

Class Hexapoda: general introduction

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Introduction to aquatic Hexapoda

In his classical paper on biodiversity, Robert May (1992) recognized that Hexapoda included the greatest proportion of global biodiversity. Nearly three-quarters of all named living animal species are insects (Mayhew, 2007). While the current insect decline worldwide is unquestionable (Cardoso et al., 2020; Hallmann et al., 2017; Wagner et al., 2021), data to assess large-scale spatial patterns in the severity of insect trends are not yet available (Montgomery et al., 2020) and veracity of alarmist insect decline statements is under revision due recent weak studies (Didham et al., 2020). Moreover, this biodiversity decline is only well documented for a few aquatic groups (Odonata, Ephemeroptera, and Plecoptera; Sánchez-Bayo & Wyckhuys, 2019) and some trends in declining abundance seem to be more related to terrestrial insects than aquatic ones (Van Klink et al., 2020 but see Desquilbet et al., 2020 and Jähnig et al., 2021). Similarly, the traditional view of the temporal trend of their biodiversity is that insect richness increased continuously over the evolutionary history of the group, but new approaches now recognize a Cretaceous peak in family richness and negligible net richness change over the past 125 Myr (Clapham et al., 2016).

In freshwater ecosystems, Hexapoda are a hyperdiverse group since the majority of the freshwater animal species are insects (60.4%; Balian et al., 2008). Moreover, some hundreds of water-dependent Collembola have also been identified (approximately 0.5% of the total diversity; Deharveng et al., 2008), although this group needs a more accurate estimate (Balian et al., 2008). Knowledge of the evolutionary patterns of freshwater hexapods is less developed than for terrestrial insects (but see Múrria et al., 2018), and this lack of knowledge contrasts with other aspects that have been widely studied, such as their ecology and habitat preferences (Dijkstra et al., 2014). Moreover, several ecological patterns of terrestrial hexapods do not seem to match the aquatic ones, showing differences in population and community dynamics (e.g., Fenoglio et al., 2016; Lancaster & Downes, 2018; Van Klink et al., 2020).

The unity of the morphological characters of hexapod organisms was already evident in the pre-Linnean taxonomies, and it was from the Linnaeus proposal that the main groups (i.e., orders such as Coleoptera, Hemiptera, Lepidoptera, Neuroptera, Hymenoptera and Diptera) were identified. In fact, Linnaeus' *Systema Naturae* named Insecta as the fifth Class of his proposal, but the term was used in a very different way than our modern concept, since it included all arthropods. The term “hexapods” appeared in some proposals of the 19th century accompanying the term Insecta to refer to the class in which insects and springtails were included (i.e., “Hexapod metamorphic insects” in John O. Westwood's two-volumes *An Introduction to the Modern Classification of Insects* (1839–1840)). Springtails were included within insects until second half of the 20th century, when cladistic analyses favoured the split of Collembola from Insecta. Some 19th century authors, such as F. M. Brauer, pointed out the differences between Collembola and wingless insects (those that lost wings secondarily). According to the morphological and phylogenetic affinities between

both groups, they were assigned to the same class (Hexapoda). A comprehensive history of Hexapoda classification was published by Engel and Kristensen (2013). Therefore, two classes of freshwater hexapods can be identified, Collembola and Insecta. The former are organisms of < 6 mm long and can be distinguished from insects by the presence of ventral tube or “collophore” on the first abdominal segment and in some species by a furca (see section *Keys to the Subclass Entognatha (Collembola)*) on the fourth segment (Hilsenhoff, 2001).

Subclass Collembola—aquatic taxa

Identification and sampling

Collembola is currently considered as a subclass of Hexapoda with four orders, two of them with elongate or cylindrical shape: Poduromorpha, with the three thoracic segments evident in dorsal view (all with chaetae); and Entomobryomorpha, with prothorax tergite reduced and without chaetae. The other two orders, Symphypleona and Neelipleona, are globular in shape, with abdominal segments indistinctly divided, or sometimes into two parts by a constriction. Neelipleona are diminute, without eyes, and with special sensilla and sensillar areas on the head and body. Many species (all groups) have a “furca,” an unpaired ventral organ on the fourth segment, that allows them to spring considerable distances. The most characteristic feature of the group is the ventral tube (or collophore), with many functions under debate but surely used for gas, water, and ion exchange with the environment, and in some groups it is a cleaning organ. The antennae have four segments (sometimes subdivided or annulated) and always possess a sensillar area at the end of the third segment. The eyes are simple, with a maximum of eight ocelli, reduced in many species and, sometimes, there is a chemical receptor near them called the PAO (post antennal organ).

Aquatic Collembola groups

In the order Entomobryomorpha, the Isotomidae is the family that can be considered more related to freshwater aquatic environments, while Entomobryidae, Tomoceridae, and Oncopoduridae accumulate many stygofauna species (living on a water film or in the surface of the water). For example, the Isotomidae species *Isotomurus palustris* is frequently cited throughout the whole Holarctic Region living at riverbanks and other freshwater habitats, probably not neustonic. It may actually be a cluster of species (Carapelli et al., 2001).

Among Symphypleona, only Bourletiellidae, Sminthurididae, Dicyrtomidae, and Katiannidae have species associated with above-ground aquatic environments, while Arrhopalitidae includes many species specialized in cave habitats (water film on surfaces or neustonic on pools). The Neelipleona, with a few species, are also present in aquatic environments.

Sampling

With low-density populations and cryptic habitats, the only efficient method is the hand collection onto a white surface or directly from the water surface, capturing the specimens with a small aspirator, using an aquarium net, or taking them directly with a paintbrush. Small pitfall traps can be used at the edges of water bodies. From sandy-river banks and beaches the specimens can be retrieved with an aquarium net after making a hole (a meter above the water limit) allowing water poured into it.

Collembola ecology

Habitats and distribution

Most collembolans found on a water surface are not actually aquatic and may have just fallen into that habitat. Instead, springtails are predominantly soil, litter, and arboreal dwellers, with many tropical species occurring on vegetation and tree canopies (Palacios-Vargas, 2013). The relationship between springtails and water was known before the description of the *Podura aquatica* Linnaeus, 1758, when in 1740 De Geer observed large groups on the water in Holland (De Geer, 1740).

Due to its way of obtaining oxygen, through its cuticle, it can be said that all springtails are dependent on high ambient humidity. In some studies, it has been demonstrated that eggs laid into the soil may hatch after a long period of flooding (Tamm, 1984). Besides the species *P. aquatica*, only a limited number of species belonging to a few genera can be considered strictly aquatic: *Isotomurus*, *Hypogastrura*, *Axelsonia*, *Anurida*, and *Sminthurides* (Yue & Fu, 2000), especially the last one, that lives on water surfaces all its life cycle (Greenslade, n.d.). The “aquatic” springtails are specialized for various damp microhabitats (Waltz & McCafferty, 1979). The first group, cryophilic species, are primary

aquatic-associated springtails, living permanently on the snow surface. This group will not be considered in this publication. The second group, epigeal hydrophilic species, can live on low vegetation close to water, on other organisms, or directly on the surfaces of freshwater or marine habitats. The last is found on the surface tension layer. Only a few species can live submerged, such as *P. aquatica*. The third group, cave hydrophilic species, need a water-saturated atmosphere. Some are dependent on the water film on rocks and have specialized claws and empodia, other are frequent on the water of gours or pools in caves (Deharveng et al., 2008), again on the surface tension layer such as some *Arrhopalites* and Neelidae. The adaptation in this group, especially for the claws and empodia, will be treated later. Some species have been also considered aquatic when found into the interstices of soil components, for example in sandy soils near rivers and sea, or on the riverbanks and pond littoral. They are also found in soils that often be flooded. The impossibility of separating the species that should be considered water dependent from those that are never found in this environment makes us discard the numerous citations that exist in the bibliography for this group (i.e., Arbea & Ariza, 2012).

Only *P. aquatica* has a widespread distribution. *Isotomurus* is the dominant genera in nontropical regions, with *I. palustris* (probably a cluster of species, not all aquatic) (Carapelli et al., 2001) are along with all Holarctic region. *Sminthurides*, although present in the northern hemisphere, is more diversified in the tropics (Deharveng et al., 2008). In many cases, the hydrophilic species have a wide range of endemism, being higher in caves. The marine species have a greater range distribution because the capacity to stay at the water surface allows them to move along long coast distances.

Physiology and morphology

The cuticle of Collembola is composed of structures that give it stiffness. The composition, including wax, also makes it hydrophobic, enabling the animal to float on water. However, only the tubercles and joints have wax, leaving the depressed areas permeable to air that is trapped among the tubercles and acts as a physical gill when submerged (Noble-Nesbitt, 1963). If Collembola eggs hatch underwater the juveniles can be totally submerged, but when the cuticle is exposed to air, it changes and starts to repel water avoiding submersion (Greenslade, n.d.). Especially among neustonic species, the claws suffer an evident elongation, and the mucro acquires a wider shape. Adaptation to aquatic or semiaquatic habitats is a derived condition that has evolved independently several times in Collembola (D'Haese, 2002).

Neanuridae: *Anurida maritima* Guerin, 1839 is frequent on seaweed in marine waters.

Poduridae: *P. aquatica* (peat bog; Lek-Ang et al., 2007) is usually observed on the freshwater surface, deposits its eggs on water plants, and is believed to hibernate under water.

Onychiuridae: *Ongulonychiurus colpus* (Thibaud & Massoud, 1986) is a stalactite water film dweller based on its peculiar morphology.

Tullbergiidae: Many of the genera have species present on marine littoral sands, and it seems that they can survive in immersion during the tides. However, it is not clear if they really are aquatic.

Hypogastruridae: *Ongulogastrura longisensilla* (Thibaud & Massoud, 1983) lives on the water film on the stones of a cave from the French Basque Country (Oyanbeltza, Urkullu range). Some species have been found near the sea, such as *Xenilla maritima*, but the reality is that it is a species with wide distribution and edaphic.

Isotomidae: *I. palustris* was also observed by De Geer (1740). Some species of the genus are riverbank species that live near freshwater and are usually caught with phytoplankton or neuston nets.

Actaletidae: *Actaletes neptuni* (Giard, 1889) has been cited on the coast of the Iberian Peninsula in Galicia (Selga, 1971) and Coimbra on *Mytilus* (Gama, 1988).

Orchesellidae: Only *Orchesella quinquefasciata* has been cited in relation to the aquatic environment, on the northern beaches of the Mediterranean coast in Spain, on the Costa Brava (Arbea & Ariza, 2012), but it may not be justified to consider it aquatic as it is present in dry environments in many parts of Europe.

Entomobryidae: Some *Entomobrya* are halophiles, but it appears that they are not strictly aquatic, although they live in riverside vegetation.

Bourletiellidae: This family seems mostly associated with dry environments, although some species are present in wet meadows or littorals. *Heterosminthurus insignis* is a species of wide distribution in northern Europe and other parts of the world; it is present on floating plants and could be present in the Mediterranean Basin.

Sminthurididae: *Sminthurides aquaticus* has mentioned feeding on *Lemna* (Klugkist, 1907), and other *Sminthurides* species have been cited in relation to freshwater courses (Bretfeld, 1999).

Dicyrtomidae: Although many of the species in the family are found in wet habitats (forests or high-altitude areas), only three species have been found clearly related to the aquatic environment. *Dicyrtomina minuta* has been cited as thalassophile and present in the littoral by several authors (Strenzke, 1955; Weigmann, 1973), although it is abundant in dry environments. *Ptenothrix cavicola* is described from a jetty in a cave, making evident its relationship with water

(Cassagnau & Delamare-Deboutteville, 1955). Lastly, *Jordanathrix articulata articulata*, although present in dry environments at various points in the Mediterranean, has been found on aquatic vegetation on the Levantine coast (Rueda & Jordana, 2020).

Katiannidae: Only some species of the genus *Sminthurinus* have been related with aquatic environment, and among them, only *Sminthurinus concolor* is present in the Mediterranean Basin, where it is found in Spain (Minorca) on *Phragmites* near the seashore (Bretfeld, 1999).

Arrhopalitidae: Many are aquatic, practically all of which live in caves. Since they feed diatoms on *neuston*, and it is not uncommon to find carbonate crystals in its gut, which indicates that they can live on the water pools in caves.

Neelidae: It seems that its presence in the water is accidental, because aquatic organisms, such as diatoms, that are common in the diet of aquatic collembolans are not present in the gut contents of this family.

Subclass Insecta

Some biological notes on the subclass Insecta

The subclass Insecta belongs to the class Hexapoda and includes a large group of arthropods characterized by having three pairs of locomotory legs and external mouthparts, at least in their adult stage (Johnson & Triplehorn, 2004). Aquatic insects spend one or more life cycle stages in the freshwater habitat, with the majority moving to terrestrial habitats as adults. They play important ecological roles in both habitats as primary consumers, detritivores, predators, and pollinators (Lancaster & Downes, 2013). Primary aquatic insects are archaic elements of the fauna of continents. There are fossils that date more than 200 million years and are amongst the oldest members of the aquatic organisms (Illies, 1969; Sinitshenkova, 2003). In evolutionary terms, aquatic insects are essentially terrestrial insects that have found the way to live in freshwaters habitats (Marden, 2008). Due to this, they developed many morphological, physiological, and ecological adaptations that made them extremely diverse and abundant, providing excellent models for research on diversification (Múrria et al., 2018; Wootton, 1988). Their habitats exhibit marked spatial and temporal gradients in stability, and their amphibiotic lifestyles link strong habitat dependence with a response to change via dispersal (Dijkstra et al., 2014).

Most aquatic insect species are included in 10 taxonomic orders and may represent in abundance and richness terms the most important community in freshwater habitats (Wichard et al., 2002). In five orders, all their species are entirely aquatic in some part of their life cycle, usually, the immature stages, whereas the adult stages are terrestrial. These orders include insects such as mayflies (order Ephemeroptera), stoneflies (order Plecoptera), dragonflies (order Odonata), caddisflies (order Trichoptera), and alderflies (order Megaloptera). The other five orders are partially aquatic and often have a minority of species with aquatic immatures. The adults of these species are mostly terrestrial, although some species also have aquatic adults. These orders contain insects such as true bugs (order Hemiptera), sponge flies and lance lacewings (order Neuroptera), beetles (order Coleoptera), moths (order Lepidoptera), and true flies (order Diptera).

Insect life cycle

All insects begin their lives as eggs. After hatching, insects pass through various development stages until they become adults. This process is called metamorphosis (McGavin, 2001). A minority of the insects are ametabolous, i.e. the immature stages are very similar to adults, but have not developed the reproductive system (external genitalia). No aquatic insects have ametabolous development. Most of them alternate between the water and the terrestrial habitats and live temporarily on land or in the air. All are grouped into one of two development cycles. In the “hemimetabolous life cycle,” a gradual metamorphosis occurs. The immature insect (larva or nymph) resembles the adult in form, eating habits, and body proportions. Nevertheless, it is different in body size and genitalia and wings development. Rudimentary wings are externally visible and develop gradually inside wing pads. The larvae or nymphaea grow gradually through a succession of molts. The term “nymph” is traditionally referred to larvae with hemimetabolous metamorphosis living in different habitats than the adults (Ephemeroptera, Plecoptera, and Odonata). However, in these cases, the term larva is also commonly accepted. In this section, we will use the simplest term and will call to all immature stages as “larvae.” In the “holometabolous life cycle” (or complete metamorphosis) the larva also grows gradually, but the developmental stages differ greatly in morphology and habits from the adult. Larvae are wingless, and the form and habits are suited for growth and development rather than reproduction. Additionally, the change to the adult occurs during the inactive nonfeeding stage called a “pupa.” Sometimes the eggs, larvae, pupae, and imagoes are not adapted to live in the water at all (Wichard et al., 2002). Aquatic insects with holometabolous metamorphosis belong to Coleoptera, Trichoptera, Lepidoptera, Megaloptera, Neuroptera, and Diptera orders.

Insect body structure

An insect's body has an exoskeleton composed of chitin, a long-chain polymer derived from glucose. In most insects, especially the adults, the exoskeleton is heavily sclerotized and forms a series of dorsal, ventral, and lateral plates (Johnson & Triplehorn, 2004). However, in many insects, mainly larvae, the entire cuticle is flexible, although clearly segmented (McGavin, 2001). The body of the adult insect consists of three parts: head, thorax, and abdomen. The head is formed from several plates that join through sutures lines. Also, it has a pair of multisegmented antennae, a complex set of mouthparts, a pair of compound eyes, and up to three simple eyes (ocelli). The thorax contains most of the organ systems. It is also the center of insect locomotion. Thus, it has three pairs of segmented legs and in most adults, one or two pairs of functional wings. The abdomen usually consists of a relatively simple structure with up to 10 visible segments. Most lack appendages, and the external genitalia occur on the last segment.

The larval body contains the same parts such as the adults, although in some cases these may be undifferentiated or reduced (e.g., in some Diptera larvae) (Johnson & Triplehorn, 2004). Larvae of the holometabolous orders lack compound eyes and ocelli but have special eyes called stemmata. The larvae thorax may contain true legs (jointed), prolegs (no jointed), or lack of them altogether. All larvae lack wings, although in hemimetabolous orders these may develop gradually inside wing pads. Also, many aquatic larvae bear gills placed between the legs or in the cervical zone (Wichard et al., 2002). The abdomen may have appendages (prolegs), filaments, or suckers. Overall, the prolegs (thoracic or abdominal) usually have a locomotory function, and neither are true legs nor lack sclerotized segments. Additionally, lateral gills are generally very common in the aquatic larvae abdomen. The last abdominal segment may bear appendages, lobes, cercus, hairs, gills, caudal prolegs, or also may lack any structure.

Endemicity of aquatic insects and singular habitats in the Mediterranean Basin

Worldwide Mediterranean regions are characterized by high levels of endemicity of several biotic groups, including aquatic insects (Table 8.1). The high taxonomic and genetic diversity observed in the aquatic insects in the Mediterranean Basin is partly explained by the complex geographical and historical events that have affected the region through geological times. Moreover, the faunal elements are mainly of Palearctic origin; but due to the location of the Mediterranean Basin close to the southern edge of the Palearctic realm, there is an influence of the Ethiopian and Oriental realms, especially in the southeastern part (Botosaneanu & Gasith, 1971; Boudot et al., 2009; Por, 1975). This diversity, as in many other groups, has been shaped by the intrinsic role of the Mediterranean Sea as a dispersal barrier, together with the complicated palaeo-geographical and palaeo-climatic history (including microplate movements, orogens formations, the salinity crisis, intermittent connections between shores, and Quaternary climatic oscillations, among others), establishing several foci of biodiversity all across the Mediterranean Basin, especially in the peninsulas and mountain systems (Balletto & Casale, 1991). Few taxa with reduced populations and with disjunct distributions among different faunistic realms are considered to be pre-Quaternary relicts from an ancient biota that was highly transformed due to the climatic oscillations of the Pleistocene (Tierno de Figueroa et al., 2013), such as the ephemeropteran *Prosopistoma* spp. (with three species in the Mediterranean Basin, and one widely distributed in the West Palearctic; Barber-James, 2009; Bojková & Soldán, 2015), the neuropteran genus *Nevrorthus* spp. (with five species in the Mediterranean Basin; Aspöck et al., 2017), and the trichopterans *Nyctiophylax gaditana*, *Pseudoneureclipsis* spp., *Calamoceras* spp., or *Larcasia* spp., among others (Malicky, 2014; Malicky, 2020; Martínez, 2014; Ruiz-García et al., 2013; Tachet et al., 2001). Other aquatic insects radiated in pre-Pleistocene times (e.g., the hemipteran *Velia* spp., or the coleopterans *Deronectes* spp., *Hydrochus* spp., *Hydraena* spp. (“*Haenydra*” lineage), *Ochthebius exsculptus* group; Berchi et al., 2018; García-Vázquez et al., 2016; Hidalgo-Galiana & Ribera, 2011; Ribera et al., 2010; Trizzino et al., 2011), some of them showing geographical distributions linked to the different geological evolutions of the western and eastern areas of the northern Peri-Tethys platforms or northern shore of the Mediterranean (Meulenkamp & Sissingh, 2003). However, climatic oscillations during the Pleistocene were very important in establishing modern biodiversity patterns in the Mediterranean, affecting all pre-Quaternary faunistic elements, as well as those aquatic insects that diversified during the Pleistocene (e.g., the odonates *Calopteryx* spp., *Aeshna cyanea*, the coleopterans *Meladema* spp., *Graptodytes* spp., *Hydraena gracilis* complex, or the trichopterans *Drusus* spp., *Annitella* spp.; García-Vázquez et al., 2017; Múrria et al., 2020; Previšić et al., 2009; Ribera & Faille, 2010; Simonsen et al., 2020; Sýkora et al., 2017; Weekers et al., 2001). Thus, the role of the Mediterranean peninsulas as refugia during this period allowed the survival of populations which accumulated higher levels of genetic diversity due to long continuities in the same areas (Hewitt, 2004), and some of these lineages were the sources of the recolonization of northern latitudes during interglacial periods. However, the roles of the Iberian, Italian, and Balkan peninsulas, as well as North Africa, were probably not

TABLE 8.1 Some data available of the endemism (percentage of endemic species) in the worldwide Mediterranean regions.

Mediterranean area	Biotic group (% of endemic species)
California	Fish (63%)
Mediterranean Basin	Crustaceans (55%) Coleopterans—Hydraenidae (57%) Dipterans—Simuliidae (51%) Amphibians (60%) Fish (63%)
South America (Chile)	Aquatic plants (80%) Trichopterans (70%) Amphibians (61%)
South Africa	Aquatic plants (86%) Crustaceans (72%) Water mites (52%) Plecopterans (92%) Trichopterans (71%) Anurans (69%) Fish (52%)
Southwestern Australia	Oligochaetes (59%) Water mites (56%) Ephemeropterans (58%) Trichopterans (82%) Plecopterans (75%) Amphibians (81%)
Data sources: Ball et al. (2013), Davies and Stewart (2013), de Moor and Day (2013), Figueroa et al. (2013), Tierno de Figueroa et al. (2013).	

similar in the evolution of the fauna due to the different origins, palaeo-geographic components, and landscape elements (Hewitt, 2011; Husemann et al., 2014). Moreover, the presence of diverging lineages within these highly heterogeneous refugial regions pointed to past isolated populations linked to high climatic stability, allowing to the existence of multiple (long-term or temporary) glacial refugia-within-refugia all across the Mediterranean Basin (Abellán & Svenning, 2014; Gómez & Lunt, 2007; Migliore et al., 2018).

The mechanisms of diversification in aquatic insects are influenced by their capacity to adapt to the varied environmental characteristics of the aquatic habitats. The habitat type can be broadly divided in lotic (running) and lentic (standing) waters, with contrasting characteristics related to the habitat stability and physical and chemical gradients. Lotic habitats are characterized by a high stability of the environment, from the geological and ecological perspectives, which results in a lower need to disperse (Ribera, 2008). In both habitat types, two main environmental gradients which create community structure have been identified: temporality and salinity (Brucet et al., 2012; Datry et al., 2014; Gasith & Resh, 1999; Leigh & Datry, 2017; Marchant et al., 2006; Wellborn et al., 1996). In this sense, temporary and saline waterbodies are not exclusive of the Mediterranean Basin, but they are not rare as in other regions, and they harbor singular communities (Álvarez-Cobelas et al., 2005; Millán et al., 2011). Temporary waterbodies had been considered as secondary habitats with respect to permanent ones; however, this point of view has changed considerably and nowadays they support significant biodiversity and provide valuable goods and services, especially in arid and semi-arid landscapes as in the Mediterranean Basin (Acuña et al., 2017; Boix et al., 2020; Calhoun et al., 2017; Vander Vorste et al., 2020). In some Mediterranean regions, comparable macroinvertebrate richness has been recorded at permanent and temporary sites in both lotic and lentic habitats (Boix et al., 2008; Bonada, Rieradevall, et al., 2007), but not in all the studies (Della Bella et al., 2005). Moreover, macroinvertebrate composition of permanent and temporary ponds showed differences and the latter support relevant biodiversity of rare and threatened species (Boix et al., 2008; Della Bella et al., 2005). Species richness in Mediterranean temporary ponds is dominated by arthropods: primarily insects and secondarily crustaceans (Boix et al., 2016 and references therein). The absence of fishes in Mediterranean temporary ponds gives to insects a relevant ecological role as main predators, but compared to other latitudes the predation pressure is not directly related to hydroperiod length (Boix et al., 2011; Schneider & Frost, 1996), since seasonal timing is also a

relevant factor (Kneitel, 2014). In colder temperate regions longer hydroperiod implies more time with optimum weather for aerial dispersal, since ponds fill after snow melt. However, the Mediterranean autumnal-winter hydroperiods can be longer than spring ones, but the latter have better weather conditions for aerial dispersion (Boix et al., 2016). Moreover, Mediterranean temporary rivers harbor greater regional diversity, beta diversity, rarity, and endemism levels of macroinvertebrates than temperate rivers (Bonada et al., 2017). This high biodiversity could be the result of anagenetic speciation due to isolation and species range contractions. On the other hand, in saline inland and coastal wetlands environmental factors, such as hydrology, have a crucial and different role with respect to freshwater in ecosystem functioning (e.g., food webs structure, eutrophication process and nutrient effects, confinement-flooding dynamics, etc.) (Bas-Silvestre et al., 2020; Beklioglu et al., 2007; Comín et al., 1992; Díaz et al., 1998). It is important to note that inland saline wetlands are mainly located in the south Mediterranean countries, with the exception of the Iberian Peninsula (Britton & Crivelli, 1993). Insect fauna of these habitats are characterized by a low richness and euryhaline species (Alcorlo et al., 2001; García et al., 1997; Gascón et al., 2008; Quintana et al., 1998). In coastal ponds, a decrease in the relative importance of the richness ratio of insects to crustaceans with increases in salinity has been reported (Boix et al., 2007). Finally, one of the most singular habitats are saline streams, which have received less attention due to their scarcity and scattered geographical distribution, and their low economic value as a water resource (Moreno et al., 2010). The harsh environmental conditions of high salinities imply an environmental filter for many species and shape the kind of organisms that inhabit them (Millán et al., 2011). These organisms showed adaptations to the extreme conditions (not only high salinity, but extreme temperatures and marked hydrological fluctuations of severe dry periods and floods). Insects are the best represented macroinvertebrates especially Diptera (mainly the families Chironomidae, Ceratopogonidae, Ephydriidae, Stratiomyidae, and Syrphidae), Heteroptera (Corixidae), and Coleoptera (Hydraenidae, Hydrophilidae, and Dytiscidae) (Millán et al., 2009; Moreno & De las Heras, 2009; Velasco et al., 2006). Although these habitats have a high conservation interest and a limited distribution (especially in the European context), the low social awareness of these habitats potentially exposes them to intense anthropogenic pressures (Millán et al., 2011).

Biological traits of the aquatic insects in Mediterranean climate

Biological traits are morphological, physiological, behavioral, or life history attributes that characterize organisms (Violle et al., 2007). They can be applied to individuals or to species (or other taxonomic levels) and have been evolutionarily acquired through the interaction of these organisms with the environment (Menezes et al., 2010; Statzner, Hildrew, et al., 2001). Therefore, according to the theory of the habitat template (based on the niche concept) (Southwood, 1977), the presence or absence of a species in a community depends on the match between their traits and the environment, acting at multiple spatial scales through a niche filtering process. More recently, local community composition is being also explained by dispersal processes of these species (another type of trait) or the landscape configuration favoring or limiting species' dispersal (Leibold et al., 2004). Trait analysis has thus become a central part of community ecology in both fundamental and applied research.

Besides their use in community ecology, traits have also been considered in other fields, such as molecular phylogenetics and biodiversity conservation (Cavender-Bares et al., 2004; Statzner, Hildrew, et al., 2001; Miatta et al., 2021). Their popular use in the last decades has resulted in a wide variety of trait databases (e.g., CESTES, Jeliakov et al., 2020) that cover multiple taxonomic groups, with plants being the most popular organisms in trait studies. There are also several trait databases that include information on aquatic insects, and some of them have been widely used in Mediterranean regions worldwide. The Tachet database and subsequent additions (Bonada & Dolédec, 2011; Tachet et al., 2010), for example, have been applied to environmental gradients in the Mediterranean Basin countries. These studies have considered large-scale traits patterns (Bonada, Dolédec, et al., 2007; Morais et al., 2009; Statzner et al., 2007) or the response of traits to specific environmental gradients related to hydrology, habitat, or pollution (García-Roger et al., 2013; Mellado-Díaz et al., 2008; Vidal-Abarca et al., 2013). More recently, the DISPERSE database compiles trait information related to dispersal of aquatic insects and its potential use in fundamental and applied research (Sarremejane et al., 2020) (Table 8.2).

Trait databases for aquatic insects consider a wide variety of traits (with several trait categories) and include information for family, genus, or species level in form of presence/absence or some type of quantification, such as the fuzzy coding approach (Chevenet et al., 1994). All these databases consider potential trait data (i.e., not real trait measured values), and therefore their use is usually limited to large-scale studies or along strong environmental gradients (Bonada & Dolédec, 2018). In particular, the Tachet database and subsequent additions include information for 473 macroinvertebrate taxa (mostly genus level), with 331 aquatic insects. It comprises 11 biological traits and 63 categories coded

TABLE 8.2 List of general biological traits and trait categories describing aquatic insects according to Tachet et al. (2010) and list of dispersal-related traits according to Sarremejane et al. (2020).

References	Trait	Category	References	Trait	Category			
Tachet et al. (2010)	Maximal size	≤ 0.25 cm	Sarremejane et al. (2020)	Maximum body size (cm)	< 0.25			
		> 0.25–0.5 cm			≥ 0.25–0.5			
		> 0.5–1 cm			≥ 0.5–1			
		> 1–2 cm			≥ 1–2			
		> 2–4 cm			≥ 2–4			
		> 4–8 cm			≥ 4–8			
		> 8 cm			≥ 8			
	Life cycle duration	≤ 1 year		Sarremejane et al. (2020)	Female wing length (mm)	< 5		
		> 1 year				≥ 5–10		
	Potential number of	< 1				≥ 10–15		
	Reproduction cycles	1				≥ 15–20		
		> 1				≥ 20–30		
	Aquatic stages	Egg				≥ 30–40		
		Larva				≥ 40–50		
		Nymph			≥ 50			
		Imago						
	Reproduction	Ovoviviparity			Sarremejane et al. (2020)	Wing pair type	1 pair + halteres	
		Isolated eggs, free					1 pair + elytra or hemelytra	
		Isolated eggs, cemented					1 pair + small hind wings	
		Clutches, cemented or fixed					2 similar-sized pairs	
		Clutches, free				Life-cycle duration	≤ 1 year	
		Clutches in vegetation (endophytic)					> 1 year	
		Clutches, terrestrial					< 1 week	
	Asexual reproduction	≥ 1 week to 1 month						
	Dissemination	Aquatic passive				Sarremejane et al. (2020)	Adult life span	≥ 1 month to 1 year
		Aquatic active						≥ 1 year
		Aerial passive						Lifelong fecundity
Aerial active		(number of eggs per female)						
Resistance form	Eggs, statoblasts, gemmules	≥ 100–1000						
	Cocoons	≥ 1000–3000						
		≥ 3000						
		< 1						
			Potential number of				< 1	

(Continued)

TABLE 8.2 (Continued)

References	Trait	Category	References	Trait	Category
		Cells against desiccation		Reproduction cycles	1
		Diapause or dormancy		Per year	> 1
		None		Dispersal strategy	Aquatic active
	Respiration	Tegument			Aquatic passive
		Gill			Aerial active
		Plastron			Aerial passive
		Spiracle (aerial)		Propensity to drift	Rare/catastrophic
	Hydrostatic vesicle (aerial)		Occasional		
	Locomotion and	Flier			Frequent
	Substrate relation	Surface swimmer			
		Swimmer			
		Crawler			
		Burrower (epibenthic)			
		Interstitial (endobenthic)			
		Temporarily attached			
		Permanently attached			
	Food	Fine sediment + microorganisms			
		Detritus < 1 mm			
		Plant detritus ≥ 1 mm			
		Living microphytes			
		Living macrophytes			
		Dead animal > 1 mm			
		Living microinvertebrates			
		Living macroinvertebrates			
		Vertebrates			
	Feeding habits	Absorber			
		Deposit feeder			
		Shredder			
		Scraper			
		Filter feeder			
		Piercer (plant or animal)			
		Predator (carver/engulfer/swallower)			
		Parasite, parasitoid			

using a fuzzy coding approach that consider within genera and across latitude variability (Table 8.2). It was built with information from c. 6000 published and unpublished studies and a time span of more than one century (the oldest publication used dated back from 1802). These studies were all performed in Europe and therefore, the Tachet database is supposed to be representative of the whole continent (Bonada & Dolédec, 2011). Despite this, its application to non-European Mediterranean Basin countries is potentially possible because most aquatic insect genera in these countries are also present in Europe and the use of the fuzzy coding provides some flexibility on its use. However, some genera found in these countries are not coded in the Tachet, and updates and adaptations of this database to all Mediterranean Basin countries are needed. For example, Bonada and Dolédec (2011) found 44 new genera present in Mediterranean Basin but not included in the Tachet database.

The particular characteristics of rivers in the Mediterranean Basin impose the presence of particular traits (Bonada & Resh, 2013; Cid et al., 2017). Mediterranean rivers are overall characterized by high seasonal and predictable flow patterns, with temporary rivers being a common river type. In comparison to other climate regions in the world, the seasonality and predictability of Mediterranean rivers (Tonkin et al., 2017) should have resulted in particular trait adaptations to the drying period. According to Lytle and Poff (2004), under these conditions, aquatic organisms should have acquired synchronized life history traits to the drying period instead of other strategies to escape the unfavorable moment. This is actually a common pattern in plants and terrestrial arthropods (Milla et al., 2010; Stamou, 1998) but also for aquatic insects. For example, the Mediterranean trichopteran *Mesophylax aspersus* have life cycles synchronized with the drying period. The pupae of this species emerge before the river dries up and adults estivate in nearby cave during the summer period and until the rewetting, when mating and egg laying take place (Salavert et al., 2008).

The characteristic hydrological variability in Mediterranean rivers has resulted in species with particular traits. In comparison to rivers in temperate Europe, aquatic insects in Mediterranean Basin have traits to cope with or recover from the dry period, along with dominant traits from pool habitats during summer (Hershkovitz & Gasith, 2013). For example, resistance forms, such as diapause or terrestrial egg laying, or resilient traits such as smaller sizes, aerial active dispersal, or multivoltinism were significantly more frequent in Mediterranean than in temperate rivers (Bonada & Dolédec, 2018; Bonada, Dolédec, et al., 2007). Many aquatic insects in the Mediterranean Basin have also traits adapted to the pool conditions, less frequent in the temperate rivers. Aquatic insects have usually larger sizes and imagos, and aerial respiration is common. This is because these pools habitats are usually characterized by Odonata, Coleoptera, and Heteroptera, whose richness values have also been considered as a measure of the temporary nature of rivers (Bonada et al., 2020; Bonada, Rieradevall, et al., 2006).

Resistance and resilience are the two response mechanisms to drying (Fig. 8.1). Several studies have found that dormancy is a common resistance mechanism in temporary rivers located in several climate regions of the world (Bogan et al., 2017; Strachan et al., 2015). Stubbington and Datry (2013) found a large proportion of aquatic insects in dry riverbeds in English temporary rivers, with dormancy stages such as eggs, larvae, pupae, or adults. Although the survival of this “seedbank” depends on the duration of the drying period (Storey & Quinn, 2013; Stubbington & Datry, 2013), some aquatic insects, such as the North American megalopteran *Neohermes filicornis*, can survive multiple periods of drying and rewetting (Cover et al., 2015). However, unless species are able to resist in disconnected pools, resilience strategies seem to be more common than resistance ones in Mediterranean Basin. The traits of most aquatic insects in these countries (smaller sizes, shorter life cycles, high dispersal ability) and the few existing rewetting experiments (Folch de la Iglesia, 2020) reveal that resilience plays a more important role than resistance when rivers completely dry up (Fig. 8.1). More studies on the potential resistance strategies of aquatic insects are, however, still needed. For example, there is evidence of the existence of aquatic insects with semivoltine life cycles in temporary rivers of the Mediterranean Basin, so specific strategies to survive the dry period in the sediments are required (e.g., the Plecoptera *Guadalgenus franzi*, López-Rodríguez et al., 2009).

Aquatic insects in the Mediterranean Basin are also supposed to be characterized by strong dispersal abilities. The alternative strategy to survive the dry period with a resistance stage is to leave the site before the river dries. This could be done by the aerial active dispersal of aquatic flying adults (i.e., Coleoptera or Heteroptera) or by synchronizing the life cycle with drying, with larvae or pupae emerging as adults and dispersing to other water bodies (Fig. 8.1). “To stay or leave” is considered an evolutionary trade-off (Bonada et al., 2017), and both strategies are related to traits allowing species to spread risk through space and time. Whereas spatial dispersal refers to the ability of species to leave a site and move to another one, temporal dispersal relies on the ability of species to enter into a dormancy stage and to remain in the site during the unfavorable conditions. Different species of aquatic insects are placed along the spatial and temporal dispersal continuum (Bonada et al., 2017). For example, the North American plecopteran *Mesocapnia arizonensis* has apterous males with aestivating nymphs (Gray, 1981), and the Iberian plecopteran *Guadalgenus franzi* most likely has similar dormancy strategies (López-Rodríguez et al., 2009), suggesting high temporal dispersal. In contrast, most beetles of the family Dytiscidae have strong dispersal abilities and unknown resistance strategies (Schäfer et al., 2006).

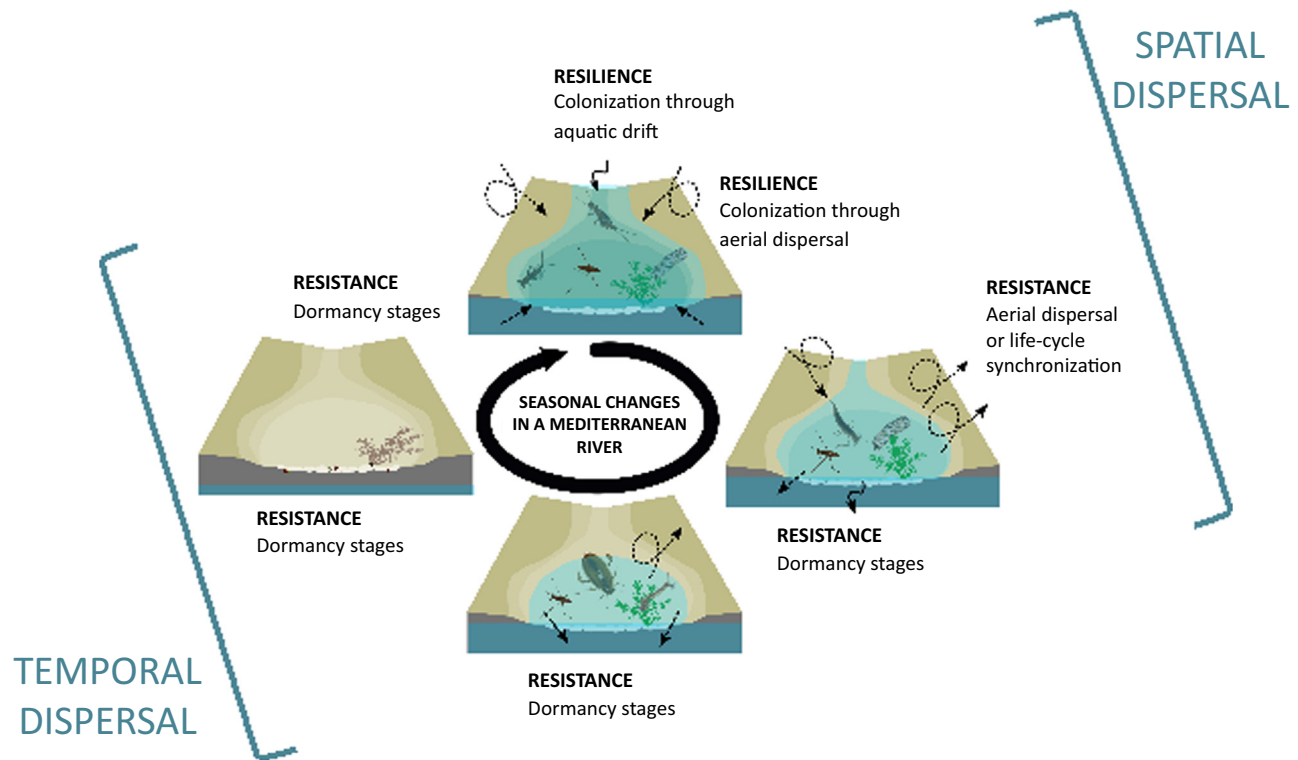


FIGURE 8.1 Resistance and resilience strategies of aquatic insects in Mediterranean rivers to drying. Spatial dispersal refers to the ability of species to leave a site and move to another one. Temporal dispersal relies on the ability of species to enter into a resistance stage and to remain in the site during the unfavorable conditions.

Most likely, as stated above, the aquatic insects in the Mediterranean Basin have a dominance of spatial dispersal but also may possess intermediate strategies (e.g., having both strategies, spatial and temporal dispersal), as in the case of *M. aspersus*. In this species adults flight dozens of kilometers to find caves where they estivate (Salavert et al., 2008). Actually, high spatial dispersal abilities are one of the most significant traits of insects in rivers of the Mediterranean Basin as a result of the higher dominance of Odonata, Coleoptera, and Heteroptera adapted to temporary rivers, as these three orders contain species known to be higher dispersers as adults (Bonada & Resh, 2013; Bonada, Dolédec, et al., 2007; Bonada et al., 2020).

Analyzing community composition by using a trait-based approach also provides information on functional processes (Violle et al., 2007). Most commonly used traits in aquatic insects are related to ecosystem functions such as body size, feeding habits, dispersal abilities, life history, and behavior characteristics (Bonada et al., 2017). Large aquatic insects, for example, contribute to increased biomass and ecosystem stability and decreased productivity, whereas shredders significantly contribute to the processing of organic matter. Species with high dispersal ability, short life cycles, and large offspring significantly increase ecosystem resilience, and some aquatic insects, such as cased-building Trichoptera, contribute to the retention of solids (Statzner, 2012). The understanding of the relationship between biodiversity and ecosystem functions is thus mediated by these traits related to functional processes. In a Mediterranean context, the high hydrological variability imposes seasonal biodiversity changes in taxonomic and trait richness and composition (e.g., García-Roger et al., 2013; Hershkovitz & Gasith, 2013) that can potentially compromise ecosystem functions. Temporal stability for functional diversity is, however, higher than for taxonomic diversity in the Mediterranean Basin (Dolédec et al., 2017), suggesting that there is a high trait redundancy and that ecosystem functions can remain relatively stable. In addition, in comparison to taxonomic diversity and composition, traits recover quickly after the dry period (Dolédec et al., 2017).

Beyond the use in fundamental research in the Mediterranean Basin, traits have been also used in applied research regarding bioassessment. The use of traits in bioassessment is considered a good approach and fulfils most criteria on rationale, implementation, and performance identified as the ideal bioassessment approach by Bonada, Prat, et al. (2006). They are able to respond to particular disturbances and, as mentioned before, to link disturbance effects to functional processes. For example, increases in organic matter would favor aquatic insects with aerial respiration by

decreasing dissolved oxygen, whereas pollution by heavy metals would favor those with smaller sizes that bioaccumulate less (Statzner, Bis, et al., 2001). This ability to respond to different disturbances has been very useful in disentangling natural from human disturbances. This is of great importance in rivers in the Mediterranean Basin where the effects of human disturbances are exacerbated by the low or no-flow periods of temporary rivers. Functional metrics seem to work well in these conditions and respond to human disturbances regardless of hydrological variability (Soria et al., 2020). In addition, traits related to dispersal have also the potential to increase the reliability of the bioassessment of these temporary rivers (Cid et al., 2020). The recurrent shifts among flow, disconnected pools, and dry riverbeds in temporary rivers imply the need for recolonization of aquatic insects and thus the arrival of aquatic insects from other water bodies. If this arrival is in addition constrained by landscape configuration, the recovery of biodiversity during the rewetting in temporary rivers may be limited. In these conditions, the use of traditional biological indices that rely on species richness is not reliable because low richness does not imply low biological quality but rather high isolation (spatially and temporally). Therefore, the incorporation of the dispersal ability of aquatic insects and spatial constraints for it (i.e., considering the metacommunity approach) would contribute to improving the bioassessment of rivers in Mediterranean Basin and in other regions worldwide (Cid et al., 2020).

Dispersal and metacommunity dynamics

Hexapods are a group that show diverse dispersal modes among taxa and development stages, a strategy that may help increasing their success in dispersing effectively depending on the environmental conditions and the inhabited system characteristics. Thus, active dispersal by flight is the usual but not exclusive mode of dispersion for adult insects (Bilton et al., 2001). Some winged adults also present passive aerial dispersal since their movement is strongly affected by winds (e.g., Ceratopogonidae, Chironomidae, Culicidae; Grönroos et al., 2013), and some larvae might passively disperse by migratory birds (Green & Figuerola, 2005). In lotic systems the main dispersal modes include drift (downstream, active or passive), active movement of aquatic larvae (up- or downstream), and aerial dispersal of adult winged stages (active, passive) (Sondermann et al., 2015). In contrast, dispersal in lentic systems exclusively relies on aerial modes (both passive and active). However, dispersal processes are highly influenced by environmental conditions. For example, insect flight may be influenced by landscape, atmospheric, and habitat conditions and biological interactions (Boix et al., 2016), and drift highly depends on river flow. In fact, some winged adults such as damselflies, stoneflies, and caddisflies have some preferred conditions (microclimatic and light conditions) for dispersal and can even stop dispersing if conditions change (Briers et al., 2002; Collier & Smith, 1998). Thus, this emphasizes their ability to modify dispersal based on environmental conditions (Bilton et al., 2001; De Bie et al., 2012). Moreover, within lotic systems, the hydrology characteristics generate distinctive features at dispersal level. In Mediterranean systems the flow cessation or bed dryness favors flying to other less-dry sites, and therefore it promotes the aerial active dispersal. By contrast, in temperate streams, the permanent action of flow increases downstream drift, and, consequently, promotes aquatic passive dispersal (Bonada, Dolédec, et al., 2007). Interestingly, in pond systems, in which drift is not possible, and so aquatic dispersion among ponds is not relevant, there are also differences between pond typologies. Thus, Mediterranean ponds are more dominated by organisms showing a passive aerial dispersal mode than continental ponds, in which active aerial dispersal is enhanced (Céréghino et al., 2012).

But why is dispersal so important? Communities are not isolated entities but connected to other communities through dispersal movements. In fact, a set of local communities that are linked by dispersal of multiple potentially interacting species is the definition of a metacommunity (Hanski & Gilpin, 1991; Wilson, 1992). In the metacommunity context, communities are structured by a combination of local processes like environmental filtering and species interactions, and regional processes driven by the dispersal of organisms among localities on a landscape (Holyoak et al., 2005; Leibold et al., 2004). Therefore, inherent in the metacommunity perspective is the comprehension of how organisms move on landscapes (Brown et al., 2018). In the case of aquatic systems, an organisms' movement over the landscape, i.e., its dispersal, greatly relies on the connectivity among the communities that form the network (Altermatt, 2013; Brown et al., 2018; Liu et al., 2013). However, this connectivity is not static, and in some cases could change along and between years, mainly due to seasonal and interannual variability. This is the case of Mediterranean rivers that present sequential seasonal flooding and drying periods, with increasing loss of habitat connectivity over an annual cycle that can result in temporary isolated habitats especially during severe droughts. This temporal pattern generates different levels of hydrological connectivity among seasons, with an expansion phase in the wet period (i.e., autumn-winter) and a contraction phase in the dry period (i.e., spring-summer) (Bernal et al., 2013). This seasonal hydrological variability affects biological communities (Robson et al., 2013) and by extension, the metacommunity dynamics (Cañedo-Argüelles et al., 2020; Sarremejane et al., 2017). Then, during the wet period, communities are mainly directionally connected due to the water flux (functioning more like temperate rivers; Carrara et al., 2014; Tonkin et al., 2018), from headwaters to downstream since downstream reaches are connected to

effectively function in a given habitat; [Leibold et al., 2017](#)) over other mechanisms as a determinant of community assembly patterns in different organisms including hexapods: macrophytes (in this case together with dispersal limitation; [García-Girón et al., 2019](#)), ostracods ([Castillo-Escrivà et al., 2017](#)), macrofauna (i.e., invertebrates and amphibians; [Tornero et al., 2018](#)), and invertebrates (including cladoceran and macroinvertebrates; [Waterkeyn et al., 2008](#)). However, it is also true that the detection of some metacommunity archetypes, like the mass effects (i.e., a mechanism in which there is net flow of individuals created by differences in population size or density in different patches; [Schmida & Wilson, 1985](#)), is highly scale dependent, being more probably detected in smaller geographical ranges than in larger ones ([Heino et al., 2014](#); [Tornero et al., 2018](#)). Besides this scale dependency, the type of organisms' dispersal is also relevant, since some types are more prone to track environmental conditions and so to show the species sorting signal (i.e., active aerial dispersers, like many insects).

On the other hand, the location of a pond within a pond network with a centrality-isolation gradient can influence insects' colonization, with the central ponds often having the highest abundance and richness of insects. In this sense, [Cunillera-Montcusí, Boix, et al. \(2020\)](#) found clearly differentiated abundance and richness patterns between central and isolated ponds for strong dispersers (i.e., Coleoptera: Dytiscidae, Helophoridae, and Hydrophilidae). Hence, when the neighboring waterbodies were drying, the central ponds experienced an increase in individual arrivals. However, weak dispersers (i.e., Diptera: Ceratopogonidae, Chironomidae, and Ephydriidae) followed more or less the same pattern of increasing abundance during the hydroperiod independently of pond location. Moreover, in highly connected systems, in which the centrality-isolation gradient is blurred, species (mainly insect species) demonstrated weak dispersal limitations ([Florescio et al., 2014](#); [Tornero et al., 2016](#)). Finally, the fact of being an active or passive disperser can also create patterns of nestedness within metacommunities (i.e., when species-poor sites contain subsets of assemblages found in species-rich sites; [McAbendroth et al., 2005](#)). In this sense, [Florescio et al. \(2011\)](#) observed that winged insects were more highly nested than nondispersing taxa, because the dispersal movements of insects after the dry period would help maintain the nested structure of the macroinvertebrate assemblages across the pond network.

In summary, aquatic insects often have adaptive strategies for effective dispersal, and especially in the case of those inhabiting the Mediterranean Basin, these type of strategies gain importance due to the recurrent drying or filling of both lotic and lentic ecosystems. Overall, the diverse literature including both lotic and lentic environments from the Mediterranean Basin has evidenced that both the dispersal mode (active or passive) and dispersal ability (weak or strong) of aquatic hexapods may have important effects on metacommunity structuring and dynamics.

The role of aquatic insects in food webs

Trophic interactions determine the structure of a community and underly crucial functions in ecosystems. Trophic relationships control energy flow from primary resources to consumers (bottom–up interactions), while, at the same time, some consumers potentially limit the biomass of some taxa through a top–down control. The strength of these consumer–resource interactions has large effects on community dynamics. The study of food webs enables the extension of the attributes of individuals and populations to ecosystem properties such as production and element cycling ([Thompson et al., 2012](#)). In this way, a food web perspective can help us better understand the links between biodiversity and ecosystem functioning and how to advance in the conservation and management of functional ecosystems.

In freshwater habitats under the Mediterranean climate, seasonality affects food source availability from terrestrial and aquatic primary producers. In streams and during the wet period (autumn–winter), longitudinal, lateral, and vertical flow connectivity is restored and the inputs of allochthonous organic matter (terrestrial origin) are distributed and processed in the river network. During the dry period (spring–summer), high temperature and flow contraction favor autochthonous (river origin) primary production although there is a reduction of river connectivity ([Gasith & Resh, 1999](#)). Ponds fed by fluvial drainage or directly by rainfall also reflect fluctuations in food availability related to the hydroperiod and interannual climate variations. In addition, the Mediterranean Basin has many karstic areas with spring-fed ponds that are highly stable ([Sahuquillo & Miracle, 2013](#)) as well as permanent streams. Thus, depending on the degree of flow intermittence, the Mediterranean inland waters span a wide range of hydrological conditions that can determine the quality and quantity of the food resources conditioning trophic relationships. The characteristics of the food resources, however, are also affected by factors other than the hydroperiod (e.g., water chemical characteristics and land uses). Since these factors interact to determine the biotic and abiotic conditions in the system, the food web in a particular freshwater system will reflect the consequences of the effects of all these factors.

Essentially, all aquatic insects are omnivorous. For example, shredders ingest not only leaf tissue and the associated microbiota, but also diatoms and other algae attached to the leaf surface, as well as small invertebrates. First described 47 years ago, the functional feeding group (FFG) approach ([Cummins, 1973](#)) is based on a correspondence between the

categories of nutritional resources present in the environment and the analysis of insect feeding based on the morpho-behavioral mechanisms of food acquisition. Six FFGs were initially proposed and linked to six food resource categories. Among the FFGs there are obligate and facultative (i.e., flexible requirements for more than one food resource) members. There are few specialists feeding on a specific food resource during the entire life cycle. Despite this, the FFG designation is based on the preponderance of a food item and on the most probable feeding mode (Merritt et al., 2019). Among the insect orders, we find representatives of all the different FFGs. Instead of only classifying a taxon into its main FFG, a more accurate approach was adopted by Tachet et al. (2010) for European freshwater macroinvertebrates that involved using a fuzzy system for the proportional assignment of a taxon (at the family, genus, or species level) to different FFGs. Nevertheless, the values given to each taxon, which result from known variations in size, season, and place of origin, cannot always be extrapolated to the same taxon in a specific place and season (a similar pattern that also occurs with other labile traits such as voltinism, Bonada & Dolédec, 2018). This is especially important in Mediterranean freshwater systems, where the source, identity, and quality of the food available for consumers change over the course of the year, requiring long-term studies to characterize the consumer diet well (Tierno de Figueroa et al., 2019).

Insects can be top predators in a food web or be part of the diet of other top predators (other invertebrates, amphibians, and fish). The most common insect predators include those belonging to Odonata, Plecoptera, Megaloptera, Trichoptera, and Diptera. Mayflies and Diptera are the common prey taxa for invertebrate predators (Peckarsky & Lamberti, 2017).

How to analyze a food web

The most common approach for the identification of trophic relationships is the analysis of gut contents. This approach provides a minimum estimate of the biomass and diversity of the diet, although these can be underestimated in most aquatic consumers since some food may be unrecognizable or the predator may ingest only fluids or soft parts. Gut analysis provides information about what is ingested, but not all ingested material is necessarily assimilated. Analyses of stable isotope ratios of C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) have contributed to food web research over the last 30 years. Values of these isotopes in animal tissues have been used as indicators of food sources and trophic level, since $\delta^{13}\text{C}$ values can distinguish primary producers and increases in the $\delta^{15}\text{N}$ value can indicate a move to a higher trophic level (e.g., Muñoz et al., 2009; Vander Zanden & Rasmussen, 2001). Therefore, biplots for C and N isotopes reveal the food web structure. However, in aquatic ecosystems, the $\delta^{13}\text{C}$ of algae in periphyton is sometimes too variable and detrital sources from different origins (terrestrial or aquatic) are mixed, making assessment difficult. Similarly, for $\delta^{15}\text{N}$, the isotope enrichment factor per trophic level of freshwater invertebrates is likely to be smaller and more variable than that of other animals. Other isotopes that are used in diet analysis are $\delta^2\text{H}$ and $\delta^{34}\text{S}$, the latter is especially useful for discriminating between marine and terrestrial nutrient sources and may have utility in wetlands and saltmarshes.

The use of fatty acids as trophic markers has provided information on trophic links in open-ocean, estuarine, lake, and river food webs. Some polyunsaturated fatty acids are good markers for diatom, bacteria, or bryophytes and have been proposed as markers for a terrestrial versus aquatic matter origin in streams (Torres-Ruiz et al., 2007). The measurement of the stable N isotopic composition of amino acids (SIAA) has recently been applied to estimate the trophic position of consumers in freshwater systems. In amino acid metabolism, glutamic acid is subjected to deamination and transamination, which lead to increased isotope enrichment per trophic level. In contrast, phenylalanine retains its amino group during metabolism as animals cannot synthesize phenylalanine themselves, resulting in little isotope enrichment in the food chain. Thus, in a single food chain, the trophic level of an animal can be estimated only from its $\delta^{15}\text{N}_{\text{Glu}}$ and $\delta^{15}\text{N}_{\text{Phe}}$ values, in a similar way to that when using C and N isotopes (Ishikawa et al., 2014).

Recent advances in DNA-based approaches have led to more accurate methods for identifying prey species from gut or fecal samples. These techniques can be used in the cases where it is difficult to obtain good results with other methods, such as for insect predators that feed on fluids or when the morphological identification of remnants is impossible. A standardized DNA region (DNA barcode) is amplified by PCR, with the amplicons sequenced and then compared to a reference database for the identification of prey. Good results have been obtained with a wide taxonomic range of predators, fish, and insect adults like the members of Odonata. However, more detailed work is needed, particularly in freshwater systems (Kaunisto et al., 2017; Pompanon et al., 2012).

Food web structure

Most undisturbed stream food webs have approximately three or four trophic levels and are characterized by a high degree of connectivity. In general, disturbed aquatic systems or those under extreme conditions (e.g., long dry periods)

typically have simplified food webs (Townsend et al., 1998). Reductions of food chain length linked to drying are associated with the loss of large top predators (fish or invertebrates) (Sabo et al., 2010). Detritus and primary producers, including algae, bryophytes, and vascular macrophytes, are the food sources that occupy the basal level. A similar structure is found in lentic systems, although the primary producers can sustain preferential and long food chains in some deep and permanent water bodies. Grazers (direct consumers of primary production) and detritivores (consumers of detritus coming from algal and terrestrial organic matter) occupy the primary consumer trophic level. As producers and detritus are associated with heterotrophic microbes and microorganisms (e.g., ciliates), these consumers function as both primary and secondary consumers. Predators often have mixed diets that include some combinations of detritus, diatoms, animal prey, and even other predators, placing them between trophic levels 3, 4, and, in some cases, 5. As in other systems, omnivores (consumers that feed on different trophic levels) often dominate communities in Mediterranean inland waters and it is common that the prey–predator interactions form a complex food web rather than a simple and linear food chain. High levels of omnivory buffer food web dynamics from fluctuations in water flow. Food depletion may increase cannibalism and intraguild predation in aquatic insects, which are common among the larvae of beetles and odonates and in omnivorous predators such as the caddisfly *Hydropsyche*.

Among detritivores, insect shredders are critical for mobilizing energy from leaf litter to consumers in streams and may play a similarly important role in small ponds (Holgerson et al., 2016). In Mediterranean rivers, the low abundance or the lack of shredders has been linked to the low quality of the organic matter when flow returns after drying (Álvarez & Pardo, 2009; López-Rodríguez et al., 2012). For example, in the permanent river Riera Major, an alder-shaded, second-order stream (NE Spain), the shredding caddisfly *Halesus radiatus* is dominant in autumn, but a high shredder biomass is present all year round because conditioned leaves are available for the insect. In contrast, in the nearby temporary river La Solana, a second-order tributary in the same basin, shredders are mainly present in autumn and significantly decline thereafter, with decreases in discharge and benthic organic matter (Muñoz, 2003).

The quantitative study of trophic link strengths in a permanent Mediterranean river food web in the south of Spain (Peralta-Maraver et al., 2017) revealed the presence of small groups of strong links and many other weak interactions and although the node with a high number of interactions was similar over time, the strength of the links differed seasonally. This structure contributed to a certain degree of stability against seasonal environmental variability in these systems.

Temporal variability of resource–consumer interactions

In most freshwater systems, detritus predominating as food source favors the heterotrophic pathway. Allochthonous matter and its associated microbiota are an important food source in many low-order streams. Small ponds are fed by abundant detritus originating from adjacent terrestrial systems. However, even in heavily shaded streams with low algal standing crops, algae support freshwater organisms with their rapid turnover and high nutritional value (low C:N ratios) compared to detritus and can strongly influence the structure of entire food webs. Similarly, most pond consumers feed on both algae and detritus coming from leaves, but algal-based pathways are prevalent, challenging the common assumption that small net-heterotrophic low-light ponds have detritus-based food webs.

In temporary Mediterranean streams, seasonality and its associated changes in hydrological conditions determine the relative importance of allochthonous versus autochthonous food sources over time. Pulses of riparian litterfall occur mostly in summer with water stress, with a second peak occurring in autumn due to leaf abscission (e.g., Sanpera-Calbet et al., 2016). When flow resumes in dry stream channels, high levels of light and temperature promote a rapid increase in periphyton biomass (Acuña et al., 2007; Álvarez & Pardo, 2009), thus increasing the importance of benthic primary producers. In Fuirosos, a third-order temporary river (NE Spain), the contribution of algal biofilm to the diet of the consumers is relevant during the entire hydrological cycle. The highest contribution of biofilm to collectors, shredders, and predators has been observed in the drying phase, but additionally for the last two groups, biofilms is also relevant when water flow is disconnected (fragmentation), coinciding with the highest abundance of autochthonous resources. The contribution of detritus is the greatest in the late recovery phase, following leaf autumn abscission (Fig. 8.3; Mas-Martí, 2014). The assimilation of resources is related more to their overall abundance than to their quality. Interestingly, the increase in the importance of autochthonous resources to the biomass of consumers is transferred up in the food web in the dry period.

The dependence of the relative dominance of a basal resource on water flow dynamics and hence, energy pathways through consumers has been observed in other Mediterranean streams with interannual differences. In the Eel River (California; Power et al., 2013), algal (*Cladophora*) growth is limited in dry years due to the control exerted by a grazer case-living caddisfly (predator resistant). During wet winters, floods kill or export these grazers and large *Cladophora* blooms proliferate in the following

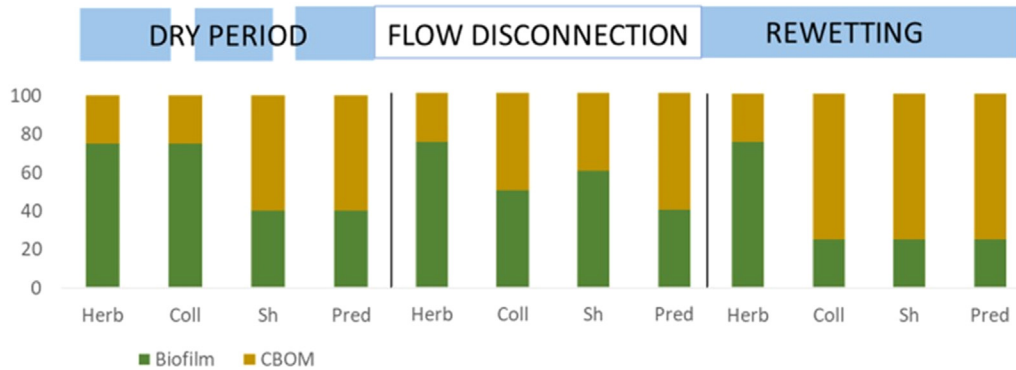
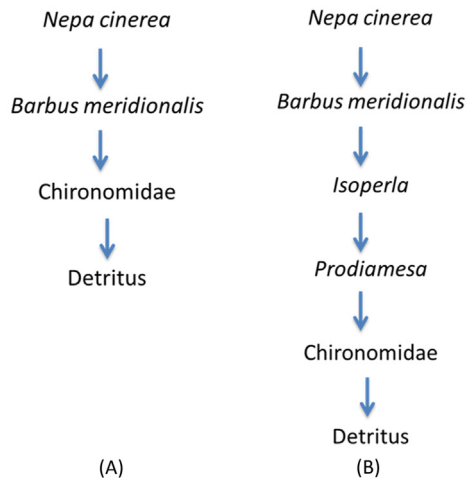


FIGURE 8.3 Mean percent contribution of epilithic biofilm and coarse benthic organic matter (CBOM) to consumers (analyzed by SIAR mixing model, using stable isotopic analysis) in the different hydrologic phases in Fuirosos stream: dry period, flow disconnection, and rewetting (flow recovery). *Herb*, Herbivores; *Coll*, collectors; *Sh*, shredders; *Pred*, predators. Adapted from Mas-Martí, E. (2014). Climate induced changes in headwater streams: Effects of warming and drought on resource-consumer trophic interactions (*Ph.D. thesis*). Spain: University of Barcelona, Barcelona. 162 pp.

2002 wet summer

2003 dry summer

FIGURE 8.4 Example of a food chain in Fuirosos stream in two consecutive summers with different hydrological characteristics. (A) Summer 2002 (wet period preceded by high precipitations in winter-spring); (B) summer 2003 (dry summer with stream flow fragmentation).



spring and summer, which sustain other grazers like mayflies and free-living midges. In Fuirosos, algal sources are more important to food webs after wet years with severe winter floods. Winter floods remove the accumulated detritus and organic matter-rich sediments (Acuña et al., 2007). With lower storage of organic matter, the overall detritivore biomass decreases. These interannual hydrological differences also lead to differences in the food web structure between years in Fuirosos. For example, over two consecutive summers characterized by different winter-spring hydroperiods, there are clear differences in the properties of the food web (Fig. 8.4, Table 8.3). A drier winter-spring period favors higher diversity in the habitat patches (pools, riffles, and isolated pools) and food sources (algae, detritus and preys), producing longer average food chain length. The proportion of intermediate consumers is higher and the number of omnivorous species also increases.

In floodplains where water dynamics are governed by a seasonal inundation regime and lateral hydrological connectivity, a rich array of temporary water bodies occurs. Complexity of the trophic structure is governed by the persistence of water (O'Neill & Thorp, 2014). Food chain length and trophic complexity are low at the beginning of an inundation period due to high trophic redundancy. Later, insects colonize the ecosystem, bringing new trophic species that can increase the food chain length and trophic structural complexity. The longer the hydroperiod, the more diverse the trophic niches are and higher the colonization and insect oviposition.

Drying also determines spatial variation in the density and composition of communities at small spatial scales. For example, drying increases the density-dependence processes that also influence trophic interactions. In isolated pools after flow

TABLE 8.3 Food web properties in two consecutive years during summer.

	Summer 2002	Summer 2003
Average long chain	1.39	1.86
Maximum trophic levels	4	6
Ratio basal species/total	0.13	0.12
Ratio intermediate species/total	0.22	0.33
Ratio top species/total	0.65	0.55
Omnivorous species	7	9

Summer 2002 was a wet period preceded by high precipitations in winter-spring that maintained connected the water flow during all summer. Summer 2003 was drier with stream flow fragmentation.

fragmentation, the density of invertebrates increases, causing changes in predation intensity (Bonada et al., 2020; Gasith & Resh, 1999). The abundance of large-bodied insect predators (e.g., Dytiscidae and Odonata) is low during high flow, but becomes dominant during low flow (Acuña et al., 2005). In Fuirosos, for example, changes in habitat dynamics induce changes in food source availability for consumers. The odonate *Onychogomphus* is a predator, consuming midges and mayflies (mainly *Baetis* and *Ephemerella*), in summer and in reaches that maintain flow connectivity. However, it is omnivorous in disconnected pools consuming diatoms and detritus in addition to *Baetis* and worms (Naididae).

In standing ponds, the diets of predatory insects vary from highly specialized to broadly general. Species with similar sizes that forage in the same microhabitat (e.g., bottom or water column) have widely overlapping diets, but separable from those insect predators with different body sizes or habitat use, although individuals can shift between food webs according to food availability (Klecka & Boukal, 2012). Spatial connectivity between temporary ponds (Tornero et al., 2016) or disconnected pools in temporary rivers facilitates dispersion and colonization of the macrofauna from one pond to another, determining their trophic structure (McIntosh et al., 2017).

Ontogeny

Ontogenetic diet shifts associated with individual growth in size are common across all major groups of predatory aquatic insects. They occur in *Notonecta* bugs and in larval odonates in both running and standing waters (see references in Klecka & Boukal, 2012). Odonate larvae begin to feed on rotifers and even protozoans after hatching, later switching to larger benthic prey. Some predatory Plecoptera and Trichoptera are herbivorous during the first larval stages. In a seasonal stream, López-Rodríguez et al. (2018) described that the stonefly *Isoperla morenica* reduces its intake of animal matter with size, whereas the dragonfly *Onychogomphus forcipatus* increases it. Plasticity in food habits could drive the success in persisting in or colonizing ecosystems. If animals must adapt to the fluctuations in their habitat to complete their life cycle (Townsend et al., 1998), they may thus adapt their food preferences during their developmental period according to the quantity and quality of the food resources available.

Donor aquatic ecosystems to terrestrial ecosystems

Freshwater and terrestrial food webs are connected at multiple trophic levels by cross-habitat flows of organic matter and organisms (Larsen et al., 2016). The importance of allochthonous terrestrial organic matter to aquatic food webs was recognized decades ago with more recent studies describing reciprocal aquatic-terrestrial subsidies that strongly affect consumers and food webs in both habitats.

Aquatic ecosystems may be important sources of energy and nutrients for adjacent terrestrial systems. A large part of aquatic productivity is exported to land consumers (spiders, ground beetles, lizards, birds, and bats) via insect emergence or even larvae (some terrestrial birds, such as *Cinclus cinclus*, can dive in pursuit of aquatic insects). Most of the data about the importance of this process come from streams in which more than 60% of the emergent insect biomass are dipteran adults, followed by adults from Ephemeroptera, Plecoptera, Trichoptera, and Odonata (Popova et al., 2017).

Aquatic algae can also be consumed directly by specialist terrestrial algivores (e.g., grasshoppers), in which nearly 90% of the $\delta^{13}\text{C}$ signature indicates that the carbon derives from epilithic algae rather than terrestrial vegetation (Power et al., 2013). This aquatic source of energy is more available to terrestrial animals when water flow decreases in

temporary rivers. The drying of lentic systems or the disconnected pools in temporary rivers can also accumulate aquatic insects in the shoreline, making them available for terrestrial predators. Aquatic insects may be a superior food quality source for terrestrial consumers, not only as a source of C, but because they contain high concentrations of essential polyunsaturated fatty acids obtained from aquatic food webs (Martin-Creuzburg et al., 2017).

Disturbance effects on aquatic insects

Aquatic insects have been acknowledged as quality indicators of freshwater systems that have been affected acute or chronically by a disturbance (Armitage et al., 1983; European Commission, 2000; Verdonschot & Nijboer, 2004). Their ubiquitous presence, high abundance, intermediate lifespan, and position in the trophic chain (i.e., between primary producers and secondary consumers) has made aquatic insects a more suitable candidate to indicate long-term environmental conditions and quality than for example chemical or physical properties of aquatic systems (see the section on “Biological assessment of water quality”). Consequently, literature focusing on aquatic insects and disturbances is abundant even within a restricted region such as the Mediterranean Basin. Thus, in this section we have focused on four main disturbances for aquatic systems: changes in water quality, habitat loss and fragmentation, climate change consequences, and invasive species (Fig. 8.5) that exemplify how aquatic insects group respond to a change in habitat conditions.

A disturbance could be defined as “(…) any relatively discrete event in the time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment” (White & Pickett, 1985). This definition gives a wide window in which to include what is a disturbance, ranging from the direct change in environmental conditions due to human intervention (e.g., heavy metals, salinization, eutrophication), the landscape structure alteration due to the direct elimination of habitats (e.g., habitat loss, damming, habitat fragmentation), the change in the frequency or harshness of already natural processes (e.g., drought, floods, wildfires) or the arrival of another species (e.g., fish introduction or insect invasive species). All these disturbances are directly or indirectly human-mediated and therefore, caused by human activity either through specific punctual activities such as pesticides

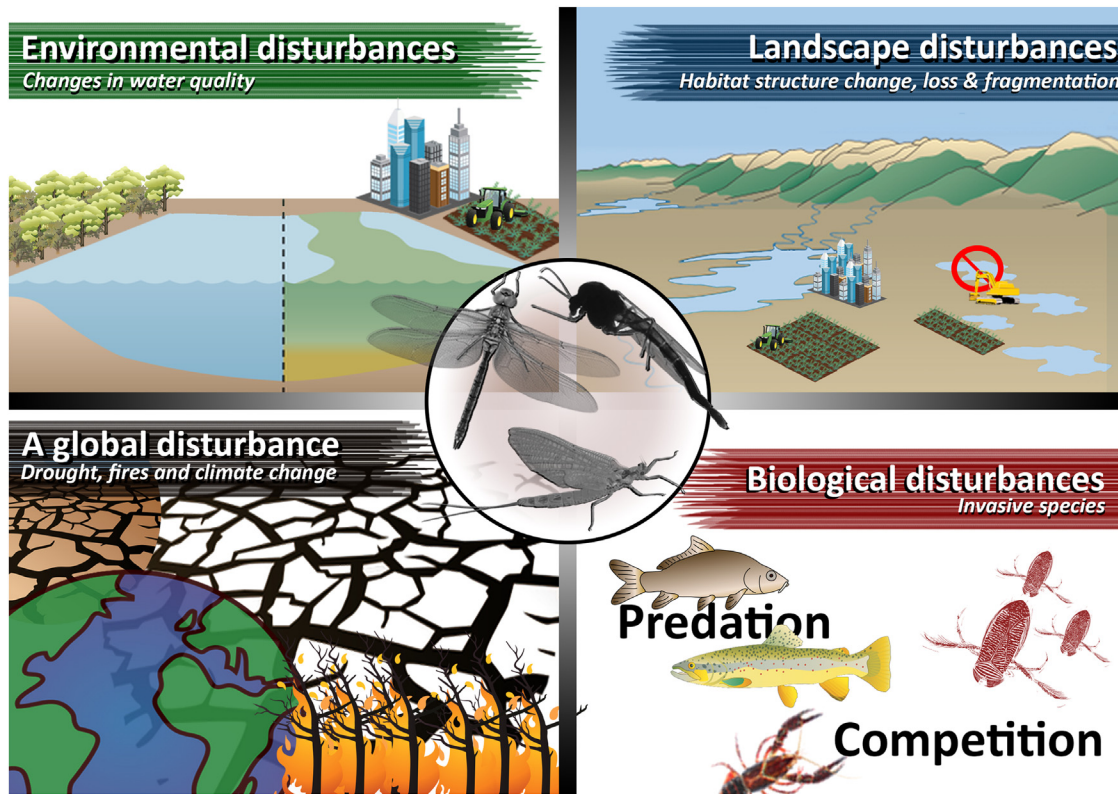


FIGURE 8.5 Schematic illustration of the four main disturbances affecting aquatic insects discussed in this chapter. Central invertebrate images (Odonata, Ephemeroptera, and Diptera) have been ceded by Jesús Ortiz and David Cunillera-Montcusí. Smaller drawings and symbols have been downloaded from IAN Image Library. Finally, small corixids, bottom-right section, are original drawings ceded by Rita Montcusí Rovira.

usage (Topaz et al., 2020) or mining activities (Solà et al., 2004) or by more diffuse and bigger-scale activities such as climate change (Alba-Tercedor et al., 2017) or land-use changes (Bruno et al., 2014). Overall, all these impacts are affecting insect abundances and diversity across the globe in what has been said as a death by a thousand cuts (Wagner et al., 2021). In contrast, some reports have detected an increase in aquatic insects' diversity but not in their abundance across Europe (Pilotto et al., 2020). Nevertheless, we still need better resolution and datasets that can provide a clearer view in this extremely complex problematic (Wagner et al., 2021).

Environmental disturbances: changes in water quality

In general, changes in water characteristics lead to a change in species presence or abundance as a consequence of species fitness limitations or direct toxicity. Nutrient increases primary production, and the consequent eutrophication can lead to dissolved oxygen depletion to which only few insect species can survive (e.g., Syrphidae dipterans which have a respiratory conduct to breath aerial oxygen). Therefore, lowland aquatic systems, where agricultural activity and human settlements (e.g., wastewaters) are more frequent, present depleted and less singular insect communities due to eutrophication (e.g., Bazzanti et al., 2017; Bruno et al., 2014; Fenoy & Casas, 2015; Mor et al., 2019; Pilotto et al., 2015; Sánchez-Morales et al., 2018), where only high tolerant taxa (e.g., Syrphidae or Ephydriidae) can survive. Furthermore, pesticides usage, directly targeted to eliminate insects, can reach high toxicity values in flooding periods causing high stress situations in aquatic habitats (Topaz et al., 2020). However, increase in nutrients, as well as entrance of dissolved salts, can lead to changes on system salinity, which is one of the main aquatic insect community determinants (Bruce et al., 2012; Damásio et al., 2011; Pallarés et al., 2016, 2017; Picazo et al., 2012; Touaylia et al., 2013). In fact, even salinity decrease due to dilution can impact aquatic insects and loss of their singularity (Boix et al., 2008; Cañedo-Argüelles & Rieradevall, 2010; Gascón et al., 2009; Gutiérrez-Cánovas et al., 2012). Salinization impacts on insects imply physiological stress due to osmoregulation, which require previous adaptations in order to tolerate them (Cañedo-Argüelles, 2020; Pallarés et al., 2016, 2017). Finally, while eutrophication and salinization might be understood as natural processes that are fostered by human activities, heavy metal inputs in aquatic systems are less frequent and their direct toxicity and consequences can erode insect diversity from aquatic habitats and remain with toxic values for years if no intervention is carried (Damásio et al., 2011; Solà et al., 2004). In particular for temporary rivers, the impacts of all these environmental disturbances are exacerbated during the drying period, where pollutants become more concentrated in low or no flows (i.e., disconnected pools; Bonada et al., 2020).

Landscape disturbances: habitat structure change, loss and fragmentation

At the regional level, changes in habitat structure (alteration of river beds, damming, canopy loss) can cause changes in habitat characteristics (e.g., available resources, habitat conditions, populations disconnection) which can lead to a loss of insect richness and impoverishment of communities (Lobera et al., 2017). Such alterations of system structure also influence hydrological connectivity which can affect dispersal dynamics between communities, and consequently generate a loss of biodiversity due to a decrease in new organism arrivals (Gallardo et al., 2014). The impact of such alterations on the loss of biodiversity can become even greater than the impact of eutrophication (Bruno et al., 2014; Pilotto et al., 2015). In lotic systems connectivity relevance is assumed, but in lentic systems it is rarely acknowledged although the maintenance of an heterogenous pondscape is key for insect diversity (Jooste et al., 2020) and, consequently, the loss of lentic habitats can lead to a loss of invertebrate species diversity (Downing, 2010; Horváth et al., 2019; Pekel et al., 2016). In temporary rivers in the Mediterranean Basin, however, these landscape disturbances are also considered natural disturbances when linked to natural drying (Soria et al., 2020). As drying in the Mediterranean Basin has been a long-term phenomenon, aquatic insects are adapted to fragmentation and thus can be more resistant and resilient to human-driven landscape disturbances, a phenomenon known as co-tolerance (Soria et al., 2020).

Global disturbances: drought, fires, and climate change

On a wider global scale, climatic alterations can foster the previously commented consequences both at the local and the regional scales. The case of the Mediterranean Basin is especially threatening as the situation and the pressures under which the aquatic communities are subject have increased in the recent years compared to central European regions (Kalkman et al., 2008). In the Mediterranean Basin an increase in temperature and a decrease in water availability during the year (i.e., increase in extreme events) are expected (Kovats et al., 2014). Drought frequency and duration are strong determinants of insect communities (Boix et al., 2016; Hershkovitz & Gasith, 2013; Williams, 2006). An

increase in drought harshness will probably lead to the loss of some currently temporary habitats and the change from permanent to temporary classification of many of the Mediterranean waterbodies. One of the consequences of drought will be the increase in salinity values in water bodies which, as indicated, will constrain insect communities to those only adapted to them (Arribas et al., 2015; Boix et al., 2008; Bruce et al., 2012; Gascón et al., 2009; Picazo et al., 2012). Insect communities will therefore be forced to cope with such harsher conditions (Pace et al., 2013), with survival of only those specialized species (e.g., Coleoptera species adapted to high salinity) that are better adapted to such new conditions (Pallarés et al., 2016, 2017). Water scarcity can also foster dissolved O₂ depletion, which can negatively affect sensitive species, thereby increasing species drift (Calapez et al., 2017). Furthermore, in lotic systems, stronger drought periods added to more frequent flood events can also decrease species diversity (López-Rodríguez et al., 2012). Overall, rises in temperature and water scarcity should increase Mediterranean aquatic systems harshness, leaving only the few species adapted to those conditions (Kefford et al., 2016). One example would be coleopterans adapted to high salinities (Pallarés et al., 2016), which would be expected to find more habitat available, unless other negative, human-induced degradations of this habitat are present (Arribas et al., 2015). However, some species, from more wet environments (e.g., high-altitude regions), which are endemic to the Mediterranean Basin might be completely lost due to the disappearance of their natural habitat (Guareschi et al., 2018; Kroll et al., 2017; Múrria et al., 2020). Therefore, future predictions based on climate change impacts in Mediterranean countries clearly forecast a generalized loss of insect species richness (Alba-Tercedor et al., 2017).

While climatic alterations due to global change can have a direct effect (i.e., average temperature increase and water scarcity), these conditions can also foster more punctual disturbances such as wildfires (Pausas & Fernández-Muñoz, 2012; Turco et al., 2018). As an example of catastrophic disturbances induced by global change, wildfires can impact aquatic systems indirectly while also fostering previously described impacts such as nutrient entrance, eutrophication, and structural changes to the habitat (McCullough et al., 2019; Minshall et al., 1989). In this sense, Mediterranean aquatic systems rapidly recover after these disturbances although some species can be impacted in the short term (Cunillera-Montcusí et al., 2019; Verkaik et al., 2013). However, at the same time, drought plays a key role in determining the normal community structure as well as their responses to wildfires (Cunillera-Montcusí, Arim, et al., 2020; Verkaik et al., 2015). Although such communities might be considered as “resilient,” future scenarios might compromise this response (Cunillera-Montcusí et al., 2020).

Biological disturbances: invasive species

All the previously described disturbances could have short-term impacts or could produce more extensive impacts on environmental conditions and thus affect habitat structure for resident biota. However, changes in the biological interactions through the introduction of a predator (i.e., fish), another competitor (i.e., invasive insect or other invertebrate species), or a primary producer (i.e., algae) can also be considered as a disturbance and generate an impact on insect communities (e.g., Céspedes, Coccia, et al., 2019; Ferreras-Romero et al., 2016; Ladrera et al., 2018). Fish predation is another main determinant of aquatic systems insect diversity, especially for traditionally fishless habitats (e.g., temporary ponds; Boix et al., 2016), but even in aquatic systems with fish presence, introductions of fish invasive species (e.g., *Gambusia spp.*) can disrupt and change insect community characteristics (Anton-Pardo & Armengol, 2014) or decrease specific groups diversity (Odonata; Ferreras-Romero et al., 2016). Moreover, although less studied for insects, the arrival of introduced competitors may impact native species, such as the introduction of *Trichocorixa verticalis* (Hemiptera, Corixidae), which are competitively stronger in saline waters than native corixid species (e.g., *Sigara spp.*) (see the section on “Alien Aquatic Hexapods”).

Use of aquatic insects in biological assessment of water quality

The pioneer studies on the relationship between environmental variables and the presence of specific species date back from the beginning of the 20th century (Elton, 1927; Grinnell, 1917; Hutchinson, 1957). This knowledge became one of the central core aspects of modern ecology and has been well established around the ecological niche concept, which is in continuous evolution and re-analysis (Chase, 2011; Leibold, 1995; Pocheville, 2015). This concept is also the fundamental background of several applied issues, such as the assessment of the ecological integrity of ecosystems based on changes on community composition in relation to disturbances. The need for the development of tools for the assessment of aquatic ecosystems favored the research on both the identification of most sensitive aquatic organisms (i.e., bioindicators) and the study of their relationship to disturbance (e.g., Liebmann, 1962; Margalef, 1955;

Woodiwiss, 1964). These tools were elaborated and validated during the second half of 20th century in many countries worldwide, including those in the Mediterranean Basin (Dallas, 2013), and many of them focused on the response of aquatic insects as part of the larger macroinvertebrate community (Birk et al., 2012; Rosenberg & Resh, 1993). In fact, the ecology and habitat preferences of aquatic insects have been intensively studied, in part because of their widespread use as bioindicators (Dijkstra et al., 2014).

Bioindicators are organisms that respond to an environmental stress or disturbance and, therefore, inform about the quality of the environment (Adams, 2002; Li et al., 2010). Diatoms, macrophytes, macroinvertebrates, and fish are the most commonly used bioindicators in aquatic ecosystems (e.g., Bonada, Prat, et al., 2006; Menetrey et al., 2011; Wright, 2000). In the case of macroinvertebrates, they have been used to evaluate pollution, heavy metals, nutrient enrichment, habitat loss, overexploitation, hydromorphological degradation, hydrology alteration, acidification, and general stressors (Li et al., 2010 and references therein). Moreover, they have been also used to assess ecological integrity (Birk et al., 2012; Rosenberg & Resh, 1993) or ecological risk (King & Richardson, 2003), and as a management tool useful in environment restoration projects (Kenney et al., 2009). Comparisons of the results obtained among bioindicators based in different biotic groups (Birk et al., 2012; Hering et al., 2006; Marzin et al., 2012) put in evidence that they have different sensitivities to human disturbances. For example, diatoms, macrophytes, and macroinvertebrates respond more quickly to nutrient enrichment or eutrophication than fish, whereas macroinvertebrates and fish are more sensitive to hydrological and morphological alteration.

Aquatic insects constitute the main bulk of macroinvertebrates used in bioassessment. Rosenberg & Resh (1993) and Bonada, Prat, et al. (2006), summarized the advantages of using macroinvertebrates for bioassessment purposes, all applicable to aquatic insects. Basically, they stated that macroinvertebrates are ubiquitous and sedentary, respond to a wide spectrum of environmental responses, can be used as “sentinel” organisms in experimental conditions, sampling is simple and inexpensive, and the taxonomy of many groups as well as their response to different types of pollution is relatively well-known (at least at family and genera level). Despite these advantages, Rosenberg and Resh (1993) also listed several methodological difficulties in using macroinvertebrates in bioassessment: invertebrates apparently do not respond to all impacts or they respond to other factors than water quality; quantitative data require exhaustive sampling and time-consuming sample processing; seasonal variation in abundance and distribution, specially of insects, could difficult comparisons among different seasons; and in lotic habitats the presence of some invertebrate taxa could be explained by the drift from other habitats.

A wide range of approaches have been developed in bioassessment using aquatic insects (Bonada, Prat, et al., 2006; Li et al., 2010; Beauger & Lair, 2014) and other macroinvertebrates. Four types of bioassessment methods or procedures based on macroinvertebrates have been identified according to Beauger and Lair (2014): two of them derived from the pioneering proposals (Trent Biotic Index (Woodiwiss, 1964) and Chandler’s Biotic Index (Chandler, 1970), respectively), predictive methods and rapid bioassessment methods. The first method assigns a water quality category according to a double entry table consisting of (1) the more sensible taxa to pollution (identifying several assemblage groups from very sensible to high tolerant) and (2) macroinvertebrate richness (often family level). In contrast, the second method assigns a coefficient to each taxa. These coefficients indicate the level of pollution sensibility of each taxon (often coefficient take values from 1 to 10, being 1 the most tolerant and 10 the most sensitive). Then, the water quality category is obtained taking into account the coefficients of all taxa present in the sample. Another differences could also exist for example in the field work: in first type sampling is habitat-specific, while in the second one sampling is conducted in all habitats of the sampled point. The third type, predictive methods predict site-specific fauna composition and compare the observed and expected fauna (Dolédéc et al., 1999; Wright, 2000). Finally, the fourth approach consists of rapid bioassessment methods. To clarify what a rapid bioassessment is, Fennessy et al. (2004) proposed the following four criteria that must characterize the method: (1) it must measure condition/integrity; (2) it should be rapid (i.e., no more than two people a half day in the field and no more than a half day of office preparation and data analysis); (3) include an on-site assessment; and (4) results must be verifiable. Rapid bioassessment is a very useful tool for managers needing easily understandable results in a short time period (Lenat & Barbour, 1994; Resh & Jackson, 1993). Such methods using aquatic insects have been developed for streams and wetlands (Barbour et al., 1999; Fennessy et al., 2004; Growns et al., 1997).

Metrics used in Mediterranean bioassessment indices include taxa richness (usually at family level), diversity indices (included those based not only on abundance distribution but also on size classes), or metrics based on pollution tolerance. In EU Mediterranean countries following the implementation of the Water Framework Directive (Directive 2000/60/EC), these metrics are assessed in relation to a particular typology of water body and its reference condition (the value of the metric in absence of disturbances). This can be done by comparing the real values of the metrics with the reference condition of the typology, or by modeling the expected community composition in reference conditions, and thus comparing the real metric

value with the expected one (i.e., using a multivariate approach). While the most common approaches used in Mediterranean countries consider the first option and combine unimetric (e.g., BMWP', EQAT, or HES; [Alba-Tercedor & Sánchez-Ortega, 1988](#); [Artemiadou & Lazaridou, 2005](#); [Cañedo-Argüelles et al., 2012](#)) or multimetric indices (e.g., AQEM, QAELS, or IMM-T; [Buffagni et al., 2004](#); [Munné & Prat, 2009](#); [Solimini et al., 2008](#)), some attempts in predictive models have been also developed (i.e., MEDPACS; [Poquet et al., 2009](#)), or are being considered, even using the metacommunity framework ([Cid et al., 2020](#)). In addition to these bioassessment methods based on taxonomic composition, recent methods that consider functional approaches are becoming useful and are considered more reliable under particular conditions. For example, [Soria et al. \(2020\)](#) found that metrics based on biological traits responded better in temporary rivers than traditional taxonomic metrics. This is because they appear to better disentangle the effect of increasing human disturbance from the increasing flow intermittence. Despite their potential good performance in Mediterranean rivers and the currently extensive knowledge of the traits of aquatic insects (and of macroinvertebrates in general) in the EU Mediterranean countries, their use is not yet routine, most likely because of the difficulty of comparing their output to those derived from other metrics. Another challenge for the use of aquatic insects in Mediterranean countries is related to taxonomic issues. Despite most methods based on family level data, there are many taxonomic gaps and some regions have been more explored than others. For example, the family of aquatic insect Nevrorthidae (Neuroptera) was cited for the first time in the Iberian Peninsula in 2012, and it is not included in the biotic indices currently used in the area ([Gavira et al., 2012](#)). Recent advances in molecular techniques may overcome some of these taxonomic limitations, although this method has not been adopted often yet for macroinvertebrates ([Blackman et al., 2019](#)).

The long tradition of using aquatic insects in bioassessment varies considerably among countries and environments (i.e., lotic and lentic). For instance, central and north Europe have a longer tradition than in Mediterranean regions. For this reason, some existing indexes in Mediterranean countries represent a transposition of existing tools elaborated in other countries. In some cases, the use of indexes needs to be adapted, since differences in fauna and community structure exist among the country where the bioindicator was created and the country in which they are to be applied. One good example is the index IBMWP, created from BMWP British index ([Hellawell, 1978](#)) and first adapted only by means of expert criteria ([Alba-Tercedor & Sánchez-Ortega, 1988](#)) and later validated in a research project (i.e., GUADALMED; [Prat & Bonada, 2002](#)). However, the bioassessment tools created in other countries have to be used with caution, since they are usually region-specific. For example, even for the IBMWP, the scores of particular Trichoptera families are not still well adapted, and they did not consider highly tolerant species endemic of the Iberian Peninsula ([Bonada et al., 2004](#)). A similar situation currently exists between northern and southern Mediterranean countries and some European tools, and even USA methods are used in other regions such as Turkey and North African countries (e.g., [Girgin, 2010](#); [Karrouch & Chahlaoui, 2009](#); [Sellam et al., 2016](#); [Souilmi et al., 2017](#)). In addition to concerns on the application of methods derived from other countries, a bigger effort is needed in the research on the ecology and impact-fauna responses in North African countries in order to obtain the essential knowledge to adapt adequately existing methodologies or to create new bioassessment tools (e.g., [Benzina et al., 2018](#); [Djitli et al., in press](#); [Haggag et al., 2018](#); [Korbaa et al., 2018](#); [Souilmi et al., 2019](#)). Similarly, the use of aquatic insects in bioassessments in lotic environments (streams and rivers) has a longer tradition than in lentic ones (wetlands, ponds, and lakes). In this sense, it is important to add that aquatic insects have a clear prevalence in the biological indicators used in lotic environments, while macroinvertebrate groups other than aquatic insects (i.e., molluscs, oligochaetes, or crustaceans; [Boix et al., 2005](#); [Mazzella et al., 2009](#); [Mouthon, 1993](#)) have more importance in lentic indexes.

Alien aquatic Hexapods

The impacts of biological invasions are considered a main component of global change and they are a leading cause of animal extinctions ([Clavero & García-Berthou, 2006](#); [Early et al., 2016](#); [Simberloff et al., 2013](#)). However, the number of aquatic alien insect species in the continental Mediterranean waters, and in world inland waters, is surprisingly low. Besides, as far as we know, no aquatic alien Collembola has been reported. Although in other world regions (i.e., South Africa and Australia) the number of exotic species could achieve the 20% of the Collembola fauna, few of these alien species are aquatic or inhabitant of wet habitats ([Greenslade, 2018](#); [Janion-Scheepers et al., 2015](#)).

Several points make to this low number of alien insects astounding: (1) the high biodiversity of this group, being the richness group in continental waters ([Balian et al., 2008](#)); (2) the high number of aquatic alien species in other faunal groups (e.g., invertebrates such as crustaceans or vertebrates as fish) reported in some Mediterranean countries ([Gherardi et al., 2008](#); [Muñoz-Mas & García-Berthou, 2020](#)) or in some waterbodies ([Ricciardi, 2015](#)); (3) the high proportion of terrestrial alien insects known in Mediterranean countries (e.g., in Italy insects represent between 80% and 90% of the introduced species in terrestrial habitats; [Zapparoli, 2006](#)), in fact insects are one of the groups with the

world highest number of invasive species (Kenis et al., 2009); (4) compared to terrestrial systems, estuarine and inland waters are highly vulnerable to either unintentional or deliberate introductions of taxa and to their spread consequences (Dudgeon et al., 2006; Gherardi, 2007); and (5) freshwater habitats seemed to be more susceptible to invasion—and experienced more impacts—than coastal habitats (Tricarico et al., 2016). Therefore, although inland waters are among the most invaded ecosystems on our planet, the number of aquatic alien insects remains very low. Fenoglio et al. (2016) proposed explanations and summarized some biological, ecological, and anthropogenic factors that could explain, at least partially, this fact. The explanations identify some characteristics of aquatic insects that diminish their potential invasive capacity: (1) economic interest in moving aquatic insects is currently limited; (2) associations between aquatic insects and host plants are extremely rare; (3) aquatic insects usually lack adaptations for overland or maritime transport; (4) aquatic insects seem to have less diverse reproductive strategies than terrestrial ones; (5) aquatic insects usually have an aquatic and a terrestrial stage; (6) aquatic insects usually have an aquatic and a terrestrial stage; (7) many aquatic insects live in running water environments. In fact, the few aquatic alien insects are exemptions of these general characteristics. For example, the hemipteran *T. verticalis*, and the dipterans *Aedes albopictus* and *Ae. japonicus* have biological adaptations that allow them to disperse by means of overland and marine transport. The water boatman *Trichocorixa* tolerates waters with high conductivity and even marine waters (Gunter & Christmas, 1959; Hutchinson, 1931), while the *Aedes* mosquitoes can survive in small amounts of water, and have high reproductive rates and desiccation-resistant eggs that allow them spread worldwide via the trade of used tyres (Benedict et al., 2007; Kaufman & Fonseca, 2013). Within continental waters, temporary ones showed less susceptibility to the establishment of nonindigenous species (Naselli-Flores & Marrone, 2019); however, several of the alien insects listed below have been located in temporary waters (i.e., *T. verticalis*, *Aedes* spp., and *Stenopelmus rufinusus*).

The lack of knowledge of the past and present distribution of aquatic insects makes it difficult to identify exotic species and, therefore, could also explain the low number of the reported alien aquatic insects. Thus, some cosmopolitan aquatic insect species could be undocumented introductions due to the difficulties to have verifiable historical data which allow us to confirm as exotic one species (de Moor, 1992). Even some species could have been described in a continent, but they are native from a different one, such as the case of gastropod *Haitia acuta* (Draparnaud) which has been described in France and it inhabits nowadays all types of freshwaters in Europe, but later it was identified as an American species (García-Berthou et al., 2007 and references therein). A similar case for aquatic insects could be *Culicoides paolae* (see below). In other situations, one species can be identified as alien because it does not have previously recorded (groups poor studied or changes in environmental conditions). One example are species that recover their native distribution ranges after the environmental constraint that had initially caused their disappearance is reversed, but historical records documenting its disappearance do not exist (this could be the case of *Ametropus fragilis* in Germany; Berger & Rothe, 1999).

The low number of alien insect species does not imply that biological invasion is not a relevant subject for aquatic insects, since some of these few species can affect human health (i.e., some Culicidae and Ceratopogonidae). Moreover, some of the most dangerous invasive species have been spread by humans as biological control of insects (e.g., *Gambusia* spp. as control of mosquitoes), and aquatic and semiaquatic insects are used to control invasive species including alien insects (Hoddle, 2004; Shaw et al., 2018). Besides, insects could be affected by invasive species in several ways. Some impacts of invasive species on aquatic insects include (1) substitution of autochthonous plants by alien ones, which are food resource for insects in riparian habitats, imply changes in nutritional value of food that in turn affect growth rates and insect production (e.g., Canhoto & Graça, 1995; Going & Dudley, 2008); (2) fish introductions is one of the main threats of insects conservation (Polhemus, 1993), since it is long known and well established that some introductions imply a high predation impact on insects (e.g., Macan, 1965; Merkley et al., 2015; Pope et al., 2009); (3) similarly, other invasive species such as birds can increase predation pressure on insects (e.g., Marion, 2013); and (4) some invasive ecosystem engineer species, including many species of crayfish, significantly reduce the insect biodiversity and alter aquatic insect composition (e.g., Freeland-Riggert et al., 2016; Geiger et al., 2005; Rodríguez et al., 2005).

In this section, we will depict the few known cases of alien aquatic insects reported in Mediterranean inland waters and we also included doubtful cases for different reasons:

(1) *Ametropus fragilis* Albarda, 1878 (Ephemeroptera: Ametropodidae)

This species is known in Italy and Croatia (Ćuk et al., 2015; Turin et al., 1997). Its presence in Italy was considered an introduction because of the known distribution of Ametropodidae in Europe (and its absence in some adjacent countries with a well-known Ephemeroptera fauna, such as France, Austria, Switzerland, and Slovenia). It seems that it was the result of an accidental introduction related to fish restocking from eastern Europe (Turin et al., 1997). In contrast, when this species was located in Germany in 1998, the researchers considered it as a native species (taking into account its global distribution); and the absence of previous records was explained because it had been extinct, but they did not

have knowledge of historic proof that supported this hypothesis (Berger & Rothe, 1999). This species has been extinct in several European countries, such as The Netherlands and Czech Republic, probably as a result of human activity, linked to fish restocking in rivers (Čuk et al., 2015). The finding in Croatia in 2014 was located near the considered native area (near Hungary border) and far away of the Mediterranean coast (Čuk et al., 2015).

(2) *Electrogena zebrata* (Hagen, 1864) (Ephemeroptera: Heptageniidae)

The distribution of this species constitutes a doubt of its origin. Although it is considered a Sardo-Corsican endemic, the only similar species is found in Lebanon and Israel. The morphology between them is very similar, so distinction of the two is impossible. This disjunct distribution cannot be explained by geological events, and some authors formulated the hypothesis that its presence in Sardinia was an involuntary introduction by the Phoenicians (Belfiore, 2006).

(3) *Trichocorixa verticalis verticalis* (Fieber, 1851) (Hemiptera: Corixidae)

This species, native to the Atlantic coast of America, is distributed throughout the Atlantic coast from Labrador to the north of Mexico, and the Caribbean islands (Jansson, 2002; Kment, 2006; Sailer, 1948). Its presence in the south western Iberian Peninsula has been documented from the last decade of 20th century (Sala & Boix, 2005), but it was in the first years of 21st century that its presence in this region was regularly documented and monitored in some areas as Doñana Natural Park where reproduction has been observed (Günther, 2004; Kment, 2006; Millán et al., 2005; Rodríguez-Pérez et al., 2009; Sala & Boix, 2005; Tornero et al., 2014). Its presence was also reported in Morocco (L'Mohdi et al., 2010), where it has significantly increased its distribution range in 2010s decade (Fouzi et al., 2020). Outside of its native range, it has also reported from New Caledonia (Jansson, 1982) and several sites in the KwaZulu-Natal region in South Africa (Nzimane River, Umhlatuze River, and Charter's Creek; Jansson & Reavell, 1999). Predictions of the potential new zones of invasion based on both climatic data and thermal physiological data (Guareschi et al., 2013) indicate that *T. v. verticalis* may expand well beyond its current distribution and find new habitable conditions in temperate areas, with an emphasis on coastal areas (including Europe, North and South America, Asia (mainly Arabian Peninsula, India and Myanmar), Australia, and New Zealand).

Fortunately, this species has attracted the attention of Mediterranean researchers and a significant number of studies on its biology in the invaded area and its interaction with native species have been done. It is a well-known halobiont species and usually inhabits brackish and saline waterbodies, even occurring in the open sea (Gunter & Christmas, 1959; Hutchinson, 1931; Sailer, 1948). Therefore, it is not surprising that in the invaded area it dominates permanent saline waters (Coccia et al., 2013). However, when its ecophysiology was compared with native Corixidae, its wide saline tolerance was lower than the tolerance range of the native species *Sigara selecta* (Carbonell et al., 2016). In contrast, *T. v. verticalis* took advantage of other environmental stress such as temperature and shows higher thermal plasticity than native *Sigara* spp. (Carbonell et al., 2016; Coccia et al., 2013). Comparison of biological traits was also done between *T. v. verticalis* and the native *Sigara* spp. (Carbonell et al., 2016; Céspedes, Coccia, et al., 2019; Coccia et al., 2016). The main conclusions were as follows: (1) according to wing morphometry, *T. v. verticalis* could be a stronger flier; (2) it shows higher fecundity, especially in saline waters; (3) it performs a continuous reproduction through the year, while native spp. mainly reproduce from spring to autumn; and (4) it changes diet preferences relying more on herbivory under the presence of native competitors. All these reasons explain that this species is a successful invader in saline waters, but they do not justify why it fails to invade freshwaters, although in experimental conditions it can reproduce and tolerate low salinities, even in the presence of native species (Carbonell et al., 2020). One explanation could be the higher infection levels by mite larvae in *T. v. verticalis* than in native corixids, and the fact that these infections are especially abundant in low saline waters (Céspedes, Stoks, et al., 2019; Sánchez et al., 2015). A complementary explanation could be predation, since differential predation by Odonata has been observed between *T. v. verticalis* and native corixids (Coccia et al., 2014), the latter being less predated (Odonata larvae achieved higher densities in low saline waters). Moreover, *T. v. verticalis* can also affect the community structure by means of predation over keystone species of saline wetlands, since its predation over *Artemia partenogenetica* implies a trophic cascade resulting a higher phytoplankton increase (Céspedes et al., 2017).

(4) *Stenopelmus rufinusus* Gyllenhal, 1836 (Coleoptera: Eriirhinidae)

This aquatic weevil is native to North America (Southern and Western United States) (Richerson & Grigarick, 1967). It has been first recorded in France, a Mediterranean country, in 1898 (Bedel, 1901), from where it reached several European countries (it was recorded in United Kingdom, and the Netherlands, Ireland, Germany, Belgium, and Ukraine) including some Mediterranean ones as Portugal, Spain, and Italy (Carrapiço et al., 2011; Dana & Viva, 2006; Florencio et al., 2015; Gherardi et al., 2008). The few observations in the Iberian Peninsula indicate that this species is present in southern, northeastern, and western locations (Fernández et al., 2005; Mor et al., 2010; Tornero et al., 2014).

The current distribution of this species is closely related to the expansion of the aquatic fern *Azolla filiculoides*, which constitutes its main food source. *Azolla filiculoides* is native to the Americas but has become naturalized throughout the

world by a variety of mechanisms, with humans as its main dispersal factor (Lumpkin & Plucknet, 1980). One of the strategies to mitigate the negative impacts of this aquatic fern is the use of *S. rufinasus* as a biocontrol agent in some countries as South Africa, but its present in Mediterranean Basin seems to be unintentional (Shaw et al., 2018).

(5) *Lissorhoptrus oryzophilus* Kuschel, 1951 (Coleoptera: Erihniidae)

L. oryzophilus is a semi aquatic beetle native to North America (Canada, United States, and Mexico; Kuschel, 1951). In 1976, it was accidentally introduced into Japan (Tsuzuki and Isogawa, 1976) and from there the distribution range of this pest has expanded to several Asian countries (i.e., China, North and South Korea, Taiwan and India). It is also present in Caribbean and South American countries (i.e., Cuba, Dominican Republic, Colombia, Suriname and Venezuela) (CABI, 2023). In Europe, its presence was detected more recently in four Mediterranean countries: Italy, France, Greece and Spain in 2004, 2014, 2016 and 2018, respectively (Caldara et al., 2004; Ferrand, 2017; Giantsis et al., 2017; Montauban et al., 2021). The rice water weevil *L. oryzophilus* is considered one of the most important rice pests globally and in North America it causes annual losses of up to 25% of rice crops (Aghaee and Godfrey, 2014).

(6) *Sternolophus solieri* Laporte, 1840 (Coleoptera: Hydrophilidae)

This species is native to Asia and Australia, but it is currently widespread in western, central, and eastern Africa, Madagascar, the Cape Verdes, and the Comoros. It has reached the Mediterranean Basin in Algeria, Egypt, Israel, and Greece (Bird et al., 2017; Nasserzadeh et al., 2017). In Italy its presence is also documented; however, there are no reports of well established (i.e., self-sustaining) populations (Gherardi et al., 2008).

(7) *Pelosoma lafertei* Mulsant, 1844 (Coleoptera: Sphaeridiidae)

Species of *Pelosoma* are native to southern and central America and are currently present in France and Italy (Bameul, 1992; Costa et al., 2017 and references therein). This species and the previous one, *Sternolophus solieri*, possibly arrived by ship transport and seem not to adapt well to the Mediterranean climate, having never been found again since their introduction (Rocchi, 2006). This species is a typical inhabitant of phytotelmata in its native range (de Oliveira et al., 2018).

(8) *Cercyon (Paracycreon) laminatus* Sharp, 1873 (Coleoptera: Sphaeridiidae)

Its native distribution includes China, Taiwan, Japan, and the Russian Far East (Jia et al., 2011). The introduction of this species has been reported in Europe and the Hawaiian Islands (Hansen, 1999), where it is well-established, and it was also reported in Chile and Australia (Fikáček, 2009). At the moment, its sole presence in the Mediterranean Basin is in Italy (Gherardi et al., 2008). Although this species is included in xenodiversity inventories of inland waters (Gherardi et al., 2008), it is described as a terrestrial species, which inhabits various kinds of decay-ing organic matter and excrements of various mammals (Fikáček, 2009).

(9) *Cryptopleurum subtile* Sharp, 1884 (Coleoptera: Sphaeridiidae)

The native range of this beetle is East Asia, and it was probably introduced in Europe, northern Asia (excluding China), North America, and southern Asia (Lobl & Smetana, 2015). In the Mediterranean Basin, it has been reported in France, Italy, and Albania (CABI, 2021; Gherardi et al., 2008). Similar to the previous species, *C. laminatus* it is considered terrestrial although it is also included in alien species inventories of inland waters (i.e., Gherardi et al., 2008) and it was observed in woody debris in river banks (Dalley, 2014).

(10–13) *Aedes* spp. (Diptera: Culicidae): *Aedes aegypti* (Linnaeus, 1762); *Aedes albopictus* (Skuse, 1894); *Aedes japonicus* (Theobald, 1901); *Aedes koreicus* (Edwards, 1917).

At least four nonnative *Aedes* species have been recorded in the Mediterranean Basin; however, their distribution is very different. For example, *Ae. albopictus* was first introduced in 1970s in Albania and was later found in many Mediterranean countries (i.e., Syria, Lebanon, Palestine, Israel, Jordan, Turkey, Greece, Albania, Montenegro, Bosnia-Herzegovina, Croatia, Slovenia, Italy, Malta, San Marino, Monaco, France, Algeria, Spain, and Portugal). In contrast, *Ae. japonicus* and *Ae. koreicus* have been only reported in few countries: *Ae. japonicus* in Bosnia-Herzegovina, Croatia, Slovenia, and Italy (it is also established in France and Spain, but not in the Mediterranean climate region); and *Ae. koreicus* in Italy. Finally, *Ae. aegypti* is present in Egypt (far from the coast) and Turkey (Black Sea coast), but not in the Mediterranean climate region. This species was present in Mediterranean basin (i.e., Turkey, Greece, Italy, Spain), but it was eradicated. However, sporadic records have been recorded in Turkey, Israel, and Italy (Aranda et al., 2006; Ballardini et al., 2019; Schaffner & Mathis, 2014; ECDC, 2021; Eritja et al., 2019).

Three of these *Aedes* species are native to Asia, being the origin of *Ae. albopictus* and *Ae. koreicus* (southeast Asia), while *Ae. japonicus* is distributed in China, Japan, Korea, south-eastern Russia, and Taiwan (Ballardini et al., 2019; Eritja et al., 2019). In contrast, *Ae. aegypti* has its origin in sub-Saharan Africa, where the ancestor of the domestic form of *Ae. aegypti* is native (the domestic form is nowadays distributed around the world; Powell & Tabachnick, 2013). The

distribution of these species is largely driven by both human movement and the presence of suitable climate; marine transport of tires, plants, and other goods seems a common pathway for several of these species (Eritja et al., 2005; Kraemer et al., 2019; Schaffner et al., 2009). However, different dispersion patterns have been reported, and some species spread by long distance importations (i.e., *Ae. aegypti*), while others (i.e., *Ae. albopictus*) expanded mainly along the fringes of its distribution (Kraemer et al., 2019). Future scenarios predict an increase of the distribution of these species related to accelerating urbanization, connectivity, and climate change conditions (Kraemer et al., 2019; Schaffner & Mathis, 2014). All these species are extensively studied because they are dispersal vectors for several viral diseases. Thus, (1) *Ae. aegypti* is vector for viral diseases such as yellow fever, dengue fever, and chikungunya (due to an effective vaccine, yellow fever is of less concern worldwide, although cases still occur; Powell & Tabachnick, 2013); (2) *Ae. albopictus* is vector of major human diseases such as chikungunya, dengue, yellow fever, West Nile virus, and encephalitis, but it is also a vector of the dog heartworm *Dirofilaria* spp. (Aranda et al., 2006; Ballardini et al., 2019; Cancrini et al., 2007); (3) *Ae. japonicus* is vector for several mosquito-borne pathogens, to date only the West Nile virus is a concern based on field evidence (Eritja et al., 2019); and (4) *Ae. koreicus* specimens were found infected by encephalitis virus and the heartworm *Dirofilaria* spp. and it is vector for the chikungunya virus (Ballardini et al., 2019 and references therein).

(14) *Culicoides paolae* Boorman, 1996 (Diptera: Ceratopogonidae)

It is a *Culicoides* species found in southern Italy (Boorman et al., 1996) that was described in 1996 and named *C. paolae*. In the following years, this species was found in several countries of the Mediterranean basin including Malta, Croatia, Tunisia, France, Algeria, Greece, and Spain (Estrada et al., 2011). However, some doubts exist on the validity of this species, since several specialists considered that it is a synonym of *C. jamaicensis* Edwards, 1922 because morphology of both species is very similar, but unusual differences were noted (Meiswinkel et al., 2004). At the moment, it has been placed in the subgenus *Drymodesmyia* which includes more than 20 endemic species to the tropical regions of the New World and, where known, breed in vegetative materials including the decaying leaves and fruits of Central American cacti. These points are used to propose the exotic origin of this species and its introduction related to the introduction of American cacti in Europe (in a similar way of the introduction of the related species *C. loughnani* (Edwards, 1922) in Australia from America; Dyce, 1969). Even it has been proposed that *C. paolae* was brought to Europe with the introduction of *Opuntia ficus-indica* by Christopher Columbus (Meiswinkel et al., 2004). However, the fact that this species was not discovered until 500 years later and that efforts to rear *C. paolae* from *Opuntia* have thus far failed make this hypothesis doubtful.

The distribution knowledge of this species in the Mediterranean Basin has been improved by national surveys (e.g., in Spain and Italy), since *Culicoides* species (i.e., *C. imicola*) are known vectors of bluetongue and deer virus (Estrada et al., 2011; Meiswinkel et al., 2004). *C. paolae* was formerly included in *Remmia* subgenus, and this fact implied that it was considered a potential new vector. However, taxonomic revisions consider that this species has differences in morphology and biology (it feeds preferentially on birds). In fact, *C. paolae* is considered a potential vector of avian haemosporidians (Veiga et al., 2018). Similarly to two coleopterans previously commented above, this species is perhaps linked to terrestrial habitats, since some *Culicoides* species select rotting parts of vegetation or even wet manure to breed over aquatic habitats, and the breeding habitats of this species are not yet well known (Meiswinkel et al., 2004).

Taxonomic keys to the Subphylum Crustacea, Class Hexapoda

How to use these keys

The designed keys in this chapter have been written to identify aquatic springtails (Collembola) and insects that can generally be found in all types of Mediterranean freshwater habitats: streams, rivers, wetlands, ponds, and lakes. It does not include communities found in brackish water nor marine estuarine habitats. The key to Entognatha (Collembola) is to species, while the key to Insecta is limited to orders knowing that more detailed keys are provided in later chapters of this book. Only the aquatic stages of insects living on or below the water surface are treated here knowing that many insects migrate to terrestrial habitats as adults. This key should only be used for adults and last stadium larvae (mature larvae). Juvenile or first stadium larvae should not be used because their morphological characteristics are not fully developed, and that can lead to mistaken identifications. Only a minute proportion of Mediterranean freshwater insects have been illustrated, and identified specimens may differ from those examples drawn and shown here. However, if the identified and illustrated specimens contrast considerably, then the identification should be checked in the later chapters of this book.

The keys do not cover insects living at the shoreline. However, because these usually are found in the field samples and often confused with aquatic stages, a list of them is also included at the end of the Insecta key.

Key to the subclass Entognatha (Collembola)

This key is a modification or compilation of others, such as those included in Jordana and Arbea (1989), Bretfeld (1999), Potapov (2001), Thibaud et al. (2004), Christiansen and Snider (2008), Jordana (2012), Bellinger et al. (1996–2020), with some own contributions.

- 1 Body elongate and segmented (Figs. 8.6, 8.8, and 8.35A) 2
- 1' Body subglobular, not or partially segmented (Figs. 8.7 and 8.9). 3
- 2(1) Th I with tergal chaetae (Fig. 8.6) Poduromorpha
- 2' Th I without tergal chaetae (Fig. 8.8) Entomobryomorpha
- 3(1') Antennae as long or longer than head (Fig. 8.7) Symphypleona
- 3' Antennae shorter than head (Fig. 8.9) Neelipleona

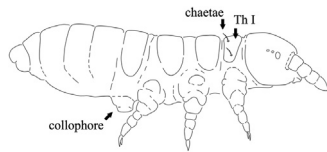


FIGURE 8.6 Habitus of a Poduromorpha showing chaetae on protoracic tergum (Th I).

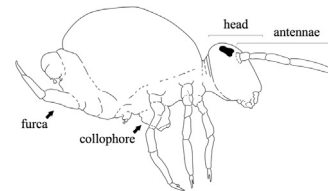


FIGURE 8.7 Habitus of a Symphypleona.

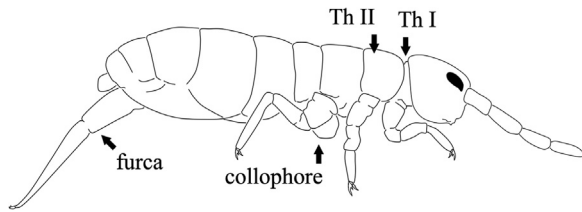


FIGURE 8.8 Habitus of an Isotomidae showing the absence of protoracic tergum.

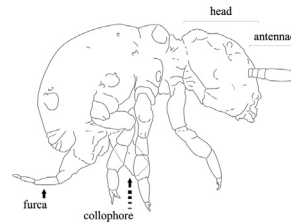


FIGURE 8.9 Habitus of a Neelipleona.

Poduromorpha

- 1 Mouthparts modified (Fig. 8.10) (Neanuridae) 2
- 1' Mouthparts with maxillae, and mandibles with a molar plate (Fig. 8.11) 7



FIGURE 8.10 An example of modified mouthparts.



FIGURE 8.11 Maxylla with denticulate molar plate.

- 2(1) Furca absent; eight “s” chaetae on Ant IV (Fig. 8.12); PAO absent (Neanurinae) *Bilobella aurantiaca*
- 2’ Furca present or absent; fourth antennal segment different of eight “s” chaetae; PAO absent or present 3
- 3(2) Maxylla head triangular (Fig. 8.13) (Frieseinae) *Friesea acuminata*
- 3’ Maxylla head not triangular (Fig. 8.14) (Pseudachorutinae) 4



FIGURE 8.12 Tip of the antenna of *Bilobella aurantiaca* showing the eight “s” chaetae (Jordana et al., 1997). Modified from Jordana, R., Arbea J. I., Simón C., & Lucíañez, M. J. (1997). *Collembola Poduromorpha*. In M. A. Ramos, et al. (Eds.), *Fauna Iberica* (Vol. 8, p. 807). Madrid, Spain: Museo Nacional de Ciencias Naturales, CSIC. *Class Hexapoda: general introduction*



FIGURE 8.13 Maxylla of a *Friesea*.



FIGURE 8.14 Maxylla with dentate lamellae of a *Pseudachorutinae*.

- 4(3) Maxylla with toothed or flabellated lamellae (Fig. 8.15) 5
- 4’ Simple and stylized maxilla; 0–2 + 0–2 eyes. Ant IV with “s” chaetae in candle-shaped flame (Fig. 8.16)
..... *Micranurida pygmaea*
- 5(4) Mandible with normal teeth (Fig. 8.17) 6

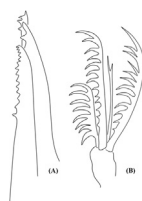


FIGURE 8.15 Maxylla dentate (A) and flabellated (B).



FIGURE 8.16 Tip of the antenna of *Micranurida pygmaea*.



FIGURE 8.17 Mandible of *Anurida*.

- 5’ Mandible with two teeth and between them a finely serrated semicircular lamella (Fig. 8.18)
..... *Anuridella calcarata*
- 6(5) Terga without additional chaetae *Anurida granaria*
- 6’ Terga plurichaetotic *A. maritima*
- 7(1) Dentes more than three times as long as manubrium, with distal rings of granules (Fig. 8.19)
..... (Poduridae) *P. aquatica*
- 7’ Dentes with other shape 8
- 8(7) Body with pseudocelli; Ant III sensory organ as in Fig. 8.20; without eyes; body without pigmentation
..... (Onychiuridae) 9
- 8’ Body without pseudocelli; Ant III sensory organ as in Fig. 8.21; 0–8 eyes; body with or without pigment
..... (Hypogastruridae) 11
- 9(8) PAO with 3–5 lobes of one vesicle (Fig. 8.22). *Oligaphorura absoloni*
- 9’ PAO with 8 or more vesicles (Fig. 8.23) 10
- 10(9) Claw as long as antenna; Ant III sensory organ with two rows of guard papillae *O. colpus*
- 10’ Claw as long as first proximal antennal segment; Ant III sensory organ with one row of guard papillae
..... *Thalassaphorura debilis*

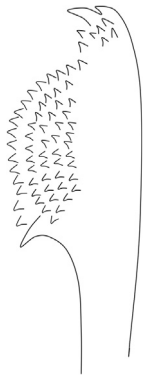


FIGURE 8.18 Mandible of *Anuridella calcarata*.

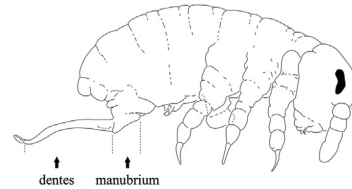


FIGURE 8.19 Habitus of *Podura aquatica*.

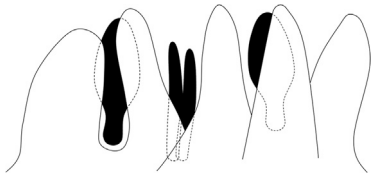


FIGURE 8.20 Ant III sensory organ of an Onychiuridae.



FIGURE 8.21 Ant III sensory organ of a Hypogastruridae.

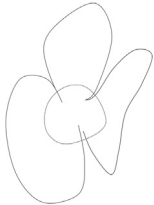


FIGURE 8.22 PAO of *Oligaphorura absoloni*.

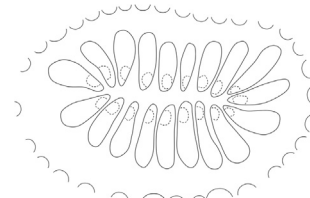


FIGURE 8.23 PAO of *Thalassaphorura debilis*.

11(8) Head with 8 + 8 eyes	12
11' Head with fewer than 8 + 8 eyes	15
12(11) Empodium 1/7th or more as long as inner claw	13
12' Empodium less than 1/9th as long as inner claw	<i>Schoettella unungiculata</i>
13(12) Tibiotarsus I–III with three knobbed tenent hairs (Fig. 8.24)	<i>Hypogastrura viatica</i>
13' Tibiotarsus I–III with one weakly knobbed tenent hair	14
14(13) Retinaculum with 3 + 3 teeth	<i>H. gisini</i>
14' Retinaculum with 4 + 4 teeth (Fig. 8.25)	<i>H. vernalis</i>
15(11) PAO absent	16
15' PAO present (Fig. 8.26)	20
16(15) Head with 2 + 2 eyes or fewer per side	<i>Acherontiella carusoi</i>
16' Head with 4 + 4–5 + 5 eyes per side	17

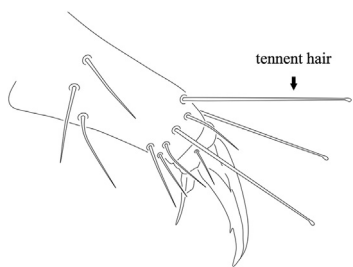


FIGURE 8.24 Tip of the leg of a *Hypogastrura viatica*.

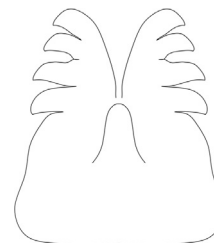


FIGURE 8.25 Retinaculum of *Hypogastrura vernalis*.

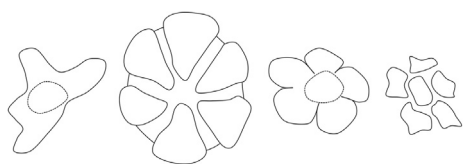


FIGURE 8.26 PAO of different species.



FIGURE 8.27 Mandible of *Paraxenylla affiniformis*.

- 17(16) Mandible with long thin apex and small apical teeth (Fig. 8.27, arrow) *Paraxenylla affiniformis*
- 17' Mandible short without long apex, apical teeth large (Fig. 8.28, arrow) 18
- 18(17) Mucro separated from dens, and with two chaetae (Fig. 8.29); Th II–III with dorsal central chaetae in three rows (Fig. 8.30) or Th III with dorsal a_2 chaeta displaced distally relative to a_1 *Xenylla humicola*
- 18' Furca diversely structured; Th II with dorsal a_2 chaeta displaced distally relative to a_1 and dorsal p_2 displaced apically relative to p_1 19
- 19(18) Mucrodens more than twice as long as claw III (Fig. 8.31) *X. maritima*
- 19' Mucrodens less than twice as long as claw III, and with inner semicircular lamella (Fig. 8.32) *X. grisea*

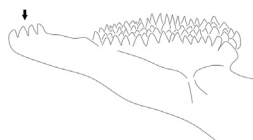


FIGURE 8.28 Mandible of *Xenylla*.



FIGURE 8.29 Dens and mucro of *Xenylla humicola*.

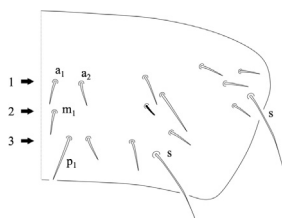


FIGURE 8.30 Th II–III of *Xenylla humicola*.

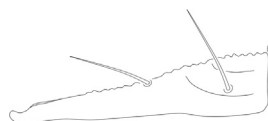


FIGURE 8.31 Mucrodens of *Xenylla maritima*.

- 20(15) Claw eight or more times as long as basal width (Fig. 8.33) *O. longisensilla*
- 20' Claw six or less times as long as basal width 21
- 21(20) 2–3 + 2–3 eyes *Typhlogastrura breuili*
- 21' 0 + 0 eyes *T. mendizabali*

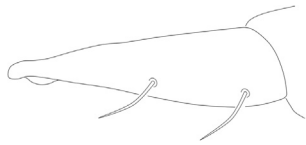


FIGURE 8.32 Mucrodens of *Xenylla grisea*.

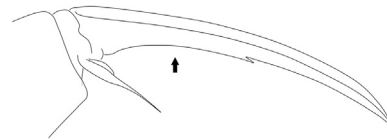


FIGURE 8.33 Claw of *Ongulogastrura longisensilla*.

Entomobryomorpha

- 1 Body chaetae smooth (Fig. 8.34A) or unilaterally ciliate (Fig. 8.34B); multilaterally ciliate macrochaetae always acuminate (Fig. 8.34C) 2
- 1' Body chaetae mostly ciliate; multilaterally ciliate macrochaetae sometimes cylindrical (Fig. 8.35B) usually truncate or broadened at the tip (Fig. 8.35C) (Entomobryidae) 20

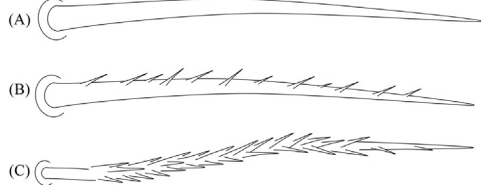


FIGURE 8.34 Some examples of chaetae of Isotomidae: (A), smooth chaeta; (B), unilaterally ciliate chaeta; (C), multilaterally ciliate macrochaetae.

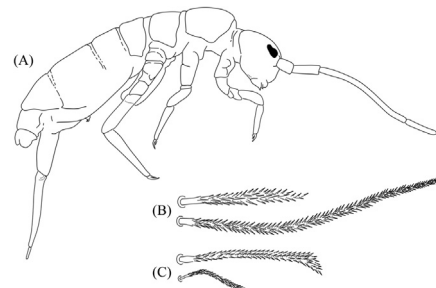


FIGURE 8.35 Habitus of Tomoceridae (A); some examples of chaetae of Entomobryomorpha except Isotomidae and Actaletidae: pointed (B) and capitate (C).

- 2(1) Abd IV–VI fused and 1.4 times the length of mesothorax to Abd III (Fig. 8.36); tenent hair leaf-shaped (Fig. 8.37, arrow) (Actaletidae) *A. neptuni*
- 2' Abd IV–VI not fused (Fig. 8.38), but if fused then shorter than the length of mesothorax to Abd III; tenent hair never leaf-like (Isotomidae) 3

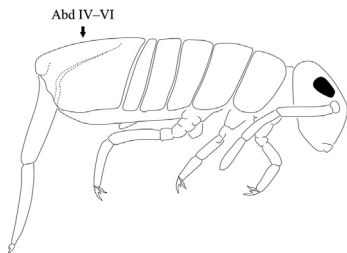


FIGURE 8.36 Habitus of *Actaletes neptuni*.

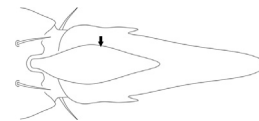


FIGURE 8.37 Tenent hair leaf-shaped of *Actaletes neptuni*.

- 3(2) Abd III larger than other abdominal segments 4
- 3' Abd III not larger than other abdominal segments 11
- (3) Dens cylindrical, distally not narrowed (Fig. 8.39), normally multilaterally chaetaceous *Hydroisotoma schaefferi*

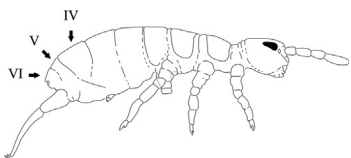


FIGURE 8.38 Habitus of Isotomidae.



FIGURE 8.39 Dens and mucro of *Hydroisotoma schaefferi*.

- 4' Dens clearly narrowed distally, dorsally crenulate, or knobbed; dorsal and ventral surfaces of dens clearly distinguished by the number and thickness of their chaetae (Fig. 8.40) 5
- 5(4) Abd II–IV without bothriotricha 6
- 5' Abd II–IV with bothriotricha (Fig. 8.41) 7



FIGURE 8.40 Dens of normal shape.



FIGURE 8.41 Two examples of bothriotricha.

- 6(5) One feathered chaeta on tibiotarsus II *Halisotoma boneti*
- 6' Two feathered chaeta on tibiotarsus II *H. maritima*
- 7(5) Ant III sensory organ with 10 or more thickened sensilla (Fig. 8.42) *Axelsonia litoralis*
- 7' Ant III sensory organ without that sensilla, bothriotricha ciliate 8
- 8(7) Pigment absent; claws long and slender; found in caves *Isotomurus subterraneus*
- 8' Pigment present, at least in eye region; claws variable in shape 9
- 9(8) Abd II–IV with 0, 1, 1 bothriotricha; Th II–Abd IV with transverse broad dark bands *Isotomurus gallicus*
- 9' Abd II–IV with 3, 3, 1 bothriotricha (absent in juvenile specimens); pigmentation variable, often with longitudinal stripes 10
- 10(9) Longitudinal median band interrupted or fainter on last abdominal segments, especially on Abd III
..... *I. palustris* species complex
- 10' Longitudinal median band continuous, broad and dark, sometimes interrupted on Abd IV and V
..... *I. unifasciatus*
- 11(3) Abd IV–VI dorsally fused (Fig. 8.43), often with a nonchaetaceous band between Abd IV and V, where this occurs the band is narrower than that among other segments 12



FIGURE 8.42 Ant III sensory organ of *Axelsonia litoralis*.

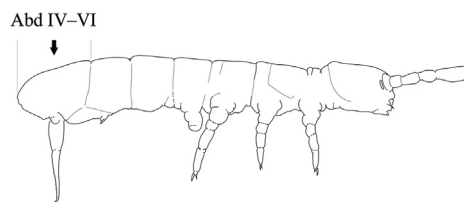


FIGURE 8.43 Habitus of *Folsomia*.

- 11' Abd IV–V not fused, if they seem fused, then the nonchaetaceous band is located with the same width as those among other segments 13
- 12(11) Head with 2 + 2 eyes *Folsomia quadrioculata*
- 12' Head with 3 + 3 eyes *F. sexoculata*

- 13(11) Cuticle granulate; dorsal surface of dens granulate, short, with ventral chaetae; mucro without chaetae, often with lamellae (Fig. 8.44) 14
- 13' Cuticle not granulate; dorsal surface of dens smooth, annulate, or with large knobs (Fig. 8.45); mucro may be chaetaceous 15
- 14(13) 2 + 2 anterior chaetae on manubrium *Pachyotoma crassicauda*
- 14' Without anterior chaetae on manubrium *P. levantina*

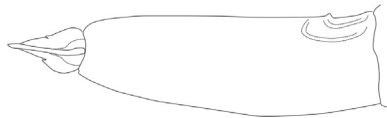


FIGURE 8.44 Dens and mucro of *Pachyotoma*.



FIGURE 8.45 Dens and mucro of *Ballistura*.

- 15(13) Manubrium with two or more ventral chaetae and/or spines 16
- 15' Manubrium without ventral chaetae and/or spines 18
- 16(15) Only males with dorsal broad and numerous spines on body (Fig. 8.46) *Dimorphotoma porcellus*
- 16' Dorsal broad spines absent or present on both sexes 17
- 17(16) Abd V–VI not fused *Proisotoma minuta*
- 17' Abd V–VI fused *Cryptopygus thermophilus*
- 18(15) Dens smooth and cylindrical; mucro characteristic (Fig. 8.47), often with chaetae *Archisotoma interstitialis*
- 18' Dens annulated or knobbed; mucro different 19

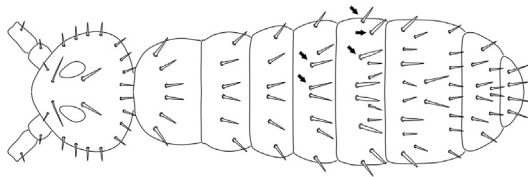


FIGURE 8.46 Habitus of *Dimorphotoma porcellus*.

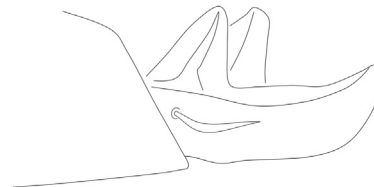


FIGURE 8.47 Mucro of *Archisotoma interstitialis*.

- 19(18) At least with the distal 2/3th of the anterior side of dens with chaetae; posterior side of dens without notches (Fig. 8.48) *Ballistura schoetti*
- 19' At most, the distal half of the anterior side of dens with chaetae; posterior side of dens with distinct notches (Fig. 8.49) *B. albertinae*

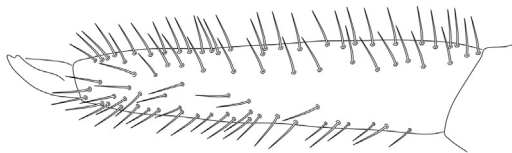


FIGURE 8.48 Dens and mucro of *Ballistura schoetti*.

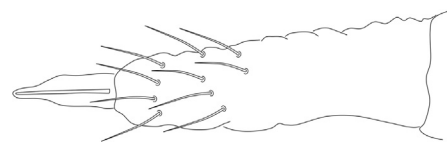


FIGURE 8.49 Dens and mucro of *Ballistura albertinae*.

- 20(1) Ventral face of dens with scales 21
- 20' Ventral face of dens without scales 24
- 21(20) Scales with coarse ribs, some pointed (Fig. 8.50) *Seira ferrarii*
- 21' Scales without ribs, finely denticulate, apical rounded (Fig. 8.51) 22

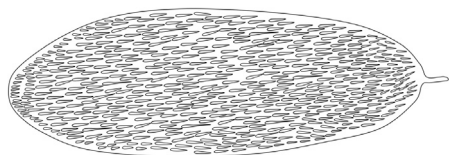


FIGURE 8.50 Scale of *Seira*.

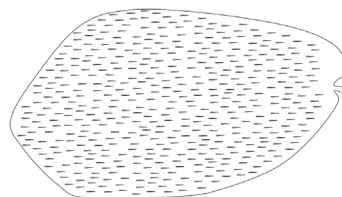


FIGURE 8.51 Scale of *Pseudosinella* or *Lepidocyrtus*.

- 22(21) Head with 0–6 + 0–6 eyes; claws with lateral teeth; first internal teeth (paired) well developed (like-wings) (Fig. 8.52) *Pseudosinella* spp.
- 22' Head with 8 + 8 eyes; claws with normal teeth (Fig. 8.53) 23
- 23(22) Body with blue color *Lepidocyrtus cyaneus*

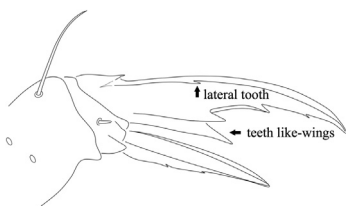


FIGURE 8.52 Claw of *Pseudosinella*.

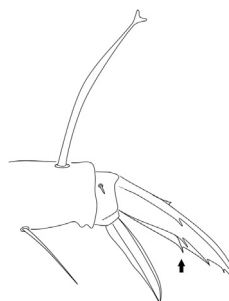


FIGURE 8.53 Claw of *Entomobrya*.

- 23' Body without color, or yellowish *L. lignorum*
- 24(20) Mucronal basal spine present (Fig. 8.54) *Entomobrya benaventii*
- 24' Mucronal basal spine absent 25
- 25(24) Nine dorsal macrochaetae on Abd II *Mesentotoma dollfusi*
- 25 Seven dorsal macrochaetae on Abd II *M. hispanica*

Symphyleona

- 1 Tenaculum with three teeth from juvenile phase II to adult (really with two teeth and a basal tubercle) (Fig. 8.55) (Bourletiellidae) *H. insignis*
- 1' Tenaculum with four teeth from juvenile phase II to adult (really with three teeth and a basal tubercle) 2

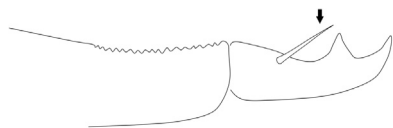


FIGURE 8.54 Mucro of *Entomobrya*.



FIGURE 8.55 Tenaculum of Bourletiellidae.

- 2(1) Females without anal appendages. Males with Ant II–III modified as a fixation organ. Two pairs of bothriotricha in the Abd V. Large abdominal bothriotricha A, B, and C equidistant and open to back or forward (Fig. 8.56) 3
- 2' Female with anal appendages. Male with unmodified antennae. At most one pair of bothriotricha on Abd V. Large abdominal bothriotricha A, B, and C in another arrangement 4

- 3(2) Tibiotarsal III organ absent; mucro without a chaeta *Sphaeridia pumilis*
 3' Tibiotarsal III organ present (Fig. 8.57) *Sminthurides* spp.

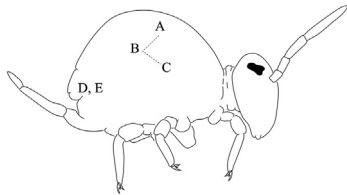


FIGURE 8.56 Habitus of Sminthuridae.



FIGURE 8.57 Tibiotarsal organ of *Sphaeridia pumilis*.

- 4(2) Ant IV shorter than III. Anal appendages clearly directed towards the anus (Fig. 8.58). Bothriotricha of the large abdominal at a backward angle, bothriotricum A apparently on a papilla (Fig. 8.59)
 (Dicyrtomidae) *Dicyrtomina* spp., *Jordanathrix* spp.

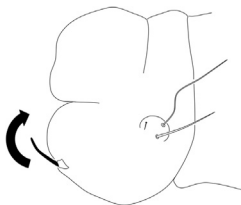


FIGURE 8.58 Small abdominal (lateral view) of a female Dicyrtomidae.

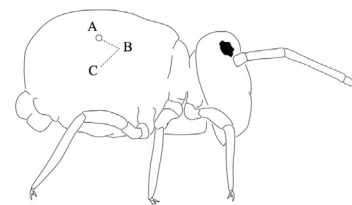


FIGURE 8.59 Habitus of a Dicyrtomidae. A, B, and C are the large abdominal bothriotricha.

- 4' Ant IV longer than Ant III. Bothriotricha form an angle open forward, with different angle (A and B or B and C near each other, and the other (Fig. 8.60). Anal appendages not clearly directed towards the anus, or directed towards genital opening (Fig. 8.61) 5

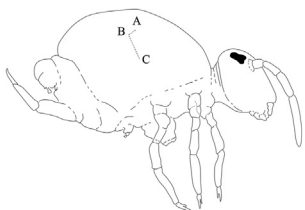


FIGURE 8.60 Habitus of a *Sminthurinus*. A, B, and C are the large abdominal bothriotricha.

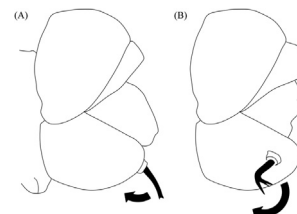


FIGURE 8.61 Small abdominal (lateral view) of a female *Arrhopalites* (A) and *Sminthurinus* (B).

- 5(4) Head with 8 + 8 eyes on each side. Tibiotarsi with erect and capitated chaetae (Fig. 8.62). Dentes without spines (Katiannidae) *Sminthurinus* spp.
 5' Head with 0–2 eyes on each side. Body without pigment or very pale; tibiotarsus without capitated chaetae. Adults with spines on dens (Fig. 8.63) (Arrhopalitidae) *Arrhopalites* spp. (Fig. 8.64)

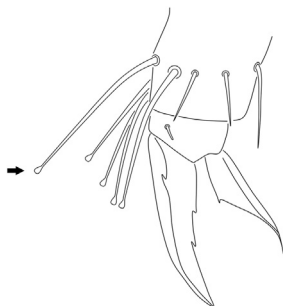


FIGURE 8.62 Tip of leg, claw, and empodium of *Sminthurinus*.



FIGURE 8.63 Dens of *Arrhopalites*.

Neelipleona (Neelidae)

- 1 Sensory fields of posterior large abdomen with two marginal chaetae (Fig. 8.65) *Neelus murinus* (Fig. 8.66)
 1' Sensory fields of posterior large abdomen with five marginal chaetae (Fig. 8.67) *Megalothorax* spp. (Fig. 8.68)

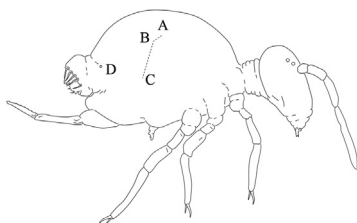


FIGURE 8.64 Habitus of a *Arrhopalites*. A, B, and C are the large abdominal bothriotricha, and D is the small abdominal bothriotricha.

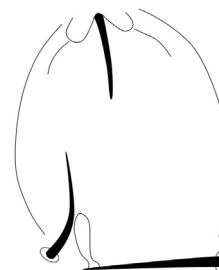


FIGURE 8.65 Sensory field of *Neelus*.

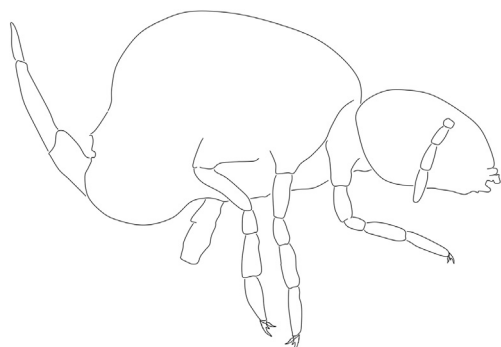


FIGURE 8.66 Habitus of *Neelus murinus*.

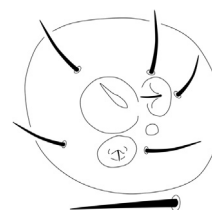


FIGURE 8.67 Sensory field of *Megalothorax*.

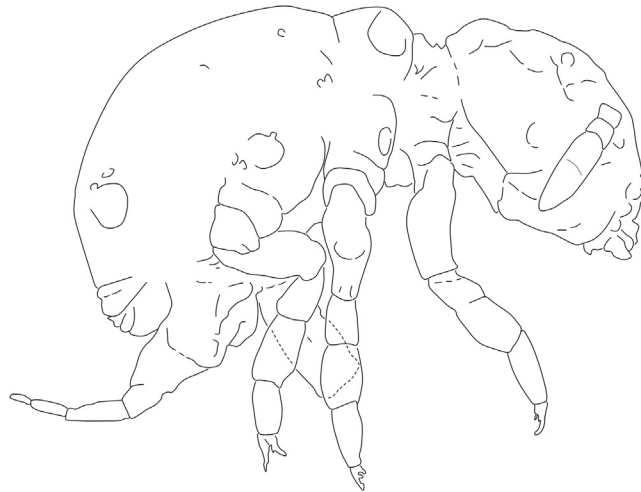


FIGURE 8.68 Habitus of *Megalothorax*.

Key to the subclass Insecta

- 1 Adults and larvae with sucking mouthparts forming a more-or-less prominent narrow tube. Thorax with three pairs of jointed legs (true legs). Forewings (if present) partly chitinized in the basal half and membranous in the distal half. Larvae similar to adults, but without developed wings. Last larval stadium usually must present wing pads **Hemiptera (Fig. 8.69)**
- 1' Adults and larvae usually without sucking mouthparts. But, if these are present, in larvae do not make up a single narrow tube and in adults have a pair of antenna with small clubs 2

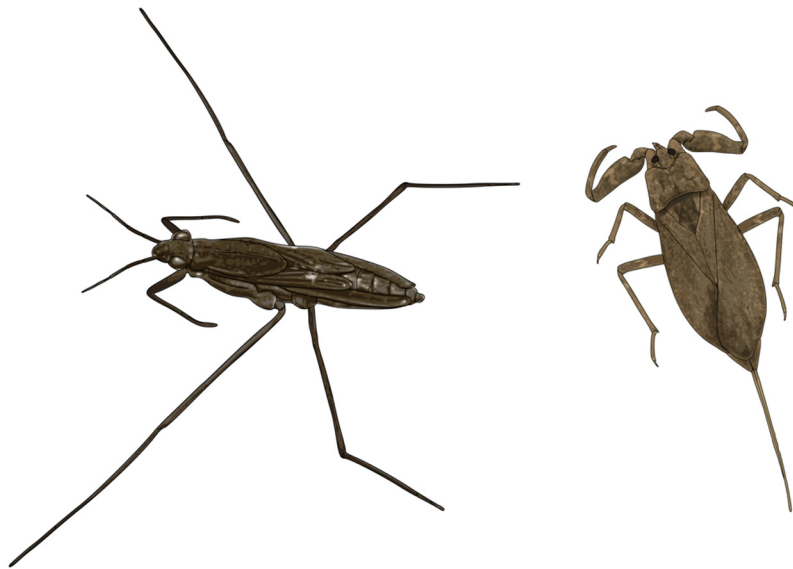


FIGURE 8.69 Two examples of Hemiptera: Gerridae (left) and Nepidae (right).

- 2(1') Adults with forewings rigid and strongly chitinized to form wing cases (elytra) **Coleoptera (Adults) (Fig. 8.70)**
- 2' Without wings. All insect immature (larvae) 3
- 3(2') Body curved to straight with short setae and usually white or yellow. Head heavily sclerotized and often brown or orange. First thoracic segment with a pair of dorsal sclerotized plates. Without thoracic legs. Abdominal segments

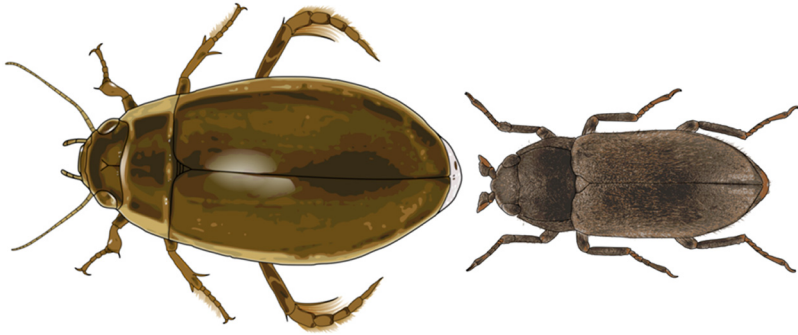


FIGURE 8.70 Two examples of Coleoptera (Adults): Dytiscidae (left) and Dryopidae (right).

- 1–8 with 2–5 dorsal transverse folds, segment 9 with 1 dorsal fold and segment 10 reduced to anal lobe **Coleoptera** (Curculionidae larvae) (Fig. 8.71)
- 3' Larvae without that combination of features 4
- 4(3') Body shape highly variable, but all without true legs. Usually with thoracic, abdominal, or caudal no jointed legs (i.e., false legs or prolegs). Although they must also be entirely absent. Filaments, suckers, extensions, setae, creeping welts, or gills may also be present throughout the body **Diptera** (Fig. 8.72)
- 4') All with true legs on each thoracic segment 5

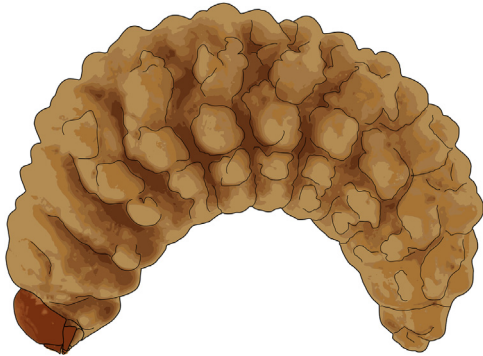


FIGURE 8.71 Larvae of Curculionidae (Coleoptera).

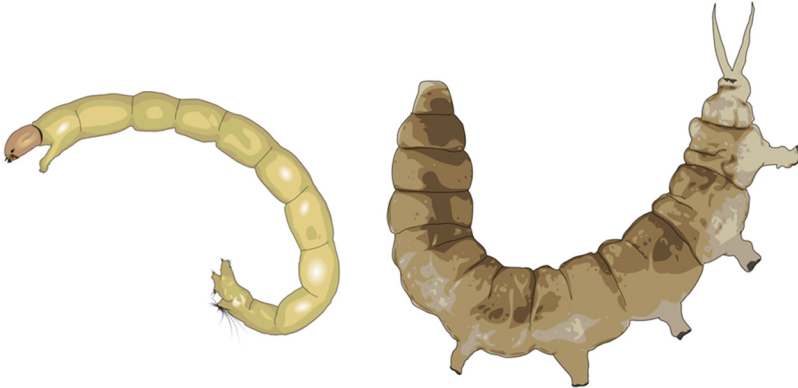


FIGURE 8.72 Two examples of Diptera: Chironomidae (left) and Limoniidae (right).

- 5(4') Larvae with caterpillar shape. Head heavily defined and sclerotized. Abdomen with ventral prolegs on segments 3–6 and the caudal segment, each with a ring of apical hooklets fine hooks (crochets) **Lepidoptera** (Fig. 8.73)
- 5' Larvae are not caterpillar-like 6
- 6(5') Mandibles are usually elongate, slender, and modified in two long sucking tubes on the head **Neuroptera** (Fig. 8.74)
- 6' Short and robust mandibles, no modified in sucking tubes 7
- 7(6') Abdomen with a single long caudal filament and with seven pairs of lateral filamentous gills **Megaloptera** (Fig. 8.75)
- 7' Abdomen without this combination of characters 8
- 8(7') Abdomen with one pair of anal prolegs, each ending in a sclerotized hook; larvae often live inside cases or nets **Trichoptera** (Fig. 8.76)
- 8' Abdomen without anal prolegs. Occasionally, two pairs of sclerotized hooks may be present. Larvae never live inside cases 9
- 9(8') Last larval stadium without wing pads developed. Thorax and abdomen highly variable. Abdominal segments may present dorsal projections, lateral gills, prolegs. Caudal segment may present gills, hooks, long filaments (urogomphi) **Coleoptera** (Larvae) (Fig. 8.77)
- 9' Last larval stadium with wing pads developed 10
- 10(9') Modified mouthparts into a mask-like structure, hinged basally and toothed apically, that can extend forward and retract rapidly. Slender species with three leaf-like, caudal gills. Stout species without caudal gills, but with spine-like processes at the body end **Odonata** (Fig. 8.78)
- 10' Mouthparts no modified into a mask 11
- 11 (10') Abdomen with three (less usually two) multisegmented caudal filaments and paired lateral gills. Legs with one tarsal claw **Ephemeroptera** (Fig. 8.79)
- 11' Abdomen with two multisegmented caudal. Without lateral abdominal gills, but cervical, thoracic, or caudal gills may be present. Legs with two tarsal claws **Plecoptera** (Fig. 8.80)

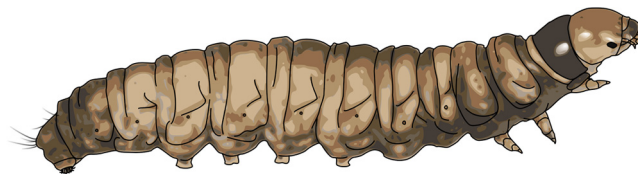


FIGURE 8.73 Example of Lepidoptera: Crambidae.



FIGURE 8.74 Example of Neuroptera: Osmylidae.

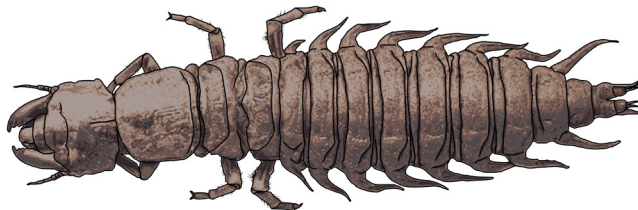


FIGURE 8.75 Example of Megaloptera: Sialidae.



FIGURE 8.76 Two examples of Trichoptera: Limnephilidae (left) and Hydropsychidae (right).



FIGURE 8.77 Two examples of Coleoptera (Larvae): Elmidae (left) and Hydrophilidae (right).



FIGURE 8.78 Two examples of Odonata: Aeshnidae (left) and Lestidae (right).



FIGURE 8.79 Two examples of Ephemeroptera: Baetidae (left) and Heptageniidae (right).

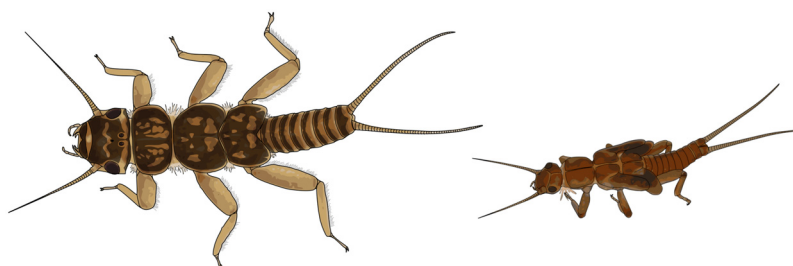


FIGURE 8.80 Two examples of Plecoptera: Perlidae (left) and Nemouridae (right).

Insect taxa marginally associated with the aquatic environment

Hymenoptera: This is a very large order of holometabolous insects that includes bees, wasps, and ants. Some species of wasps have terrestrial adults and larvae that are parasitic upon other aquatic organisms, often other insects. Most aquatic Hymenoptera are endoparasites of larvae that occur in aquatic plants (Lancaster & Downes, 2013). However, some are ectoparasitic and oviposit on larvae, prepupae, or pupae. Larvae are generally worm-like, and their morphology is the typical of internal parasites. These do not have legs, and the head is often very reduced (without ocelli and absent or reduced antennae). Hymenoptera will be treated more extensively in Chapter 16 of this book.

Shoreline insects often found in aquatic samples

The following three insect orders include insects that are primarily terrestrial, but because they live in the shoreline of rivers or lakes, are often found in aquatic samples, and thus could easily be confused with aquatic taxa:

Suborder Homoptera: The suborder Homoptera are grouped within Hemiptera. Consequently, they also have sucking mouthparts forming a prominent narrow tube, and their first pair of wings are membranous. Two families frequently found in the shoreline are Cicadellidae (leafhoppers) and Aphididae (aphids). The Cicadellidae are easily recognized by having the hind tibiae with one or more distinct keels and a row of movable spines on each side. Most Aphididae are wingless and have long antennae. Their main characteristic is the presence of a pair of abdominal tubes on the dorsal surface of their fifth abdominal segment.

Order Coleoptera: Excluding the aquatic species, most Coleoptera have terrestrial habits. But some species live in the shoreline. Two families can be found frequently in the shoreline. The Carabidae are predatory ground beetles with long and filamentous antennae, shiny black or metallic elytra, and long and run-adapted legs. The Staphylinidae (or rove beetles) are primarily distinguished by their short elytra typically leaving more than half of their abdominal segments exposed. Larvae of Carabidae and Staphylinidae are also frequently found in the shoreline and confused with Hydrophilidae or Dytiscidae. Both can be recognized by having in the last abdominal segment, two long cerci and a ventral tube or supporting structure.

Order Thysanoptera: Commonly called thrips, Thysanoptera are hemimetabolous minute insects whose distinctive characteristic is the presence of two pairs of wings fringed with hairs and asymmetrical rasping-sucking mouthparts.

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