Evolutionary adaptations to flows in aquatic invertebrates and management consequences.

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1) Macroevolutionary versus microevolutionary adaptations to the environment
   a) Macroevolution- Evolution at the level of the species or above
      i) Macroevolution could involve the evolution of one species to another and can also be used to discuss evolutionary trends that differ above the level of the species. These trends can include different adaptations to deal with environmental challenges. For example, groups of organisms possess different modes of adaptation (life-history, behavioural, or morphological) to deal with the dynamic nature of river flows.
   b) Microevolution- Evolution below the level of the species
      i) Microevolution involves changes in alleles and resulting phenotypic changes within the same species. Aquatic invertebrate populations may evolve to different flow regimes at local scales.
2) Hydrograph of the Green River in Utah before and after installation of the Flaming Gorge Dam[1].
   a) Directional evolution is driven by changes in alleles and their frequencies resulting from differential survival under environmental conditions. Organisms are inherently adapted to the environment under which they evolved. If this environment drastically changes, organisms may or may not be adapted to survive under the new conditions. Regulation of rivers has drastically changed flow environments, often reducing the frequency and magnitude of floods and droughts, as shown in this example. Aquatic invertebrates may or may not be able to survive these changes, and some may be able to adapt to these changes.
3) Macroevolutionary modes of adaptation.
   a) Life history- Life-history adaptations include those related to growth, development, and reproduction.
      i) Within aquatic invertebrates, organisms which have life stages that can survive certain disturbances may have life-history adaptations.
      ii) Short developmental periods coupled with an aerial life stage and lack of seasonality allows for survival of floods by aerial adults at any time of the year and continuation of the population[2]. Gray (1981) noted that all mayflies and small dipteran larvae in Sycamore Creek, AZ (arid creek in American Southwest with flash flooding) had rapid developmental times and continuous emergence. The larval stages of mayflies and dipterans in this creek have mortality rates due to flooding from 80-96% loss[2]. In creeks with more predictable flooding, emergence may be timed so that the majority of individuals emerge before the flood season.
      iii) Lytle (2002) found that on average 86% of the caddisfly *Phylloicus mexicanus* in three montane American Southwest creeks emerged before the 100 year average arrival date of the first seasonal flood, indicating that its developmental timing is adapted for flood survival.

        Size at emergence also decreased as the probability of a flash flood occurring increased, indicating a trade-off in fecundity and survival probability[3].

   b) Behavioral- Behavioral adaptations include specific behaviours that allow an organism to better survive environmental challenges.
      i) Some groups of aquatic invertebrates with aquatic adults (for example, Hemiptera and Coleoptera) exhibit rainfall response behaviour (RRB), in which rainfall acts as a cue for the individuals to leave the affected aquatic habitat[4,5].
      ii) Some invertebrates may also use rainfall as a cue to change microhabitats within the water, such as seeking refuge beneath submerged rocks[5].
      iii) Some invertebrates and fish change their posture during high flows to avoid becoming dislodged[6].
   c) Morphological- Morphological adaptations include body shape, size, and evolution of specific body structures.
      i) Blephariceridae larvae (Diptera) possess ventral suckers that allow them to withstand velocities of up to 450 cm/s[7].
      ii) Simuliidae larvae (Diptera) possess hooks on their prolegs and produce large quantities of silk that allow them to withstand high velocities[8].
      iii) The streamlined bodies and small size of many aquatic invertebrates may allow them to withstand higher flow velocities[9].

4) Flood escape behaviour in Belostomatidae (Hemiptera).
   a) *Abedus herberti* (Hemiptera: Belostomatidae) have been shown to exit the stream during periods of heavy rainfall, and to crawl in a negative geotactic manner away from the stream until a sheltered area is reached[4].
   b) *A. herberti* and *Lethocerus medius* (Hemiptera: Belostomatidae) respond to simulated rainfall in behavioural arenas by crawling out in a negative geotactic manner[10].
5) Flood escape behaviour in other taxa.
   a) Flood excape behaviour was tested in seven desert aquatic insects. These include *Curicta pronotata* (Hemiptera: Nepidae), *Ranatra quadridentata* (Hemiptera: Nepidae), *Ambrysus woodburyi* (Hemiptera: Naucoridae), *Aquarius regimis* (Hemiptera: Gerridae), *Rhantus atricolor* (Coleoptera: Dytiscidae), *Gyrinus plicifer* (Coleoptera: Gyrinidae), and *Corydalus texanus* (Megaloptera: Corydalidae)[5].
   b) *C. pronotata* responded significantly to rainfall experiments by crawling out of the water and up the sides of the behavioural arena as long as light rainfall was contacting them[5].
   c) *A. regimis* responded significantly to rainfall experiments by crawling out of the water and up the sides of the behavioural arena for at least 10cm[5].
6) Drought escape.
   a) The Santa Maria River in Arizona was observed to be receeding at a rate of .16 cm/s on 10 April 2007[12].
   b) An estimated 3600 individuals of *Postelichus immsi* (Coleoptera: Dryopidae) were observed crawling upstream in a 37 meter long column[12].

c) An estimated 690 larvae/m^2 of *Progomphus borealis* (Odonata: Gomphidae) were observed burrowing upstream at a rate of .17 cm/s[11].
d) The exact method of detection of drought and subsequent rheotaxic behaviour is unknown, but this could be further examined by a mark-and-recapture field study.

7) Flood experiments on the Bill Williams River, AZ
   a) The Bill Williams River in Arizona, USA is a Nature Conservancy Sustainable Rivers Project river. It is regulated by Alamo Dam, primarily for recreation and flood control.
   b) There is a collaboration between managers and researchers to implement planned environmental flows, including floods, on the river. This allows examination of species-level and community-level reactions to changes in flow regime, and specifically to floods.
   c) In spring of 2006 a 2500 cfs multi-day drawdown flood was released from the dam, and in spring of 2007 a 1000 cfs pulse flood was released.
   d) We are examining the effect of the planned floods on the benthic invertebrate community.
8) Results of the 2006 2500cfs release flood on benthic invertebrates.
   a) The overall proportion of snails was significantly decreased (ANOVA, $p=.04$).
   b) The overall proportion of ostracods was significantly decreased (ANOVA, $P<.001$).
   c) The overall proportion of invertebrates with a terrestrial stage, and thus potentially available as food to birds, was significantly increased ($p<.01$).
   d) Snails and ostracods may share traits that decrease survivorship during floods (heavy shells, no aerial stage) while invertebrates potentially available as food to birds may share traits that allow them to be better adapted to floods (aerial stages escape flood mortality, streamlined bodies).
9) What to expect from floods
   a) An organism's mode of adaptation (or lack thereof) to flood events will determine which components of a flood are important to its survival probability.
   b) For organisms that have life-history patterns timed with the natural flow cycle, the timing of floods is important.
   c) For organisms that respond behaviourally to avoid floods, environmental cues such as rainfall are important to their survival.
10) Conclusions
   a) Many taxa possess adaptations to survive flood and drought.
   b) Knowing whether an organism has the ability to adapt to specific changes in flow regime will allow careful management of specific populations of aquatic organisms.

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