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1   **Freshwater invertebrate life history strategies for surviving desiccation**

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10   **Motivation**

11   • Climate change is prolonging dry periods in intermittent rivers and wetlands in many regions across the world,
12   increasing the potential for desiccation stress in the fauna. Invertebrates comprise the greatest proportion of
13   biodiversity in these systems, but there are no recent reviews on the response of invertebrates to desiccation in the
14   context of climate change.
15   • This review elaborates on the idea that the degree of desiccation that fauna experience is likely to be critical for
16   survival as climates dry because this idea has not previously been considered in the literature. Most research talks
17   of wet or dry, but does not deal with degree of drying or moisture content, which are probably associated with
18   assemblage composition (Stubbington & Datry 2013, see empirical data supporting this in Strachan et al., 2014).
19   • This review uses pre-electronic era literature which often includes detailed observations of species behavioural
20   responses to drying, but which has often been ignored in more recent studies. Also, it brings together this pre-
21   electronic era literature with contemporary ideas of species traits and how they affect ecology.
22   • Confusion in the terminology used to describe species' responses to desiccation is currently a barrier to coherent
23   synthesis and understanding. This review provides, for the first time, a diagrammatic key to enable researchers to
24   identify the correct term to use to describe the response to desiccation by a particular species.

25

26 **ABSTRACT**

27 In many regions, climate change is prolonging dry periods in rivers and wetlands, exposing freshwater

28 invertebrates to increased periods of desiccation. Invertebrates show a range of strategies for surviving

29 desiccation, but the effects of the degree of exposure to desiccation on the expression of particular traits is

30 unknown. This review synthesizes existing information on the desiccation-responses of freshwater invertebrates

31 to examine the flexibility of these survival strategies and the relationship between strategies and the degree of

32 desiccation to which individuals are exposed. It focuses on desiccation at the small spatial scales experienced by

33 individuals and clarifies the terminology of resting stages present during desiccation. We provide a key to

34 terminology used for different forms of dormancy so that appropriate terms may be used. All invertebrate

35 groups showed a range of strategies for surviving desiccation. Sometimes, different traits were expressed among

36 different populations of a species however it is unclear how many species show multiple desiccation-response

37 strategies. Many crustacean taxa showed physiological dormancy responses to desiccation that enabled survival

38 for long periods (years). Insects often rely on emigration from drying waterbodies as flying adults, or on larvae

39 occupying damp refuges on the benthos. Altered water regimes may alter the phenology of desiccation

40 responses, potentially increasing local extinctions, even in species capable of prolonged dormancy because of

41 constraints on life cycles. However, there is limited empirical evidence demonstrating the flexibility of, or

42 limitations to, expression of these survival strategies and their potential fitness costs.

43 **Key words:** Climate change, Diapause, Dormancy, Drought, Intermittency, Rivers, Traits, Wetlands

Introduction

44

45   It is predicted that by 2090, the proportion of the global land surface in extreme drought will increase tenfold

46   from current levels (Kundzewicz et al. 2008) leading to decreased hydroperiods in affected wetlands. The areas

47   affected by climatic drying include large areas of southern Australia, north-eastern Brazil, Mexico, the

48   Mediterranean and southern Africa. Many of these areas already contain temporary waterbodies, but climatic

49   drying has the potential to change water regimes from perennial to temporary and for existing temporary waters,

50   hydroperiods are likely to further decrease. Temporary waters are diverse in form and geography; they include

51   small depressions, large lakes, riparian wetlands and ephemeral streams that dry to pools and are found in

52   tropical, arid, semi-arid, temperate and mediterranean climate regions (Williams 1996; Schwartz and Jenkins

53   2000). Many wetland processes are interrelated and will have cumulative or synergistic effects, for example

54   changes in air temperature will affect the biota directly, as well as indirectly via changes in evaporation rates

55   and rainfall patterns, and will influence wetland hydrology, stratigraphy and hydrochemistry (Semeniuk and

56   Semeniuk 2012). Altered sediment dynamics can have a large effect on the survival of buried eggs (the egg

57   bank, Hairston 1996). Furthermore, decreased hydroperiods combined with changes in phenology (arising from

58   increased temperatures) will shift the geographical distribution of many species (Grimm et al. 1997). For

59   example, an increase in the mean temperature of 3°C is predicted to result in a loss of 10-25% of the mean

60   species richness in upland streams in the United Kingdom (Durance and Ormerod 2007). In south-western

61   Australia, Sim et al. (2013) have documented change in wetland hydroperiods from perennial to seasonal and

62   from seasonal to ephemeral (or terrestrial) arising from the previous 50 years of drying climate in that region.

63   Although many of the plants and animals living in temporary waters possess traits that enable them to survive

64   dry periods, little is known of the flexibility of these traits and whether they will enable populations to withstand

65   prolonged or more frequent dry periods (Robson et al. 2011). Conceptually, this scenario is one of an

66   increasingly harsh habitat templet (*sensu* Southwood 1977) interacting with species life histories to determine

67   site occupancy by species (Robson et al. 2011). As drying alters the templet, there is an increased risk of species

68   not possessing the traits required for survival in the new water regime. For some taxa, probably those that are

69   good dispersers, existing survival strategies will enable them to withstand prolonged drying (e.g. Sim et al.

70   2013). For other species, their survival may depend on whether the traits within each population are sufficiently

71   flexible to allow their persistence under the new water regimes. Existing research shows that many species

72   possess multiple strategies for surviving drying and these may be used by different life history stages (Robson et

73   al. 2011). Thus, the interaction between species survival strategies and aquatic habitat as waterbodies dry out for

74 longer (or fail to fill at all) is likely to be a major driver of reductions in species geographic range. Thus, a

75 review of the existing terminology and knowledge of the strategies available to taxa inhabiting intermittent

76 waterbodies is timely to provide a foundation for hypotheses of change in response to climatic drying.

77 During summer drying, aquatic animals are exposed to high levels of ultraviolet light, high temperature, large

78 fluctuations in salinity, pH and oxygen, and the rapid disappearance of water (Alekseev et al. 2007). The timing

79 and intensity of this combination of conditions determine the species that survive to reproduce or recolonize

80 during the wet phase. The composition of the fauna emerging from dry basins may change dramatically

81 depending on the time of year that inundation occurs (Dietz-Brantley et al. 2002; Beche and Resh 2007; Kneitel

82 2014) and the volume of precipitation that determines habitat area (Beche and Resh 2007; Vanschoenwinkel et

83 al. 2009). This dependence on timing is important because changing climates may show increasingly

84 unpredictable timing and frequency of rainfall events and thereby no longer meet the needs of some species.

85 Some changes may benefit species dependent on hatching propagules. For example, species that are able to

86 survive harsh periods in dormancy may profit from habitat instability, as the temporarily unsuitable habitat can

87 exclude all competitors (Altermatt et al. 2009). However, other species will suffer disadvantage due to hatching

88 at inopportune times when they cannot complete their life cycle. With respect to climate change impacts, much

89 emphasis has been placed on species' changes in phenology driven by changes in temperature, but for aquatic

90 animals, changes in the timing of hydroregime may be of equal significance. Furthermore, in the scenario of

91 warmer, drier conditions, water temperatures will be warmer and waterbodies shallower, so the effects of

92 decreased hydroperiod and increased temperatures are likely to be synergistic (Davies 2010). Increased

93 temperatures influence the duration of egg incubation periods, hatching success, duration of hatching and the

94 induction and termination of resting stages (Oliver 1971; Alekseev et al. 2007), minimum size at pupation, sex

95 of insects, and increased rate of metabolic function (Terblanche et al. 2005). However, increased temperatures

96 may also exceed physiological tolerances and lead to local extinction (Portner and Knust 2007, Davies 2010).

97 Water quality will also be altered by increased temperatures, influencing oxygen and carbon dioxide levels,

98 salinity and eutrophication in aquatic ecosystems (Portner and Farrell 2008, Davies 2010). Although these

99 multiple stressors caused by climate change will all affect aquatic assemblages, loss of water is among the most

100 deleterious despite many species possessing traits enabling them to survive dry periods (Robson et al. 2011).

101

102   Observations of invertebrates surviving harsh conditions have been made for centuries. Leeuwenhoek (1702

103   cited in Hand et al. 2007) studied animals that survived loss of all cellular water for prolonged periods. Baker,

104   (1764 cited in Hall 1992) revived nematodes after they had been dried for 27 years. Observations of anostracans

105   and notostracans emerging from desiccation resistant eggs date back to the early 18th century (Fryer 1996).

106   Straus (1819-1820) recognized that ephippia on *Daphnia* were used to withstand the northern winter, and this

107   was the first genuine report of diapause (Fryer 1996). Dormancy in invertebrates is not a single trait but rather a

108   large group of individual strategies and physiological states (Caceres 1997); and it is only one of the options that

109   species may use to cope with desiccation. The effect of desiccation is different for each life-cycle stage of a

110   species, especially under different environmental conditions (Danks 2000). This variation may provide

111   opportunities for species to adjust to changed water regimes. For example, copepods that can enter a resting

112   stage as an egg, juvenile or adult, can survive desiccation at any life stage. In contrast, some aquatic taxa

113   sensitive to desiccation die within a few hours of the sediment drying if they cannot find an aquatic refuge

114   (Datry et al. 2012). Even though these processes and mechanisms have been studied for a long time, knowledge-

115   gaps exist, especially the variation in strategies among related species and the flexibility of these strategies

116   under different environmental conditions. Until relatively recently, dry sediments in temporary aquatic habitats

117   were often considered to be biologically inactive (Stanley et al. 1997; Steward et al. 2012).

118   It is important to correctly identify each desiccation response to make predictions about the effects of increased

119   frequency, duration or intensity of drying upon populations. Similarly, understanding the effects of levels of

120   exposure to desiccation upon the expression of traits increases the ability to predict the consequences of

121   changing climatic regimes for freshwater invertebrates. Therefore, this review aims to synthesize existing

122   information on the desiccation responses of freshwater invertebrates, to examine the flexibility of these

123   strategies and the relationship between survival strategies and the degree of desiccation to which individuals are

124   exposed. That is, responses to desiccation at the small spatial scales experienced by individual invertebrate

125   animals. To do this, we have clarified the definitions of the types of resting stages that occur during desiccation

126   and made an effort to include the older (pre-electronic) literature which often included detailed observations of

127   invertebrate behaviour.

128   **What is desiccation?**

129   Desiccation from drought is a major factor in mortalities of insects in temporary pools (Renshaw et al. 1993;

130   Jeffries 1994), but not all drying leads to complete desiccation. Desiccation arises from different mechanisms

131   leading to the loss of water. In high latitudes, desiccation occurs in systems that freeze in the winter and there is

132   no free water for invertebrates; in lower latitudes, desiccation is associated with long periods of drought. In arid

133   and semi-arid areas where invertebrates are exposed to desiccation for most of the year they have adapted to

134   cope with a very short period of inundation, and in mediterranean climate ecosystems, drying is usually an

135   annual occurrence (Hershkovitz and Gasith 2013). Desiccation tolerance is defined as the ability to dry to

136   equilibrium with air (<0.1g H_2Og^{-1}) that is moderate to extremely dry and then to regain normal function after

137   rehydration (Alpert 2005; Rebecchi et al. 2007). The highest post-desiccation survival rates occur after slow

138   drying that gives individuals sufficient time to adjust their metabolism (Ricci and Pagani 1997).

139   While many terms describe individual responses to drying, drying itself is often vaguely defined. A 'dry'

140   riverbed or wetland that has no free surface water can have a gradient of sediment moisture levels ranging from

141   totally dry through to saturated, and this gradient will affect the response of individual invertebrates exposed to

142   it. Where groundwater lies below (sometimes metres below) the exposed surface of wetland or riverbeds, but the

143   interstitial spaces are filled with water through wicking, an intermediate degree of drying is created, that we

144   term 'damp'. At the wetter end of the gradient, 'saturated' conditions occur when the water table is level with

145   the sediment surface. Neither damp nor saturated sediment conditions are necessarily desiccating for

146   invertebrates (although they may also present other environmental challenges, such as low dissolved oxygen),

147   and they may contain subsurface microhabitats accessible to invertebrates (Strachan et al. 2014).

148   There is also an important distinction to be made between an organism being desiccated and an environment

149   being desiccated. The absence of surface water does not mean that habitat is desiccated, and especially does not

150   mean that the invertebrates in it are also desiccated (Strachan et al. 2014). A much greater amount of

151   information is necessary about habitat conditions at the scale at which individual animals are exposed to them,

152   to interpret information on strategies such as dormancy (Brendonck 1996). From afar (as in satellite images), a

153   wetland may appear dry and potentially desiccated, but it may contain damp or inundated microhabitats

154   occupied by invertebrate that do not possess physiological adaptations to desiccation (Strachan et al. 2014).

155   Microhabitats such as cracks in sediments or crayfish burrows that lead to the groundwater table may allow

156   invertebrates to survive periods without surface water and prevent them from becoming desiccated (e.g.

157   Johnston and Robson 2009).

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159

How do individuals respond to desiccation?

Individual animals survive adverse conditions by using physiological adaptations and/or behavioural responses. Some invertebrate groups have profound physiological adaptations to drying, such the desiccation resistant eggs produced by many micro-crustaceans (Robson et al. 2011). These physiological responses include strategies that have been defined as resistance traits or strategies because they allow individuals to resist the drying of waterbodies (Robertson et al. 1995; Lake 2003) and have been included as forms of refuge from disturbance (Chester and Robson 2011; Robson et al. 2013). Resistance strategies may also include the use of refuge (micro) habitats within the benthos. Other groups, such as adult Coleoptera, have behavioural responses like flying away from drying habitat to more permanent water. Winged stages allow recolonization of habitats that have experienced localized extinction due to drought and serve as an important source of colonizers (Bunn and Hughes 1997). These have been termed resilience traits because they permit recovery of populations following loss of individuals during disturbances (Robertson et al. 1995; Lake 2003; Chester and Robson 2011). These strategies may be stimulated by the degree of desiccation to which individuals are exposed, however, in some cases behaviour such as flying away from drying habitat may also be triggered by other processes including life history stage or other forms of disturbance. Similarly, some other traits such as a rapid growth rate or early age at reproduction, which may lead to a population being able to respond to the drying of a waterbody through rapid reproduction, is a response that may be triggered by processes other than drying. In the case of rapid reproduction, several traits (and potentially various combinations of traits) from across two trait domains (reproduction and development *sensu* Verberk et al. 2008) are involved in producing the observed response. To describe this complexity clearly, Verberk et al. (2008) described suites of co-evolved species traits that combine to make adaptations permitting species to deal with a range of ecological problems as 'life-history strategies'. Consequently, because some responses are specific to drying (e.g. aestivation) and others are not (e.g. rapid growth), and because some are combinations of traits rather than single traits, we describe them as 'responses' to desiccation or as 'drought survival strategies'.

To maintain life processes, rather than suspending them, many aquatic invertebrates survive dry periods in refuges comprising microhabitats with high humidity; including beneath algal mats (Strandine 1941), in cracks in the sediment (Strachan et al. 2014), damp areas beneath woody debris or stones (e.g. Chester and Robson 2011; Stubbington 2012) and inside crayfish burrows (e.g. Johnston and Robson 2009). Shallow groundwater such as the hyporheic zone present beneath some streams may also provide refuge for species able

189   to access it (Stubbington 2012). The potential for hyporheic refuges from drying is variable and depends on the

190   presence of saturated interstitial spaces, determined by stream gradient and local geology (Stubbington 2012). If

191   the bottom of a waterbody is concave then resting stages and surviving life stages may move down slope as the

192   water recedes and gather in the deeper zones ('the coffee ground effect'), which are both the last and first place

193   inundated (Stubbington and Datry 2013). Small scale conditions, especially heterogeneity, on the benthos are

194   therefore likely to be important for the survival of invertebrates that seek refuge in the water that remains during

195   the dry period.

196   **The terminology of dormancy responses**

197   Textbook definitions and dictionary meanings of the terminology used to describe resting stages differ markedly

198   (Table 1). For example abiosis and anabiosis are terms used in the literature to describe a state resembling death

199   but their definitions are broad and imprecise. Similarly, Bishop (1967a) stated "students of Crustacea have used

200   the word 'diapause' loosely and did not distinguish between diapause and quiescence". Quiescence is simply the

201   appearance of inactivity, regardless of physical or metabolic state, where as diapause emphasizes a more

202   profound difference between the active and inactive forms; it might require a physiological change to a specific

203   life stage (Fig. 1). A 'Web of Knowledge' search showed some broadly defined words being commonly used

204   while more specific words were used rarely (Table 1).

205   It is important that researchers use the correct terminology to describe species responses to drying, because these

206   terms may describe physiological mechanisms and thereby indicate how much is known about the particular

207   physiological process used (Fig. 1). We have constructed a key to assist researchers to identify the correct term

208   for a species under study, reflecting what is known of its response to drying (Fig. 1). Use of precise terminology

209   also enables more accurate prediction of the outcome of environmental change for species. Usually the

210   appropriate term can be determined by the degree of knowledge of the physiological processes involved in

211   producing the observed state, such as by following the key to terms shown in Figure 1. Often, authors do not

212   know which process or mechanism is occurring and wrongly use a precise term such as 'diapause' where they

213   should be using the term 'dormancy' instead.

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217 **Desiccation resistance among freshwater invertebrates**

218 Most taxonomic groups have several strategies for surviving drought (Table 2), so although individual species

219 might only use one method, ancestral genotypes contained the potential for multiple survival strategies. Some

220 taxa have extraordinary abilities to resist desiccation *in situ*.

221 *Anhydrobiosis*

222 Although many taxa have desiccation resistant eggs, some also have desiccation resistant larvae and adults

223 capable of entering anhydrobiosis (dehydrated state). Nematodes, for example, may produce a resistant third

224 stage juvenile known as "daver larvae" which have a modified cuticle to withstand drying (Wharfton 1986 cited

225 in Caceres 1997) and may survive extended dry periods (longer than 200 days) in a state of anhydrobiosis

226 (Guidetti and Jonsson 2002; Larned et al. 2007). Rotifers also use anhydrobiosis, and some (*Mnibbila* sp.) can

227 survive nine years in a desiccated state (Guidetti and Jonsson 2002). Some leeches are also capable of

228 anhydrobiosis (Kenk 1949, Table 2); for example, a leech survived drying at 13°C for 17 days (Hall 1992).

229 However, the physiological mechanism and fitness cost of anhydrobiosis in most species is unknown. For

230 example, it is not known whether animals can enter and emerge from anhydrobiosis repeatedly. Consequently,

231 while anhydrobiosis is a strategy specific to surviving desiccation and appears to be suitable for long periods

232 without surface water, it is not clear whether it is a flexible or costly strategy for individuals.

233 *Diapause*

234 Diapause is present in life cycles of the majority of crustaceans (Table 2), usually only one form of diapause is

235 specific to order (but exceptions are not rare; Alekseev et al. 2007). Diapause may be used to survive drying,

236 but also freezing, or may occur as part of the life cycle in the absence of disturbance. Copepods have diapausing

237 eggs, juveniles (Conover 1988) and adults (Naess and Nilssen 1991), late copepodites (Sarvala 1979) and adults

238 may encyst (Yaron 1964), and the eggs of some species are very resistant to desiccation (Williams 1980). It has

239 even been reported that some copepods were "desiccation" resistant for 200 years or more (Hairston et al. 1995

240 cited in Bilton et al. 2001). Although copepods are probably very desiccation resistant, the mechanisms that

241 allow prolonged diapause are unknown and therefore the likely effects of drier water regimes on populations

242 cannot be predicted. This is true for other taxa that use diapause to resist drying, such as some stonefly species

243 that have early instars capable of diapause.

244 *Alternative life cycle*

245 For some taxa, the life cycle changes profoundly at the onset of a disturbance such as drying. This type of

246 response to declining water levels comprises reproductive flexibility and the capacity to alter development; it

247 thus combines traits from two domains (i.e. Verberk et al. 2008). Male Cladocera (water fleas, Crustacea) occur

248 in populations only at the onset of unfavourable conditions; usually populations are entirely made up of females

249 reproducing parthenogenetically. Following fertilization, females produce a resting egg (ephippium) by

250 thickening a section of the carapace which forms the ephippium (after her death, Williams 1980). Ephippia have

251 been successfully hatched from dry pond sediments after 200 years (Gooderham and Tsyrlin 2002) and they can

252 withstand both freezing and desiccation (Mellors 1975), suggesting that they would be a robust response to

253 prolonged drying. However, in floodplain sediments, Jenkins and Boulton (2007), found that "cladoceran

254 production fell by more than an order of magnitude as the duration of drying increased from 6 to 20 years",

255 showing that effects of prolonged drying can be detected in wild populations, and indicating that climate change

256 may affect the viability of ephippia.

257 *Resistant eggs and cysts*

258 There are a wide range of other taxa that produce forms of resistant eggs or cysts, some of which must

259 experience a period of dormancy (either quiescence or diapause) prior to hatching. The physiological processes

260 leading to the formation of eggs and cysts differ markedly and eggs may be formed parthenogenetically or

261 through meiosis and sexual reproduction. Even the details of the parthenogenetic process differ among species.

262 In most cases, little is known of the processes by which eggs or cysts develop in response to drying or the

263 triggers that commence these processes. Many Crustacea, such as anostracans (brine shrimp) and copepods,

264 produce desiccation resistant eggs. Anostracan eggs can survive 15-20 years of desiccation (Clegg 1967; Steiert

265 1995 cited in Belk 1998), and may persist in the sediment over many hydrological cycles. Hildrew (1985) used

266 an experiment where 28 day wet/dry periods were oscillated nine times over a 504 day period and observed

267 anostracans hatching during every wet phase. This shows that egg banks can supply hatchlings over repeated

268 cycles of wetting and drying without new egg production contributing to the egg bank. Some genera (e.g.

269 *Branchinella*), require the desiccation of eggs as part of their life history (Williams 1980). Notostraca (tadpole

270 shrimp) are one of the few invertebrate groups found only in temporary waters and their desiccation resistant

271 eggs last for long periods; in at least one species eggs require desiccation for further development (Fox 1949;

272 Williams 1980). Conchostracan (clam shrimp) eggs are also desiccation resistant although the free swimming

273   stages are killed by drying (Bishop 1967b). Anostracans and notostracans are likely to be taxa that adapt well to

274   prolonged dry periods.

275   Other taxa have resting stages that may last for shorter periods, but still up to around two years, representing a

276   form of quiescence. Turbellarians (flatworms, Platyhelminthes) have dormant eggs lasting up to two years

277   (Young 1974) and may also form resistant cysts enclosing young, adults or fragments of animals; they also may

278   survive in permanent pools (Castle 1928, Table 2). Oligochaetes (Annelida) also have resistant cysts enclosing

279   young and can also survive as adults or fragments of adults or dormant eggs (Kenk 1949). The rotifer *Bdelloidea*

280   sp. secretes a cyst with a layer of protective gel (Williams 2006; Alekseev et al. 2007), which is thick shelled

281   and only hatches after a dormant period (Williams 1980).

282   Insects, including many dipterans and some coleopterans, may produce desiccation resistant eggs. For example,

283   the chironomid midge *Polypedilum vanderplanki* produces desiccation resistant eggs capable of surviving

284   drying for 17 years (Adams 1985 cited in Rebecchi et al. 2007). Simuliidae (black flies) and Culicidae

285   (mosquitoes) have drought resistant eggs which hatch once the water returns (Hawley 1988 cited in Alto and

286   Juliano 2001; Robson et al. 2011). *Aedes aegypti* and *A. albpictus* eggs become resistant to desiccation

287   approximately 24-48 hours after deposition (Christophers 1960 cited in Sota and Mogi 1992). *Eurosta*

288   *solidaginis* (Diptera: Tephritida) found in North America, withstand exceptionally dry conditions for 6-8

289   months; among the driest reported for any insect (Ramlov and Lee 2000). Some species of Plecoptera

290   (stoneflies) have eggs that pass through dormancy periods (Table 2); while other species show delayed hatching

291   (e.g. members of the Perlidae, Perlodidae and Pteronacyidae) (Marten and Zwick 1989). These are forms of

292   quiescence and diapause, respectively.

293   *Aestivation*

294   Some taxa rely on shorter term resistance to drying by constructing special resistant structures in which to

295   aestivate or hibernate (Fig. 1). Some species of Hirudinea are able to survive the summer and autumn period

296   buried in the ground and some surround themselves in a secreted layer of slime in small cavities in the dry mud,

297   forming an aestivation chamber (Herter 1937 cited in Kenk 1949; Davies 1991; Hall 1992). Enchytraeids

298   (oligochaetes) use two survival strategies to survive drying: migration to deeper and moister microhabitats (only

299   for periods of days) or a desiccation tolerant cocoon stage (Maraldo et al. 2009). Burial in deeper, moister

300   sediments is also a strategy used by some bivalve molluscs (Table 2). Hyriidae (freshwater mussels) are able to

301   tolerate prolonged dry spells by burying themselves in the mud and sealing their shell (quiescence). Sphaeriidae

302   may survive drying for short periods (Davis and Christidis 1999), by closing their shells. Many sphaerids are

303   endemic to ephemeral waters where they survive drying for many months (McMahon 1991).

304   Aestivation has not been recorded for amphipods and has only been observed in isopods in two studies: Chester

305   and Robson (2011) observed adult *Synamphisopus doegi* (erroneously named *Paraphreatoicus relictus*)

306   aestivating in damp sediment beneath stones in dry stream beds; Mackie et al. (2012) found two species of

307   isopod (*Heterias* sp. and *S. doegi*) aestivating under boulders in damp places in intermittent streams; both

308   studies were in the Victoria Range, western Victoria, Australia. Aquatic amphipods and isopods therefore

309   probably have a reliance on permanent water sources (e.g. Murphy et al. 2010). Under climate change these

310   refuges may be more difficult to access. If the ability to aestivate is rare among amphipods and isopods, this

311   could place them at significant risk of local extinction during climatic drying.

312   Similarly, freshwater crayfish may construct aestivation chambers (Chester and Robson 2011), burrow down to

313   the water table (Williams 1980; Fig. 2), or enter the burrows of other crayfish species (Johnston and Robson

314   2009). Some are able to survive several years of drought in burrows connected to the water table and some

315   species seal the burrow entrance with a mound of excavated earth to further reduce drying (Riek 1969), another

316   form of aestivation. Responses to prolonged drying and water regime change arising from climatic drying will

317   probably vary widely among freshwater crayfish species. Aestivation is rarer among insects than crustaceans but

318   has been recorded for some caddisfly (Leptoceridae, Wickson et al. 2012) and dragonfly larvae (Telephlebiidae,

319   Chester and Robson 2011). The caddisflies seal their cases up with silk and the dragonfly larvae burrow beneath

320   stones on the streambed. For all the taxa that aestivate, the construction of aestivation chambers probably

321   entails fitness costs.

322   False start events may occur where an intense rainfall event causes the partial filling of a dry waterbody, which

323   then dries out again before aquatic invertebrates can complete their life cycles. Mortality will occur in some

324   species, and other species may encounter a fitness cost such as having to repeatedly construct (and emerge from)

325   aestivation chambers. An experiment with caddisfly larvae showed that drier sediment conditions reduced the

326   success of aestivation (Wickson et al. 2012), so aestivation will have limits to its viability that may be exceeded

327   for some species and some locations as a result of climatic drying.

328   *Resistance by use of moist microhabitat refuges within a waterbody*

329 Where invertebrates survive drying within moist sites within a waterbody they are resisting desiccation in that

330 waterbody. However, there are other survival strategies that involve invertebrates leaving the waterbody to seek

331 out moist or wet habitats elsewhere and these are resilience strategies (discussed below).

332 Some species exploit damp microrefuges on the benthos (Fig. 2). For example, the adults of some cladoceran

333 and gastropod species can survive and remain active in damp sediment. Other freshwater gastropods, both adults

334 and young, survive drying in patches of moist air and sediment beneath dried algal mats (Strandine 1941; Facon

335 et al. 2004). The production of an epiphragm or operculum to seal the shell aperture and retain moisture

336 prolongs the time that they can remain in these microrefuges. However, juvenile gastropods are more

337 susceptible to drying than adults (Facon et al. 2004), so if a false start occurs and they hatch out, the whole

338 cohort may be killed. These types of microrefuge are likely to become smaller and occur less frequently under

339 drier climates.

340 Amphipods and isopods have been commonly found in temporary ponds where they take advantage of the

341 pholeteros (burrow water; Lake 1977); but they are also found in waterbodies without crayfish burrows (Harris

342 et al. 2002), so they exploit refuges such as the groundwater table, which they access by burrowing (Fig. 2,

343 Williams and Hynes 1976), or perennial springs associated with temporary waters (Murphy et al. 2010).

344 Shallow groundwater can be a refuge and corridor for dispersal for these crustaceans (Harris et al. 2002), and

345 cracks in the substrate may give access to ground water, as observed for *Paramphisopus palustris* (Strachan et

346 al. 2014). If groundwater tables decline with climatic drying, these refuges are likely to become unavailable in

347 some places, leading to local extinction of species like these that have few alternatives (Table 2).

348 **Desiccation resilience among freshwater invertebrates**

349 *Cohort splitting*

350 Cohort splitting occurs when a single generation divides because of differing duration of a dormant stage (Bunn

351 1988; Robson et al. 2011). This mechanism occurs together with diapause, where individuals remain viable for

352 longer than their usual life cycle and may occur in the absence of disturbances as well as in response to

353 disturbances, including drying (Bunn 1988). Unlike the strategies listed above, it occurs at the population level.

354 For example, Hildrew (1985) found that during inundation in a Kenyan rain pool, only about 3% of the fairy

355 shrimp population hatched and this reproductive population produced offspring equalling 7 times the

356 population, showing the productive potential of egg banks. Female conchostracans also use cohort splitting

357 where they deposit very large numbers of eggs at times of favourable conditions so that they can persist for the

358 next few years even if the conditions become unfavourable (Dobrynina 2011). Cohort splitting probably occurs

359 in many groups of invertebrates as a means of resisting desiccation but goes unnoticed, being difficult to detect

360 unless studied directly. It may become more important as climate change progresses and warrants further

361 research to determine the limits to its flexibility. A few studies of the egg bank and aestivation are beginning to

362 address these questions (e.g. Jenkins and Boulton 2007; Wickson et al. 2012; Stubbington and Datry 2013).

363 *Dependence on perennial waters*

364 Lastly, some species rely on perennial waters, such as permanent pools that exist amongst temporary wetlands

365 or streams (e.g. Fig. 7.19 in Boulton et al. 2014; Rayner et al. 2009; Murphy et al. 2010; Chester and Robson

366 2011). Those insect larvae unable to accelerate their growth or enter a dormant state to avoid desiccation may

367 rely entirely on perennial waters. They include some species of mayfly (Ephemeroptera), water pennies

368 (Psephenidae: Coleoptera), as well as some Crustacea such as decapod shrimps, some isopod and amphipod

369 species and some freshwater crayfish (Boulton et al. 2014).

370 *Rapid Growth*

371 Rapid growth during periods of inundation in temporary waters is a strategy used to complete the aquatic stage

372 of a life cycle seen in several invertebrate groups, particularly insects (Table 2). This strategy is not confined to

373 drought but is potentially beneficial for a range of circumstances. Furthermore, under warmer conditions, many

374 invertebrates are likely to increase their growth rate. For example, mosquitoes take advantage of small

375 temporary waters to reproduce and rapidly complete their life cycle as an aerial adult. Odonates may respond to

376 drying by developing faster, reducing their size at metamorphosis (Murdoch 1971). However, final instar size

377 may be directly related to fecundity in females (Rowe and Ludwig 1991; De Block et al. 2008), so this may

378 entail a fitness cost.

379 Ostracods that live in temporary waters may grow rapidly and are short lived, potentially having multiple

380 generations in one season, permitting cohort splitting (Marmonier et al. 1994) and showing how resistance and

381 resilience traits can combine to create highly effective strategies for surviving desiccation. Hatching has been

382 observed in sediment during damp periods but most hatching occurs after refilling (Aguilar-Alberola and

383 Mesquita-Jones 2011, Strachan et al. 2014) suggesting quiescence. With immature stages already in the dry soil,

384 ostracods may have a developmental head start when the water returns and an advantage over other species of

385   invertebrates, given that they are already well developed (Horne 1993). It also appears likely that the amount of

386   time juvenile ostracods take to become active once re-immersed is proportional to the duration of desiccation

387   (Horne 1993; Aguilar-Alberola and Mesquita-Jones 2011). Strachan et al. (2014) observed two strategies for

388   surviving drying among six species of ostracods (Cyprididae) in one intermittent wetland: one group (4 species)

389   closed their carapace and aestivated and the other group (2 species) relied on the hatching of desiccation

390   resistant eggs.

391   *Emigration by flying adults*

392   Emigration is a drought-avoidance strategy seen in many insects but also in most species of Acarina (water

393   mites). They have larvae that attach to migrating insect hosts and leave the water (phoresis), remaining attached

394   to their host throughout its stay in permanent water and returning to temporary waterbodies with the host when

395   water returns (Wiggins et al. 1980). Insects generally have a separate aquatic larval stage and an aerial adult

396   stage with varying degrees of dependence on water, so this form of resilience strategy is common (Table 2).

397   Therefore, once hatched, insects may have to complete their aquatic life stage before surface water disappears,

398   although the ability of most species to accelerate their growth, and any associated fitness costs, are unknown

399   (except for some odonates e.g. De Block et al. 2008).

400   Aquatic coleopterans (beetles) show a range of traits to resist drying including recolonizing adults (Table 2,

401   Jackson 1956 cited in Williams 2006). Aquatic Hemiptera (true bugs) do not appear to have life stages tolerant

402   to drying, instead relying on recolonizing adults (Macan 1939 cited in Williams 2006) but like beetles they are

403   able to efficiently exploit temporary water bodies. Adult beetles are usually capable of flying away and

404   effectively avoid drought through rapid colonization of more permanent waters via flight (Wissinger 1995 cited

405   in Smith and Golladay 2011). Many predatory adult water beetles and bugs are able to survive in harsh aquatic

406   environments such as drying pools where levels of dissolved oxygen are low (Anderson 1976), because they are

407   air-breathers, in order to prey or scavenge upon trapped animals.

408   Although short-lived, Ephemeroptera (mayflies) have mobile adult stages that may fly to permanent water

409   (Lehmkuhl 1973; Williams 1980) as do the Plecoptera (stoneflies). Wing length is important in flight dispersers;

410   rare species frequently have relatively shorter wings while common species have long wings and are therefore

411   better dispersers (Malmqvist 2000). Ephemeroptera are susceptible to drying and while a few species have

412   desiccation resistant eggs (Williams 1980; Robson et al. 2011), most species survive in permanent water and

413   repopulate temporary waters via oviposition. Most Plecoptera have a mobile adult stage that migrates by flight

414   to survive the summer around permanent water (Harper and Hynes 1970; Boulton et al. 2014). Some species are

415   very selective in their choice of oviposition sites, for example, ovipositing almost exclusively on substrata that

416   protrude above the water surface (Lancaster et al. 2010), which may provide a humid environment that keeps

417   eggs moist.

418   **Life history strategies that combine desiccation resistance and resilience traits may show the greatest**

419   **flexibility, despite their complexity**

420   Odonata (dragonflies and damselflies) and Trichoptera (caddisflies) have some of the most complex

421   combinations of drought survival strategies, including: diapausing eggs within desiccation resistant gelatinous

422   egg masses and terrestrial pupae (Trichoptera); desiccation resistant nymphs (odonates) and recolonizing adults.

423   Most species that inhabit temporary waterbodies show rapid growth (Wiggins 1973; Watson et al. 1991; De

424   Block and Stoks 2005) and some species of caddisfly have larvae that can burrow and survive deep in substrata

425   (Wiggins 1973); and probably undergo quiescence. Larvae of the dragonflies *Telephlebia* and *Antipodophlebia*

426   can be found quiescent in damp leaf litter; Petaluridae larvae are semi-aquatic burrowers while Archipetaliidae

427   and Austropetaliidae larvae are semi-terrestrial and can be found under damp logs (Daborn 1971; Gooderham

428   and Tsyrlin 2002). Some damselfly species in wetlands deposit eggs endophytically (within the stems of

429   vegetation) (Silsby 2001) where they undergo quiescence until the habitat refloods. When nymphs of the

430   dragonfly *Anax* sp. reach their last instar, they either metamorphose or enter mesopause (Fig. 1) depending on

431   the photoperiod; in long photoperiods the dragonfly will metamorphose within a couple of days but if the

432   photoperiod is shorter it will enter mesopause, where it will stay for at least 105 days (Corbet 1956).

433   Those trichopterans having cases built from silk, twigs, leaves or stones probably experience some protection

434   from drying. Some species deposit their eggs in a terrestrial location which is thought to reduce the risk of

435   autumn rain providing a 'false start' (Wissinger et al. 2003). Leptoceridae and Limnephilidae may enter

436   dormancy as eggs (Wiggins 1973), a form of hibernation; the eggs are also capable of diapause and the aquatic

437   larvae of aestivation (Colburn 1984; Wickson et al. 2012). Diapause (Colburn 1984) has also been shown in

438   larvae of the Glossosomatidae (Anderson and Bourne 1974), Sericostomatidae (Elliott 1969) and

439   Calamoceratidae (Anderson and Cummins 1979). Life histories for Trichoptera can differ considerably from one

440   location to another within the same species (Elliott 1968) suggesting that the use of these survival traits might

441   vary among populations. For example, the suspension-feeding caddisfly *Smicrophylax australis*

442   (Hydropsychidae) showed autumn-winter hatching, followed by rapid growth in spring and adult emergence in

443   late summer in a warm shallow perennial stream. In contrast, in a nearby cooler and deeper stream, larval

444   growth rates of *S. australis* were slower: larvae hatched in autumn-winter failed to emerge the following

445   summer and instead emerged the following year over a shorter period during spring and early summer (Bunn

446   1988). Both populations showed cohort-splitting (Bunn 1988) but the pattern differed between streams,

447   presumably because the warmer stream facilitated faster growth but perhaps also provided a cue (warm shallow

448   conditions) to larvae to accelerate growth to avoid potential stream drying, because these larvae lack a

449   desiccation resistance mechanism. Other caddisfly strategies can include migration from intermittent habitats

450   shortly before drying (e.g. some species of the genus *Ironquia* sp. (Limnephiloidea)); *I. plattenis* migrate as a

451   fifth instar and aestivate for 4 months before pupating (Flint 1958; Whiles et al. 1999). Although some caddis

452   larvae aestivate by sealing their cases with silk (e.g. Wickson et al. 2012), it is unclear whether they can

453   repeatedly emerge from and re-enter this state, as would be required with increased occurrence of false start

454   events during dry periods. However, even if they can repeatedly aestivate, emerge and aestivate again, there is

455   likely to be an eventual fitness cost for adults.

456   The capacity for survival strategies to differ between populations in some species permits adaptation to local

457   conditions, a form of flexibility that will assist species to adapt to climatic drying. For example, the bivalve

458   *Pisidum moitessieranum* in southern Finland produces only one cohort per year, eggs are laid in the summer and

459   shelled larvae emerge the following spring. But in the Upper Rhone (France) the same species produces two

460   cohorts per year and the first cohort are incubated in the mother's shell for three months and then released

461   (Marmonier et al. 1994). Similar examples have been reported for other invertebrate species, but more research

462   is required into the flexibility of life history traits related to surviving desiccation and whether there is a

463   possibility of species being able to switch from one strategy (combination of traits) to another and maybe

464   'hedging their bets' with multiple strategies among populations.

Invertebrate life cycles and their interaction with drying climates

466   There are many advantages for species that can persist *in situ* despite desiccation. Aestivation allows species to

467   exploit habitats not available to other taxa and potentially to dominate temporary waterbodies through early

468   emergence (Strachan et al. 2014), as does the ability to hatch and develop in damp sediment (Horne 1993;

469   Robson et al. 2011; Wickson et al. 2012). However, life cycle lengths for aquatic invertebrates differ under

470   different temperatures and among species (e.g. Nilsson-Ortman et al. 2013). This is important because where

471   hydroperiods decrease, species with shorter life cycles may be more likely to survive than species with longer

472   life spans, depending on which life stage is affected. However, if species able to survive desiccation as an egg

473   experience hydroperiods too short for hatchlings to reach either emergence or reproductive age, the population

474   risks localized extinction unless cohort-splitting prevents all the eggs from hatching. So far, studies suggest that

475   delayed hatching occurs in many, perhaps most, species that rely on desiccation-resistant eggs but further

476   research is needed to determine how hatching cues will respond to drier water regimes.

477   The biggest difference in traits related to desiccation is between crustaceans and insects. Many crustacean taxa

478   have physiological adaptations to survive desiccation; although most amphipods, isopods and decapod shrimp

479   are exceptions. Crustaceans can also survive for longer periods of time in resting states compared to insects.

480   Insects mainly rely on either emigration as adults to permanent waterbodies or as larvae dwelling in either damp

481   microrefuges or inundated refuge habitat to survive. However, we do not know whether survival in microrefuges

482   occurs because individuals are simply in the right spot at the right time when drying occurs or whether

483   individuals are capable of seeking out and moving into suitable microrefuges (Robson et al. 2013), although

484   there is increasing evidence of deliberate movement into refuges by some species (e.g. Lytle et al. 2008;

485   Johnston and Robson 2009; Strachan et al. 2014). Overall, crustaceans are more likely to emerge in large

486   numbers from refuges on the bed when surface water becomes available, provided that fine sediments are

487   present to harbour them (Stubbington and Datry 2013). Thus, it appears likely that crustaceans will be more

488   resistant to climatic drying than insects, although because of other climatic changes that accompany drying,

489   species with resilience traits may ultimately adapt more successfully (Chester and Robson 2011).

490   The altered timing of seasonal floods that may accompany climatic drying could limit distributions of more

491   desiccation resistant species by disrupting matches between life stages and resource availability (Sponseller et

492   al. 2010). For example, emergence following dormancy may coincide with an abundance of food, but with

493   altered flood timing there may be more missed opportunities where emergence and the abundant food source no

494   longer coincide. These effects may be transmitted to all trophic levels, with ecological and environmental

495   consequences (Winder and Schindler 2004). Although this review demonstrates knowledge of a range of

496   desiccation resistance and resilience traits, less is known about the phenology of these traits, their flexibility or

497   the potential fitness costs entailed by climate change. This comprises a large knowledge gap in our ability to

498   predict the consequences of climate change on ecosystems.

499   Some desiccation survival traits are better developed to survive higher temperatures and longer dry periods than

500   others, but all traits have limits. Aerial adults may be the most successful way for insects to survive drying as

501 they are able to disperse to find permanent water, however, drier landscapes with little vegetation may also limit

502 adult movement (Collier and Smith 2000). However, we know from genetic studies that many aquatic insects

503 are surprisingly poor dispersers (Hughes et al. 2013). Insect larvae need to have a hydroperiod duration

504 sufficient to reach their final larval instar and then, depending upon their dispersal ability, (or the availability of

505 'stepping stones'), the length of the adult life stage will determine whether they reach suitable habitat. A few

506 long term studies of the impact of drought and increasingly intermittent flow regimes now show that some taxa

507 will be 'filtered out' by prolonged drying, reducing biodiversity and leading to lasting change in community

508 composition (Sponseller et al. 2010; Bogan & Lytle 2011). The most successful strategies for surviving

509 prolonged drying and higher temperatures are shown by crustaceans with eggs that are viable for long periods

510 and capable of cohort splitting and by insects with strongly dispersing flying adults and rapidly growing larval

511 stages. More research is required into invertebrate physiology so we can predict the mechanisms involved in

512 survival of desiccation and the environmental limits of these mechanisms. Furthermore, studies are now

513 showing that even congeneric species can show remarkably different trait functions (e.g. Nilsson-Ortman et al.

514 2013), meaning that more species-level investigations are needed to understand the diversity of responses to

515 environmental change.

516 This review has highlighted the need for further research into life history traits and strategies, their flexibility

517 and the physiological processes used in resisting desiccation. One difficulty for research is that traits for

518 surviving dry periods are species or life-stage specific, even different populations of the same species may

519 display different survival strategies. However, initial responses to climate change in ecological communities will

520 be by individuals, and thus will be reflected in the population dynamics of individual species. Groups of species,

521 whether functional or taxonomic will not respond as a single unit (Steffen et al. 2009) so species responses must

522 be investigated to predict the outcomes of climate change.

523 One of the questions we posed at the beginning of this article was: does the degree of exposure to desiccation

524 affect the expression of life history strategies for surviving desiccation? Unfortunately, the knowledge we have

525 about species responses to desiccation does not yet enable us to answer this question. More field and laboratory

526 studies are needed to investigate the tolerances of species, the flexibility of their life history traits and the effects

527 of water regime change on individual and population fitness. Specifically, how much moisture is retained in

528 different habitats as they dry and the effect of this on species responses is a key knowledge gap that limits our

529 ability to predict the consequences of changes in water regime in both running and standing waters. Those few

530   studies that have examined different degrees of drying (Stubbington and Datry 2013, Strachan et al. 2014)

531   suggest that moisture content will be a key variable in invertebrate persistence in freshwater ecosystems.

532

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825

Figure captions

827   Figure 1. Key to terminology of the types of dormancy shown by freshwater invertebrates. Using literature listed

828   in the Table 1, this key was constructed to assist researchers to identify the correct terminology for

829   dormant states. Begin on the left hand side and proceed according to the level of knowledge about the

830   physiology and traits of a particular species.

831   Figure 2. Refuges that aquatic animals use to survive dry periods in wetlands. Image: South Lake, Perth.

Table 1. Terminology and definitions for the 'dormant stages' shown by invertebrates in response to habitat drying.

Term	Description of meaning	Web of science usage*	Our definition	Taxa shown to use strategy
Resting stages		1739	A broad collective term for the different types of dormancy and diapause; should be used when more specific processes is not understood.	
Resistant stages		2394	A broad collective term for the different types of dormancy and diapause; should be used when more specific processes is not understood.	
Suspension of life		536	A broad collective term for the different types of dormancy and diapause; should be used when more specific processes is not understood.	
Dormancy	"Is a suspension of the vital functions in an organism for a certain, sometimes very long, period of time to overcome harsh environmental conditions; with long term cessation of development, growth and breeding. In insects it may occur in embryonic, immature or adult stages" (Gordh & Headrick, 2001; Alekseev, DeStasio & Gilbert, 2007).	2956	The slowing of metabolism to overcome a harsh environment	
Hypobiosis	"dormancy" (Allaby, 2009)	16	Another term for dormancy	

Diapause	"Is a type of dormancy; it is determined by a predictive mechanism combining environmental signals and an internal biological clock, driven by hormones and induced by both signal and vital factors (e.g. a larval damselfly or ephippial eggs). Development is not resumed, even if the conditions become favourable, until diapause is broken. It is regarded as adaptive and increases the probability of survival during environmentally unfavourable conditions" (Gordh & Headrick, 2001; Brendonck & DeMeester, 2003; Alekseev *et al.*, 2007)	4772	Is the slowing of the metabolism cued by seasonal cues and biological clock, driven by hormones and will not end when favourable conditions return but rather when diapause is broken	Nematoda, Turbellaria, Oligochaeta, Bivalves, Gastropods, Acarina, Cladocera, Copepoda, Conchostracha, Ostracoda, Anostraca, Notostraca, Chironomidae, Diptera, Culicidae, Ephemeroptera, Odonata, Plecoptera, Trichoptera, Rotifers
Quiescence	"Quiescence is an immediate response to a limiting factor, and metabolism and development is resumed as soon as conditions permit" (Gordh & Headrick, 2001; Brendonck & DeMeester, 2003; Alekseev *et al.*, 2007).	1389	Is a period of slowed metabolism to survive a period of limiting factor and is resumed as soon as conditions become favourable	Bivalves, Gastropods, Acarina, Cladocera, Copepoda, Conchostracha, Ostracoda, Plecoptera, Trichoptera
Aestivation	"Is a physical state in which an organism is metabolically inactive or physically dormant during summer or during periods of continued high temperatures in temperate areas or during a dry season in tropical areas" (Gordh & Headrick, 2001).	543	Is a time of slowed metabolism usually during summer to survive a hot and dry period	Nematodes, Hirudinea, Amphipoda/Isopoda, Decapoda, Odonata
Hibernation	"winter dormancy, a period of suspended development in organisms that occurs during seasonally low temperatures" (Gordh & Headrick, 2001).	2515	Is a time of slowed metabolism usually during winter to survive a cold period	Acarina, Cladocera, Ostracoda, Trichoptera
Athermopause	"Is a physiological condition or expression of dormancy that is influenced by one or more non-thermal factors" (Gordh & Headrick, 2001).	0	Is a period of slowed metabolism influenced by a non-thermal factor (e.g. food shortage)	
Summer diapause	May be induced obligatorily or facultatively by such seasonal cues as day length and temperature, different from winter diapause as the two types involve different physiological processes (Resh & Carde, 2003)	591	Diapause that occurs in the summer months triggered by cues such as day length and temperature	

Term	Definition	Count	Description	Taxa
Abiosis	"Is suspension of life, a mode of living, vitality" (Gordh & Headrick, 2001).	1		
Anabiosis	"A condition of apparent death or suspended animation where productive metabolic process in which biochemical reactions within the animal body produces proteins, fats and carbohydrates from food material" (Lawrence et al. 1998; Gordh & Headrick, 2001)	66		
Superpause	"Is diapause for more than 1 year" (Gordh & Headrick, 2001)	0	Diapause for a period of more than a year	
Mesopause	"Is diapause for between 3-12 months" (Gordh & Headrick, 2001)	12	Diapause for a period of 3-12 months	
Oligopause	"Is diapause for less than 3 months"(Gordh & Headrick, 2001)	13	Diapause for a period of less than 3 months	
Cryptobiosis	"Is a hidden life, continuing at a low metabolic level, without obvious signs of activity" (Anderson, 2001) (e.g. Collembola).	118	Is a physiological adaption where the animal is camouflaged and period of low metabolic function	
Anhydrobiosis	"Is the maintenance of life in the absence of water induced by low humidity or by desiccation" (Anderson, 2001; Gordh & Headrick, 2001)	305	Is a physiological adaption of being able to dehydrate and then rehydrate and survive	Nematodes, Turbellaria, Hirudinea, Trichoptera, Rotifers
Cyclomorphosis	"Seasonal changes in body shape found in rotifers and in cladocerans. In cladocerans the changes in shape involve the head, which is rounded from midsummer to spring and then progressively becomes helmet shaped from spring to summer reverting to the rounded shape by midsummer. The process is poorly understood and may be a result of genetic factors interacting with external conditions (e.g. temperature)" (Allaby, 1994; Williams, 2006).	143	Is a physiological adaption of change in body shape over the summer period, only observed in rotifers and cladocerans	Rotifers, Cladocera

*Web of science search conducted on 6/11/12; related search included web of science categories: anatomy morphology, biodiversity conservation, biology, cell biology, developmental biology, ecology, entomology, environmental sciences, environmental science ecology, evolution biology, fisheries, limnology, marine freshwater biology, microbiology, physiology, reproductive biology and zoology. Usage: numbers are numbers of articles identified in the search as using a particular term.

Table 2. Drought survival strategies across life stages in freshwater invertebrate taxa and their known duration of dormancy (where applicable). Strategies and life stages in bold are specific responses to desiccation, others are used for other types of disturbance.

Group	**Aestivation**	**Anhydrobiosis**	Cryptobiosis	Diapause	Hibernation	Quiescence	Cohort splitting	Commensalism	Rapid growth	**Sealing shell/carapace**	Burrows	Aerial adults	**Egg**	**Larvae/Juvenile**	**Adult**	**Pupae**	**Fragment**	Pholeteros	Moist sediment	Moist leaf litter	Algal mats	Silk /mucus cocoons/cyst	Permanent waters	Survival time dormant state	References
Nematoda	X	X		X									X	X	X		X	X	X				X	10 years	Boulton et al. (2014); Baker (1764) cited in Hall (1992); Caceres (1997); Gooderham & Tsyrlin (2002); Guidetti & Jonsson (2002); Larned et al. (2007); Poinar (1991); Wharfton (1986) cited in Caceres, (1997)
Turbellaria		X		X									X	X	X		X					X			Boulton et al. (2014); Castle (1928); Davis & Christidis (1999); Young (1974)
Hirudinea	X	X												X	X		X					X		17 days	Davies (1991); Hall (1992); Herter (1937) cited in Kenk (1949); Kenk (1949)
Oligochaeta				X									X	X	X		X	X	X			X		Months	Kenk (1949); Maraldo et al. (2009)
Bivalves	X			X	X					X				X	X				X					Many months	Byrne & McMahon (1994); Davis & Christidis (1999); Way et al. (1980); McMahon (1991)
Gastropoda				X		X								X	X				X		X	X		Extremely long time	Barbosa & Barbosa (1959); Davis & Christidis (1999); Eckbald (1973); Falcon et al. (2004); Gooderham & Tsyrlin (2002); Pilsbry (1896) cited in Strandine (1941); Strandine (1941)
Acarina	X			X	X	X						X			X							X			Belozerov (2008); So & Takafuji (1991); Wiggins et al. (1980);
Rotifers		X		X									X									X		9 years	Alekseev et al. (2007); Guidetti & Jonsson (2002); Williams (1988); Williams (2006)
Cladocera	X			X	X	X							X		X				X					200 years	Alekseev et al. (2007); Gooderham & Tsyrlin (2002); Jenkins & Boulton (2007); Mellors (1975); Williams (1988)
Copepoda				X		X							X	X	X							X		200 years	Conover (1988); Hairston et al. (1995) cited in Bilton et al. (2001); Larned et al. (2007); Naess & Nilssen (1991); Sarvala,(1979); Williams (1988); Yaron (1964)

Group	Survival strategy												Life stage capable					Refuge						Survival time dormant state	References
	Aestivation	Anhydrobiosis	Cryptobiosis	Diapause	Hibernation	Quiescence	Cohort splitting	Commensalism	Rapid growth	**Sealing shell/carapace**	Burrows	Aerial adults	**Egg**	**Larvae/Juvenile**	**Adult**	**Pupae**	**Fragment**	Pholeteros	Moist sediment	Moist leaf litter	Algal mats	Silk /mucus cocoons/cyst	Permanent waters		
Conchostracha				X		X	X			X			X											Long periods	Bishop (1967a); Bishop (1967b); Davis & Christidis (1999); Dobrynina (2011); Gooderham & Tsyrlin (2002); Rzoska (1961); Williams (1985); Williams (1988)
Ostracoda				X	X	X	X			X	X		X	X	X				X					Years	Aguilar-Alberola & Mesquita-Jones (2011); Davis & Christidis (1999); Delorme (1991); Gooderham & Tsyrlin (2002); Horne (1993); Larned et al. (2007); Marmonier et al. (1994); Williams (1988)
Amphipoda/ Isopoda	X													X	X			X	X			X			Chester & Robson (2011); Harris et al. (2002); Lake (1977); Mackie et al. (2012); Marsden (1991); Swanson (1984); Williams & Hynes (1976); Williams (1988); Wilson (2008)
Decapoda	X					X					X							X						3 years	Johnston & Robson (2009); Riek (1969); Williams (1988)
Anostraca				X						X			X											15-20 years	Clegg (1967, 2005); Hildrew (1985); Hinton (1954) cited in William (2006); Steiert (1995) cited in Belk (1998); Williams (1988)
Notostraca				X			X						X											Long periods	Fox (1987); Hildrew (1985); Williams (1988)
Collembola		X									X		X	X	X				X					4 months	Alvarez et al. (1999); Bahrndorff et al. (2006); Bayley & Holmstrup (1999); Butcher et al. (1971); Davidson (1932); Gooderham & Tsyrlin (2002); Greenslade (1981) cited in Alvarez et al. (1999); Wallace (1968); Williams (1988)
Coleoptera											X	X			X	X				X					Anderson (1976); Jackson (1956) cited in Williams (2006); Lake et al. (1989) cited in Smith & Golladay (2011); Smith & Golladay 2011; Verberk et al. (2008); Wissinger (1995) cited in Smith & Golladay (2011)
Chironomidae				X										X	X	X						X		17 years	Adams (1985) cited in Rebecchi et al. (2007); Bishop (1974); Danks (1971); Jones (1975); Larned et al. (2007); Horsfall (1955) cited in Williams & Hynes (1976)
Diptera				X		X								X	X	X								6-8 months	Ramlov & Lee (2000); Robson et al. (2011)
Culicidae				X									X							X					Christophers (1960) cited in Sota & Mogi (1992); Hawley (1988) cited in Alto & Juliano (2001); Renshaw et al. (1993)
Ephemeroptera				X		X							X	X					X			X			Lehmkuhl (1973); Malmqvist (2000); Robson et al. (2011); Williams (1988)

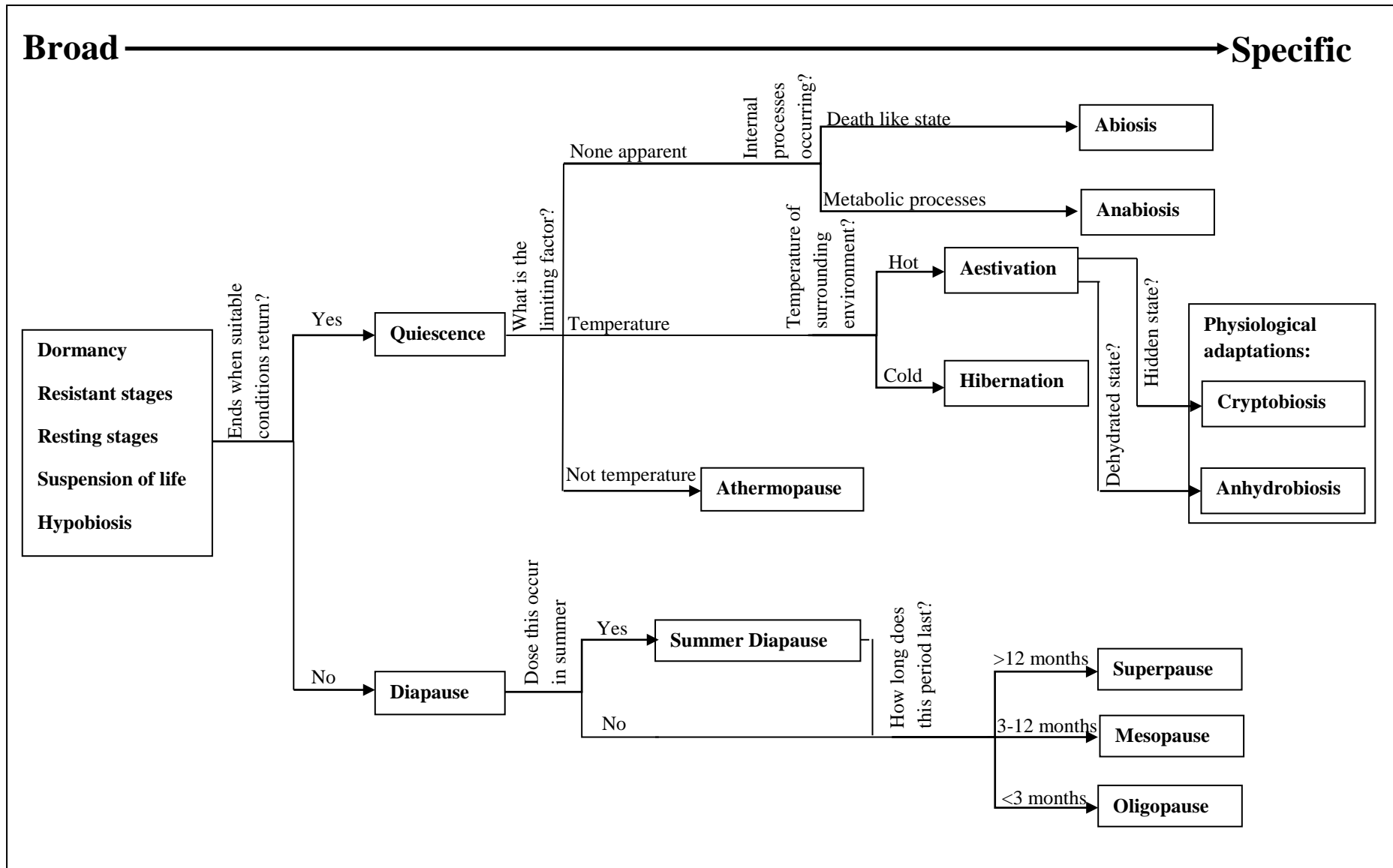| Group	Survival strategy											Life stage capable							Refuge					Survival time dormant state	References
	Aestivation	Anhydrobiosis	Cryptobiosis	Diapause	Hibernation	Quiescence	Cohort splitting	Commensalism	Rapid growth	Sealing shell/carapace	Burrows	Aerial adults	Egg	Larvae/Juvenile	Adult	Pupae	Fragment	Pholeteros	Moist sediment	Moist leaf litter	Algal mats	Silk /mucus cocoons/cyst	Permanent waters		
Hemiptera												X											X		Macan (1939) cited in Williams (2006); Pajunen & Jasson (1969) cited in Wiggins et al. (1980); Popham, (1964) cited in Wiggins et al. (1980)
Odonata	X			X	X	X			X			X	X	X						X			X		Corbet (1956); Daborn (1971); Gooderham & Tsyrlin (2002); Murdoch (1971); Raebel et al. (2010); Ludwig & Rowe (1990); Silsby (2001); Watson et al. (1991)
Plecoptera				X		X						X	X	X									X		Boulton et al. (2014); Harper & Hynes (1970); Lancaster et al. (2010); Marten & Zwick (1989)
Trichoptera		X		X	X	X	X						X	X	X	X			X					4 months	Anderson & Bourne (1974); Anderson & Cummings (1979); Colburn (1984); Decamps (1967) cited in Ward & Stanford (1982); Elliott (1968); Elliott (1969); Flint (1958); Gooderham & Tsyrlin (2002); Imhof & Harrison (1981); Lamberi et al. (1987); Lloyd (1921) cited in Kenk (1949); StClair (1993); Whiles et al. (1999); Wickson et al. (2012); Wiggins (1973); Wissinger et al. (2003)

Figure 1

Figure 2