis techniques allow researchers to include widely disparate papers in a single analysis, while recognizing that studies with greater temporal or spatial scope may provide more robust conclusions. To that end, we weighted studies in our analysis by multiplying the number of sites by years of data available for both the control and experimental areas. The weighting scheme resulted in weights that did not seem unreasonable given the contrasting study designs (Table 1).

Experimental habitat manipulations involved both additions and removals. We accounted for the expected contrary outcomes using reversal markers (Gurevitch et al. 1992). Reversal markers are used to keep the expected effects comparable among studies, as some studies were measured in such a way that a positive response for those studies is in the opposite direction from other studies. In our study, habitat additions were expected to have a positive effect on fish abundance and biomass, while habitat removal was expected

to have either negative (lotic studies) or positive (lentic studies) effects. The lentic studies all involved vegetation removal, which was expected to benefit fish populations by removing overly abundant macrophytes.

Meta-analyses were conducted on abundance or biomass data separately, using various combinations of data to test if the robustness of results depended on the literature included. The most common experimental design was one that presented fish abundance data from both reference and experimental sites or streams post-habitat manipulation (19 studies). Biomass data were less frequently presented in this type of design (11 studies). A moderate number of papers included a pre-treatment assessment of fish abundance (14 studies), and least frequent were studies with pre-treatment data of fish biomass (6 studies). To generate one number for the reference and control system a ratio of the post:pre periods was calculated, again using propagation of error rules to generate the error term. When data for multiple species and cohorts were given, we analyzed all fish species and cohorts separately, then by blending cohorts (by species), and finally blending across all species and cohorts to generate total fish numbers or biomass within a study. Abundance data (both post-post and post-pre designs) were analyzed across all scales and at the site and stream scales separately.

As both the choice of metric and data selected for the analysis can influence meta-analyses results, we decided for a broad approach in our analysis. For all meta-analyses we calculated both the standardized mean difference (Hedges' d) statistic and the log response ratio ($\ln R$) to generate an effect size for each study to examine how the choice of metric influenced our results and conclusions. Hedges' d is the most commonly used meta-analysis statistic, first introduced by Cohen (1965) and later refined by Hedges and Olkin (1985) as

$$[1] \qquad d = \left(\frac{\bar{y}^{E} - \bar{y}^{C}}{S} \right) J$$

where $\bar{y}^{E}$ and $\bar{y}^{C}$ are the experimental and control group means, respectively, and S is the within-group standard deviation. J corrects for bias due to small sample size, and is defined as

$$[2] \qquad J = 1 - \left(\frac{3}{4(N^{C} + N^{E} - 2) - 1} \right)$$

where N^{C} and N^{E} are the sample sizes for the control and experimental groups, respectively. The response ratio, a ratio of some measured quantity in control and experimental groups, is increasingly used in ecology because it quantifies the proportional change from an experimental manipulation (Hedges et al. 1999) and is defined as

$$[3] \qquad \ln R = \ln\left(\frac{\bar{X}^{E}}{\bar{X}^{C}} \right)$$

where $\bar{X}^{E}$ and $\bar{X}^{C}$ are the mean of the experimental and control groups, respectively.

For both metrics, the overall effect size (E_{++}) was calculated as

$$[4] \qquad E_{++} = \frac{\sum_{i=1}^{n} w_i e_i}{\sum_{i=1}^{n} w_i}$$

where e_i is the effect size calculated for the ith study, and w_i is the recriprocal of the sampling variance of the ith study. Interpretation of the overall effect size includes its sign (+, −), which is directly related to the direction of response to habitat manipulation, and magnitude, where by convention values around 0.2 are considered weak, around 0.5 are considered moderate, around 0.8 are considered strong, and 1.0 or greater are considered very strong. The overall effect size was considered significant if the 95% confidence intervals did not overlap with zero.

Categorical analyses were then conducted to determine if responses by different system types (lotic, lentic), by different fish groups (salmon, trout, other), or to different manipulations (add wood, add other, remove structure, remove vegetation) were consistent, using the heterogeneity statistic (Q). The total heterogeneity for all effects tested (Q_{T}) was calculated, as were the heterogeneity between (Q_{B}) and within (Q_{W}) groups, and their significance was evaluated using a chi-square distribution (Hedges and Olkin 1985). We expected that the use of the two most common meta-analysis metrics and performing a number of analyses would provide a robust assessment of the benefits of fish habitat manipulations. Analyses were conducted using Metawin 2.1 (Rosenberg et al. 2000).

Lotic (streams and rivers)

There is a predominance of literature addressing the habitat preferences of salmonids in flowing water systems, likely due to the perceived greater value of this group of fishes or ease of study in such habitats. Habitat preference or use can be dependent on age-class, level of predation and competition (Bustard and Narver 1975a; Glova 1984; Schlosser 1987; Lonzarich and Quinn 1995; Rosenfeld et al. 2000; Rosenfeld and Boss 2001), season (Bustard and Narver 1975a; Peterson 1982; Tschaplinski and Hartman 1983; Rimmer et al. 1983, 1984; Swales et al. 1986; Swales and Levings 1989; Nickelson et al. 1992; Whalen and Parrish 1999; Solazzi et al. 2000), and geographical region (Ford and Lonzarich 2000; Healy and Lonzarich 2000). However, generalizations in salmonid habitat preferences can be made that include a preference for pools or deeper channel units (Bustard and Narver 1975b; 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), cooler tributaries (Stein et al. 1972; Bisson et al. 1988; Bugert et al. 1991), and instream structures (Mundie 1969; Fausch 1993). Increasing the availability of these preferred habitats has been a frequently chosen method of improving fish production, although the production-habitat link remains largely untested.

Morphology and cover

Experimental addition
The role of channel morphology (width, depth, percent

Table 1. Summary of studies included in meta-analysis for (*a*) habitat addition studies and (*b*) habitat removal studies. LWD, large woody debris; FWD, fine woody debris; MPR, multiple pass removal using blocking nets; MR, mark-recapture; efishing is electro-fishing; N is abundance; and B is biomass.

Type	Name	Habitat change	Scale	Census method	N control – sites × years	N expt. – sites × years	Data Available	Location in source	Source
(a) Habitat Addition									
Lotic	North Fork Porter Creek, WA	LWD addition	Sites	MPR efishing	1×3	1×3	Post-Post N	Figs. 3–5	Cederholm et al. 1997
					1×6	1×6	Pre-Post N		
Lotic	Elk Creek, OR	LWD addition	Streams	Spawner counts	2×4	1×4	Post-Post N	Fig. 1	Crispin et al. 1993
					2×11	1×11	Pre-Post N		
Lotic	Jumping Pound Creek, AB	FWD simulation	Sites	MPR efishing	20×1	20×1	Post-Post N, B	Figs. 4–5	Culp et al. 1996
Lotic	McMichaels Creek, PA	Half logs	Sites	MPR efishing	6×3	6×3	Post-Post N, B	Table 3	Hartzler 1983
					6×5	6×5	Pre-Post N, B	Table 4	
Lotic	East Fork Lobster Creek, OR	Boulder, gabions	Sites	MPR efishing or beach seine	6×8	6×8	Post-Post N, B	Table 4	House 1996
					6×9	6×9	Pre-Post N, B		
Lotic	Tenmile Creek, OR	LWD addition, riparian planting	Streams	MPR/MR efishing, diver counts, smolt traps	3×4	6×4	Post-Post N	Figs. 5–7	Johnson et al. 2005
					3×8	6×8	Pre-Post N		
Lotic	NWT	Artificial stream with habitat structures	Sites and Streams	MPR efishing	3×1, Site	(2–6)×1	Post-Post N, B	Fig. 4	Jones and Tonn 2004
					10×2, Stream	14×2	Post-Post N, B	Fig. 6	
					10×3, Stream	14×3	Pre-Post N, B		
Lotic	Noel Paul's Brook, Nfld.	Boulders, undercut bank, wing deflectors	Sites	Day and night counts, MPR efishing at end of each experiment	6×1	6×1	Post-Post N	Fig. 3	Mitchell et al. 1998
Lotic	Mack Creek, OR	Lateral habitat (boulder movements)	Sites	Snorkeller counts, efishing	3×1	3×1	Post-Post N	Tables 2–3 and text	Moore and Gregory 1988*b*
					3×1	3×1	Post-Post B		
Lotic	Creeks in Oregon	Log addition, alcove creation	Streams	Snorkeller counts and MR or MPR efishing	2×4	2×4	Post-Post N	Fig. 3	Solazzi et al. 2000
					2×7	2×7	Pre-Post N		
Lotic	Mühlebach Stream (channelized)	Trees felled into river every 20 m	Sites	MPR efishing	1×4(days)	1×4(days)	Post-Post N	Table 2	Zika and Peter 2002
					1×4(days)	1×4(days)	Post-Post B	Table 3	

Table 1 (*concluded*).

Type	Name	Habitat change	Scale	Census method	N control – sites × years	N expt. – sites × years	Data Available	Location in source	Source
(*b*) Habitat Removal									
Lentic	Lakes in Arkansas	Vegetation removal; 5%–100%	Lakes	Rotenone treatment	8×2	20×3	Post-Post B	Figs. 1–25	Bailey 1978
					8×6	20×6	Pre-Post B		
Lotic	Streams in Alaska	Cover manipulations (removals, additions)	Sites	MPR efishing	6×1	6×1	Post-Post N	Table 2	Bjornn et al. 1991
					6×1	6×1	Pre-Post N	Table 3	
Lentic	Lakes in Minnesota	Vegetation removal	Lakes	Trap net, boat efishing	1×2	2×2	Post-Post N	Table 4	Cross et al. 1992
					1×4	2×4	Pre-Post N	Table 11, Table 17	
Lotic	Tye and Toad Creeks, AK	LWD removal, 1/2 each reach, 10%–15%	Sites	Two-way fish traps, MR using minnow traps	2×2	2×2	Post-Post N	Figs. 8–9	Dolloff 1986
					2×3	2×3	Pre-Post N	Table 3	
					2×3	2×3	Post-Post B		
Lotic	Spring Pond Creek, AK	LWD removal - logging slash	Stream	MR minnow traps,	1×5	1×5	Post-Post N, B	Fig. 2	Elliott 1986
					1×10	1×10	Pre-Post N, B	Fig. 3	
Lentic	Lakes in Minnesota	Vegetation removal; 37%–67%	Lakes	Seine, gill net, trap net	3×1	2×1	Post-Post N	Fig. 1	Pothoven et al. 1999
					3×2	2×2	Pre-Post N	Fig. 2	
Lentic	Lakes in Minnesota	Vegetation removal; 100%	Lakes	Seine, trap net	1×3	1×3	Post-Post N, B	Table 4	Radomski et al. 1995
					1×5	1×5	Pre-Post N, B		
Lentic	Lakes in Michigan	Vegetation removal; 19%	Lakes	Seine	2×2	4×2	Post-Post N	Table 1	Valley and Bremigan 2002
					1×2	1×2	Pre-Post N		

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 has the compound effect of forming pools, increasing side channel habitat, and providing instream cover (e.g., 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 and low-gradient sand substrate streams can cause substantial pool formation (Beechie and Sibley 1997), wood addition to high gradient streams dominated by large substrate can result in little change in habitat structure (Hilderbrand et al. 1997). Design specifications are available for a variety of instream channel structures intended to improve habitat of modified stream channels (Shields 1983), although reviews of the physical durability of structures have found high occurrence of damage or failure in such modified systems (House and Boehne 1986; Frissell 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 effects of morphology changes or changes in instream cover, but instead we will describe the biotic response to deliberate actions by resource managers or researchers.

Salmonids

Salmonid populations have been extensively studied in regard to stream habitat needs and response to placement of instream structures, and a number of narrative critical reviews on the topic have already been published. However, frequent experimental design problems exist with these studies, with a lack of reference sites, seasonal coverage, and narrow temporal scope being some of the main problems (Roni et al. 2002). For example, of 29 instream habitat restoration projects, 12 of which suggested significant increases in juvenile salmonid abundance, only five were monitored beyond 5 years (House 1996; Cederholm et al. 1997; Reeves et al. 1997; Solazzi et al. 2000). Ambiguity also remains regarding the absolute nature of the change (increased production or simply redistribution of existing fish) or the sustainability of population response. A review of 13 projects designed to enhance instream structural cover (Smokorowski et al. 1998) found that only two studies measured fish production. Both studies measured increases in fish production at the site of the enhancement, yet monitoring reference – reduced habitat reaches found a decrease in fish production that ultimately balanced the total production in the streams to no net change (Hunt 1974, 1976; Moore and Gregory 1988).

Bayley (2002) reviewed 441 abstracts, 30 full papers, and 7 review articles dealing with the 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. Bayley (2002) concluded that 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. 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. Below we summarize results from specific studies to demonstrate the wide variety of approaches taken, the disparate results that followed, and to provide a narrative description of studies included in our meta-analysis (Table 1), and of those not included in the analysis due to incompatible data requirements.

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. Experimental placement of large woody habitat in western Washington and Oregon streams significantly increased densities of coho salmon (*Oncorhynchus kisutch*) across seasons at the sites of enhancement (House 1996; Cederholm et al. 1997; Solazzi et al. 2000; Roni and Quinn 2001; Johnson et al. 2005), with either no change or decreases found at unaltered sites (Crispin et al. 1993). Cutthroat (*Oncorhynchus clarki*) or steelhead trout (*Oncorhynchus mykiss*) responded inconsistently to the placement of woody material (Solazzi et al. 2000; Roni and Quinn 2001). The creation of new off-channel ponds successfully increased winter survival of coho salmon (Cederholm and Scarlett 1991), increased density in age-0 cutthroat trout (Moore and Gregory 1988) but produced little response in Chinook salmon (*Oncorhynchus tshawytscha*) (Richards et al. 1992). Coho salmon response to changes in wood density was dependent on temperature (Giannico and Hinch 2003) and food level (Giannico 2000). Differences in seasonal response both within and among species were generally attributed to differences in species-specific seasonal habitat preferences.

The addition of smaller bushy woody material may not alter channel morphology or elicit the accompanying predicted response (Spalding et al. 1995), or it may aggregate fish in the new complex habitat (Culp et al. 1996). Manipulation of habitat complexity in experimental channels demonstrated shifts in use of habitat but not total density or growth (Bugert and Bjornn 1991; Imre et al. 2002). Fausch (1993) experimentally placed artificial habitat in a natural stream and reported that coho salmon showed a strong preference for velocity barriers regardless of level of cover, whereas steel-

head trout 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 (*Thymallus arcticus*) at sites of enhanced structural habitat in an artificial stream channel (NWT), but failed to detect an improvement at the stream scale. Jones and Tonn (2004) suggested that deficiencies existed at the catchment scale, specifically a paucity of allochthonous and autochthonous organic matter, which prevented improvement in grayling production.

Moving east we find that enhancement of brook (*Salvelinus fontinalis*), rainbow (*Oncorhynchus mykiss*) or brown (*Salmo trutta trutta*) trout habitat dominate the literature, with most studies reporting positive results such as improvements in angler harvest (Shetter et al. 1946), biomass (Boussu 1954; Burgess and Bider 1980), and abundance (Saunders and Smith 1962), within 2 years after placement of current deflectors, cover, and log or rock dams, respectively. Yet the success of habitat additions could be dependent on quantity and quality of existing habitat (Hartzler 1983), and response can be season dependent (Vehanen et al. 2000; Zika and Peter 2002). Complexity of habitat may (Sundbaum and Naslund 1998) or may not (Saunders and Smith 1962) affect fish growth rate. Level of aggression and activity can depend on complexity of habitat (Butler and Hawthorne 1968; Sundbaum and Naslund 1998). Trout demonstrate a strong preference for cover and will respond by changing distribution to its manipulation (DeVore and White 1978; Cunjak and Power 1986). 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.

In Eastern Canada, brook trout and Atlantic salmon (*Salmo salar*) often occur in sympatry, with juvenile salmon generally occupying riffles and brook trout occupying pools (Gibson et al. 1993). Habitat enhancement projects intended to increase variability in depth, velocity, and cover were sometimes successful in achieving their physical habitat goals (e.g., van Zyll de Jong et al. 1997), but not always (e.g., Mitchell et al. 1998). Biological response was still unpredictable with widespread increases in juvenile salmon, but no significant change in brook trout densities (the target species) except where pool habitat increased (van Zyll de Jong et al. 1997). When Atlantic salmon density increased even though habitat addition failed to create pools, Mitchell et al. (1998) hypothesized 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).

Non-salmonids

Warmwater habitat enhancement has mainly been carried out in highly degraded channel like habitats, so it is not surprising that localized results are positive. Increasing complexity of warmwater incised channel habitat, particularly by forming pool habitat, increased fish abundance, size, and richness (Shields et al. 1995), and changed fish species composition from small colonists (principally cyprinids and small centrarchids) toward larger centrarchids, catostomids, and ictalurids (Shields et al. 1998). Other studies of similar channels have shown that 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 (Shields and Hoover 1991). Cyprinids and centrarchids were more abundant in complex habitats supplied by woody debris compared with cleared reaches (Angermeier and Karr 1984), whereas some smaller fish (such as johnny darter, *Etheostoma nigrum*) preferred open reaches (Angermeier and Karr 1984).

Experimental removal

The effects of experimental simplification of fish habitat appear more consistent. Removal of large debris was shown to generally reduce wetted width, reduce pools, and increase water velocity (Elliott 1986; Collins et al. 2002) and can potentially seriously degrade rearing habitat for salmonids (Pess et al. 2002). Immediate and short-term reductions can occur in invertebrate density (Elliott 1986), with the more persistent, longer-term effect of reducing abundance, biomass or production of fish in the affected reaches (Boussu 1954; Chapman and Knudsen 1980; Elliott 1986; Dolloff 1986; Hesse 1994; Abe and Nakamura 1999). Some authors have found less of an effect on age-0 fishes (Chapman and Knudsen 1980; Dolloff 1986), possibly due to increased survival via reduced predator densities.

Indirect effects from land use can be significant. Unlogged sections of a creek contained more pools, spawning gravel, secondary channels, meanders, undercut banks, and three times the density of coho salmon and trout fry relative to the logged section (House and Boehne 1986). However, after adding gabions intended to mimic woody debris in the logged section, and the resulting improvement in gravel retention and pool formation, there was no significant difference in the salmonid biomass between sections. Beechie et al. (1994) concluded that the loss of side-channels off the main-stem Skagit River, Washington, was the major factor limiting coho salmon smolt production. Age-0 cutthroat trout were virtually eliminated from stream sections with reduced area of lateral habitat (Moore and Gregory 1988).

Substrate

Salmonids have been shown to have a preference for larger and varied substrates, and to avoid sand or other fine substrates (Bustard and Narver 1975b; Heggenes 1988; Kondolf and Wolman 1993; Montgomery et al. 1999; Rosenfeld et al. 2000). On the other hand, some species, such as prairie river cyprinids (Quist and Hubert 2004) or the Eastern sand darter (*Ammocrypta pellucida*; Daniels 1993), may be most abundant over fine substrates, avoiding gravel and large rocky substrate. Substrate composition has been implicated as a factor in fish growth, varying by species (Putman and Pierce 1995).

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 assumed to be limiting (Roni et al. 2002). Placement of instream structures may trap gravel and improve

spawning habitat (House 1996), and the addition of large cobble and boulder habitat can increase localized densities of salmon (Gilbert 1978) and trout (Brittain et al. 1993), but the effect may be temporary if fines inundate interstitial spaces over time (Hillman et al. 1987; Greenberg and Stiles 1993). Demonstration of increased spawning activity in newly created spawning habitat (Lacroix 1996; Geiling et al. 1996) does not necessarily translate to an increase in total egg deposition or adult abundance (Geiling et al. 1996).

Aquatic vegetation

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. It is thought that vegetation, if available, will be used as cover in the absence of suitable cover provided by substrate (Boussu 1954; Eklöv and Greenberg 1998; Beland et al. 2004). Removal of aquatic vegetation can have the effect of reducing biomass and density of some fish species (Eklöv and Greenberg 1998; Roussel et al. 1998) but may increase density of species preferring higher velocities (Roussel et al. 1998).

Riparian vegetation

The effect of riparian vegetation on streams has received empirical examination in a number of studies surveying the effects of logging on aquatic biota. As with other habitat features, clear correlations between extent of riparian cover and (or) buffer strips and aquatic productivity are elusive, and some results are contradictory. In general, two schools of thought predominate: (1) riparian cover improved habitat by controlling temperature, filtering runoff, moderating the hydrograph, and providing significant input of terrestrial productivity (Newbold et al. 1980; Wesche et al. 1987; Platts and Nelson 1989; Hartman et al. 1996; Watson and Hillman 1997; Wipfli 1997; Kawaguchi and Nakano 2001; Allan et al. 2003; Johansen et al. 2005); and (2) riparian cover reduces solar input and in situ primary productivity, with the accompanying trophic consequences (Lyford and Gregory 1975; Newbold et al. 1980; Murphy and Hall 1981; Behmer and Hawkins 1986; Glova and Sagar 1994; Lester et al. 1994; Putman and Pierce 1995; Growns et al. 2003). The benefits of increasing solar input with removal of riparian vegetation can be lost if an increase in fine substrate or temperature also result (Murphy and Hall 1981; Murphy et al.1981; Hawkins et al. 1983), or also may not continue through winter (Johnson et al. 1986).

Few riparian studies have directly manipulated overhead or riparian cover in a controlled experimental setting. We could find only one example where controlled removal of stream bank vegetation and the subsequent addition of cover were tested, both of which failed to elicit a significant response in localized salmonid abundance, although abundance of older fish was lower after removal (Bjornn et al. 1991). The manipulation consisted of the removal of 3 m of vegetation along each streambank in 6 of 13 habitat units, for a total of 18 m of canopy removed on each bank. Habitat units were defined as pools or runs bounded by riffles that ranged in area from 7.3 to 25.9 m^2. Given that most of the stream widths were 2–4 m, we can deduce that the fraction of streambank deforested ranged from 23% to 100% of a habitat unit. While this may seem like a large percentage, the overall small scale of the study (and subsequent low and variable abundances) may be part of the reason for a lack of a significant result.

Many studies assessing the role of riparian vegetation dealt with the effect of uncontrolled livestock grazing on lotic habitat productivity. Allowing unimpeded livestock grazing negatively affects fish habitat through changes in channel morphology, increased water temperature through sun exposure, altering the hydrograph, bank trampling and accelerated erosion, and decreased biomass or loss of vegetation (Fitch and Adams 1998; Belsky et al. 1999), while restricting livestock results in measurable improvements in habitat (Platts and Rinne 1985; Kauffman et al. 2002). On the other hand, fish have not responded in a consistently negative fashion to livestock-induced habitat changes (Kauffman et al. 2002). Rinne's (1999) review concluded that few studies could directly and quantitatively link grazing to fish diversity, density or biomass, largely due to poor experimental design and the indirect nature of the relationship. 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).

Forage base

Because lower trophic levels form the basis of the aquatic food web, and ultimately fish production, the effect of habitat alterations on plankton and macroinvertebrates has also been studied. 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). Not surprisingly, habitat modifications that were found to enhance site-specific fish abundance or biomass also had a positive effect on macroinvertebrates.

Fish have considerable flexibility in their diet, and can adapt to changes in available forage base. Fish can directly forage on invertebrates attached to hard or stable substrates in lotic environments (Benke et al. 1985), or feed primarily on invertebrate drift (Keeley and Grant 1995, 1997), which is composed of both benthic and terrestrial invertebrates (Esteban and Marchetti 2004; Mookerji et al. 2004). 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 complexity of habitat that subsequently traps organic matter resulted in increased macroinvertebrate abundance (Dobson et al. 1995; Wallace et al. 1995; Negishi and Richardson 2003), but not always (Hilderbrand et al. 1997; Muotka and Laasonen 2002). While total abundance may not change, composition of invertebrate taxa (Hilderbrand et al. 1997) and overall trophic relations (Lemly and Hilderbrand 2000) could be affected.

Abundance, diversity, and composition of invertebrate taxa vary by substrate type (wood, sand, gravel etc.), condition, and complexity (e.g., O'Connor 1991; Downes et al.

1998; Magoulick 1998; Drury and Kelso 2000; Lee and Hershey 2000). Changes in invertebrate communities through disturbance can be proportional to the level of disturbance, with factors returning to pre-harvest within 5 years (Collier and Bowman 2003). Lake et al. (1989) reported invertebrate density recovered only 33 days post disturbance, and that frequency of disturbance had no effect on species richness, density, or diversity. 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.

Lentic (lakes, ponds, and 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 (i.e., 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). As per above, this section of the review will not attempt to document the specific habitat requirements of all Canadian lentic fishes, as such reviews have already been undertaken (Lane et al. 1996*a*, 1996*b*, 1996*c*, 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.

Substrate

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 and rubble reefs. Structurally complex habitats, with large and variables substrate sizes, 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 preferred 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. 1996*a*, 1996*b*, 1996*c*; 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.

Correlational evidence suggests that fine 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 type (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, 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 fine 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, resulting in large areas of fine substrates, produced rapid shifts in fish communities, with losses of diversity but no change in lake-wide biomass (Whitfield 1986; Bettoli et al. 1993).

It is hypothesized 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 fine 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 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. 1996*a*, 1996*b*, 1996*c*; Bradbury et al. 1999; Langhorne et al. 2001; Richardson et al. 2001; Roberge et al. 2002).

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 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 (e.g., 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 2000; Osenberg et al. 2002).

There has been little effort expended in resolving the attraction–production issue 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 1957; 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. 2005). 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.

Macrophytes

Aquatic macrophytes are an important 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. 1996*a*, 1996*b*, 1996*c*; 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. 1996*a*, 1996*b*, 1996*c*). Many of the most ubiquitous Canadian species (i.e., northern pike, *Esox lucius*; 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 a substrate for growth of epiphytic algae and macroinvertebrates that make up the base of the food chain.

A number of correlative investigations have identified the importance 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 fish species richness, diversity, and abundance (Brazner and Magnuson 1994; Chick and McIvor 1994; Weaver et al. 1996, 1997; Pratt and Smokorowski 2003). Presumably, increasing macrophyte 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 (e.g., pondweeds, stoneworts, muskgrasses), emergent (e.g., reeds, bulrushes, cattails), floating-leaved (e.g., waterlilies), and free-floating (e.g., duckweeds) (Nichols 1997). Submersed macrophytes likely contribute more to habitat heterogeneity than other macrophyte forms, and comprise the vast majority of aquatic macrophytes used in fish habitat research performed to date (Keast et al. 1978; Durocher et al. 1984; Miranda and Hubbard 1994; Hoyer and Canfield 1996; Randall et al. 1996; Miranda and Pugh 1997; Trebitz et al. 1997; Killgore et al. 1997; Weaver et al. 1997; Pratt and Smokorowski 2003). Findings to date indicate that fish production likely depends on both the species composition and density of submersed aquatic macrophytes (Krecker 1939; Gerrish and Bristow 1979; Cyr and Downing 1988; Diehl 1988; Dionne and Folt 1991; Paterson 1993; Hargeby et al. 1994; Dibble and Harrel 1997), and fish foraging success is significantly higher in submersed macrophytes with simple (i.e., non-branching) structure, thus both species composition and density need to be considered when managing for submersed macrophyte communities. The floating-leaved or free-floating macrophytes are not thought to be important fish habitat (Bruno et al. 1990; Moore et al. 1994; Parr and Mason 2004), although emergent macrophytes are important habitats for certain life stages in some species (Franklin and Smith 1963; Johnson and Moyle 1969; Dewey and Jennings 1992; Pope and Willis 1997; Paukert and Willis 2002; Cooperman and Markle 2004).

Non-experimental situations where vegetation was lost or removed demonstrate that fish communities can radically change without corresponding changes in system-wide fish biomass or productivity. For example, after the introduction of grass carp (*Ctenopharyngodon idella*), which consumed 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 to be was dominated by planktivorous species (Bettoli et al.

1993). However, no obvious change in lake-wide biomass of fish 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 (*Micropterus salmoides*) or bluegill (*Lepomis macrochirus*) abundance were detected in an uncontrolled vegetation removal study where 50% of the Eurasian watermilfoil was removed, though changes in growth were apparent for some year classes of largemouth bass and bluegills (Unmuth et al. 1999). In a review of fisheries assessment studies in 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) provided two examples of apparent system-wide losses in biomass and species diversity with the introduction of grass carp to two small lakes.

An intermediate level of submersed aquatic macrophytes is believed to be necessary 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 macrophyte 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 2002*a*), 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).

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 removals of submersed macrophytes 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 three-years post treatment. The authors did not look for changes in fish abundance because these changes were considered too difficult to detect (Carpenter et al. 1995). Pothoven et al. (1999) determined that, with a 50% reduction in submersed macrophytes, significantly fewer age-0 bluegills were found, 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 (2002*b*) 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.

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 (e.g., Scheffer et al. 1993; Stephen et al. 2004). The fine line between a fish, zooplankton, and submerged macrophyte dominated vs. a turbid phytoplankton dominated system is one of the few examples of a threshold response 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).

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 increasing human development (Christensen et al. 1996; Schindler and Scheuerell 2002; Jennings et al. 2003). Woody habitat supports similarly high macroinvertebrate densities as aquatic macrophytes (Bowen et al. 1998), supports greater invertebrate biomass than open sediments (Smokorowski et al. 2006), and it 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 (e.g., Lane et al. 1996*a*, 1996*b*, 1996*c*; 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; Sass et al. 2006).

For decades, wood has been added to lakes to improve fisheries (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 of 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 rare, 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). Lake-wide wood removal experiments, conducted over a number of years, have provided conflicting results, finding either no (Pratt et al. 2005) or significant negative effects (Sass et al. 2006) on fish biomass or productivity.

Role of biotic interactions

There is a body 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 (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 (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 Eklov 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 that provided little or no refuge and where foraging opportunities were 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 Eklov 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, although 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 understand-

ing of what fishes are present is required to understand fish-habitat dynamics in a given lake.

Bottom-up influences on fish productivity

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).

There are a number of papers that successfully correlate nutrient inputs (Moyle 1956; Vollenweider 1968; Hanson and Leggett 1982; Yurk and Ney 1989; Downing et al. 1990; 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 and Jones 1991), although 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 management goals and objectives are required to determine what habitat types are important to protect in a given system.

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 (*Oncorhynchus nerka*) fertilization experiments resulted in an increase in sockeye salmon 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 that alters trophic dynamics and food web cycling (Carpenter et al. 1995; Hyatt et al. 2004).

Meta-analysis results

A total of 19 studies contributed to the meta-analyses (Table 1). The post-post abundance analyses contained the largest datasets, consisting of 54 estimates of abundance; the pre-post abundance included the responses of 43 fish groups (Table 2). Only two of the 32 separate analyses showed a weak response opposite to our expectations (ln R, site scale), and only 6 others were not significant. Therefore, the majority of analyses (75%) showed some level of direct response to the habitat manipulation. The significance level of the results depended on the metric used and on how the data were grouped, but overall, fish biomass responded more strongly than abundance, and the pre-post design, which is a more rigorous statistical examination of the problem, produced a stronger positive response than studies that measured responses post-treatment only, which only compared treated sites to the control (Table 2).

Grouping the data clarified the drivers of the overall results (Figs. 1–4), although in some cases a lack of studies limited the ways we could partition the data. For both abundance and biomass data, the effect sizes were significantly different between groups regardless of design, metric, or category. In the post-post abundance analysis, lotic salmonids in wood addition habitat were driving the moderate positive effect obtained using Hedges' d (Fig. 1). The pre-post abundance negligible and weak responses were largely driven by the lentic studies, which also comprise all of the vegetation removal studies (Fig. 2). In the post-post biomass design, it was the lotic system studies, mainly removal of structure or addition of non-woody structure, that drove the negligible to weak positive response (Fig. 3). The design that demonstrated the strongest positive response to the habitat change, those involving pre- and post-manipulation biomass data, were significant in both habitat types, but mostly by the lentic system studies (Fig. 4).

Linking physical habitat and productive capacity

It is clear from the narrative 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 habitat complexity has a positive influence on diversity, and sometimes abundance, of aquatic biota, and that habitat can shape the fish community. The results of the meta-analysis provide much clearer support for the importance of physical habitat to fish, given that most of our analyses resulted in at least a weak collective positive response to habitat change. Given that the attraction–production debate is based on the premise that localized improvements do not translate to the system scale, it was surprising that the only negative, and therefore unexpected, response to the habitat change was when the studies were conducted at the site scale, but this result was dependent on the metric chosen.

The diversity of fishes response to change in physical habitat is attributable to a variety of factors that are 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, semiquantitative measures, poor sampling techniques leading to poor data, or flawed analyses among others, as reasons to 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 specific ways in which we feel the relationship could be elucidated.

Spatial and temporal scale

From this review and from the results of the meta-analysis, we contend that the most significant factor contributing to the problem of linking physical habitat and productive capacity is a mismatch in the spatial and temporal scale over which functional relationships 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 reachscale 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, and pre-treatment data is not always included in the monitoring program, likely because it is not always required by regulators. 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. 1996; 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

Table 2. Meta-analysis results summary table including the number of cases included in the analysis (*N*), overall mean effect size, 95% confidence interval (C.I.) and the interpretation of the strength of the result.

| Habitat	Scale	Design	Measure	Metric	Fish groups*	N	Mean effect size	95% C.I.	Result
Lotic & Lentic	Site & Stream	Post-Post	Abundance	ln R	Separate	54	0.0005	–0.0246 to 0.0256	n.s.
Lotic & Lentic	Site & Stream	Post-Post	Abundance	Hedges' d	Separate	54	0.3613	0.2178 to 0.5049	moderate
Lotic & Lentic	Site & Stream	Post-Post	Abundance	ln R	Species	47	0.0181	–0.0083 to 0.0445	n.s.
Lotic & Lentic	Site & Stream	Post-Post	Abundance	Hedges' d	Species	47	0.3174	0.1638 to 0.4709	weak
Lotic & Lentic	Site & Stream	Post-Post	Abundance	ln R	Total	29	0.0142	–0.0137 to 0.0421	n.s.
Lotic & Lentic	Site & Stream	Post-Post	Abundance	Hedges' d	Total	29	0.1859	–0.0318 to 0.4036	n.s.
Lotic & Lentic	Site & Stream	Post-Post	Biomass	ln R	Separate	26	0.0466	0.0172 to 0.0759	negligible
Lotic & Lentic	Site & Stream	Post-Post	Biomass	Hedges' d	Separate	26	0.3221	0.1357 to 0.5085	weak
Lotic & Lentic	Site & Stream	Post-Post	Biomass	ln R	Species	23	0.0554	0.0252 to 0.0857	negligible
Lotic & Lentic	Site & Stream	Post-Post	Biomass	Hedges' d	Species	23	0.3567	0.1607 to 0.5527	moderate
Lotic & Lentic	Site & Stream	Post-Post	Biomass	ln R	Total	15	0.0506	0.0192 to 0.0819	negligible
Lotic & Lentic	Site & Stream	Post-Post	Biomass	Hedges' d	Total	15	0.3723	0.1468 to 0.5977	moderate
Lotic & Lentic	Site & Stream	Post-Pre	Abundance	ln R	Separate	43	0.1498	0.1380 to 0.1616	negligible
Lotic & Lentic	Site & Stream	Post-Pre	Abundance	Hedges' d	Separate	43	0.1331	0.0142 to 0.2521	negligible
Lotic & Lentic	Site & Stream	Post-Pre	Abundance	ln R	Species	36	0.1548	0.1429 to 0.1668	weak
Lotic & Lentic	Site & Stream	Post-Pre	Abundance	Hedges' d	Species	36	0.2415	0.1104 to 0.3726	weak
Lotic & Lentic	Site & Stream	Post-Pre	Abundance	ln R	Total	19	0.0572	0.0040 to 0.1105	negligible
Lotic & Lentic	Site & Stream	Post-Pre	Abundance	Hedges' d	Total	19	0.3421	0.1449 to 0.5392	weak
Lotic & Lentic	Site & Stream	Post-Pre	Biomass	ln R	Separate	13	1.6532	1.5943 to 1.7120	strong
Lotic & Lentic	Site & Stream	Post-Pre	Biomass	Hedges' d	Separate	13	0.5558	0.4007 to 0.7110	moderate
Lotic & Lentic	Site & Stream	Post-Pre	Biomass	ln R	Species	12	1.8794	1.8147 to 1.9441	strong
Lotic & Lentic	Site & Stream	Post-Pre	Biomass	Hedges' d	Species	12	0.5289	0.3673 to 0.6904	moderate
Lotic & Lentic	Site & Stream	Post-Pre	Biomass	ln R	Total	6	0.6237	0.4574 to 0.7899	moderate
Lotic & Lentic	Site & Stream	Post-Pre	Biomass	Hedges' d	Total	6	0.3993	0.1356 to 0.6630	moderate
Lotic	Site	Post-Post	Abundance	ln R	Separate	31	–0.1359	–0.1631 to –0.1086	negligible
Lotic	Site	Post-Post	Abundance	Hedges' d	Separate	31	0.2578	0.0825 to 0.4330	weak
Lotic & Lentic	Stream & Lake	Post-Post	Abundance	ln R	Separate	23	0.6399	0.5793 to 0.7006	moderate
Lotic & Lentic	Stream & Lake	Post-Post	Abundance	Hedges' d	Separate	23	0.5974	0.3343 to 0.8604	moderate
Lotic	Site	Post-Pre	Abundance	ln R	Separate	20	–0.1952	–0.2580 to –0.1324	weak
Lotic	Site	Post-Pre	Abundance	Hedges' d	Separate	20	0.1375	–0.0371 to 0.3121	n.s.
Lotic & Lentic	Stream & Lake	Post-Pre	Abundance	ln R	Separate	23	0.1635	0.1511 to 0.1758	weak
Lotic & Lentic	Stream & Lake	Post-Pre	Abundance	Hedges' d	Separate	23	0.1288	–0.0441 to 0.3016	n.s.

*Separate = all cohorts and species included separately; Species = cohorts combined into one number by species; Total = cohorts and species combined into one number representing all fish measured in study.
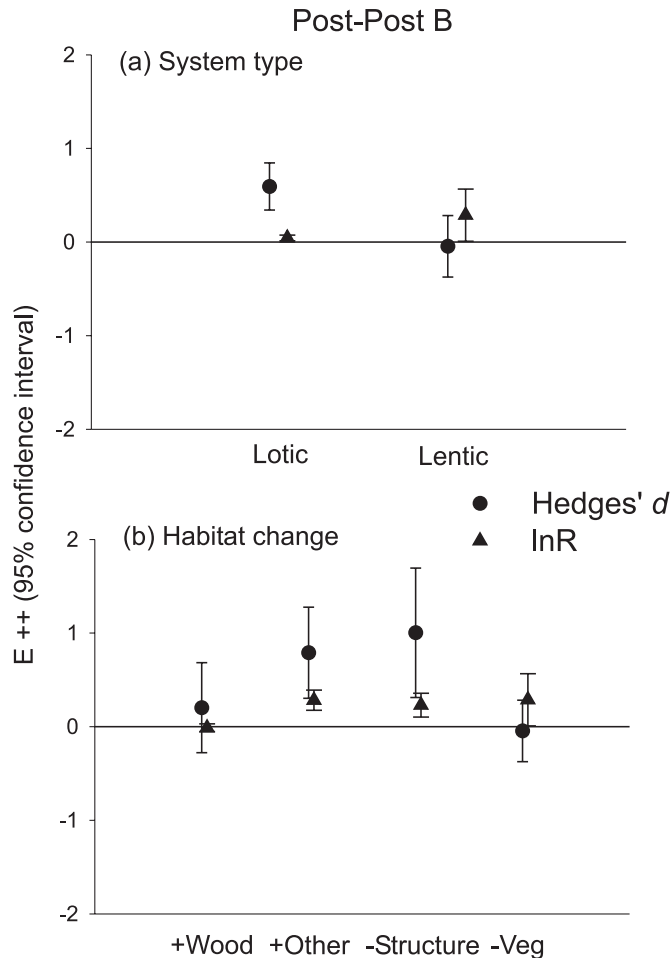
Fig. 1. Categorical meta-analysis results from the post-post abundance (N) design for both Hedges' d and ln R, partitioning the overall mean effect size by (*a*) system type; (*b*) habitat change; and (*c*) fish group.


Post-Post N

(a) System Type

(b) Habitat change

(c) Fish group

Fig. 2. Categorical meta-analysis results from the pre-post abundance (N) design for both Hedges' d and ln R, partitioning the overall mean effect size by (*a*) system type; (*b*) habitat change; and (*c*) fish group.

Pre-Post N

(a) System type

(b) Habitat change

(c) Fish group
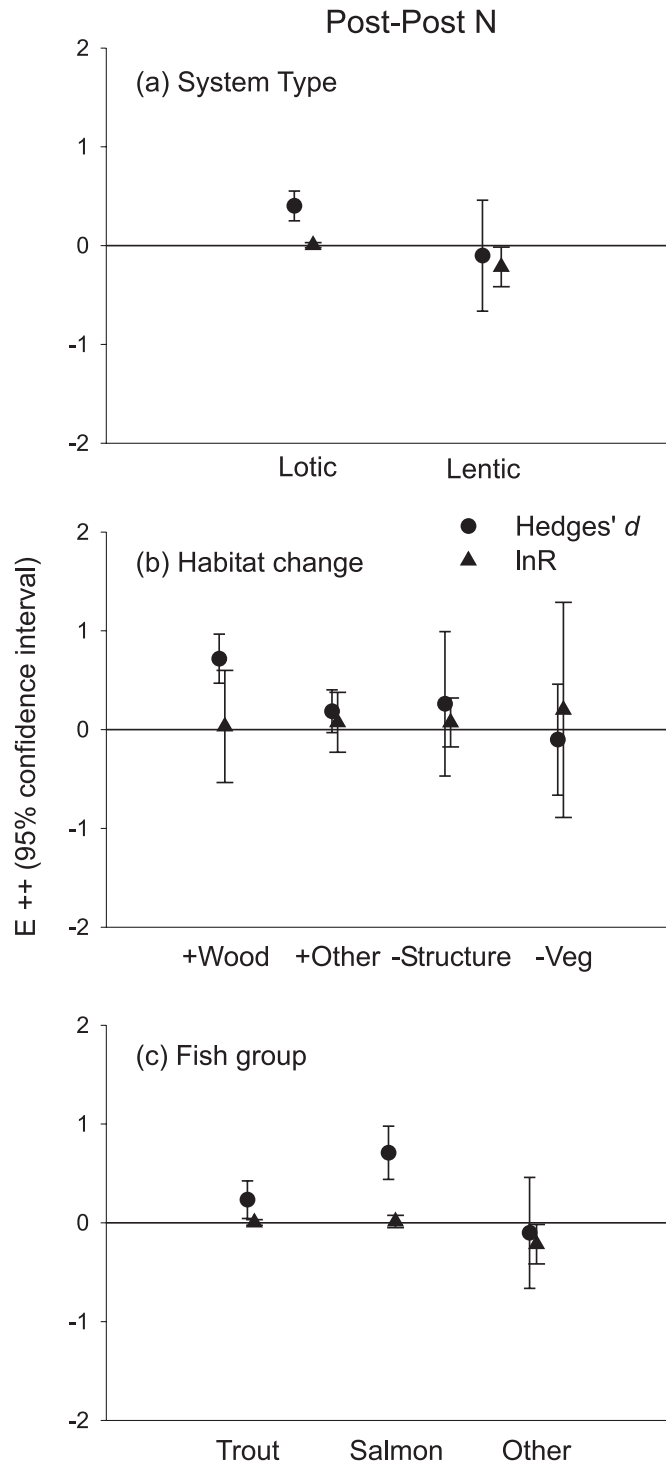
addition, it is important to measure community response to change as opposed to individual species, since individuals and populations do not react in isolation of others. However, species-specific restoration efforts to achieve fisheries management objectives may be more easily attainable, given the relatively greater knowledge of habitat needs of individual,
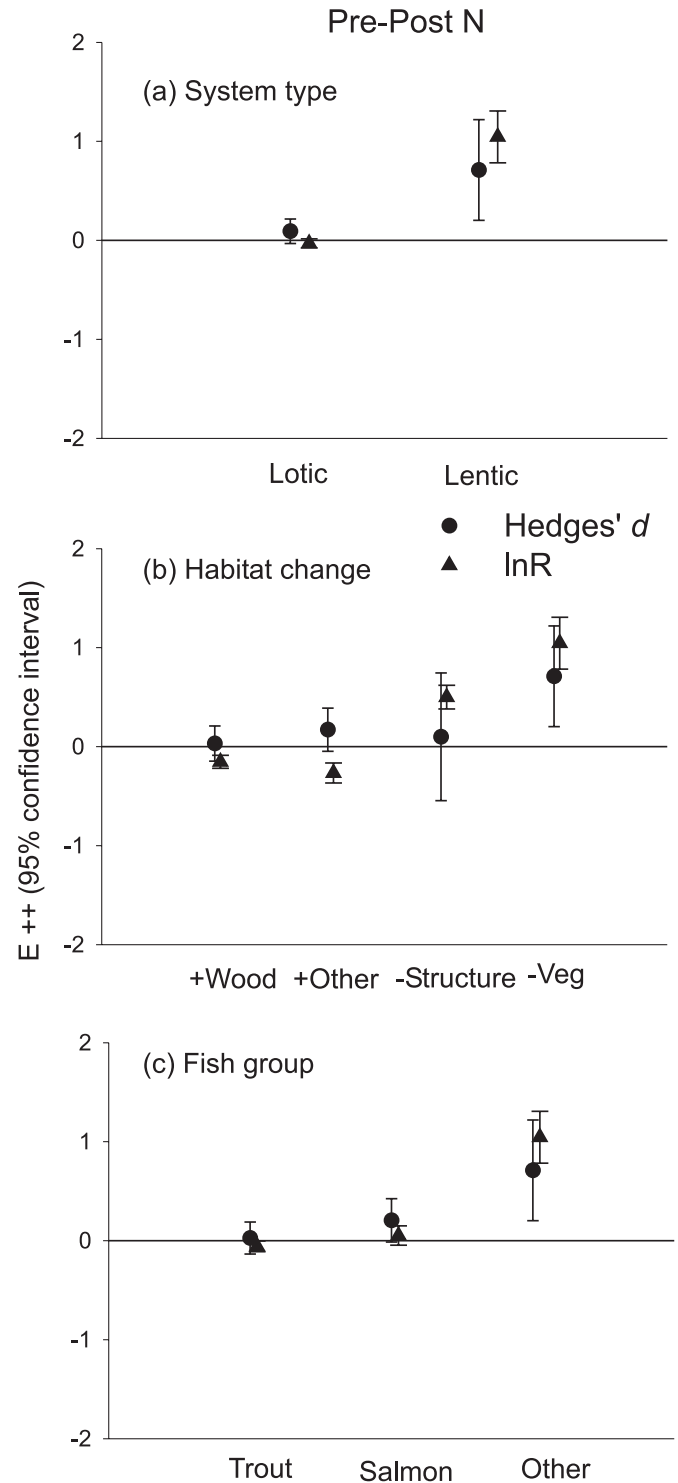
valued species. Yet, species-specific restoration efforts must consider all aspects of life history when different habitat requirements are associated with different life stages.

In fairness to the studies reviewed herein, it must be noted that the spatial and temporal scale of an experimental design required to clarify habitat–biota relationships would almost

Fig. 3. Categorical meta-analysis results from the post-post biomass (B) design for both Hedges' *d* and ln *R*, partitioning the overall mean effect size by (*a*) system type and (*b*) habitat change.
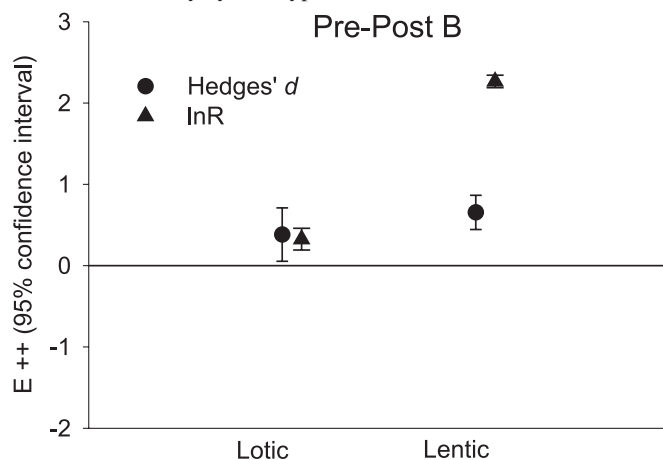
over the long term, and pool results to provide more clear answers to resource managers (Kelso et al. 2001).

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 mortality 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.

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 reassuring that the quantitative meta-analysis generally supported the prevailing belief despite the apparently disparate results from the narrative review. Habitat managers 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 aquatic resource 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 different studies showing increases, decreases, or no measurable changes in species and (or) communities. 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.

Fig. 4. Categorical meta-analysis results from the pre-post biomass (B) design for both Hedges' *d* and ln *R*, partitioning the overall mean effect size by system type.

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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

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