

# Chapter 5

## Invertebrates of Freshwater Temporary Ponds in Mediterranean Climates

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### Introduction to Mediterranean Temporary Ponds

#### *Long Known But Neglected Until Recently*

Temporary ponds have long attracted the attention of Mediterranean people. In “History of Animals,” Aristotle described the seemingly spontaneous generation of life from mud or sand using observations from a temporary pond (“fish” probably refers to the aquatic invertebrates, such as fairy shrimp, that he was observing):

*The great majority of fish, then, as has been stated, proceed from eggs. However, there are some fish that proceed from mud and sand, even of those kinds that proceed also from pairing and the egg. This occurs in ponds here and there, and especially in a pond in the neighbourhood of Cnidos. This pond, it is said, at one time ran dry about the rising of the Dogstar, and the mud had all dried up; at the first fall of the rains there was a show of water in the pond, and on the first appearance of the water shoals of tiny fish were found in the pond. [Aristotle (350 BC) Book VI. Chapter 15. In: The History of Animals (translated in 1907 by D’Arcy Wentworth Thompson. London: John Bell)]*

The lack of scientific publications on Mediterranean temporary ponds does not reflect their ecological importance (Grillas et al. 2010), and research in these environments has increased significantly over the last two decades (Boix et al. 2012). The absence of comparative studies on aquatic ecosystems in regions with a Mediterranean-type climate has been reported (Gasith and Resh 1999) and partially addressed for Mediterranean-climate streams and rivers (Bonada and Resh 2013). However, studies have emphasized the importance, abundance, functioning, and biodiversity of Mediterranean temporary ponds in the last several decades (e.g., Balla and Davis 1995; Witham 1998; Diget and Rioux 1998; Blaustein and Schwartz 2001), highlighting the need to develop conservation plans for these systems (Zedler 2003; Grillas et al. 2004; Fraga et al. 2010; Sancho and Lacombe 2010).

## ***Mediterranean Biome: The Five Mediterranean Regions***

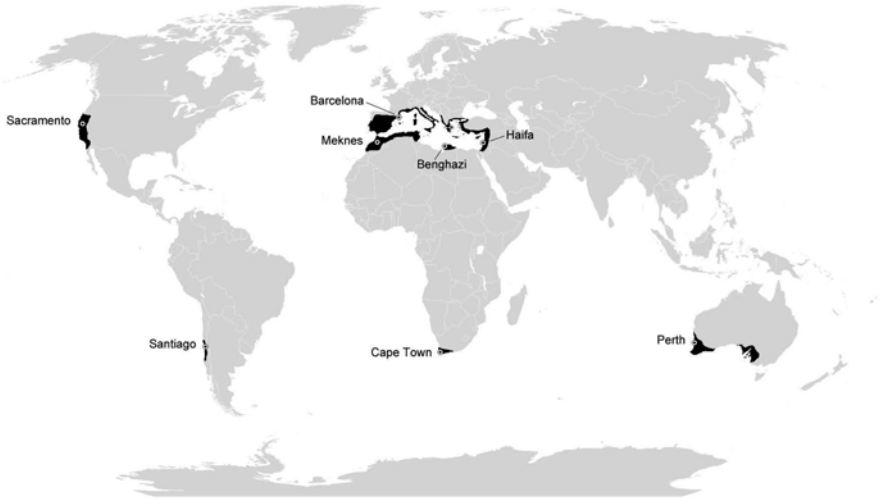
The term “Mediterranean” as a biome is not recognized in the same way as other biomes (e.g., boreal forest, desert, or savannah). Although it is named for a particular geographic region, the term is used to designate regions with a similar climate around the world. Mediterranean climates are typically located in a narrow latitudinal band between 30° and 40°, although in the Mediterranean basin itself the biome expands to 45° (Bolle 2003). This habitat is located on five continents (Eurasia, Africa, South and North America, and Australia), and thus five biogeographic regions (Palearctic, Afrotropic, Neotropic, Nearctic, and Australasian) (Fig. 5.1). The concept of a Mediterranean biome remains controversial (Stamou 1998) because some define the habitat with a definite drought period, while others take into account two features: dry summers and cool winters. However, biogeographic studies have clearly identified Mediterranean forests, woodlands, and scrub, as well as wetlands, since they share similar bioclimatic conditions.

The area covered by the Mediterranean biome is quite small compared to other biomes (Olson et al. 2001). It covers only 5 % of the earth’s surface (Fig. 5.1), and the subregions vary tremendously in size (Underwood et al. 2009). South and North America and South Africa combined are small, roughly 100,000 km<sup>2</sup> each (11 % of the Mediterranean area). The south-western Australian Mediterranean-climate region covers more than 750,000 km<sup>2</sup> (25 % of this biome) divided into two separate areas. However, the biome has its maximum extent (64 % of the total area covered by this biome) around the Mediterranean Sea, from which it takes its name. The Circum-Mediterranean region forms an incomplete belt around the Mediterranean Sea (Fig. 5.1), with the maximum width of this belt located on the Iberian Peninsula.

Temporary water bodies predominate in Mediterranean regions because of their typically long, hot, dry summers. Their widespread occurrence and abundance therefore make temporary habitats the characteristic wetlands of this biome. In this chapter, we use “Mediterranean temporary ponds” in a broad sense, including all the temporary freshwater wetlands located in Mediterranean regions, and not restricted by any legal definition. For example, the European Habitats Directive (European Directive 92/43/CEE) considers “Mediterranean temporary ponds” a priority habitat to conserve, but the Directive defines this wetland type strictly by the presence of particular plant species (European Commission 2003; Bagella et al. 2007). Curiously, this protected habitat is identified in the United Kingdom (McAbendroth 2004), outside of the Mediterranean-climate region.

### ***Climate: Hot Dry Summers and Mild Winters***

Mediterranean climates are transitional between temperate and tropical climates, hence their prevalence between 30° and 40° of latitude (Aschman 1973; Daget 1984). The climate can be summarized as follows:



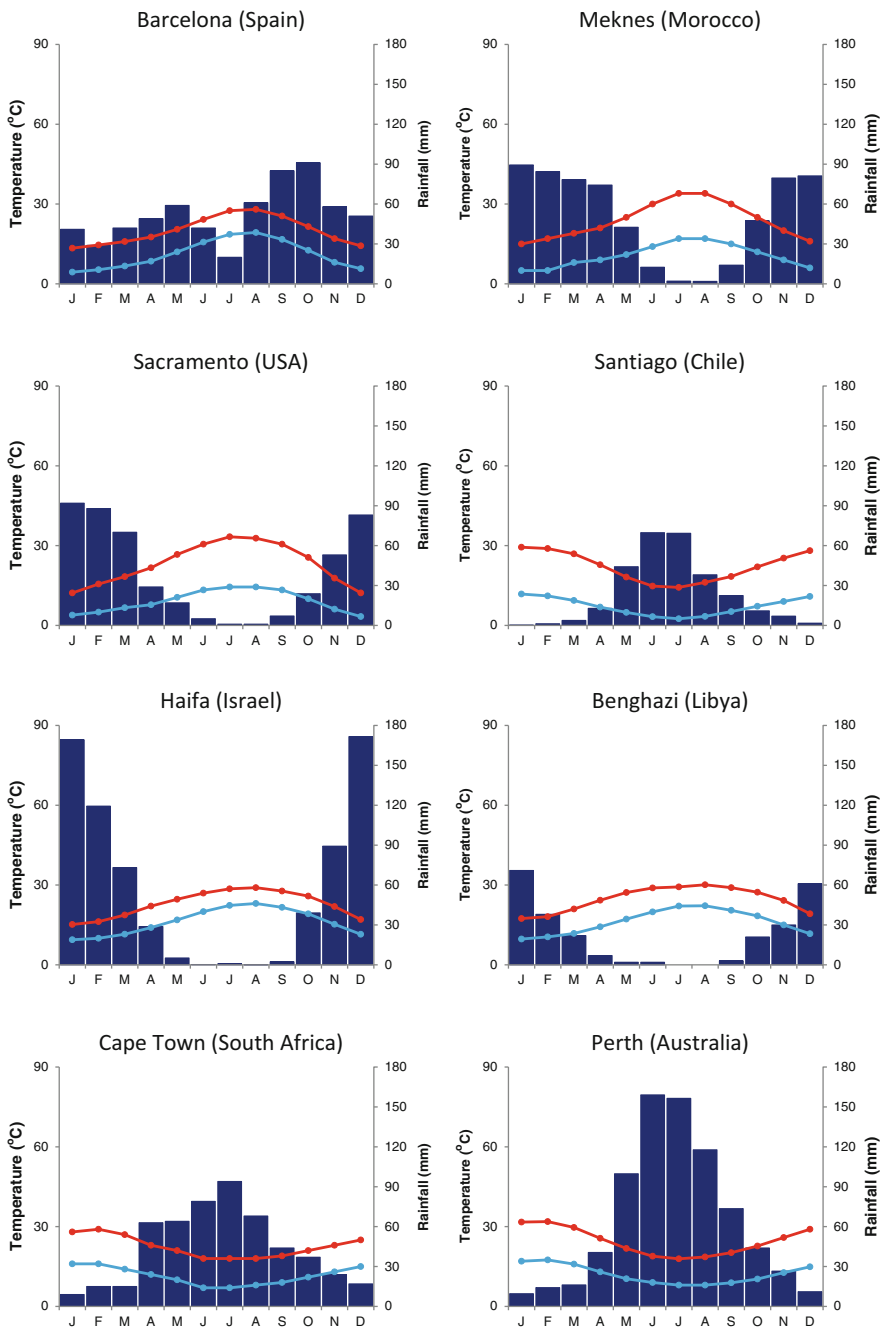
**Fig. 5.1** World map showing the location of Mediterranean-climate regions. The sites indicated on the map correspond to the ombrothermic diagrams shown in Fig. 5.2

1. Hot summers which coincide with the dry period
2. Mild, but cool winters
3. High temporal variability (i.e., high intra- and inter-annual differences)

These characteristics determine the hydrology and ecological functioning of the wetlands. The combination of dry weather and high temperatures causes large water-level fluctuations (Álvarez-Cobelas et al. 2005; Beklioglu et al. 2007) and thereby regulates the presence of temporary waters in Mediterranean areas. The mild winters mean that most Mediterranean wetlands remain ice-free (Britton and Crivelli 1993). Freezing of wetlands affects both limnological processes (e.g., thermal or oxygen vertical gradients in the water column) and the availability of habitat and resources for the biota. This particular combination of annual drying and the absence of freezing typify Mediterranean wetlands and distinguish them from wetlands in most other biomes. Moreover, high inter-annual climate variability is also characteristic of Mediterranean regions (Gasith and Resh 1999) (Fig. 5.2).

Despite the narrow latitudinal range and small area of Mediterranean regions, extreme gradients of aridity (i.e., duration of the dry period) and temperature exist (Bolle 2003) (Fig. 5.2). Those gradients have been used to distinguish various climate types and are used to classify Mediterranean climates (Stamou 1998):

1. Duration of the dry period
  - (a) Perarid: 11–12 months
  - (b) Arid: 9–10 months



**Fig. 5.2** Ombrothermic diagrams for eight locations in Mediterranean-climate regions. *Upper* diagrams correspond to sites in the Mediterranean Basin and *lower* diagrams correspond to sites located in other Mediterranean regions. Monthly mean maximum (red line) and minimum (blue line) temperature, and monthly mean rainfall (bars) were shown. The high intra-annual variability characteristic of mediterranean climates is evident, as well as variability among and within regions (i.e., Mediterranean Basin)

- (c) Semiarid: 7–8 months
- (d) Subhumid: 5–6 months
- (e) Humid: 3–4 months
- (f) Perhumid: 1–2 months

2. Mean temperature of the coldest month

- (a) Warm winter: more than 7 °C (no periods of freezing)
- (b) Mild winter: between 3 and 7 °C (freezing is rare)
- (c) Cold winter: between 0 and 3 °C (freezing is frequent)
- (d) Severe winter: less than 0 °C (freezing may be extensive)

Division of Mediterranean climates into subclasses using a numerical approach has been proposed by Nahal (1981). The use of Ebergers' index of drought ( $Q$ ) is the most widely accepted approach:

$$Q = \frac{2P}{(M + m)(M - m)}$$

where

$P$  is annual rainfall

$M$  the mean maximum temperature of the hottest month

$m$  the mean minimum temperature of the coldest month

Thus, we can distinguish the following subclasses of Mediterranean climate:

1. Arid:  $Q$  values between 20 and 30; annual rainfall between 300 and 500 mm
2. Semiarid:  $Q$  values between 30 and 50; annual rainfall between 500 and 700 mm
3. Subhumid:  $Q$  values between 50 and 90; annual rainfall between 700 and 1000 mm
4. Humid:  $Q$  values more than 90; annual rainfall more than 1000 mm

Mediterranean regions are characterized by an annual precipitation in the range of 275 to 900 mm with over 65% occurring in the 6 colder months (Aschman 1973). However, Mediterranean areas with annual rainfall less than 275 mm do exist (e.g., in Morocco, Spain, and Israel). Two seasonal patterns of precipitation have been described in Mediterranean regions: (1) a single rainfall maximum in winter, and (2) two rainfall maxima, one in spring and the other in autumn. In those Mediterranean regions with strong oceanic influences, winter rainfalls are heavy due to storms moving from high latitudes towards the equator (e.g., southern Australia). In contrast, in areas with less oceanic influence (e.g., coast of the western Mediterranean basin), the storms are weaker, so winter rains are meagre, while spring and autumn rains that are generated by cold air masses are more important to hydrology (Ferrés 1993).

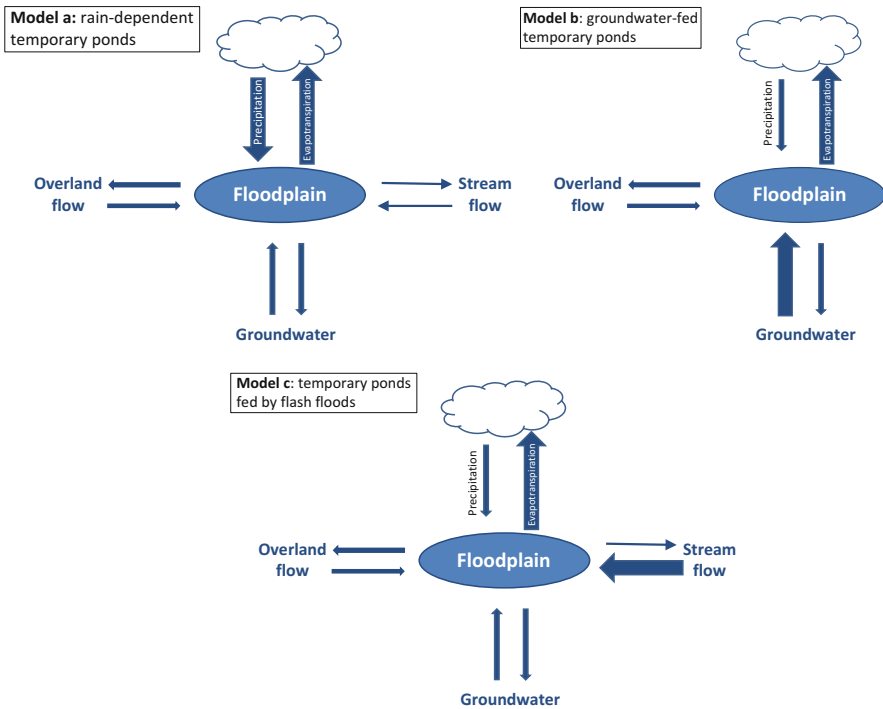
## Hydrology

Mediterranean temporary wetlands are usually flooded by rainfall and evaporation is the primary mechanism of drying (Fig. 5.3a). However, there are exceptions. Groundwater-fed temporary wetlands (Fig. 5.3b) are abundant in the southern Australia (Sim et al. 2006a; Horwitz et al. 2009; Boulton et al. 2014) and the African Cape (Mlambo et al. 2011; de Moor and Day 2013) Mediterranean regions, and they are present in some areas of the Mediterranean basin (Rodríguez-Rodríguez 2007). Groundwater-fed temporary wetlands are also found in karstic limestone areas (Boix et al. 2001). Temporary pools or riverine-floodplain wetlands resulting from flash floods (ultimately caused by rains), or by springs that vary in output, resulting in areas that flood (sometimes with fossil water), recede and dry (Issar 1990) (Fig. 5.3c).

Although rain and evaporation are the main inputs and outputs, respectively, freshwater temporary ponds rarely accumulate ions in their basins. Runoff of ions (on the surface or via ground water) must therefore occur from these waterbodies. However, athalassic lakes and ponds (saline water isolated from the sea, sensu Williams 1981) occur in endorheic basins of the more arid locations of Mediterranean climates, such as the Iberian Peninsula, North Africa, California, Australia, and South Africa. In these systems, ions accumulate in the basin because water output occurs only by evaporation. Groundwater-dependent wetlands have water levels that rise and fall seasonally as groundwater tables fluctuate and thus moderate concentrations of ions develop as water levels decline.

Several classifications for temporary ponds have been proposed using hydrological patterns. Duration and predictability of the hydroperiod are frequently used criteria (Comín and Williams 1994; Keeley and Zedler 1998; Boulton et al. 2014; Williams 2006). Our proposal, following Boulton et al. (2014), distinguishes five types of temporary lentic waters:

- (a) *Ephemeral*: Filled only after unpredictable rain and by runoff. The flooded area dries out during the days following the flooding and supports low numbers of macroscopic aquatic species.
- (b) *Episodic*: Dries in 9 out of 10 years, with rare and irregular flooding (or wet periods) which may last for a few months.
- (c) *Intermittent*: Alternating wet and dry periods, but a more irregular frequency of filling than seasonal wetlands. Flooding may persist for months or years.
- (d) *Seasonal*: Alternating wet and dry periods annually, in accordance with the season. Usually fill during the wet season of the year, and dry out in a predictable way every year. The flooding lasts for several months, long enough for macroscopic animals and plants to complete their life cycles.
- (e) *Near-permanent*: Predictable flooding, though water levels may vary. The annual input of water is greater than the losses (does not dry out) in 9 out of 10 years. The majority of organisms living here cannot tolerate desiccation.



**Fig. 5.3** Water budget diagram characteristics of Mediterranean temporary ponds. Model (a) represents rain-dependent temporary ponds such as vernal pools; model (b) represents groundwater-fed temporary ponds unconnected to rivers commonly found across southern Australia and Cape Mediterranean region, and also present in karst geologies; and model (c) shows temporary ponds fed by flash-floods (occurring in some countries of the Mediterranean basin (e.g., Israel))

In this chapter we focus on two of these types, intermittent and seasonal, because these are the types most commonly found in Mediterranean regions. However, these categories represent points along a gradient. For example, some waterbodies dry more often than 1 year in 10 (e.g., 1 year in 3). For these types of ponds, the term “semipermanent” (dry but not every year) is commonly used (e.g., Stewart and Kantru 1972; Collinson et al. 1995; Gascón et al. 2005).

## Invertebrate Assemblages of Mediterranean Temporary Ponds

The similar climatic conditions among Mediterranean regions have led to convergent evolution in the flora (Matesanz and Valladares 2014) characterized in part by remarkably high species diversity. However, the regions’ isolation and geologic history have resulted in differences in the aquatic fauna (Bonada et al. 2008). For example, fauna

groups (e.g., aquatic coleopterans) are characterized by very restricted distributions in the Mediterranean basin region, very likely a consequence of two evolutionary processes: (1) the Mediterranean basin as a refugium during the glacial maxima and (2) the Mediterranean as an area of endemism during isolation in the glacial cycles (Hewitt 2000; Ribera et al. 2003). Similarly, the south-western Australian Mediterranean-climate region has been isolated by surrounding arid zones for millennia, and as a result of this isolation is depauperate in some aquatic fauna, such as stoneflies (Davies and Stewart 2013). Therefore, Mediterranean temporary ponds are characterized by a unique combination of isolation and connectedness at different spatial scales, which can result in the evolution of endemic species (Zedler 2003).

Appendix 1 provides a list of the families of aquatic invertebrates reported from the five Mediterranean regions. The list is geographically and taxonomically biased due to different research efforts among regions and taxonomic groups. The data were obtained in an extensive review of the literature and complemented by unpublished data of the authors (see Appendix 1 for references). Biodiversity (number of genera) in Mediterranean temporary ponds is dominated by arthropods: primarily insects and secondarily crustaceans (Appendix 1). In the case of insects, two families have the highest biodiversity in all Mediterranean regions: Dytiscidae (Coleoptera) and Chironomidae (Diptera). Another six insect families possess at least ten genera (in decreasing order of genera richness): Hydrophilidae, Corixidae, Libellulidae, Ceratopogonidae, Coenagrionidae, and Hydraenidae. Similarly, two families of crustaceans have the highest biodiversity in all Mediterranean regions: Chydoridae (Branchiopoda) and Cyprididae (Ostracoda). These two families are followed by two copepod families: Cyclopidae and Diaptomidae. For non-arthropods, two other families have high genera richness: typhloplanid turbellarians and planorbid gastropods. This pattern of richness among taxonomic groups is in accordance with published comparisons among temporary ponds around the world, regardless of the climate region (e.g., Boix et al. 2001; Boix and Sala 2002; Williams 2006).

### ***Large Branchiopods: Flagship Invertebrate Species of Mediterranean Temporary Ponds***

Large branchiopods are a group of crustaceans that almost exclusively inhabit temporary ponds (Hartland-Rowe 1972) and they have a worldwide distribution (Brendonck et al. 2008). In the Mediterranean they are often considered a flagship group of invertebrates for temporary ponds (Belk 1998; Thiéry 2004) and they are promoted to monitoring ecological status of temporary ponds, since they are very sensitive to habitat and landscape degradation (Gascón et al. 2012; van den Broeck et al. 2015a, b). Appendix 2 provides a list (and references) for the large branchiopod species present in Mediterranean ponds to show the high species richness of this group and the high level of endemism. We only included species specifically observed in the temporary ponds located in the Mediterranean biome, below 1500 m.a.s.l., and in fresh water. Species present in the Mediterranean basin but only



located at high altitude (e.g., *Chirocephalus algidus*, *C. marchesonii*, *C. ruffoi*, *C. sibyllae* or *C. tauricus*; Cottarelli and Mura 1983; Cottarelli et al. 2010) were not included, nor were saline species (the genus *Parartemia* in Australia has up to 15 species in Australian Mediterranean regions, 11 of them being endemic: Timms 2014 and references therein). Some early-described species are not included in the Appendix because our existing knowledge consists only of very old records, and taxonomic revision is probably needed; this is especially true for the Spinicaudata (Hartland-Rowe 1967; Thiéry 1996) and for some Anostraca of the Mediterranean basin area (such as *Chirocephalus recticornis* and *Chirocephalus festae*; Brauer 1877; Colosi 1922). Only species that appear in the scientific literature during the second half of the twentieth century have therefore been included.

Large branchiopods are known in four of the five Mediterranean regions (no species have been identified from the South American Mediterranean region) and their species richness is high (Appendix 2). The degree of endemism is also quite high, except in South Africa, where only a single endemic species has been recorded. The proportion of endemic species is 55 %, 46 %, and 45 % in the Mediterranean basin, southern Australia, and North America, respectively. At generic level, the anostracan *Linderiella* (California and Mediterranean basin) and the spinicaudatan *Maghrebetheria* (Mediterranean basin) can be considered as endemic to the Mediterranean regions. Some genera have broad distributions across several Mediterranean regions, although endemic species within these genera occur. They represent an example of faunal complexes persisting over millennia with locally adapted endemic species (Keeley and Zedler 1998). This is especially evident in the Notostraca (e.g., *Triops*), Spinicaudata (e.g., *Cyzicus*, *Eulimnadia*), and Laevicaudata (e.g., *Lynceus*), although it also occurs in some anostracan genera (e.g., *Streptocephalus*, *Branchinecta*). It is interesting to note that some genera are highly speciose in a particular Mediterranean region, such as *Streptocephalus* and *Branchipodopsis* in South Africa, *Branchinecta* in North America, *Branchinella*, *Eulimnadia*, and *Limnadopsis* in southern Australia, and *Chirocephalus*, *Tanymastigites* and *Triops* in the Mediterranean basin.

## **Dynamics of Invertebrate Assemblages of Mediterranean Temporary Ponds**

### ***Key Environmental Factors***

Hydroperiod is an important factor determining the faunal composition and structure of Mediterranean temporary ponds (e.g., Boix et al. 2004; Ripley and Simovich 2009; Sim et al. 2013; Kneitel 2014). However, pond size is also considered a determinant factor (e.g., Ebert and Balko 1987; March and Bass 1995; Meintjes 1996; Spencer et al. 1999). Indirect effects of pond size on community structure (i.e., larger ponds have different environmental characteristics than smaller ones) seems to be weak in temporary Mediterranean ponds (Ballón et al. [in press](#)). The effects of both hydroregime and habitat size depend on the dispersal modes of the taxa.

Hydroregime has been found to be more important for passive dispersers than for active dispersers (Vanschoenwinkel et al. 2009), for instance, and interactions between inundation length and timing can differentially affect dispersal modes (Kneitel 2014). Further, nested community patterns have been observed in Mediterranean temporary ponds and found to be most associated with environmental variation (hydroperiod and pond size), but the presence of species with poor dispersal abilities can also increase nestedness (Ripley and Simovich 2009; Florencio et al. 2011).

Water quality has also been related to community structure, although it shows an inconsistent pattern over invertebrate successional phases. Water quality fluctuations probably coincide with changes in invertebrate assemblages, rather than causing them (Barclay 1966; Meintjes 1996). The main physical and chemical variables related to species richness and community composition in Mediterranean temporary ponds are salinity (Boix et al. 2008; Waterkeyn et al. 2009; Mlambo et al. 2009), turbidity (Alonso 1998; Mlambo et al. 2009; Ruhí et al. 2014), light (Mokany et al. 2008) and nutrient concentration (Balla and Davis 1995; Mlambo et al. 2009). Although local pond characteristics, and intra- and inter-annual variability are of greater importance than biological factors for shaping the physical and chemical characteristics of temporary ponds, bottom-up and top-down trophic effects are also influential (e.g., Magnusson and Williams 2006), but few studies have specifically addressed this topic in Mediterranean temporary ponds (but see Balla and Davis 1995; Waterkeyn et al. 2013).

## *Seasonal Succession*

### **Successional Phases**

Change in community composition during inundation was the focus of early studies in temperate temporary ponds of the northern hemisphere (e.g., Murray 1911; Mozley 1932; Kenk 1949). These pioneering studies built a general conceptual model, which described the seasonal succession of invertebrate communities. This model has subsequently been improved and/or validated in studies in temperate regions of the southern hemisphere (Barclay 1966; Lake et al. 1989) and in more arid zones with short hydroperiods (e.g., Rzóska 1961; Meintjes 1996; Lahr et al. 1999).

Kenk (1949) identified several different community structures during the hydroperiod of temporary ponds in cool-temperate Michigan (USA) and described them as “stages or phases.” Two aquatic phases were described based on water temperature and season: the cold-water and the spring phase. In the southern hemisphere, in New Zealand, Barclay (1966) also observed similar time periods with distinguishable temporary pond communities (autumn-winter stage and spring-early summer stage), but described a third phase during drying (dry stage). Lake et al. (1989) constructed a three-phase conceptual model in which phases were called: “filling,” “middle or aquatic” and “drying.” The com-

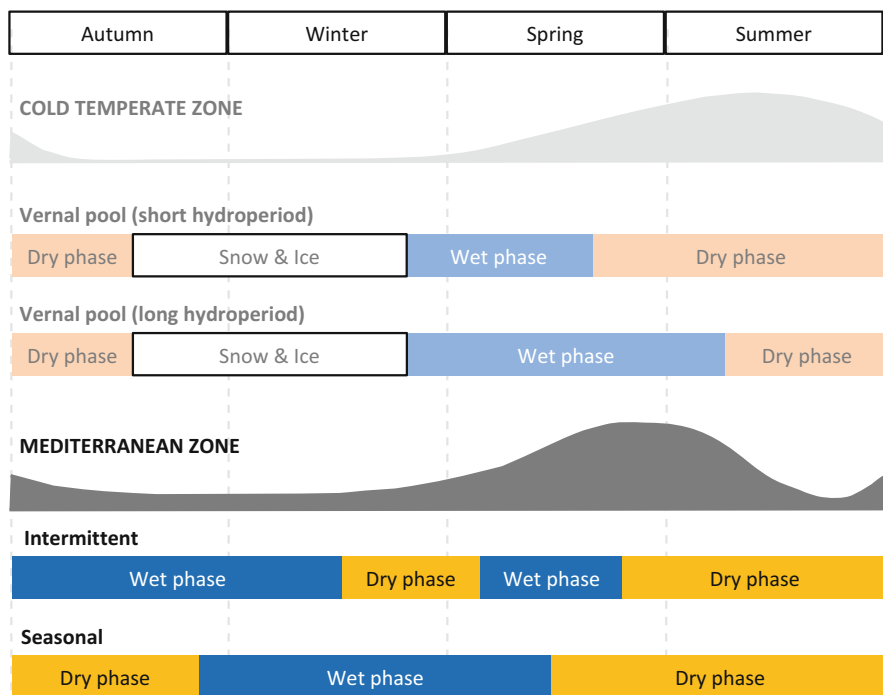
munity dynamics of filling and drying phases represent allogenic succession driven by environmental processes. During flooding, resources become abundant, and biotic interactions have limited effect on community composition. During drying, environmental variables change dramatically (e.g., temperature increases, dissolved oxygen fluctuates), and although higher faunal densities intensify biotic interactions, changes in community composition are again mostly driven by environmental conditions. However, the succession observed between these two phases is autogenic, that is, the result of biological processes (i.e., predation and competition). Case studies of faunal community succession in Mediterranean basin ponds are consistent with the three-phase model (Bazzanti et al. 1996; Boix et al. 2004; Florencio et al. 2009; Sahuquillo and Miracle 2010). Additionally, comparisons among the same phases of different hydroperiods suggest that secondary changes in community composition related to season exist in Mediterranean temporary ponds (Yaron 1964; Boix et al. 2004; Culioli et al. 2006). In these studies, invertebrate species compositions for the three successional phases were identified, but species were also identified that only appeared in spring or in autumn-winter hydroperiods. Similarly, in a temporary wetland in the south-western Australian Mediterranean region, Strachan et al. (2014) observed three distinct phases of invertebrate community structure during the process of wetland drying and reflooding, with an almost complete turnover of species between hydrologically defined phases (damp phase, sediment damp but surface water absent; dry phase, groundwater at its lowest level and sediment surface dry; reflooded phase, surface water had returned). These results suggest that groundwater-fed Mediterranean temporary ponds are likely to show very large shifts in community composition over short time periods driven by the marked hydrological changes that occur there.

The study of temporal changes in community structure based on body size is complementary, rather than a replacement for the taxonomic approach (Rodríguez and Magnan 1993). Successional analyses based on taxonomic or functional approaches clearly show temporal changes in the community related to different life-history strategies of the organisms, such as dispersal or resistance to drought (Kenk 1949; Wiggins et al. 1980). In contrast, succession analyses based on body size emphasize the temporal changes in the community related to trophic structure (Quintana et al. 2015). In Mediterranean temporary ponds, differences in biomass-size spectra were observed during succession, while permanent ponds remained more static (Solimini et al. 2005). Size-based approaches have also been used to identify successional phases (Boix et al. 2004).

### **Mediterranean Versus Cold-Temperate Regions**

Although temporary ponds are very important in arid and semiarid areas, such as Mediterranean-climate regions, most ecological knowledge, and the resulting paradigms are biased by studies developed in cold-temperate areas. The general successional models for temporary pond communities may be valid for

Mediterranean ponds, but important distinctions must be recognized. First, in contrast with the mild winters in Mediterranean region, ponds in cold-temperate regions freeze and become snow-covered in winter (e.g., Kenk 1949; Wiggins et al. 1980; Boix et al. 2011) (Fig. 5.4). Consequently, these colder temperate regions may have lower densities of invertebrates and decreases in certain faunal activities, such as aerial dispersal, when compared to Mediterranean temporary ponds (see Ruhí et al. 2012 for an example in created wetlands). Second, the life-history traits and distribution of species differ in cold-temperate and Mediterranean regions (Ruhí et al. 2013a). Species in Mediterranean regions tend to have narrower thermal tolerances and allocate more to reproduction and resistance than species found in colder habitats (Ruhí et al. 2012). Third, precipitation, and hence hydroperiod, is more variable in Mediterranean ponds: annual rainfall vary markedly in some regions across years, and a deviation of 30 % or more from a long-term average is not uncommon (Gasith and Resh 1999; Florencio et al. 2009; Sahuquillo and Miracle 2010; Chester and Robson 2011). Moreover, this inter- and intra-annual variability can result in



**Fig. 5.4** Schematic diagram of temporary pond hydroperiods in cold-temperate and some Mediterranean regions (duration of wet phases can be different depending on the geographical or inter-annual variability of each site). Shaded area indicates favorable environmental conditions for aerial colonizers. In cold-temperate regions, an increase in hydroperiod length implies an increasing number of days with good environmental conditions for aerial dispersers, but this is not the case in all Mediterranean regions

basins flooding in autumn, winter, spring, and occasionally in summer, and ponds can also dry in different seasons, sometimes remaining dry for consecutive years (Fig. 5.4). In contrast, many vernal and autumnal temporary ponds in cold-temperate regions follow a more consistent seasonal pattern, both drying in summer and flooding in spring or autumn, respectively (Wiggins et al. 1980).

### Trait-Based Groups During Succession

In cold-temperate temporary ponds, community structure exhibits consistent temporal patterns of functional-feeding groups. Initially, filtering collectors, gathering collectors, and shredders dominate followed by increasing predator densities with increasing hydroperiod (Wiggins et al. 1980; Williams 1983). The majority of predator species cannot persist in the temporary pond during the dry phase. Moreover, predation pressure tends to increase with increasing hydroperiod length (Schneider and Frost 1996). These patterns are commonly associated with changes in resource availability (Wiggins et al. 1980) and the hydrological limitations imposed on certain functional-feeding and life-history groups (Schneider and Frost 1996; Higgins and Merritt 1999). There are similarities between cold-temperate and Mediterranean temporary ponds, but there are many differences.

Temporal patterns of invertebrate composition in temporary Mediterranean ponds can be explained by life-history strategies (Wiggins et al. 1980; see also Chap. 1). Passive dispersers that are desiccation-resistant often dominate at the beginning of the hydroperiod, whereas taxa that are non-desiccation-resistant active dispersers may dominate in both the beginning and in the final stages of the hydroperiod (Culioli et al. 2006; Boix et al. 2009). The dominance of detritivores at the beginning and of predators at the end of the hydroperiod has been observed in many Mediterranean and arid ponds (Lahr et al. 1999; Culioli et al. 2006), although this pattern is not ubiquitous (Bazzanti et al. 1996; Spencer et al. 1999; Boix et al. 2004). Other sequences have been observed, including the dominance of desiccation-resistant taxa at both the beginning (aerially colonizing insects) and in the middle (passive-colonizers) of the hydroperiod (Bazzanti et al. 1996). An absence of a pattern resulting in similar proportions among all life-history groups can also develop (Sim et al. 2013). Predators can be present at the beginning of the hydroperiod after mild winters, or the dominant predators can emerge from pond sediment rather than via flight (i.e., they have drought-resistant stages). For example, when Mediterranean temporary ponds fill in winter, heteropterans (mainly Corixidae) colonize quickly (e.g., Bazzanti et al. 1996; Boix et al. 2001; Florencio et al. 2009). Additionally, it is known communities in which the main predators, such as the notostracan *Triops cancriformis* and the coleopteran *Agabus nebulosus*, are desiccation-resistant and become active during initial flooding (Boix et al. 2006). In these communities the highest predation pressure occurred 20–25 days after flooding with no increase over the rest of the hydroperiod.

High inter-annual variability of hydroperiod length in Mediterranean ponds causes variability in life-history groups (Boix et al. 2009; Sim et al. 2013; Kneitel

2014). Sim et al. (2013) proposed a conceptual model of the relationships between hydroperiod length, proportions of the different life-history groups, and the dominant recolonization strategy (dispersal or egg-bank hatching). The model showed how hydroperiod variability could interact with life-history traits that result in community structural differences (see also Chap. 1). One persistent limitation to progress in understanding these dynamics is the lack of life-history information for many freshwater invertebrates (Robson et al. 2011). Recent studies show that invertebrates might be capable of adapting to variable hydroperiods in ways not previously understood (e.g., Strachan et al. 2015).

### ***Dry Period: Drought Resistance and Dispersal***

Drought-tolerance, microrefuges, or high dispersal capacity allow aquatic animals of temporary ponds to survive dry periods. Colonization from other wetlands and persistence in a wetland are not mutually exclusive strategies for some invertebrate taxa (Anderson and Smith 2004). The dry period is considered a constraint for the aquatic fauna, causing lower taxa richness in temporary than in permanent ponds. Studies (e.g., Wiggins et al. 1980; Williams 1996; Boulton et al. 2014; Strachan et al. 2015) have shown, however, that a wide variety of invertebrate groups are adapted to desiccation. For this reason, some authors consider desiccation a mythical constraint rather than a strong ecological filter (Biggs et al. 1994). Although some evidence shows higher species richness in permanent ponds (Della Bella et al. 2005; but see Boix et al. 2008), this may be caused by single sampling events underestimating species richness in temporary wetlands with high temporal turnover in species (Robson and Clay 2005). However, the duration and the predictability of the dry period implies a selection of the fauna, since resistance to desiccation by some groups is related to the duration of the dry period and the existence of suitable refuges (Strachan et al. 2014, 2015). For example, in a temporary pond located in the NE of the Iberian Peninsula, three abundant pioneering macroinvertebrates (*Physa acuta*, *Galba truncatula*, and *Berosus signaticollis*) were always present during previous hydroperiods (dry period length between hydroperiods was less than 6 months), but became absent after the pond was dry for more than 2 years (Boix et al. 2001). Freshwater gastropods can survive short-term exposure to air (Havel et al. 2014), resting in microrefuges such as surface depressions of temporary ponds during the dry period, and some species can also aestivate in the sediment (Strachan et al. 2014). Beetles of the genus *Berosus* rest in the sediment during the metamorphosis from larval instar III to imago while waiting for the pond to reflood (Thiéry 1979; Barbero et al. 1982). Although crustacean eggs may be viable in sediment for long periods (300 years in some copepods; Hairston et al. 1995), surviving numbers decline over time (Jenkins and Boulton 2007). Besides drying stress, aestivating crustacean eggs can be consumed by predators (Waterkeyn et al. 2011a).

Studies of egg-bank dynamics in Mediterranean temporary ponds are scarce (but see Mura 2004), but the presence of species in ponds has been related to their

optimal water temperatures (Nourisson and Aguesse 1961; Waterkeyn et al. 2009). Temperature not only determines the presence of species, but can also determine the presence of different clones, as in the case of the ostracod *Heterocypris incongruens* (Rossi and Menozzi 1990). In laboratory experiments, photoperiod variation can produce clones with different life-history traits (Rossi and Menozzi 1993). In fact, both photoperiod and temperature have been identified as cues for diapause in several species of crustaceans and insects (e.g., Sawchyn and Church 1973; Otero et al. 1998). Temporal hatching patterns, whether bet-hedging or synchronous, can vary for invertebrates. Some crustacean species use bet-hedging in more unstable, temporary habitats, and use synchronous hatching in the more stable places (Simovich and Hathaway 1997; Waterkeyn et al. 2013). Other factors playing a role in the hatching process include salinity (Waterkeyn et al. 2009), light (Pinceel et al. 2013), and predation (Spencer and Blaustein 2001), among others.

Different temporal patterns should be expected among groups that differ in dispersal abilities, such as active vs. passive dispersers, aerial vs. terrestrial dispersers, or large- vs. small-bodied organisms (Bilton et al. 2001; De Bie et al. 2012; Ruhf et al. 2013b). For example, large-bodied species are more dispersal-limited if they are passive dispersers, whereas the opposite is true for active dispersers (De Bie et al. 2012). Small organisms producing resting stages have not been considered dispersal-limited, under the so-called *cosmopolitan paradigm*, but the generality of this paradigm is currently being debated (Incagnone et al. 2015 and references therein). Several vectors for passive dispersers have been described, each acting at different spatial scales: wind (Parekh et al. 2014), insects (Van de Meutter et al. 2008), amphibians (Bohonak and Whiteman 1999), fishes (Beladjal et al. 2007), birds (Frisch et al. 2007), and mammals (Vanschoenwinkel et al. 2008) including human (Valls et al. [in press](#)). With animal dispersal, eggs can be transported externally, but there are also cases of dispersal following ingestion and defecation (Bohonak and Whiteman 1999). Different dispersal abilities among active dispersers interact with local and regional factors resulting in different spatiotemporal diversity patterns (Miguel-Chinchilla et al. 2014). Insect flight may be influenced by atmospheric conditions (mainly air temperature, wind speed, air humidity; Boix et al. 2011 and references therein) as well as landscape type, habitat conditions, and biological interactions, such as predation and competition. These factors may also act as cues for the initiation of colonization flights (e.g., Velasco and Millán 1998; Pajunen and Pajunen 2003; Yee et al. 2009), or may be important to insects in their selection of a suitable habitat (Blaustein et al. 2004).

### ***Predation, Competition, and Trophic Webs***

Along the hydroperiod gradient, the importance of abiotic and biotic factors both change. In the schematic model proposed by Wellborn et al. (1996), ephemeral habitats were considered as refuges against predation, while increased hydroperiod length led to increased predation pressure. In contrast, permanent wetland

invertebrates were viewed as being under higher predation pressure, mainly by fish. This model is widely accepted, but it also generates misunderstandings. First, it is incorrect to assume that predation is absent in temporary ponds, even in those ponds with short hydroperiod length (e.g., Blaustein 1998; Brendonck et al. 2002; Boix et al. 2006; Strachan et al. 2014). Second, in Mediterranean temporary waters, longer hydroperiods are not always associated with the highest predation pressure (Spencer et al. 1999). Wetlands with short spring hydroperiods can show stronger effects of insect predation than wetlands with long autumn-winter hydroperiods (Fig. 5.4). Third, autogenic changes at community level (as described in the Seasonal Succession section) are caused, at least in part, by predation (Higgins and Merrit 1999; Boix et al. 2006). Fourth, indirect effects of predation were also reported in these habitats; for example, bioturbation created by *Triops* negatively affected microcrustaceans by impeding filtering capacities (Waterkeyn et al. 2011a) and altering water physico-chemistry (Croel and Kneitel 2011). Therefore, predation is particularly important in structuring communities in temporary waters because the inhabitants typically lack defences against predation (Wilcox 2001; Petrussek et al. 2009), and the abundance of predaceous insects can be very high in short-duration habitats (Batzler and Wissinger 1996).

From an evolutionary point of view, temporary ponds have been considered faunal refuges from predation (Kerfoot and Lynch 1987). The reduction of the global distribution of branchiopods and the rise of cladocerans (small-sized species) coincided with the increase in fish predation during the Mesozoic. Large branchiopods now almost exclusively inhabit temporary (fish-free) waters (Kerfoot and Lynch 1987). However, some defences against predators, which are exclusive of temporary waters (i.e., *Triops cancriformis*), have been observed in the invertebrate fauna. Morphological changes that increase prey survival (i.e., formation of heart-shaped lobes armed by long spines in the head shield, increased tail spine length, increased body lengths and widths) have been observed in individuals of *Daphnia* spp. when those individuals were incubated with chemical cues released by predatory tadpole shrimp (Petrussek et al. 2009; Rabus et al. 2012).

Other ways of avoiding or reducing the risk of predation also exist. For example, some diel patterns observed in zooplankton species of Mediterranean temporary ponds can be interpreted as adaptations to the effects of predators (Compte et al. [in press](#)). In non-Mediterranean fishless ponds, predatory invertebrates that inhabit temporary ponds generate diel responses in zooplankton prey (Neill 1990; Gilbert and Hampton 2001; Trochine et al. 2009). In these studies, the diel pattern varied markedly among zooplankton-prey species, but examples also exist showing that zooplankton diel patterns cannot be explained by predation (Arranz et al. 2015). Other adaptations that reduce exposure to predators also exist in Mediterranean temporary ponds. For example, some culicid (mosquito) females avoid ovipositing in pools that contain predators (Blaustein et al. 2004). Although the cue for oviposition avoidance is generally chemical (Blaustein et al. 2004; Silberbush et al. 2010) mosquitoes appear to use other cues for detecting predators (odonates; Stav et al. 2000), or may not avoid certain kinds of predators (urodeles) when ovipositing (Blaustein et al. 2014).



Predation can also have population-level effects. *Triops*, potentially a keystone predator, may selectively prey upon particular sizes or sexes of prey. Populations of *Daphnia magna* and the mayfly *Callibaetis californicus* exposed to *Triops* predation were size-biased, and characterized by preying on a high proportion of larger individuals (Walton et al. 1991; Rabus et al. 2012). In another study, *Triops* targeted male copepods (*Megacyclops viridis*) (Boix et al. 2006). The role of predation in temporary ponds may therefore be important for population-level, as well as community, dynamics.

Unlike predation, only a few studies have addressed competition in Mediterranean temporary ponds. One interesting feature of these studies is the important effect of predation interacting indirectly with competition through: (1) keystone predation (sensu Paine 1969); and (2) intraguild predation. The most competitively dominant cladoceran genus, *Daphnia*, is also the preferred prey of *Notonecta maculata* (Eitam and Blaustein 2010), so densities of less competitive and smaller cladocerans increase with increasing predator abundance. Consequently species diversity increases, as is typical of keystone predation. Two examples of intraguild predation have been reported: mosquito versus toad competition in a temporary pool in Israel (Blaustein and Margalit 1994), and fairy shrimps versus microcrustaceans in French and Spanish temporary ponds (Sánchez and Angeler 2007; Waterkeyn et al. 2011b). Mosquito larvae (*Culiseta longiareolata*) and toad tadpoles (*Bufo variegatus*) compete for periphyton food, but late-stage *Culiseta* larvae also prey on *Bufo* hatchlings. Fairy shrimps compete with and potentially also prey on microcrustaceans.

Analyses of food web structure and top-down and bottom-up dynamics are rare in temporary ponds, and the few existing examples are from studies performed outside the Mediterranean biome (Magnusson and Williams 2009; Schriever and Williams 2013; O'Neill and Thorp 2014). These studies illustrate, however, that (1) food-chains are short (average of 3.3 trophic levels, range of 1.7–4.6) regardless of pond size (Schriever and Williams 2013); (2) food-chain length increases as temporary waterbodies approach the end of the hydroperiod (O'Neill and Thorp 2014); and (3) strong top-down effects generated by insect predators (Odonata and Coleoptera) have been observed, regulating the abundance of dipterans and zooplankton with the effects propagating downwards through the food web to lower trophic levels (i.e., trophic cascades; Magnusson and Williams 2009). Short food-chains and trophic cascades have been also observed in temporary brackish waters in coastal Mediterranean ponds (Compte et al. 2012).

## Conservation and Management of Mediterranean Temporary Ponds

From a global perspective, conservation of temporary aquatic environments is precarious, because historically they have been neglected. For example, degradation and disappearance of temporary wetlands and streams progressed continuously during the last century (Holland et al. 1995; Brown 1998), in part due to the negative

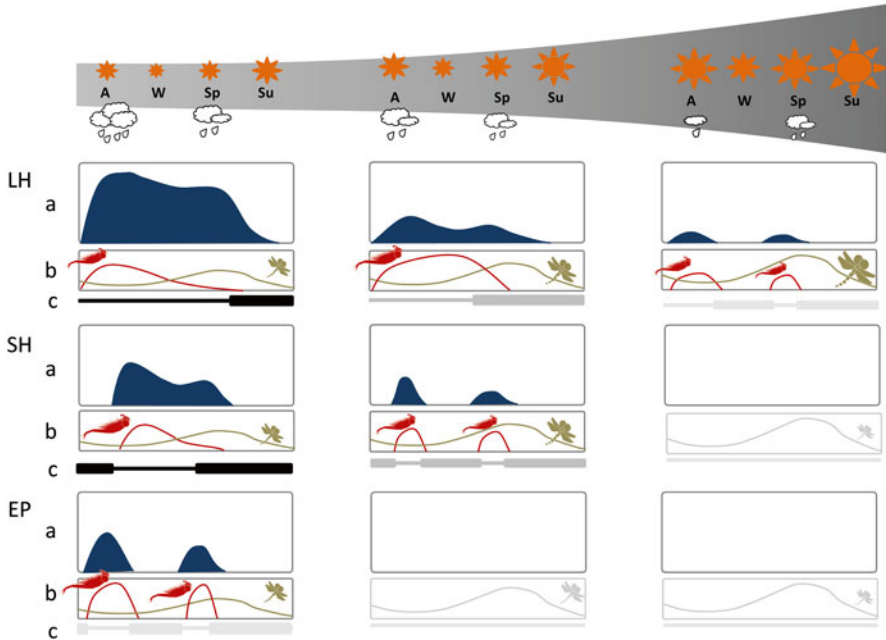
effects of both intensive (Euliss and Mushet 1999; Barry and Davies 2004; Underwood et al. 2009) and expansive (Robson and Clay 2005; Sim et al. 2006a, b) agricultural practices. Temporary ponds in the Mediterranean basin that were compatible with agricultural activity for thousands of years (Grillas et al. 2004) are now clearly negatively affected by current intensive agriculture (Beja and Alcazar 2003; Parra et al. 2005) as they are in other Mediterranean regions (e.g., southern Australia: Robson and Clay 2005; Sim et al. 2006a, b). Remote sensing and historical comparison studies performed in several Mediterranean regions (e.g., De Roeck et al. 2008; Levin et al. 2009; Gómez-Rodríguez et al. 2010; Rhazi et al. 2012; Tulbure et al. 2014) reveal degradation (i.e., reduced hydroperiod due to human activities) and drastic reduction in the number of temporary ponds. The shallowness and the small size of many Mediterranean temporary ponds have made them very vulnerable to human impacts: they can easily be drained for agriculture, urbanization, tourism, or industrial purposes (Grillas et al. 2004; Zacharias et al. 2007). In other cases, temporary waterbodies have been converted to permanent ones for waste disposal, water storage, or (perceived) aesthetics (e.g., Davis et al. 2001). Thus, Mediterranean temporary ponds are endangered habitats, and consequently the scientific community has emphasized the need to reverse the situation (Giudicelli and Thiéry 1998; Boix et al. 2001; Horwitz et al. 2009; Díaz-Paniagua et al. 2010; Zacharias and Zamparas 2010), so as to restore and preserve these unique and valuable environments.

Negative impacts continue despite the existence of preservation initiatives for Mediterranean temporary ponds and their species (e.g., Europe, European Habitat Directive 92/43/CEE; US Federal Register 2003; but see Zedler 2003). The great value of the flora of Mediterranean temporary aquatic environments has been widely reported (e.g., Holland and Jain 1981; Boutin et al. 1982; Ferchichi-Ben Jamaa et al. 2010; Rhazi et al. 2012), as well as the importance of these aquatic environments for amphibian conservation (e.g., Beja and Alcazar 2003; Gómez-Rodríguez et al. 2009; Ferreira and Beja 2013; Escoriza et al. 2014). Invertebrates have received less attention, with the exception of some crustaceans (e.g., King et al. 1996; Belk 1998; De Roeck et al. 2007). However, the need to protect these environments and even to create new ones for the conservation of endangered invertebrate species has been noted (Baltanás et al. 1992; Valdecasas et al. 1992; Fugate 1998; Chester and Robson 2013). In recent years, public perception, scientific knowledge, and management efforts have improved. For example, the number of scientific symposia and publications for both scientific and general audiences has increased significantly in the last two decades (Witham 1998; Diget and Rioux 1998; Blaustein and Schwartz 2001; Grillas et al. 2004; Fraga 2009). Pioneering examples of vernal pool restoration, mitigation against damage, and conservation activities were developed in California in the 1980s (Black and Zedler 1998; Ferren et al. 1998), and more followed in the other Mediterranean regions. For example, in Europe, local and international projects to establish the value of Mediterranean temporary ponds, and to improve their management, have flourished in the last 15 years (including continen-

tal France, Corsica, Minorca, València, southwest of Portugal, Crete and Sardinia; Grillas et al. 2004; Fraga et al. 2010; Sancho and Lacomba 2010). In southern Australia, recent research has focused on understanding the effects of water regime change on temporary wetlands (e.g., Robson and Clay 2005; Chambers et al. 2013; Chester et al. 2013; Sim et al. 2013), the biodiversity and recolonization dynamics of temporary wetland biota (Horwitz et al. 2009; Tuckett et al. 2010; Strachan et al. 2014), and whether artificial wetlands can play a role in conservation as more and more natural wetlands become drier (Chester and Robson 2013; Chester et al. 2013). Globally, several new tools or methods have been proposed for Mediterranean temporary ponds to evaluate the impact of human socioeconomic pressure (Zacharias et al. 2008), estimate their environmental status (Dimitriou et al. 2006), establish their habitat condition or ecological integrity (Sala et al. 2004; Sutula et al. 2006; Chester et al. 2013; van den Broeck et al. 2015a), assess their water quality using invertebrates (Chessman et al. 2002; Boix et al. 2005), and assess the contribution anthropogenic wetlands could make to conservation goals (Chester and Robson 2013; Chester et al. 2013).

Common threats to temporary wetlands are prevalent among Mediterranean regions: habitat loss, hydrological perturbation, disconnection and habitat fragmentation, fire damage, pollution, eutrophication, sedimentation, physical disturbance of the sediment, invasive species, livestock impacts, and climate change (Grillas et al. 2004; Zacharias et al. 2007; Zacharias and Zamparas 2010). However, the relative importance of each differs among countries. For example, increased livestock herd size has caused overgrazing and disturbance of sediments in North Africa (Bouahim et al. 2014, but see Ferchichi-Ben Jamaa et al. 2012). In contrast, the use of livestock has been proposed as a management tool to maintain disturbances that favor rare plant germination and amphibian reproduction in Europe (Grillas et al. 2004), and to reduce invasive plant species and promote natives in California (Marty 2005). Water extraction and diversion can dramatically affect the hydrology of temporary ponds in some areas (Serrano and Serrano 1996; Levin et al. 2009; Sim et al. 2013; Boulton et al. 2014). Habitat loss through drainage appears to be a universal issue across Mediterranean-climate regions (e.g., Hambright and Zohary 1998; Robson and Clay 2005; Horwitz et al. 2009). Moreover, annual rainfall has been declining substantially since 1900 in several Mediterranean regions owing to climate change (IPCC 2007) and already dry periods in rivers and wetlands have been markedly prolonged (Davies 2010; Sim et al. 2013). Many formerly perennial wetlands are now seasonal, and several formerly seasonal wetlands are now rarely inundated. These changes in hydroregime (duration, timing, and frequency of inundation) will imply changes in the populations and metacommunities dynamics, and different patterns between organisms with different dispersion mode or ability are expected (Pyke 2005; Sim et al. 2013; Kneitel 2014; Fig. 5.5).

Although many threats are common among temporary ponds in Mediterranean regions, legal protections and conservation plans differ among locations with very different political and social contexts. However, three fundamental concepts are



**Fig. 5.5** Schematic diagram showing changes in hydroregime and to invertebrates in some future climate change scenarios. Three types of Mediterranean temporary ponds are shown: long hydroperiod (LH); short hydroperiod (SH); and ephemeral (EP). The *left panels* represent the present situation, the *middle panel* shows moderate effects of climate change and the *right-hand panel* shows severe effects of climate change along with the expected changes to hydroperiod length for each pond type. Larger clouds and suns indicate higher rainfall and temperature, respectively. Each panel shows three variables: hydroregime (a), organism dynamics (b), egg-bank dynamics (c). In the hydroregime plots (a) the *blue area* shows seasonal water levels (A autumn, W winter, Sp spring, Su summer) and hydroperiod length. In the organism dynamic plots (b) the bigger the icons (red for passive dispersal invertebrates and green for the active ones) the higher the population size, and red and green lines represent the change of population size during the year. Finally, the pattern in (c) plots identifies three statuses of the egg-bank: *black*, high density and diversity of propagules; *dark gray*, low density and diversity of propagules; *light gray*, depleted egg-bank. Rainfall reduction and temperature increase cause shorter hydroperiod lengths with decreased life cycle duration and, in turn, a gradual depletion of the egg-bank. For active dispersers, optimal dispersal conditions (i.e., late spring) will be decoupled from hydroperiod since these conditions would occur when ponds would probably be dry. Thus, metapopulation sizes will decrease in time, and taxa presence can be only explained by neighboring ponds (*gray panels*)

shared: (1) habitat loss continues to be the primary challenge to conservation and management; (2) integration of freshwater and terrestrial biodiversity priorities in systematic conservation planning is a major challenge to conservation planners (Amis et al. 2009; Davies and Stewart 2013) and it is especially relevant in areas with a high abundance of temporary ponds (Chester and Robson 2013); and (3)

biodiversity protection requires networks of ponds with diverse hydroperiods, where the natural hydrologic regimes are preserved (Beja and Alcazar 2003; Díaz-Paniagua et al. 2010; Chester and Robson 2013; Chester et al. 2013; Florencio et al. 2014). Pond networks in regions under strong human pressure exhibit poorly developed invertebrate metacommunities (Gascón et al. 2012). More knowledge of plants and vertebrates in these environments means that these organisms are sometimes used as surrogates for total biodiversity, but evidence exists that biodiversity patterns and spatiotemporal dynamics of plants, vertebrates, and invertebrates, and even among invertebrate groups, are different (Alexander and Schlising 1998; Gascón et al. 2009; Bagella et al. 2010, 2011; Davies and Stewart 2013; Ruhí et al. 2014; Rouissi et al. 2014). Thus the use of surrogates may be ineffective in Mediterranean-climate regions.

To solve these conservation dilemmas and improve the sustainability of biodiversity and ecosystem function in Mediterranean temporary wetlands, much more research is needed into the dynamics of populations and communities. Comparatively little is known of local and regional patterns of biodiversity, of invertebrate population genetics and dispersal (with the exception of some groups such as large branchiopods; e.g., Aguilar 2011, 2012; Simovich et al. 2013), and of the dynamics of invertebrates in the wide range of habitats and microhabitats present in these wetlands. For example, only recently have invertebrate movements into sediment microrefuges during the drying process been documented in a Mediterranean-climate wetland, showing dynamics not previously observed (Strachan et al. 2014). Finally, progress is being made in elucidating how changes in the hydroregime or in the climate characteristics affect community structure (Ruhí et al. 2014; Kneitel 2014), and further research in this subject should allow improved conservation management of Mediterranean temporary ponds in future scenarios (Fig. 5.5).

**Acknowledgement** We especially thank Christopher Rogers and Brian Timms for their help with the appendix on large branchiopods, and Valentina Pieri with ostracod genera included in the first appendix. We also thank Laura Serrano for her valuable comments in the preparation of this text.

## Appendix 1

Invertebrate taxa observed in Mediterranean temporary ponds of the five world regions (data from published and non-published studies). The figures correspond to the number of identified genera in each family. The symbol+ indicates the presence of a certain taxa, but without any genera identified. MED. REG., total number of genera identified in all Mediterranean regions.

		Med. Basin	North America	South America	Southern Australia	South Africa	MED. REG.
<b>NEMATODA</b>							
	Nematoda undet.	+	+	+	+	+	+
<b>Dorylaimida</b>	Dorylaimidae	1	-	-	-	-	1
	Thornemematidae	1	-	-	-	-	1
<b>Enoplida</b>	Tripylidae	1	-	-	-	-	1
<b>Monhysterida</b>	Monhysteridae	1	-	-	-	-	1
<b>Rhabditida</b>	Rhabditida undet.	+	-	-	-	-	+
<b>BRYOZOA</b>							
<b>Plumatellida</b>	Plumatellidae	1	-	1	-	-	1
<b>CNIDARIA</b>							
<b>Hydroida</b>	Hydridae	1	+	1	2	1	2
<b>TURBELLARIA</b>							
	Turbellaria undet.	+	+	+	+	+	+
<b>Catenulida</b>	Stenostomidae	1	-	-	-	-	1
<b>Dalryelloida</b>	Dalryelloidae	2	-	-	-	-	2
<b>Rhabdocoela</b>	Polycystidae	1	-	-	-	-	1
	Typhloplanidae	10	-	-	-	1	10
<b>Tricladida</b>	Tricladida undet.	-	-	-	+	-	+
	Dugesidae	1	-	1	-	-	1
	Planariidae	-	+	-	-	-	+
	Rhynchodemidae	1	-	-	-	-	1
<b>TARDIGRADA</b>							
	Tardigrada undet.	+	-	-	+	+	+
<b>NEMERTEA</b>							
	Nemertea undet.	-	-	-	+	-	+
<b>NEMATOMORPHA</b>							
	Nematomorpha und.	-	-	-	-	+	+

<b>Gordioidea</b>	Gordioidea	1	1	1	-	-	-	-	1
<b>ROTIFERA</b>									
<b>Bdelloidea</b>	Rotifera undet.	-	-	-	-	-	+	+	+
	Bdelloidea undet.	+	+	+	+	-	-	-	+
	Philodinidae	1	-	-	-	-	-	-	1
<b>Monogononta</b>	Asplanchnidae	2	-	1	1	-	-	-	2
	Atrochidae	1	-	-	-	-	-	-	1
	Brachionidae	6	2	3	3	-	-	-	6
	Conochilidae	1	-	1	1	-	-	-	1
	Euchlanidae	2	-	1	1	-	-	-	2
	Filiniidae	1	-	-	-	-	-	-	1
	Flosculariidae	1	-	-	-	-	-	-	1
	Hexarthridae	1	1	1	1	-	-	-	1
	Lecanidae	1	2	2	2	-	-	-	2
	Lepadellidae	2	2	2	2	-	-	-	3
	Mytilinidae	1	-	-	-	-	-	-	1
	Notommatidae	2	-	1	1	-	-	-	2
	Proalidae	1	-	-	-	-	-	-	1
	Scaridiidae	-	1	1	1	-	-	-	1
	Synchaetidae	2	1	1	1	-	-	-	2
	Testudinellidae	1	-	-	-	-	-	-	1
	Trichocercidae	1	1	1	1	-	-	-	1
	Trichotriidae	1	-	1	1	-	-	-	1

(continued)

(continued)

		Med. Basin	North America	South America	Southern Australia	South Africa	MED. REG.
<b>MOLLUSCA</b>							
<b>Gastropoda</b>							
	Ancylidae	2	-	-	1	1	2
	Chilimidae	-	-	1	-	-	1
	Glacidorbidae	-	-	-	1	-	1
	Hydrobiidae	-	-	1	-	-	1
	Lymnaeidae	3	2	-	1	2	5
	Physidae	1	1	1	1	2	2
	Planorbidae	6	-	-	4	2	10
	Pomatopsidae	-	-	-	1	1	2
	Succineidae	1	-	-	1	-	1
	Tateidae	1	-	-	-	-	1
	Sphaeriidae	2	-	+	2	-	2
<b>Bivalvia</b>							
<b>ANNELIDA</b>							
<b>Polychaeta</b>							
	Polychaeta undet.	-	-	+	-	-	+
	Aelosomatidae	1	-	-	1	1	1
	Oligochaeta undet.	-	+	+	+	-	+
	Enchytraeidae	2	-	-	+	-	2
	Lumbricidae	2	-	-	-	-	2
	Lumbriculidae	+	-	-	-	-	+
	Naididae	3	+	+	3	+	4
	Tubificidae	2	+	+	3	+	5
<b>Hirudinea</b>							
	Hirudinea undet.	-	-	+	+	-	+
	Erpobdellidae	2	-	-	-	-	2
	Glossiphoniidae	2	-	-	+	-	3
	Hirudimidae	2	-	-	+	-	2
	Richardsonianidae	-	-	-	+	-	+



<b>CRUSTACEA</b>										
<b>Branchiopoda</b>										
Bosminidae	1	1	1	2	1	1	2	1	1	2
Branchinectidae	1	1	-	-	-	-	-	-	-	1
Branchipodidae	1	-	-	1	-	-	1	1	3	3
Chirocephalidae	2	2	-	-	-	-	-	-	-	3
Chydoridae	16	8	5	16	7	7	16	7	7	24
Cyzicidae	2	1	-	1	-	-	1	-	-	3
Daphniidae	4	4	3	5	5	5	5	5	6	6
Ilyocryptidae	1	-	1	1	-	-	1	-	-	1
Leptostheriidae	3	-	-	-	-	-	-	-	-	3
Limnadiidae	2	1	-	3	-	-	3	-	-	5
Lynceidae	1	1	-	1	-	-	1	-	-	1
Macrotrichidae	1	1	-	2	-	-	1	-	-	2
Moinidae	1	1	-	1	-	-	1	-	-	1
Sidae	2	1	1	2	-	-	2	-	-	3
Streptocephalidae	1	1	-	-	-	-	-	-	-	1
Tanyrastigidae	2	-	-	-	-	-	-	-	-	2
Thamnocephalidae	-	-	-	1	-	-	1	-	-	1
Triopsidae	2	2	-	2	-	-	2	-	-	2
Canthocamptidae	4	3	2	1	-	-	1	-	-	5
Centropagidae	-	-	-	-	-	-	-	-	-	2
Cyclopidae	12	5	5	3	5	5	3	5	5	13
Diaptomidae	9	5	-	-	3	3	-	-	-	15

(continued)

(continued)

		Med. Basin	North America	South America	Southern Australia	South Africa	MED. REG.
<b>Ostracoda</b>	Candonidae	6	2	1	1	2	7
	Cypridae	14	11	7	15	8	33
	Darwinulidae	1	-	-	1	-	1
	Hemicytheridae	1	-	-	-	-	1
	Ilyocyprididae	1	-	-	1	-	1
	Limnocytheridae	2	2	-	3	1	4
	Notodromadidae	1	-	-	2	-	3
	Amphisopidae	-	-	-	1	-	1
	Asellidae	1	-	+	-	-	1
	Scyphacidae	-	-	-	1	-	1
<b>Amphipoda</b>	Ceinidae	-	-	-	1	-	1
	Crangonyctidae	-	1	-	-	-	1
	Hyalellidae	-	-	1	-	-	1
	Perthiidae	-	-	-	1	-	1
	Aegidae	-	-	1	-	-	1
	Cambaridae	1	1	-	-	-	1
	Parastacidae	-	-	1	3	-	4
	Hydrozetidae	1	-	-	-	-	1
	<b>ARACHNIDA</b>						
<b>Oribatida</b>							

<b>Prostigmata</b>	Prostigmata undet.	-	-	-	+	-	-	-	+	
	Arrenuridae	1	1	1	-	1	-	1	-	
	Eylidae	1	1	1	-	1	-	1	-	
	Hydrachnidae	1	-	-	-	1	-	1	-	
	Hydrodromidae	1	-	-	-	1	-	1	-	
	Hydryphantidae	2	-	-	-	+	3	-	4	
	Hygrobatidae	1	-	-	-	-	-	-	1	
	Limnesiidae	-	-	1	-	-	-	-	1	
	Limnochariidae	-	-	-	-	-	1	-	1	
	Oxidae	-	-	-	-	-	1	-	1	
	Pionidae	2	-	-	-	-	2	-	3	
	Teutonidae	1	-	-	-	-	-	-	1	
	Unionicolidae	-	-	-	-	-	2	-	3	
	Pisauridae	-	-	-	-	-	+	-	-	
	<b>Araneae</b>									
	<b>INSECTA</b>									
	<b>Ephemeroptera</b>	Baetidae	1	1	1	-	1	-	1	2
Caenidae		1	-	-	1	-	-	-	2	
Coloburiscidae		-	-	-	+	-	-	-	+	
Leptophlebiidae		1	-	-	1	-	-	-	2	

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(continued)

		Med. Basin	North America	South America	Southern Australia	South Africa	MED. REG.
<b>Odonata</b>	Aeshnidae	3	2	+	3	1	5
	Austrocordulidae	-	-	-	1	-	1
	Calopterygidae	1	-	-	-	-	1
	Coenagrionidae	6	3	+	4	3	11
	Corduliidae	1	-	-	2	-	3
	Gomphidae	-	-	-	2	+	2
	Lestidae	3	-	+	1	-	4
	Libellulidae	5	5	+	7	4	13
	Megapodagrionidae	-	-	-	2	-	2
	Petaluridae	-	-	-	1	-	1
	Platycnemididae	1	-	-	-	-	1
	Synthemistidae	-	-	-	2	-	2
	Telephlebiidae	-	-	-	1	-	1
	Capniidae	1	-	-	-	-	1
	Gripopterygidae	-	-	2	-	-	2
Perlidae	-	-	+	-	-	+	
Notonemouridae	-	-	1	-	-	1	
<b>Plecoptera</b>							

<b>Hemiptera</b>	Belostomatidae	1	1	-	1	1	1	3
	Corixidae	10	4	+	4	2	13	
	Gerridae	2	1	-	-	2	3	
	Hebridae	-	-	+	-	-	+	
	Hydrometridae	1	-	-	+	-	1	
	Mesoveliidae	1	1	+	+	1	1	
	Naucoriidae	2	-	-	-	-	2	
	Nepidae	2	-	-	1	-	2	
	Notonectidae	3	2	-	3	2	5	
	Pleidae	1	-	-	2	1	2	
	Saldidae	1	-	-	-	-	1	
	Veliidae	2	-	-	1	-	2	
	Sialidae	-	-	1	-	-	1	
	Osmylidae	-	-	+	-	-	+	
	Sisyridae	-	-	-	1	-	1	

(continued)

(continued)

	Med. Basin	North America	South America	Southern Australia	South Africa	MED. REG.
<b>Coleoptera</b>						
Alleculidae	+	-	-	-	-	+
Carabidae	-	-	+	-	-	+
Chrysomelidae	1	-	-	+	-	1
Curculionidae	2	+	-	1	-	2
Dryopidae	1	-	-	-	1	1
Dytiscidae	27	14	+	23	12	52
Elmidae	1	-	2	-	-	3
Eirithinidae	1	-	-	-	-	1
Georissidae	-	-	-	-	+	+
Gyrinidae	1	1	-	-	1	2
Halplidae	3	3	-	1	1	4
Helophoridae	1	1	-	-	-	1
Heteroceridae	-	1	-	-	-	1
Hydraenidae	3	2	+	2	9	10
Hydrochidae	1	-	1	1	1	1
Hydrophilidae	14	6	1	7	11	21
Hygrobiidae	1	-	-	-	-	1
Limnichidae	-	-	-	+	-	+
Noteridae	1	-	-	1	-	2
Ptiliidae	-	-	-	+	+	+
Ptilodactylidae	-	-	-	+	-	+
Scarabaeidae	-	1	-	-	-	1
Scirtidae	2	-	1	1	+	3
Spercheidae	-	-	-	-	+	+
Staphylinidae	-	-	+	-	-	+

<b>Trichoptera</b>	Ecnomidae	-	-	-	-	-	+	-	+
	Hydropsychidae	-	-	1	1	-	-	-	1
	Hydroptilidae	2	-	1	1	1	1	1	3
	Leptoceridae	-	-	2	2	4	-	-	5
	Limnephilidae	5	1	-	-	-	-	-	5
	Phryganeidae	1	-	-	-	-	-	-	1
	Polycentropodidae	1	-	1	1	-	-	-	2
	Sericostomatidae	1	-	-	-	-	-	-	1
	Stenopsychidae	-	-	+	+	-	-	-	+
	Crambidae	-	-	-	-	+	-	-	+
	Pyralidae	1	-	+	+	+	-	+	1
	<b>Lepidoptera</b>								

(continued)

(continued)

	Med. Basin	North America	South America	Southern Australia	South Africa	MED. REG.
<b>Diptera</b>						
Anthomyiidae	-	+	-	+	+	+
Athericidae	-	-	+	-	-	+
Ceratopogonidae	6	4	+	8	1	11
Chaoboridae	1	-	-	1	1	2
Chironomidae	40	13	+	21	10	49
Chloropidae	+	-	-	-	-	+
Culicidae	5	5	+	4	5	7
Dixidae	2	1	-	-	+	2
Dolichopodidae	1	+	-	+	-	1
Empididae	+	-	+	+	-	+
Ephydriidae	4	4	+	+	+	6
Limoniidae	3	-	+	-	-	3
Psychodidae	2	1	-	1	1	2
Rhagionidae	1	-	-	-	-	1
Scatophagidae	-	1	-	-	-	1
Sciomyzidae	2	-	-	1	-	2
Simuliidae	2	+	+	-	-	2
Stratiomyidae	3	2	-	+	+	4
Syrphidae	1	2	-	-	-	2
Tabanidae	1	1	-	+	+	1
Thaumaleidae	-	-	-	+	-	+
Tipulidae	3	3	+	+	+	4
<b>MINIMUM NUMBER OF GENERA</b>	394	169	101	253	150	633
<b>MINIMUM NUMBER OF FAMILIES</b>	149	73	77	112	71	204



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## Appendix 2

Large branchiopods species observed in temporary ponds in four of the five Mediterranean regions (data from published studies; no species have been identified from South American Mediterranean region). **P** means that this species occurs both in and outside the Mediterranean areas, whereas **E** means that it is endemic to one Mediterranean area. For the species inclusion criteria see section “Invertebrate assemblages of Mediterranean temporary ponds?” means that this taxon cannot be included in one of the two previous categories, because taxonomic identity is not at species level.

	Med. Basin	North America	Southern Australia	South Africa
<b>O. NOTOSTRACA</b>				
<b>F. Triopidae</b>				
<i>Lepidurus apus apus</i>	<b>P</b>	–	–	–
<i>Lepidurus apus viridis</i>	–	–	<b>P</b>	–
<i>Lepidurus couesii</i>	<b>P</b>	–	–	–
<i>Lepidurus lubbocki</i>	<b>P</b>	–	–	–
<i>Lepidurus packardi</i>	–	<b>E</b>	–	–
<i>Triops australiensis</i>	–	–	<b>P</b>	–
<i>Triops baeticus</i>	<b>E</b>	–	–	–
<i>Triops cancriformis</i>	<b>P</b>	–	–	–
<i>Triops emeritensis</i>	<b>E</b>	–	–	–
<i>Triops gadensis</i>	<b>E</b>	–	–	–
<i>Triops granarius</i>	<b>P</b>	–	–	<b>P</b>
<i>Triops longicaudatus</i>	–	<b>P</b>	–	–
<i>Triops mauritanicus</i>	<b>E</b>	–	–	–
<i>Triops simplex</i>	<b>E</b>	–	–	–
<i>Triops vicentinus</i>	<b>E</b>	–	–	–

(continued)

(continued)

	Med. Basin	North America	Southern Australia	South Africa
<b>O. SPINICAUDATA</b>				
<b>F. Cyzicidae</b>				
<i>Cyzicus bucheti</i>	<b>E</b>	–	–	–
<i>Cyzicus californicus</i>	–	<b>E</b>	–	–
<i>Cyzicus gihoni</i>	<b>E</b>	–	–	–
<i>Cyzicus grubei</i>	<b>E</b>	–	–	–
<i>Cyzicus tetracerus</i>	<b>P</b>	–	–	–
<i>Eocyzicus saharicus</i>	<b>P</b>	–	–	–
<i>Ozestheria mariae</i>	–	–	<b>E</b>	–
<i>Ozestheria packardi</i>	–	–	<b>P</b>	–
<b>F. Limnadiidae</b>				
<i>Eulimnadia</i> sp. <sup>1</sup>	?	–	–	–
<i>Eulimnadia feriensis</i>	–	–	<b>E</b>	–
<i>Eulimnadia datsonae</i>	–	–	<b>E</b>	–
<i>Eulimnadia palustera</i>	–	–	<b>E</b>	–
<i>Eulimnadia vinculum</i>	–	–	<b>E</b>	–
<i>Eulimnadia texana</i>	–	<b>P</b>	–	–
<i>Imnadia yeyetta</i>	<b>P</b>	–	–	–
<i>Limnadia lenticularis</i>	<b>P</b>	–	–	–
<i>Limnadopsis occidentalis</i>	–	–	<b>P</b>	–
<i>Limnadopsis paradoxa</i>	–	–	<b>E</b>	–
<i>Limnadopsis tatei</i>	–	–	<b>P</b>	–
<i>Paralimnadia badia</i>	–	–	<b>E</b>	–
<i>Paralimnadia cygnorum</i>	–	–	<b>E</b>	–
<i>Paralimnadia sordida</i>	–	–	<b>P</b>	–
<b>F. Leptestheriidae</b>				
<i>Eoleptestheria ticinensis</i>	<b>P</b>	–	–	–
<i>Leptestheria dahalacensis</i>	<b>P</b>	–	–	–
<i>Leptestheria mayeti</i>	<b>P</b>	–	–	–
<i>Leptestheria rubidgei</i>	–	–	–	<b>P</b>
<i>Maghrebestheria maroccana</i>	<b>E</b>	–	–	–
<b>O. LAEVICAUDATA</b>				
<b>F. Lynceidae</b>				
<i>Lynceus</i> sp. <sup>2</sup>	?	–	–	–
<i>Lynceus baylyi</i>	–	–	<b>P</b>	–
<i>Lynceus brachyurus</i>	–	<b>P</b>	–	–
<i>Lynceus tatei</i>	–	–	<b>P</b>	–
<i>Lynceus macleayanus</i>	–	–	<b>P</b>	–
<i>Lynceus magdaleanae</i>	–	–	<b>P</b>	–
<i>Lynceus susanneae</i>	–	–	<b>E</b>	–

	Med. Basin	North America	Southern Australia	South Africa
<b>O. ANOSTRACA</b>				
<b>F. Streptocephalidae</b>				
<i>Streptocephalus cafer</i>	–	–	–	<b>P</b>
<i>Streptocephalus dendyi</i>	–	–	–	<b>P</b>
<i>Streptocephalus gracilis</i>	–	–	–	<b>P</b>
<i>Streptocephalus ovamboensis</i>	–	–	–	<b>P</b>
<i>Streptocephalus papillatus</i>	–	–	–	<b>P</b>
<i>Streptocephalus purcelli</i>	–	–	–	<b>P</b>
<i>Streptocephalus torvicornis</i>	<b>P</b>	–	–	–
<i>Streptocephalus woottoni</i>	–	<b>E</b>	–	–
<b>F. Tanymastigidae</b>				
<i>Tanymastix affinis</i>	<b>E</b>	–	–	–
<i>Tanymastix stagnalis</i>	<b>P</b>	–	–	–
<i>Tanymastix stellae</i>	<b>E</b>	–	–	–
<i>Tanymastigites brteki</i>	<b>E</b>	–	–	–
<i>Tanymastigites cyrenaica</i>	<b>P</b>	–	–	–
<i>Tanymastigites lusitanica</i>	<b>E</b>	–	–	–
<i>Tanymastigites perrieri</i>	<b>P</b>	–	–	–
<b>F. Branchipodidae</b>				
<i>Australbranchipus parooensis</i>	–	–	<b>P</b>	–
<i>Branchipodopsis dayae</i>	–	–	–	<b>P</b>
<i>Branchipodopsis hodgsoni</i>	–	–	–	<b>P</b>
<i>Branchipodopsis karroensis</i>	–	–	–	<b>E</b>
<i>Branchipodopsis wolfi</i>	–	–	–	<b>P</b>
<i>Branchipus cortesi</i>	<b>E</b>	–	–	–
<i>Branchipus pasai</i>	<b>E</b>	–	–	–
<i>Branchipus schaefferi</i>	<b>P</b>	–	–	–
<b>F. Thamnocephalidae</b>				
<i>Branchinella affinis</i>	–	–	<b>P</b>	–
<i>Branchinella australiensis</i>	–	–	<b>P</b>	–
<i>Branchinella basispina</i>	–	–	<b>E</b>	–
<i>Branchinella complexidigitata</i>	–	–	<b>E</b>	–
<i>Branchinella erosa</i>	–	–	<b>E</b>	–
<i>Branchinella kadjikadji</i>	–	–	<b>E</b>	–
<i>Branchinella halsei</i>	–	–	<b>P</b>	–
<i>Branchinella hattahensis</i>	–	–	<b>P</b>	–
<i>Branchinella hearnii</i>	–	–	<b>E</b>	–
<i>Branchinella longirostris</i>	–	–	<b>E</b>	–
<i>Branchinella lyrifera</i>	–	–	<b>P</b>	–
<i>Branchinella nana</i>	–	–	<b>P</b>	–
<i>Branchinella occidentalis</i>	–	–	<b>P</b>	–
<i>Branchinella papillata</i>	–	–	<b>P</b>	–
<i>Branchinella vosperi</i>	–	–	<b>E</b>	–

(continued)

(continued)

	Med. Basin	North America	Southern Australia	South Africa
<b>F. Branchinectidae</b>				
<i>Branchinecta campestris</i>	–	<b>P</b>	–	–
<i>Branchinecta coloradensis</i>	–	<b>P</b>	–	–
<i>Branchinecta conservatio</i>	–	<b>E</b>	–	–
<i>Branchinecta dissimilis</i>	–	<b>P</b>	–	–
<i>Branchinecta ferox</i>	<b>P</b>	–	–	–
<i>Branchinecta gigas</i>	–	<b>P</b>	–	–
<i>Branchinecta lindahli</i>	–	<b>P</b>	–	–
<i>Branchinecta longiantenna</i>	–	<b>E</b>	–	–
<i>Branchinecta lynchi</i>	–	<b>E</b>	–	–
<i>Branchinecta mackini</i>	–	<b>P</b>	–	–
<i>Branchinecta mesovallensis</i>	–	<b>E</b>	–	–
<i>Branchinecta orientalis</i>	<b>P</b>	–	–	–
<i>Branchinecta sandiegonensis</i>	–	<b>E</b>	–	–
<b>F. Chirocephalidae</b>				
<i>Chirocephalus anatolicus</i>	<b>E</b>	–	–	–
<i>Chirocephalus bairdi</i>	<b>E</b>	–	–	–
<i>Chirocephalus brteki</i>	<b>E</b>	–	–	–
<i>Chirocephalus diaphanus</i>	<b>P</b>	–	–	–
<i>Chirocephalus kerkyrensis</i>	<b>E</b>	–	–	–
<i>Chirocephalus murae</i>	<b>E</b>	–	–	–
<i>Chirocephalus neumanni</i>	<b>E</b>	–	–	–
<i>Chirocephalus salinus</i>	<b>P</b>	–	–	–
<i>Eubbranchipus bundyi</i>	–	<b>P</b>	–	–
<i>Eubbranchipus oregonus</i>	–	<b>P</b>	–	–
<i>Eubbranchipus serratus</i>	–	<b>P</b>	–	–
<i>Linderiella africana</i>	<b>E</b>	–	–	–
<i>Linderiella baetica</i>	<b>E</b>	–	–	–
<i>Linderiella massaliensis</i>	<b>E</b>	–	–	–
<i>Linderiella occidentalis</i>	–	<b>E</b>	–	–
<i>Linderiella santarosae</i>	–	<b>E</b>	–	–

<sup>1</sup>The taxonomic identity at species level of this population in Tunisia (Rabet et al. 2015) is not determined

<sup>2</sup>According to Hartland-Rowe (1967) this species is not the ubiquitous *L. brachyurus*

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