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CRUSTACEANS OF EXTREME ENVIRONMENTS

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This chapter is dedicated to Brenton, a dear friend and outstanding colleague, who dedicated much of his life to the study of crustaceans. Brenton, your legacy will continue.

Abstract

Crustaceans are a remarkably diverse group of organisms that have colonized and occupied a broad variety of niches. Many crustacean species are found in extreme environments, inhospitable to the majority of animal taxa, including Antarctic lakes, subterranean waters, hydrothermal vents, dry deserts, hypersaline lakes, and highly acidic habitats. Particular adaptations have evolved in response to the environmental conditions in these extreme habitats, shaping the lifestyle of crustaceans. In this chapter, some of the morphological, physiological, and life history adaptations that enabled crustaceans to colonize these habitats are reviewed. An overview of the main crustacean taxa in these extreme environments is given, and their evolutionary adaptations are briefly compared to those of other organisms co-occurring in the same habitats. Although not exhaustive, this review highlights how successful crustaceans have been in adapting to extreme conditions. Nowadays, anthropogenic activities risk irreversibly altering the delicate equilibrium these crustaceans have achieved in extreme environments.

INTRODUCTION

Crustaceans, a very speciose group of organisms surpassed only by insects, mollusks, and chelicerates, present an impressive array of morphological diversity, the highest among metazoans (Martin and Davis 2001). Their variety in morphological traits, combined with physiological, ecological,

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and behavioral differences, underscores a high level of adaptation to a wide range of environments and conditions (Thiel and Duffy 2007). Crustaceans have colonized and filled almost every type of niche available, including the most inhospitable places on our planet, such as Antarctic lakes, subterranean waters, hydrothermal vents, xeric deserts, hypersaline lakes, and highly acidic habitats. These environments are hostile to the majority of other multicellular organisms, yet selected crustaceans thrive within them.

Ecosystems are regulated by complex interactions among organisms. The ecological dynamics connecting these organisms are arguably the most important factors shaping species' distributions. In extreme environments, the ecosystem is usually much simpler, and abiotic factors play a major role in determining species' presence and abundance (e.g., Convey 1997), even though biotic factors are still important (Camacho 2006). Abiotic factors include physical (e.g., temperature, pressure, light) and chemical (e.g., salinity, pH, dissolved oxygen) parameters. Extreme environments constitute an array of abiotic factors beyond the extremes of the limits of tolerance of the majority of organisms.

Extremophiles "love" these extreme conditions, or at least can resist and persist in them (Rothschild and Mancinelli 2001). The sense of wonder for these creatures contributed to the creation of names that highlight their ability to survive in extreme conditions: thermophiles, psychrophiles, acidophiles, alkaliphiles, halophiles, xerophiles, and piezophiles resist extreme high temperature, coldness, acidity, alkalinity, salinity, desiccation, and pressure, respectively. Furthermore, many organisms are indeed poly-extremophiles, enduring in environments where more than one parameter is "extreme" (Rothschild and Mancinelli 2001). Depending on the ability to sustain narrow or large variations in abiotic parameters, organisms are classified as "steno" or "eury," respectively. Steno-organisms can survive only within limited variations of the parameters to which they are adapted. We might regard them as the best examples of extremophiles because they are perfectly adapted to specific extreme conditions (low or high temperatures, low or high salinity, etc.). Alternatively, extreme environments may present considerable variation in one or more parameters that can be tolerated by eury-organisms (Peck 2004). When environmental conditions fluctuate greatly over time (e.g., in temporary environments, such as ephemeral pools filled by rain only for a short season or Antarctic lakes that freeze solid in winter), specific stress-avoidance strategies can be used by organisms (Badyaev 2005), including migration, production of desiccation-resistant cysts to survive the lack of water, hibernation, or supercooling to persist in cold conditions.

Some crustacean species are adapted to extreme environments and share their habitats with many microorganisms and a few other multicellular organisms. Because of specialized biological adaptations, many species are endemic to their extreme habitats (Rogers et al. 2007). Here, we summarize the characteristics of extreme environments and present an overview of some of the morphological, physiological, and life history adaptations that enabled crustaceans to colonize these habitats. These evolutionary adaptations are briefly compared to those of other organisms cohabiting the same environments (Tables 14.1 and 14.2).

CRUSTACEANS IN ANTARCTIC LAKES

Antarctica is the most extreme of all continents. Large and isolated, it is the coldest and windiest continent of our planet, characterized by extremely dry weather and almost completely covered by snow and ice during most of the year (Convey 1997, Peck et al. 2006). A biological designation of the Antarctic includes not only continental and maritime areas but also subantarctic islands.

Antarctic lakes display considerable diversity in terms of size, depth, salinity, temperature, age, and seasonality: some freeze solid or dry out completely (temporary lakes), others are permanently

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Table 14.1. Extreme environments: organisms other than crustaceans

	Conditions/ Characteristics	Taxa Present	Adaptations
Antarctic Lakes	Low temperature Poor light climate Nutrient limitation Salinity ↓ Truncated food webs Species poor biota	Acarina[1]	(littoral species)
		Anellida: Oligochaeta[2–4]	
		Bacteria/Cyanobacteria[5, 6]	Biochemical adaptations
		Diptera: Chironomidae[3, 4]	Flexible life cycle; overwintering as larvae and/or adults
		Gastrotricha[2]	
		Nematoda[2, 9, 10]	Euryhaline species in saline lakes; anhydrobiosis and cryobiosis
		Phytoplankton/ Diatoms[5, 6, 11]	Mixotrophy; starch reserves; cysts; nutritional versatility; high mobility
		Platyhelminthes[2]	
		Protozoa[5]	Mixotrophy
		Rotifera[2, 6, 12]	
		Tardigrada[2, 12]	Anhydrobiosis and cryobiosis
Subterranean Environments	Scarce food Anoxia Aphotic environment ↓ Truncated food web	Amphibia[13, 14]	
		Arachnida[13, 15]	Pigment reduction in the eyes or lack of eyes
		Chilopoda[13]	
		Coleoptera[13, 16]	Lack/reduction of eyes; pigment reduction; wing reduction
		Diplopoda[13]	
		Fish[13, 17, 18]	Eye reduction; pigment reduction
		Insecta [Collembola; Diplura; Diptera][13]	
		Molluska[13, 19, 20]	Eye loss; shell size reduction; lack of tegument pigmentation
		Oligochaeta[13, 20]	
		Protozoa[20]	
		Turbellaria[13]	

(*Continued*)

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Table 14.1 (*Continued*)

	Conditions/ Characteristics	**Taxa Present**	**Adaptations**
Hydrothermal Vents	High temperatures High hydrostatic pressure Anoxia Presence of hydrogen sulfide and heavy metals Aphotic environment	Annelida/Tubeworm[21–23]	Symbiotic chemolithoautotrophic bacteria; use of carbonic anhydrase to concentrate carbon; protection by a chitinous tube; phenotypic plasticity; use of myohemerythrin instead of hemoglobin; escape responses
		Chemosynthetic bacteria[24]	
		Gasteropoda/Bivalves[22]	Symbiotic methanotrophic and sulfur oxidizing bacteria
Desert Environments Temporary Freshwater Pools	Extreme hydrological regimes	Acarina[25]	(aquatic mites)
		Amphibia[25–27]	
		Diptera: Chironomidae[25–27]	
		Fish[28, 29]	Fossorial habit; cutaneous respiration
		Heteroptera[27]	
		Insecta [Coleoptera[27]/ Notonectidae/ Corixidae/Culicidae/ Ceratopogonidae][25, 26]	
		Molluska[25]	
		Nematoda[25]	
		Odonata[26, 27, 30]	
		Rotifera[25]	
		Tardigrada[25]	
		Turbellaria[30]	
Desert Rivers	Extreme hydrological regimes	Acarina[31]	
		Annelida[31]	
		Insecta: Coleoptera/ Diptera[31]	
		Molluska[31]	

Table 14.1 (*Continued*)

	Conditions/ Characteristics	Taxa Present	Adaptations
Desert Spring		Insecta: Coleoptera/ Diptera/ Ephemeroptera/ Hemiptera/ Lepidoptera/Odonata/ Trichoptera[32]	
		Molluska[32]	
		Turbellaria[32]	
Desert Saltwater Ponds/ Lakes	Extreme hydrological regimes Salinity ↓ Species poor biota	Acarina[33]	
		Coleoptera[33, 34]	
		Diptera[33]	
		Fish[34]	
		Hemiptera[34, 35]	
		Molluska: Gastropoda[33]	
		Nematoda[35]	
		Odonata[35]	
Acidic Environments	pH <5–6 Possible presence of heavy metals ↓ Species poor biota	Amphibia[36, 37]	Reduced sodium content in the body
		Bacteria[38]	Chemolithoautotrophic; sulfur-oxidizing; resistant spores
		[Coleoptera[39], Megaloptera][40]	
		Diptera: Chironomidae[41–43]	Enlarged anal papillae[44]
		Fish[40]	Chloride cells
		Salamanderfish[29]	Internal fertilization
		Heteroptera[45]	Highly impermeable cuticle[44]
		Molluska; Bivalvia[39]	
		Phytoplancton[38]	
		Protozoa[38]	Eterothrophy
		Rotifera[46]	
		[Trichoptera[43], Plecoptera[43], Ephemeroptera][39, 40, 42]	

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[1] Pugh and Dartnall 1994; [2] Dartnall et al. 2005; [3] Toro et al. 2007; [4] Vincent et al. 2008; [5] Laybourn-Parry 2002; [6] Gibson et al. 2006; [7] Arnold and Convey 1998; [8] Hansson and Tranvik 1996; [9] Andrássy and Gibson 2007; [10] McSorley 2003; [11] Laybourn-Parry and Pearce 2007; [12] Pugh and Convey 2008; [13] Culver et al. 2003; [14] Holsinger et al. 2006; [15] Paquin and Hedin 2004; [16] Leys et al. 2003; [17] Humphreys 2001; [18] Protas et al. 2006; [19] Bichain et al. 2007; [20] Botosaneanu 1986; [21] Cottin et al. 2008; [22] Prieur 2007; [23] Ruan et al. 2008; [24] Crespo-Medina et al. 2009; [25] Chan et al. 2005; [26] Dodson, 1987; [27] Graham 2002; [28] Martin et al. 1993; [29] Berra and Allen 1991; [30] Brendonck et al. 2002; [31] Stanley et al. 1994; [32] Sada et al; 2005; [33] Pinder et al. 2005; [34] Martínez-Pantoja et al. 2002; [35] McCulloch et al. 2008; [36] Pierce and Wooten 1992; [37] Pierce 1985; [38] López-Archilla et al. 2001; [39] Petrin et al. 2007; [40] Collier et al. 1990; [41] Löhr et al. 2005; [42] Winterbourn and Collier 1987; [43] Horecký et al. 2006; [44] Havas and Advokaat, 1995; [45] Wollmann 2000; [46] Deneke 2000.

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Table 14.2. Species of crustaceans in extreme environments

	Type	Taxa	Species	Notes
Antarctic Lakes	Epishelf/ freshwater	Copepoda	*Boeckella poppei*†[1–10]; *Gladioferens antarcticus**[2–5]	†Dwarfism; low fecundity; feeding strategies; adaptation to fluctuating environments
	Freshwater	Anostraca	*Branchinecta gaini*[3, 5, 9, 11–14]	metabolic flexibility/cysts
		Cladocera	*Alona* (*A. quadrangularis*[a15]; *A. rectangular*[16]; *A. weinecki*[15, 17]; *Chydorus patagonicus*[a15]; *Daphnia gelida**[a]‡[15]; *Ilyocryptus brevidentatus*‡[17, 18]; *Macrothrix* (*M. ciliata*[17, 19]; *M. hirsuticornis*[15]); *Pleuroxus macquariensis**[a15]	([a]Macquarie Island) ‡Ephippial and parthenogenetic females
		Copepoda	*Acanthocyclops mirni**[4, 5] *Boeckella* (*B. brevicaudata*[15]; *B. michaelseni*[5, 6, 10]); *Parabroteas sarsi*[5, 6]	
		Ostracoda	*Cypretta* cf. *seurati*[a15]; *Eucypris fontana*[5]; *Notiocypridopsi sfrigogena*[5]	([a]Macquarie Island) endogenous fat reserves; feeding on microbial plankton; overwinters as juveniles, adults or ephippial eggs; carotenoid pigmentation (protection against UV-B)
	Freshwater/ brackish	Cladocera	*Daphniopsis studeri**[3–5, 7, 8, 20]	
	Saline	Copepoda	*Amphiascoides* sp[3, 5]; *Harpacticus furcatus*[5]; *Idomene scotti*[5]; *Paralabidocera antarctica*[a3, 5, 7, 8, 21]	[a]Slow development

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Subterranean Environments		Amphipoda	[*Alloteiweckelia hirsute; Artesia* (*A. subterranean; A. welbourni; Allocrangonyx hubrichti*][22]; *Bactrurus* (*B. brachycaudus*[22, 23]; *B. hubrichti*[22, 23]; *B. pseudomucronatus*[23]; *B. speleopolis*[23]; [*Crangonyx* (*C. grandimanus; C. hobbsi; C. antennatus; C. dearolfi; C. packardi*)][22]; *Hadzia fragilis*[24]; *Holsingerius* (*H. samacos; H. smaragdinus*)[22]; *Mexiweckelia hardeni*[22]; *Microniphargus leruthi*[25]; *Niphargus* (*N. aquilex*[26]; *N. fontanus*[26] *N. hebereri*[24]; *N. kochianus irlandicus*[*][25]; *N. pectencoronatae*[24]; *N. rhenorhodanensis*[b][27]; *N. schellenbergi*[26]; *N. timavi*[28]; *N. virei* [b][29]; *N. wexfordensis*[*][25]); *Gammarus* (*G. acherondytes*[22, 30]; *G. duebeni celticus*[25]; *G. minus*[a][31]; *G. Troglophilus*[30]); *Parabogidiella americana*[22]; *Parameiweckelia ruffoi*[22]; *Seborgia* (*S. hershleri; S. relicta*)[22]; [*Stygobromus* (*S. abditus; S. ackerlyi; S. allegheniensis; S. baroodyi; S. barryi; S. biggersi; S. clantoni; S. conradi; S. cooperi; S. culveri; S. cumberlandus; S. dicksoni; S. emarginatus; S. ephemerus; S. estesi; S. exilis; S. fecundus; S. fergusoni; S. finleyi; S. frani; S. gracilipes; S. grandis; S. hoffmani; S. inexpectatus; S. interitus; S. leensis; S. mackini; S. onondagaensis; S. oarkensis; S. smithi; S. minutus; S. morrisoni; S. mundus; S. nanus; S. nortoni; S. parvus; S. pollostus; S. pseudospinosus; S. redactus; S. sparsus; S. spinatus; S. stegerorum; S. subtilis; S. vitreus; S. balconies; S. bifurcates; S. dejectus; S. flagellatus; S. hadenoecus; S. longipes; S. pecki; S. russelli; S. gradyi; S. grahami; S. harai; S. iowae*)][22];*Texiweckelia texensis*[22]; *Texiweckeliopsis insolita*[22]	[a]Reduction in eye size, number of ommatidia (spring and cave populations); [b]depigmentation, anophtalmy, long life cycle, resistance to anoxia and starvation

(Continued)

Table 14.2 (*Continued*)

Type	Taxa	Species	Notes
	Decapoda/ Astacidea	*Cambarus*[b] (*C. aculabrum*[22, 32]; *C. Cryptodtes*[32]; *C. nerterius*[22]; *C. hamulatus*[22, 32]; *C. jonesi*[22, 32]; *C. veitchorum*[22, 32]; *C. hubrichti*[22, 32]; *C. laconensis**[32]; *C. nerterius*[a22]; *C. setosus*[22, 32–34]; *C. speleocoopi**[32]); *C. subterraneus*[22, 32]; *C. tartarus*[22, 32]; *C. ophonastes*[22, 32]); *Orconectes*[a] (*O. australis*[35]; *O. australis australis*[22]; *O. australis packardi*[22]; *O. barri*[35]; *O. inermis inermis*[22, 35]; *O. inermis testii*[22, 35]; *O. incomptus*[22, 35]; *O. packardi*[35]; *O. pellucidus*[22, 35]; *O. sheltie**[22, 35]; *O. stygocaneyi*[22, 35]); *Procambarus* (*P. acherontis*[22]; *P. attiguus*[22]; *P. cavernicola*[33, 34]; *P. delicatus*[22]; *P. erythropus*[33, 34]; *P. frani*[22]; *P. horsti*[22]; *P. leitheuseri*[22]; *P. lucifugus alachua*[22]; *P. lucifugus lucifugus*[22]; *P. morrisi*[22]; *P. oaxacae reddelli*[33, 34]; *P. orcinus*[22]; *P. pallidus*[22, 33, 34]; *P. pecki*[22]); *Troglocambarus maclanei*[22, 34]	[a]Reduction of eyes and reproductive system; loss of body and eye pigmentation; elongated antennae and limbs/"enlargement of ambulatory appendages, short eyestalk; increase of setae on several parts of the body"; physiological adaptations (oxygen consumption rates); eye reduction; pigment reduction [b]Eye reduction; pigment reduction (with the exclusion of [a]); albinism
	Decapoda/ Caridea	*Antecaridina lauensis*[36]; *Caridina* (*C. spelunca; C. steineri; C. thermophila*)[36]; *Halocaridina rubra*[36]; *Palaemonetes* (*P. cummingi;P. antrorum;P. holthuisi*)[22]; *Palaemonias* (*P. alabamae; P. ganteri*)[22]; *Parisia* (*P. gracilis; P. unguis*)[36]; *Pycneus morsitans*[36]; *Pycnisia* (*P. bunyip; P. raptor*)[36]; *Spelaeocaris pretneri*[36]; *Stygiocaris* (*S.lancifera*; S. stylifera; S.* sp)[36]; *Troglocaris* (*T. anophthalmus*[36]; *T. bosnica*[37]); *Typhlatya pearsei*[36]	
	Copepoda	*Badijella jalzici*[24]; *Bryocamptus* (*B. morrisoni elegans; B. morrisoni morrisoni*)[22]; *Cauloxenus stygius*[22]; *Dyacyclops* (*D. bicuspidatus; D. crassicaudis; D. languidoides*)[24]; *Diacyclops* (*D. clandestinus; D. jeanneli jeanneli*)[22]; *Halicyclops dalmatinus*[24]); *Hondurella verrucosa*[37]; *Megacyclops donnaldsoni donnaldsoni*[22]; *Metacyclops sp*[24]	

	Isopoda	[*Amergoniscus* (*A. curvatus; A. georgiensis; A. henroti; A. nicholasi; A. paynei; A. proximus*); *Antrolana lira; Brackenridgia* (*B. cavernarum; B. reddelli*); *Caecidotea* (*C. antricola*[23]; *C. dimorpha; C. fustis; C. macropropoda; C. bilineata; C. reddelli; C. packardi; C. salemensis; C. serrata; C. spatula; C. steevesi; C. stiladactla; C. whitei C. ancyla; C. jordani; C. nickajackensis; C. stygia; C. whitei; C. hobbsi; C. bicrenata bicrenata; C. bicrenata whitei; C. cannula; C. circulus; C. cyrtorhynchus; C. frani; C. henroti; C. holsingeri; C. incurve; C. nortoni; C. pricei; C. recurvata; C. richardsonae; C. scypha; C. simonini; C. sinuncus; C. vandeli*); *Cirolanides texensis; Ligidium* (*L. elrodii chatoogaensis; L. elrodii hancockensis; L. elrodii leensis; L. elrodii scottensis*); *Lirceus* (*L. culveri; L. usdagalun*); *Lirceolus* (*L. bisetus; L. hardeni; L. pilus; L. smithii*); *Miktoniscus* (*M. alabamensis; M. barri; M. racovitai racovitai*); *Remasellus parvus; Speocirolana hardeni*][22]
	Ostracoda	*Cavernocypris subterranea*[25]; Cypria *ophtalmica*[25]; *Cryptocandona vavrai*[25]; [*Dactylocythere* (*D. arcuata; D. prionata;D. steevesi; D. susanae*); *Donnaldsoncythere tuberosa*][22]; *Fabaeformiscandona* (*F. breuili*[25]; *F. wegelini*[25]); *Potamocypris zschokkei*[25]; *Pseudocandona* (*P. jeanneli*[22]; *P. marengoensis*[22]; *P. albicans*[25]); [*Sagittocythere* (*S. barri; S. stygia*); *Sphaeromicola moria; Uncinocythere* (*U. ambophora; U. pholetera; U. xania*)][22]
	Thermosbaenacea	*Monodella texana*[22]
Hydrothermal Vents	Decapoda/ Anomura	[*Uroptychus* (*U.bicavu; U. edisonicus; U. thermalis U.* sp)][39]
	Decapoda/ Astacidea	[*Acanthacaris cf. tenuimana; Homarus gammarus; Thymopides laurentae**][39]
	Decapoda/ Brachura	[*Allograea tomentosa*; Austinograea* (*A. alaseae; A. rodriguezensis; A. williamsi; A. yunohana*); *Bathplax typhla; Bythograea** (*B. galapagensis; B. intermedia; B. laubieri; B. microps; B. thermydron; B. vrijenhoeki; B.* sp); *Carcinoplax* sp; *Chaceon affinis; Cyanagraea** (*C. praedator; C.* sp); *Dorhnchus thomsoni; Hyas* sp; *Ovalipes molleri; Macroregonia macrochira; Paromola cuvieri; Pilumnoplax sp; Platymaia sp; Segonzacia mesatlantica*; Tutankhamen* sp; *Xenograpsus* (*X. noveainsularis; X. testudinatus*)][39]

(*Continued*)

Table 14.2 (Continued)

	Type	Taxa	Species	Notes
		Decapoda/ Caridea	[Alvinocaris* (A. brevitelsonis; A. dissimilis; A. leurokolos; A. longirostris, A. lusca; A. markensis; A. methanopila; A. niwa; A. stactophila; A. williamsi; A. sp); Chorocaris* (C. chacei*[40, 41]; C. paulexa; C. vandoverae; C. sp); Mirocaris fortunate*[40, 41]; Nautilocaris saintlaurentae*; Opaepele loihi*; Paracrangon sp; Periclimenes hydrothermophilus*; Rimicaris exoculata*[40, 41]; Rimicaris kairei*][39]	Metals are accumulated in the exoskeleton; metal detoxification system
Desert Environments	Temporary Freshwater Pools	Anostraca	Branchinecta (B. belki[42]; B. ferox[43]; B. ferrolimneta[44]; B. gaini[45]; B. lindahli[42, 46]; B. mackini[46]; B. packardi[42, 47, 48]); [Branchinella ondonguae; Branchipodopsis (B. barnardi[49]; B. browni; B. dayae; B. drakensbergensis[49]; B. drepane; B. hodgsoni; B. hutchinsoni; B. kalaharensis*; B. kaokoensis; B. karroensis; B. natalensis[49]; B. scambus; B. simplex; B. tridens; B. underbergensis[49]; B. wolfi[49, 50];B. cf. wolfi)][51]; Branchipus schaefferi[43]; Chirocephalus diaphanous[43]; Eubranchipus bundi[42]; Pumilibranchipus deserti[51]; Rhinobranchipus martensi[51]; Streptocephalus (S. bidentatus[51]; S. cf. bidentatus[51]; S. bourquinii[51]; S. cafer[51]; S. cirratus[49, 51]; S. cladophorus[51]; S. cf. cladophorus/dendrophorus[51]; S. dendrophorus[51]; S. dendyi[51]; S. dorothae[42, 46]; S. dregei[51]; S. gracilis[51]; S. gumani[42]; S. indistinctus[51]; S. (Parastreptocephalus) kaokoensis[51]; S. linderi[42]; S. mackini[42]; S. macrourus[51]; S. moorei[42]; S. namibiensis[51]; S. ovamboensis[51]; S. papillatus[51]; S. proboscideus[51]; S. propinquus[51]; S. purcelli[51]; S. sealii[42];S. similes[42]; S. spinicaudatus[49, 51]; S. texanus[42, 46, 48]; S. torvicornis bucheti[43]; S. trifidus[51]; S. vitreus[51]; S. wirminghausi[51]; S. zuluensis[51]); Tanymastigites (T. jbiletica[43]; T. brteki[43]); Tanymastix affinis[43]; Thamnocephalus (T. mexicanus[42, 46]; T. platyurus[42, 46, 47])	Development of highly resistant "cysts" that can be completely dried and are viable for decades or longer
		Cladocera	Alona cf. diaphana[52]; Ceriodaphnia quadrangula[52]; Chydoridae sp[48]; Daphnia (D. similis[52]; D. obtusa[48]); Macrothrix hirsuticornis[52]; Moina brachiata[52]; Pleuroxus letourneuxi[52]	
		Copepoda	Acanthocyplos vernalis[48]; Diaptomus (D. clavipes; D. siciloides)[48]	

	Laevicaudata	*Lynceus* (*L. alleppeyensis*[53]; *L. brachyurus*[42]; *L. brevifrons*[42]; *L. lobatsianus*[51]; *L. macleayanus*[54]; *L. tatei*[54]); *Paralimnetis mapimi*[42]	Development of highly resistant "cysts" that can be completely dried and are viable for decades or longer
	Notostraca	*Lepidurus lemmoni*[46]; *Triops* (*T. cancriformis mauritanicus*[43]; *T. granarius*[43, 49, 51]; *T. longicaudatus*[47, 55]; *T. newberryi*[55])	Development of highly resistant "cysts" that can be completely dried and are viable for decades or longer
	Ostracoda	*Caboncypris nunkeri*[56]; *Cypridopsis* sp[47, 48]; *Cypriconcha* sp[47, 48]; *Eucyprinotus rostratus*[52]; *Heterocypris* sp[52]; *Ilyocypris* sp[52]; [*Lacrimicypris kumbar; Mytilocypris* (*M. coolcalalaya; M mytiloides*); *Trigonocypris timmsi*][56]; *Potamocypris arcuata*[52]; *Tonnacypris lutaria*[52]	
	Spinicaudata	*Caenestheria* (*C. berneyi*[54]; *C. diction*[54]; *C. lutraria*[54]; *C. elliptica*[54]; *C. rubra*[54]; *C. sarsii*[54]; *Caenestheriella* (*C. austlis*[49]; *C. mariae*[54]; *C. packardi*[54]; *C. setosa*[42]); *Cyclestheria hislopi*[54]; *Cyzicus* (*C. bucheti*[43]; *C. rufa*[54]); *Eocvzicus* (*E. digueti*[42]; *E.* sp[51]); *Eulimnadia* (*E. africana*[49]; *E. belki*[57]; *E. brasiliensis*[58]; *E. colombiensis*[44, 58]; *E. cylindrova*[42, 46, 58]; *E. dahli*[54, 59]; *E. Diversa*[60]; *E. feriensis*[54, 59]; *E. follisimilis*[58]; *E. geayi*[58]; *E. inflecta*[47, 48]; *E. magdalenensis*[58]; *E. ovilunata*[61]; *E. ovisimilis*[61]; *E. texana*[42, 58]); *Leptestheria* (*L. compleximanus*[42, 47, 48]; *L. mayeti*[43]); *Leptestheriella* (*L. inermis; L. calcarata*)[51]; *Limnadia* (L. *cygnorum*[54]; *L. badia*[54, 59]; *L. grobbeni*[54]; *L. sordida*[54, 59]; *L. stanleyana*[54, 59]; *L. urukhai*[54]; *L. victoriensis*[54]; *L. sp*[59]); *Limnadopsis* (*L. birchii*[54]; *L. brunneus*[54]; *L. parvispinus*[54]; *L. tatei*[54, 59]); *Maghrebestheria maroccana*[43]; *Metalimnadia serratura*[58]	Development of highly resistant "cysts" that can be completely dried and are viable for decades or longer
Desert Rivers	Copepoda	Not specified[62]	
	Ostracoda	*Cipridae*[63]	
Desert Springs	Amphipoda	*Gammarus*(*G. pecos*[64]; *G. sp.*[65]); *Hyalellidae*[66]; *Hyalella* (*H. azteca*[67, 68]; *H. montezuma*[67]; *H. sandra*[68]; *H. sp.*[65]); *Stygobromus* sp[65]	

(*Continued*)

Table 14.2 (*Continued*)

Type	Taxa	Species	Notes
Desert Saltwater Ponds/Lakes	Anostraca	*Artemia* (*A. parthenogentica*[69]; *A. tunisiana*[70]); *Branchinecta ferox*[70]; *Branchinectella media*[70]; *Branchinella* (*B. affinis*[69]; *B. australiensis*[69]; *B. buchananensis*[69]; *B. compacta*[69]; *B. frondosa*[69]; *B. nana*[69]; *B. ornata*[51, 71]; *B. papillata*[69]; *B. simplex*[69]; *B. spinosa*[51, 70, 71]); *Branchipus schaefferi*[70]; *Chirocephalus* (*C. diaphanous; C. salinus*)[70]; *Parartemia* (*P. contracta; P. cylindrifera; P. extracta; P. informis; P. longicaudata; P. minuta; P. serventyi; P. Zietziana*[72]; *P.* sp)[69]; *Phallocryptus spinosa*[72]; *Tanymastigites* (*T. mzabica*; T. perrieri*)[70]; *Tanymastix stagnalis*[70]; *Streptocephalus* (*S. proboscideus*[51]; *S. Rubricaudatus*[70]; *S. torvicornis bucheti*[70])	Osmoregulation in *P. zieztiana*
	Cladocera	*Daphnia barbata*[71]; *Moina belli*[71] *Daphniopsis*[74]	
	Copepoda	*Boeckella poopoensis*[75]; *Calamoecia* (*C. clitellata; C. salina; C.trilobata*)[76]; *Lovenula africana*[71]; *Metadiaptomus transvaalensis*[71]	
	Ostracoda	*Australocypris* (*A. bennetti; A. beaumonti; A. insularis; A. dispar; A. mongerensis*)[56]; *Caboncypris kondininensis*[56]; *Diacypris* sp[76]; *Heterocypris* sp[76]; *Limnocythere tudoranceai*[71]; *Mytilocypris* (*M. mytiloides; M. ambiguosa*)[56]; *Plesiocypridopsis aldabrae*[71]; *Potamocypris* sp*[71]; *Repandocypris* (*R. gleneagles; R. austinensis*)[56]; *Reticypris* sp[76]; *Sclerocypris exserta makarikarensis**[71]; *Trigonocypris globulosa*[56]	
	Notostraca	*Lepidurus apus lubbocki*[70]; *Triops* (*T.nr australiensis*[69]; *T. cancriformis simplex*[70]; *T. granarius*[70])	
	Spinicaudata	*Caenestheria diction*[69]; *Caenestheriella packardi*[69]; *Cyzicus tetracerus*[70]; *Eocyzicus* (*E. parooensis*[54, 69];*E. diguetti*[77]; *E. politus*[78]); *Leptestheria* (*L. compleximanus*[77]; *L. cortieri*[70]; *L. mayeti*[70]; *L.sStriatoconcha*[51, 71]); *Limnadia nr cygnorum*[69]	
Terrestrial	Isopoda	[*Agabiformius obtusus; Armadillo albomarginatus; Hemilepistus reaumuri*[a][79]; *Porcellio* (*P. olivieri; P. barroisi*); *Porcellionides* sp.[80]	Fossorial habits [a]Resistance to water loss

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Acidic Environments	Input from catchments	Cladocera	*Bosmina longirostris*[81]; *Chydorus sphaericus*[81]	
		Copepoda	*Cyclops strenuous*[81]	
	Brown waters	Amphipoda	*Paraleptamphopus caeruleus*[82]	
		Decapoda	*Paranephrops planifrons*[83, 84]; *Parastacoides tasmanicus*[85]	Variation of ion concentration in the hemolymph
	Sulfur acidic lakes	Cladocera	*Chydorus sphaericus*[81]	
		Copepoda	*Cyclops viridis (robustus)*[81]; *Paracyclops fimbriatus*[81]	
	Volcanic lakes	Cladocera	*Chydorus sphaericus*[81]; *Simocephalus vetulus*[81]	
		Copepoda	*Cyclops strenuus*[81]; *Macrocyclops fuscus*[81]	
	Saline lakes	Anostraca	*Parartemia contracta**[56, 72]	
		Copepoda	*Calamoecia trilobata*[56]	
		Ostracoda	*Australocypris bennetti*[56]; *Reticypris* sp[56]	

For species in acidic waters, our main reference is Deneke 2000 (see references therein); for Antarctic lakes, it is Pugh et al. 2002 (see references therein) as updated by Gibson and Bal 2007 (see references therein). For species in subterranean habitats, we present only a reduced list (please refer to Botosaneanu 1986 and Culver and Pipans 2009 for a complete list). The same applies for decapods in hydrothermal vents (please refer to Martin and Haney 2005).

*Endemic

[1] Almada et al. 2004; [2] Bayly et al. 2003; [3] Gibson and Bayly 2007; [4] Gibson et al. 2006; [5] Pugh et al. 2002; [6] Hansson and Tranvik 1996; [7] Laybourn-Parry 2002; [8] Laybourn-Parry and Pearce 2007; [9] Pociecha and Dumont 2008; [10] Tranvik and Hansson 1997; [11] Hawes et al. 2008; [12] Peck 2004; [13] Peck 2005; [14] Pociecha 2007; [15] Dartnall et al. 2005; [16] Vincent et al. 2008; [17] Pugh and Convey 2008; [18] Kotov et al. 2002; [19] Toro et al. 2007; [20] Bayliss and Laybourn-Parry 1995; [21] Swadling and Gibson 2000; [22] Culver et al. 2003; [23] Holsinger et al. 2006; [24] Gottsteinet al. 2007; [25] Arnscheidt et al. 2008; [26] Hartke et al. 2011; [27] Lefébure et al. 2006; [28] Luštrik et al., 2011; [29] Lefébure et al. 2007; [30] Wilhelm and Venarsky 2009; [31] Culver 1987; [32] Buhay and Crandall 2009; [33] Mejía-Ortíz and López-Mejía 2005; [34] Mejía-Ortíz and Hartnoll 2005; [35] Buhay and Crandall 2008; [36] Page et al. 2008; [37] Zakšek et al., 2009; [38] Suárez-Morales and Iliffe 2007; [39] Martin and Haney 2005; [40] Gonzalez-Rey et al. 2008; [41] Prieur 2007; [42] Maeda-Martínez et al. 1997a; [43] Thiéry 1991; [44] Rogers and Ferreira 2007; [45] De los Ríos et al. 2008; [46] Maeda-Martínez et al. 1997b; [47] Chan et al. 2005; [48] Dodson 1987; [49] Hamer and Martens 1998; [50] Brendonck et al., 2002; [51] Brendonck and Riddoch 1997; [52] Eitam et al. 2004; [53] Balaraman and Nayar 2004; [54] Richter and Timms 2005; [55] Sassaman et al. 1997; [56] Halse and McRae 2004; [57] Martin 1989; [58] Pereira and García 2001; [59] Weeks et al. 2006a; [60] Mattox 1937; [61] Martin and Belk 1989; [62] Stanley et al. 1994; [63] Meffe and Minckley 1987; [64] Sei et al. 2009; [65] Myers and Resh 2002; [66] Sada et al. 2005; [67] Thomas et al. 1997; [68] Witt et al. 2006; [69] Timms 2009; [70] Samraoui et al. 2006; [71] McCulloch et al. 2008; [72] Conte and Geddes 1988; [73] Rogers 2003; [74] Hebert and Wilson 2000; [75] De los Ríos and Crespo 2004; [76] Halse and McRae 2001; [77] Martínez-Pantoja et al. 2002; [78] Baid 1968; [79] Baker and Rao 2004; [80] Warburg 1995; [81] Deneke 2000; [82] Winterbourn and Collier 1987; [83] Collier et al. 1990; [84] Olsson et al. 2006; [85] Newcombe 1975.

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or seasonally covered by ice and snow (thereby limiting transmission of light to the underlying water), and almost all are nutrient-limited (Laybourn-Parry and Pearce 2007). Salinity varies greatly, from freshwater through to hypersaline lakes. Tidal, epishelf lakes are stratified: freshwater overlays saltwater (Gibson and Andersen 2002, Laybourn-Parry 2002, Vincent et al. 2008). Subglacial lakes are permanently buried under a thick cover of ice, as in the large Vostok lake in central east Antarctica (Kapitsa et al. 1996). Meromictic lakes have a well-defined separation between oxygenated (uppermost) and anoxic (lowermost) layers that never mix (Gibson 1999). Although presenting extreme environmental conditions, Antarctic lakes are, on average, less severe than those of adjacent terrestrial and intertidal regional zones (Peck et al. 2006), being oases in cold deserts, maintaining liquid water and presenting milder temperatures, at least in summer (Laybourn-Parry 2002, Laybourn-Parry and Pearce 2007, Toro et al. 2007).

Lentic freshwater systems in the Antarctic are inhabited by a very limited number of species. There are no fish (Laybourn-Parry 2002, Vincent et al. 2008), and vertebrates, when present, are restricted to seabirds, ducks, and marine mammals (Peck et al. 2006). There are only a few invertebrate groups (Tables 14.1 and 14.2) and, generally, the food web is dominated by plankton. Consequently, the trophic structure is very simple and truncated, restricted to a few levels: primary producers (benthic and planktonic), consumers (represented by detritivores/scavengers/suspension feeders), and predators/omnivores (Hogg et al. 2006). Invertebrate predators are restricted to *Lancetes* diving beetles in South Georgia (Hansson and Tranvik 1996, Arnold and Convey 1998) and the platyhelminth *Minona amnica* in Macquarie Island (Dartnall et al. 2005), both feeding on crustaceans. The copepod *Boeckella poppei* shows an unexpected omnivorous feeding mode and can prey upon protozoa (Almada et al. 2004, Butler et al. 2005, Camacho 2006). In many lakes, copepods represent the highest level of the trophic chain (Tranvik and Hansson 1997).

In this simplified trophic structure, bottom-up processes seem to control the food web through a "microbial loop." In this pathway, nanoplankton (bacteria and protozoa) recycle energy and carbon (Laybourn-Parry 1997). Recently, though, grazing has been reevaluated as an important factor controlling microbial biomass (e.g., Camacho 2006), implying a top-down influence in the trophic cascade (e.g., grazing by the calanoid copepods *Paralabidocera antarctica* [Swadling and Gibson 2000] and *B. poppei* [Almada et al. 2004, Butler et al. 2005]).

The lack of vertebrates in the lakes, vegetation, and human input all limit the allochthonous nutrient contribution. Lakes are oligotrophic or even ultra-oligotrophic (Laybourn-Parry and Pearce 2007). The markedly seasonal variation in photosynthetic active radiation (PAR) results in winter decreases in primary production. Ice cover, reducing the penetration of light, further augments this seasonal effect. The ice layer also prevents the wind from mixing the water column and impedes the exchange of gases with the atmosphere (Peck et al. 2006, Laybourn-Parry and Pearce 2007).

According to their physiochemical characteristics, Antarctic lakes accommodate various (albeit few) species (Tables 14.1 and 14.2). Historical (i.e., isolation) and physiochemical conditions affect biodiversity (number of species and endemicity) and also have a strong effect on the life history, physiology, and behavior of the organisms inhabiting these lakes. In general, organisms are affected mainly by nutrient scarcity, low light levels, and low temperatures (Laybourn-Parry 2002). Organisms have evolved adaptations to these constraints and, in particular, to their seasonality (Peck et al. 2006).

The crustaceans inhabiting Antarctic lakes comprise copepods, ostracods, anostracans, and cladocerans (Table 14.2). Palaeolimnological studies indicate that some of these lakes might have acted as refugia for some species during the last glacial maximum (Gibson and Bayly 2007, Pugh and Convey 2008), implying a long-term presence of crustaceans in the Antarctic instead of a more recent colonization from other continents (as previously suggested by Pugh et al. 2002). Some populations, mostly of copepods inhabiting saline lakes, appear to have derived from marine populations (Pugh et al. 2002, Gibson and Bayly 2007).

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The life cycles of these crustaceans are different from those of their relatives in temperate and tropical climates or even of Antarctic marine conspecifics (Swadling et al. 2004). Low temperature and low nutrient levels (particularly during winter months) impose a reduction in physiological and metabolic rates (Peck et al. 2006). Development is slow, and life cycles are extended in this enemy-free environment. Dwarfism sometimes evolves as a strategy, exemplified in copepods by the dwarf form of *B. poppei* (Laybourn-Parry 2002, Bayly et al. 2003) and by the reduced size of *P. antarctica* (much smaller in lacustrine than marine populations; Swadling et al. 2000). These minute dimensions are probably determined by reduced resource availability in such oligotrophic environments (Laybourn-Parry 2002) rather than by lack of predation. Indeed, in temperate habitats, amphipods of the genus *Hyalella* present a "small ecomorph" in lakes with intense predation and a "large ecomorph" in lakes with reduced predation (Wellborn and Cothran 2007).

A key factor to survival in this hostile environment is a certain degree of plasticity in feeding strategies. Some crustaceans are omnivores and feed on alternative food sources when their main nutritional resources are scarce. The herbivorous *B. poppei* also utilizes heterotrophic prey (Almada et al. 2004, Butler et al. 2005), and mixotrophic Antarctic phytoplankton, primarily photoautrophic, feed on protozoa when necessary (Laybourn-Parry 2002). Some members of the phytoplankton also have evolved adaptations, such as the use of highly efficient photosynthetic pigments, to make better use of the limited PAR (Hawes and Schwarz 2000).

Physiological flexibility allows for long-term survival in a highly seasonal environment: the anostracan *Branchinecta gaini* withstands daily temperature variations of up to 25°C during the summer (Peck 2004, 2005). Flexibility in life cycle is also important: populations of the copepod *P. antarctica* in lakes are not linked to ice cover, as marine populations are (Swadling et al. 2000), and they store more lipids (triacylglycerol) than do marine conspecifics (Swadling et al. 2000), possibly due to lower and inconsistent feeding rates in lakes. Similarly, the cladoceran *Daphniopsis studeri* utilizes fat reserves during the winter (Laybourn-Parry 2002). The use of endogenous energy supplies is not limited to crustaceans. Other organisms employ the same strategy: phytoplankton accumulate starch organelles to be used in dark periods when photosynthesis is not possible (Laybourn-Parry 2002, Laybourn-Parry and Pearce 2007). Flexible life cycles are also reported for *D. studeri* (Bayliss and Laybourn-Parry 1995, Laybourn-Parry and Pearce 2007) and, among non-crustaceans, for the beetle *Lancetes angusticollis* (Arnold and Convey 1998). Both these organisms are capable of overwintering in different stages of their life cycle, as juveniles (or larvae in the case of the beetle) and/or adults. The overwintering stage depends on the trophic state and/or thermal conditions of their environment: warmer and more productive lakes allow for the overwintering of adults.

Feeding adaptations, life cycle/physiological flexibility, and use of stored energy are all strategies to resist and persist during the adverse season and enter the summer ready to reproduce. Overwintering is thus important in order to have a major growing season during the short summer (Convey 1997, Laybourn-Parry 2002, Laybourn-Parry and Pearce 2007). Extended life cycles, coupled with the ability to overwinter, reduce the number of univoltine species (Convey 1997) with the exception of species inhabiting ephemeral lakes. Specific mating strategies, such as parthenogenesis, can also contribute to a fast growing season in summer, reducing time and effort to find mates (Laybourn-Parry and Pearce 2007). Parthenogenetic females are found, for example, in populations of the cladocerans *Ilyocryptus brevidentatus* (Kotov et al. 2002) and *Daphnia gelida* (Dartnall et al. 2005).

Overwintering is not possible in ephemeral pools, which dry or freeze: resting cysts are employed in these situations. Cysts of the fairy shrimp *B. gaini* are still viable at −25°C (Peck 2005), and cladocerans' ephippial eggs represent resistant stages. This same adaptation is commonly used by crustaceans in ephemeral pools in hot deserts, with opposite thermal conditions. Cryobiosis (quiescent state to resist cold temperature) and anhydrobiosis (desiccation) are common in nematodes (McSorley 2003) and tardigrades (Everitt 1981).

Organisms living in subzero temperatures employ various adaptations to cold climate. "Antifreeze" proteins and biochemical adaptations in membranes are common in terrestrial invertebrates, such as collembolans and acari (Peck 2005), as well as marine fish (Peck et al. 2006, Clarke et al. 2007) and have also been reported for bacteria in Antarctic lakes (Gilbert et al. 2004). Other strategies include lowering the freezing point (thermal hysteresis performed by marine invertebrates), supercooling, and tolerance of ice in body fluids (Waller et al. 2006). When internal ice is not tolerated, material that could initiate the formation of ice crystals is removed (i.e., gut contents or gut epithelium). A similar function might be attributed to the peeling of tissue in female *B. gaini* (Hawes 2008). This fairy shrimp is well adapted to a polar climate: its respiration is more efficient at low temperatures whereas highest oxygen consumption rates occur when the crustacean approaches 15°C, the thermal limit for the species (Peck 2004, Pociecha 2007). It is the largest invertebrate in Antarctic lakes (Pociecha 2007) and can survive for short periods of time completely encased in ice (Hawes et al. 2008).

CRUSTACEANS IN SUBTERRANEAN ENVIRONMENTS

Subterranean spaces inhabited by animals (biotopes) occur in considerable diversity and complexity, and both spaces and animals have attracted attention since the beginning of speleology in the 19th century (Culver 1982, Botosaneanu 1986, Gibert et al. 1994). Culver and Pipan (2009) paint a succinct, current history of biospeleology, highlighting the comparatively recent expansion of studies beyond national boundaries and embracing experimental studies investigating core biological themes, such as the evolution and ecology of cavernicoles (cave-dwelling organisms).

Subterranean biotopes are constantly changing, either by enlargement through dissolution of the substrata or by constriction through deposition or compaction. These biotopes may comprise air-filled spaces (vertically or horizontally aligned) permanently above the water table in the inactive vadose (the dry upper) zone, the active vadose zone (periodically flooded), or the phreatic zone below the water table (Culver 1986). The size of subterranean living spaces ranges widely, from small interstitial spaces (<1 mm diameter) to large voids (caves; Culver and Pipan [2009] cite the volume of Lubang Nasib Bagus [Good Luck Cave], Sarawak, Malaysia, as $>21 \times 10^6$ m^3) that may be permanently inundated or have lakes or streams.

Initially, limited access by humans into caves had a significant impact on the rate of development of biospeleology, but during the past three decades pumps and nets have been used to sample bores and reveal a rich diversity of animals inhabiting water-filled interstitial spaces, especially in the hyporheic zones beneath river channels (Culver and Pipan 2009).

Caves frequently are derived by dissolution of the calcium carbonate of limestone rocks; this dissolution produces a range of characteristic structures, ranging from small to large scale, called karst (Jennings 1985). Subterranean biotopes are characterized by lack of light and so may be predicted, a priori, to be hostile to animal habitation. Consequently, it is not surprising that speleologists have long been attracted by the diverse and frequently spectacular forms inhabiting caves, especially the arthropods from the vadose zones—chelicerates including spiders, opilionids (harvestmen), pseudoscorpiones, and schizomids (Table 14.1). Botosaneanu (1986) edited a comprehensive systematic review of the world's stygofauna (i.e., aquatic groundwater fauna), thereby identifying a preponderance of crustaceans (Cladocera, Copepoda, Remipedia, Mystacocarida, Syncarida, Isopoda, Amphipoda, Thermosbaenacea, Decapoda; Table 14.2); the list, however, includes single-celled protists (rhizopods, ciliates), blastocoelomates, mollusks, annelids, and chordates. Culver and Pipan (2009) list 21 invertebrate orders with 50 species inhabiting subterranean waters, of which the 17 arthropod orders include seven crustaceans (Cyclopoida, Harpacticoida, Podocopida, Bathynellacea, Amphipoda, Isopoda, Decapoda). Culver and Holsinger (1992) estimated that the total world fauna of subterranean metazoans (terrestrial plus aquatic) comprised approximately

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50,000 species. Cavernicoles are classified according to their ecological relationships: *troglobionts* (= *troglobites*), obligate cave-dwellers, spend their entire life cycles underground; the facultative *troglophiles* may occur in cave and surface biotopes; *trogloxenes* inhabit caves sporadically; and *accidentals* find their ways into caves by chance. There is continuing confusion with the terms (Culver and Pipan 2009): troglobiont may apply to both terrestrial and aquatic species or just terrestrial species. Stygobionts inhabit aquatic subterranean habitats.

Subterranean aquatic ecosystems operate under two major differences from epigean ecosystems. The first is the reduction in daily and seasonal variation in signals such as day length and temperature variation. The second is the amount of photosynthetically driven primary productivity, which is limited to the area of the cave entrance and is completely lacking in the deeper recesses of the cave. Consequently, stygobionts need to gain access to chemoautotrophic production (Culver and Pipan 2009), alternate sources of food such as biofilms, or rely on sporadic and unpredictable supplies of food. The latter include the transport into a cave of autochthonous detritus by an inflowing sinking stream (swallet) or the carcasses of "accidental inputs." Stygobionts of the majority of caves, therefore, rely on food derived from surface environments.

In the shallow caves of the Tamala calcarenite at Yanchep, near Perth, Western Australia, roots of the tuart tree, *Eucalyptus gomphocephala*, reached the streams at the surface of the underlying, unconfined aquifer and formed into tree root–mat fungi myccorhizal associations. These root mats provided a reliable supply of substrata driving diverse stygobiont communities (Jasinska et al. 1996). The adaptive response to food limitation/unpredictability of supply seemingly would constitute the reduced metabolic rates characteristic of stygobionts. Enzymatic activities of hypogean amphipods and isopods that correlate with metabolic rates of Krebs cycle and glycolysis are 1.2–8.6 times lower in hypogean than epigean forms (Hervant 1996). Stygal crustaceans can survive more than 200 days without food (>1 year in the case of the amphipods *Niphargus virei* and *N. rhenorhodanensis*), reducing their metabolic, locomotory, and ventilatory rates in the process (Hervant et al. 1999). Hervant and Renault (2002), studying aquatic isopods, suggest that during long-term starvation, stygal crustaceans rely on large energy stores, subsisting mainly on lipids and sparing proteins and glycogen; surface crustaceans going into fasting show an immediate decrease in all energy stores. Cave waters typically show low oxygen concentrations, and stygobiontic amphipods and isopods survive severe hypoxic conditions far longer than do epigean forms (Hervant and Mathieu 1995).

Crustacean stygobionts show a characteristic morphofacies or troglomorphy: lacking pigment, eyeless, and having elongate limbs and sensory structures (Fig. 14.1). Because there is no debate

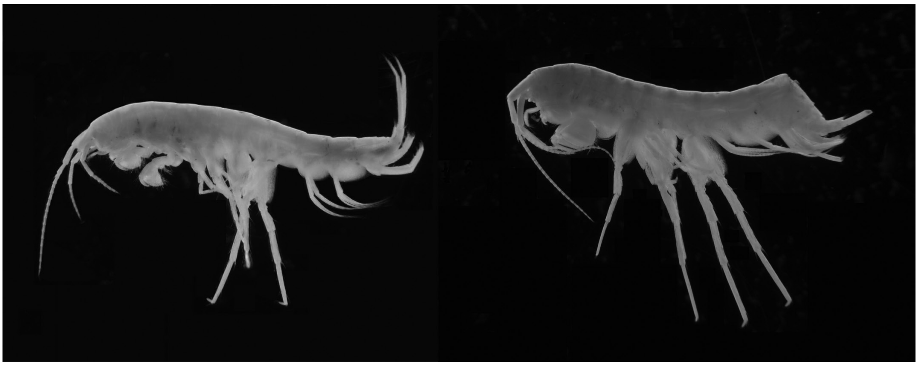

Fig. 14.1.
Troglomorphy exemplified in the subterranean amphipods *Niphargus aquilex* (left) and *N. fontanus* (right). Photo courtesy of Dr. Joerg Arnscheidt.

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about the ultimate source of stygobionts—namely, from surface populations—the lack of both pigment and eyes exemplifies regressive evolution. There has been, however, considerable debate concerning the mechanism(s) leading to these losses. What are the selective advantages of lacking pigment, of being eyeless in a subterranean environment? Arguments in support of selection invoke energy economy (in an energy-depleted environment, the limited reserves available are better expended on producing adaptive structures and reproduction rather than on producing nonadaptive structures) and pleiotropy (the regression may be due to negative pleiotropy linked with, for example, elongation of antennae that may be selected for in completely dark environments or exemplify positive pleiotropy associated with structures selected against in caves). Alternatively, structures with no adaptive benefit may be lost by the accumulation of neutral mutations and genetic drift (Poulson 1964, Culver 1982, Howarth 1987). Deleterious mutations for pigment and eye development may accumulate because they would have no effect on fitness of cavernicoles and would not be eliminated by selection; thus, these characters may be lost by drift in the absence of selection.

Studies on natural systems have not generated a consistent model explaining the regressive morphological features of cavernicoles. In one detailed study into the adaptation of the amphipod *Gammarus minus* to the groundwaters of the eastern United States (where the morphofacies range from troglomorphic populations in two cave areas in Virginia to amphipods from springs with no troglomorphic expression), Culver et al. (1995) assessed five criteria proposed by Brandon (1990) by which adaptation might be accepted as an explanation for how cavernicoles have evolved. The five criteria include (i) evidence of selection, (ii) an ecological accounting for differential rates of reproduction, (iii) evidence that the cave morphofacies have heritable components, (iv) data concerning gene flow and genetic relatedness of surface and subterranean populations, and (v) information on ancestral and derived character states. Culver et al. (1995) concluded that eye size of this amphipod changes through selection and neutral mutations, but antennae and body size change through selection only.

Enlargement of nonvisual sensory structures is widely interpreted to exemplify a selective advantage, but supporting evidence is meager. Holsinger and Culver (1970), comparing cave and spring populations of *G. minus* in Virginia, argued, on the evidence of significantly different slopes plotting average body length of males from seven cave and eight spring populations, that there was an increase in length of antennae 1—but the genetic basis was unknown.

Although subterranean communities often are simpler than epigean communities in terms of species number, interactions nonetheless occur. In Appalachian caves, amphipods and isopods concentrate in riffle zones of cave streams away from predators and in the zone where the oxygen content is increased and leaves accumulate. Interactions between the two crustaceans in the riffles may involve competition for food, with small or damaged specimens being cannibalized/eaten by larger specimens or being swept from protective spaces into the water column and into pools harboring predators (Culver 1975). However, the valviferan isopods *Caecidotea cannulas* and *C. holsingeri* co-occur in Alpena Cave, Virginia, without any evidence of competition between the species (Culver 1994). The two may coexist *sans* competition because their size difference (*C. annulas* is larger than *C. holsingeri*) enables them to exploit differences in sizes of rocks and gravel. Habitat partitioning is implemented also to manage intra- and interspecific interactions (Luštrik et al. 2011): small individuals of the surface amphipod *Gammarus fossarum* and the subterranean amphipod *Niphargus timavi* inhabit finer substrata, less used by adults of these two coexisting species (to avoid predation/cannibalism as well as competition). Stygobionts, and especially the crustacean representatives, are important because of the insights they provide into past geographical connections. The freshwater stygobiontic crustaceans from the Pilbara region of northern Western Australia (Amphipoda, Thermosbaenacea, Remipedia) through to related forms from the Caribbean constitute significant evidence of a Tethyan connection, now disjunct through continental drift (Humphreys 1993, Knott 1993).

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In view of this discussion of evidence of the success at which crustaceans colonized the underworld, it may not be cynical to suggest that the greatest problem confronting living underground stems not from the obvious biological issues of lack of light (restricting primary productivity) and lack of diurnal and seasonal cues to control life cycle activities, for example, but rather the human-driven, seemingly cosmopolitan trend to deplete aquifers of their water. The ecological and physiological problems have been solved, during the time available for the evolution of a wide diversity of stygobionts. In marked contrast, the depletion of aquifers through anthropogenic activities is immediate, leaving many stygobionts with no time to “find solutions” other than to be driven extinct.

CRUSTACEANS IN HYDROTHERMAL VENTS

Dwellers of the abyss cope with considerable pressure—and they share two constraints with subterranean faunae: the lack of light precluding photosynthetically driven primary productivity and lack of reliable food supplies. Light of blue wavelengths penetrates much deeper into the water column than those of other wavelengths, with the depth depending on a number of factors including the angle of refraction and the clarity of the water column; photosynthesis (PS) is possible in the upper 100–200 m, but the depth to 1,000 m is dimly lit and thus not sufficient for PS. The depth across 90% of the area of the world’s oceans exceeds 1,000 m, and the water column at these depths lacks light (is aphotic).

As with probably all habitable places, continuing study has identified heterogeneity of biotopes where originally it was thought homogeneity prevailed. For example, the great abyssal plains are not uniformly flat and covered with a uniform blanket of sediment. Instead the flatness may be interrupted in places by sea mounts (mountains derived from extinct volcanoes rising generally 1,000 m above the abyssal plain but not reaching sea level; 30,000 are estimated to occur) and the 55,000 km of ridges separating the continental plates that are the sources of spreading of tectonic plates. As recently as 1977, very localized hydrothermal vent chimneys (known as “black smokers”) were discovered at the comparatively shallow depth of 2,500 m on the East Pacific Rise (Corliss et al. 1979). Since then, numerous other hydrothermal vents have been recorded from the mid-ocean ridges of the globe, both fast spreading (≥12 cm/yr^{-1}) and slow spreading (<2 cm/yr^{-1}). Black smoker chimneys comprise hollow spires that may develop to heights of several tens of meters; they are formed initially through deposition of sulfate minerals and then, in a second phase of development, from deposition of iron and copper-zinc-sulfide minerals on the inner surface and in the pores of the spire. There is considerable diversity in the vent fields reflecting local variations in geology, chemistry, and physics (Reed 2006).

The sulfides of deep-sea hydrothermal vents provide a source of energy, driving an ecosystem based ultimately on chemosynthesis fixing CO_2 through sulfide oxidation. Crustaceans, including shrimp and crabs, sometimes in large swarms, hug the narrow zones (of centimeter scales) of steep thermal and sulfur-to-oxygen gradients that occur about deep vent sulfide chimneys. One might expect, a priori, for crustaceans of the deep to be eyeless, as in the above noted subterranean forms. However, the fissure shrimp, *Rimicaris exoculata*, although “eyeless” as originally described has, in fact, a pair of reflective dorsal cephalothoracic structures containing visual pigment with a blue-green sensitive, rhodopsin-like absorption spectrum (Van Dover et al. 1989). Although photoreceptors are present, no images are formed, and Van Dover et al. (1989) conclude that the structures are sensitive to the “eerie” bioluminescent glow emanating from chemiluminescence as sulfide is oxidized and associated with mid-ocean ridge hot springs. Thus, these decapods may use the glow to avoid the lethal temperatures of the fluid discharging from the mouths of chimneys. Consistent

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with this hypothesis, Pelli and Chamberlain (1989) calculated that the plume discharged from a vent of 10 cm diameter would be detectable by the shrimp from a distance of 2.3 m. Land (1989) questions whether the function of the “eye” is not to resolve point sources of light but to detect a bioluminescent source—and concluded that an “eye” with naked retina would be capable of such coarsely directional detection. Another decapod inhabitant of deep-sea hydrothermal vents, the predatory crab *Bythograea thermydron*, has bioluminescence detectors similar in structure and function to those of *R. exoculata* (Jinks et al. 2002). Jinks et al. (2002) measured the spectral sensitivity of the ontogenetic stages of *B. thermydron* and recorded maximal sensitivity to increase from 447 nm (blue light in the planktonic zoea larvae) to 479 nm (blue-green light in the benthic megalopa larvae) to 489 nm (longer wavelength blue-green light in adults), a trend opposite to what may be predicted based on the depth to which sunlight penetrates the seawater column. They conclude that this “opposite” trend is due to the spectral composition of the bioluminescence of the hydrothermal vents.

If vent fields are small objects in huge expanses of the abyssal plains, how are they colonized? Plumes of water from the black smokers may form into vortices of about 2 km diameter and approximately 200 m thick, 300 m above the sea floor. Planktonic stages may be swept into such vortices, which revolve due to the Earth’s rotation, and be carried substantial distances through the ocean basins. Association with vortices may provide a mechanism for transport between deep hydrothermal vent fields (Lupton et al. 1998).

CRUSTACEANS IN DESERT ENVIRONMENTS

Because crustaceans are almost entirely aquatic, one does not commonly think of them as widespread inhabitants of desert environments. Indeed, the few crustaceans that are terrestrial do not call deserts their home, except for rare exceptions (Warburg 1995, Baker and Rao 2004; Table 14.2). However, a number of aquatic crustaceans can eke out an existence in the desert habitat (Table 14.2).

Desert aquatic habitats primarily are of four types: temporary freshwater pools, desert rivers, isolated springs, or larger (mostly temporary) saltwater ponds/lakes. In each of these habitats, we find crustaceans.

Temporary Freshwater Pools

By definition, water is not a plentiful commodity in desert environments. Webster’s dictionary defines a desert as land that receives “less than 25 cm of sporadic rainfall annually.” Commonly, when rain does come, it is voluminous and often pools into small to quite large earthen depressions, gathers in rock (potholes), or fills dry lake beds. In such pools/lakes, a community of desiccation-resistant plants and animals will hatch or rehydrate to take advantage of these short-term aquatic conditions (Tables 14.1 and 14.2).

A most extreme example of temporary pools in arid environments can be found in the “wheatbelt” region of Western Australia. This region of Australia is dotted with an array of granite outcrops (i.e., “inselbergs”; Withers 2000) that well up from the surrounding otherwise flat landscape to varying degrees (York Main 1997). On the tops of these outcrops are a series of small depressions ranging in size from 1 to 26 m^2 (surface area) and from 1 to 7 cm in depth (Calabrese 2009). The large surface area-to-depth ratio means that these pools dry out exceptionally fast after fillings, especially in the summer season, and they can fluctuate quite broadly in temperature, conductivity, dissolved oxygen, and pH. For example, several rock pools measured diurnally in 2009 ranged from 6°C to 20°C in a single day in Kent, Lake Grace, Kondinin, and Wagin Shires in Western Australia (Calabrese 2009).

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These extreme outcrop pool habitats are dominated by crustaceans (Weeks et al. 2006a, Calabrese 2009), particularly branchiopods in the orders Spinicaudata and Anostraca (Fig. 14.2).

The trophic structure of temporary pools is different from that of other permanent aquatic ecosystems. Fish are usually not present, with the exception of the salamanderfish *Lepidogalaxias salamandroides* in Western Australia (Berra and Allen 1991), but turbellarians, dragonfly larvae, beetle larvae, tadpoles, and some crustaceans fill this predatory gap (Blaustein et al. 1999, Brendonck et al. 2002, Dumont and Negrea 2002, Pfennig and Murphy 2002). Nutrients and minerals are usually not in short supply (Brendonck and Riddoch 1997) due to allochthonous input and high productivity of the photosynthetic microbial mat and algae (Chan et al. 2005).

The animals that dominate ephemeral pool communities are crustaceans (Table 14.2), particularly branchiopod crustaceans, although ostracods and copepods are also common inhabitants of such pools (Yevdokimov and Yermokhin 2009). Branchiopods are primitive Crustacea that are commonly filter feeders, scavengers, and some predators (Dumont and Negrea 2002). Branchiopods (Fig. 14.2) frequently found in desert pools are in the orders Anostraca ("fairy shrimp"), Notostraca ("tadpole shrimp"), Cladocera ("water fleas"), Spinicaudata, and Laevicaudata (the latter two commonly named "clam shrimp").

All of these orders share several similarities that allow them to dominate these freshwater desert pools. Due to the short hydroperiod duration, the life cycle of these crustaceans is accelerated. Crustaceans present rapid hatching, fast development, high fecundity, and short life span (Hildrew 1985). For example, in the clam shrimp *Eulimnadia texana*, eggs hatch in 24 h, maturity is reached in 5–6 days, and up to two clutches of eggs are produced each day for a total lifespan of 2–3 weeks (Weeks et al. 1997; Fig. 14.3). These life history traits vary among species and in the same species (Marcus and Weeks 1997), depending on the hydration length of the pond.

Because temporary pools undergo dramatic abiotic changes over their short lives (Chan et al. 2005, Calabrese 2009), the branchiopods inhabiting them have adaptations allowing them to withstand broad ranges of water quality parameters and temperature. pH varies from 7 to 10 over a filling, and, in some cases, pools can vary over this range in a single day (Chan et al. 2005). Additionally, the small volumes of many of these water bodies means that temperatures can vary from 0°C to 35°C over the course of a season and by as much as 17.5°C over a single day (Chan et al. 2005, Calabrese 2009). Salinity variation is relatively low compared with pH and temperature (Chan et al. 2005, Calabrese 2009).

One of the most important and unique adaptations to a desert environment that the branchiopods possess is their exceptionally desiccation-resistant cysts. These cysts have no detectable water and show no sign of the slightest metabolic activity (Clegg 2001). The cysts are surrounded by a thick and ornamented shell (Rabet 2010; Fig. 14.4) that is porous to water but provides protection from solar radiation and mechanical degradative processes (Belk 1970). The cysts are

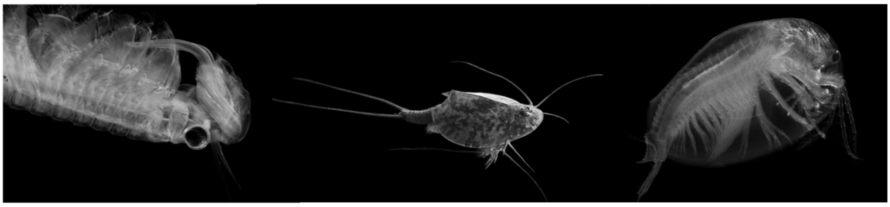

Fig. 14.2.
Examples of large branchiopods commonly found in desert environments. *Phallocryptus spinosa* (order Anostraca; photo on the left) are found in desert saltwater lakes; *Triops cancriformis* (order Notostraca; central photo) and *Eulimnadia texana* (order Spinicaudata; photo on the right) inhabit temporary pools in the desert. Images are not in scale. Photo courtesy of Jean-François Cart.

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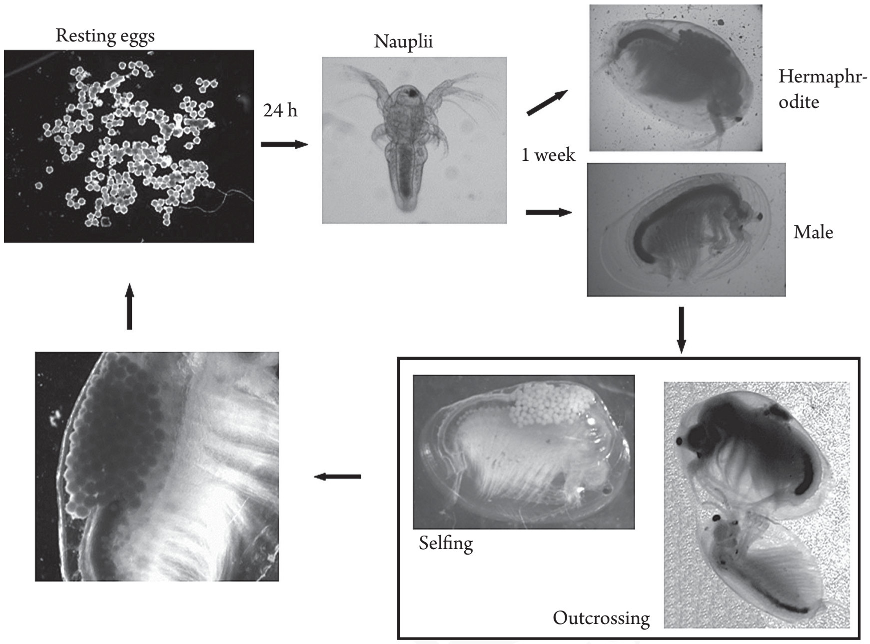

Fig. 14.3.
Life cycle of *Eulimnadia texana*. The life cycle of these branchiopod crustaceans is well-adapted to the ephemeral environments they inhabit (such as temporary pools in the deserts of southwestern United States).

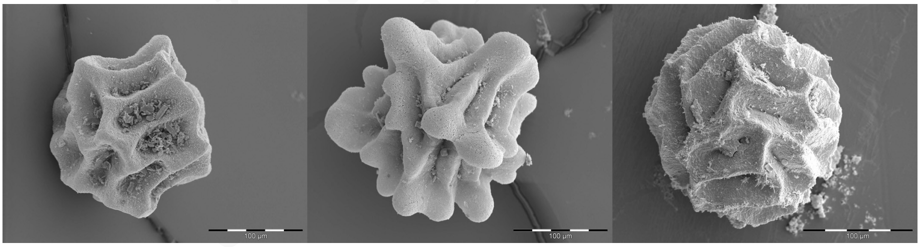

Fig. 14.4.
Scanning electron microscopy pictures of encysted eggs of *Eulimnadia geayi* (left), *E. mauritiana* (center), and *E. aethiopica* (right). Photo courtesy of Dr. Nicolas Rabet.

actually embryos (Fig. 14.5) that have divided to the approximately 4,100 cell stage (Nakanishi et al. 1962) and then arrested development 24–48 h after being deposited into the pools (Weeks et al. 2002). They can withstand extremes in temperatures, ranging from −271°C up to 98°C (Carlisle 1968, Iwasaki 1973), and can stand anoxic conditions for up to 4 years (Clegg 1997). These cysts can lie dormant for decades, and there are reports of cysts from soil cores in Utah that have hatched after 6,000 years of dormancy (Dumont and Negrea 2002). Because of the variable length of standing water in the deserts, these cysts employ a type of "bet-hedging" in which only a portion of the cyst bank hatches at any one hydration (Simovich and Hathaway 1997). This allows a sufficient number of remaining cysts after "failed" hydrations; that is, those in which the pools dry before the shrimp can reproduce.

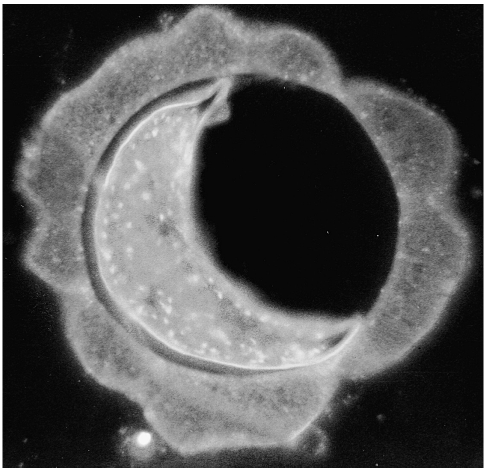

Fig. 14.5.
Section of encysted egg of *Eulimnadia texana*. The crescent-shaped body is the developing embryo.

Given the ephemeral nature of these pools, dispersal to new pools is imperative to the species that inhabit these environments. Dispersal of these cysts by wind is the most commonly assumed dispersal method for branchiopod crustaceans (Tasch 1987). However, Brendonck and Riddoch (1999) found little evidence of wind dispersal for fairy shrimp cysts: they found fewer than 2% of the 423 sites examined had any evidence of wind-blown eggs, and, even at these few sites, the eggs were not found at distances greater than 50 cm from their source pools. Other options for cyst movement among pools is via animal vectors, either attaching to the outside of animals (e.g., on the legs of birds; termed "epizoochory") or through the digestive tracts of predators (termed "endozoochory"). Several studies have shown both mechanisms to be possible for crustacean dispersal, including in branchiopods (Charalabidou and Santamaria 2002, Figuerola and Green 2002, Green and Figuerola 2002). However, the relative importance of either of these animal-vectored dispersal mechanisms relative to wind transport has yet to be determined.

Another life history strategy that is advantageous in such temporary habitats is the ability to produce offspring without the need for a mate. "Reproductive assurance" is the notion that plants/animals that can produce offspring without a mate are advantageous under conditions of low population sizes, which might be common in early-colonizing species (Baker 1955, Ghiselin 1969). Temporary pool habitats have repeatedly favored the evolution of self-compatible hermaphrodites from gonochoristic ancestors in both Spinicaudatan and Notostracan crustaceans (Weeks 2012). In these crustacea, two types of self-compatible species have been noted: 100% self-compatible hermaphroditic species and "androdioecious" species that are mixes of males and hermaphrodites, commonly in about 1:3 proportions, respectively (Weeks et al. 2008). Self-compatible hermaphroditism has independently evolved from gonochorism in the Notostraca at least five times (Mathers et al. 2013) and at least four times in the Spinicaudata (Brantner 2011, Brantner et al. 2013a,b). Androdioecy is rare in most animals, including crustaceans (Weeks et al. 2006b, Weeks 2012), but is fairly common in these ephemeral pool branchiopods (Weeks et al. 2006b, 2008, Weeks 2012) and appears to be a very successful strategy in the Spinicaudata, being maintained in the genus *Eulimnadia* for 25–180 million years (Weeks et al. 2006c), the longest known for any plant or animal species (Weeks 2012).

All of these attributes combine to provide an efficient and effective mechanism to persist under these harsh desert conditions and are quite likely the reason that these crustaceans dominate these temporary pools (Fryer 1996).

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Desert Rivers

"Desert river" seems to be an oxymoron, and yet many deserts have either permanent or temporary rivers/streams with their associated ecosystems (Kingsford 2006). Desert rivers flow through arid regions that receive 500 mm or less of annual rainfall (Kingsford and Thompson 2006). Such ecosystems are dominated by the cycle of flooding and drying, and thus the crustaceans that live in these ecosystems (Table 14.2) have evolved to deal with this variation. Commonly, desert communities (Tables 14.1 and 14.2) are much less diverse than their non-desert-living counterparts (Boulton et al. 2006), but abundances of species can be exceptionally high (Meffe and Minckley 1987).

Most desert river systems may not be truly considered "extreme" environments for aquatic organisms. The primary difference between these rivers and their mesic counterparts is the variability of water input and thus flow (Kingsford and Thompson 2006). Many desert rivers flow through both mesic and xeric habitats and thus combine attributes of both systems. These rivers tend to be more stable than wholly xeric-system rivers. Those that are primarily desert rivers may have full flow during some portions of the year and at other times may partially or wholly dry up. Clearly, these latter river systems can be considered "extreme" to their wholly aquatic residents.

As with mesic rivers, desert rivers are dominated by aquatic insects, comprising between 55% and 75% of the species (Fisher et al. 1982, Meffe and Minckley 1987, Boulton et al. 2006). Nonetheless, these ecosystems are home to a number of important crustacean species (Table 14.2). River/stream crustacean species include primarily cladocerans, copepods, ostracods, and some decapod shrimp, the latter being primarily in more permanent rivers (Jenkins and Boulton 2003, Boulton et al. 2006). Cladocerans and copepods dominate streams that dry periodically (Jenkins and Boulton 2003).

In desert rivers that predominately get their water from xeric habitat input, there are two aspects of the environment that can be considered "extreme." The first is the obvious threat of drying of part or most of the stream/river during low-input periods. In these systems, repopulation of the streams is primarily by aerial recruitment or by desiccation-resistant stages that hatch after rehydration (Boulton et al. 2006). Clearly, the latter method is all that is available for crustaceans. Ostracod and copepod adults can withstand up to 6 days of drying in these systems, but any longer kills all crustacean adults (Stanley et al. 1994). The second extreme condition is the threat of flash floods washing away the invertebrate community. Fisher et al. (1982) estimated that up to 98% of the invertebrate community can be washed away during a flash flood. However, the rapid population growth capability of these desert systems allows repopulation of these streams back to preflood levels in as little as 2–4 weeks (Fisher et al. 1982).

Desert Springs

Desert springs are commonly isolated refugia of freshwater embedded in a desert landscape. These springs/pools offer permanent water supplies and thus have a very different biota from the temporary freshwater pools that are much more common in these systems (Tables 14.1 and 14.2). Habitat variability in these springs is much lower than in temporary pools, with temperatures ranging between 5°C and 20°C, pH between 7 and 8.6, and alkalinity between 16 and 165 mg/L (Myers and Resh 2002). Because of the permanence of these systems, the animal communities are dominated by fish, often endemic species localized to the small pools surrounding the spring (Sei et al. 2009). Therefore, the crustacean communities in these springs are very much shaped by these dominant predators, which completely exclude the larger branchiopod crustaceans that dominate the fishless desert pools.

Desert spring crustacean communities comprise ostracods, copepods, and cladocerans (Pavlik 2008) but are dominated by amphipods (Meffe and Marsh 1983, Myers and Resh 2002, Sada et al. 2005).

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The disconnected nature of these systems is reflected in the endemic nature of these crustacean species, as well as in the genetic divergence among those crustaceans that are more widespread (Thomas et al. 1997, Witt et al. 2006, Sei et al. 2009).

Desert Saltwater Ponds/Lakes

Salt lakes with athalassic (nonmarine) water occur worldwide in arid basins, in rain shadows of mountains, conspicuously along the western mountainous spine of North and South America, and on the Tibet Plateau. "Least favorable" conditions for their formation are deserts with low relief (Eugster and Hardie 1978). Nevertheless, the playa lakes of southern Western Australia in a terrain of very low relief are remnants of Cainozoic rivers (van de Graff et al. 1977) and are sufficiently prominent for recognition of a geomorphic region, Salinaland (Jutson 1934). The lakes of Salinaland are zoologically significant for the anostracans they harbor. Another significant category of salt lakes are coastal lakes with water of marine derivation.

Inland (athalassic) salt lakes show considerable diversity in terms of depth/ephemerality and ionic composition and concentration ranges. The Dead Sea is a perennially stratified brine; the playa lakes of Salinaland in Western Australia are less than 1 m deep and ephemeral. Inland playa salt lakes form through a balance between high evaporation rates and limited freshwater inputs (commonly derived from melting snows). The lower salt concentration boundary of a salt lake is set at 5 ppt, based on biological tolerances; the upper boundary is approximately 400,000 ppt. Eugster and Hardie (1978) defined salt lakes according to the salts precipitated: alkaline ($Na\text{-}CO_3$), bitterns ($Na_2SO_4.MgSO_4.4H_2O$), $Na\text{-}SO_4\text{-}Cl$ waters, and halite (NaCl). Significantly, salt lakes harbor a range of salt-tolerant microbes, plants, and animals, with the microbes completely dominating at the extreme upper salinity concentrations. However, some crustacean species in the order Anostraca occur in salt lakes and in no other environments. They do not co-occur with fish, so their upper boundary of salt tolerance in each lake presumably controls, in part, the shift from absence to presence of anostracans.

The two genera of salt lake anostracans are *Artemia* and *Parartemia*. The genus *Artemia* occurs on all continents of the world except Antarctica. In all, seven species have been described across this "cosmopolitan" distribution: six sexual and one parthenogenetic, *Artemia parthenogenetica*. In marked contrast, there is significantly higher diversity of members of the genus *Parartemia*, with eight species formally described (and more awaiting formal description) and endemic to Australia. All *Parartemia* are awaiting studies of their biology.

Undoubtedly, one reason for the success of salt lake anostracans is their ability to switch between ovoviviparous and oviparous development (Clegg and Conte 1980, Criel 1991). Development may proceed to (i) the formation of eggs (fertilized in sexual species) that hatch directly to release a nauplius larva (ovoviviparous development), or (ii) the embryo may proceed only to the gastrula stage of embryonic development, when it is then enclosed within a multilayered wall (i.e., encysted) and held in diapause until reactivated; the nauplius eventually emerges from the cyst via the process of excystment (oviparous development).

Artemia show wide ecophysiological tolerances. *Artemia* have been recorded from waters supersaturated (150%) in oxygen to less than 1 ppm dissolved oxygen. The ability to tolerate low oxygen levels is facilitated by the formation of the oxygen-carrying molecule hemoglobin. At a constant salinity, nauplii from three strains of *Artemia* (sexual, diploid parthenogenetic, and tetraploid parthenogenetic) maintained constant rates of oxygen consumption over a wide range of oxygen concentrations (Varo et al. 1993). However, oxygen consumption of the nauplii of the two parthenogenetic strains increased progressively with increasing temperature to 35°C, whereas oxygen consumption of the sexual strain nauplii declined at temperatures greater than 30°C. Additionally, *Artemia* survive in water of salinity varying from 10 to 340 ppt (Persoone and

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Sorgeloos 1980). The impacts of salinity on 10 life history parameters, including hatching success, survival, length, weight, ovigery, and brood size of *A. franciscana monica*, were determined based on published and laboratory studies (Dana et al. 1993). Between 40% and 93% of the variation in the 10 life history parameters was explained by salinity. As salinity increased from 76 to 168 ppt, survival, length, weight, percent of ovigerous females, brood size, and hatching success all decreased, and interbrood duration, time to hatching, and reproduction all increased in value. However, the effects on life history characteristics appeared to be gradual rather than exhibiting salinity thresholds, with one exception: naupliar survival, which was constant between 76 and 133 ppt but dramatically decreased at salinities greater than 133 ppt.

Artemia survive temperatures below 6°C encysted; the upper temperature tolerated is about 35°C, but the tolerance is strain-specific. Persoone and Sorgeloos (1980) suggest the optimum to be within the range of 25°C to 30°C. *Artemia* from the high-altitude saline lakes in Tibet are likely to experience water temperatures ranging between 0°C and 16°C (Williams 1991), that is, well outside the optimum temperature range suggested by Persoone and Sorgeloos (1980). There is also evidence of an ability to adapt rapidly to local temperature conditions: brine shrimp from Macau, Brazil, survived at 40°C in Thailand (Persoone and Sorgeloos 1980). Indeed, rapid adaptations of some strains are causing a loss of biodiversity in local native strains (Pinto et al. 2013), facilitated by the widespread used of *Artemia* species as live food in aquaculture.

There is considerable variability in *Artemia* life history patterns relating to specific localities. Individual *Artemia* strains do not have the capacity to switch from sexual to parthenogenetic reproduction: each strain is fixed regarding its reproductive mode. However, as noted above for other anostracans, female *Artemia* can switch between ovoviparous and oviparous development and generally do so depending on the prevailing environmental and endogenous conditions. Population numbers can be increased rapidly through ovoviparous development thereby enabling the population to exploit some transient resource(s). However, with a decline in environmental conditions, by switching to production of diapausing cysts, oviparity provides the population with protection against unfavorable conditions.

There are four agencies by which *Artemia* may be dispersed. Dispersal over long inter- and intracontinental distances, particularly of the cyst stage, may be achieved by human intervention, birds, and wind. Flowing water may serve to disperse within a river catchment all stages of *Artemia*, particularly during flood events.

CRUSTACEANS IN ACIDIC ENVIRONMENTS

Freshwater ecosystems are usually characterized by a neutral concentration of protons (i.e., pH ≈7). Low pH characterizes acidic environments, such as those produced by volcanic activity (e.g., crater lakes), by the weathering of catchment soil, or in the buttongrass swamps of southwestern Tasmania. The list of naturally acidic freshwater environments is augmented by sites where anthropogenic activity has lowered the natural pH of the water; for example, as a result of mining activity or deposition of acidic substances from the atmosphere. Natural and anthropogenic acidic environments present different community structures (Collier et al. 1990, Dangles et al. 2004, Petrin et al. 2008) probably because organisms in naturally acidic environments have developed specific adaptations to the chemophysical characteristic of these extreme habitats (Dangles et al. 2004, Petrin et al. 2008).

Acidic freshwater systems present high concentrations of protons, but this characteristic is usually coupled with high concentration of heavy metals (Löhr et al. 2007) or high salinity (e.g., acidic salt lakes in Australia). The few organisms able to cope with these extreme environments are often poly-extremophiles. Highly acidic environments have a pH of lower than 3. In the Tinto River in Spain (pH = 2.2), only microbes are found (López-Archilla et al. 2001); in the river system fed by the Kawah Ijen crater lake (East Java, Indonesia: pH = 2.3) no invertebrates are present with the exception of chironomids (Löhr et al. 2005). In brown water streams in New Zealand, acidity is decoupled from heavy metal toxicity because metal ions are not free but instead form less toxic complexes with organic acid from the humic soil (Collier et al. 1990).

Increased anthropogenic acidity is often correlated with a decrease in biodiversity and species abundance (e.g., Økland and Økland 1986, Horecký et al. 2006). Fish are often highly sensitive to low pH, and thus natural or artificial decrease of pH can indirectly modify the food web, reducing the predatory impact of fish (Bendell and McNicol 1987, Olsson et al. 2006). The food web is also altered because some functional groups (e.g., scrapers and shredders) are less tolerant to acidity than other groups or generalists (Horecký et al. 2006).

Acidity affects respiration, ion regulation, and membrane permeability in animals (Økland and Økland 1986, Havas and Advokaat 1995), but some organisms cope with these physiological stresses. Such tolerance varies not only among taxa (Petrin et al. 2007), but also within a single species. Intraspecific variation of endurance in acidic environments possibly depends on size, life stage, or genetic makeup. Small macroinvertebrates suffer higher mortality than larger ones (Courtney and Clements 1998), early developmental stages are more sensitive than juveniles and adults (Økland and Økland 1986, Havas and Advokaat 1995), and genetic variation (and maternal factors in amphibians) seems to play a role in individual sensitivity to acidity (Collier et al. 1990, Pierce and Wooten 1992).

Sodium and calcium ions are involved in membrane permeability, and their uptake is inhibited by low pH (Økland and Økland 1986). In naturally acidic habitats, organisms present high osmoregulatory capability. Crayfish can regulate ion concentration in the hemolymph (Collier et al. 1990) even though not all species are capable of doing so (Appelberg 1985). The brine shrimp *Parartemia contracta* inhabits acid salt lakes in Australia. In this highly stressful environment, osmoregulation is probably achieved by utilizing active pumps for sodium and protons (Conte and Geddes 1988). Cladocerans can survive transient periods of anthropogenic acidification in the form of encysted eggs and thus have the potential to recolonize the body of water once recovered (Nilssen and Wærvågen 2002).

Acidity can affect shell formation in mollusks and molting processes in crustaceans (Økland and Økland 1986, Havas and Advokaat 1995). Calcium intake is reduced with high hydrogen ion concentration in the water. The more acidic-tolerant mollusk species are those that can obtain calcium from the diet instead of relying completely on calcium in the water (Økland and Økland 1986). Many crustaceans eat their exuvia after molting, but probably this is not their major source of calcium: they often reabsorb ions during premolt (Roer and Dillaman 1984, Wheatly and Gannon 1995). Endogenous ions reabsorbed during premolt are stored in gastroliths or other calcareous concretions and used during postmolt. Nonetheless, it seems that difficulty in molting is mainly due to the low concentration of CO_2 in the water, typical of acidic environments, rather than from the pH itself (Wheatly and Gannon 1995). High proton concentration in aquatic environments also reduces oxygen uptake, affecting respiration. Aquatic insects capable of breathing oxygen from the air and amphibian larvae able to use cutaneous respiration can tolerate low pH better than species that utilize only aquatic respiration (Havas and Advokaat 1995). Acidity can also affect reproduction. Sperm motility is reduced under acidic conditions in amphibians (Schlichter 1981), and failure in egg hatching or embryo development has been reported in mollusks and crayfish in habitats with low pH (Økland and Økland 1986).

Thanks to their osmoregulatory capability, crustaceans thrive in many acidic environments (Table 14.2). Certain species of crayfish that are indigenous to New Zealand and Tasmania are highly tolerant of natural acidic conditions (Newcombe 1975, Collier et al. 1990); cladocerans are found in many natural and anthropogenic acidic environments (Deneke 2000) and are colonizers of newly acidified waters (Belyaeva and Deneke 2007). More sensitive species, such as *Gammarus pulex* and *Daphnia pulex*, are used as ecological indicators to assess the health of the environment (Felten et al. 2008) or study physiological variation under acidic stress (Weber and Pirow 2009).

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FUTURE DIRECTIONS

Significant advances have been made in the investigation of the mechanisms that allow organisms to survive under extreme conditions, and we are thus attaining a clearer understanding of the evolutionary adaptations involved. Nevertheless, we are still lacking a comprehensive picture of life in extreme environments. This remains a key challenge, given the fact that extreme environments are, by definition, difficult to access and sample, thus complicating field studies. Many organisms inhabiting extreme habitats are specialized to their harsh conditions: there is a high degree of endemism as well as a variety of cryptic species that are yet to be thoroughly investigated (Peck et al. 2006, Brandt et al. 2007, Zakšek et al. 2009). All of this has great implications for the conservation and management of these remarkable species. To preserve and protect this biodiversity, we need to improve our knowledge: more extensive sampling needs to be undertaken to document the variation of forms of life present in extreme environments. These remote and poorly accessible environments are pristine but already influenced by anthropogenic impacts (e.g., Quayle et al. 2002, Lyons et al. 2006, Rogers et al. 2012).

Recent studies have laid a strong groundwork for future research. Still, we need more scientific data collection and multidisciplinary approaches to attain an integrative view. Extreme habitats represent natural workbenches where we can assess evolutionary responses to multiple and extreme stressors; species adapted to extreme conditions can thus play a key role in enhancing our understanding of the influences, effects, and responses that climate change can cause in organisms. We should thus integrate ecology with physiology, with molecular evolution, and with the study of the genetic makeup of organisms and their behavioral responses to abiotic stressors. The molecular, genetic, metabolic, physiological, ecological, and behavioral adaptations required to survive in extreme environments can also be analyzed to address the origin and evolution of pathways, networks, and processes related to organismal–environmental interactions (Clegg 2001, Rothschild and Mancinelli 2001, Clarke 2003, Schwenk et al. 2009).

Current new molecular techniques are available to explore gene expressions and functional genomics to understand the underlying mechanisms involved in species adapted to extreme environments, and these findings can be related to other organisms inhabiting less challenging habitats (White 2001, Clark et al. 2004, Laybourn-Parry and Pearce 2007, Magazù et al. 2012). Crustaceans from extreme environments are unique and valuable candidates to address these topics (e.g., Gajardo and Beardmore 2012). Understanding adaptations and responses to extreme environmental and climatic conditions will be essential to address current challenges due to climate changes.

CONCLUSIONS

The documented morphological and physiological diversity of crustaceans has allowed this group to colonize the most extreme habitats on our planet. From “aquatic” habitats that are wet for less than a week, to deep-sea and subterranean habitats that lack all light and have minimal food, to ponds extreme in salinity, pH, and temperature—in all these, we find crustaceans. Often these crustaceans represent the highest trophic level in their respective extreme habitats (e.g., branchiopods in temporary desert pools and anostracans in hypersaline lakes). In other cases, crustaceans are important for regulating their respective communities, such as the top-down regulation of microbial communities by copepods in Antarctic ponds. Crustaceans can exist in these extreme environments by either being “extremophiles” that are specifically adapted to their extreme environments (e.g., polar-adapted fairy shrimp or eyeless cave-dwelling amphipods and decapods) or by being broadly tolerant to a range of habitats that includes these extremes (e.g., the amphipod *G. minus* that is found in caves as well as

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surface springs). In all cases, we can safely state that these crustaceans are exceptionally interesting and provide a wealth of opportunities for studying how life can adapt to extreme conditions.

It is clear that species overviewed here have been able to overcome extremely adverse conditions to thrive in their respective extreme environments. However, these species that have adapted to such hostile habitats now face another challenge: the rapid environmental change imposed by anthropogenic activities. Many extreme environments (such as those in Antarctica) are particularly susceptible to climate warming, exposure to ultraviolet radiation, acidification, pollution, and more (Quayle et al. 2002), all of which are posing new threats to the species inhabiting them. It would be sadly ironic if these species, which have been able to withstand the most extreme habitats this planet has to offer, fall to human-induced habitat loss or alteration. It would indeed be a strong statement about our influence on our planet's biota.

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REFERENCES

Almada, P., L. Allende, G. Tell, and I. Izaguirre. 2004. Experimental evidence of the grazing impact of *Boeckella poppei* on phytoplankton in a maritime Antarctic lake. Polar Biology 28:39–46.

Andrássy, I., and J.A.E. Gibson. 2007. Nematodes from saline and freshwater lakes of the Vestfold Hills, East Antarctica, including the description of *Hypodontolaimus antarcticus* sp. n. Polar Biology 30:669–678.

Appelberg, M. 1985. Changes in haemolymph ion concentrations of *Astucus astacus* L. and *Pacifastacus leniusculus* (Dana) after exposure to low pH and aluminium. Hydrobiologia 121:19–25.

Arnold, R.J., and P. Convey. 1998. The life history of the diving beetle, *Lancetes angusticollis* (Curtis) (Coleoptera: Dytiscidae), on sub-Antarctic South Georgia. Polar Biology 20:153–160.

Arnscheidt, J., H.-J. Hahn, and A. Fuchs. 2008. Aquatic subterranean Crustacea in Ireland: results and new records from a pilot study. Cave and Karst Science 35:53–58.

Badyaev, A.V. 2005. Stress-induced variation in evolution: from behavioural plasticity to genetic assimilation. Proceedings of the Royal Society London Biological Sciences B 272:877–886.

Baid, I.C. 1968. The arthropod fauna of Sambhar Salt Lake, Rajasthan, India. Oikos 19:292–303.

Baker, H.G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9:347–349.

Baker, M.B., and S. Rao. 2004. Incremental costs and benefits shape natal dispersal: theory and example with *Hemilepistus reaumuri*. Ecology 85:1039–1051.

Balaraman, U., and C.K.G. Nayar. 2004. A new species of the clam shrimp genus *Lynceus* (Branchiopoda, Conchostraca, Laevicaudata) from Kerala, India. Crustaceana 77:407–416.

Bayliss, P.R., and J. Laybourn-Parry. 1995. Seasonal abundance and size variation in Antarctic populations of the Cladoceran *Daphniopsis studeri*. Antarctic Science 7:393–394.

Bayly, I.A.E., J.A.E. Gibson, B. Wagner, and K.M. Swadling. 2003. Taxonomy, ecology and zoogeography of two East Antarctic freshwater calanoid copepod species: *Boeckella poppei* and *Gladioferens antarcticus*. Antarctic Science 15:439–448.

Belk, D. 1970. Functions of the conchostracan egg shell. Crustaceana 19:105–106.

Belyaeva, M., and R. Deneke. 2007. Colonization of acidic mining lakes: *Chydorus sphaericus* and other Cladocera within a dynamic horizontal pH gradient (pH 3-7) in Lake Senftenberger See (Germany). Hydrobiologia 594:97–108.

Lifestyles and Feeding Biology. Edited By Martin Thiel and Les Watling.

Bendell, B.E., and D.K. McNicol. 1987. Fish predation, lake acidity and the composition of aquatic insect assemblages. Hydrobiologia 150:193–202.

Berra, T.M., and G.R. Allen. 1991. Population structure and development of *Lepidogalaxias salamandroides* (Pisces: Salmoniformes) from Western Australia. Copeia 1991:845–850.

Bichain, J.-M., P. Gaubert, S. Samadi, and M.-C. Boisselier-Dubayle. 2007. A gleam in the dark: phylogenetic species delimitation in the confusing spring-snail genus *Bythinella* Moquin-Tandon, 1856 (Gastropoda: Rissooidea: Amnicolidae). Molecular Phylogenetics and Evolution 45:927–941.

Blaustein, L., J.E. Garb, D. Shebitz, and E. Nevo. 1999. Microclimate, developmental plasticity and community structure in artificial temporary pools. Hydrobiologia 392:187–196.

Botosaneanu, L. 1986. Stygofauna Mundi: a faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters. E.J. Brill/Dr. W. Backhuys Publishers, Leiden, The Netherlands.

Boulton, A.J., F. Sheldon, and K.M. Jenkins. 2006. Natural disturbance and aquatic invertebrates in desert rivers. Pages 133–153 *in* R. Kingsford, editor. Ecology of desert rivers. Cambridge University Press, Cambridge.

Brandon, R. 1990. Adaptation and environment. Princeton University Press, Princeton, NJ.

Brandt, A., C. De Broyer, I. De Mesel, K.E. Ellingsen, A.J. Gooday, B. Hilbig, K.Linse, M.R.A. Thomson, and P.A. Tyler. 2007. The biodiversity of the deep Southern Ocean benthos. Philosophical Transactions of the Royal Society B: Biological Sciences 362:39–66.

Brantner, J.S. 2011. Mating system inferences in representatives from two clam shrimp families (Limnadiidae and Cyzicidae) using histological and cellular observations. Master's Thesis. The University of Akron, Akron, OH.

Brantner, J.S., D.W. Ott, R.J. Duff, J.I. Orridge, J.R. Waldman, and S.C. Weeks. 2013a. Evidence of selfing hermaphroditism in the clam shrimp *Cyzicus gynecia* (Branchiopoda, Spinicaudata). Journal of Crustacean Biology 33:184–190.

Brantner, J.S., D.W. Ott, R.J. Duff, L. Sanoamuang, G.P. Simhachalam, K.K.S. Babu, and S.C. Weeks. 2013b. Androdioecy and hermaphroditism in five species of clam shrimp (Crustacea: Branchiopoda: Spinicaudata) from India and Thailand. Invertebrate Biology 132:27–37.

Brendonck, L., and B. Riddoch. 1997. Anostracans (Branchiopoda) of Botswana: morphology, distribution, diversity, and endemicity. Journal of Crustacean Biology 17:111–134.

Brendonck, L., E. Michels, L. De Meester, and B. Riddoch. 2002. Temporary pools are not "enemy-free." Hydrobiologia 486:147–159.

Buhay, J.E., and K.A. Crandall. 2008. Taxonimic revision of cave crayfishes in the genus *Orconectes*, subgenus *orconectes* (Decapoda: Cambaridae) along the Cumberland plateau, including a description of a new species, *Orconectes barri*. Journal of Crustacean Biology 28:57–67.

Buhay, J.E., and K.A. Crandall. 2009. Taxonimic revision of cave crayfish in the genus *Cambarus*, subgenus *aviticambarus* (Decapoda: Cambaridae) with descriptions of two new species, *C. speleocoopi* and *C. laconensis*, endemic to Alabama, U.S.A. Journal of Crustacean Biology 29:121–134.

Butler, H., A. Atkinson, and M. Gordon. 2005. Omnivory and predation impact of the calanoid copepod *Boeckella poppei* in a maritime Antarctic lake. Polar Biology 28:815–821.

Calabrese, A. 2009. A survey of the Branshiopoda and community associates in rock pools with respect to abiotic habitat parameters across outcrops in Western Australia and northern AZ, USA. Master's thesis, University of Akron, OH.

Camacho, A. 2006. Planktonic microbial assemblages and the potential effects of metazooplankton predation on the food web of lakes from the maritime Antarctica and sub-Antarctic islands. Reviews in Environmental Science and Biotechnology 5:167–185.

Carlisle, D.B. 1968. *Triops* (Entomostraca) eggs killed only by boiling. Science 161:279.

Chan, M.A., K. Moser, J.M. Davis, G. Southam, K. Hughes, and T. Graham. 2005. Desert potholes: ephemeral aquatic microsystems. Aquatic Geochemistry 11:279–302.

Charalabidou, I., and L. Santamaria. 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. Acta Oecologica 23:165–176.

Clark, M.S., A. Clarke, C.S. Cockell, P. Convey, H.W. Detrich III, K.P.P. Fraser, I.A. Johnston, B.A. Methe, A.E. Murray, L.S. Peck, K. Römisch, and A.D. Rogers. 2004. Antarctic genomics. Comparative and Functional Genomics 5:230–238.

Lifestyles and Feeding Biology. Edited By Martin Thiel and Les Watling.

Clarke, A. 2003. Costs and consequences of evolutionary temperature adaptation. Trends in Ecology & Evolution 18:573–581.

Clarke, A., N.M. Johnston, E.J. Murphy, and A.D. Rogers. 2007. Introduction. Antarctic ecology from genes to ecosystems: the impact of climate change and the importance of scale. Philosophical Transactions of the Royal Society B 362:5–9.

Clegg, J.S. 1997. Embryos of *Artemia franciscana* survive four years of continuous anoxia: the case for complete metabolic rate depression. Journal of Experimental Biology 200:467–475.

Clegg, J.S. 2001. Cryptobiosis—a peculiar state of biological organization. Comparative Biochemistry and Physiology Part B 128:613–624.

Clegg, J.S., and F.P. Conte. 1980. A review of cellular and developmental biology of *Artemia*. Pages 11–54 *in* G. Persoone, P. Sorgeloos, O. Roels, and E. Jaspers, editors. The brine shrimp *Artemia*. Universa Press, Wetteren, Belgium.

Collier, K.J., O.J. Ball, A.K. Graesser, M.R. Main, and M.J. Winterbourn. 1990. Do organic and anthropogenic acidity have similar effects on aquatic fauna? Oikos 59:33–38.

Conte, F.P., and M.C. Geddes. 1988. Acid brine shrimp: metabolic strategies in osmotic and ionic adaptation. Hydrobiologia 158:191–200.

Convey, P. 1997. How are the life history strategies of Antarctic terrestrial invertebrates influenced by extreme environmental conditions? Journal of Thermal Biology 22:429–440.

Corliss, J.B., J. Dymond, L.I. Gordon, J.M. Edmond, R.P. von Herzen, R.D. Ballard, K. Green, D. Williams, A. Bainbridge, K. Crane, and T.H. van Andel. 1979. Submarine thermal springs on the Galapagos Rift. Science 203:1073–1083.

Cottin, D., J. Ravaux, N. Léger, S. Halary, T.J.-Y., P.-M. Sarradin, F. Gaill, and B. Shillito. 2008. Thermal biology of the deep-sea vent annelid *Paralvinella grasslei*: in vivo studies. The Journal of Experimental Biology 211:2196–2204.

Courtney, L.A., and W.H. Clements. 1998. Effects of acidic pH on benthic macroinvertebrate communities in stream microcosms. Hydrobiologia 379:135–145.

Crespo-Medina, M., A.D. Chatziefthimiou, N.S. Bloom, G.W. Luther, D.D. Wright, J.R. Reinfelder, C. Vetriani, and T. Barkay. 2009. Adaptation of chemosynthetic microorganisms to elevated mercury concentrations in deep-sea hydrothermal vents. Limnology and Oceanography 54:41–49.

Criel, G.R.J. 1991. Morphology of *Artemia*. Pages 119–154 *in* R.A. Browne, P. Sorgeloos, and C.N.A. Trotman, editors. *Artemia* biology. CRC Press, Boca Raton, FL.

Culver, D.C. 1975. Interaction between competition and predation in cave stream communities. International Journal of Speleology 7:229–245.

Culver, D.C. 1982. Cave life: evolution and ecology. Harvard University Press, Cambridge, MA.

Culver, D.C. 1986. Cave faunas. Pages 427–443 *in* M.E. Soule, editor. Conservation biology, the science of scarcity and diversity. Sinauer, Sunderland, MA.

Culver, D.C. 1987. Eye morphometrics of cave and spring populations of *Gammarus minus* (Amphipoda: Gammaridae). Journal of Crustacean Biology 7:136–147.

Culver, D.C. 1994. Species interactions. Pages 271–286 *in* J. Gibert, D.L. Danielopol, and J.A. Stanford, editors. Groundwater ecology. Academic Press, Inc., San Diego, CA.

Culver, D.C., and J.R. Holsinger. 1992. How many species of troglobites are there? National Speleological Society Bulletin 54:79–80.

Culver, D.C., and T. Pipan. 2009. The biology of caves and other subterranean habitats. Oxford University Press, Inc., Oxford, UK.

Culver, D.C., T.C. Kane, and D.W. Fong. 1995. Adaptation and natural selection in caves. The evolution of *Gammarus minus*. Harvard University Press, Cambridge, MA.

Culver, D.C., M.C. Christman, W.R. Elliott, H.H. Hobbs III, and J.R. Reddell. 2003. The North American obligate cave fauna: regional patterns. Biodiversity and Conservation 12:441–468.

Dana, G.L., R. Jellison, J.M. Melack, and G.L. Starrett. 1993. Relationships between *Artemia monica* life-history characteristics and salinity. Hydrobiologia 263:129–143.

Dangles, O., B. Malmqvist, and H. Laudon. 2004. Naturally acid freshwater ecosystems are diverse and functional: evidence from boreal streams. Oikos 104:149–155.

Lifestyles and Feeding Biology. Edited By Martin Thiel and Les Watling.

Dartnall, H.J.G., W. Hollwedel, and J.C. De Paggi. 2005. The freshwater fauna of Macquarie Island, including a redescription of the endemic water-flea *Daphnia gelida* (Brady) (Anomopoda: Crustacea). Polar Biology 28:922–939.

De los Ríos, P., and J.E. Crespo. 2004. Salinity effects on the abundance of *Boeckella poopoensis* (Copepoda, Calanoida) in saline ponds in the Atacama Desert, Northern Chile. Crustaceana 77:417–423.

De los Ríos, P., D.C. Rogers, and N. Rivera. 2008. *Branchinecta gaini* Daday, 1910 (Branchiopoda, Anostraca) as a bioindicator of oligotrophic and low conductivity shallow ponds in southern Chilean Patagonia. Crustaceana 81:1025–1034.

Deneke, R. 2000. Review of rotifers and crustaceans in highly acidic environments of pH values < = 3. Hydrobiologia 433:167–172.

Dodson, S.I. 1987. Animal assemblages in temporary desert rock pools: aspects of the ecology of *Dasyhelea subletiei* (Diptera: Ceratopogoidae). Journal of the North American Benthological Society 6:65–71.

Dumont, H.J., and S.V. Negrea. 2002. Introduction to the Class Branchiopoda. Backhuys Publishers, Leiden.

Eitam, A., L. Blaustein, K. Van Damme, H.J. Dumont, and K. Martens. 2004. Crustacean species richness in temporary pools: relationships with habitat traits. Hydrobiologia 525:125–130.

Eugster, H.P., and L.A. Hardie. 1978. Saline lakes. Pages 237–293 *in* A. Lerman, editor. Lakes: chemistry, geology, physics. Springer-Verlag, New York.

Everitt, D.A. 1981. An ecological study of an Antarctic freshwater pool with particular reference to Tardigrada and Rotifera. Hydrobiologia 83:225–237.

Felten, V., G. Charmantier, M. Charmantier-Daures, F. Aujoulat, J. Garric, and O. Geffard. 2008. Physiological and behavioural responses of *Gammarus pulex* exposed to acid stress. Comparative Biochemistry and Physiology Part C 147:189–197.

Figuerola, J., and A.J. Green. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshwater Biology 47:483–494.

Fisher, S.G., L.J. Gray, N.B. Grimm, and D.E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecological Monographs 52:93–110.

Fryer, G. 1996. Diapause, a potent force in the evolution of freshwater crustaceans. Hydrobiologia 320:1–14.

Gajardo, G.M., and J.A. Beardmore. 2012. The brine shrimp *Artemia*: adapted to critical life conditions. Frontiers in Physiology 3:185.

Ghiselin, M.T. 1969. The evolution of hermaphroditism among animals. The Quarterly Review of Biology 44:189–208.

Gibert, J., D.L. Danielopol, and J.A. Stanford. 1994. Groundwater ecology. Academic Press, San Diego, CA.

Gibson, J.A.E. 1999. The meromictic lakes and stratified marine basins of the Vestfold Hills, East Antarctica. Antarctic Science 11:175–192.

Gibson, J.A.E., and D.T. Andersen. 2002. Physical structure of epishelf lakes of the southern Bunger Hills, East Antarctica. Antarctic Science 14:253–261.

Gibson, J.A.E., and I.A.E. Bayly. 2007. New insights into the origins of crustaceans of Antarctic lakes. Antarctic Science 19:157–164.

Gibson, J.A.E., A. Wilmotte, A. Taton, B. Van De Vijver, L. Beyens, and H.J.G. Dartnall. 2006. Pages 71–100 *in* D.M. Bergstrom, P. Convey, and A.H.L. Huiskes, editors. Trends in antarctic terrestrial and limnetic ecosystems. Springer, Dordrecht, The Netherlands.

Gilbert, J.A.E., P.J. Hill, C.E.R. Dodd, and J. Laybourn-Parry. 2004. Demonstration of antifreeze protein activity in Antarctic lake bacteria. Microbiology 150:171–180.

Gonzalez-Rey, M., A. Serafim, R. Company, T. Gomes, and M.J. Bebianno. 2008. Detoxification mechanisms in shrimp: comparative approach between hydrothermal vent fields and estuarine environments. Marine Environmental Research 66:35–37.

Gottstein, S., M. Ivković, I. Ternjej, B. Jalžić, and M. Kerovec. 2007. Environmental features and crustacean community of anchihaline hypogean waters on the Kornati islands, Croatia. Marine Ecology 28:24–30.

Graham, T.B. 2002. Survey of aquatic macroinvertebrates and amphibians at Wupatki National Monument, Arizona, USA: an evaluation of selected factors affecting species richness in ephemeral pools. Hydrobiologia 486:215–224.

Green, A.J., and J. Figuerola. 2005. Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. Biodiversity Research 11:149–156.

Halse, S.A., and J.M. McRae. 2001. *Calamoecia trilobata* n sp (Copepoda: Calanoida) from salt lakes in southwestern Australia. Journal of the Royal Society of Western Australia 84:5–11.

Halse, S.A., and J.M. McRae. 2004. New genera and species of "giant" ostracods (Crustacea: Cyprididae) from Australia. Hydrobiologia 524:1–52.

Hamer, M.L., and K. Martens. 1998. The large Branchiopoda (Crustacea) from temporary habitats of the Drakensberg region, South Africa. Hydrobiologia 384:151–165.

Hansson, L.-A., and L.J. Tranvik. 1996. Quantification of invertebrate predation and herbivory in food chains of low complexity. Oecologia 108:542–551.

Hartke, T.R., C. Fišer, J. Hohagen, S. Kleber, R. Hartmann, and S. Koenemann. 2011. Morphological and molecular analyses of closely related species in the stygobiontic genus *Niphargus* (Amphipoda). Journal of Crustacean Biology 31:701–709.

Havas, M., and E. Advokaat. 1995. Can sodium regulation be used to predict the relative acid-sensitivity of various life-stages and different species of aquatic fauna? Water, Air and Soil Pollution 85:865–870.

Hawes, I., and A.-M.J. Schwarz. 2000. Absorption and utilization of irradiance by cyanobacterial mats in two ice-covered Antarctic lakes with contrasting light climate. Journal of Phycology 37:5–15.

Hawes, T.C. 2008. Feeding behaviour in the Antarctic fairy shrimp, *Branchinecta gaini*. Polar Biology 31:1287–1289.

Hawes, T.C., M.R. Worland, and J.S. Bale. 2008. Physiological constraints on the life cycle and distribution of the Antarctic fairy shrimp *Branchinecta gaini*. Polar Biology 31:1531–1538.

Hebert, P.D.N., and C.C. Wilson. 2000. Diversity of the genus *Daphniopsis* in the saline waters of Australia. Canadian Journal of Zoology 78:794–808.

Hervant, F. 1996. The activities of enzymes associated with the intermediary and energy metabolism in hypogean and epigean crustaceans. Comptes Rendus De L'Academie Des Sciences Serie Iii-Sciences De La Vie-Life Sciences 319:1071–1077.

Hervant, F., and J. Mathieu. 1995. Ventilatory and locomotory act in anoxia and subsequent recovery of epigean and hypogean crustaceans. Comptes Rendus De L'Academie Des Sciences Serie Iii-Sciences De La Vie-Life Sciences 318:585–592.

Hervant, F., and D. Renault. 2002. Long-term fasting and realimentation in hypogean and epigean isopods: a proposed adaptive strategy for groundwater organisms. Journal of Experimental Biology 205:2079–2087.

Hervant, F., J. Mathieu, and H. Barre. 1999. Comparative study on the metabolic responses of subterranean and surface-dwelling amphipods to long-term starvation and subsequent refeeding. Journal of Experimental Biology 202:3587–3595.

Hildrew, A.G. 1985. A quantitative study of the life history of a fairy shrimp (Branchipoda: Anostraca) in relation to the temporary nature of its habitat, a Kenyan rain pool. Journal of Animal Ecology 54:99–110.

Hogg, I.D., S.C. Cary, P. Convey, K.K. Newsham, A.G. O'Donnell, B.J. Adams, J. Aislabie, F. Frati, M.I. Stevens, and D.H. Wall. 2006. Biotic interactions in Antarctic terrestrial ecosystems: are they a factor? Soil Biology and Biochemistry 38:3035–3040.

Holsinger, J.R., and D.C. Culver. 1970. Morphological variation in *Gammarus minus* Say (Amphipoda, Gammaridae) with emphasis on subterranean forms. Postilla 146:1–24.

Holsinger, J.R., T.R. Sawicki, and G.O. Graening. 2006. *Bactrurus speleopolis*, a new species of subterranean amphipod crustacean (Crangonyctidae) from caves in northern Arkansas. Proceedings of the Biological Society of Washington 119:15–24.

Horecký, J., E. Stuchlík, P. Chvojka, D.W. Hardekopf, M. Mihaljevič, and J. Špaček. 2006. Macroinvertebrate community and chemistry of the most atmospherically acidified streams in the Czech Republic. Water, Air, and Soil Pollution 173:261–272.

Howarth, F.G. 1987. Evolutionary ecology of aeolian and subterranean habitats in Hawaii. Trends in Ecology & Evolution 2:220–223.

Humphreys, W.F. 1993. Stygofauna in semi-arid tropical Western Australia: a Tethyan connection? Memoires de Biospeologie 20:111–116.

Humphreys, W.F. 2001. *Milyeringa veritas* (Eleotridae), a remarkably versatile cave fish from the arid tropics of northwestern Australia. Environmental Biology of Fishes 62:297–313.

Iwasaki, T. 1973. Tolerance of *Artemia* dry eggs for temperature, vacuum and radiation. Bulletin Institut International du Froid Supplément 5:79–88.

Lifestyles and Feeding Biology. Edited By Martin Thiel and Les Watling.

Jasinska, E.J., B. Knott, and A.J. McComb. 1996. Root mats in ground water: a fauna-rich cave habitat. Journal of the North American Benthological Society 15:508–519.

Jenkins, K.M., and A.J. Boulton. 2003. Connectivity in a dryland river: short-term aquatic microinvertebrate recruitment following floodplain inundation. Ecology 84:2708–2723.

Jennings, J.N. 1985. Karst geomorphology. Basil Blackwell, Inc., New York.

Jinks, R.N., T.L. Markley, E.E. Taylor, G. Perovich, A.I. Dittel, C.E. Epifanio, and T.W. Cronin. 2002. Adaptive visual metamorphosis in a deep-sea hydrothermal vent crab. Nature 420:68–70.

Jutson, J.T. 1934. The geomorphology of Western Australia. Geological Survey of Western Australia Bulletin 95:1–366.

Kapitsa, A.P., J.K. Ridley, G.D.Q. Robin, M.J. Siegert, and I.A. Zotikov. 1996. A large deep freshwater lake beneath the ice of central East Antarctica. Nature 381:684–686.

Kingsford, R., editor. 2006. Ecology of desert rivers. Cambridge University Press, Cambridge, U.K.

Kingsford, R., and R.T. Thompson. 2006. Desert or dryland rivers of the world: an introduction. Pages 3–10 *in* R. Kingsford, editor. Ecology of desert rivers. Cambridge University Press, Cambridge, U.K.

Knott, B. 1993. Stygofauna from Cape Range peninsula, Western Australia: tethyan relicts. Records of the Australian Museum Supplement 45:109–127.

Kotov, A.A., J.C. Paggi, and M. Elías-Gutiérrez. 2002. Redescription of *Ilyocryptus brevidentatus* Ekman, 1905 (Anomopoda, Cladocera, Branchiopoda). Hydrobiologia 481:1–18.

Land, M.F. 1989. Animal behavior—The sight of deep wet heat. Nature 337:404.

Laybourn-Parry, J. 1997. The microbial loop in Antarctic lakes. Pages 231–240 *in* W.B. Lyons, C. Howard-Williams, and I. Hawes, editors. Ecosystem processes in Antarctic ice-free landscapes. A.A. Balkema, Rotterdam, The Netherlands.

Laybourn-Parry, J. 2002. Survival mechanisms in Antarctic lakes. Philosophical Transactions of the Royal Society B 357:863–869.

Laybourn-Parry, J., and D.A. Pearce. 2007. The biodiversity and ecology of Antarctic lakes: models for evolution. Philosophical Transactions of the Royal Society B 362:2273–2289.

Lefébure, T., C.J. Douady, M. Gouy, P. Trontelj, J. Briolay, and J. Gibert. 2006. Phylogeography of a subterranean amphipod reveals cryptic diversity and dynamic evolution in extreme environments. Molecular Ecology 15:1797–1806.

Lefébure, T., C.J. Douady, F. Malard, and J. Gibert. 2007. Testing dispersal and cryptic diversity in a widely distributed groundwater amphipod (*Niphargus rhenorhodanensis*). Molecular Phylogenetics and Evolution 42:676–686.

Leys, R., C.H.S. Watts, S.J.B. Cooper, and W.F. Humphreys. 2003. Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. Evolution 57:2819–2834.

Löhr, A.J., T.A. Bogaard, A. Heikens, M.R. Hendriks, S. Sumarti, M.J. Van Bergen, C.A.M. Van Gestel, N.M. Van Straalen, P.Z. Vroon, and B. Widianarko. 2005. Natural pollution caused by the extremely acidic crater lake Kawah Ijen, East Java, Indonesia. Environmental Science & Pollution Research 12:89–95.

Löhr, A.J., T. De Kort, N.M. Van Straalen, and C.A.M. Van Gestel. 2007. Unraveling the causes of the toxicity of extremely acid waters of volcanic origin. Environment International 33:743–749.

López-Archilla, A.I., I. Marin, and R. Amils. 2001. Microbial community composition and ecology of an acidic aquatic environment: the Tinto River, Spain. Microbial Ecology 41:20–35.

Lupton, J.E., E.T. Baker, N. Garfield, G.J. Massoth, R.A. Feely, J.P. Cowen, R.R. Greene, and T.A. Rago. 1998. Tracking the evolution of a hydrothermal event plume with a RAFOS neutrally buoyant drifter. Science 280:1052–1055.

Luštrik, R., M. Turjak, S. Kralj-Fišer, and C. Fišer. 2011. Coexistence of surface and cave amphipods in an ecotone environment. Contributions to Zoology 80:133–141.

Lyons, W.B., J. Laybourn-Parry, K.A. Welch, and J.C. Priscu. 2006. Antarctic lake systems and climate change. Pages 273–295 *in* D.M. Bergstrom, P. Convey and A.H.L. Huiskes, editors. Trends in Antarctic terrestrial and limnetic ecosystems—Antarctica as a global indicator. Springer, Dordrecht, The Netherlands.

Maeda-Martínez, A.M., H. Obregón-Barboza, and H. García-Velazco. 1997a. New records of large branchiopods (Branchiopoda: Anostraca, Notostraca, and Spinicaudata) in Mexico. Hydrobiologia 359:63–68.

Maeda-Martínez, A.M., D. Belk, H. Obregón-Barboza, and H.J. Dumont. 1997b. Large branchiopod assemblages common to Mexico and the United States. Hydrobiologia 359:45–62.

Magazù, S., F. Migliardo, M. Gonzalez, C. Mondelli, S. Parker, and B.G. Vertessy. 2012. Molecular mechanisms of survival strategies in extreme conditions. Life 2:364–376.

Marcus, V., and S.C. Weeks. 1997. The effects of pond duration on the life history traits of an ephemeral pond crustacean, *Eulimnadia texana*. Hydrobiologia 359:213–221.

Martin, J.W. 1989. *Eulimnadia belki*, a new clam shrimp from Cozumel, Mexico (Conchostraca, Limnadiidae), with a review of central and South American species of the genus Eulimnadia. Journal of Crustacean Biology 9:104–114.

Martin, J.W., and D. Belk. 1989. *Eulimnadia ovilunata* and *Eulimnadia ovisimilis*, New species of clam shrimps (Crustacea, Branchiopoda, Spinicaudata) from South America. Proceedings of the Biological Society of Washington 102:894–900.

Martin, J.W., and G.E. Davis. 2001. An updated classification of the recent Crustacea. Natural History Museum of Los Angeles County, Los Angeles, CA.

Martin, J.W., and T.A. Haney. 2005. Decapod crustaceans from hydrothermal vents and cold seeps: a review through 2005. Zoological Journal of the Linnean Society 145:445–522.

Martin, K.L.M., T.M. Berra, and G.R. Allen. 1993. Cutaneous aerial respiration during forced emergence in the Australian salamanderfish, *Lepidogalaxias salamandroides*. Copeia 1993:875–879.

Martínez-Pantoja, M.A., J. Alcocer, and A.M. Maeda-Martínez. 2002. On the Spinicaudata (Branchiopoda) from Lake Cuitzeo, Michoacán, México: first report of a clam shrimp fishery. Hydrobiologia 486:207–213.

Mathers, T.C., R.L. Hammond, R.A. Jenner, T. Zierold, B. Haenfling, and A. Gomez. 2013. High lability of sexual system over 250 million years of evolution in morphologically conservative tadpole shrimps. BMC Evolutionary Biology 13:30.

Mattox, N.T. 1937. Studies on the life history of a new species of fairy shrimp, *Eulimnadia diversa*. Transactions of the American Microscopical Society 56:249–255.

McCulloch, P.G., K. Irvine, F.D. Eckardt, and R. Bryant. 2008. Hydrochemical fluctuations and crustacean community composition in an ephemeral saline lake (Sua Pan, Makgadikgadi Botswana). Hydrobiologia 596:31–46.

McSorley, R. 2003. Adaptations of nematodes to environmental extremes. Florida Entomologist 86:138–142.

Meffe, G.K., and P.C. Marsh. 1983. Distribution of aquatic macroinvertebrates in three Sonoran desert springbrooks. Journal of Arid Environments 6:363–371.

Meffe, G.K., and W.L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran desert stream. The American Midland Naturalist Journal 117:177–191.

Mejía-Ortíz, L.M., and R.G. Hartnoll. 2005. Modifications of eye structure and integumental pigment in two cave crayfish. Journal of Crustacean Biology 25:480–487.

Mejía-Ortíz, L.M., and M. López-Mejía. 2005. Are there adaptational levels to cave life in crayfish? Journal of Crustacean Biology 25:593–597.

Myers, M.J., and V.H. Resh. 2002. Trichoptera and other macroinvertebrates in springs of the Great Basin: species composition, richness, and distribution. Western North American Naturalist 62:1–13.

Nakanishi, Y.H., T. Iwaski, T. Okigaki, and H. Kato. 1962. Cytological studies of *Artemia salina*. I. Embryonic development without cell multiplication after the blastula stage in encysted dry eggs. Annotationes Zoologicae Japonenses 35:223–228.

Newcombe, K.J. 1975. The pH tolerance of the crayfish *Parastacoides tasmanicus* (Erichson) (Decapoda, Parastacidae). Crustaceana 29:231–234.

Nilssen, J.P., and S.B. Wærvågen. 2002. Recent re-establishment of the key species *Daphnia langispina* and cladoceran community changes following chemical recovery in a strongly acid-stressed region in southern Norway. Archiv für Hydrobiologie 153:557–580.

Økland, J., and K.A. Økland. 1986. The effects of acid deposition on benthic animals in lakes and streams. Experientia 42:471–486.

Olsson, K., P. Stenroth, P. Nyström, N. Holmqvist, A.R. McIntosh, and M.J. Winterbourn. 2006. Does natural acidity mediate interactions between introduced brown trout, native fish, crayfish and other invertebrates in West Coast New Zealand streams? Biological Conservation 130:255–267.

Page, T.J., W.F. Humphreys, and J.M. Hughes. 2008. Shrimps down under: evolutionary relationships of subterranean crustaceans from Western Australia (Decapoda: Atyidae: *Stygiocaris*). PloS ONE 3:e1618.

Lifestyles and Feeding Biology. Edited By Martin Thiel and Les Watling.

Paquin, P., and M. Hedin. 2004. The power and perils of "molecular taxonomy": a case study of eyeless and endangered *Cicurina* (Araneae: Dictynidae) from Texas caves. Molecular Ecology 13:3239–3255.

Pavlik, B.P. 2008. The California deserts. University of California Press, Berkeley, CA.

Peck, L.S. 2004. Physiological flexibility: the key to success and survival for Antarctic fairy shrimps in highly fluctuating extreme environments. Freshwater Biology 49:1195–1205.

Peck, L.S. 2005. Prospects for surviving climate change in Antarctic aquatic species. Frontiers in Zoology 2:9–16.

Peck, L.S., P. Convey, and D.K.A. Barnes. 2006. Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. Biological Reviews 81:75–109.

Pelli, D.G., and S.C. Chamberlain. 1989. The visibility of 350 degrees-C black-body radiation by the shrimp *Rimicaris exoculata* and man. Nature 337:460–461.

Pereira, G., and J.V. García. 2001. A review of the clam shrimp family Limnadiidae (Branchiopoda, Conchostraca) from Venezuela, with the description of a new species. Journal of Crustacean Biology 21:640–652.

Persoone, G., and P. Sorgeloos. 1980. General aspects of the ecology and biogeography of *Artemia*. Pages 3–24 *in* G. Persoone, P. Sorgeloos, O. Roels, and E. Jaspers, editors. The brine shrimp *Artemia*. Vol. 3. Ecology, culturing, use in aquaculture. Universa Press, Wetteren, Belgium.

Petrin, Z., H. Laudon, and B. Malmqvist. 2007. Does freshwater macroinvertebrate diversity along a pH-gradient reflect adaptation to low pH? Freshwater Biology 52:2172–2183.

Petrin, Z., H. Laudon, and B. Malmqvist. 2008. Diverging effects of anthropogenic acidification and natural acidity on community structure in Swedish streams. Science of the Total Environment 394:321–330.

Pfennig, D.W., and P.J. Murphy. 2002. How fluctuating competition and phenotypic plasticity mediate species divergence. Evolution 56:1217–1228.

Pierce, B.A. 1985. Acid tolerance in amphibians. BioScience 35:239–243.

Pierce, B.A., and D.K. Wooten. 1992. Genetic variation in tolerance of amphibians to low pH. Journal of Herpetology 26:422–429.

Pinder, A M., S.A. Halse, J.M. McRae, and R.J. Shiel. 2005. Occurrence of aquatic invertebrates of the wheatbelt region of Western Australia in relation to salinity. Hydrobiologia 543:1–24.

Pinto, P.M., A. Bio, F. Hontoria, V. Almeida, and N. Vieira. 2013. Portuguese native *Artemia parthenogenetica* and *Artemia franciscana* survival under different abiotic conditions. Journal of Experimental Marine Biology and Ecology 440:81–89.

Pociecha, A. 2007. Effect of temperature on the respiration of an Antarctic freshwater anostracan, *Branchinecta gaini* Daday 1910, in field experiments. Polar Biology 30:731–734.

Pociecha, A., and H.J. Dumont. 2008. Life cycle of *Boeckella poppei* Mrazek and *Branchinecta gaini* Daday (King George Island, South Shetlands). Polar Biology 31:245–248.

Poulson, T.L. 1964. Animals in aquatic environments: animals in caves. Pages 749–771 *in* D.B. Dill, editor. Handbook of physiology, sect. 4, adaptation to environment. American Physiological Society, Washington, DC

Prieur, D. 2007. An extreme environment on Earth: deep-sea hydrothermal vents lessons for exploration of Mars and Europa. Pages 319–345 *in* M. Gargaud et al., editors. Lectures in astrobiology. Vol. II, Advances in Astrobiology and Biogeophysics.

Protas, M.E., C. Hersey, D. Kochanek, Y. Zhou, H. Wilkens, W.R. Jeffery, L.I. Zon, R. Borowsky, and C.J. Tabin. 2006. Genetic analysis of cavefish reveals molecular convergence in the evolution of albinism. Nature Genetics 38:107–111.

Pugh, P.J.A., and P. Convey. 2008. Surviving out in the cold: Antarctic endemic invertebrates and their refugia. Journal of Biogeography 35:2176–2186.

Pugh, P.J.A., and H.J.G. Dartnall. 1994. The Acari of fresh- and brackish water habitats in the Antarctic and sub-Antarctic regions. Polar Biology 14:401–404.

Pugh, P.J.A., H.J.G. Dartnall, and S.J. McInnes. 2002. The non-marine Crustacea of Antarctica and the Islands of the Southern Ocean: biodiversity and biogeography. Journal of Natural History 36:1047–1103.

Quayle, W.C., L.S. Peck, H. Peat, J.C. Ellis-Evans, and P.R. Harrigan. 2002. Extreme responses to climate change in Antarctic lakes. Science 295:645.

Rabet, N. 2010. Revision of the egg morphology of *Eulimnadia* (Crustacea, Branchiopoda, Spinicaudata). Zoosystema 32:373–391.

Lifestyles and Feeding Biology. Edited By Martin Thiel and Les Watling.

Reed, C. 2006. Marine science: boiling points. Nature 439:905–907.

Richter, S., and B.V. Timms. 2005. A list of the recent clam shrimps (Crustacea: Laevicaudata, Spinicaudata, Cyclestherida) of Australia, including a description of a new species of Eocyzicus. Records of the Australian Museum 57:341–354.

Roer, R., and R. Dillaman. 1984. The structure and calcification of the crustacean cuticle. American Zoologist 24:893–909.

Rogers, A.D., E.J. Murphy, N.M. Johnston, and A. Clarke. 2007. Introduction. Antarctic ecology: from genes to ecosystems. Part 2. Evolution, diversity and functional ecology. Philosophical Transactions of the Royal Society of London B 362:2187–2189.

Rogers, A.D., N.M. Johnston, E.J. Murphy, and A. Clarke. 2012. Antarctic ecosystems: an extreme environment in a changing world. Blackwell Publishing, London.

Rogers, D.C. 2003. Revision of the thamnocephalid genus *Phallocryptus* (Crustacea; Branchiopoda; Anostraca). Zootaxa 257:1–14.

Rogers, D.C., and A. Ferreira. 2007. A new species of *Branchinecta* (Crustacea: Anostraca) from Brasil. Zootaxa 1445:27–34.

Rothschild, L.J., and R.L. Mancinelli. 2001. Life in extreme environments. Nature 409:1092–1101.

Ruan, L., X. Bian, X. Wang, X. Yan, F. Li, and X. Xu. 2008. Molecular characteristics of the tubeworm, *Ridgeia piscesae*, from the deep-sea hydrothermal vent. Extremophiles 12:735–739.

Sada, D.W., E. Fleishman, and D.D. Murphy. 2005. Associations among spring-dependent aquatic assemblages and environmental and land use gradients in a Mojave Desert mountain range. Diversity and Distributions 11:91–99.

Samraoui, B., K. Chakri, and F. Samraoui. 2006. Large branchiopods (Branchiopoda: Anostraca, Notostraca and Spinicaudata) from the salt lakes of Algeria. Journal of Limnology 65:83–88.

Sassaman, C., M.A. Simovich, and M. Fugate. 1997. Reproductive isolation and genetic differentiation in North American species of *Triops* (Crustacea: Branchiopoda: Notostraca). Hydrobiologia 359:125–147.

Schlichter, L.C. 1981. Low pH affects the fertilization and development of *Rana pipiens* eggs. Canadian Journal of Zoology 59:1693–1699.

Schwenk, K., D.K. Padilla, G.S. Bakken, and R.J. Full. 2009. Grand challenges in organismal biology. Integrative and Comparative Biology 49:7–14.

Sei, M., B.K. Lang, and D.J. Berg. 2009. Genetic and community similarities are correlated in endemic-rich springs of the northern Chihuahuan Desert. Global Ecology and Biogeography 18:192–201.

Simovich, M.A., and S.A. Hathaway. 1997. Diversified bet-hedging as a reproductive strategy of some ephemeral pool anostracans (Branchiopoda). Journal of Crustacean Biology 17:38–44.

Stanley, E.H., D.L. Buschman, A.J. Boulton, N.B. Grimm, and S.G. Fisher. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. American Midland Naturalist 131:288–300.

Suárez-Morales, E., and T.M. Iliffe. 2007. A new genus of *Ridgewayiidae* (Copepoda: Calanoidea) from a karstic cave of the Western Caribbean. Journal of Crustacean Biology 27:339–350.

Swadling, K.M., and J.A.E. Gibson. 2000. Grazing rates of a calanoid copepod (*Paralabidocera antarctica*) in a continental Antarctic lake. Polar Biology 23:301–308.

Swadling, K.M., P.D. Nichols, J.A.E. Gibson, and D.A. Ritz. 2000. Role of lipid in the life cycles of ice-dependent and ice-independent populations of the copepod *Paralabidocera antarctica*. Marine Ecology Progress Series 208:171–182.

Swadling, K.M., A.D. McKinnon, G. De'ath, and J.A.E. Gibson. 2004. Life cycle plasticity and differential growth and development in marine and lacustrine populations of an Antarctic copepod. Limnology and Oceanography 49:644–655.

Tasch, P. 1987. Fossil Conchostraca of the southern hemisphere and continental drift: paleontology, biostratigraphy, and dispersal. The Geological Society of America, Inc., Boulder, CO.

Thiel, M., and J.E. Duffy. 2007. The behavioral ecology of crustaceans: a primer in taxonomy, morphology, and biology. Pages 3–28 *in* J.E. Duffy and M. Thiel, editors. Evolutionary ecology of social and sexual systems—crustaceans as model organisms. Oxford University Press, New York.

Thiéry, A. 1991. Multispecies coexistence of branchiopods (Anostraca, Notostraca & Spinicaudata) in temporary ponds of Chaouia plain (western Morocco): sympatry or syntopy between usually allopatric species. Hydrobiologia 212:117–136.

Lifestyles and Feeding Biology. Edited By Martin Thiel and Les Watling.

Thomas, P.E., D.W. Blinn, and P. Keim. 1997. Genetic and behavioural divergence among desert spring amphipod populations. Freshwater Biology 38:137–143.

Timms, B.V. 2009. Biodiversity of large branchiopods of Australian saline lakes. Current Science 96:74–80.

Toro, M., A. Camacho, C. Rochera, E. Rico, M. Bañón, E. Fernández-Valiente, E. Marco, A. Justel, M.C. Avendaño, Y. Ariosa, W.F. Vincent, and A. Quesada. 2007. Limnological characteristics of the freshwater ecosystems of Byers Peninsula, Livingston Island, in maritime Antarctica. Polar Biology 30:635–649.

Tranvik, L.J., and L.-A. Hansson. 1997. Predator regulation of aquatic microbial abundance in simple food webs of sub-Antarctic lakes. Oikos 79:347–356.

van de Graff, W.J.E., R.W.A. Crowe, J.A. Bunting, and M.J. Jackson. 1977. Relict early Cainozoic drainages in arid Western Australia. Zeitschrift für Geomorphologie N. F. 21:379–400.

Van Dover, C.L., E.Z. Szuts, S.C. Chamberlain, and J.R. Cann. 1989. A novel eye in eyeless shrimp from hydrothermal vents of the Mid-Atlantic Ridge. Nature 337:458–460.

Varo, I., A.C. Taylor, and F. Amat. 1993. Comparative study of the effects of temperature, salinity and oxygen-tension on the rates of oxygen-consumption of nauplii of different strains of *Artemia*. Marine Biology 117:623–628.

Vincent, W.F., J.E. Hobbie, and J. Laybourn-Parry. 2008. Introduction to the limnology of high-latitude lake and river ecosystems. Pages 1–23 *in* W.F. Vincent, and J. Laybourn-Parry, editors. Polar lakes and rivers—limnology of Arctic and Antarctic aquatic ecosystems. Oxford University Press, Oxford, UK.

Waller, C.L., M.R. Worland, P. Convey, and D K.A. Barnes. 2006. Ecophysiological strategies of Antarctic intertidal invertebrates faced with freezing stress. Polar Biology 29:1077–1083.

Warburg, M.R. 1995. Growth and reproduction in a rare desert isopod: *Porcellio barroisi* (Oniscidea; Porcellionidae) from the Central Negev Mountains. Journal of Arid Environments 31:199–204.

Weber, A.K., and R. Pirow. 2009. Physiological responses of *Daphnia pulex* to acid stress. BMC Physiology 9:9.

Weeks, S.C. 2012. The role of androdioecy and gynodioecy in mediating evolutionary transitions between dioecy and hermaphroditism in the Animalia. Evolution 66:3670–3686.

Weeks, S.C., V. Marcus, and S. Alvarez. 1997. Notes on the life history of the clam shrimp, *Eulimnadia texana*. Hydrobiologia 359:191–197.

Weeks, S.C., V. Marcus, R.L. Salisbury, and D.W. Ott. 2002. Cyst development in the conchostracan shrimp, *Eulimnadia texana* (Crustacea: Spinicaudata). Hydrobiologia 486:289–294.

Weeks, S.C., M. Zofkova, and B. Knott. 2006a. Limnadiid clam shrimp biogeography in Australia (Crustacea: Branchiopoda: Spinicaudata). Journal of the Royal Society of Western Australia 89:155–161.

Weeks, S.C., C. Benvenuto, and S.K. Reed. 2006b. When males and hermaphrodites coexist: a review of androdioecy in animals. Integrative and Comparative Biology 46:449–464.

Weeks, S.C., T.F. Sanderson, S.K. Reed, M. Zofkova, B. Knott, U. Balaraman, G. Pereira, D.M. Senyo, and W.R. Hoeh. 2006c. Ancient androdioecy in the freshwater crustacean *Eulimnadia*. Proceedings of the Royal Society London Biological Sciences B 273:725–734.

Weeks, S.C., T.F. Sanderson, M. Zofkova, and B. Knott. 2008. Breeding systems in the clam shrimp family Limnadiidae (Branchiopoda, Spinicaudata). Invertebrate Biology 127:336–349.

Wellborn, G.A., and R.D. Cothran. 2007. Ecology and evolution of mating behavior in freshwater amphipods. Pages 147–166 *in* J.E. Duffy and M. Thiel, editors. Evolutionary ecology of social and sexual systems—crustaceans as model organisms. Oxford University Press, New York.

Wheatly, M.G., and A.T. Gannon. 1995. Ion regulation in crayfish: freshwater adaptations and the problem of molting. American Zoologist 35:49–59.

White, K.P. 2001. Functional genomics and the study of development, variation and evolution. Nature Reviews Genetics 2:528–537.

Wilhelm, F.M., and M.P. Venarsky. 2009. Variation in gnathopod morphology of cave amphipods and its use in determination of sex. Journal of Crustacean Biology 29:26–33.

Williams, W.D. 1991. Chinese and Mongolian saline lakes—a limnological overview. Hydrobiologia 210:39–66.

Winterbourn, M.J., and K.J. Collier. 1987. Distribution of benthic invertebrates in acid, brown water streams in the South Island of New Zealand. Hydrobiologia 153:277–286.

Withers P.C. 2000. Overview of granite outcrops in Western Australia. Journal of the Royal Society of Western Australia 83:103–108.

Lifestyles and Feeding Biology. Edited By Martin Thiel and Les Watling.

Witt, J.D.S., D.L. Threloff, and P.D.N. Hebert. 2006. DNA barcoding reveals extraordinary cryptic diversity in an amphipod genus: implications for desert spring conservation. Molecular Ecology 15:3073–3082.

Wollmann, K. 2000. Corixidae (Hemiptera, Heteroptera) in acidic mining lakes with pH ≤ 3 in Lusatia, Germany. Hydrobiologia 433:181–183.

Yevdokimov, N.A., and M.V. Yermokhin. 2009. Zooplankton crustaceans of ephemeral waterbodies on the territory of various natural zones in Saratov oblast. Inland Water Biology 2:59–66.

York Main, B. 1997. Granite outcrops: a collective ecosystem. Journal of the Royal Society of Western Australia 80:113–122.

Zakšek, V., B. Sket, S. Gottstein, and D. Frannjević. 2009. The limits of cryptic diversity in groundwater: phylogeography of the cave shrimp *Troglocaris anophthalmus* (Crustacea: Decapoda: Atyidae). Molecular Ecology 18:931–946.

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