The Abiotic Environment

5

At all spatial scales in fluvial ecosystems, studies of stream-dwelling organisms support the expectation that greater physical complexity of the environment promotes increased biological richness. That organisms are adapted to aspects of habitat, such that the traits of organisms reflect features of the environment, is a fundamental idea in ecology referred to as the habitat template concept (Southwood 1988). The key habitat needs of a species commonly are identified from the subset of environmental variables that best correlate with its distribution and abundance. Although additional factors also influence the composition and diversity of biological assemblages, including interactions among species and taxon richness at the regional scale, the abiotic environment provides an important starting point for investigations of species distributions and abundances. This view has two important corollaries. First, environments that are either structurally simple or extreme tend to support fewer species, whereas more moderate and heterogeneous habitats support more species. Second, a high frequency of disturbance tends to diminish biological richness, although a moderate level of disturbance potentially may enhance diversity by maintaining an ever-changing spatial mosaic of conditions. These principles forecast the consequences of human disturbance: anthropogenic degradation and homogenization of habitat will lead to biodiversity decline with unpredictable consequences for ecosystem function.

Habitat is often described as where a species lives, and thus is an important component of a species' niche. The latter term is broader, describing a species' place in a biological community and incorporating all of the physical and biological conditions needed for a species to maintain its population in an area (Begon et al. 2005). The niche concept incorporates species interactions, distinguishing between the space that a species could occupy in the absence of predators and competitors (the fundamental niche) and the more restricted space where a species is found (the realized niche). In this chapter we focus on key abiotic aspects of habitat that influence the distribution and abundance of the biota of fluvial ecosystems; later, in Chap. 10, the influence of species interactions will be explored.

Habitat features vary across small to large spatial scales, referred to as micro-, meso-, and macrohabitat (Vinson and Hawkins 2003); and from very short to long time scales. Individual taxa are adapted to a specific range of habitat conditions, and will be more or less abundant depending on the matching of their morphological, behavioral, and physiological traits to environmental conditions. Thus the abiotic environment, acting on species traits, serves as a filter that determines which taxa of the region are likely to be found at the local scale (Poff 1997).

In fluvial ecosystems, key abiotic features of the environment usually are those related to current, substrate, temperature, and sometimes water chemistry variables such as alkalinity and dissolved oxygen. Water chemistry and dissolved oxygen are important under natural conditions only in some unusual environments and under low flows, but both factors can be very influential when human activities result in polluted waters. Current is the defining feature of rivers and streams. It conveys benefits, such as transport of resources to the organism and removal of wastes, but also risks, of which being swept away is the most obvious. Physical habitat includes the substrate composition of the stream bed, boulders and large wood that influence local current and scour patterns, and also larger-scale channel features including riffles, pools, bars, and channel meanders. The substrate of running waters differs greatly from place to place, and is important to algae and many invertebrates as the surface on which they dwell. For many organisms, substrate is where their food is found. Larger physical elements, such as large wood, are important to many fishes as the structure near which they find shelter from current or enemies. Temperature affects all life processes, and because most stream-dwelling organisms are ectothermic, growth rates, life cycles, and the productivity of the entire system are strongly under its influence. Thus, current, physical habitat, and temperature are three key aspects of the abiotic

J. D. Allan et al., *Stream Ecology*,
https://doi.org/10.1007/978-3-030-61286-3_5

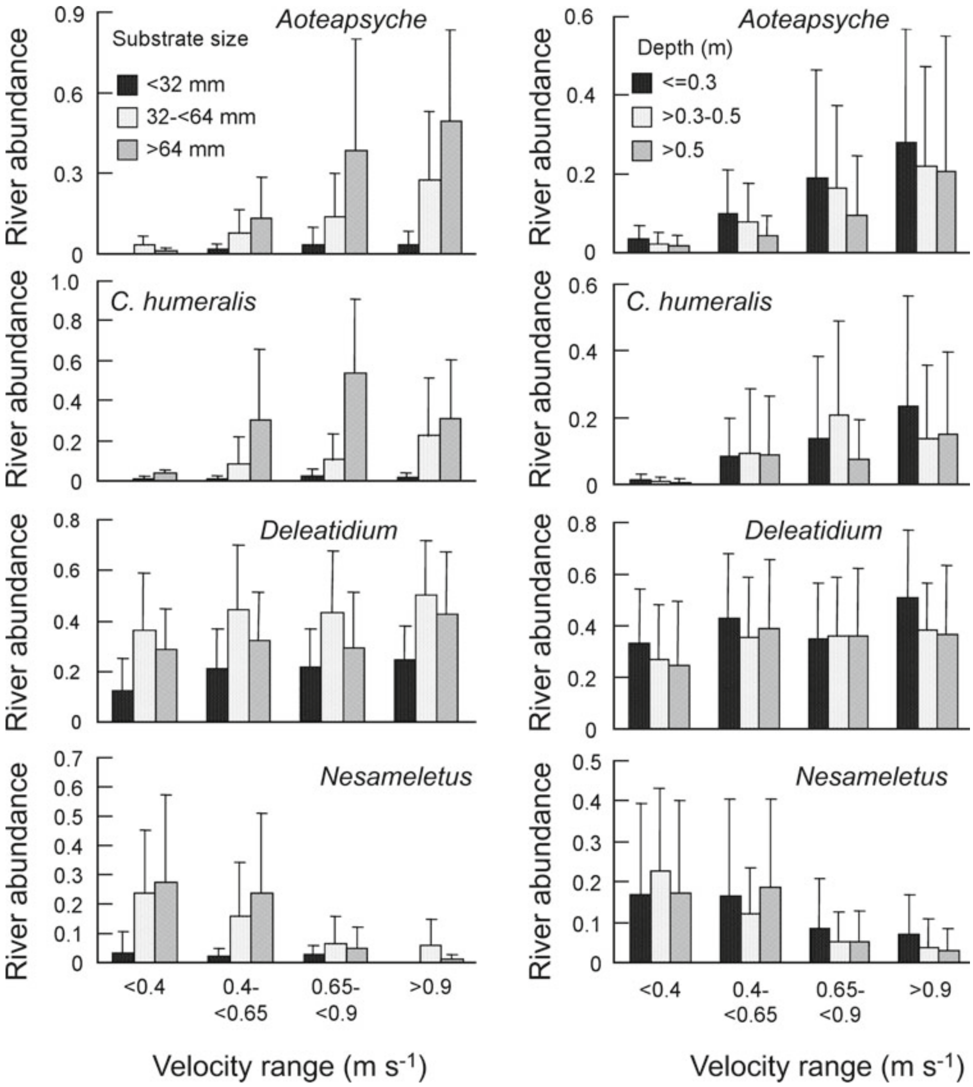

Fig. 5.1 The relative abundance of some macroinvertebrate taxa in four large New Zealand rivers within substrate size (left), depth (right), and velocity ranges. *Aoteapsyche* (Trichoptera); *Coloburscius humeralis*, *Deleatidium*, and *Nesameletus* (Ephemeroptera). Error bars are 1 standard deviation (Reproduced from Jowett 2003)

environment that we should understand in order to appreciate the functioning of a lotic ecosystem and the adaptations of its denizens.

To decipher how organisms respond to individual habitat variables is complicated because organisms are subject to the simultaneous and interactive effectives of multiple abiotic factors. The relationship of macroinvertebrate abundances to velocity, substrate size, and depth (Fig. 5.1) nicely illustrates differences in habitat preferences, but because these environmental factors are inter-related, it can be difficult to distinguish causal from correlated responses. Often, we focus on the influence of average conditions on aquatic organisms, but the variance in average conditions and the frequency and magnitude of extremes may be equally important to organismal abundance and the structure of aquatic communities. When environmental conditions episodically become unfavorable, such as an area of substrate that receives excessive scour or a stream section that becomes too warm for days or weeks, then patches of remaining suitable habitat provide critical refuge until the disturbance passes and recolonization can occur. Species traits, such as motility or tolerance to high temperatures, determine how populations will respond to unfavorable conditions and play an important role in shaping aquatic communities.

5.1 The Flow Environment

In fluvial systems the flow of water is a dominant and characterizing variable that influences diverse aspects of the stream environment (Hart and Finelli 1999). It affects channel shape and substrate composition, and episodically disturbs both. Flow strongly influences the hydraulic forces operating in the benthic and near-bed microhabitats occupied by much of the biota, and is important to ecological interactions, rates of energy transfer, and material cycling

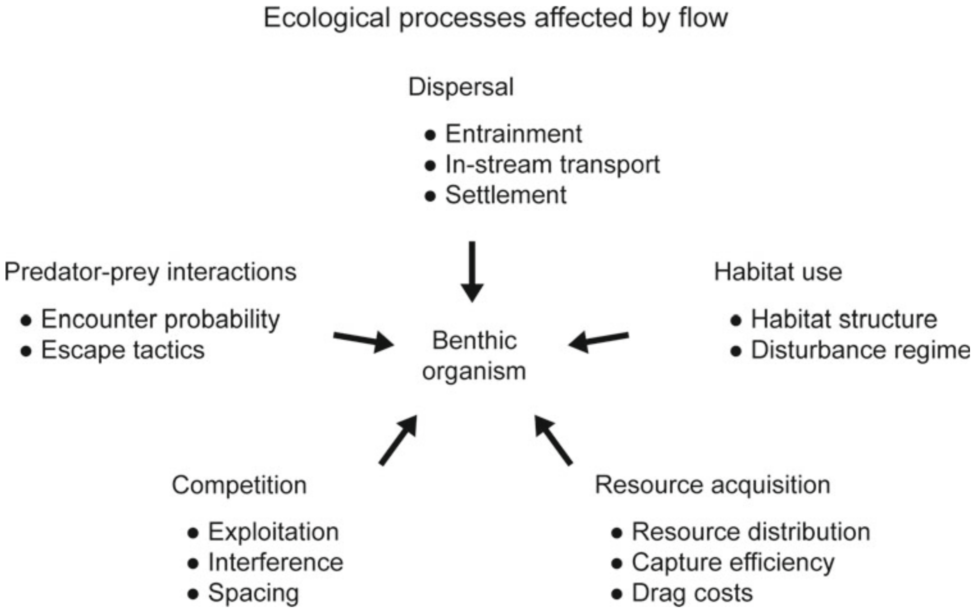

Fig. 5.2 Multiple causal pathways by which flow can affect organisms. Potential interactions among pathways are not shown (Reproduced from Hart and Finelli 1999)

(Fig. 5.2). Current velocity is a physical force that organisms experience within the water column as well as at the substrate surface. Organisms are directly affected by current velocity when eroded from a substrate and displaced downstream, or when their energy reserves are depleted as they attempt to maintain position against current. They are indirectly affected when the delivery of food particles, nutrients, or dissolved gasses—factors that influence their metabolism and growth—change with changes in current velocity. Relevant definitions and methods of measurement were given in Chap. 2; recall that current is the speed of moving water (usually in cm s^{-1} or m s^{-1}), and flow or discharge is volume per unit time (usually m^3 s^{-1} or cfs). Turbulence refers to rapidly varying and unpredictable fluctuations in current velocity, and may be more influential than mean velocity. It can be quantified from the standard deviation of velocity divided by the mean, or from time series analyses.

Current velocity varies enormously, not only along a river's length and with the rise and fall of the hydrograph, but also from place to place within stream channels at meso- and micro-habitat scales owing to bed friction, topography, and bed roughness due to large substrate particles and wood. The vertical velocity profile (Fig. 2.7) is of fundamental importance to any consideration of the effects of current on organisms, as the flow conditions near the streambed may differ markedly from open-channel flow. When the depth of flow is substantially greater than the height of roughness elements, one expects an outer layer in which velocities vary little with depth (free stream velocity) and a logarithmic layer of declining velocity near the streambed (Fig. 5.3). In reality, the velocity profile is usually more complex.

Water in contact with the streambed has zero velocity, referred to as the no-slip condition, and velocity increases above the bed to its free stream value. The boundary layer is defined as a flow region where water velocity increases from zero in contact with the stream bed to the free stream velocity with increasing distance away from the streambed (Vogel 1996). An average velocity within this boundary layer can be estimated from fine-scale measurement of the velocity profile, provided that the profile is semi-logarithmic. This is based on a principle of fluid dynamics called the "law of the wall", which states that the average velocity of a turbulent flow at a certain point is proportional to the logarithm of the distance from the "wall". In laboratory settings the wall is the surface of a pipe or smooth surface of a flume, whereas in a natural stream that surface is usually rough (Fig. 5.3), creating turbulence and an irregular velocity profile. In theory this near-bed profile provides an estimate of shear velocity, which expresses the force, or shear stress, of near-bed flows in units of velocity. Shear stress is useful in predicting sediment mobilization and transport, and thus is also a plausible measure of the hydraulic forces experienced by an organism on the streambed.

Three fundamental types of flow characterize moving fluids: laminar, turbulent, and transitional. In laminar flow, fluid particle movement is regular and smooth, and particles can be thought of as "sliding" in parallel layers with little mixing. Turbulent flow is characterized by irregular movement with considerable mixing. Intermediate conditions are described as transitional. In order to understand the flow environment experienced by benthic organisms, much interest has focused on the nature of flows within the boundary layer down to within a few millimeters of a stone

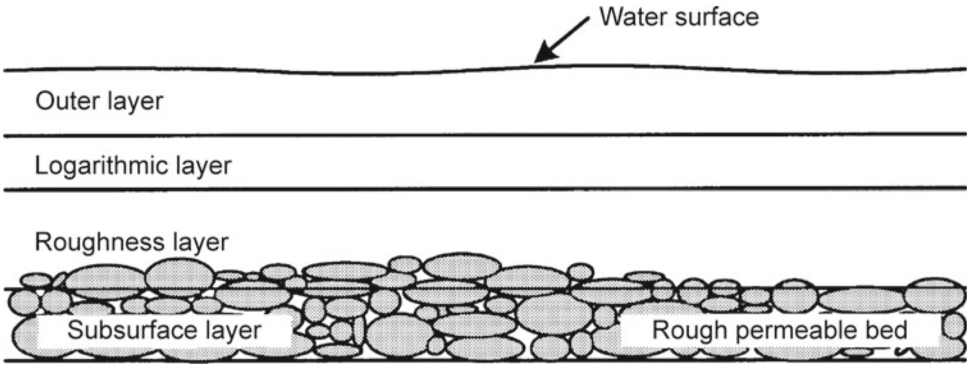

Fig. 5.3 Subdivision of hydraulically rough open-channel flow into horizontal layers. Flow velocities within the roughness layer are unpredictable based solely on knowledge of flow in the logarithmic layer. This figure is not drawn to scale (Reproduced from Hart and Finelli 1999)

surface. Flume studies indicate the possibility of much lower current velocities, less turbulence, and laminar flows very close to the substrate surface. In most natural circumstances, however, friction with an uneven streambed induces three-dimensional flows and turbulence within the near-bed environment where most stream organisms dwell (Hart and Finelli 1999).

5.1.1 Characterizing the Flow Environment

Table 5.1 summarizes some hydraulic variables in common use. Mean velocity (U) and depth (D) are the same variables described in Chap. 2, although here we use the symbols of hydraulic engineers rather than of hydrologists. Surface roughness (k_s) can be estimated in a number of ways, including from sediment dimensions such the D84 (Sect. 3.2.1) multiplied by an empirical roughness constant, and with bed profiler devices that use acoustic signals, lasers, or stereophotogrammetry to quantify topography (Bertin et al. 2014). Mean velocity, depth, and surface roughness are simple hydraulic variables that provide useful information about the flow environment. When channel depth is shallow relative to substrate roughness, such as in riffles and broken water, flow will be very complex.

The size and longitudinal spacing of roughness elements along the streambed influences the complexity of flow in the near-bed environment (Davis and Barmuta 1989). Large roughness elements such as pebble clusters and boulders are common features of poorly sorted gravel-bed rivers, where their presence generates intense turbulence downstream (Fig. 5.4). Velocity and turbulence estimates can differ appreciably on a centimeter scale downstream of these elements (Lacey and Roy 2008). Depending on their density and positioning, the wake behind each element may dissipate before the next element is encountered, which Davis and Barmuta (1989) called isolated roughness flow. When spacing between roughness elements is less, their wakes interfere with one another, producing high local velocities and turbulence, termed wake interference flow. Lastly, skimming flow describes the circumstance when roughness elements are very closely spaced, which allows flow to skim across the tops of elements and produces a relatively smooth flow environment and slow eddies in the intervening spaces.

Bed surface roughness is due not only to stones of various sizes, but also wood and vegetation. Flow measured in and around a common lotic macrophyte *Ranunculus penicillatus* showed that velocities dropped to a low and constant value within 5 cm into the plant bed, forcing most of the flow over and around it. A dead-water zone formed immediately downstream, and then a region of high turbulence (Green 2005). As Nepf (2012) has shown, the presence of vegetation in stream channels alters the velocity field across several scales, ranging from individual branches and blades on a single plant, to vegetation patches, to the channel reach.

Using open-channel measurements and certain constants, one can estimate two widely used hydraulic parameters, channel Reynolds number (R_e) and Froude's number (*Fr*). The Reynolds number quantifies the ratio of inertial forces of the moving fluid to the viscous properties of a fluid that resist mixing (Newbury and Bates 2017). It is a dimensionless number that can be used to distinguish types of flow and the forces experienced by an organism. Depth is used to estimate R_e for the channel, and the length of a fish or insect can be used to estimate the forces that act directly on an organism. At low R_e flow is laminar and viscous forces predominate, whereas at high R_e turbulence occurs and inertial forces predominate. Laminar flow usually requires current velocities well below 10 cm s^{-1}, especially if depth exceeds 0.1 m; in short, quite shallow and slow-moving water. Hence turbulent flow is the norm in the channels of rivers and streams.

Fr is a dimensionless velocity-to-depth ratio, and it differentiates tranquil flow from broken and turbulent flow (Davis and Barmuta 1989). Low values of *Fr* are characteristic of pool habitats and higher values of riffle habitats. In

Table 5.1 Some terms and equations useful in describing streamflow. It is the convention of this literature to represent velocity with U, depth with *D*, and the constant for kinesmatic viscosity of water as *v*

Terms	Description	Units	Measurement	
$\bar{U}$	Mean velocity	cm s^{-1}	Measured at 0.4 depth from bottom or from open-channel velocity profile	
U_*	Shear velocity	cm s^{-1}	Estimated from fine-scale velocity plotted against log depth near the streambed	
D	Water depth	cm	Total depth, surface to bed	
k_s	Substrate roughness	cm	Height of surface roughness elements measured individually or with bed profiler	
k_s/D	Relative roughness	Dimensionless	Height of roughness elements in relation to stream depth	
g	Acceleration due to gravity		9.8 m s^{-2}	
v	Kinematic viscosity		1.004×10^{-6} m^2 s^{-1} at 20 °C	
Equations				
R_e	Bulk flow Reynolds number	Dimensionless	$Re = U\ D/v$	$R_e < 500 \rightarrow$ laminar flow
				$500 < R_e < 10^3$ to $10^4 \rightarrow$ transitional flow
				$R_e > 10^3$ to $10^4 \rightarrow$ turbulent flow
Fr	Froude number	Dimensionless	$Fr = U(gD)^{-0.5}$	$Fr < 1 \rightarrow$ subcritical flow
				$Fr = 1 \rightarrow$ critical flow
				$Fr > 1 \rightarrow$ super-critical flow
R_{e*}	Roughness Reynolds number	Dimensionless	$Re_* = U_*\ k/v$	$R_{e*} < 5 \rightarrow$ hydraulically smooth flow
				$>5\ R_{e*} < 70 \rightarrow$ transitional flow
				$R_{e*} > 70 \rightarrow$ hydraulically rough flow

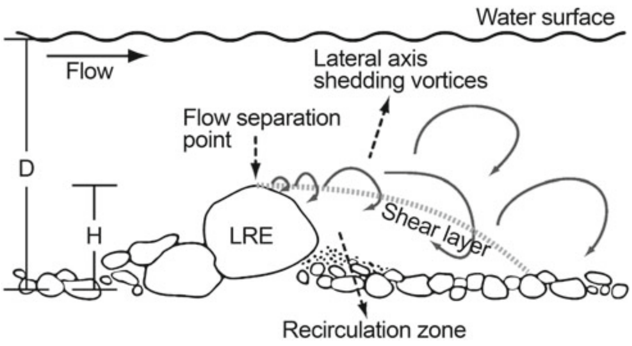

Fig. 5.4 Sideview schematic of a typical large roughness element (LRE) and associated wake characteristics, showing flow separation at a downstream point on the stone surface, flow reversal, and shear. H is large roughness element protrusion height, D is water depth (Reproduced from Lacey and Roy 2008)

some New Zealand streams, *Fr* generally was less than 0.18 and rarely as high as 0.4 in pools, greater than 0.41 and as high as 1 in riffles, and intermediate in runs (Jowett 1993).

Using an estimate of shear velocity (U_*), which can be derived from the velocity profile near the streambed, and substituting the height of roughness elements for water depth, one can estimate boundary (roughness) Reynolds number (R_{e*}) (Table 5.1). This variable and the dimensionless shear stress τ describe the conditions under which particle movement is likely to be initiated (Sect. 3.2.3). Both near-bed velocity and bed shear stress increase with increasing relative roughness (k_s/D) and mean velocity (U).

5.1.2 Flows at the Scale of Organisms

Spatial variation in hydraulic parameters has been shown to correlate with the local distribution of stream macroinvertebrates. Parameters including those based on the main channel such as mean velocity, Froude number, and Reynolds number (Statzner and Muller 1989; Mérigoux and Dolédec 2004), and those based on near-bed measurements of velocity, turbulence, and shear stress, have been found to be important (Hart et al. 1996; Bouckaert and Davis 1998; Enders et al. 2003). Such relationships are unsurprising as micro-scale studies in laboratory flumes reveal how crawling movements and posture shifts by benthic invertebrates respond to very fine-scale velocity and turbulence patterns (Weissenberger et al. 1991; Rice et al. 2008).

Efforts to understand the actual forces experienced by organisms whose profile extends less than 10 mm into the water column have been informed by fluid dynamics theory, studies of sediment dynamics, and laboratory flume studies conducted with both inanimate and living invertebrates.

From the former, we know that flow separation occurs when frictional shearing between the layers of water closest to the substrate surface becomes too great for the layer closest to the surface to remain attached. Simply put, the fluid's flow is not able to follow the shape of the stone surface or body of an organism, but instead becomes detached and reverses flow, creating eddies and vortices (Fig. 5.4). The force of fluid moving in opposite direction to the main flow is referred to as resistance or drag, and increases with the square of velocity when flow is turbulent. Even low-profile larval mayflies on a flat plate experience lift and drag as flows impinge on and separate from their bodies (Weissenberger et al. 1991). Collectively these findings indicate that most of our knowledge about the association of organisms with current are useful correlations, but a mechanistic understanding of how they cope with the forces of current requires improved methods of measurement.

Investigators have had some success in explaining macroinvertebrate distributions using average shear velocity and boundary Reynolds number estimated from the near-bed velocity profile, provided the stream bed is not too irregular and the vertical velocity profile is semi-logarithmic. Using an electromagnetic current meter to within approximately 2 cm of the stream bed in two New Zealand rivers, Quinn and Hickey (1994) found good log-normal velocity profiles at most sites sampled, and strong relationships between benthic invertebrate distribution patterns and bed hydraulic variables (shear velocity and boundary Reynolds number) under baseflow conditions. Similarly, in riffle microhabitats of the Kangaroo River of southeastern Australia, the majority of the macroinvertebrate community was associated with riffle areas of lowest near-bed turbulence (Brooks et al. 2005). Macroinvertebrate abundance and number of taxa were negatively related to velocity, roughness Reynolds number, shear velocity, and Froude number. In particular, some mayflies of the families Leptophlebiidae and Baetidae, and the water penny Psephenidae, were associated with low Reynolds numbers (Fig. 5.5).

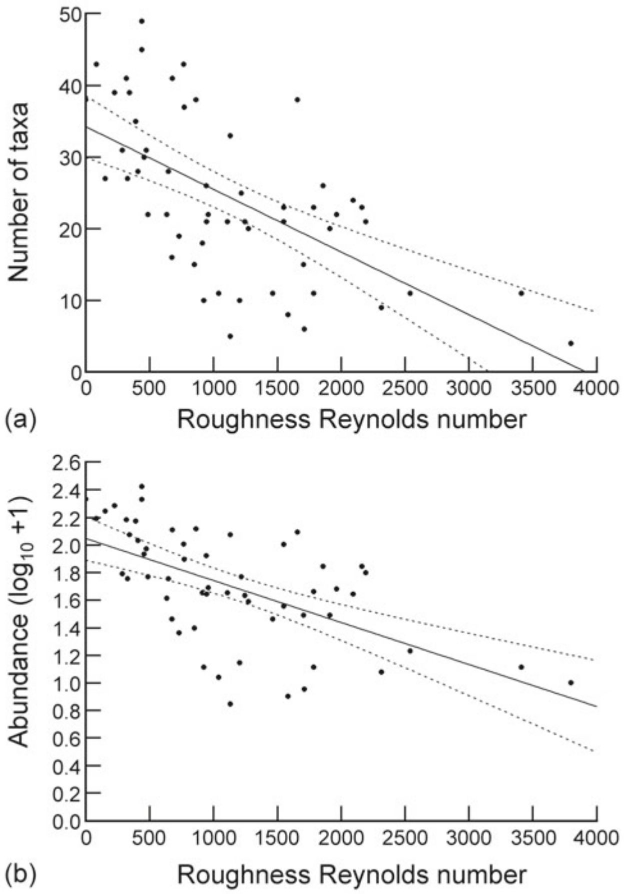

Fig. 5.5 Relationship between roughness Reynolds number and (**a**) number of invertebrate taxa and (**b**) macroinvertebrate abundance in sampled areas of 0.07 m^2 within three riffles in the Kangaroo River, New South Wales, Australia. Dotted lines indicate 95% confidence intervals (Reproduced from Brooks et al. 2005)

Commonly used current meters such as propeller and electromagnetic flow meters have a spatial resolution of one to many centimeters, and bed roughness elements in natural streams will generally cause near-bed currents to be highly variable and to deviate from log-normal (Hart et al. 1996; Hoover and Ackerman 2004). Together these considerations point to the need for fine-scale measurements that can describe the spatial and temporal variability of near-bed flows. Several new approaches have been explored in recent years in hope of more accurately characterizing flows at the scale of an invertebrate on the streambed, including the acoustic Doppler velocimeter (ADV), hot-film anemometry, syringe-like pressure devices, and a series of hemispheres of standard size but different mass placed on a flat plate on the streambed. The ADV emits sound energy that is reflected back by particles in the water, whose movement with the current causes a frequency (Doppler) shift that is proportional to current velocity. Use of ADVs is increasing because they allow three-dimensional, fine-scale velocity measurements in field settings and thus estimation of shear stress and turbulence. Hot-film anemometry is based on heat transfer and voltage drop recorded on a very fine sensor covered with a heat conducting film, calibrated against current speed for a given temperature. Using this instrument, Hart et al. (1996) were able to measure velocities only millimeters above stone surfaces, documenting extensive spatial and temporal variation at very fine scales and short intervals. Finally, methods have existed for some years to estimate current velocity using a small capillary tube and pressure differences near stone surfaces (Vogel 1996). Ackerman and Hoover (2001) have elaborated on this approach, referred to as the Preston-static tube, employing a small diameter syringe connected to a differential pressure transducer, oriented with a micro-positioning device, and positioned using dye release and an underwater periscope viewer.

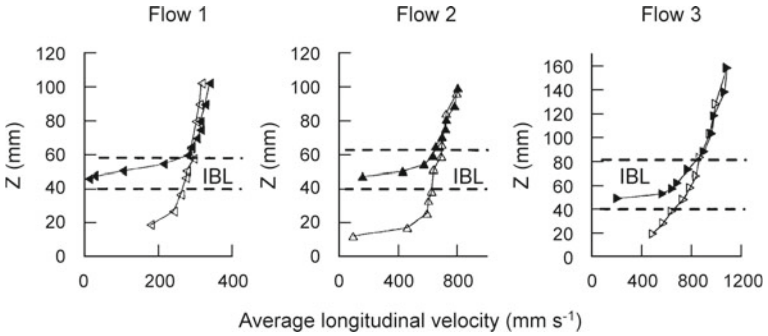

Fig. 5.6 Average longitudinal velocity over cobbles with (closed triangles) and without (open triangles) the moss *Frissidens rigidulus* in a laboratory flume at three flow levels (1 is lowest, 3 is highest). The vertical axis is distance above the stream bed. The existence of the internal boundary layer (IBL) and influence of the moss are clearly evident (Reproduced from Nikora et al. 1998)

While the above methods and devices have shown promise for measuring velocity and turbulence at centimeter and finer scales, their use is still relatively limited. ADVs and hot film anemometry are expensive instruments and the latter is vulnerable to damage and fouling under field conditions. The Preston tube does not have these limitations, but detailed measurements are laborious, and spatial and temporal variation seems almost without limit. Despite these challenges, careful studies of near-bed flows have led to very useful insights.

Nikora et al. (1998) used an ADV to examine how the presence of the aquatic moss *Fissidens rigidulus* influenced near-bed flow environment in a stream flume by measuring flow around cobbles with moss, and then repeating the measurements after removing the moss without disturbing the cobbles' position. Velocities in the upper layer followed the standard logarithmic profile, but within the lower sublayer the interaction of flow with roughness due to moss had a marked effect, reducing velocity, stress measures, and turbulence (Fig. 5.6). Using an ADV to measure flows in a flume with a constructed gravel bed, Rice et al. (2008) found that the crawling behavior of the cased caddisfly *Potamophylax latipennis* was associated with low elevations, low flow velocities, and low turbulent kinetic energies. Discrimination among locations was greater at higher discharges, indicating that caddisfly movement was contingent upon flow conditions.

Using hot-film anemometry to study the spatial positioning of blackfly larvae (*Simulium vittatum*) in a Pennsylvania stream, Hart et al. (1996) showed that larval abundance was positively related to current speed at 2 mm above the stone surface (the approximate height of the feeding appendages), but not to velocity at a height of 10 mm. In addition, velocities at 2 and 10 mm were not significantly correlated. Semi-logarithmic velocity profiles were observed in only a few instances, making estimating of shear stress from the law of the wall impractical. Near-continuous measurement of current velocity within 4-second time series revealed large fluctuations, often by at least 30 cm s^{-1} and occasionally by as much as 100 cm s^{-1}. The conclusions from this study were that velocities of 30–50 cm s^{-1} occur at 2 mm height above a stone surface, and flow is turbulent, as shown by rapid and chaotic changes in flow velocity. Hart et al. (1996) further concluded that complex bed topography was responsible for highly turbulent flow, and that much of the turbulence they observed very close to the surface of individual stones was produced not by local shear but was inherited from upstream roughness elements.

Following a month of colonization of experimentally deployed stones in a Canadian Rocky Mountain stream, Ackerman and Hoover (2001) found more algae on rougher, higher areas of the substrate and very high densities of mayfly nymphs (*Epeorus longimanus*) on high-shear regions of the upper, exposed stone surfaces. Nymphs avoided regions of flow separation at the downstream end of stones and appeared less tolerant of spatially variable or oscillatory flows. When stone orientation was reversed by the investigators, nymphs repositioned, indicating a proximate response to near-bed flows. Shear stress was measured with a Preston-static tube at grid points across the surface of each stone, and 15 measurements over a 30-s interval were time-averaged. Similar to results with hot-film anemometry, data from the Preston-static tube showed pronounced differences among points 2.5 cm apart, and vertical velocity profiles that often were not log-normal (Hoover and Ackerman 2004).

A surrogate method to estimate shear stress on the stream bed uses a set of 24 FST (FliesswasserStammTisch) hemispheres of identical size (diameter 7.8 cm) and surface texture, but different densities, calibrated against shear stress in flumes (Statzner and Muller 1989). Hemispheres are exposed sequentially on a small, weighted plexiglass plate on the stream bed near the location of invertebrate sampling, and the heaviest hemisphere moved by the flow provides an estimate of hydraulic forces experienced by the organisms.

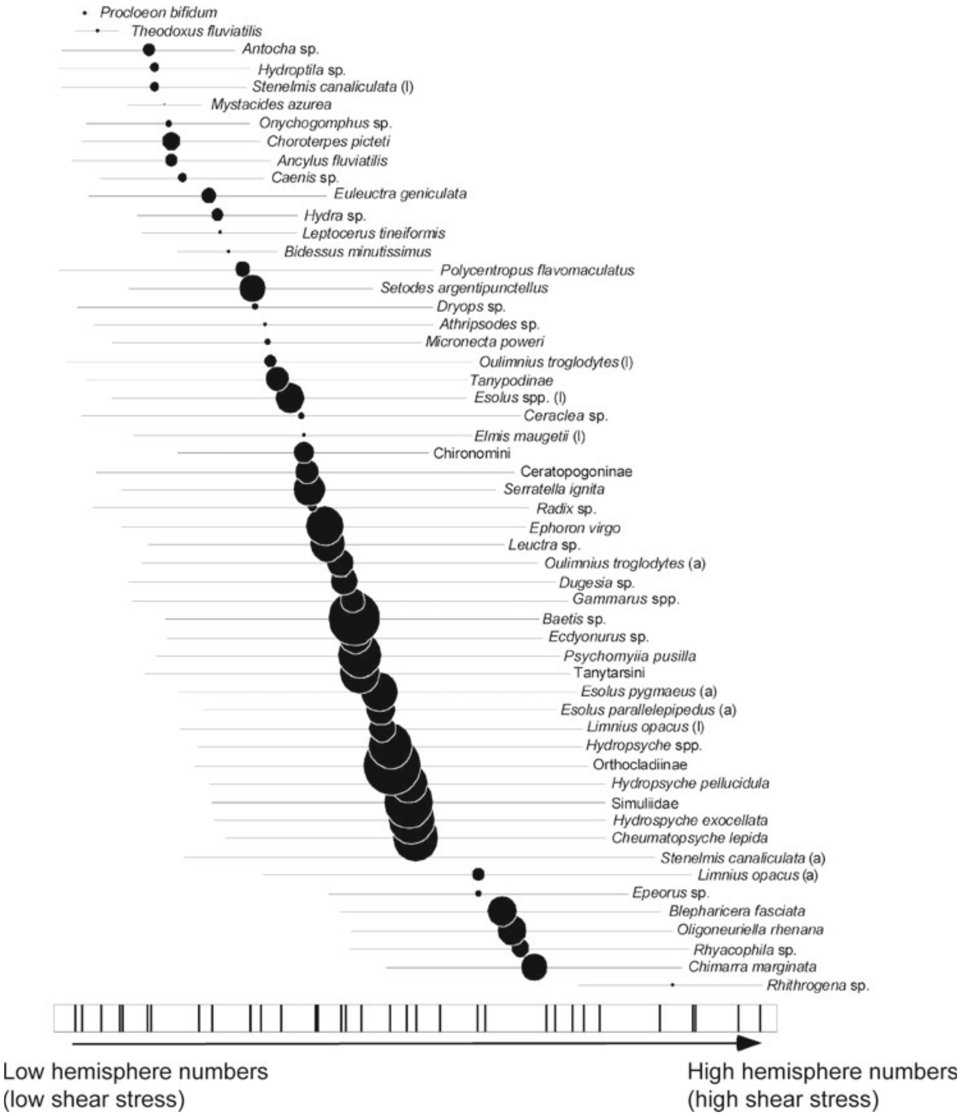

Fig. 5.7 Ordination of the fauna collected from the Ardèche River, France during spring sampling versus a hydraulic axis constructed from hydraulic parameters including shear stress estimated using the FST hemisphere method, Froude number, and depth and substrate measures. The bottom axis denotes the hydraulic axis. Taxa are positioned according to their locations along the axis, and the area of each circle is proportional to taxon abundance. Horizontal lines represent the standard deviation of the hydraulic score (Reproduced from Mérigoux and Dolédec 2004)

Their relative ease of use is an advantage, although given their size and placement on a weighted plate on the streambed, the hemispheres obviously are not a direct measure of the forces that organisms experience. Nonetheless, studies have shown that the distribution or abundances of the majority of taxa show a significant relationship to FST hemisphere numbers (Mérigoux and Dolédec 2004, Fig. 5.7). It should be noted that the shear stress axis in this figure is a linear combination of coefficients including those for FST number, depth, substrate particle size, Froude number, and bed roughness. FST number and Froude number were the most influential parameters on the sheer stress axis in this study. In another FST application, Sagnes et al. (2008) showed that some species of macroinvertebrates were found at similar shear velocities, regardless of developmental stage and body size, while others showed differing velocity preferences with size changes. Statistical associations can be quite strong for some taxa, but for many others FST number explains only about one-fourth of the total variation in densities (e.g., Dolédec et al. 2007). The FST method has been criticized for its modest level of predictive power (Frutiger and Schib 1993), which presumably indicates the importance of other environmental variables, some imprecision in the hydraulic estimates, or that some combination of factors influence habitat selection by macroinvertebrates.

The above studies demonstrate that benthic invertebrates can experience high current velocities, turbulence, and shear stress within 5–10 mm above the surface of a stone. They also draw our attention to the three-dimensional, rapid, and often extreme velocity fluctuations that occur around the time-averaged velocity across multiple scales, that is, to turbulence rather than mean velocity. Turbulence can be characterized statistically using the ratio of the standard deviation of velocity to its mean, although this also is a kind of averaging. A time series of near-bed velocities measured with an ADV more fully describes turbulence.

Turbulence is strongly influenced by bed roughness, as illustrated in Fig. 5.4. Estimating turbulent flow from current velocity measured with an ADV at 10 cm above the bed of a gravel-bed river, Roy et al. (2010) concluded that standard habitat variables had a relatively low capacity to explain turbulent properties. Mean flow velocity explained the largest proportion of the turbulent flow variation, which is unsurprising as the Reynolds number increases linearly with U, while depth and substrate showed less influence. In this study, turbulence was confined to a relatively small, localized zone in the lee of large roughness elements.

Fisheries scientists have long known that fish take advantage of roughness elements and uneven flows, sheltering behind large clasts on the stream bed. When water velocity microhabitats were quantified at the scale of millimeters, rainbow darters (*Etheostoma caeruleum*) in the Mad River, Ohio, were consistently found in microhabitat shelters where velocities were significantly lower than at adjacent (<5 cm distance) sites (Harding et al. 1998). Similarly, by holding positions in low-velocity water behind current obstructions, stream-dwelling salmonids optimize the tradeoff between the energy supply from drifting invertebrates and the energy cost of swimming (Fausch 1984). Position choice in drift-feeding Arctic grayling (*Thymallus arcticus*) was explained by a model in which net energy intake depended on capture rate, which was a function of visual reaction distance, depth, and velocity; and on the velocity-dependent cost of swimming (Hughes and Dill 1990). Because grayling must intercept prey entering their field of view before the prey is swept downstream, velocity increases the encounter rate but decreases the proportion of macroinvertebrates captured by fish.

Precisely how fish utilize or avoid turbulent conditions, which can vary at the scale of cm downstream of a roughness element, is not fully resolved. Laboratory studies show that turbulence can induce higher swimming costs (Enders et al. 2003), but also reveal the adoption of energy-saving swimming synchronized to shedding vortices (Liao et al. 2003). Brown trout in a Michigan stream take advantage of spatial variation in flows, based on turbulence measured during the day when trout presumably are in resting locations. Individuals selected positions near cover with low average velocities and low turbulence values, and avoided low velocity, high-turbulence locations (Cotel et al. 2006). In a flume experiment with hemispheric boulders that generated a range of flow velocities and turbulence, measured using an ADV, guppies exhibited different microhabitat preferences depending on size, sex, and parasite load, presumably reflective of swimming costs (Hockley et al. 2014). Larger guppies spent more time in areas of high velocity and low turbulence beside boulders, whereas smaller guppies frequented areas behind boulders with lower velocities and higher turbulence. Males, with their larger fins, spent more time in low velocities, and individuals infected with a parasite frequented low turbulence locations. In addition to differences among species and size classes in swimming ability, other factors including food availability and safety from predators is likely to influence flow microhabitat selection.

A detailed understanding of the physical forces experienced by organisms in flowing water remains a challenge for freshwater scientists. However, this field is advancing due to the arrival of more sophisticated measurement and analytic tools, as well as greater cross-fertilization among disciplines. Recent years have seen an integration of hydraulic and biological studies creating the new, interdisciplinary field of ecohydraulics (Maddock et al. 2013), which seeks to predict ecological responses to hydraulic conditions and inform management regarding habitat restoration, hydropower operations, and other flow-related impacts on the ecosystem. Although we lack a full understanding of the relationships between hydraulic characteristics and organismal behavior, there is no question that the distribution and abundance of many and perhaps most organisms exhibit a statistical association with a subset of measurable hydrodynamic parameters. These findings can be shown to have practical use in predicting how the fauna will respond to human-induced changes in flow conditions.

5.1.3 Influence of Extreme Flows

In addition to the challenge of determining the flow-associated habitat preferences of benthic invertebrates and fish under ‘normal’ flows, we would also like to know how organisms cope with extremes. This includes floods of sufficient magnitude to scour the bed, as well as sudden and rapid increases in flow (often referred to as spates or freshets) that follow a heavy rain or are due to rapid snowmelt. Recall from Sect. 3.2.5 that floods of modest magnitude are frequent, may result in episodes of streambed scour and fill, and are likely to be affect some areas of streambed more than others. At water velocity and shear stress below the levels that cause sediment entrainment, benthic organisms are affected only by the shear force exerted by flowing water. As water velocity and shear stress increase, movement of fine sediments and then coarse sediments takes place, affecting the biota through abrasion, bed scour, and habitat disruption. Floods sufficient to induce bedload transport can dramatically alter the composition, density, and biomass of benthic invertebrate communities (Holomuzki and Biggs 2000; Death 2008), and periphyton (Biggs et al. 1998).

During high-flow events, some locations may serve as refuges for aquatic organisms. These include floodplains, stream margins, depositional areas, and debris dams at the meso-scale (Lancaster and Hildrew 1993; Palmer et al. 1995; Francoeur et al. 1998), and crevices and surface roughness at the micro-scale (Dudley and D'Antonio 1991; Bergey 2005). Studies in New Zealand streams have examined the stability of local habitats at the stone or patch scale. For instance, Matthaei et al. (2000) compared invertebrate densities on stones that were well-embedded and stable, versus less stable stones lying loosely on top of the stream bed, in response to flooding. There were no differences in invertebrate densities before a moderate flood, but there were significantly higher densities of macroinvertebrates on stable stones after the event. Notably, changes were ephemeral as most differences disappeared within less than 3 weeks, largely due to animals leaving stable substrates to colonize other parts of the streambed. Effenberger et al. (2006) also documented similar, short-lived "refuge effects" in macroinvertebrate communities subjected to souring events. Freshwater mussel distribution is thought to be strongly linked to hydraulic variables because they are long-lived, filter-feeding organisms that colonize the surface substrate of the streambed. Supporting this expectation, Strayer (1999) found that mussel beds occurred in flow-protected locations of two rivers in New York, US.

Occupation of flow refuges may be the result of strong habitat preferences, simple chance in which some fraction of the population happens to be in a more protected location, or active response to changing flows. In flume studies, snails and the mayfly *Deleatidium* moved into low-velocity crevices on all substrates as current velocities increased, and caddisfly larvae *Pycnocentrodes* unreeled their silken drag-lines to reach more sheltered locations (Holomuzki and Biggs 2000). In one intriguing example, the giant water bug *Abedus herberti* apparently uses rainfall as a cue to avoid flash floods in its desert stream habitat (Lytle 1999). Fish, being larger and more mobile, are likely to shift habitat in response to rising flows. Using prepositioned electrofishing devices, Schwartz and Herricks (2005) showed that the fish assemblage of small, low-gradient Illinois streams occupied different habitats depending on flood stage. At near-bankfull flows, fish were associated with vegetated point bars and concave-bank benches, at half-bankfull conditions fish abundance and biomass were greatest in low-velocity eddies, and at base flow the main channel habitat of pools, riffles, and glides contained higher numbers and greater biomass than did lateral habitat units. Juvenile fish may be especially vulnerable to displacement and thus especially dependent on flow refuges. When juvenile rainbow trout *Oncorhynchus mykiss* were acclimated to low current speeds of 0.2 m s^{-1} in a flume with a cobble bed and then subjected to much higher currents, individuals sought cover in cobble interstices as current increased, generally to the deepest extent possible. The number of deep interstices (>20 cm depth, measured with a fine probe) determined the number of individuals that were able to find refuge, suggesting that the availability of suitable interstitial habitat may limit abundances of juvenile fishes in natural streams (Ligon et al. 2016).

Studies of streams experiencing large floods have found major changes in aquatic community distribution and structure in some instances, while others have found that stream communities were highly resistant and resilient to major floods. Comparing invertebrate and fish abundance before and after a major flood event in the northeastern US among sites that differed with respect to flood intensity, Nislow et al. (2002) observed the smallest change in fish and invertebrate abundance at a site experiencing the lowest-magnitude flood (approximately bankfull). Two other sites experienced more intense, overbank flooding and greater subsequent changes in species abundance, particularly where geomorphic change was greatest. In response to greater flood intensity, the abundance of macroinvertebrates and yearling fish declined, while over-yearling salmonids exhibited normal or greater than normal abundance.

Mortality events can also occur when streams experience intense flooding. A radiotelemetry study of tagged brown trout in a New Zealand stream, designed to study movement patterns, was interrupted by a severe, 50-year flood that caused substantial scouring, bed load movement, and removal of riverbed and bank vegetation (Young et al. 2009). Subsequent location of radio signals originating from beneath gravel banks, within debris piles, and out in the flood plain indicated that the flood killed 60–70% of the tagged fish. Though hardly fortuitous from the perspective of the investigators or the fish, this rare example confirms that flood-induced mortality can affect a substantial proportion of adult fishes in a population. This is noteworthy, as most studies of the effects of floods on fishes have shown that relative to juveniles, adults typically are impacted less.

Resistance and recovery of benthic invertebrates and fishes to flow-induced disturbance clearly depends on a number of variables. For example, the physical effects of a pronounced increase in flow will depend on the rate and magnitude of increase, channel morphology, the availability of refuges, and overall geomorphic disturbance. Impacts on the biota likely are affected by the availability of stable patches of substrate, the organisms' ability to find refuge and/or withstand increased current forces, and the timing of the event with respect to growth and recruitment. This serves as a reminder that in order to persist in a given location, populations of organisms must be able to cope with extreme events in addition to average conditions, and that episodic extreme conditions can have a large effect on the composition of stream assemblages.

5.1.4 Flow Management Applications

Knowledge of hydraulic habitat preferences and species traits that are associated with flow (e.g., Reynold's number, swimming ability, etc.) inform our ability to anticipate changes in faunal assemblages in response to flow manipulation, and our design of infrastructure (e.g., fish passages at dams) and management actions (e.g., mimicking natural flow regimes) to mitigate the effects of flow modification on aquatic communities. Fishways to allow passage by migrating fish around weirs, dams, and natural barriers have been in use in Europe since as early as the mid-eighteenth century (Katopodis and Williams 2012). However, many were ineffective, and efforts to improve fishway design after the mid-20th century benefited from testing of hydraulic relationships among various fishway types and biological assessment of their effectiveness. Studies of fishway effectiveness often have focused on salmonids due to their high economic and recreational value, and passage through dams by fish of different swimming behaviors and low commercial value has been largely neglected. Surveying 37 fishways in Portugal, Santos et al. (2012) found that more than half were unsuitable for fish species for which passage was required under the European Water Framework Directive.

In response to the widespread reduction in current velocities and total discharge due to impoundments and water withdrawals, a number of methods have been developed to estimate the necessary amount of water, termed instream flows, to meet the basic habitat needs of the biota. These methods vary in the complexity of the models used to predict changes in hydrology and in the number of habitat variables, species, and life-stages that are included. The widely used Physical Habitat Simulation System (PHABSIM) was developed as a flow assessment tool to ensure sufficient flows for aquatic life (Bovee 1982). Field sampling identifies those habitat conditions where higher densities of fish are found, and statistical models then relate preferred fish habitat to flow. PHABSIM provided managers with a basis for identifying the flows that provided sufficient amounts of the preferred habitat to sustain desired population densities of focal species. PHABSIM is relatively simple to apply, as it is based on univariate curves relating the abundance of individual species to the amount of preferred habitat (expressed as current velocity, depth, and substrate), which can be combined to develop a habitat index that varies with discharge. Applying this approach to predict spawning habitat for chinook salmon (*Oncorhynchus tschawytscha*) and steelhead trout (*O. mykiss*) in several California rivers, Gard (2009) found that occupied nest locations accorded well with model predictions. As discussed below, however, this approach has critics as well as supporters.

Throughout the 20th century, numerous channel segments in the mainstem of the French Rhône River experienced flow reductions due to diversion dams that directed river discharge through artificial channels to hydroelectric plants. After 2000, restoration efforts were undertaken to increase flows in by-passed channels. From published information about flow preferences of many species (e.g. Fig. 5.8), it was possible to predict how the species assemblage would respond to flow restoration. In reaches where the increase in minimum flow was greatest, the abundance of fish species preferring fast-flowing and deep microhabitats roughly doubled, whereas the abundance of other species declined (Lamouroux and Olivier 2015). Macroinvertebrate taxa found near the banks prior to restoration tended to decline; however, approximately equal numbers of species found in the main channel experienced either increases or decreases in abundance (Mérigoux et al. 2015). The coupling of habitat preference with hydraulic data in this study effectively predicted the ecological response of individual species, measured as the natural log of change in density. Because the habitat preference models were developed at other locations, these results also provide some confidence that statistical habitat models are transferable across sites. Lastly, when the responses were re-examined using traits

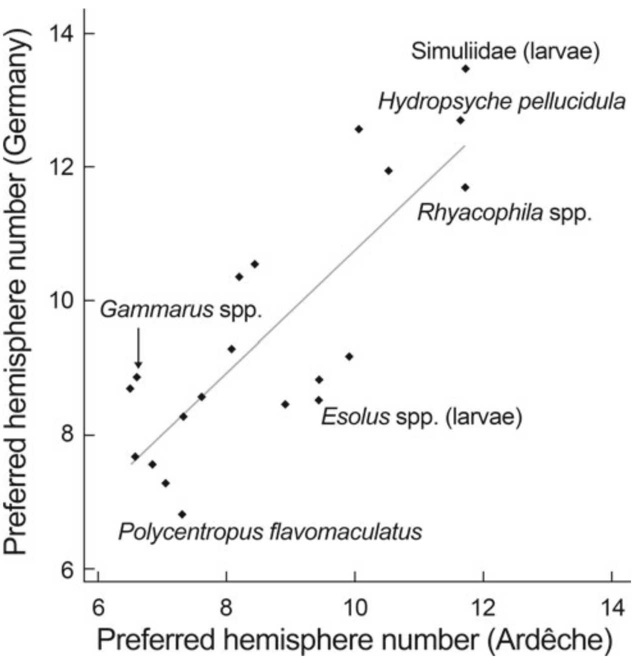

Fig. 5.8 The average 'preferred' bottom shear stress in the Ardèche River in France (data from Mèrigoux and Dolèdec 2004) predicts the average 'preferred' bottom shear stress observed in German streams (data from Dolèdec et al. 2007), for 20 taxa involved in both studies ($R^2 = 0.68$, $p < 0.001$). Some taxa, defined at different biological levels, are indicated by labels (Reproduced from Lamouroux et al. 2010)

rather than taxa, traits related to locomotion and attachment, as well as general biology and physiology, proved useful in understanding the effects of hydraulic restoration on aquatic communities (Dolédec et al. 2015). After restoration, clingers and passive filter feeders dominated invertebrate communities in the main channels. Within fish communities, species exhibiting the life-history strategy characteristic of downstream river segments (long life span, large body, late sexual maturity) increased with restoration.

Managing rivers to ensure that flow conditions support diverse assemblages of native species is an on-going, global challenge. Early models such as PHABSIM remain in use, but its shortcomings are widely acknowledged, including that it is too simple both in its description of habitat and in its modeling approach (Railsback 2016). More detailed and dynamic models that can simulate more complex flow conditions and more fully represent population processes are becoming more widely used, and may well become the standard approach in the future. This topic shares many considerations with discussions about natural flow regimes and environmental flows (Sect. 2.5) although they emphasize different outcomes. Environmental flow modelling tends to emphasize restoring the overall hydrograph in the direction of its unaltered or reference state to benefit ecosystem processes. In comparison, the motivation behind integrating habitat preferences and flow modelling is to ensure adequate environmental conditions for particular species in specific locations. Sound management strategies obviously will require both approaches applied together to support flow-related management decisions that restore or maintain the desired structural and functional attributes of rivers and streams.

5.2 Physical Habitat

Physical habitat structure is widely held to be a major determinant of assemblage composition in all types of ecosystems, as structural complexity and heterogeneity are considered to influence both individual abundances and taxon richness (number of species). Heterogeneous habitat mosaics and structurally complex habitats are expected to provide a greater range of niches, thus enabling a greater number of species to co-exist; more effective refuge from predators and physical disturbance; and a greater range and abundance of food resources. In streams and rivers, physical habitat structure includes a wide variety of inorganic and organic substrates of varying size, large objects such as boulders and submerged wood, and channel units such as pools, riffles, and bends. Substrate is especially important to macroinvertebrates, small in size and dwelling on or within the stream bed. Larger elements, including boulders and wood, are of particular importance to fish, especially larger species found in the water column. Large substrate elements in a segment of stream influence flow and scour that affect the characteristics and diversity of substrate, so they are strongly interrelated. This makes it challenging to quantify and compare the influence of physical habitat structure on organisms (Kovalenko et al. 2012). First, there are many types of substrate and habitat elements, both inorganic (bedrock, silt, sand, gravel, pebbles, cobbles, up to large boulders) and organic (leaf litter, tree roots, wood of various sizes and textures). Second, terms such as heterogeneity and complexity are often used interchangeably and are loosely defined. Third, relationships between taxon richness and habitat structure often are further confounded by variations in surface area. Complex habitats typically have a larger surface area that supports more individuals, and because the number of species generally increases logarithmically with number of individuals, more complex habitats may support more species as a consequence of greater numbers, referred to as a passive sampling effect.

Because much of the focus on habitat complexity concerns its relationship with assemblage diversity, it is useful to define a few terms. Habitat heterogeneity can be defined as both the composition (number and relative abundance) and configuration (spatial arrangement) of habitat patches or types. Habitat complexity can be defined as the total abundance of structural features, such as crevices on a stone surface or number of accumulations of large wood, in relation to surface area. A variety of statistical approaches have been employed to describe habitat heterogeneity and complexity, including fractal dimensions (a statistical index of complexity that describes how some pattern changes with the scale of measurement), and various concepts from landscape ecology that examine the surrounding mosaic in terms of the diversity, distribution, and patch size attributes of surrounding habitat types (Palmer et al. 2000; Kovalenko et al. 2012). Unfortunately, because the terms “heterogeneity” and “complexity” have been used inconsistently in published studies, it is not feasible to distinguish between them in reviewing the literature; hence, in our discussion we generally follow the terminology used by the authors of the original studies.

Species diversity generally refers to the number of species at a location, typically referred to as species or taxon richness. The latter is more general, as it can be used for datasets using genus- or family-level classification. There are also formulae that take into account the relative abundance of species, based on the premise that an assemblage in which one species makes up the majority of total individuals is less diverse than one in which dominance is reduced and a greater number of species are well represented. Total diversity can be sub-divided into the diversity within each habitat type (α-diversity; e.g., the diversity within just riffle or just pool habitats in a given reach), and the additional diversity resulting from differences in assemblage composition between habitat types or locations (β-diversity; e.g., the number of species found only in riffles, plus the number of species found only in pools). β-diversity is sometimes referred to as dissimilarity or species turnover. In practice, field studies often collect macroinvertebrates by disturbing the substrate at a number of locations and/or habitat types, and collect fish by electroshocking an entire stream reach, combining data across habitats and effectively making it impossible to distinguish α- from β-diversity. Although less commonly measured, β-diversity is a useful metric for evaluating the extent to which habitat diversity is linked to species diversity in a given system, as it identifies the total number of species that are uniquely associated with each habitat.

5.2.1 Inorganic Substrates

Many of the important features of inorganic substrate were described previously from the perspective of fluvial geomorphology (Sect. 3.2.1), where the emphasis was on the interaction of sediment supply and flow on particle transport and channel form. Relevant measurements and concepts include the size categories of inorganic particles (Table 3.3) and their quantification using pebble counts to determine the median size (D50) and range (D16 and D84); the relationship between particle size eroded and current velocity (Fig. 3.8); and the development of channel features including riffles, pools, point bars, and undercut banks, which are meso-scale physical features often referred to as habitat units. Surface substrate usually is coarser than sub-surface substrate and at least partially protects this finer material from transport, resulting in vertical heterogeneity within the stream bed. The stability of the substrate depends on the magnitude and frequency of hydrological events and particle size. Permeability of the sub-surface region (the interstitial zone or hyporheos) adds a vertical dimension to available habitat by allowing water to circulate and transport gases, nutrients, and fine organic material. Texture and the availability of crevices also can influence a particle's suitability as habitat. Low levels of siltation may be beneficial, particularly for species adapted to consuming silt for its organic content, but high silt levels usually have a negative influence on habitat for surface-dwelling organisms by reducing habitat heterogeneity, filling interstitial spaces, and coating consumers and their food resources.

Stream beds of gravel, cobble, and boulders occur in a great many regions around the world, harboring a diverse fauna of lithophilous taxa that Hynes (1970) remarks is broadly similar almost everywhere. Sand generally is considered to be a poor substrate, especially for macroinvertebrates, due to its instability and because tight packing of sand grains reduces the trapping of detritus and can limit the availability of oxygen. Nevertheless, a variety of taxa, termed psammophilous, are specialists of this habitat. The meiofauna, defined as invertebrates passing a 0.5 mm sieve but retained on a smaller sieve of 0.05 mm, can be very abundant, dwelling interstitially to considerable depth (Palmer 1990). Burrowing taxa can be quite specific in the particle size of substrate they inhabit. The mayflies *Ephemera danica* and *E. simulans* burrow effectively in gravel. *Hexagenia limbata* cannot, but does well in fine sediments. Substrates composed of finer sediments generally are low in oxygen, and *H. limbata* meets this challenge by beating its gills to create a current through its U-shaped burrows (Eriksen 1964). Invertebrates living in poorly oxygenated environments have a variety of means to create current and move oxygenated water over their bodies, including gill beating, body undulations, and other movements (Resh et al. 2008).

A number of species of fishes and other vertebrates of rivers also occur on or near particular substrates, and some fishes are quite specialized in their affinities. For example, the mud darter *Etheostoma asprigene* is restricted primarily to the backwaters of larger tributaries of the Mississippi River, the southern sand darter *Ammocrypta meridiana* to clean, sandy substrates of the Mobile River basin, and the Blenny darter *Etheostoma blennius* to the gravel and rubble bottom of fast riffles in Tennessee River tributaries in the south-eastern US (Lee et al. 1980). For gravel-spawning fish, gravels of an appropriate size that are neither compacted nor embedded with fine particles are essential for reproduction so that water flows into interstices and oxygen is transported to buried eggs. The requirements of salmonids have been especially well-studied. Substrate material must be moveable to allow the female to excavate a nest, termed a redd, and the size of stones that can be moved varies with size of fish (Kondolf 2004). Successful incubation requires circulation of water to supply oxygen, and so an excess of fines within the interstitial matrix can be harmful to egg and larval survival.

Aquatic insects also select particular substrates for oviposition. Egg masses of the mayfly *Baetis* were highly aggregated under protruding stones with specific characteristics associated with lower probabilities of desiccation in a Rocky Mountain stream (Encalada and Peckarsky 2006). Similarly, hydrobiosid caddis flies were observed lay their eggs in single masses beneath emergent rocks in an upland Australian stream, and "landing pad size" was thought to influence oviposition choice (Reich and Downes 2003).

5.2.2 Organic Substrates

Organic substrates including algae, moss, macrophytes, dead leaves, and wood vary greatly in size, the conditions where they occur (depth, current, stream size), and in their temporal persistence. Small organic particles less than 1 mm usually serve as food rather than as substrate, except perhaps for the smallest invertebrates and microorganisms. Macroinvertebrates generally are more abundant where greater amounts of fine organic matter occur on the surfaces of mineral substrates, within their interstices, and in depositional zones behind obstructions. Autumn-shed leaves and the fungi and bacteria they support are a major energy source for invertebrate consumers, especially in woodland streams, and often are most abundant in depositional zones where fine particles often are trapped. Thus, aggregations of leaves on the streambed provide food as well as habitat and typically support a high abundance and diversity of invertebrates (Mackay and Kalff 1969). On the other hand, higher plants and submerged wood are consumed by only a few specialists, and support high animal abundances mainly because these large organic substrates serve as perches from which to capture food items transported in the water column, as sites where fine detrital material accumulates, and as surfaces for algal and biofilm growth. The presence of wood in streams also adds substantially to meso-scale habitat complexity, acting both as a geomorphic agent influencing channel shape and pool formation (Sect. 3.1.5), and as important habitat.

The invertebrate taxa that live in association with aquatic plants are referred to as phytophilous. A number of species are found primarily on moss, including the free-living caddis larva *Rhyacophila verrula* and a number of mayflies with backward-directed dorsal spines that are thought to minimize entanglement (Hynes 1970). Most commonly, mosses and filamentous algae provide habitat rather than food, serving as a refuge and a trap for silt and organic matter (Steinman and Boston 1993). Macrophytes add to the physical complexity of aquatic environments, creating habitat that algae, microbes, and invertebrates may colonize (Tokeshi and Pinder 1985), and providing refuge for fishes from high flows and predators (Grenouillet et al. 2000). Some fish species preferentially spawn on submerged vegetation, attaching adhesive eggs to live or dead plants and submerged roots (Balon 1981). For examples, certain darters in the very diverse genus *Etheostoma* specialize in spawning on rotting vegetation (*E. exile*), the macroalga *Cladophora* (*E. blennioides*), and other rooted plants (*E. lepidum*, *E. punctulata*).

Xylophilous, or wood-dwelling, taxa attest that wood constitutes yet another substrate category of lotic environments. In the headwater streams of forested areas, as much as one-quarter to one-half of the streambed can be wood and wood-created habitat (Anderson and Sedell 1979). Similar to aquatic mosses, wood appears to be substrate more often than it is food. Some taxa, such as the beetle *Lara avara*, feed mainly on wood. However, this beetle has an exceptionally slow growth rate and long life cycle among stream insects (Huryn and Wallace 2000). Many wood-associated taxa actually obtain their nourishment from biofilms occurring on wood surfaces, rather than the wood itself (Hax and Golliday 1993). In lowland rivers where the substrate is largely sand, fallen trees are especially important as a substrate coated with periphyton and biofilm, and as a perch from which to collect particles in suspension (Benke et al. 1985).

5.2.3 The Influence of Physical Habitat on Stream Assemblages

The density and richness of invertebrates have been shown to correlate with amount of detritus, algal biomass, substrate stability and complexity, depth, and velocity (Rabeni and Minshall 1977; Barmuta 1989; Quinn and Hickey 1994); and the strength of correlation has been found to depend upon the spatial scale at which substrate-related variables are measured (Beisel et al. 2000). In gravel-bed rivers, a diverse macroinvertebrate fauna exhibits a patchy spatial distribution that surely is determined at least in part by the heterogeneity of the substrate. In fact, abundance and taxon richness typically are low in fine substrates and increase with substrate size at least up to gravel and cobble (Minshall 1984; Mackay 1992). Substrate size tends to decline downstream, for reasons discussed in Chap. 3, but tributaries can interrupt the longitudinal fining of substrate with inputs of coarse material. In gravel-bed rivers of western Canada, Rice et al. (2011) found an increased abundance of taxa that prefer coarse substrate at these points of sediment recruitment, as well as an overall increase in diversity.

Studies of substrate-induced habitat complexity conducted in Steavenson River, a stony upland stream in southeastern Australia, found that stone surface area accounted for some 70–80% of variation in species richness, small stones had fewer species because they had less surface roughness, and the filamentous red alga *Audouinella hermannii* enhanced roughness and the presence of macroinvertebrates (Downes et al. 1998). Using clay bricks as experimental substrate, Downes et al. manipulated three aspects of habitat structure: large surface pits and cracks, surface texture (small pits), and abundance of macroalgae. Sampled after 14 and 28 days of macroinvertebrate colonization, the majority of common species reached higher abundances on rough substrates, there was a disproportionate accumulation of small individuals, and each of the three manipulated elements of habitat structure had separate, additive effects on both the total abundance of individuals and the total number of species. Because the number of taxa increased disproportionately relative to increases in the numbers of individuals, it appeared that species richness was augmented by habitat complexity. Although this study provided strong evidence for the importance of substrate roughness, the mechanisms by which crevices and surface roughness affected the biota were unclear. Surface roughness appears to be influential for algal colonization in the Downes et al. study, but because *A. hermannii* responded strongly to surface texture, it was not possible to separate the effects on the fauna of increased algal cover alone from that of increased algae in combination with a rough surface. Similarly, following 45 days of colonization in a 4th-order stream in southern Brazil, total species richness of algae was higher on rough than on smooth substrates, and species composition differed between substrates, likely due to differences in species' capabilities to colonize substrates with or without crevices (Schneck et al. 2011).

The frequently observed positive relationship between taxon richness and measures of habitat complexity could be mediated through a positive effect of complexity on habitat area and total abundances, i.e., a passive sampling effect. In a study of macroinvertebrate richness and abundance in small patches (<0.1 m^2) in small streams in Wales, UK, surface area had the greatest influence on both abundance and richness, and richness was largely the consequence of abundance (Barnes et al. 2013). The authors detected a modest effect of complexity (estimated by a fractal dimension of surface area) but not of heterogeneity (estimated from the mix of surrounding habitats). Interestingly, habitat type (bedrock, silt, sand, gravel, pebbles and cobbles) was the single best explanatory variable (Fig. 5.9) and rendered complexity and surface area redundant in predictive models. Habitat type also was the most important variable determining assemblage composition of macroinvertebrates in three streams of Brazil. Estimating β-diversity to evaluate the relative importance of between-stream versus between-habitat effects, Costa and Melo (2008) found that microhabitat was most important in determining community composition. In essence, macroinvertebrate assemblages from adjacent but different microhabitats (stones in riffles, submerged roots of terrestrial plants, mosses at the air-water interface zone, and litter deposited in pools) in a single stream site were more dissimilar than those found in a single microhabitat at different stream sites.

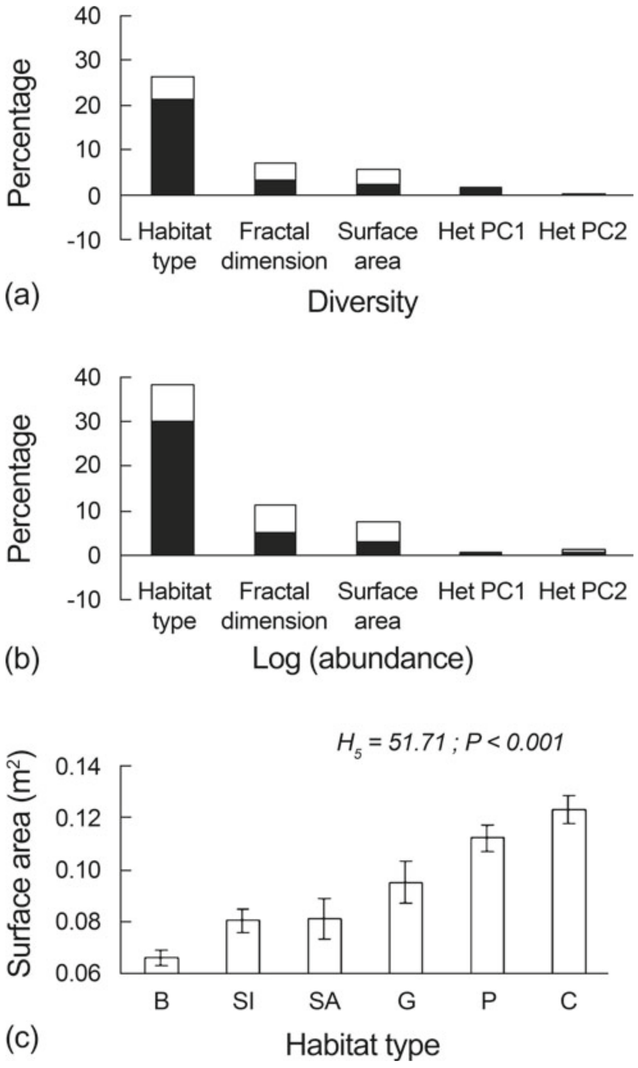

Fig. 5.9 Percentage of the variance in macroinvertebrate diversity and abundance found on different habitat types (bedrock, silt, sand, gravel, pebbles, cobbles) in a stream in Wales, UK. (**a**) diversity, (**b**) logarithmically transformed abundance. Fractal dimension and surface area were derived from profile measurements of bed surface. A Principal Components Analysis of patch size attributes and surrounding habitat types resulted in two measures of heterogeneity (Het PC1, Het PC2). Bars show amount of variance explained independently (☐) and jointly (■) by habitat type. (**c**) Surface area is highly dependent on habitat types (mean ± 95% confidence interval) B, bedrock; SI, silt; SA, sand; G, gravel; P, pebbles; C, cobbles (Reproduced from Barnes et al. 2013)

5.2.3.1 Fine Particles

Fine sediments <1–2 mm in diameter are a natural component of aquatic ecosystems, but they have become a world-wide environmental concern due to their accumulation within stream beds and clogging of substrate interstices. An increase in fine sediments within gravel-bed streams typically results in declines in total abundance and taxonomic richness for both the benthic and hyporheic faunas, with pronounced declines of aquatic insects in the Ephemeroptera, Plecoptera, and Trichoptera (EPT) groups, and increasing dominance by Oligochaeta and Chironomidae (Lenat et al. 1981; Waters 1995). By clogging interstitial pore-spaces, fine sediments restrict the circulation of water, resulting in less oxygen exchange and a shift from mostly aerobic to anaerobic biogeochemical processes.

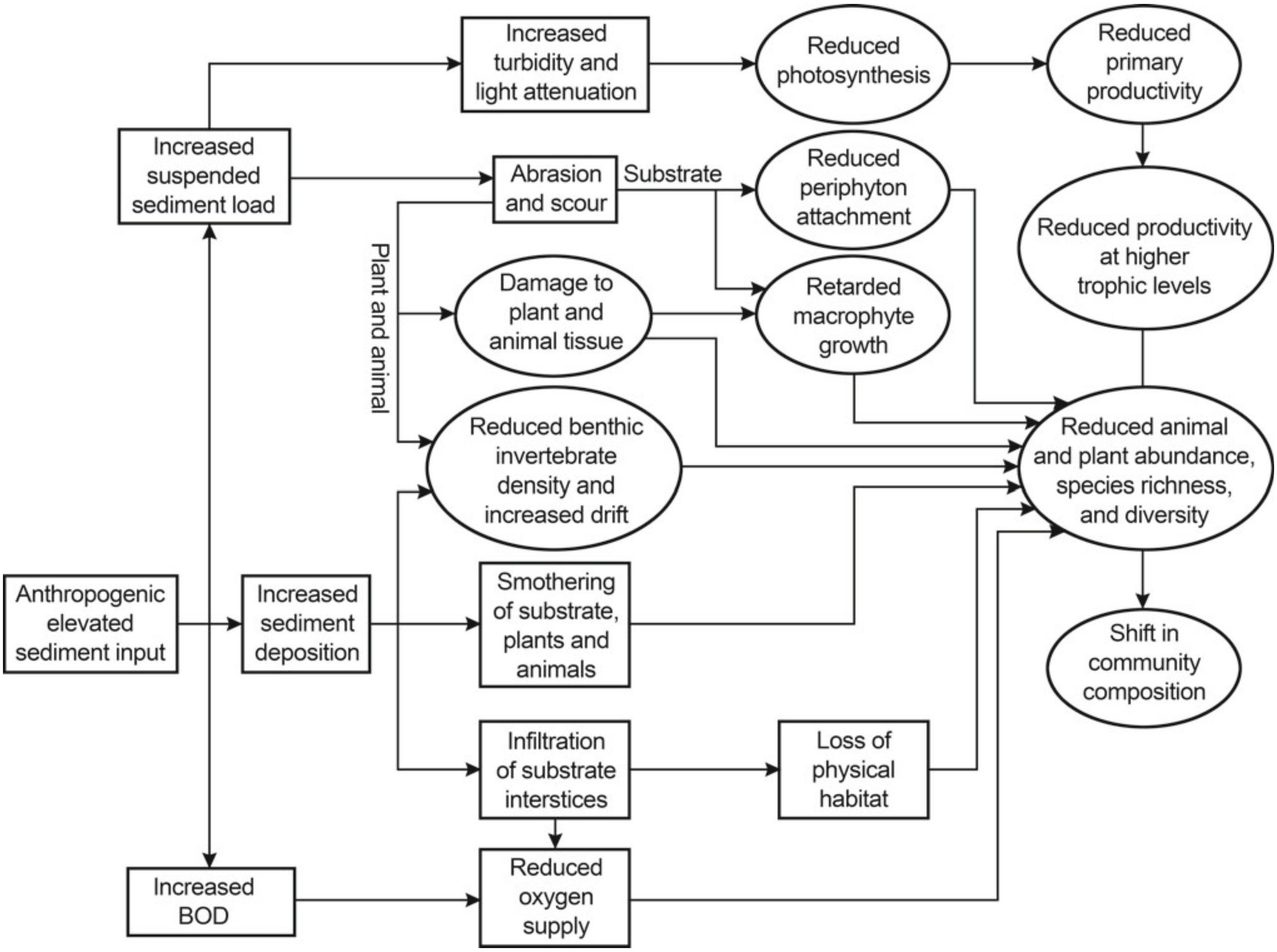

Fig. 5.10 Negative impacts of anthropogenically enhanced sediment input on lower trophic levels in stream ecosystems. Rectangles and ovals respectively denote physicochemical effects and direct and long-term biological and ecological responses. BOD is a measure of oxygen demand by aerobic organisms (Reproduced from Kemp et al. 2011)

Substrates with a high proportion of fine sediment affect lower trophic levels through a number of mechanisms (Fig. 5.10). The associated fauna frequently is dominated by taxa with low dissolved oxygen requirements (e.g., Oligochaeta and Chironomidae). Burrowing taxa of small size and deposit feeders tend to be common, while taxa sensitive to fine sediments, because of their filter-feeding or respiratory adaptations, may be absent. Surveys of macroinvertebrates and fine sediments in tributaries of the River Usk, a temperate, montane catchment in rural Wales, UK, showed pronounced changes in invertebrate composition at the patch scale (~ 3 m^2). Numbers of EPT taxa decreased by 20 and 25% at the most sediment-impacted sites relative to sediment-free sites (Larsen et al. 2009). Comparing lightly, moderately, and heavily clogged locations in three rivers of the Rhône basin of eastern France, Descloux et al. (2013) found that numbers of individuals and taxa of benthic invertebrates were significantly lower in the heavily clogged reaches than in the lightly clogged ones. Total density, number of taxa, and number of EPT taxa all exhibited a negative relationship with increasing fines following colonization of perforated cylinders that were filled with a coarse gravel matrix and 10–60% fines (<2 mm) by volume, and inserted into the stream bed for 40 days (Fig. 5.11). While benthic (the first 5 cm of the streambed) and hyporheic (deeper sediment layers) densities and taxonomic richness both were affected, the decline in taxonomic richness with an increasing percentage of fine sediment was especially pronounced for the hyporheic fauna. In a similar experiment using faunal colonization columns inserted vertically into the bed of two small lowland rivers in Rutland, UK, macroinvertebrate communities after 14 days strongly differed between those filled with washed gravel >8 mm diameter vs those with gravel plus fine sand <2 mm sufficient to fill all interstices (Mathers et al. 2017). Results varied with the date when the columns were deployed, suggesting that life cycle timing affected whether the presence of fines strongly influenced colonization.

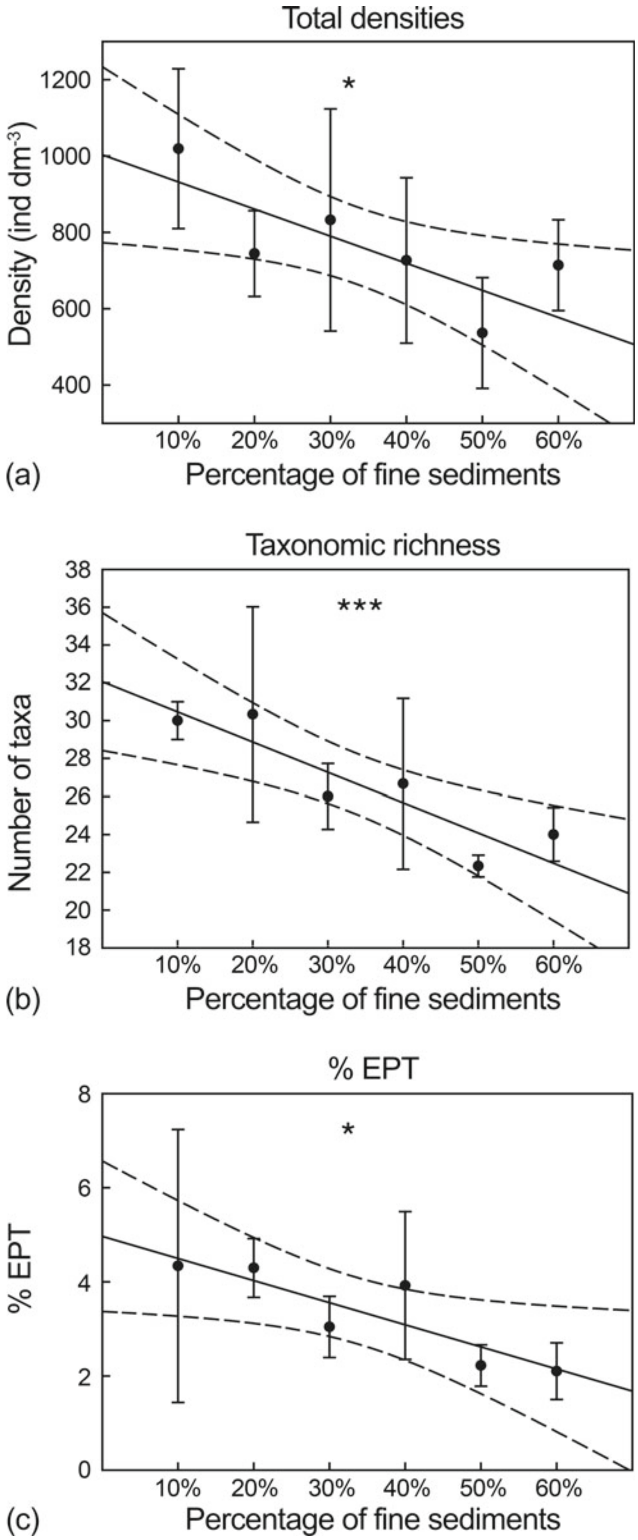

Fig. 5.11 Invertebrates colonizing vertical columns of artificial substrate containing coarse gravel and varying amounts of fine (<2 mm) sediments exhibited declines in (**a**) total densities, (**b**) taxonomic richness, (**c**) % Ephemeroptera, Plecoptera and Trichoptera (% EPT) with increases in percentage of fines. (dots: mean density for each percentage of fine sediment, n = 3 bars are standard deviation, dash line: 95% confident band). (***P < 0.001, **P < 0.01, *P < 0.05, ns non significant) (Reproduced from Descloux et al. 2013)

Studies describing indirect and direct impacts of fine sediment on freshwater fish have focused on relatively few families, notably the Salmonidae, but negative effects have been reported across a broad range of fish families (Kemp et al. 2011). Increased loading of fine sediments can have negative effects on fish via their prey populations, indirectly through changes to water quality, directly by coating gills and abrading tissue, and by degrading interstitial habitat for gravel-spawned embryos, developing eggs, and embryonic stages of fish species that excavate gravel nests. Degradation of spawning habitat due to sedimentation of fine particles is generally considered a key impact for fishes. In addition, turbidity due to fine particles in suspension has been shown to have negative effects on feeding behavior, including feeding rate and prey detection, although the strength of effect varied between species known to be turbidity-tolerant versus intolerant (Chapman et al. 2014). Fish managers frequently use various sediment control devices to manage sediments, but studies of their effectiveness are few.

Compiling lists of sediment-sensitive macroinvertebrate taxa is a useful tool in characterizing biological impairment due to excess sediments. For example, Turley et al. (2016) developed a biomonitoring tool to identify the impacts of fine sediments using data from 835 field sampling sites throughout the UK. Sensitive taxa at the family level were those whose 75th percentile of abundance corresponded with a fine sediment value of <33%. Because species assemblages differ geographically, sensitive taxa lists will require some level of regional specificity, as Relyea et al. (2012) did for separate ecoregions of the western US. One difference between that study and Turley's is that the latter had good success with family-level classification, whereas Relyea et al. (2012) found that sensitivities varied within invertebrate families and concluded that family level was insufficient for effective classification. Recognizing that the identification of sediment-sensitive taxa is for practical management applications, ease of use and accuracy of classification may be the most important factors to consider when developing classification schemes.

5.2.3.2 Macrophytes

Aquatic macrophytes acting as physical structure increase habitat complexity and heterogeneity, thereby affecting numerous species of invertebrates, fishes, and water birds (Thomaz and Cunha 2010). They do so through a chain of mechanisms that involve the availability of shelter and feeding sites (Fig. 5.12). Macrophytes of greater structural complexity typically support more abundant and richer communities of invertebrates (Taniguchi et al. 2003). As Fig. 5.13 illustrates, habitat complexity provided by macrophytes operates over a range of scales, and so can be important to epiphytic algae, to the smallest invertebrates, and to larger organisms including fishes. Greater taxon

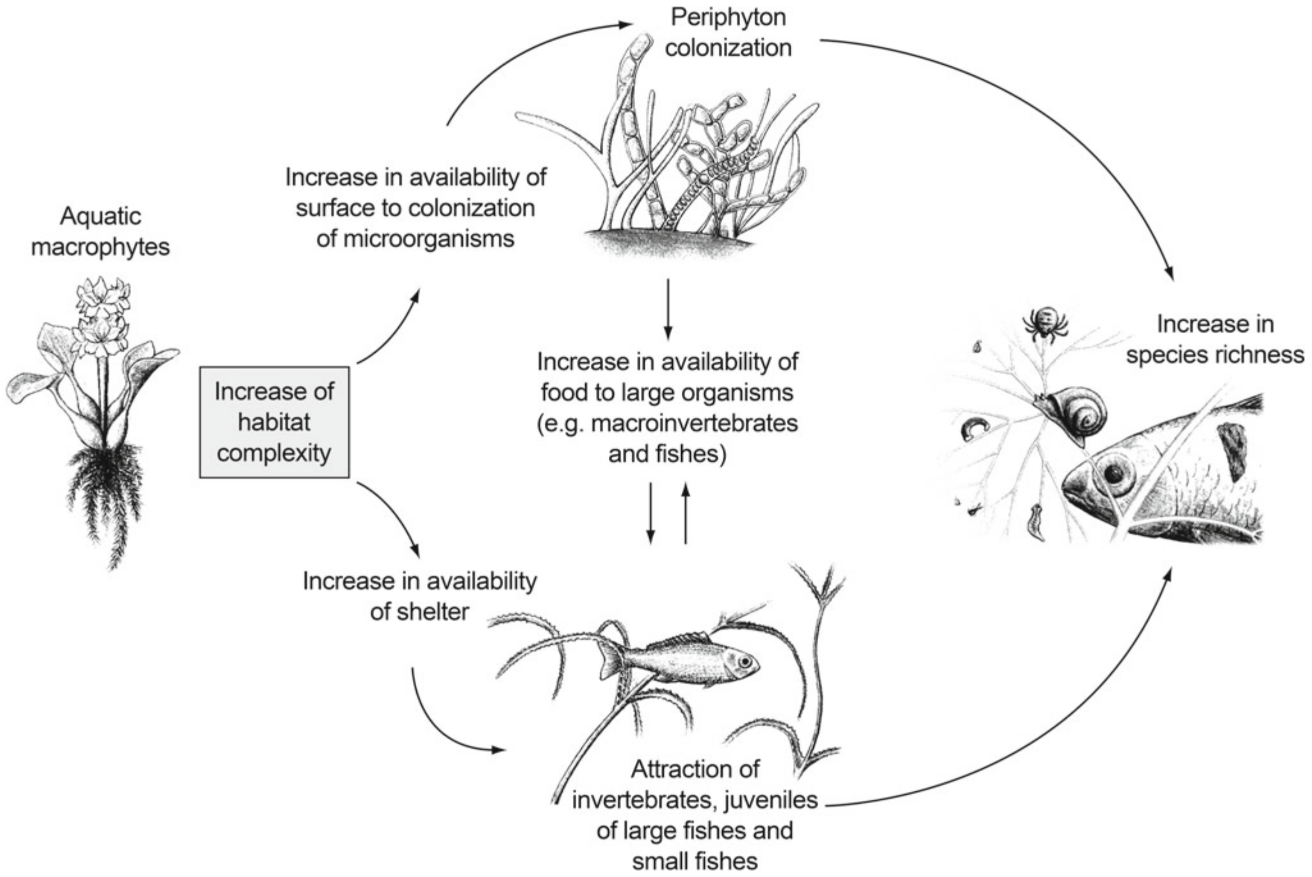

Fig. 5.12 A conceptual model depicting how the structural complexity provided by macrophytes may increase the diversity of other species in the aquatic assemblage (Reproduced from Thomaz and Cunha 2010)

richness can be explained by a greater variety of niches, whereas greater abundances may be due to more space for attachment, avoidance of predators and negative effects of current, and greater food supply for consumers of epiphytes and smaller invertebrates.

Because macrophyte complexity is influenced by details of plant architecture and is manifested at different scales, investigators have found it challenging to develop standardized measurements for cross-study comparisons. Area-adjusted number of leaves and stems, size and frequency of interstitial spaces, and fractal dimensions have been explored in various studies (Kovalenko et al. 2012). St. Pierre and Kovalenko (2014) quantified macrophyte complexity by measuring vertical and horizontal interstitial distances, finding that space-size heterogeneity was a more important contributor to macroinvertebrate taxon richness than overall complexity and the other complexity attributes examined. In a study of six representative plant species with varying physical features from lagoons and backwaters of the Upper Paraná River, Thomaz et al. (2008) examined invertebrate response as a function of plant area, a fractal dimension derived from a regression of number of objects observed against the scale of analysis, and plant identity. Their findings (Fig. 5.14), based on comparing several statistical models, indicated that invertebrate density best explained number of species, suggesting a passive sampling effect. However, complexity was also important since it appeared in the second-best model selected, and plant identity was least important. Plant area, fractal dimension, and species identity shared approximately the same importance in explaining variation in number of individuals.

Aquatic macrophytes become invasive species in many settings, as they have been dispersed around the world for ornamental objectives, human food supply, mitigation of impacted areas, and other anthropogenic interests (Schultz and Dibble 2012). Displacement of native species and biological homogenization are common outcomes of a successful invasion, but studies have also found neutral and positive effects of non-native macrophytes on macrophyte-associated species, depending upon environmental setting (Strayer et al. 2003). In some circumstances, macrophyte introduction can play a constructive role in restoring degraded aquatic environments by adding habitat complexity, which in turn supports biodiversity recovery. In

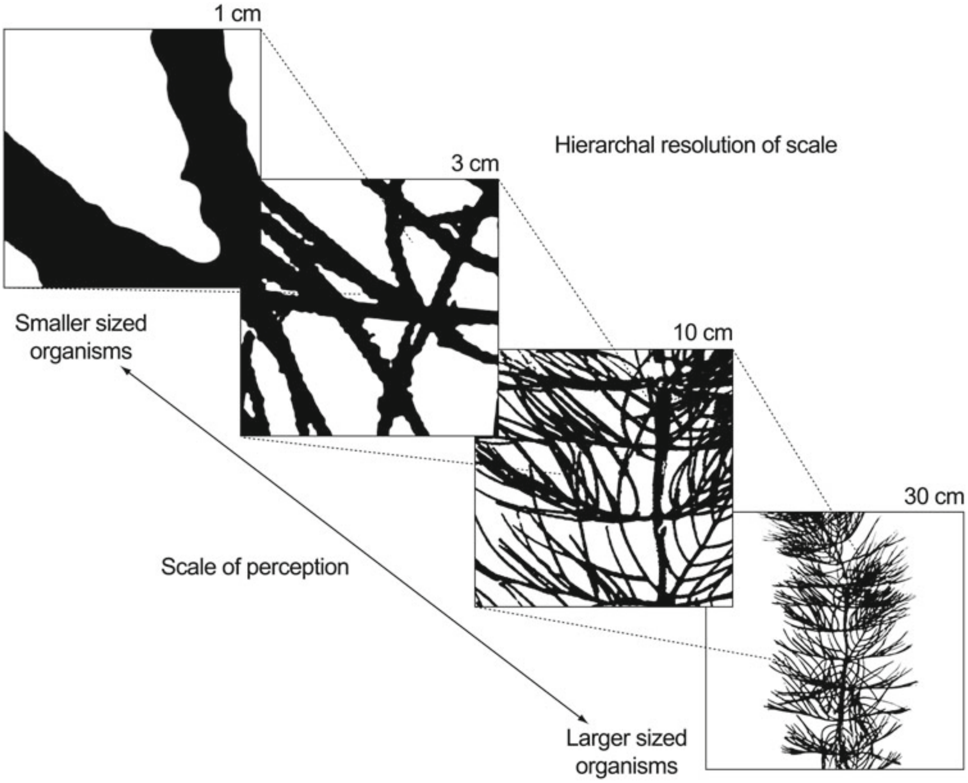

Fig. 5.13 Different hierarchal scales within the aquatic macrophyte *Myriophyllum spicatum* showing different structural complexity at different scales (Reproduced from Thomaz and Cunha 2010)

other circumstances, the control or eradication of invasive plants may be the best course of action in order to restore the original community.

5.2.3.3 Wood

Downed wood in aquatic systems is a major component of habitat complexity, provides an important substrate for biological activity, and increases the diversity of organisms (Benke and Wallace 2003). Dudley and Anderson (1982) considered 52 taxa in the northwestern US to be closely associated with wood, and another 129 to be facultatively associated. A survey of invertebrates associated with wood in Central Europe concluded that 15 taxa inhabiting freshwater ecosystems were obligate xylophagous, 22 taxa were facultatively xylophagous, and additional taxa potentially fed on wood but had not been confirmed (Hoffman and Hering 2000). Even in agricultural streams in the Midwestern US where wood was not abundant, the majority of the recorded taxa (~90%) used wood as habitat, and the presence of wood substantially increased the number of taxa at a site (Johnson et al. 2003). Wood plays key roles in streams by influencing velocity and sedimentation profiles, forming pools, and strengthening banks. For the biological community, wood provides habitat for fauna, substrate for biofilms, refuge from predators and flow extremes, and enhances in-stream diversity of fish and macroinvertebrates. It can be especially important in the simplified channels typical of many agricultural streams (Lester and Boulton 2008).

A number of studies have documented high levels of invertebrate biomass and diversity on wood (Benke et al. 1985; Scholz and Boon 1993). Wood affects a variety of invertebrate habitat conditions in streams and rivers (Benke and Wallace 2003). Dams formed by wood in small streams create pools and eddies, influencing fine-scale patterns of substrate and trapping organic matter. Trees from undercut banks that fall into the main channel may be the only stable habitat for invertebrates, especially in low-gradient, sand-bed rivers, and benefit fishes as flow refuge and source of invertebrate prey. In lowland rivers where the substrate is largely sand, fallen trees, also called snags, are especially important as a substrate for aquatic organisms. In the Satilla River, Georgia, Benke et al. (1985) estimated that snag, mud, and sand substrates occurred in the ratio 1:1.4:14 at an upriver site, and 1:3.6:18 at a downriver site. Though snag substrates were relatively limited, compared to mud and sand, snags supported more taxa and a far higher biomass of invertebrates than both mud and sand—more than half of the estimated invertebrate biomass in the river channel (Table 5.2). Interestingly, total numbers of organisms per unit area did not differ markedly between snags and sand. However, the invertebrates in the sand substrate were mostly oligochaetes and psammophilous midges of very small size,

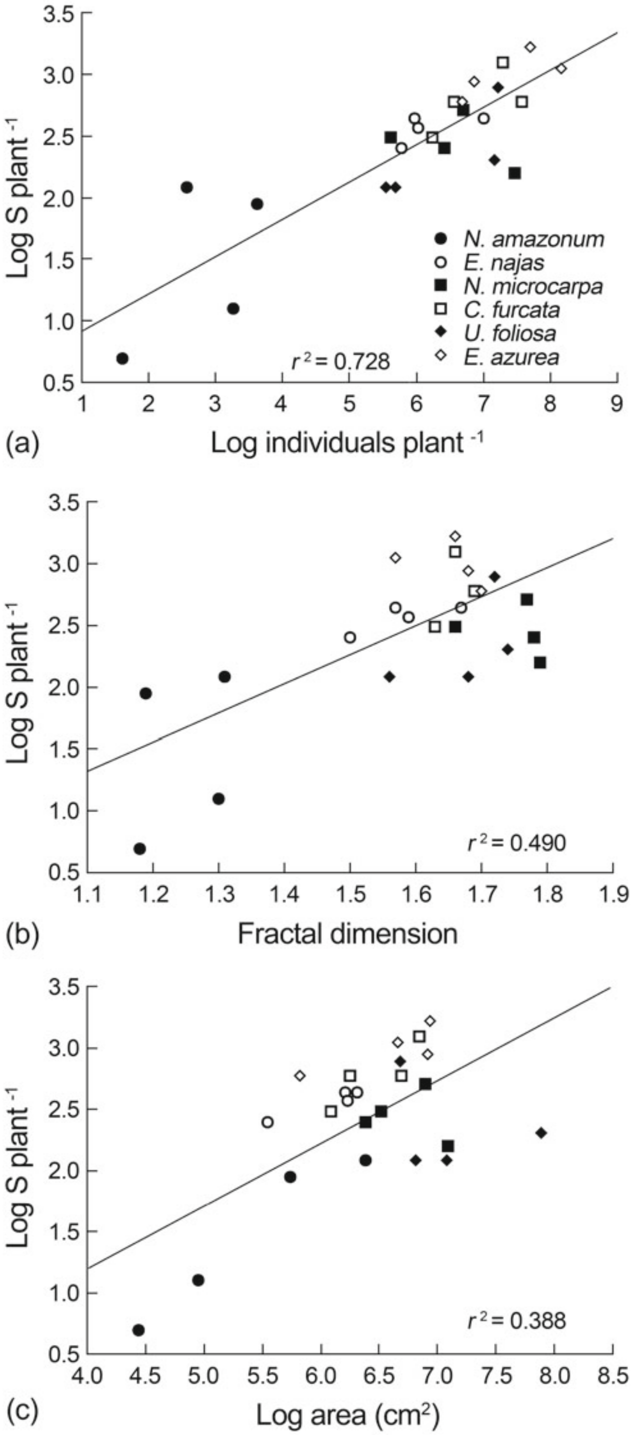

Fig. 5.14 Relationships between number of invertebrate taxa (S) and invertebrate abundances (cm^{-2}) from six plant species from lagoons and backwaters of the Upper Paraná River exhibiting different architectures: *Nymphaea amazonum*, *Egeria najas*, *Cabomba furcata*, *Najas microcarpa*, *Utricularia foliosa*, and *Eichhornia azurea* (Reproduced from Thomaz et al. 2008)

and so their biomass was modest relative to many of the organisms colonizing snags.

Although some invertebrates use wood as food or tunnel into it as habitat, most reside on its surface and feed on biofilm, periphyton, or accumulated organic particles. Biofilm (bacteria and fungi) biomass and periphyton on wood surfaces can be an important food source for detritivores (Eggert and Wallace 2007). Due to its slow breakdown, wood serves as a long-lasting substrate for biofilm development. More work is needed to understand the contribution of wood, as a food source and as a substrate, to aquatic food webs.

Numerous factors influence the recruitment and storage of wood in river systems, including forest dynamics that influence wood supply, flood and channel dynamics, and the presence of snags that provide an anchoring point for log jams (Wohl 2017). More than half of large wood in a 177-km survey of the lower Roanoke River, Virginia, US, was in log jams (Moulin et al. 2011). Individual large wood is produced mainly by bank erosion and is isolated on the mid and upper banks at low flow, where it does not appear to be important as aquatic habitat. Log jams occur near or at water level, creating bank complexity in an otherwise homogenous fine-grained channel. They occur most frequently in areas with high snag concentrations, low to intermediate bank heights, high sinuosity, high local wood recruitment rates, and narrow channel widths.

5.2.3.4 Physical Habitat and Ecosystem Processes

In addition to its effects on species abundances and diversity, physical habitat heterogeneity also may influence ecosystem processes. Following experimental manipulation of substrate heterogeneity in a low gradient stream in northern Virginia, US, Palmer et al. (2002) observed significant increases in the primary productivity of stream algae and the respiration of the benthic biofilm in high-heterogeneity riffles. Increased near-bed flow velocity and turbulence intensity, and their influence on the supply of nutrients, gasses, and organic matter, were suggested mechanisms. Habitat complexity also increases the opportunity for water exchange between the channel and interstitial spaces within the substrate. Using the transit time for dye in streams of simple versus complex habitat, Kaufmann and Faustini (2012) found that transient storage, a measure that reflects the retention of water mass due to interstitial mixing, eddies and so on, was greater in channels with wood habitat and in more complex relative to less complex channels.

Increased hydraulic complexity is expected to provide more favorable conditions for ecosystem processes. Spatial

Table 5.2 The number of taxa and standing crop biomass of invertebrates found in snag, sand and mud habitats in the Satilla River, Georgia. Wood was a small percentage of habitat but contributed over half of the total biomass to the river reach (From Benke et al. 1985)

	Wood substrates			Sand			Mud		
	No. of genera	Biomass (mg m^{-2})		No. of genera	Biomass (mg m^{-2})		No. of genera	Biomass (mg m^{-2})	
		Lower site	Upper site		Lower site	Upper site		Lower site	Upper site
Diptera	17	243	696	15	64	124	11	148	309
Trichoptera	9	4222	1581	0	–	–	3	24	30
Ephemeroptera	5	97	56	0	–	–	0	–	–
Plecoptera	2	137	109	0	–	–	0	–	–
Coleoptera	3	218	117	1	8	11	0	–	–
Megaloptera	1	379	259	0	–	–	0	–	–
Odonata	3	529	578	1	–	–	0	–	–
Oligochaeta	0	–	–	3	22	22	0	420	290
Totals	40	5825	3396	20	94	157	17	592	629

heterogeneity of flow conditions influenced bacterial diversity and ecosystem processes within 40-m-long streamside flumes constructed with different bedform heights so as to create landscapes of differing velocity variance (Singer et al. 2010). Flow heterogeneity, quantified by Acoustic Doppler Velocimetry, was positively associated with bacterial biodiversity within biofilms on the substrate as quantified by RNA fingerprinting, and also with the diversity of dissolved organic carbon (DOC) compounds removed from the water (Fig. 5.15). While the mechanisms are not yet fully understood, bacterial uptake of glucose, a highly bioavailable compound, was thought to be related primarily to turbulence-enhanced diffusion into the boundary layer overlaying the biofilm. In contrast, because DOC leached from terrestrial leaves is thought to be less easily assimilated, the influence of flow heterogeneity on its uptake may have been mainly the result of enhanced bacterial biodiversity.

5.2.4 Physical Habitat Restoration

Rapidly expanding interest in stream restoration has led to many attempts to improve stream condition and benefit biological assemblages via improvements to physical habitat. The expectation is that, by providing more habitat elements and presumably more habitat complexity, these structural improvements will benefit individual species and potentially support higher taxon richness. Weirs, flow deflectors, cover structures, boulder placements, and large woody debris are common practices for restoring habitat in rivers, as well as gravel additions for gravel-spawning fish (Roni et al. 2008). By altering flow and scour patterns, these physical structures are expected to result in more diversified physical habitat, and thereby bring about increases in fish abundance and biomass. Compiling data from 211 stream restoration projects intended to benefit habitat and salmonid populations, Whiteway et al. (2010) quantified the effect size for a number of physical and biological variables in a statistical analysis of this large data set, called a meta-analysis. Following installation of in-stream structures, pool area, average depth, large woody debris, and percent cover all increased significantly (Fig. 5.16), while riffle area decreased.

Today, many streams and rivers have greatly reduced amounts of wood, as human activities have removed wood to benefit navigation, reduce damage to bridges and other infrastructure, and constrained channels to make more riparian land available for development and agriculture. Empirical evidence attests to the positive impact wood has on habitat complexity that supports biodiversity at all trophic levels, justifying management programs to re-introduce wood to rivers with simplified channels (Roni et al. 2008). Following the placement of engineered log jams in two large Pacific Northwest, US, river systems, periphyton biomass and invertebrate densities were significantly higher on log jams than on cobbles within the same reach (Coe et al. 2009). Because these rivers experience high flows capable of moving relatively large substrate, wood serves as a more complex and stable colonization surface compared to cobble. However, invertebrate communities on wood were dominated by meiofauna, whereas larger chironomids dominated on cobbles, evidently reflecting different preferences for substrate type among these taxa.

Placement of wood in streams typically leads to improvements in physical habitat characteristics including increases in pools, cover, and habitat complexity known to

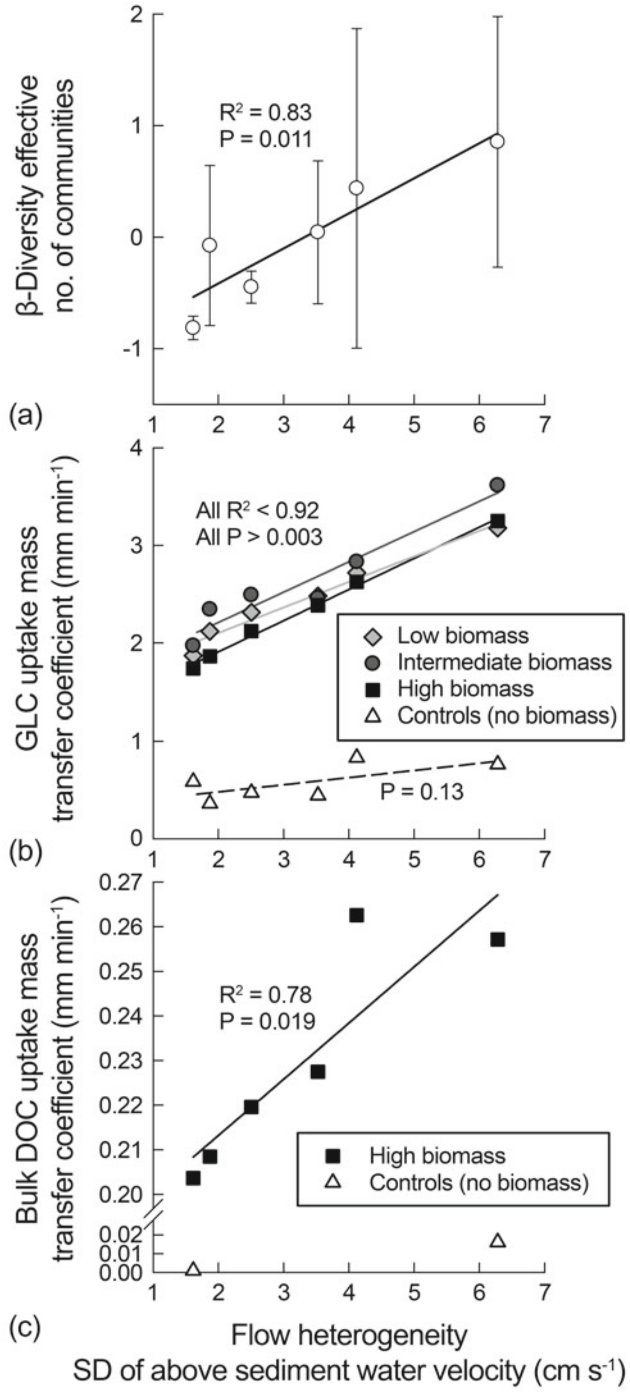

Fig. 5.15 Bacterial diversity, glucose uptake and leaf leachate DOC uptake all increased as a function of flow heterogeneity in experimental flumes. Flow heterogeneity was quantified as the standard deviation of 3-dimensional velocity measured with an Acoustic Doppler Velocimeter. (**a**) β-diversity is a measure of diversity of bacterial types among microhabitats. Diversity was classified using RNA fingerprinting. (**b**) Glucose is a highly bioavailable compound to bacteria. Its uptake is estimated by a mass transfer coefficient derived from declines in concentration over time. (**c**) Uptake of dissolved organic carbon (DOC) derived from terrestrial leaf leachate. DOC is a mix of compounds considered much less biologically available than glucose. Experimental flumes employed a range of bedform topographies to create flow heterogeneity. A flume without bedforms served as a control. Triangles indicate controls with no biofilms in (**b**) and (**c**) (Reproduced from Singer et al. 2010)

be important to fish (Roni et al. 2014). Although a few studies have reported high structural failure rates, most additions of wood remain stable in stream channels for more than a decade. A long-term study of five small streams in Colorado, US, illustrates the benefits (White et al. 2011). All streams supported wild populations of primarily brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta),* or a mixture of brook, brown, and rainbow trout (*Oncorhynchus mykiss*). Log weirs installed as trout habitat survived well over more than two decades and brought about rapid and long-lasting increases in trout abundance. Pool volume was more than three times higher in treatment sections of a 500-m study reach, and mean depth was also greater. Adult trout benefited but no response was detected for juveniles, probably because their recruitment is strongly influenced by the variable effects of snowmelt runoff. In the more than 200 projects reviewed by Whiteway et al. (2010), salmonid local density and biomass both increased significantly, with 73% of projects resulting in increased densities and 87% in increased biomass. Results differed among size classes and species, with greater response by larger individuals and by rainbow trout. Studies of non-salmonid fishes, while fewer and limited in scope and duration, suggest a positive response of species richness in more diverse systems (Roni et al. 2008). Wood addition is not always a panacea for enhancing native biodiversity, however. An experiment involving the placement of 20 engineered log jams over an 1100 m reach of a river in south-eastern Australia substantially improved sediment storage and somewhat improved pool and bar areas, but after four years there was no significant increase in richness or abundance of fishes in the test reach compared to the control (Brooks et al. 2006).

Often it is unclear whether to attribute increased numbers and biomass to population gains resulting from higher recruitment, survival, and growth, or to population redistribution due to movements of individuals into the restored reach (Gowan and Fausch 1996; Roni et al. 2008). The population in question may not be limited primarily by habitat, or different life stages may be limited by different factors, creating a population bottleneck that better habitat alone cannot fix. Immigration almost certainly contributes to rapid increases in fish abundance following habitat enhancement, especially by large, dominant individuals seeking more complex habitat or more profitable feeding positions.

Studies of the response of macroinvertebrates, while fewer in number, nonetheless are adequate to indicate that the meso-scale physical habitat elements provided to benefit fish or create a more natural appearance, at best have mixed success for benthic invertebrates. The review by Roni et al. (2008) found that effects on macroinvertebrates were highly variable based on a number of response metrics, including abundance, diversity, and traits such as functional feeding groups. Although a few studies reported positive responses,

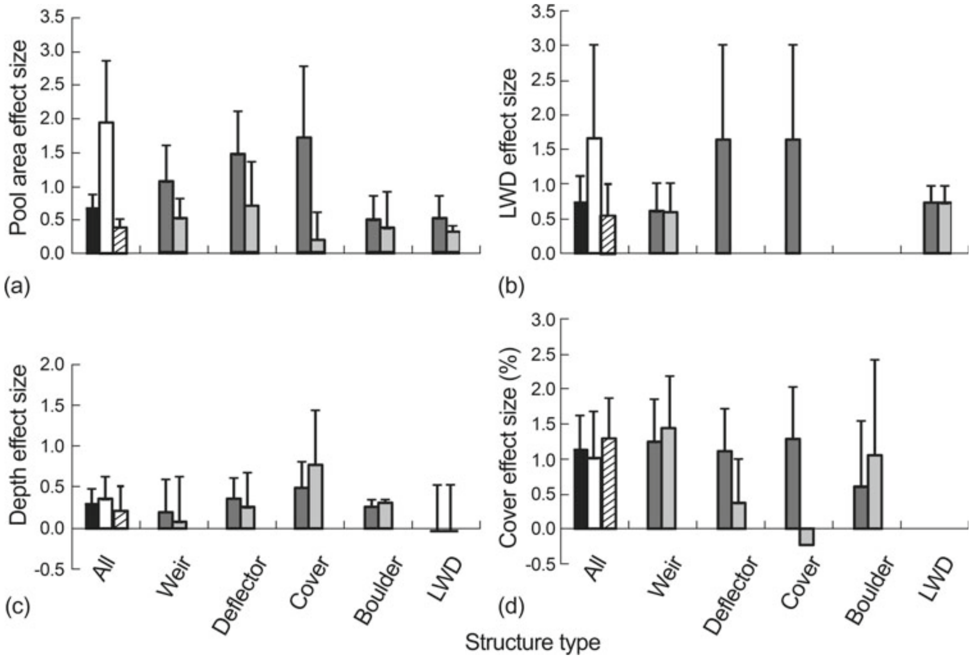

Fig. 5.16 Effect size (mean +95% confidence interval) estimated as the natural log of (treatment mean/control mean) of (**a**) pool area, (**b**) pieces of large woody debris (LWD), (**c**) stream depth, and (**d**) cover. Within the "all" bars, the solid bar represents the average effect for all structure types, the open bar represents projects that utilized only one type of structure, and the hatched bar represents projects that used two or more structure types. Within each structure type, the darker shaded bar represents the mean for all projects that used that structure (whether or not another type of structure was used) and the lighter shaded bar represents the mean for projects that only used that type of structure (Reproduced from Whiteway et al. 2010)

many did not, leading Roni et al. to suggest that macroinvertebrates may be neither sensitive to nor appropriate as success indicators for fish habitat enhancement projects. A review of 78 individual projects found that most were successful in enhancing physical habitat, but only two showed statistically significant increases in macroinvertebrate biodiversity that made them more similar to reference sites (Palmer et al. 2010). However, a meta-analysis that included only a small number of well replicated studies did find significant, positive effects of habitat restoration on macroinvertebrate richness relative to unrestored control reaches or pre-restoration conditions (Miller et al. 2010). Density also increased in restored reaches, but not significantly so due to variability in the direction and magnitude of density responses. Addition of large wood resulted in significantly greater increases in macroinvertebrate richness than did boulder additions, by adding pool–riffle morphologies and increasing the proportion of low velocity depositional habitats characterized by finer particle sizes, organic matter retention, and favorable conditions for shredders, collector-gatherers, and predatory macroinvertebrates that otherwise are rare or absent within channelized reaches. Using land use as a proxy for watershed-scale conditions, restoration projects implemented in forested upland environments exhibited more consistent, positive density and richness responses than projects located in agricultural or urban areas (Fig. 5.17). Similarly, channel re-configuration in four degraded urban streams in the Piedmont region of North Carolina resulted in no improvement in habitat or biological condition (Violin et al. 2011). Restored urban streams were indistinguishable from those not restored, and did not transition in the direction of forested streams chosen as the reference or desired condition. The authors inferred that watershed-level hydrologic processes prevented change.

Habitat improvements to benefit macrophytes have received less study, but the evidence that exists is encouraging. Surveys of macrophyte communities of 40 restored river reaches in the lowland and lower mountainous areas of Germany when compared with upstream, unrestored reaches documented significant responses to a mix of hydrologic and morphological channel improvements (Lorenz et al. 2012). In comparison with the deep, uniformly flowing character of the unrestored reaches, restored reaches had wider and shallower stream channels that were less shaded, thus enhancing macrophyte growth, and more diverse flow and depth patterns, providing conditions for a more diverse assemblage. Macrophyte cover, abundance, and diversity all were greater in restored reaches (Fig. 5.18), despite the fact that restored and unrestored reaches were on average 0.5 km apart, and no restoration at the watershed scale took place. More natural and diverse substrates and an increased

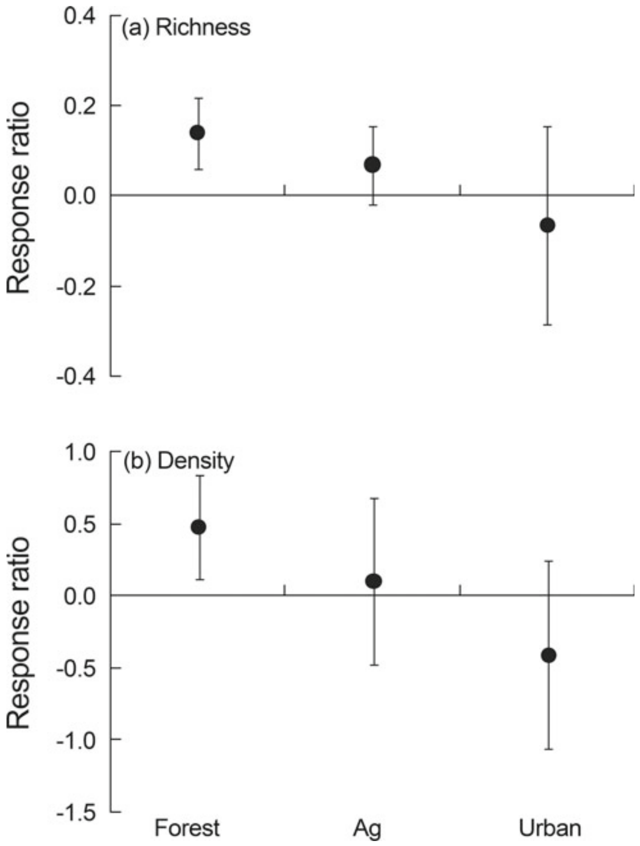

Fig. 5.17 Average response ratios to restoration with 90% confidence intervals for (**a**) macroinvertebrate richness and (**b**) macroinvertebrate density compared among forested, agricultural, and urban reaches (Reproduced from Miller et al. 2010)

floodplain area in the restored reaches were primarily responsible, as well as a greater variability of current and depth patterns.

The mixed success of restoration projects has multiple plausible explanations, including how well executed and long-lasting is the project, conditions in the upper watershed, and whether the outcome was evaluated based on population response or taxon richness, among others (Roni et al. 2008; Stewart et al. 2009; Kail et al. 2015). Because restoration measures often are reach-scale, covering short stretches of rivers, it is not surprising that outcomes can be offset by problems at the watershed scale that remain unresolved. The most important predictors of restoration success in a meta-analysis by Kail et al. (2015) were project age and agricultural land use in the upstream catchment. The negative influence of these two variables indicate that restoration actions often deteriorate over time, and that other environmental variables for which agricultural land use is a proxy, including water quality, sediment loading, and hydrologic variability, may offset the anticipated benefits of instream habitat improvements. Some of the variability in the effectiveness of instream devices is because instream devices tend to be less effective in larger streams (Stewart et al. 2009).

Despite the mixed verdict on the success of stream restoration to date, and in particular the uneven benefits to macroinvertebrates, improvements to physical habitat frequently benefit fish—usually the intended target—and may benefit other taxa as well. Loss of habitat complexity in streams and rivers is widespread, the result of wood removal, channel alteration, the floating of logs by river to market, altered hydrology, and more. Efforts to increase habitat complexity in streams are based on scientific understanding of organism-habitat relationships, and result in significant improvement when well designed and well matched to the geomorphic processes at work (Roni et al. 2015). Consideration of other factors such as water quality, hydrology, and habitat connectivity acting at larger scale than the typical single project can do much to ensure a successful biological outcome. As with all aspects of river restoration, learning from experience is critical to improving practices for the deployment of physical habitat structures and to ensure that the return on investment justifies the effort.

5.3 Temperature

Figure 5.19 illustrates the main factors that influence stream water temperatures. The heat flux at the air-water interface results from energy exchange mainly from solar and long-wave radiation, evaporation, and convective heat transfer resulting from temperature differences between the river and the atmosphere (Caissie 2006; Olden and Naiman 2010). Detailed heat budgets find that radiative fluxes account for most (>70%) of heat inputs, but friction of the water with the bed and the banks and heat transfer from the atmosphere were also significant sources of heat energy (Webb et al. 2008). Evaporative heat transfers can account for significant cooling. Topography or geographical setting is important because it influences atmospheric conditions, and stream discharge because it influences the volume of water to be heated or cooled. Heat flux at the streambed, though considerably smaller than at the air-water interface, may be important in some settings, the result of geothermal heating and of heat transfer through groundwater inputs and hyporheic exchange.

The processes that influence stream temperature vary in their relative importance along a river's length from headwaters to mouth (Poole and Berman 2001). Mean daily water temperature generally is close to the groundwater temperature in headwater streams, and increases in the downstream direction. In temperate climates, groundwater inputs usually are cooler than channel water in spring and summer, and

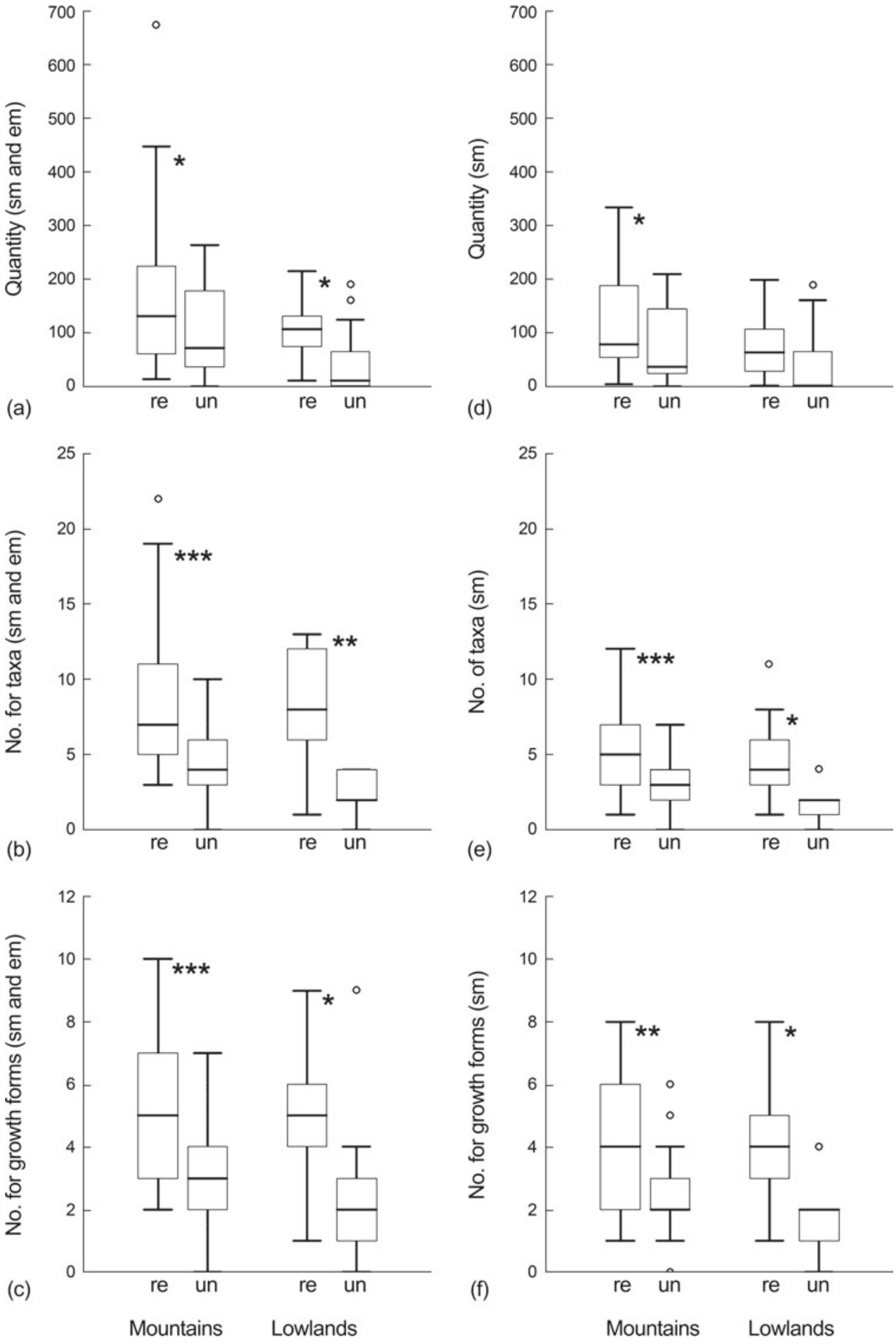

Fig. 5.18 Macrophyte quantity, number of taxa, and number of growth forms were significantly higher in restored reaches than in unrestored reaches. Box–Whisker plots show differences in restored (re) and unrestored (un) mountain and lowland reaches in macrophyte quantity (**a**, **d**), richness (**b**, **e**), and number of growth forms (**c**, **f**). Left panel (**a**–**c**) submerged and emergent macrophytes, right panel (**e**–**f**) only submerged macrophytes. sm, submerged macrophytes; em, emergent macrophytes, *P < 0·05, **P < 0·01, ***P < 0·001 (Reproduced from Lorenz et al. 2012)

warmer than channel water in fall and winter. As a consequence, headwater streams that have strong groundwater influence commonly are cooler than would otherwise be expected in spring and summer, and warmer in fall and winter. Additionally, in alluvial streams with highly permeable gravel and cobble streambeds, there can be considerable bidirectional exchange of water between the channel and alluvial aquifer, referred to as hyporheic exchange (Arrigoni et al. 2008). When surface water flows into the hyporheic zone it is referred to as downwelling or hyporheic recharge; the reverse is upwelling or hyporheic discharge. Because the annual range in hyporheic water temperature is typically less than that of channel water, hyporheic discharge commonly reduces the diel range in channel water temperature. In streams and rivers with substantial but spatially variable hyporheic exchange, considerable thermal

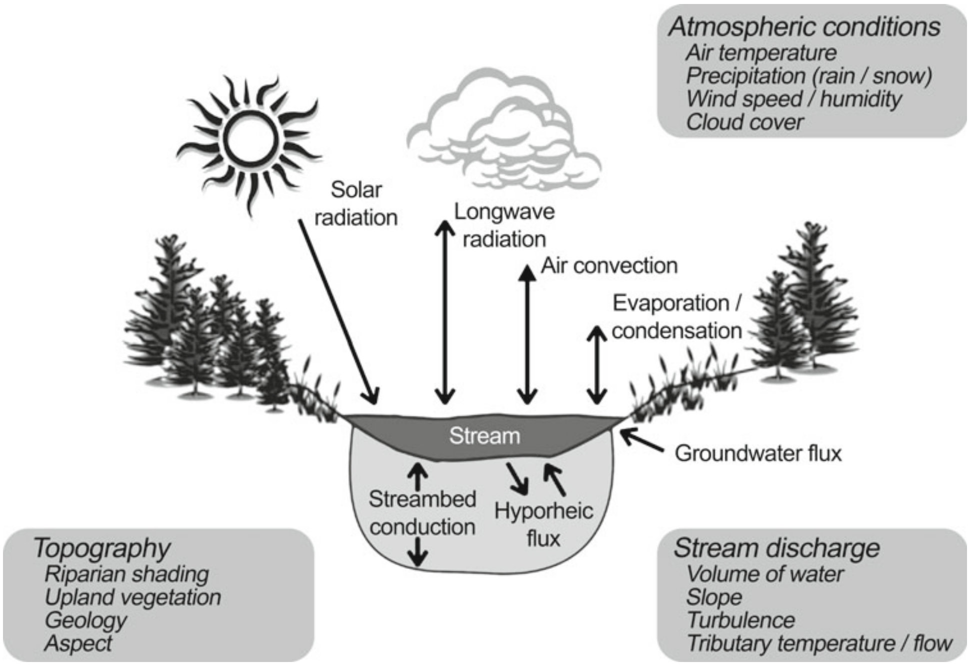

Fig. 5.19 Heat exchange processes responsible for variability in water temperatures and the physical drivers that control the rate of heat and water delivery to stream and river ecosystems (italics) (Reproduced from Olden and Naiman 2010)

heterogeneity can occur. In the gravel- and cobble-bedded Umatilla River, Oregon, Arrigoni et al. (2008) recorded diverse daytime and nighttime mosaics of surface water temperatures across main and small channels, despite only minor differences in daily mean temperatures among the channels.

As a small stream becomes a larger river, increasing width lessens the moderating influence of riparian shade on heat inputs, and the influence of groundwater lessens as well. Tributaries entering the main channel may be warmer or colder, interrupting the gradual downstream increase in average temperature that would otherwise be expected. Floodplain pools and lakes when isolated can reach different temperatures and when re-connected can influence temperature in the main channel. In most temperate rivers, the annual temperature range is between 0 and 25 °C, but desert streams can reach nearly 40 °C, which is near the thermal tolerance even of fishes adapted to these extreme environments (Matthews and Zimmerman 1990). At high latitudes and elevations, maximum temperatures rarely exceed 15 °C, and they can be cooler yet in very cold climates where ice-cover can extend for over half the year.

Temporal variability is observed on daily, annual, and longer timeframes. Streamwater temperature generally reaches a daily minimum in the early morning and a maximum in late afternoon to early evening, and this diel variation is most pronounced in wide, shallow rivers of medium size. Groundwater dominance in small streams and thermal inertia in large rivers are responsible for dampening diel fluctuations. Tropical rivers can have very constant river temperatures owing to the constancy of solar radiation throughout the year and, in the case of large rivers, their thermal inertia. The Amazon River at Manaus, Brazil, at 29 ± 1 °C, is one of most thermally stable water masses in the world (Sioli 1984).

Air and stream temperatures usually are well correlated, both seasonally and across locations, allowing air temperature to be used in predictive modeling. Simple regression models using weekly or monthly data have proven effective in predicting water temperature from air temperature, and more complex models may include heat flux estimates and some measure of long-term temperature fluctuations (Caissie 2006). Because the water–air temperature relationship departs from linearity both at low and high air temperatures, such models may be linear using a limited range (roughly 0–25 °C), or sigmoid using a wider range of air temperatures. For temperatures above freezing, Crisp and Howson (1982) found that mean weekly water temperatures (and the growth rate of brown trout) could be predicted from air temperatures using a 5–7 day lag. Some 60% of their estimates were within ±1 °C, and 80% within ±1.5 °C, of the measured stream temperatures. Despite the frequent use of correlations between air and water temperatures, however, solar radiation, not convective warming of water by the air, is the main heat input to streams, and so air temperature is better viewed as a surrogate rather than as a causal variable (Johnson 2003). In fact, statistical models to predict stream temperatures based on more readily available data on air temperatures, although widely used, have limited ability to project stream temperatures over time. This is because the underlying processes governing heat budgets of air and water are distinctive in each medium (Arismendi et al. 2014).

Comparison of modeled to observed streamwater temperatures also provides insight into departures from expectations that implicate anthropogenic influences. Using weather data to estimate the water temperature at which the sum of all heat fluxes through the water surface is zero, termed the equilibrium temperature, Bogan et al. (2003) compared stream and equilibrium temperatures for 596 stream gaging stations in the eastern and central US as a way to identify moderating influences. Weekly equilibrium temperature was a good estimator of weekly stream temperature for approximately one-fourth of stream gaging stations, those with no or minimal wind sheltering or sun shading. For the remaining three-fourth of streams, weekly equilibrium temperature was still a good predictor of weekly stream temperature, but with a significantly reduced slope, indicating the importance of other factors in addition to surface heat exchange.

In geologically complex regions, the source water of the tributaries of a single river system can be very different, resulting in a wide range of thermal habitats among headwaters that in turn may favor greater biodiversity as well as provide unique thermal niches for endemic taxa. In alpine streams of the French Pyrenees, where source waters include glaciers, snowpack, karst groundwater, and hillslope aquifers, karstic groundwater streams are coolest and most stable, hillslope groundwater streams are warmest and most variable, and glacial streams warm and become more variable downstream (Brown et al. 2007). Temperature variation due to source water and flow paths can be observed at much finer scales as well. In floodplain sections of the Tagliamento, a large, braided river of the Swiss Alps, cool-water habitats governed by groundwater inputs differ by as much as 15 °C from warm-water habitats of semi-isolated backwaters (Arscott et al. 2011). Microhabitat-scale temperature variation also is observed when stream water is forced into or drawn out from the streambed due to topographic undulations, meanders, bars, or other channel obstructions (White et al. 1987).

In addition to atmospheric, groundwater, topographic, and other physical controls on stream temperatures, various human influences significantly affect water temperatures. Most often the result is to warm rather than to cool, with the notable exception of bottom release reservoirs. Human influences likely to result in stream temperature warming include loss or reduction of riparian and upland forest cover and stream widening, which increase heat flux into the stream; reduced stream flows, which lower the volume of water to absorb heat; reduced groundwater exchange, usually a source of cooler water; discharge of warm-water effluents from municipal and industrial sources and from runoff over paved surfaces; and the effects of global warming, including increased air temperatures. Lakes and small impoundments are likely to have a warming effect. Large reservoirs that release cold bottom water typically lower stream temperatures in summer and warm them in winter. Hester and Doyle (2011) concluded that most human influences typically altered stream or river temperatures by 5 °C or less, but warming due to loss of riparian shading and cooling brought about by deep-release dams could exceed 10 °C. Most effects are relatively localized, but the effects of deep-release dams can extend for many kms. In contrast, thermal heterogeneity resulting from hyporheic flows may occur at the scale of only a few m^2.

5.3.1 Shade

The presence of a forest canopy is known to modify the amount of solar radiation and other meteorological factors influencing stream temperatures (Fig. 5.19). In addition to blocking solar radiation from reaching the channel, riparian vegetation reduces near-stream windspeed and traps air against the water surface, thereby reducing heat exchange with the atmosphere (Poole and Berman 2001). Numerous studies have documented the impact of streamside forest removal on river water temperature (Beschta et al. 1987). Following timber harvest of a headwater stream in British Columbia, Canada, maximum daily temperatures increased by as much as 5 °C, and were positively associated with maximum daily air temperature and negatively with discharge (Moore et al. 2005a). Even greater increases in summer maximum temperature of about 8 °C were observed for two streams in the western Cascades in Oregon, US. Stream temperatures often recover to pre-harvest levels within 10 years but may take longer. When riparian buffers are left in place following timber harvest, stream warming is not observed or greatly reduced, although what buffer width is sufficient depends on such conditions as stream width and forest type (Moore et al. 2005b). Based on a review of the literature that evaluated the effectiveness of streamside forest in protecting water quality, habitat, and biota for small streams, Sweeney and Newbold (2014) concluded that riparian buffers should be at least 30 m in width. Benefits are most pronounced in small streams and lessen with increasing stream width because more stream surface is exposed to direct sun.

Stream reaches of alternating open and closed canopy have been observed to warm and cool over distances of less than one km, but not in all cases, indicating that not only changing solar radiation but also cooler groundwater inputs may be involved. A small stream in the central interior of British Columbia, Canada, cooled by approximately 3 °C as it passed from an open into a shaded reach, and groundwater inflow was responsible for about 40% of this cooling (Story et al. 2003). Thermal patches at least 3 °C colder than ambient stream water were identified at multiple sites of the Grand Ronde basin in northern Oregon, US, associated with side channels, alcoves, seeps, and floodplain spring brooks

(Ebersole et al. 2003). Experimental shading cooled maximum daily temperatures within cold patches by 2–4 °C, demonstrating the influence of riparian shade on the expression of cold-water micro-habitats.

5.3.2 Hydrologic Influences

Any reduction in river discharge due to water withdrawals or water diversion projects for municipal, hydroelectric power, or agricultural use will decrease the volume of water receiving heat inputs. This can result in substantial warming during summer when heat flux is greatest and flows may be naturally low. Water withdrawals can also deplete groundwater resources, thereby reducing cool inflows during warm seasons. The presence of lakes and impoundments along a river's course has a further influence on seasonal and diel water temperatures (Jones 2010). Due to the thermal inertia of large standing bodies of water, lakes tend to reduce diel variation downstream. At its outlet a lake drains from surface waters that often are warmer than river temperatures in summer and into the autumn, but cooler in the spring because of thermal inertia and the time required to warm lake surface waters.

Following a century of dam construction, many of the world's rivers are regulated rivers (Stanford et al. 1996). Water released from large reservoirs as well as from small impoundments usually modify downstream water temperatures by releasing water that is colder or warmer than would otherwise be the case (Olden and Naiman 2010). In temperate climates, large, deep reservoirs exhibit thermal stratification similar to large, deep lakes. The density of water is greatest at 4 °C, and so bottom water in deep reservoirs during winter is warmer than the near 0 °C temperature of the reservoir's upper layers, and of river water. During summer, reservoir surface waters may warm into the 20 °C range, but bottom waters typically are in the 4–8 °C range, hence bottom-release dams can cool river water substantially and for many km downstream. Temperatures in the lower Colorado River below Glen Canyon Dam are 9–12 °C year-round, compared to the historic temperature range of 2–26 °C. The Green River, Utah, below the Flaming Gorge Dam (Fig. 5.20) illustrates the extent to which temperatures downstream from bottom-release dams are much cooler during summer and exhibit greatly dampened seasonal amplitude. A number of management options exist for mitigating the thermal impacts of dams, most commonly by means of multi-level water withdrawals that exploit the reservoir's temperature stratification by selectively withdrawing water of the desired temperature. This was implemented for the Flaming Gorge Dam, resulting in significant increases in spring–summer temperatures toward unregulated conditions, but without reducing thermal alteration during the winter months.

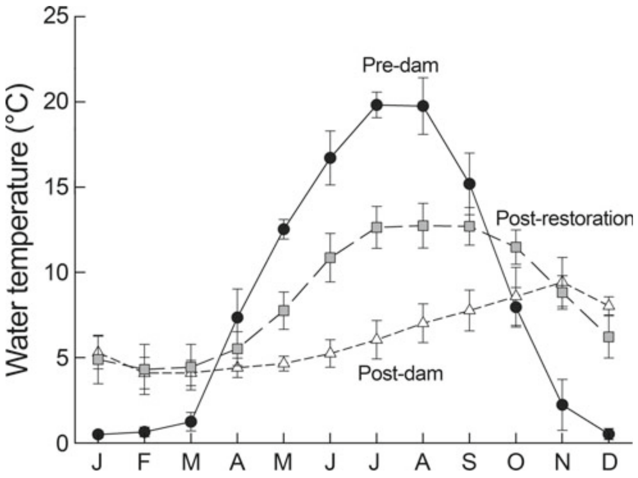

Fig. 5.20 Differing annual temperature regimes of the Green River, Utah, US, below Flaming Gorge Dam. Comparisons of monthly water temperature during pre-dam (1958–62, circles) and post-dam (1963–77, triangles) years shows the thermal dampening effect of the release of deep, cold water. Use of a multi-level water release structure during thermal restoration years (1978–2007, squares) resulted in significant increases in spring–summer temperatures toward unregulated conditions, but not during winter months (Reproduced from Olden and Naiman 2010)

The majority of impoundments are the result of small, surface release dams, and they are most likely to raise downstream temperatures during summer. Small impoundments act like lakes and beaver ponds that tend to increase stream temperatures because they increase the residence time of water and the surface area exposed to solar radiation. By sampling upstream and downstream of small impoundments on ten rivers throughout Michigan, US, Lessard and Hayes (2003) observed temperature increases in nine of the ten locations, by more than 5 °C at some sites and an overall average near 3 °C. As expected, the densities of several cold-water fish species including brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and slimy sculpin (*Cottus cognatus*) declined.

5.3.3 Urbanization

Anthropogenic factors associated with urban and industrial development can influence stream temperatures, usually causing warming. Thermal pollution refers to water released as industrial effluent, including from thermal-electric power generating plants, wastewater treatment facilities, construction holding ponds, and urban stormwater runoff (Webb et al. 2008). The release of heated, once-through condenser cooling water from power plants to the mainstem significantly increased summer temperatures in the Missouri River (Wright et al. 1999). Stream temperatures in the Ara River system, an urban river flowing through central Tokyo, increased in winter and early spring by 0.11–0.21 °C per year from 1978 through 1998 in segments that experienced a substantial increase in heat inputs from urban wastewater treatment plants over the same time period (Kinouchi et al. 2007). Changes in effluent temperature rather than air temperature best explained the result. Urban stream temperatures were observed to warm by 1–10 °C as a result of water retained in construction site sedimentation basins in Pennsylvania (Ehrhart et al. 2013). Localized rainstorms at urbanized sites in small watersheds of the Piedmont region of Maryland, US, resulted in temperature surges that averaged about 3.5 °C and dissipated over about three hours, presumably due to stormwater runoff over warm pavement (Nelson and Palmer 2007). At the most urbanized sites, these surges could occur on up to 10% of summer days and could briefly increase maximum temperature by 7 °C. A comparison of two watersheds in Puerto Rico shows that warming due to urbanization also affects tropical streams. Water temperatures in the Rio Piedras and the Espiritu Santo were similar during the early 1980s, but average annual temperatures are now higher in the urbanized Rio Piedras watershed, which experiences temperatures above 28 °C with greater frequency than its more forested counterpart (Ramírez et al. 2009).

5.3.4 Climate Change

Anthropogenic climate warming is likely to warm stream and rivers. However, although temperature records may span as long as a century, and some rivers indeed show a warming trend, it is difficult to attribute any observed changes to human influences on climate, in part because of large-scale climatic oscillations, and especially because urbanization and reservoir construction throughout the 20th century are additional drivers of warming water temperatures. No trend was observed for 90 years of water temperature data from north-central Austria (Webb and Nobilis 1997) but a significant increase of 0.8 C was seen over a similar time period in the River Danube, with greatest increases in autumn and early winter months (Webb and Nobilis 1994). Because no statistically significant trends were evident for air temperature or river discharge, the increase in river temperature does not appear to be purely a function of changing climatic conditions since 1900. Instead, rising water temperatures likely reflect increasing human modification of this heavily altered river system, including increases in the volume of heated effluent discharges and construction schemes that canalize and regulate the Danube. Compiling historical time series of water temperatures from 40 different stream and river sites located throughout the US, Kaushal et al. (2010) documented statistically significant, long-term warming of mean annual water temperatures of 0.009–0.077 °C per year. The most rapid rates of increase were observed for streams and rivers near urban areas of the mid-Atlantic US. These trends likely have multiple causes, including air temperature warming, urbanization, and potentially other factors including loss of riparian shade and reduced groundwater inputs. Thus, while it is highly likely that observed increases are due mostly to human activities, the amount that can be attributed to climate change is uncertain.

Clearly, rivers can be warmed by human influences other than climate change, but future climate warming is likely to contribute further to temperatures increases. Over the next several decades, air temperatures are projected to warm by about 0.2 °C per decade for a range of projected emissions scenarios (IPPC 2007). Mohseni et al. (1996) projected weekly stream temperatures under a climate scenario of a doubling of atmospheric CO_2 based on nonlinear models relating air to stream temperatures developed for 803 stream gaging stations in the contiguous US. Their projections showed that for all but 5% of the sites, mean annual stream temperatures would increase by 2–5 °C, and maximum and minimum weekly stream temperatures were projected to experience a 1–3 °C warming on average. Largest weekly changes were forecast for spring, and less change was projected for winter and summer.

5.3.5 Temperature and Ecological Processes

Temperature is a critical environmental variable determining the metabolic rates of organisms, their distribution along a river's length and over geographic regions, and their success in interacting with other species. Because species composition and biological rates are temperature dependent, ecosystem processes including leaf breakdown, nutrient uptake, and biological production are affected as well. Stream temperature changes in response to a variety of human actions, and so management intervention may be required to maintain a natural range of stream temperatures.

Every species is restricted to some temperature range that also limits its geographic distribution to a certain range of latitude and elevation. Species that occupy a narrow temperature range are referred to as stenothermal, while those that thrive over a wide range are called eurythermal. In addition, a species may be considered adapted to cold, cool-, or warm-water thermal environments. Few taxa are able to cope with very high temperatures, however. Coldwater fishes cannot survive water temperatures above 25 °C for very long, and most warmwater fishes including the pike family (Esocidae) and many minnows (Cyprinidae) have upper limits near 30 °C. Some fishes of desert streams can tolerate nearly 40 °C, a few invertebrates live at up to 50 °C, and specialized Cyanobacteria of hot springs survive 75 °C (Hynes 1970). In the heterogeneous glaciated landscape of Michigan, streams exhibit substantial regional variation in weekly mean temperature and in temperature fluctuation during warm seasons, allowing Wehrly et al. (2004) to determine the realized thermal niche of stream fishes based on three temperature categories (cold, less than 19 °C; cool, 19–22 °C; and warm, greater than or equal to 22 °C) and three temperature fluctuation categories (stable, less than 5 °C; moderate, 5–10 °C; and extreme, greater than 10 °C). The brook trout *Salvelinus fontinalis* and smallmouth bass *Micropterus dololieu* are good examples of cold-water and warm-water species, respectively. Overall fish diversity increased with mean water temperature across some 300 Michigan sites, documenting the well-established higher diversity of warmwater over coldwater streams. This pattern has often been reported as a longitudinal gradient in which downstream temperature increase is accompanied by an increase in river size and change in many other variables. However, because the Michigan study provided a wide range of temperature regimes within a relatively modest range of stream sizes, these results strongly implicate temperature as the causal variable.

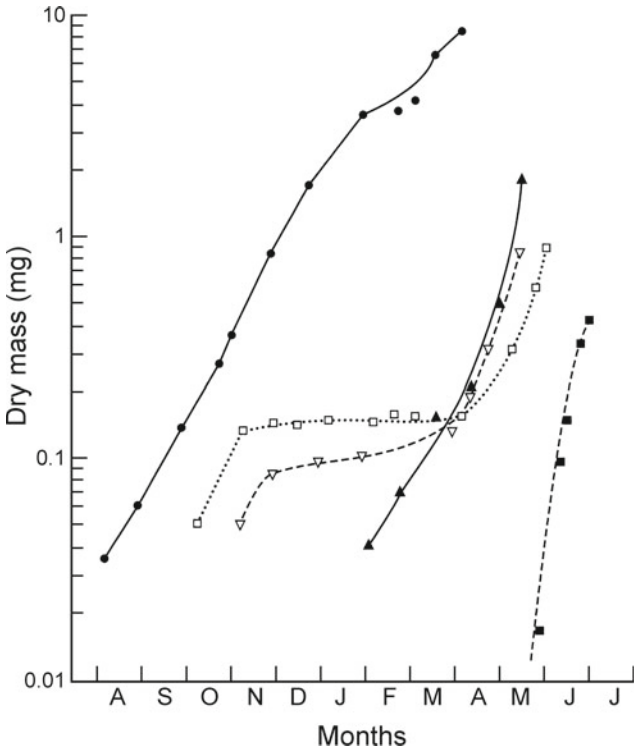

Fig. 5.21 Larval growth period for five species of riffle-inhabiting ephemerellid mayflies in White Clay Creek, Pennsylvania. (●) *Ephemerella subvaria*; (▲) *E. dorothea*; (☐) *Seratella deficiens*; (■) *S. serrata*; (inverted open triangle) *Euryophella verisimilis* (Reproduced from Sweeney and Vannote 1981)

There are a number of reasons for the specific temperature requirements of a particular species. The taxonomic lineage to which it belongs may have originated and diversified in cool waters at high latitudes (e.g., Plecoptera, Hynes 1988), or in warmer water at low latitudes (e.g., Odonata, Corbet 1980). The timing of an insect's life cycle, which often is both cued and regulated by temperature, determines the seasons when it most actively grows, consumes resources, and is exposed to predators. Thus, resource availability and predation risk, two topics that will re-appear in later chapters, can be important evolutionary pressures that are responsible for a particular life cycle and suite of temperature adaptations. A number of studies document how closely related species hatch, grow, and emerge in such a neatly staggered sequence that their life cycle separation appears to ameliorate competition (Sweeney and Vannote 1981; Elliott 1987) (Fig. 5.21). By determining when an insect hatches and grows, temperature synchronizes the life cycle to changing seasonal conditions, coordinating growth with resource availability and ensuring the availability of mates. When the growing season is very short, a common life cycle is to alternate short periods of rapid growth separated by long periods of dormancy or diapause (Danks 1992). Such life cycles often are seen at high latitudes and may require exposure to near-freezing temperatures followed by a rapid temperature rise in order to break egg diapause. When a deep release dam was built on the Saskatchewan River, Canada, water temperatures were maintained near 4 °C throughout the year, and so the cue to ending egg diapause was eliminated. Virtually all insect taxa disappeared from the stretch of river with modified temperatures. A fauna that previously included 12 orders, 30 families, and 75 species was reduced to only the midge family Chironomidae (Lehmkuhl 1974).

The influence of temperature on stream biota has been demonstrated in the laboratory, from life cycle studies, and from their distributions. For 12 invertebrate taxa from New Zealand, the lethal temperature that killed half of the individuals in 96 h (the LT_{50}) ranged from 22.6 to 32.6 °C (Quinn et al. 1994). Laboratory results on thermal tolerances also were consistent with field observations that Plecoptera and Ephemeroptera were much less abundant in rivers where typical summer temperatures exceeded 19 and 21 °C, respectively (Quinn and Hickey 1990). Sampling of 20 sites in streams located in the lower mountainous area of western Germany revealed that summer temperature variation explained more of the variability in the macroinvertebrate assemblage among sites than did other environmental factors including conductivity, substrate type, and the percent coverage of local riparian forest (Haidekker and Hering 2008). Temperature was more important for the macroinvertebrate composition of smaller than of larger streams, indicating that the latter possessed more tolerant, eurythermic species.

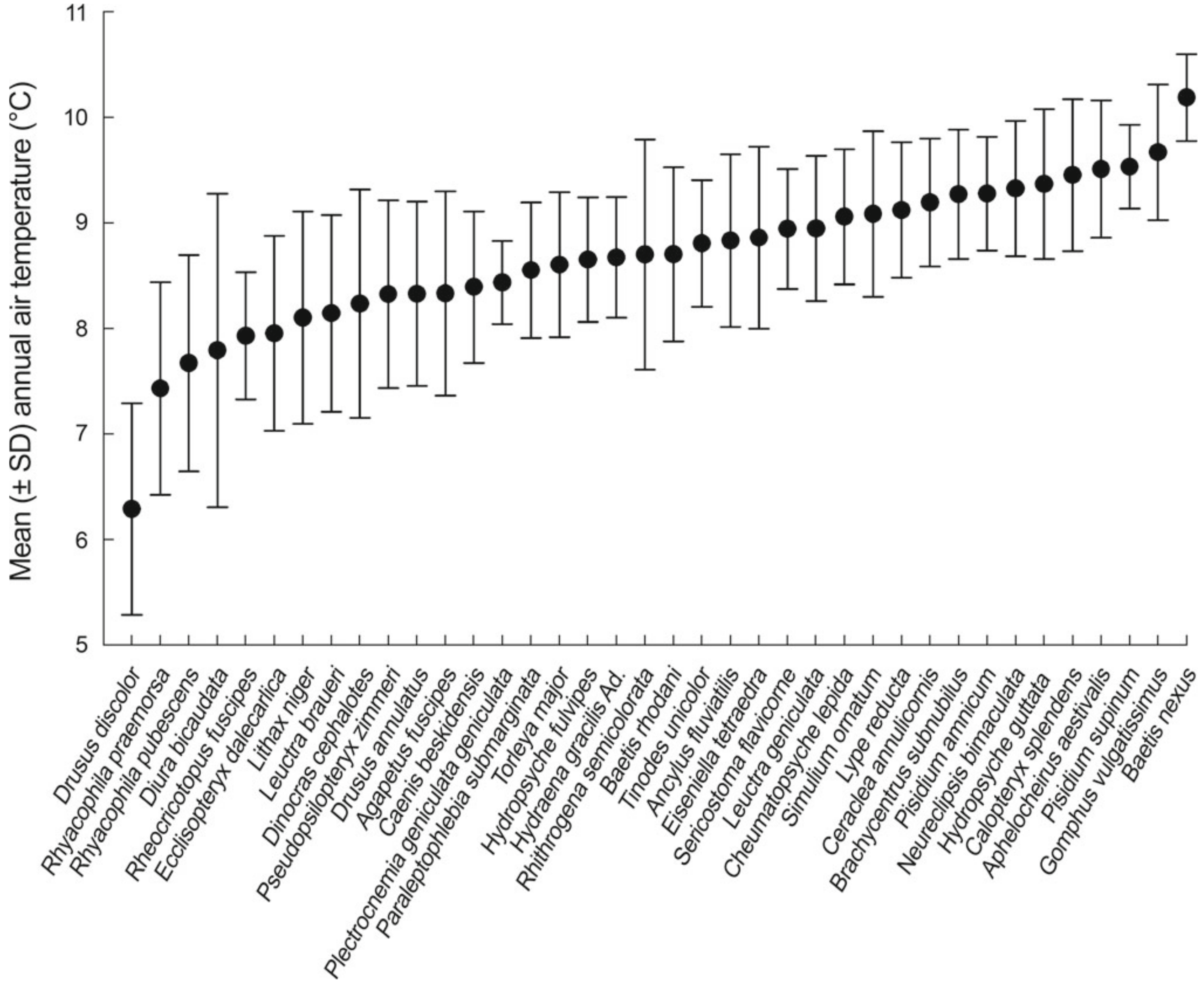

Fig. 5.22 Mean (± SD) annual air temperatures corresponding to the occurrence of 38 species of stream macroinvertebrates, based on presence-absence data for species occurring in submontane streams in Germany. Species were selected to represent those occurring only in upper reaches, hence with a preference for cooler temperatures (12 species); those occurring only in the lower reaches, hence with a preference for warmer temperatures (12); and species occurring over a wide range of zones and thereby exhibiting a broad temperature range preference (14). Air temperature was used as a surrogate for water temperature because data were more readily available, and the air-water temperature correlation is well established (Reproduced from Domisch et al. 2011)

Using climate warming scenarios and the known temperature range (Fig. 5.22) associated with the distribution of 38 species of benthic stream macroinvertebrates for the same region, species ranges were predicted to shift upward in elevation by approximately 80–120 m, contract for species occupying cool environments, and expand for those occupying warmer environments. Assemblage composition was expected to change, and headwater species to decline (Domisch et al. 2011).

Much research has been done on the thermal requirements and life cycles of salmonid species, making them excellent candidates to evaluate how future warming may affect populations. Temperature influences all aspects of the life cycle, including growth, time of spawning, egg hatching, and larval emergence, with best performance at optimal temperatures. Within a species' thermal tolerance zone, rates increase up to an optimal temperature, above which rising metabolic costs take a toll (Fig. 5.23). Under global warming, salmonid populations at the southern end of their range in the northern hemisphere are likely to be extirpated, while more northerly populations likely will benefit and expand northward (Jonsson and Jonsson 2009). For cool-water, northern hemisphere species at their southern-most range extent and thus near their upper thermal limits in warm water streams, canopy shade may be particularly important to their continued survival. In lowland rivers in the New Forest of

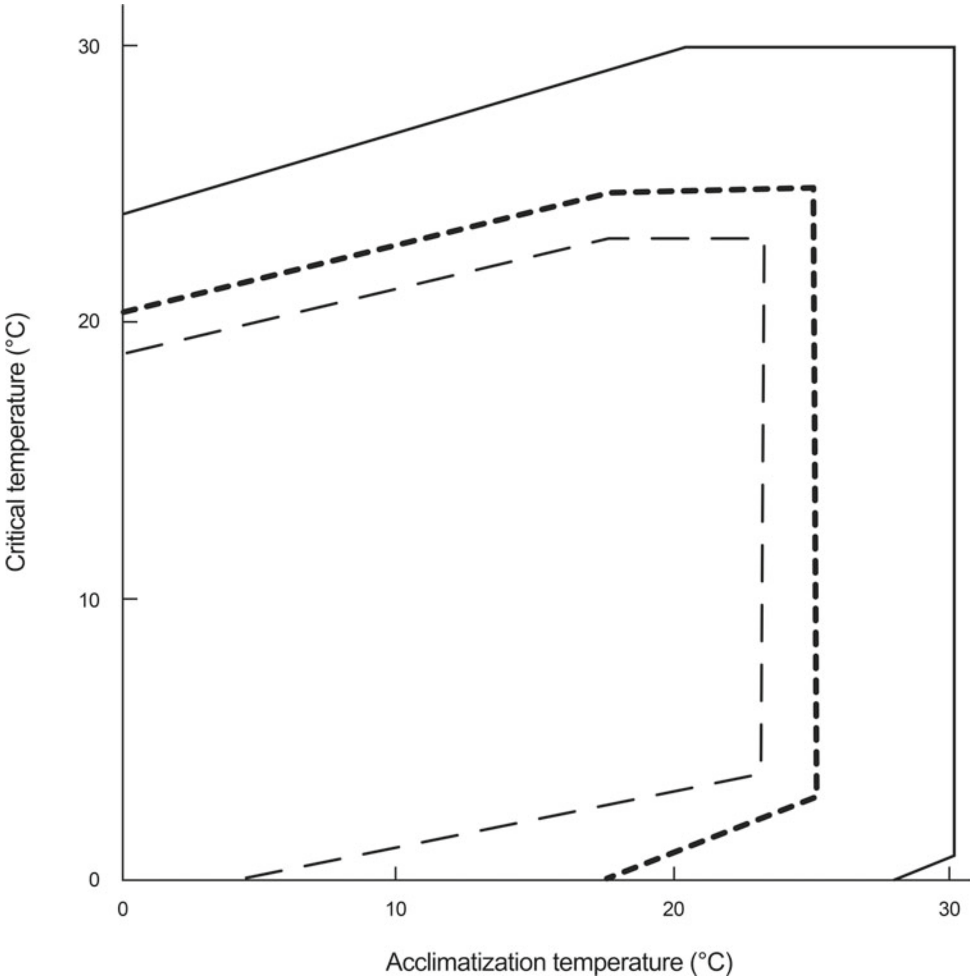

Fig. 5.23 Temperature tolerance polygon for *Salmo trutta* showing growth zone (inside the thin broken line), tolerance zone inside incipient lethal level (thick broken line) within which *S. trutta* feed, and ultimate lethal level where death is almost instantaneous (solid line). Growth at temperatures below 4 °C can occur during winter but usually not from spring to autumn (Reproduced from Jonsson and Jonsson 2009)

southern England, brown trout occur in streams that occasionally experience temperatures in excess of their upper limit for growth of 19.1 °C and their incipient lethal limit of 24.7 °C, depending upon extent of shade (Broadmeadow et al. 2011). A relatively low level of shade (20–40%) sufficed to keep summer temperatures below the incipient lethal limit for brown trout, but more extensive shade of at least 80% was necessary to ensure that water temperatures did not exceed the range for optimum growth. Expansion of riparian woodland thus is a management opportunity to protect temperature-sensitive species from anticipated climate warming.

By shifting both southern and northern distributional limit, climate warming is expected to shift species ranges to higher latitudes or elevations, causing species replacements. Locally, there will be both winners and losers, assuming that habitat is suitable as species disperse to follow their migrating thermal niche. Unfortunately, some species will have nowhere to go, including some adapted to the cool waters found at high elevations. Limited headwater habitat area may result in substantial reduction in population size and even local extirpation of some species. Using data spanning 25 years (1981–2005) from the headwaters of a stream in the uplands of Wales, UK, Durance and Ormerod (2007) observed a warming trend that was detectable after accounting for effects of the North Atlantic Oscillation, implicating directional climate change. As stream temperatures increased, macroinvertebrate abundances fell and assemblage composition changed significantly, although this result was not detected in species-poor streams of low pH. Extrapolating their finding to future increases of 1, 2, and 3 °C, reasonable given current model scenarios, total macroinvertebrate abundance could decline by up to 60%.

A warming environment has implications beyond individual species, of course, as multiple species disperse into new thermal conditions and encounter a different mix of competitors and predators. At the southern limit of brown trout in Europe, warm-adapted species such as pike, cyprinids, and percids may move into habitat from which salmonids have been displaced. At the northern limit of trout in Europe, arctic rivers, which are currently unsuitable or marginally suitable for salmonids, may become habitable

(Jonsson and Jonsson 2009). At present, these locations are more suitable for the arctic char *Salvelinus alpinus* because of its high growth efficiency at low water temperatures, but warming will set the stage for competition between brown trout and char. Temperature changes also can have indirect effects on populations by providing more favorable conditions for their enemies. The northern pikeminnow *Ptychocheilus oregonensis* is an important predator of juvenile Pacific salmon migrating to sea through the Columbia River. Using data from previous warm and cold periods associated with climate oscillations in the North Pacific Ocean and a bioenergetics model, Petersen and Kitchell (2001) predicted that predation on salmonids would have been 26–31% higher during warm than cold periods, and 68–96% higher when comparing the warmest with the coldest year. Climate regime shifts have the potential to significantly alter predation rates, and presumably yearly recruitment success of young salmon in this system.

Small-scale thermal heterogeneity can also be important to organisms, especially to fish that are able to seek out and reside in patches of water with more favorable temperatures. When surface waters are too warm, fish are able to avoid stressful high temperatures and behaviorally thermoregulate by moving into area where cool groundwater enters the surface channel, thereby maintaining optimal body temperatures. In winter, when groundwater is often warmer than surface waters, areas of groundwater upwelling are likely to allow faster growth rates and stable, warmer conditions for developing embryos of winter-spawning species. Thermal refuges can be very important to species near the limits of their thermal niche, such as the brown trout in southern England described above. Juvenile rainbow trout are able to persist in northeast Oregon streams where maximum temperatures exceeded 26 °C for several hours a day, although abundances were negatively correlated with maximum stream temperatures (Ebersole et al. 2001). Reaches of the Klamath River below the Iron Gate Dam in northern California, US, often have daily maximum temperatures during summer that exceed 25 °C as a result of reduced flows and other climatic and within-basin anthropogenic changes. This is well above the optimal temperatures for juvenile salmonids, including coho salmon (*Oncorhynchus kisutch*), Chinook salmon (*O. tshawytscha*) and migratory rainbow trout that occur in this system. By monitoring temperatures and counting fish using daytime snorkeling, Sutton et al. (2007) showed that most juvenile salmonids moved into thermal refuges associated with a tributary junction when main-stem temperatures exceeded 22–23 °C.

Finally, temperature controls the metabolism of all producers and ectothermic consumers in fluvial ecosystems, thus climate warming is likely to cause a number of changes in stream ecosystem structure and function, including greater productivity by benthic algae and microbes, which in turn may influence nutrient demand and efficiency of use. Laboratory incubation of stones taken from the Thur River in Switzerland showed that respiration of the benthic biofilm increased with incubation temperature similarly across locations with mean temperatures ranging from 8 to 19 °C (Acuña et al. 2008). Extrapolating from these results indicates that an increase of 2.5 °C will increase river respiration by an average of 20%. Ecosystem production and respiration increased with water temperature along a gradient of mean water temperatures (7.5–23.6 °C) in small streams of a geothermally active area of southwestern Iceland (Williamson et al. 2016), and in response to a ~3.3 °C experimental warming of a 35 m reach of one stream using a geothermal heat exchanger (Hood et al. 2018). Because these streams were low in nutrients, especially nitrogen, nutrient supply might have been expected to limit system productivity. This was not the case, apparently due to greater efficiency of nutrient uptake and especially to N-fixation by cyanobacteria. The broader implication is that future climate change may alter the relationship between photosynthetic carbon fixation and nutrient dynamics in unanticipated ways.

5.4 Summary

Abiotic factors include all physical and chemical variables that influence the distribution and abundance of organisms. Current, physical habitat, and temperature often are the most important variables in fluvial environments, and all organisms show adaptations that limit them to a subset of conditions. Species differ in the specific environmental conditions under which they thrive, and whether those conditions are narrow or comparatively broad. Habitat preferences can be inferred from the subset of environmental variables that best correlate with a species' distribution and abundance, with the important caveat that interactions with other species may further restrict the habitat occupied. Environments that are either structurally simple or extreme tend to support fewer species, and habitats that are more complex tend to support more species. How patterns in the abiotic environment are manifested across spatial scale, and the persistence of suitable conditions over temporal scale, add challenge to the task of deciphering organism-habitat relationships.

Current and related hydraulic forces affect diverse aspects of the stream environment including channel shape and substrate composition, the physical structure and hydraulic forces operating in the benthic and near-bed microhabitats, and the balance between physical drag processes and the benefits due to the delivery of food, nutrients, and gasses and the removal of wastes. Most organisms live attached to, within, or associated with the streambed, where flows are turbulent and difficult to measure, especially at relevant scales. Considerable effort has gone into theoretical approaches and methods of measurement that can better characterize the flow environment experienced by organisms. Both simple and complex hydraulic variables can be effective predictors of the distribution of individual species and the overall abundance and richness of the invertebrate fauna.

Even under 'normal' flows, many organisms will experience the varied effects of current, including shear stress from current velocity at the scale and location of the organism, and the rapid changes in velocity that create turbulence. Episodic increases in flow, termed spates and floods, can cause abrasion by suspended sediments and erosion of the substrate on which organisms reside, with more serious and even catastrophic effects on organisms. Thus, the association of organisms with particular currents and substrates can reflect the ability of particular habitats to serve as refuges. Some invertebrates and fishes have been shown to move quickly into more sheltered habitats as flows increase, but in other cases it may be happenstance whether an organism is protected from flow during a spate.

Physical habitat includes a wide variety of inorganic and organic substrates of varying size, large objects such as boulders and submerged wood, and channel units such as pools, riffles, and bends. Thus, physical habitat varies from the micro to the meso and macro scales. It interacts strongly with current, which both influences substrate stability and is in turn influenced by bed friction; and with roughness, which creates complex, near-bed flow environments. The quantification of physical habitat requires multiple approaches, including size analyses for inorganic substrates, counts of wood and estimates of biomass or volume, and descriptive categories such as leaf accumulations and debris dams. At the mesohabitat scale, channel units such as riffles and pools, and channel depth, while not strictly substrate categories, are important habitat categories for larger organisms, especially fishes. Among inorganic substrates, gravel of intermediate size supports a diverse, lithophilous flora and fauna that have received a great deal of study by lotic ecologists. Terrestrial leaves that accumulate in streams and wood that modifies habitat and channel shape are important and well-studied organic substrates.

Studies of the importance of physical habitat frequently are simultaneously studies of current, as these two abiotic factors are linked. Substrate size and heterogeneity appear to promote species richness, at least to a degree, and surface texture and roughness additionally promote abundance and diversity. The stability of the substrate and the protection it affords from the forces of current clearly are critical aspects as well.

Temperature is a key environmental variable determining the metabolic rates of organisms, their distributions, and quite possibly their success in interacting with other species. Stream temperature usually varies on seasonal and daily time scales and among locations due to climate, extent of streamside vegetation, and the relative importance of groundwater inputs. For these reasons thermal regimes are highly diverse, and can vary on all spatial scales from micro-scale patches to the longitudinal gradient from headwaters to river mouth. Human activities can alter the natural temperature regime in many ways, including removal of shade-enhancing vegetation, changes to flow paths such as increased impervious surface, construction of impoundments, and of course by influencing the climate.

Freshwater organisms exhibit a wide range of thermal tolerances that correspond to the thermal environment they inhabit, which may be cool or warm, constant or fluctuating. With few exceptions the organisms of running waters are ectotherms, and so external temperature governs their metabolism and growth. Although warmer temperatures generally allow greater activity, they also impose greater metabolic costs. Whether the evidence is based on lethal temperatures in the laboratory, detailed analysis of energy budgets, or field surveys, it is evident that temperature strongly affects distributions and abundances. The thermal tolerances of fishes have received a great deal of study, and it is common in the temperate zone to speak of coldwater and warmwater fishes, which typically are arrayed along latitudinal and elevational gradients. The extreme sensitivity of coldwater fishes to micro-patch differences in temperature is evident in their ability to at least temporarily reside in warmwater systems by using locations where groundwater inputs and shade provide suitable thermal conditions.

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