The importance of context dependence for understanding the effects of low-flow events on fish

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Abstract: The natural hydrology of streams and rivers has been extensively altered by dam construction, water diversion, and climate change. An increased frequency of low-flow events will affect fish by changing habitat availability, resource availability, and reproductive cues. I reviewed the literature to characterize the approaches taken to assess low-flow events and fish, the main effects of low-flow events on fish, and the associated mechanistic drivers. Most studies are focused on temperate streams and are comparative in nature. Decreased stream flow is associated with decreased survival, growth, and abundance of fish populations and shifts in community composition, but effects are variable. This variability in effects is probably caused by context dependence. I propose 3 main sources of context dependence that drive the variation in fish responses to low-flow events: attributes of the low-flow event, attributes of the habitat, and attributes of the fish. Awareness of these sources of context dependence can help managers interpret and explain data, predict vulnerability of fish communities, and prioritize appropriate management actions.
Key words: drought, disturbance, hydrology, prioritization, stream flow, variability

Low-flow events are increasing in frequency because of human alteration of streamflow regimes through dams and water diversion and natural and human-induced climate shifts (Barnett et al. 2008, Brown et al. 2013). Fisheries managers would like to be able to predict the response of fish to low-flow events, but this capability requires an understanding of the relationship between stream flow and fish population and community dynamics (Poff et al. 2010). In a review of the ecological effects of low-flow events, Poff and Zimmerman (2010) found that fish abundance, diversity, and demographic rates generally declined with decreased flow, but the extent of declines was highly variable, and Poff and Zimmerman (2010) were unable to put together general, transferrable relationships. One reason for this difficulty may be that the ecological responses to low-flow events are highly context dependent, i.e., vary based on characteristics of the low-flow event (Bonner and Wilde 2000), the habitat (Aadland 1993), and the fish species (Magalhaes et al. 2007, Bêche et al. 2009). Context dependence is an important factor in understanding how ecological communities respond to disturbance (Shears et al. 2008, Dorn and Volin 2009, Clements et al. 2012).

My goals are to explore the effects of low-flow events on fish and to characterize the major sources of context dependence. I first review the literature to characterize the approaches taken to assess the effects of low-flow events on fish, the main effects of low-flow events on fish, and the associated mechanistic drivers. The objective is to provide insight into why previous investigators have had difficulty finding general transferrable relationships between decreased stream flow and fish responses. I propose 3 main sources of context dependence that drive variation in responses to low-flow events: attributes of the low-flow event (e.g., intensity, severity, predictability), attributes of the habitat (e.g., presence of refuges, complexity, degradation), and attributes of the fish (e.g., size, life history). I argue that a better understanding of the sources of context dependence could increase our ability to predict and understand the response of fish to low-flow events and potentially our ability to manage aquatic ecosystems to increase the resistance and resilience of fish communities to low-flow events.

DEFINITION OF A LOW-FLOW EVENT

Many factors can lead to low-flow events. Streams experience seasonal variation in flow, and many temperate streams are characterized by decreased flow in late summer or during seasonal drought. Especially dry years can lead to extended periods of decreased flow, referred to as supraseasonal droughts (Humphries and Baldwin 2003, Bond et al. 2008). In addition to natural events, human alteration of the flow regime through dams and water diversion for consumptive use, irrigation, and industry leads to decreased flow (Postel et al. 1996, Jackson et al. 2001).

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Defining what constitutes a low-flow event or drought is difficult, but a general definition is that it is a period of low stream flow that is unusual in its duration, extent, severity, or intensity (Humphries and Baldwin 2003). For this article, I use a broad definition of low-flow events and define them to include natural and artificial low-flow events and events that are seasonal and supraseasonal in nature. I focus on streams and rivers, but lakes, wetlands, and estuaries also are affected by reduced water availability.

THE EFFECTS OF LOW-FLOW EVENTS ON FISH

I conducted a literature search to examine and quantify the types of studies of low-flow events and fish and the effects found. Using Web of Science (Thomson Reuters, Philadelphia, Pennsylvania), I searched for "topic = 'low flow' and fish" (348 hits; 15 January 2014) and "topic = drought and fish" (759 hits; 7 February 2014) for "year published = 2000–2013". I examined the title and abstract of each study and selected all studies that examined the effect of a low-flow event on fish. I selected 144 articles and of these was able to obtain 143. After reading the articles, I reduced the number of relevant articles to 88. In both stages of the process, I excluded review articles, studies of nonlotic ecosystems, studies of floods, studies in which effects on habitat were examined and effects on fish were hypothesized, and studies of habitat selection in which variation in velocity was examined at a single discharge level. I included studies with models only if they were based on relevant empirical data. I did not supplement these 88 studies with other relevant studies of which I was aware because my reason for using the Web of Science search was to provide a relatively unbiased approach to selecting studies. However, I discuss additional studies in the text as appropriate. For each study, I noted geographical context, temporal extent, spatial extent, study design, how the authors quantified the low-flow event, habitat characteristics, fish-assemblage characteristics, effects, and hypothesized mechanisms (Appendix S1).

Most studies were conducted in North America (58%), and there was relatively strong representation from Europe and Australia/New Zealand but very few studies in South America, Asia, or Africa (Fig. 1A). Studies were

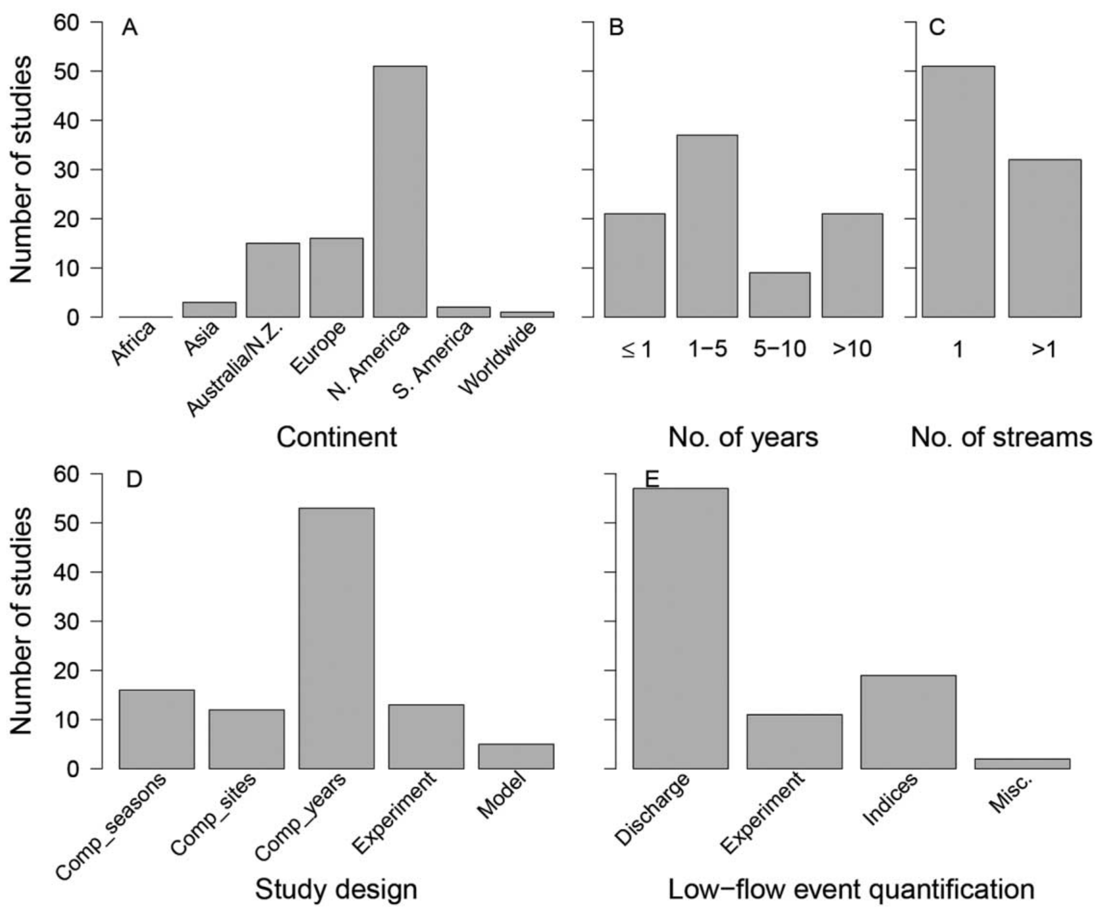

Figure 1. The selected studies broken down by geographic context (A), temporal scale (B), spatial scale (C), study design (D), and low-flow event quantification (E). N.Z. = New Zealand, N. = North, S. = South, No. = number, Comp_ = comparison of, Misc. = miscellaneous.

conducted for as little as 2 mo to >40 y, but most lasted 1 to 5 y (Fig. 1B). Spatial extent was difficult to quantify because it includes the extent of sampling in each stream reach, the number of stream reaches sampled within each stream, and the number of streams sampled. I focused on the number of streams and found that authors of most studies examined just 1 stream (Fig. 1C). Five experimental studies were not included in the spatial-extent graphs.

The vast majority of the selected studies were comparative in nature, specifically comparing across years with differing flow regimes (Fig. 1D). I differentiated between studies in which the primary comparison was among years, across a season, or among sites. The among-years comparison was most common and included both long-term studies that monitored flow variation for many years (Stefferud et al. 2011) and contrasts between just 2 years (Stanley et al. 2012). The among-site comparison was often among sites that differed in the degree to which flow had been altered by water diversion. Experimental studies were less common (13%) and ranged from studies conducted in circulating tanks and stream channels (Allouche and Gaudin 2001, Becker et al. 2003) to studies in which dam operations were altered (Berland et al. 2004). In 10 studies, approaches were combined, so the total number of designs was greater than the number of studies (Fig. 1D).

I also noted how the low-flow event was characterized and found that 65% of authors used direct comparisons of measured discharge to quantify the extent of the low-flow event. An additional 21% of authors used measured discharge but included some type of index calculation to place the discharge measurement in an historical context (Fig. 1E). Examples of indices used include recurrence intervals (Bêche et al. 2009, Hayes et al. 2010), exceedance values (Gauld et al. 2013), 7Q10 (the lowest 7-d average flow that occurs on average once every 10 y; Kanno and Vokoun 2010), and drought or rainfall indices (Boix et al. 2010). Most studies in which indices were used involved longer-term studies with hydrologic time-series data available, but some authors also were able to relate local discharge to a nearby gauged system to calculate indices for shorter-term studies (Walters and Post 2008, Bêche et al. 2009). The miscellaneous category for low-flow-event quantification included studies in which a qualitative assessment was done or another metric, such as pool volume, was used.

I wanted to assess the habitat context of each study, but habitat characteristics that were reported across all studies were hard to find. Even a simple metric, such as stream size, was surprisingly difficult to obtain. Therefore, I classified streams as wadeable or nonwadeable based on sampling gear used, watershed area, discharge measurements, or depth measurements. I classified intermediate sites where streams might have been wadeable at low flow, but not year-round, based on the time of sampling because one of the primary determining characteristics was sampling method. Sixty-three percent of studies were conducted in wadeable streams, 28% in nonwadeable streams, 3% included both, and 6% were experiments in which stream size was not applicable. I also examined whether landuse information that could give insight into the degree of stream degradation was provided. Forty percent of authors provided landuse information, 54% did not, and for 6% it was not applicable. I searched only the methods section for landuse information so cases in which information was provided in the discussion might have been overlooked. Last, I examined characteristics of fish in the studies. I classified studies as focused on a single species, multiple species, or an assemblage. Studies were split among categories, with 40% single species, 26% multiple species, and 34% assemblage. Of the single species studies (35), 54% were focused on a salmonid and 46% were of nonsalmonid species.

Low-flow events have effects ranging from the individual to the ecosystem and evolutionary level, but population-level effects are studied most often (Matthews and Marsh-Matthews 2003). The most common effects examined in the selected studies were recruitment, survival, growth, condition, abundance, species richness, community composition, habitat use, and movement (Fig. 2A, B). Shifts in community composition generally occur when some species increase in abundance while others decrease, but I did not count studies focused on community composition as examples of shifts in species abundance. Other effects of low-

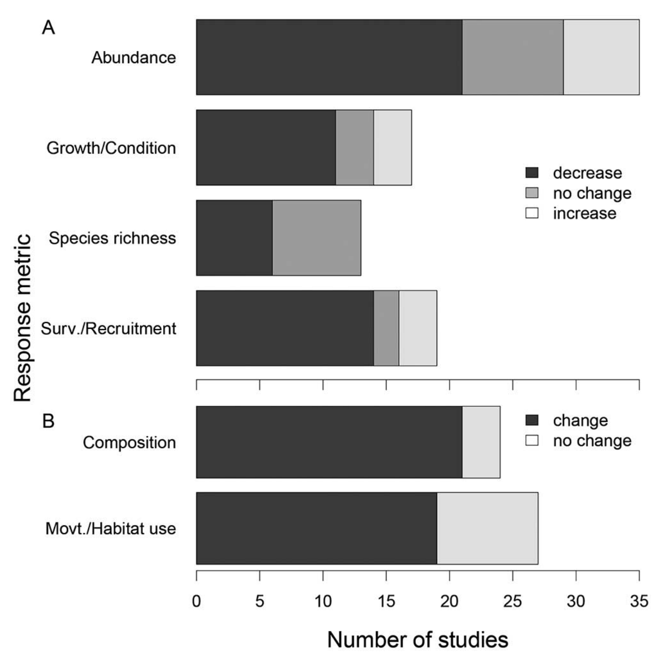

Figure 2. The number of studies in which investigators found a decrease, no change, or increase (A) or change or no change (B) in the response metric. Surv. = survival, Movt. = movement.

flow events included increased transmission of disease (Becker et al. 2003), decreased fish index of biotic integrity scores (Elkin et al. 2013), shifts in timing of spawning (Franssen et al. 2007), shifts in microbial communities on fish eggs (Fujimoto et al. 2013), shifts or no shift in resource use (Kaminskas and Humphries 2009, Hladyz et al. 2012), foodweb effects (Schlosser et al. 2000, Power et al. 2008), and altered size structure (Walters and Post 2008) (Appendix S1).

Fish populations generally showed decreased survival and recruitment (74% of studies) and decreased body condition and growth (65% of studies) in response to low-flow events (Fig. 2A). The direction of effects was fairly consistent, but their magnitudes varied. For example, Stormer and Maceina (2008) found decreases in survival from 82 to 22% with decreased flow, whereas Falke et al. (2010) found a decrease from 89 to 90% down to 84%. The response of fish population abundance was more varied. Most investigators found a decrease (60%), but some found no change (23%) or increases (17%) in abundance. Forty-six percent of investigators found decreased species richness and 54% found no change. Shifts in community composition were common, and 88% of authors reported altered fish community composition. More lentic (Freeman and Marcinek 2006), more tolerant (Ostrand and Wilde 2004), more generalist (Wedderburn et al. 2012), and nonnative species (Stefferud et al. 2011) were favored during low-flow events. Behavioral effects were somewhat more variable, and 70% of authors reported altered movement or habitat use. Investigators found both directed movement in response to decreased flow (Davey and Kelly 2007, Hodges and Magoulick 2011) and no change in movement patterns (Conallin et al. 2011, Gregory et al. 2011). In addition, in studies that examined multiple species or size classes, the effects often varied among species (Hodges and Magoulick 2011), size classes (Xu et al. 2010), and age classes (Riley et al. 2009). For example, Petty and Grossman (2004) found that movement of juveniles increased with flow, but adults showed no change in movements with changes in flow. Understanding reasons for these diverse and sometimes contradictory responses of fish to low-flow events is a major challenge for fish ecologists and natural resource managers.

CONTEXT DEPENDENCE

The 3 most commonly hypothesized mechanisms for the effects seen in the selected studies were related to the low-flow event, habitat, and fish traits (Fig. 3). Several other common mechanisms, such as water quality and connectivity, were related to habitat. Some investigators had data to support the hypothesized mechanism, e.g., data showing shifts in habitat or resource availability, but supporting data were not necessary for me to note the mechanism (see Fig. 4 for key mechanisms and associated important attributes of the mechanisms). I included reproductive cues in Fig. 4 because, in many cases, the importance of attributes of the low-flow event or fish was related to spawning cues or reproductive strategy. These multiple mechanisms suggest that variability in responses of fish to low-flow events among studies might be explained by attributes of the low-flow event, habitat, and fish species.

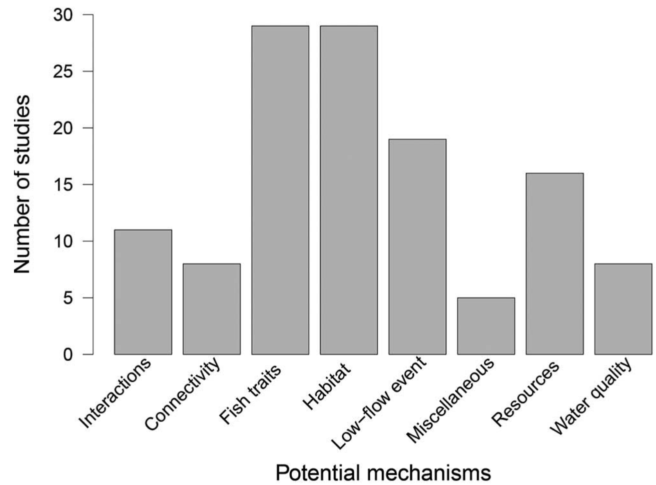

Figure 3. The number of studies in which investigators mentioned that the effects seen in the study could be caused by an indicated potential mechanism(s). Nine studies did not include any potential mechanisms.

Attributes of the low-flow event

More severe low-flow events generally have greater effects on fish, but defining what constitutes more severe is challenging. Low-flow events often are ramp disturbances that build through time (Lake 2003). As a result, both the magnitude of flow loss and the duration of the low-flow event are important. Rolls et al. (2012) identified 6 ecologically important attributes of low-flow events that can influence flow–ecological relationships. These attributes overlap closely with the 5 critical components of a natural flow regime (Poff et al. 1997) and include antecedent conditions, duration, magnitude, frequency, timing and seasonality, and rate of change.

Magnitude, duration, and frequency all determine the severity of the low-flow event, but magnitude is the most commonly measured of these attributes. The magnitude of stream drying is related to the magnitude of effects on fish (Jowett et al. 2005, Dekar and Magoulick 2007, Poff and Zimmerman 2010). For example, Matthews and Marsh-Matthews (2006) found shifts in community composition after only an extreme drought. Similarly, on the Canadian River, a 38% decrease in flow had no effect, but a 78% decrease led to large changes in species composition (Bonner and Wilde 2000). Duration also is important. In Med-

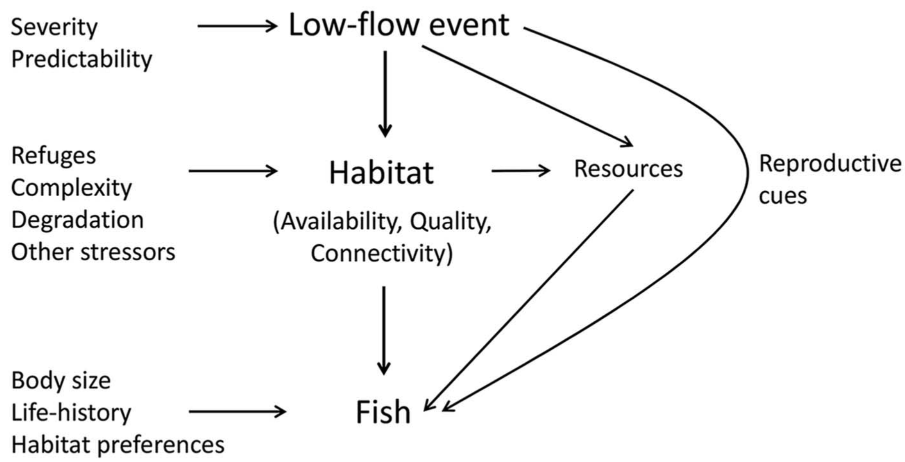

Figure 4. Key mechanisms and attributes affecting the response of fish to low-flow events.

iterranean stream fish assemblages, short low-flow events often led to only small, transient effects, whereas multiyear low-flow events caused larger shifts in species assemblages (Magalhaes et al. 2007). These cumulative effects of multiyear low-flow events highlight the importance of frequency. If low-flow events are very frequent, no temporal refuge is available during which fish can recover. The spatial extent, or the amount of the watershed affected by a low-flow event, is similarly important for refuge availability (Stanley et al. 1997).

The timing and seasonality of the low-flow events are important because relationships between flow and effects on fish can vary seasonally. For example, Tonkin et al. (2011) found that early fish growth was high during low flows, but later in the season highest growth was seen with higher flows. A seasonal low-flow event may have a smaller effect on fish than an unexpected event, especially if the timing of the unexpected event corresponds to an important period from a life-history standpoint. Fish seem to be especially sensitive to low-flow events during spawning and growth periods (Sotiropoulos et al. 2006, McCargo and Peterson 2010). Low-flow events can affect fish through the loss of cues for reproduction or the conditions needed for successful reproduction (Bonner and Wilde 2000, Perkin and Gido 2011). Many species appear to require an increase in flow to initiate spawning or experience reduced recruitment in low-flow years (Brown and Ford 2002, Stefferud et al. 2011). Reproductive guilds of fish that require a passive drift phase for eggs and larvae are especially susceptible to lower flows (Perkin and Gido 2011). Last, the rate of change in flow can determine whether a fish is able to respond behaviorally and seek refuge. A sudden drop in flow could leave fish stranded, whereas more gradual declines would allow fish to move out of areas that soon would be dewatered (Nagrodski et al. 2012).

Together, these components can be used to characterize whether the low-flow event is within the bounds of the natural flow regime. One would expect higher resistance and resilience to natural low-flow events or artificial low-flow events within the natural range of variation to which fish have adapted over evolutionary time (Lytle and Poff 2004). The historical flow regime also influences fish species composition. In a system with a historically harsh flow regime, the only fish species remaining are those adapted to that harsh flow regime. As a result, they may be more resistant to low-flow events (Matthews and Marsh-Matthews 2003).

Attributes of the habitat

The effects of low-flow events on fish are often mediated by shifts in habitat availability and quality, so attributes of the habitat can play an important role in flow–ecological relationships (Hilderbrand et al. 1999, Boulton 2003). Decreased stream depth, wetted width, and water velocity are direct effects of decreased flow that can affect fish (Hilderbrand et al. 1999, Dewson et al. 2007a). Riffle habitats are often the first habitat type lost, and as a result, shifts in community composition from fluvial or riffle specialists to generalists or pool-dwelling species are common (Freeman and Marcinek 2006, Kanno and Vokoun 2010). Habitat size, complexity, geomorphology, substrate, and condition also can influence how habitat conditions change and how fish will respond to decreased flow (Magoulick 2000).

One of the most important components of habitat is the presence of refuges (Magoulick and Kobza 2003). Refuges exist at different scales (longitudinal, lateral, and vertical) and include deep pools, the hyporheic zone, off-channel habitat, and upstream or downstream stream sections that retain water (Sedell et al. 1990, Magoulick and

Kobza 2003, Kawanishi et al. 2013). The geomorphic form of the stream channel contributes to whether refuges are present, with simple channelized streams less likely than more complex channels to maintain refuges, such as deep pools (Sedell et al. 1990). The location and connectivity of the refuges will determine how useful they are for fish (Davey and Kelly 2007). Griswold et al. (1982) found that fish recolonized a connected stream reach quickly, whereas a section above a low-head dam did not recover to the same extent. Barriers to migration are especially problematic for anadromous species (Gauld et al. 2013). In general, fish in more complex, well connected habitat probably will be more resistant and resilient to low-flow events in part because of the greater presence of refuges.

Habitat quality and condition are other important components. Increased temperatures and decreased dissolved O_2 levels are stressors associated with low-flow events that can be influenced by habitat conditions and that have repercussions for fish (Larimore et al. 1959, Cowx et al. 1984). Streams with extensive riparian cover are buffered from the temperature effects of decreased flow. Conversely, small, wide, or shallow streams have limited thermal and chemical buffering capacity and experience earlier shifts in water temperature and dissolved O_2 (McCargo and Peterson 2010). Increased fine sediment is another stressor associated with decreased flow that can affect fish (Boulton 2003, Hakala and Hartman 2004). In one of the few studies in which multiple stressors were examined explicitly, Matthaei et al. (2010) found that low-flow events had more substantial effects in streams with higher fine sediment loads. This response to multiple stressors is probably not unusual, and as a result one would expect fish to be less resistant to decreased flow in a degraded stream that is also subject to other stressors.

Attributes of the fish

Attributes of the fish themselves play an important role, and many of the authors who considered multiple species found effects that varied among species (Jowett et al. 2005, Leprieur et al. 2006, Hodges and Magoulick 2011). Species probably differ in their susceptibility because of variation in size, trophic position, behavior, morphology, mobility, habitat preference, or reproductive strategies. Even within a species, the susceptibility of an individual can vary with its size and life-history stage (Nislow and Armstrong 2012). All of these characteristics affect how well adapted a fish is to low-flow events (Lytle and Poff 2004).

One important trait that explains between and within species variation in effects of decreased flow is size. In general, larger individuals appear to be more susceptible than smaller individuals to low-flow events (McCargo and Peterson 2010, Xu et al. 2010). The loss of large, top predators has been a relatively consistent finding in studies of drought in streams (Walters and Post 2008, Woodward et al. 2012, Ledger et al. 2013). The loss of larger fish is probably because they require more habitat and face increased exposure to terrestrial predators in shallow pools (Harvey and Stewart 1991). However, large-bodied species are often longer-lived. They may be more vulnerable to low-flow events, but if they can live long enough to experience sufficient flow for reproduction they may have an advantage over short-lived fish that have to spawn every year (Magalhaes et al. 2007, Moyle et al. 2013).

Life-history theory often is used to help understand how fish respond to a disturbance (Mims et al. 2010). Winemiller and Rose (1992) identified 3 suites of life-history traits (opportunistic strategists, periodic strategists, and equilibrium strategists) that represent trade-offs between juvenile survivorship, generation time, and fecundity. Shifts in the dominance of these strategies can respond to shifts in flow variability, predictability, and seasonality, but magnitude has not been examined directly (Mims and Olden 2012, 2013). In a study of the effects of drought in Texas streams, Stanley et al. (2012) found that opportunistic species typical of temporary waters and equilibrium species that rely on stable pool habitat did better than periodic species during the drought. A rise in opportunistic species and decline in periodic species also has been observed in other studies of low-flow events (Anderson et al. 2006, Freitas et al. 2013). Several investigators found that nonnative species with high recruitment in stable low-flow years (suggestive of an equilibrium strategy) were able to establish at the expense of native species, which required a high-flow pulse for successful recruitment (Brown and Ford 2002, Stefferud et al. 2011).

Other important factors affecting sensitivity include habitat preferences and physiological tolerances. Species with a preference or requirement for lentic habitat were less affected by the loss of riffle habitats than species that preferred faster flows (Freeman and Marcinek 2006, McCargo and Peterson 2010). Specialist taxa that require a specific habitat often decline compared with generalist taxa (Wedderburn et al. 2012). Physiological tolerances, which are often related to habitat preferences, also play an important role in explaining differing responses among species. For example, introduced Brown Trout (*Salmo trutta*) are more sensitive to increased temperatures associated with decreased flow than are native galaxiids, so water abstraction favored galaxiids in New Zealand streams (Leprieur et al. 2006).

Interaction of attributes and other attributes

Attributes of the low-flow event, habitat, and fish can interact. Boulton (2003) designated several habitat thresholds that correspond to ecological responses. These thresholds occur when the stream becomes disconnected from the riparian habitat, when riffles are lost and the stream becomes a series of disconnected pools, and when the stream becomes completely dry and only hyporheic flow persists (Boulton 2003). Whether one of these thresholds is passed depends on the magnitude of the low-flow event and the geomorphology of the stream. Similarly, the attributes of the fish (e.g., riffle vs pool-dwelling species) will influence which thresholds are most important.

In addition, these 3 main factors have implications for other sources of context dependence, such as biotic interactions. For example, decreases in habitat availability can lead to an increased intensity of inter- and intraspecific interactions caused by increased densities as fish are crowded into the remaining habitat (Magoulick and Kobza 2003). In addition, fish traits, such as size, have implications for predator susceptibility. Stefferud et al. (2011) found that smaller fish were more susceptible than larger fish to low-flow events because of increased predation by nonnative fish, which were at higher densities during periods of decreased flow. However, predatory fish often are large and, therefore, highly susceptible to decreased flow, so their loss could lead to decreased predation pressure (Closs and Lake 1996). Predation risk from terrestrial predators also gains more importance as pools become shallower (Harvey and Stewart 1991).

Resource availability is another potentially important factor. Decreased flow can reduce macroinvertebrate drift and zooplankton abundance (Harvey et al. 2006, Wedderburn et al. 2013), increase algal growth (Dewson et al. 2007a), and affect the availability of fish prey (Franssen et al. 2007). In several studies of low-flow events, decreases in fish condition were attributed to reduced resource availability (Mas-Marti et al. 2010, Balcombe et al. 2012). However, the link between flow and resource consumption can be quite complex because fish that eat macroinvertebrates must balance multiple factors that are influenced by flow: drift rates, detection and capture rates, and bioenergetic costs of station holding and swimming (Fausch 1984, Nislow et al. 1999). As a result, the exact relationship between flow and resource consumption will vary.

	Weak effect	Strong effect
Low flow attributes		
Flow reduction:	Low	High
Duration:	Short	Long
Predictability:	High	Low
Habitat attributes		
Refuges:	Many	Few
Complexity:	High	Low
Other stressors:	None	Many
Fish attributes		
Body size:	Small	Large
Habitat:	Pools	Riffles
Stress tolerance:	High	Low

Figure 5. A low-flow event would be expected to have a stronger or weaker effect depending on the attributes of the event, habitat, and fish. Specific attributes and the expected direction of effect are shown.

MANAGEMENT IMPLICATIONS

The lack of consistent, predictable effects of low-flow events on fish is a management challenge. Recognition of potential sources of context dependence can help explain and interpret unexpected results. In addition, a framework that incorporates context dependence (Figs 4, 5) can help predict vulnerable streams and prioritize management actions.

Considering the 3 potential sources of context dependence can provide insight into why results may differ among studies. For example, a low-flow event caused decreased abundance and lower body condition in one study (Hakala and Hartman 2004) and decreased abundance but no change or increased body condition in another study (James et al. 2010). In both studies, the focal species was a salmonid and decreased habitat availability probably contributed to decreased abundances. However, in the study by Hakala and Hartman (2004), the magnitude of flow reduction was greater and led to increased water temperatures and suspected decreased resource availability. In the study by James et al. (2010), water temperature was not altered (partly because of habitat characteristics) and no evidence of decreased resource availability was found. Thus, differences in the response of fish among studies can be attributed to differences in the low-flow event and habitat.

Context dependence also can help explain the varied response of fish species richness to decreased flow. Low-flow events can increase (Grossman et al. 1998), decrease (Rogers et al. 2005, McCargo and Peterson 2010, Ferguson et al. 2013), or have no effect on species richness (Magalhaes et al. 2007, Balcombe et al. 2011). In the studies with decreased species richness, other stressors, such as fishing (Ferguson et al. 2013) or impoundments (Rogers et al. 2005), often were present, but in the study by Magalhaes et al. (2007), in which no change in species richness was found, the river was relatively undisturbed with no pollution, no impoundments, no fishing, and an intact riparian zone. McCargo and Peterson (2010) explicitly considered the effect of varying habitat conditions and found that smaller streams and unconfined streams showed a steep decline in species richness with decreased flow, whereas no shift occurred in confined large streams. This difference was attributed to quicker declines in water quality of smaller, shallower unconfined streams (McCargo and Peterson 2010). Attributes of the habitat can drive variation in the response of fish species richness to low-flow events.

An important task for fisheries managers is predicting the vulnerability of species or streams to low-flow events and carrying out appropriate management actions. Species traits are being used increasingly often to predict vulnerability to disturbances, such as climate change and water diversion (Poff et al. 2006, Webb et al. 2010, Walters 2011, Chessman 2013). However, despite the hope that this approach will produce more transferable relationships, the relationships can have limited application beyond the species assemblage and environment upon which they are based (Chessman 2013). Expanding the species trait framework to consider the characteristics of the habitat and low-flow event (Fig. 5) may increase predictive capabilities when assessing vulnerability to low-flow events. For example, in a prioritization assessment, habitat, species, and low-flow event traits could be analyzed, and if all suggested high vulnerability, management actions could be prioritized accordingly.

In highly vulnerable streams, management actions could consist of altering the low-flow event, habitat, or species composition. For example, the timing and extent of water use could be altered to minimize the magnitude, duration, or frequency of low-flow events in highly vulnerable streams (Poff et al. 2010). Water releases have been conducted successfully in many streams to increase spawning and recruitment of native fish species (King et al. 2010, Kiernan et al. 2012, Hardie 2013). Environmental flow allocations can increase resource availability for fish (Wedderburn et al. 2013). In some cases, a shift in the timing of water delivery to correspond to biologically important periods, such as spawning, has been sufficient to improve fish recruitment (Kiernan et al. 2012). Improvements were seen with a limited additional release of water when the flow regime was tailored to match the attributes of the fish (Kiernan et al. 2012).

Changes to water diversion practices are politically difficult to implement for some streams, and efforts could be focused instead on habitat availability and quality. Habitat restoration could be used to create more complex habitat and refuges. For example, increases in riparian vegetation can increase water quality and have positive effects on macroinvertebrate composition (Thomson et al. 2012). Similarly, addition of wood appeared to buffer against drought-induced declines in River Blackfish (*Gadopsis marmoratus*) and Southern Pygmy Perch (*Nannoperca australis*) (Bond and Lake 2005). Aquatic ecosystems often experience multiple stressors, and these stressors can mediate the effects of decreased flow. Fish assemblages in more degraded and disturbed sites are generally less resistant and resilient to hydrologic variability than are fish assemblages in high-quality sites (Matono et al. 2012). Therefore, restoration efforts that target other stressors may indirectly contribute to increased resistance of fish to low-flow events. Altering fish composition is impossible or undesirable in many situations but may be appropriate in some cases. In waterbodies that are stocked, managers could focus on fish that are well suited for the current flow regime and are less sensitive to decreased flow.

CONCLUSIONS

The effects of low-flow events on fish are increasingly well studied, but the geographic scope of studies is still very limited. Strong attention has been given to temperate streams and very limited attention to tropical streams. Moreover, most studies have been focused on smaller wadeable streams. The lack of research on large tropical streams is a major limitation for predicting the effects of increasing water diversion and flow alteration in Africa, South America, and Asia. However, a wide variety of temporal scales has been explored, and 21% of studies had durations >10 y. Another positive note is that both individual species and species assemblages have been studied. Our understanding of low-flow events and fish would benefit from expanding the spatial extent of studies in terms of geographic scope, size of streams, and number of streams examined in a study.

Most study designs were comparative in nature. However, comparing among studies is challenging because low-flow events were not quantified in a way that allowed easy comparison between studies. A major limitation was that few authors provided the necessary hydrologic indices to assess whether a low-flow event was unusual. Investigators might compare 2 years in which flow was 78% lower in one year than in the other, but without an historical context, the reader has no way to know whether the low-flow year corresponded to a 100-y drought or a 10-y drought or both years actually had higher-than-average flows. To be able to compare studies of low-flow events, researchers need to provide more comparable flow indices, such as exceedance values (the percentage of time a given flow was exceeded). For example, an exceedance value of 98, or the flow was exceeded 98% of the time, would be indicative of a low-flow event and would allow easy comparison across studies (Tharme 2003, Walters and Post 2011). Habitat indices, such as pool area or % of riffles lost, also could provide insight. Future studies would benefit from a clear description of the low-flow event and the habitat context. Low-flow indices are one promising approach for increasing our ability to compare studies and understand the results.

Authors of the selected studies generally found decreased survival, decreased growth, and altered species composition in response to low-flow events. The results were more variable for species richness, abundance, movement, and habitat use. However, despite clear trends, some investigators reported opposite responses, suggesting that context dependence is common. Many authors reported that the effects of low-flow events varied with the vulnerability of the fish species (Freeman and Marcinek 2006, Kiernan and Moyle 2012) or the magnitude of the low-flow event (Jowett et al. 2005). This context dependence can complicate our understanding, predictive capabilities, and identification of appropriate management actions. However, awareness of the major sources of context dependence could provide a framework for thinking about these issues (Figs 4, 5). The attributes of a low-flow event, habitat, or fish species provide an assessment of vulnerability, and streams that are highly vulnerable to low-flow events can be prioritized for habitat restoration efforts or flow regulations. The framework also could be used to predict when a flow–ecological relationship is likely to be transferrable to another stream. For example, a flow–ecological relationship developed for fish species in a minimally developed stream may be appropriate for another fish with similar traits in undisturbed streams but may be inappropriate for an urban stream or a fish with different life-history or ecological traits.

I reviewed low-flow events, but context dependence is ubiquitous in ecology. The same 3 categories of context dependence (event, habitat, and fish) probably are applicable to other disturbances, such as floods, fire, logging, and chemical spills. In broad reviews of how streams respond to disturbance, the importance of stream geomorphology, life history of the fish, and the timing and frequency of the disturbance have been noted for understanding responses (Resh et al. 1988, Niemi et al. 1990). These results extend beyond fish. Macroinvertebrate communities (McKay and King 2006, Dewson et al. 2007b) and crayfish (Acosta and Perry 2001, Larson et al. 2009) also show a variety of responses to low-flow events.

Low-flow events are an increasing occurrence because of extensive human diversion and global climate change (Vörösmarty et al. 2010). Low-flow events often have negative effects for fish, but the variability in responses complicates management. Several sources of context dependence may help explain the effects of low-flow events, and I propose that they can generally be grouped into 3 categories: attributes of the low-flow event, attributes of the habitat, and attributes of the fish. Recognizing the sources of context dependence driving fish responses to low-flow events can enable one to better understand, explain, and predict the effects of low-flow events, assess vulnerability to low-flow events, and apply appropriate management actions.

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