

Chapter 2

A Remarkable Anomuran: The Taxon *Aegla* Leach, 1820. Taxonomic Remarks, Distribution, Biology, Diversity and Conservation

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Abstract The family Aeglididae comprises three genera, one extant (*Aegla*) and two extinct genera (*Protaegla* and *Haumuriaegla*), the latter two genera are known only from fossils from marine sediments (indicating a marine origin for the group). *Aegla* contains all extant species and constitutes a monophyletic group within the Anomura. All 78 species and subspecies described so far are entirely adapted to freshwater habitats and are endemic to temperate and subtropical regions of continental South America. While most species are found in epigeal habitats, there are a few cave-dwelling species in southeastern Brazil. The reproductive period varies from 8 to 12 months (in species from colder higher latitudes), to 4–7 months (in species from lower latitudes where warm-rainy and cold-dry seasons alternate). The adult males of seasonally breeding species include two morphotypes, one non-reproductive and the other reproductive. Eggs are large and few in number, and post-embryonic development is epimorphic. Juveniles have limited dispersal capacity and recruits tend to remain with the parental population. *Aegla* is the most severely threatened group among South American freshwater decapods because of habitat degradation, high endemism, a restricted area of occupancy, and a severely fragmented spatial distribution with reproductively isolated subpopulations.

Keywords Aeglididae · Decapoda · Freshwater · Threatened species · Review

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2.1 Introduction

This chapter offers a multidisciplinary overview of the taxonomy, diversity, distribution, general biology, and conservation of a remarkable group of freshwater anomuran. The uniqueness of the genus *Aegla* Leach, 1820 was recognised well over 60 years ago when Schmitt (1942b) stated “There are no fresh-water Crustacea at all like *Aegla* anywhere else in the world.” This contribution is timely because *Aegla* is probably the most severely threatened taxon of freshwater decapods in South America, with more than half (55.13 %) of the 78 known species and sub-species assessed as either Critically Endangered (15.38 %), Endangered (28.21 %), or Vulnerable (11.54 %).

2.1.1 Taxonomic Remarks

The family Aeglidæ Dana, 1852 currently comprises three genera: *Haumuriaegla* Feldmann 1984; *Protaegla* Feldmann et al. 1998, and *Aegla*. The first two genera are monotypic and known only from fossil records (Fig. 2.1): *Protaegla miniscula* is found in Early Cretaceous marine deposits (about 110 million years old) in Mexico (Feldmann et al. 1998), and *Haumuriaegla glaessneri* is found in Late Cretaceous marine deposits (about 75 million years old) in New Zealand (Feldmann 1984). These fossil findings provide strong support for the marine origin of the family Aeglidæ, possibly in the Indo-Pacific region (Feldmann 1986).

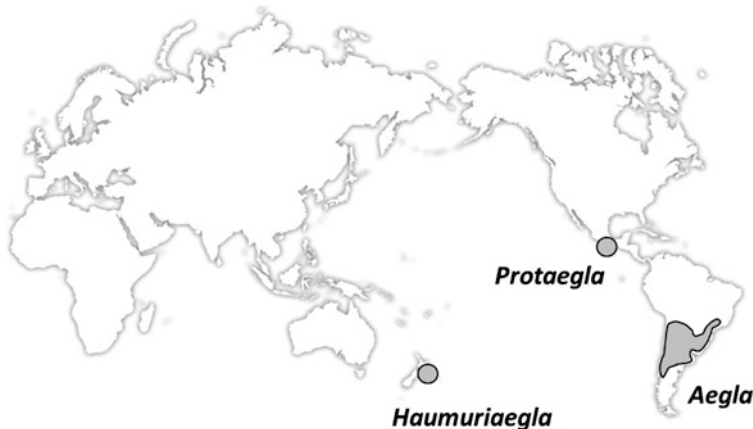


Fig. 2.1 World distribution of the family Aeglidæ. World map represents today's configuration of the continents, and it is freely used here to show proximate locations of the marine fossil genera *Haumuriaegla* and *Protaegla* in the Indo-Pacific Region. All extant aeglids, genus *Aegla*, are endemic to temperate and subtropical regions of continental South America and are entirely adapted to freshwater habitats

The third genus, *Aegla*, contains all extant aeglid species. It is the only anomuran taxon entirely adapted to freshwater habitats and it is endemic to temperate and subtropical regions of continental South America (Schmitt 1942b; Bond-Buckup et al. 2008) (Fig. 2.1). With 78 described species and subspecies, these freshwater aeglids represent only 3 % of the extant anomuran assemblage of approximately 2500 species (sensu De Grave et al. 2009).

Until recently, the family Aeglididae was included in the superfamily Galatheoidea Samouelle, 1819, together with three other anomuran families: Chirostylidae Ortmann, 1892, Porcellanidae Haworth, 1825, and Galatheididae Samouelle, 1819 (Schmitt 1942b; Bowman and Abele 1982; Martin and Abele 1986; Martin and Davis 2001). This traditional view is based on morphological similarities such as the pyriform body shape, the dorso-ventral flattening of the cephalothorax and pleon, the presence of a well-developed rostrum, and the distinct dorsal cervical groove on the carapace; but none of these traits is exclusive to the aeglids, and many are also found in other anomurans (Martin and Abele 1988).

Recent investigations based on spermatozoal ultrastructure (Tudge and Scheltinga 2002), molecular data, and phylogenetic analyses (Martin and Abele 1988; Pérez-Losada et al. 2002a, c, 2004) have challenged the traditional view that the Aeglididae is part of the superfamily Galatheoidea. Furthermore, McLaughlin et al. (2007) proposed that the Aeglididae should be placed in the superfamily Aegloidea Dana, 1952.

The phylogenetic relationships of the Aegloidea with other anomuran taxa, however, still remains controversial and close phylogenetic affinities with the Paguroidea Latreille, 1802 and Hippoidea Latreille, 1825 have been suggested by several authors (Martin and Abele 1988; Pérez-Losada et al. 2002c; McLaughlin et al. 2007). Data from sperm morphology (Tudge and Scheltinga 2002) and phylogenetic analyses (Schnabel and Ahyong 2010; Tsang et al. 2011) strongly support close affinities between the Aegloidea and the Lomisoidea Bouvier, 1895, a monotypic taxon for *Lomis hirta* Lamarck, 1818 from the Australasian and Indo-Pacific regions.

Freshwater aeglids have unique traits that set them apart from other galatheid families, such as *lineae* on the carapace, gill morphology, and postembryonic development.

1. *Lineae* on the carapace (Fig. 2.2a, b). Aeglids exhibit a unique pattern of sutures, or *lineae*, on the lateral and dorsal surfaces of the carapace. The dorsal sutures on the posterior half of the carapace demarcate well defined cardiac and branchial areas. The calcification along the *lineae* is weaker than the exoskeletal plates (Martin and Abele 1988) and the branchial plates can be easily broken along the *lineae* and gently removed creating an access window to the gill chamber that allows observation of the gills (Fig. 2.2c).
2. Gill morphology. *Aegla* has trichobranchiate gills and this separates them from the galatheid families which have the phyllobranchiate gills seen in many marine anomurans (Martin and Abele 1986). Trichobranchiate gills are found in anomurans such as the blepharopodids (Hippoidea) (Boyko 2002).

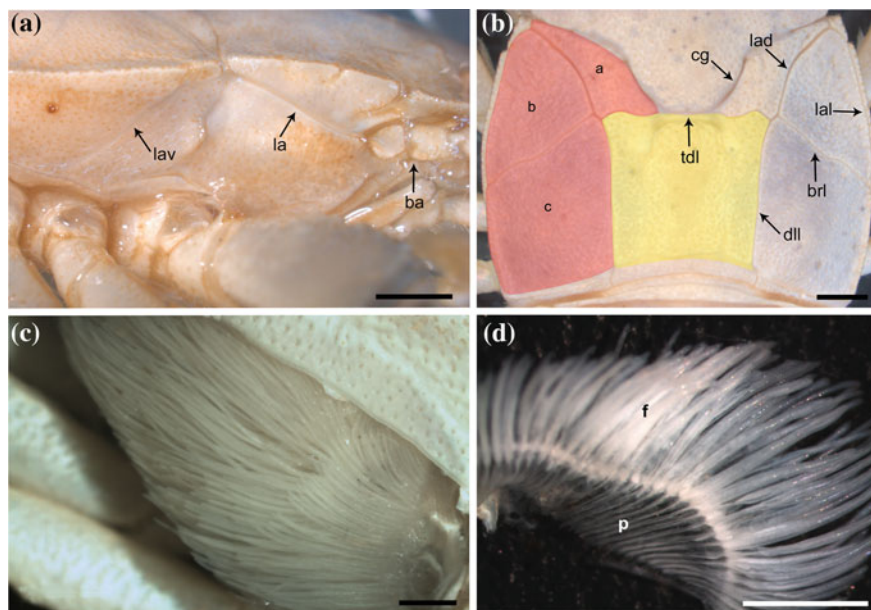


Fig. 2.2 Lineae and gill morphology. **a** *Aegla paulensis*: Lateral view of the carapace showing the *linea aeglica* (la) and the *linea aeglica ventralis* (lav); ba: base of the antenna. Bar 2 mm. **b** *Aegla strinati*: Dorsal view of the posterior region of the carapace showing the cardiac area (yellow) and the three subdivisions of the branchial area (red): interior area (a), anterior area (b) and posterior area (c). Cervical groove (cg), *linea aeglica dorsalis* (lad), *linea aeglica lateralis* (lal), branchial linea (brl), transverse dorsal linea (tdl), and dorsal longitudinal linea (dll). Bar 2 mm. **c** *Aegla perobae*: General view of trichobranchiate gills in the branchial chamber as seen after the exoskeleton plates covering the anterior and posterior branchial areas have been removed. Bar 1 mm. **d** *Aegla perobae*: Trichobranchiate gill removed from the branchial chamber; arrangements of finger-like lamellae (f) on distal portion and of plate-like lamellae (p) on proximal portion. Bar 1 mm

The trichobranchiate gills in freshwater aeglids (Fig. 2.2d) have a unique structure, which was well described by Martin and Abele (1988, p. 23, 25) as follows: (The gills) “resemble trichobranchiate gills distally in that the gill filaments are long finger-like tubes; these extend forward from the base of the gill. The proximal portion of the gill resembles that of a brachyuran phyllobranch in having plate-like lamellae extending out over the branchial axis...” McLaughlin and de Saint Laurent (1998, p. 161) emphasized that “... It is not the shape of the gill elements, so much as their insertion on the rachis of the gill that determines gill type.” McLaughlin et al. (2007) described the gills of freshwater aeglids as having a quadriserial arrangement whereby the lamellar elements are not regularly inserted around the gill axis. Gills with quadriserial arrangements of lamellar elements have also been described in some paguroids (McLaughlin and de Saint Laurent 1998). It is clear that the gill morphology of freshwater aeglids needs further investigation.

3. Postembryonic development. The postembryonic development in marine anomurans is indirect, with eggs releasing zoeal larval stages. The zoeal stages are then followed by the megalopal stage that then moults into a juvenile “crab”. Examples of this general pattern of development in marine anomurans are available in the literature for several families, such as Chirostylidae (Clark and Ng 2008; Fujita and Clark 2010), Galatheidae (Pike and Wear 1969; Fagetti and Campodonico 1971; Christiansen and Anger 1990; Fujita and Shokita 2005; Fujita 2010), Porcellanidae (Fujita et al. 2002; Fujita and Osawa 2005), Coenobitidae (Harvey 1992; Brodie and Harvey 2001), Hippidae (Knight 1967; Stuck and Truesdale 1986), Paguridae (McLaughlin et al. 1989, 1993; Gherardi and McLaughlin 1995; Barria et al. 2006), Lithodidae (Haynes 1982; Crain and McLaughlin 2000a, b; McLaughlin et al. 2003) and Lomisidae (Cormie 1993). The postembryonic development of marine fossil aeglids is not known, but it was most probably characterized by the presence of free-swimming larval form with a high capability for dispersal in ocean currents, similar to larval development observed in marine anomurans. Dispersal of ancient larval aeglids toward South America would have probably been favored by the counter-clockwise gyre of ocean circulation in the Pacific Ocean during the Oligocene Epoch (Feldmann 1986). In the freshwater aeglid genus *Aegla*, however, the postembryonic development is direct (=epimorphic), a life-history strategy that is a derived trait in this family. Aeglids hatch from eggs as benthic juveniles that resemble the adult form in general morphology (Mouchet 1932; Bahamonde and López 1961; Rodrigues and Hebling 1978; Bond-Buckup et al. 1996, 1999; Bueno and Bond-Buckup 1996; Francisco et al. 2007; Teodósio and Masunari 2007; Moraes and Bueno 2013, 2015).

2.1.2 *Origin and Biogeography*

The taxon *Aegla* probably originated in freshwater habitats in the Early Tertiary Period of the Cenozoic Era, about 60 mya (Pérez-Losada et al. 2004). While *Protaegla* and *Haumuriaegla* did not survive the great extinction of the Mesozoic/Cenozoic transition (Schweitzer and Feldmann 2005), the successful survivorship of *Aegla* during that geological period has been attributed to the occupation of buffered habitats less susceptible to the effects of the Cretaceous/Paleocene (K/P) transition (Schweitzer and Feldmann 2005). Factors that could have increased survivability of *Aegla* include inhabiting a refugium and eurytopy (Schweitzer and Feldmann 2005). The radiation and speciation of freshwater aeglids throughout the Cenozoic Era up to the present time corroborate the successful adaptation and colonization of freshwater habitats after the K/P event.

The point of origin of freshwater aeglids, whether from the Pacific side or from the Atlantic side of continental South America, was a matter of debate by past naturalists (Ortmann 1902; Schmitt 1942b; Ringuelet 1949; Morrone and Lopretto

1994). Over the past decades, however, the Pacific hypothesis has increasingly gained acceptance as data from different sources became available. This included evidence from fossil findings (Feldmann 1984; Feldmann et al. 1998), studies on the possible ancestral larval dispersal route of marine predecessor aeglids in the Indo-Pacific region (Feldmann 1986), and molecular phylogenetic analyses made in conjunction with data on the geological history and paleodrainage systems formations of continental South America (Pérez-Losada et al. 2004).

The dispersal of ancient marine aeglids on the western side of South America was favoured by marine transgressions during the early formation of the Andes Cordillera, in the Late Cretaceous-Early Tertiary Period, about 90–60 mya (Pérez-Losada et al. 2004). The evolutionary path of populations of land-locked marine aeglids would favour the acquisition of physiological adaptations and changes to life history strategies that helped them cope with increasing exposure to less saline waters. The successful adaptation to freshwater habitats marks the origin of the taxon *Aegla* and the beginning of its dispersal and speciation history throughout southern regions of South America from the Pacific to the Atlantic.

The uplifting of the Andes Cordillera represented an important physical barrier leading to the separation of *Aegla* populations on the western side of the Cordillera (mostly found in Chile today) from those on the eastern side. The uplifting of the Andes caused the drainage of many Pacific paleobasins to flow eastward toward the Atlantic side of South America (Potter 1997; Lundberg et al. 1998; Almeida et al. 2000). The west-to-east dispersal routes of *Aegla* through South American paleobasins were made possible by the eventual interconnection of continental western water masses with the paleobasins of Paraná and Uruguay rivers in the Late Eocene—Early Oligocene Epoch (43–30 mya) (Pérez-Losada et al. 2004). The east-northward dispersal route through the Paraná River paleobasin was one of the latest major events in the evolutionary radiation of the freshwater aeglids. Freshwater aeglids form a monophyletic assemblage with five recognized clades (sensu Pérez-Losada et al. 2004), and their current geographic distribution reflects the dispersal history of *Aegla* as described above.

2.1.3 Diversity, Distribution and Habitat

The present-day distributional range of freshwater aeglids includes six South American countries: Chile, Argentina, Bolivia, Paraguay, Uruguay, and Brazil (Bond-Buckup et al. 2008). The northernmost and the southernmost limits of the distributional range of *Aegla* are latitude 20 °S at Claraval, Brazil (*Aegla franca* Schmitt, 1942) and latitude 50 °S at Duque de York Island, Chile (*Aegla alacalufi* Jara and López 1981) (Bueno et al. 2007; Oyanedel et al. 2011). The highest known altitude (3613 m) is that for *Aegla septentrionalis* Bond-Buckup and Buckup 1994 from the Province of Jujuy, Argentina (Bond-Buckup et al. 2010a).

Based on a recent annotated checklist (McLaughlin et al. 2010), updated thereafter by descriptions of new species (Santos et al. 2012, 2013, 2014, 2015), the

number of known species of freshwater aeglids is currently 78 (Table 2.2). More than half of these species ($n = 47$) are found in the south and southeastern regions of Brazil of which 89.4 % ($n = 42$) are endemic to Brazilian freshwaters (Fig. 2.3). Chile ranks second in number of species (21) and has the highest percentage of species that are country endemics (95.2 %, $n = 20$). There are currently 14 species reported for Argentina, with 7 (50 %) being endemic to that country. Uruguay follows next with 4 species, including *Aegla carinata* Bond-Buckup and Loureiro 2014 as the only endemic species (25 %) (Santos et al. 2014). Paraguay and Bolivia have one species each, *Aegla platensis* Schmitt 1942 and *A. septentrionalis* Bond-Buckup and Buckup 1994, respectively, neither of which is country endemic, because the distribution of these two species extends to other countries. Species richness increases from south to north in the distributional range of the genus, and this may be due to the latitudinal gradient effect (Morrone and Lopretto 1994).

Most species of *Aegla* inhabit lotic habitats, such as rivers and streams with fast moving and well oxygenated water flowing over bedrock strata (Fig. 2.4a). A few species inhabit lentic habitats such as lakes [e.g., *Aegla denticulata lacustris* Jara 1989 from Chile, and *Aegla prado* Schmitt, 1942 from Brazil and Uruguay (Jara 1989; Bond-Buckup et al. 2008)].

Most species of aeglids inhabit epigeal habitats and show marked allopatric distributional patterns, and are usually restricted to one or more drainage systems belonging to a major hydrographic basin (Schmitt 1942b; Morrone 1996), although there are a few instances where two or more species with a sympatric distribution have been reported (Buckup and Rossi 1977; Castro-Souza and Bond-Buckup 2004; Santos et al. 2012). Several species of freshwater aeglids from epigeal habitats are highly stenotopic and are restricted either to the type-locality or have a limited area of occupancy (Rodrigues and Hebling 1978; Bueno et al. 2007; Santos et al. 2010, 2012, 2013).

A few species (*Aegla microphthalma* Bond-Buckup and Buckup 1994, *A. cavernicola* Türkay 1972 and *A. leptochela* Bond-Buckup and Buckup 1994) are obligate cave dwellers or troglobites (Fig. 2.4b). Troglotic species exhibit troglomorphic traits, such as depigmentation of the cuticle (Fig. 2.3i), shorter eyestalks, a reduced pigmented area of the cornea (Fig. 2.5), proportionately longer walking legs (Fig. 2.3d), and longer antennal flagella (Bond-Buckup and Buckup 1994; Moracchioli 1994; Alves 2007). Troglotic species are highly endemic, with distributions restricted to the type-locality inside the cave (Türkay 1972; Trajano 1987; Bond-Buckup and Buckup 1994; Gnaspini and Trajano 1994; Moracchioli 1994, Maia et al. 2013; Fernandes et al. 2013).

Aegla strinati Türkay 1972 (Fig. 2.3g) is an example of a facultative cave dwelling species, or troglophile, because it forms a self-sustaining, non-isolated reproductive population that moves about freely between both epigeal and subterranean habitats (Türkay 1972; Rocha and Bueno 2004, 2011). Troglitic and trogliphilic species are found in the karst region of the Alto Ribeira in the State of São Paulo, southeastern Brazil.

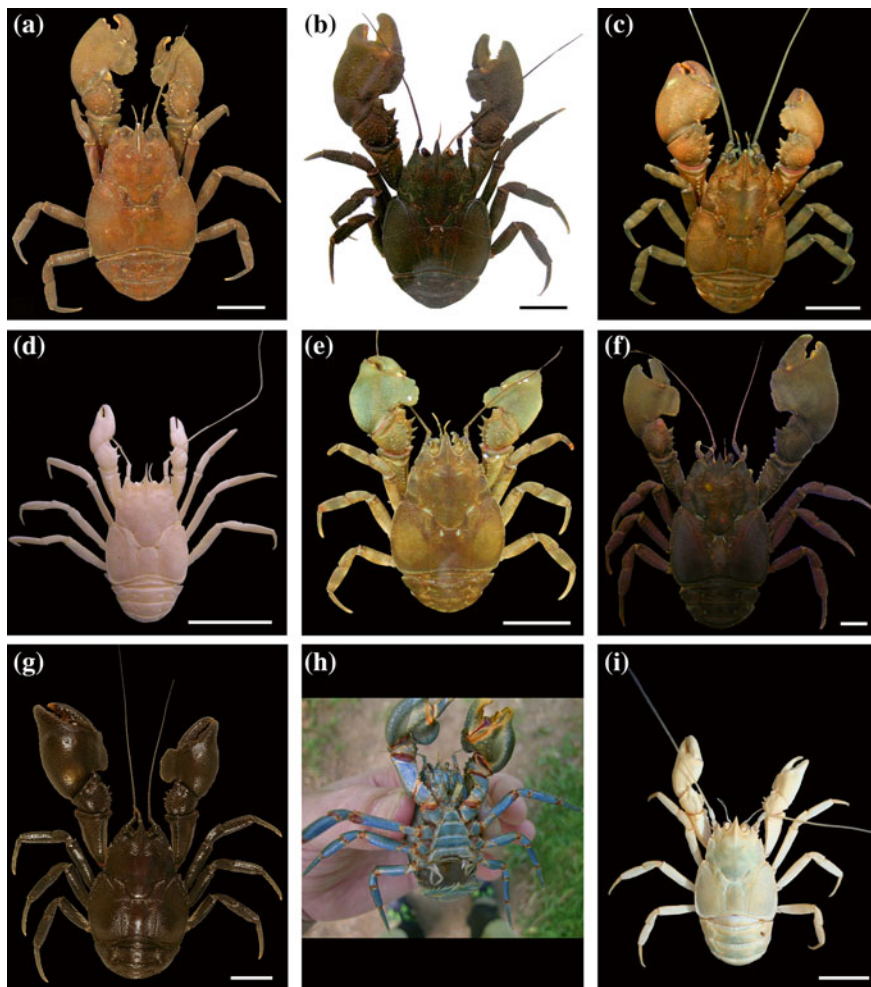


Fig. 2.3 A selection of *Aegla* species from Brazil. **a** *Aegla castro*, male, live specimen from Itatinga (SP), Bar 1 cm. **b** *Aegla franca*, male, live specimen from Claraval (MG), Bar. 1 cm. **c** *Aegla marginata*, male, live specimen from the type-locality, Morretes (PR), Bar 1 cm. **d** *Aegla microphthalma*, male, alcohol preserved specimen from the type-locality, Caverna Santana, Iporanga (SP), Bar 1 cm. **e** *Aegla paulensis*, male, live specimen from the type-locality, Paranapiacaba, Alto da Serra de Cubatão, (SP), Bar 1 cm. **f** *Aegla perobae*, male, live specimen from the type-locality, São Pedro (SP), Bar 5 mm. **g** *Aegla strinatii*, male, live specimen from the type-locality, das Ostras River/Gruta da Tapagem (also known as Caverna do Diabo), Jacupiranga (SP), Bar 1 cm, modified from original photo by Sérgio Schwarz da Rocha. **h** *Aegla schmitti*, male, live specimen from Iporanga (SP), note general body coloration on the ventral surface and leg joints; no bar included. **i** *Aegla cavernicola*, female, live specimen from the type-locality, Gruta das Areias, Iporanga (SP), Bar 1 cm; modified from original photo by Bruno Fernandes Takano. Key to Brazilian States: São Paulo (SP), Minas Gerais (MG), and Paraná (PR)

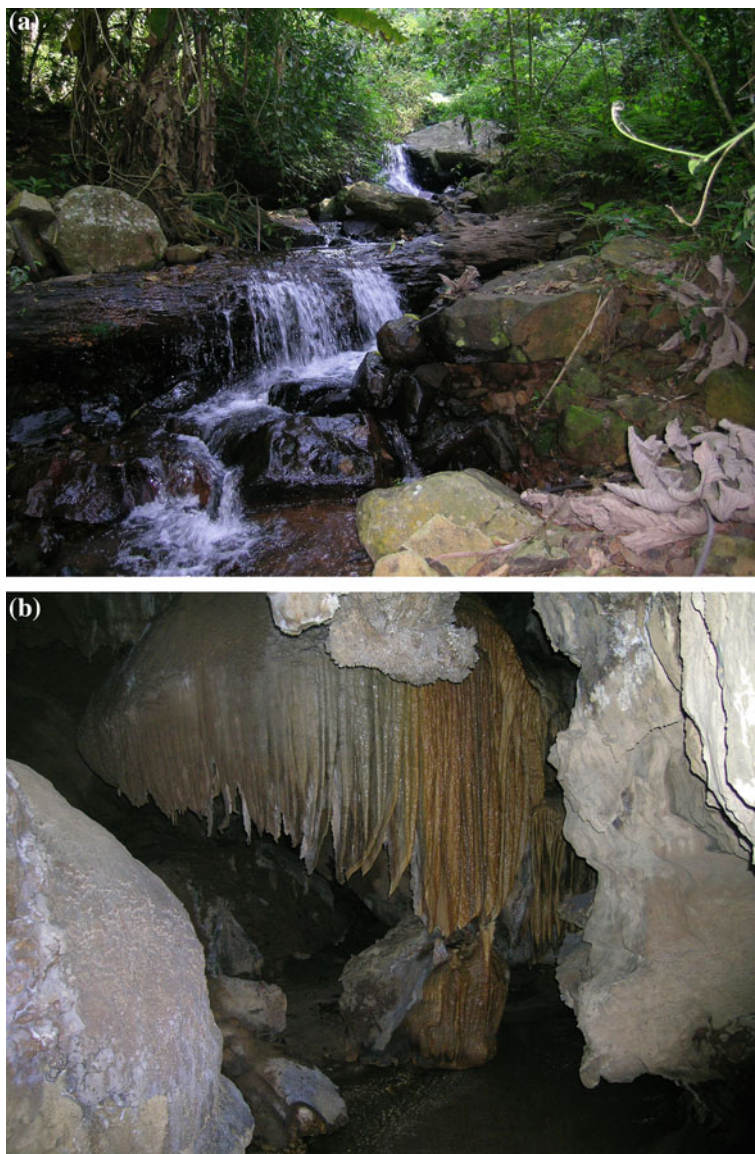


Fig. 2.4 Habitats. **a** Epigeal habitat: type-locality of *Aegla perobae*, São Pedro, São Paulo state, Brazil. **b** Subterranean habitat: type-locality of an undescribed troglobite species from Gruta do Furo da Agulha, Alto Ribeira karst region, São Paulo state, Brazil

Freshwater aeglids are omnivorous, and feed on animal debris, algae, and the larvae of aquatic invertebrates (Bahamonde and López 1961; Rodrigues and Hebling 1978; Magni and Py-Daniel 1989; Castro-Souza and Bond-Buckup 2004; Bueno and Bond-Buckup 2004; Santos et al. 2008). During the day aeglids are

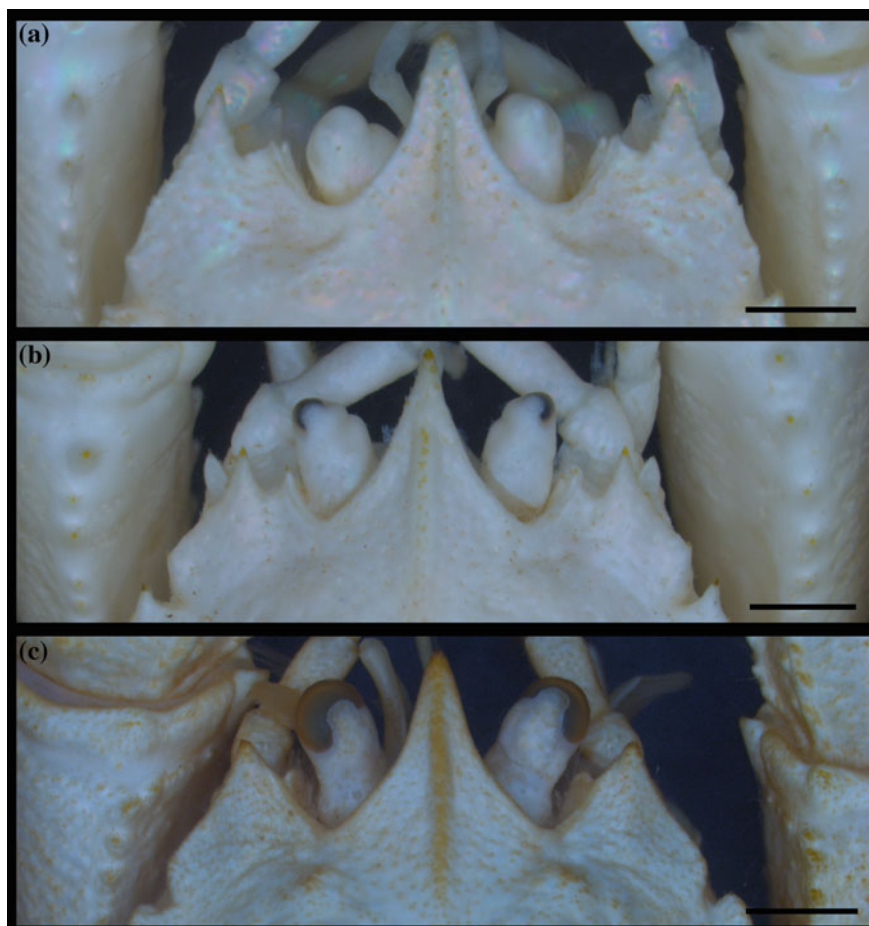


Fig. 2.5 Compound eyes. **a** Depigmentation of the cornea in the troglitic species *Aegla microphthalma*. **b** Reduced pigmentation of the cornea in the troglitic species *Aegla cavernicola*. **c** Pigmentation area of the cornea in *Aegla marginata* from epigeal habitat. Bar 1 mm (**a**) and 2 mm (**b** and **c**)

usually inactive and seek protected spaces under rocks, pebbles, and leaf litter that accumulates on the riverbed (Noro and Buckup 2002; Gonçalves et al. 2006; Bueno et al. 2014). They are more active at night and move about in their quest for food and, when the time comes, for reproduction (Sokolowicz et al. 2007a; Bueno et al. 2007; Ayres-Peres et al. 2011b).

Population density estimates are available for a few species only. Density estimates for the troglitic species, *Aegla microphthalma* and *A. leptochela*, are low, and less than one individual/m² (Moracchioli 1994; Maia et al. 2013). For species from epigeal habitats, density estimates varied from as low as 2.8/m² for *Aegla*

franca to as high as 9.05/m², 11.5 m² and 12/m² for *Aegla perobae*, *A. paulensis* and *A. platensis*, respectively (Bueno and Bond-Buckup 2000; Bueno et al. 2007, 2014b; Cohen et al. 2013).

2.2 Biology

2.2.1 Population Size Structure and Sexual Dimorphism

As a rule, male aeglids attain a larger body size than females (Swiech-Ayoub and Masunari 2001b; Noro and Buckup 2002; Fransozo et al. 2003; Boos et al. 2006; Viau et al. 2006; Bueno and Shimizu 2009; Teodósio and Masunari 2009; Cohen et al. 2011; Chiquetto-Machado et al. 2016). Body size dimorphism is a common feature in pleocyemate decapods, and has been generally interpreted to reflect different energy use by males and females (whereby females divert a significant amount of their energy toward reproduction, while males allocate most of their energy toward growth) (Hartnoll 1985). Other possible causes of body size dimorphism suggested for *Aegla* are differences in mortality rate, migration, responses to environmental conditions (Gonçalves et al. 2006), resource use (Silva-Gonçalves et al. 2009), and sexual selection (Cohen et al. 2011). Female aeglids tend to live longer than males (Silva-Castiglioni et al. 2006; Silva-Gonçalves et al. 2009; Cohen et al. 2011; Chiquetto-Machado et al. 2016), although the opposite (Trevisan and Santos 2011) as well as similar longevity in both sexes (Bahamonde and López 1961; Bueno and Bond-Buckup 2000; Swiech-Ayoub and Masunari 2001b; Boos et al. 2006) have also been reported.

Both adult male and female aeglids lack the first pair of abdominal pleopods. Female aeglids have well-developed uniramous two-segmented pairs of pleopods 2 through 5 (Fig. 2.6a), which they use for egg attachment and incubation. In males, pleopods 2 through 5 are either lacking altogether or are vestigial and resemble calcified knobs (Martin and Abele 1988) (Fig. 2.6b). This sexually dimorphic abdominal appendage trait can be used to determine the gender of freshwater aeglids. However, adult males with rudimentary pairs of pleopods 2–5 have been observed in two species: *Aegla perobae* Hebling and Rodrigues, 1977 (Moraes and Bueno 2015), and an undescribed troglobitic species (Bueno et al. 2014a) from Brazil (Fig. 2.6c). These rudimentary male pleopods are clearly shorter and less setose than the corresponding pairs of pleopods observed in adult females, but they are not vestigial, and, they are either one- or two-segmented.

Freshwater aeglids are heterochelous whereby the propodus and dactylus of the first pair of pereopods have a different size and shape to each other (Bueno and Shimizu 2009; Trevisan and Santos 2011) (Fig. 2.3), and there is only one reported exception (Noro and Buckup 2003). The heterochelous condition of the chelipeds is conspicuous in both sexes, and may even be noticeable in the late juveniles of some species (Bueno and Shimizu 2009). The chelipeds show a clear predominance for

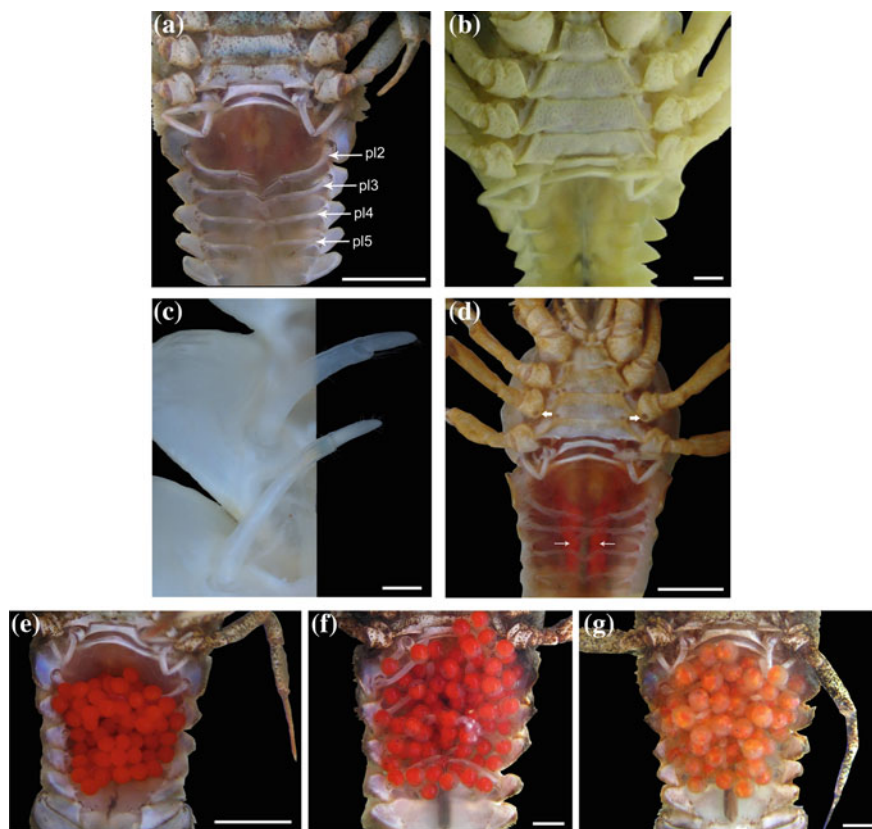


Fig. 2.6 Pleopods, late ovaries and eggs. **a** *Aegla franca*, adult female, live specimen from Claraval (MG); ventral view of pleon showing four pairs of well-developed uniramous and two-segmented pleopods 2 through 5; Bar 5 mm. **b** *Aegla paulensis*, adult male, alcohol preserved specimen from Jaraguá State Park, São Paulo (SP); ventral view of pleon. Note absence of pleopods 2 through 5; Bar 2 mm. Photo: Felipe P. A. Cohen. **c** Ventral view of pleon (one side only) of an undescribed troglobite, adult male, alcohol preserved specimen from Gruta do Lago Subterrâneo, Alto Ribeira karst region (SP), showing two (out of four) short two-segmented pleopods. Black background was positioned underneath distal portion of pleopods to provide contrast. Bar 0.5 mm. **d** *Aegla paulensis*, adult female, live specimen from Jaraguá State Park, São Paulo (SP). Ventral view of pleon showing the two posterior lobes of the ovaries at late maturation stage (*thin arrows*). Gonopore openings are also indicated (*bold arrows*) on the coxa of the third pair of pereopods. Bar 5 mm. **e–g** *Aegla franca*, ovigerous females, live specimens from Claraval (MG); **e** early eggs, Bar 5 mm; **f** intermediate eggs, Bar 2 mm; **g** late eggs, Bar 2 mm. Key to Brazilian States: São Paulo (SP) and Minas Gerais (MG)

left handedness, whereby the left is prevalently the most robust of the pair (Bahamonde and López 1961; López 1965; Rodrigues and Hebling 1978; Viau et al. 2006; Bueno and Shimizu 2009; Trevisan and Santos 2011). Adult males typically exhibit heavier and larger first chelipeds than adult females (Martin and Abele 1988) (Fig. 2.7a), and this sexually dimorphic trait has been well

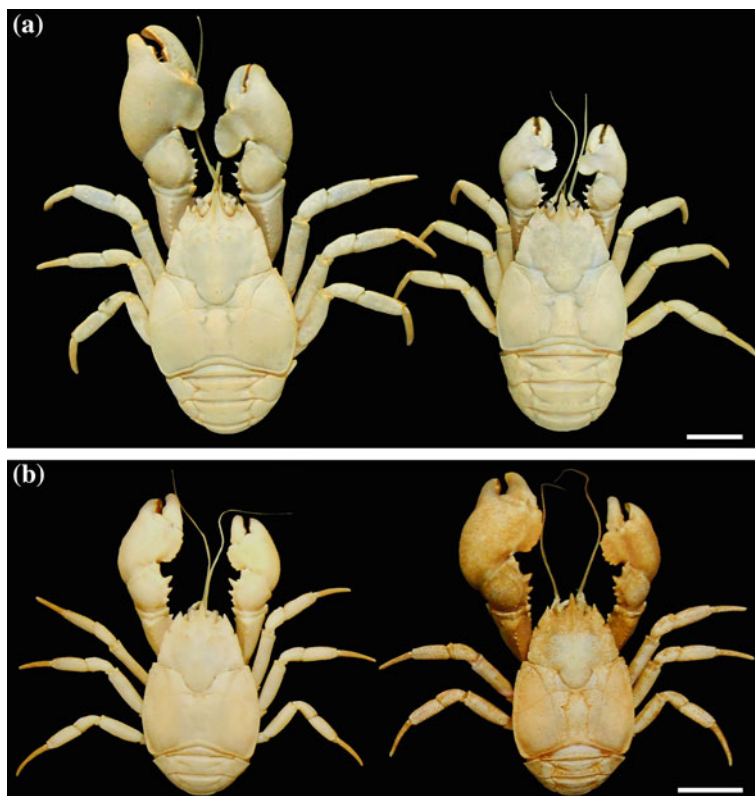


Fig. 2.7 Chelipeds: Sexual dimorphism and male morphotypes. **a** *Aegla schmitti*, sexual dimorphism of the pair of chelipeds between male (*left*) and female (*right*). Sexual dimorphism regarding the size of pleonal somites 2, 3 and 4 can also be noted. **Bar** 1 cm. **b** *Aegla franca*, morphotype I male (CL = 17.7 mm) and morphotype II male (CL = 18.7 mm) sampled in November 2005 and February 2006, respectively. CL: carapace length taken from right orbital sinus to posterior midpoint border of carapace. **Bar** 1 cm

documented in freshwater aeglids (Bahamonde and López 1961; López 1965; Colpo et al. 2005; Viau et al. 2006; Bueno and Shimizu 2009).

The increase in claw dimensions in adult male decapods is often associated with agonistic and/or reproductive behaviour (Mariappan et al. 2000). In most heterochelous decapod species reproductive activities are associated with the major chela, while non-sexual activities (such as food capturing and manipulation, and grooming) are usually associated with the minor claw (Mariappan et al. 2000). In *Aegla*, the major chela is often used in agonistic confrontations (Ayres-Peres et al. 2011a; Palaoro et al. 2014), and in *A. uruguayana* Schmitt, 1942, males use their major chela to defend females from other males (Viau et al. 2006).

The transition from juvenile to adult phase is referred to as morphometric maturity, and is usually marked by a pubertal molt to sexual maturity that has been

achieved by allometric growth in some parts of the body in decapod crustaceans (e.g., chelipeds, abdomen, pleopods) (Hartnoll 1978). Dimensions of the chelae and the pleon are used to determine the average size at the onset of morphometric maturity in *Aegla* (Colpo et al. 2005; Viau et al. 2006; Bueno and Shimizu 2009). Females attain morphometric maturity at a smaller size than males (Swiech-Ayoub and Masunari 2001a; Colpo et al. 2005; Viau et al. 2006; Bueno and Shimizu 2009).

2.2.2 Reproduction

The development of gonads and the maturation of gametes probably start soon after the pubertal molt in both sexes. In females, the early development of the ovaries is initially confined to the cephalothoracic region (Viau et al. 2006; Sokolowicz et al. 2007b). Towards the end of the maturation phase the two posterior lobes of the ovaries gradually extend posteriorly into the pleon as two bright red colored strips, which can be easily observed through the thin and translucent cuticle covering the ventral surface of the pleon (Bueno and Shimizu 2008) (Fig. 2.6d). In the field, determination of the maximum extension of the posterior lobes of the ovaries along the pleon in relation to the pairs of pleopods is a helpful indicator of full ovarian maturation (gonadal or physiological maturity) and impending oviposition (Bueno and Shimizu 2008; Rocha et al. 2010). Functional maturity in female aeglids, therefore, coincides with full gonadal maturity.

Mating behavior has been described in detail in *Aegla platensis* by Almerão et al. (2010). Those authors report that males use their chelipeds to lift and rotate the body of the female during mating with fertilization probably occurring externally in the brood pouch. Fertilized eggs are held firmly attached to the pleopods. Eggs are large in size and few in number, usually in the lower hundreds [see Bueno and Shimizu (2008) for compilation on average egg size and number in some aeglid species]. There is a positive relationship between the number of eggs and the size of the female (Noro and Buckup 2002; Bueno and Shimizu 2008; Silva-Gonçalves et al. 2009). Three sequential stages of embryonic development are recognized according to the criteria established for *Aegla franca* by Bueno and Shimizu (2008): (1) early eggs, with an evenly distributed red yolk mass that occupies over 80 % of the egg volume, with no sign of developing compound eyes (Fig. 2.6e); (2) intermediate eggs, in which the yolk mass fills 50–80 % of the egg mass, with narrow dark pigmented area in each of the compound eyes (Fig. 2.6f); (3) late eggs, with the yolk mass reduced to less than 50 % of egg volume, with the embryo clearly discernible, and with large, round dark pigmented areas in the compound eyes (Fig. 2.6g).

The occurrence of ovigerous females in the population indicates the reproductive period in freshwater aeglids, and varies from markedly seasonal (4–7 months) to

extended (8–12 months) (Table 2.1). In the southern hemisphere the seasonal reproductive period usually occurs between mid fall and late winter/early spring. Species with an extended reproductive pattern can be found in their reproductive phase for most of the year but they exhibit a conspicuous period of higher reproductive intensity that coincides with the same period of the year as the markedly seasonal pattern (López 1965; Bueno and Bond-Buckup 2000; Noro and Buckup 2002; Chiquetto-Machado et al. 2016), but *A. longirostri* Bond-Buckup and Buckup 1994 may be an exception to this (Colpo et al. 2005).

Aegla franca exhibits two adult male morphotypes (I and II), the latter (II) exhibiting larger and more robust first chelipeds than the former (I) (Fig. 2.7b). This difference is accomplished through changes in the allometry coefficient of claw dimensions (Bueno and Shimizu 2009). Adult male morphotypes have also been observed in *Aegla castro* (Takano et al. in press), *A. perobae*, *A. strinatii* and *A. paulensis* Schmitt, 1942 (Bueno, unpublished data), and all these species have a markedly seasonal reproductive period (Rodrigues and Hebling 1978; Rocha et al. 2010; Cohen et al. 2011; Bueno et al. 2014; (Takano et al. in press). It is not known whether adult male morphotypes also occur in aeglids that have an extended reproductive period.

Temporal variation in the proportion of coexisting morphotypes in the population of *Aegla franca* support the hypothesis that morphotype II adult males are the reproductive forms, because the proportion of morphotype II male in the population increases dramatically at the beginning of the mating season, coinciding with the period of late ovarian development of females (Fig. 2.8). Morphotype II male becomes numerically dominant by the time females are fully mature. Bueno and Shimizu (2009) suggested that morphotypes I and II represent a sequential shift from the non-reproductive to the reproductive phases respectively in the adult male population of *Aegla franca*. Functional maturity in adult males is therefore associated with the appearance of morphotype II, although mating will only take place when females are fully mature and ready to spawn. Larger and stronger chelae in adult males are advantageous in aggressive interactions between males during the mating period (Viau et al. 2006). In the case of *Aegla franca*, however, sexual selection would only involve adult male morphotype II individuals.

2.2.3 Postembryonic Development

The postembryonic development in *Aegla* is direct (see Sect. 2.1 this chapter), though morphological traits associated with zoeal and megalopal stages can still be recognized within the developing egg (Lizardo-Daudt and Bond-Buckup 2003) (Fig. 2.9a).

Morphological descriptions of newly-hatched juveniles are currently available for the following species from Brazil: *A. prado*, *A. violacea* Bond-Buckup and Buckup 1994, *A. platensis*, *A. ligulata* Bond-Buckup and Buckup 1994, *A. longirostri*, *A. franca*, *A. schmitti* Hobbs III, 1978, *A. paulensis* and *A. perobae*

Table 2.1 Reproductive period of freshwater aeglid species from different geographic localities

Aeglid species	Location (country)	Latitude (S)	Reproductive period (number of months)	References
<i>Aegla franca</i> (a)	Claraval (Brazil)	20°18'	May–August (4)	Bueno and Shimizu (2008)
<i>Aegla parana</i> (a)	União da Vitória (Brazil)	26°00'	April–July (4)	Grabowski et al. (2013)
<i>Aegla castro</i> (a)	Itatinga (Brazil) Ponta Grossa (Brazil)	23°09' 25°05'	April–August (5) May–October (6)	Takano et al., (in press) Swiech-Ayoub and Masunari (2001b)
<i>Aegla perobae</i> (a)	São Pedro (Brazil)	22°31' 22°33'	April–August (5) April–October (7)	Bueno et al. (2014) Rodrigues and Hebling (1978)
<i>Aegla paulensis</i> (a)	Paranapiacaba (Brazil) Jaraguá, (Brazil)	23°47' 23°27'	May or June–October (5–6) March–July or August (5–6)	López (1965) Cohen et al. (2011)
<i>Aegla strinatii</i> (a)	Jacupiranga (Brazil)	24°38'	May–September (5)	Rocha et al. (2010)
<i>Aegla franciscana</i> (a)	São Francisco de Paula (Brazil)	29°26'	June–October (5)	Gonçalves et al. (2006)
<i>Aegla leptodactyla</i> (a)	São José dos Ausentes (Brazil)	28°38'	April–September (6)	Noro and Buckup (2002)
<i>Aegla schmitti</i> (b)	Alto Ribeira Touristic State Park (Brazil) Piraquara (Brazil)	24°31' 25°29'	April–December (9) April–November (8)	Chiquetto-Machado et al. 2016 Teodósio and Masunari (2009)
<i>Aegla laevis</i> (b)	El Monte (Chile)	33°42'	March–October (8)	Bahamonde and López (1961)
<i>Aegla longirostri</i> (b)	Itaára (Brazil)	29°24'	July–March (9)	Colpo et al. (2005)
<i>Aegla platensis</i> (b)	Taquara (Brazil)	29°46'	January–December (12)	Bueno and Bond-Buckup (2000)
<i>Aegla uruguayana</i> (b)	San Antonio de Areco (Argentina)	34°14'	January–December (12)	Viau et al. (2006)

All species are from lotic environment

Reproductive period: (a) markedly seasonal, (b) extended. Modified and updated from Bueno and Shimizu (2008)

(Bond-Buckup et al. 1996; Bueno and Bond-Buckup 1996; Bond-Buckup et al. 1999; Francisco et al. 2007; Teodósio and Masunari 2007; Moraes and Bueno 2013, 2015). The resemblance between newly-hatched juvenile and adult forms in aeglids include general similarities in body shape, a complete set of body segments

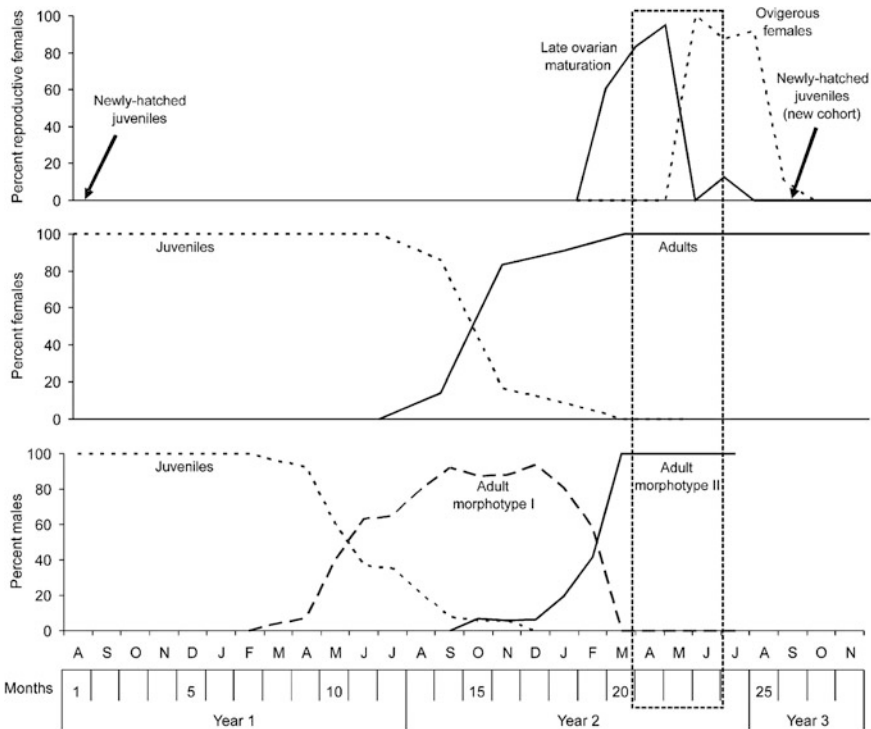


Fig. 2.8 Life cycle of *Aegla franca*. All representations refer to one single cohort. The following selected biological aspects are depicted: *Top section* the hatching moment of juveniles starting cohort, late ovarian development as seen through the thin cuticle of the pleon, followed by the markedly seasonal reproductive pattern (ovigerous females). *Middle and Bottom sections* Morphometric maturity for females (*middle*) and males (*bottom*) indicating the temporal transition from the juvenile to the adult phase. *Bottom section* includes temporal transition from morphotypes I and II in adult males. *Dashed line rectangle* indicates mating period (20–22 months after hatching of juveniles) when late maturation of the ovaries and the subsequent appearance of ovigerous females are highest, and when only the reproductive morphotype II males are present in the population

with corresponding functional pairs of appendages (except for pleopods), their general behavior, and benthic habits (Fig. 2.9b).

Though pleopods are reported to be absent in newly-hatched juveniles of *Aegla platensis*, *A. longirostri*, *A. ligulata*, *A. prado*, *A. violacea* and *A. schmitti* (Bond-Buckup et al. 1996, 1999; Bueno and Bond-Buckup 1996; Teodósio and Masunari 2007), four pairs of rudimentary pleopods have been observed in unsexed hatchlings of *Aegla franca* (Bueno unpublished data), *A. paulensis* and *A. perobae* (Moraes and Bueno 2013, 2015) (Fig. 2.9c). Moraes and Bueno (2013) speculated that those rudimentary pleopods might develop further in adult females, or might regress to calcified knobs in adult males [or develop further but still remain rudimentary as in males of *Aegla perobae* and males of an undescribed troglobitic species (Bueno et al. 2014a; Moraes and Bueno 2015)].

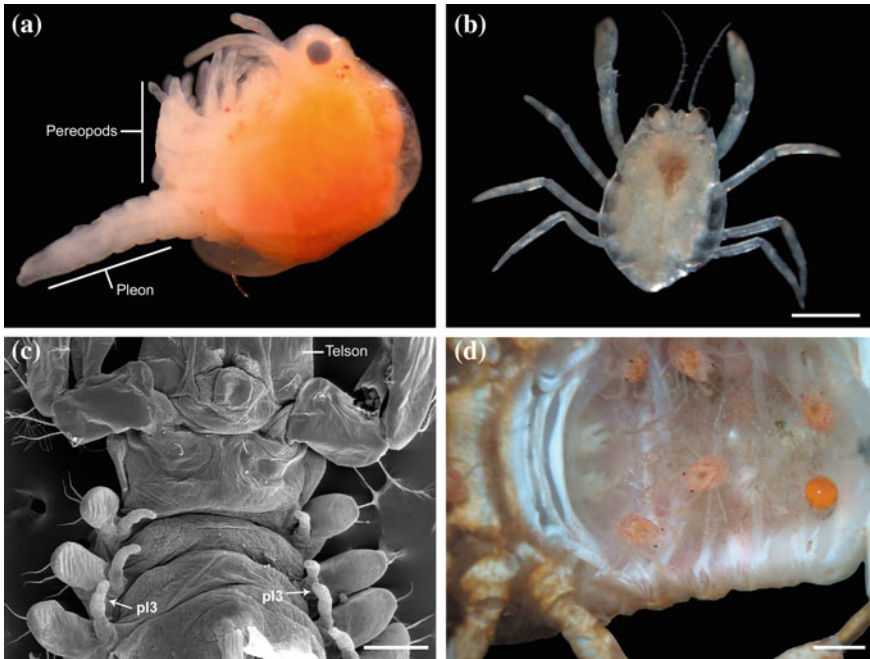


Fig. 2.9 Embryonic and post-embryonic development, and parental care. **a** Late embryo of *Aegla franca* removed from the egg shell. Note presence of larval traits such as non-functional pereopods, absence of uropods and slender pleon (as compared to the broader pleon in the newly-hatched juvenile); no bar included. **b** Newly-hatched juvenile of *Aegla perobae*. Bar 500 μ m. **c** Newly-hatched juvenile of *Aegla paulensis*: Scanning Electron Microscopy (SEM) micrograph of the ventral surface of pleon showing pairs of rudimentary pleopods (third pair indicated). Bar 100 μ m. From Moraes and Bueno (2013); Zootaxa 3635(5): 501–519. **d** *Aegla paulensis*: Live female still carrying one egg and few live newly-hatched juveniles in the brood chamber. Bar 2 mm

Newly-hatched juveniles remain in the abdominal brood chamber formed by the flexed female pleon where they are under maternal care for a few days (Bahamonde and López 1961; Rodrigues and Hebling 1978; Bueno and Bond-Buckup 1996; Bond-Buckup et al. 1999; López-Greco et al. 2004; Francisco et al. 2007; Moraes and Bueno 2013) (Fig. 2.9d). Later on, the epibenthic juveniles leave the brood chamber and move to areas of low water flow and seek protection under rocks, pebbles, and leaf and debris accumulated on the riverbed (López 1965). Aeglid juveniles tend to remain with the parental population and show limited dispersal capacity. Direct development, parental care, and limited juvenile dispersal are important life-history strategies observed in several true freshwater decapods, and these traits are related to the successful colonization of freshwater habitats (Vogt 2013; Chap. 6 in this book).

2.2.4 Latitudinal Gradient and Climate Effect

Extreme climatic conditions found within the distributional range of aeglids affects their distribution, development, and evolution (Schmitt 1942b). The latitudinal range of aeglid distribution (from 50 °S in Chile to 20 °S in Brazil) includes temperate and subtropical regions of Neotropical South America. The reproductive period in freshwater aeglids may also vary according to latitude and regional environmental differences in temperature and rainfall (Bueno and Shimizu 2008). Freshwater aeglids from colder temperate areas that live at high latitudes have an extended reproductive period (Bueno and Bond-Buckup 2000; Colpo et al. 2005; Viau et al. 2006), while those from streams at low latitudinal regions have a marked seasonal reproductive pattern (López 1965; Rodrigues and Hebling 1978; Bueno and Shimizu 2008; Rocha et al. 2010; Cohen et al. 2011; Grabowski et al. 2013; Bueno et al. 2014) (Fig. 2.10a). The effect of latitudinal gradient on the reproductive period of freshwater aeglids is the opposite of that observed in benthic marine decapods (where the reproductive period is extended in tropical species living at lower latitudes and seasonal in species from temperate regions at higher latitudes) (Bauer and Rivera Vega 1992; Bauer 1992; Castilho et al. 2007).

Contrasting regional climatic conditions of temperature and rainfall have a strong influence on the reproductive pattern in freshwater aeglids (Bueno and Shimizu 2008). The reproductive period is shorter in localities with a wide variation in rainfall (expressed as standard deviation >60 mm) than in sites with the opposite climate conditions (Bueno and Shimizu 2008; Fig. 2.10b). For example, the climate of Itaára, State of Rio Grande do Sul, southern Brazil (latitude 29 °S) is characterized by alternating warm and cool seasons and evenly distributed monthly rainfall that has only a minor effect on water flow velocity throughout the year (Fig. 2.11a). The reproductive period of *Aegla longirostri* extends for 9 months, from winter (July) to late summer (March), when species breed twice with two recruitment pulses per year (Colpo et al. 2005). Itaára has favorable conditions for the hatching and recruitment of juveniles for most of the year, which could explain the long reproductive and recruitment periods in the populations of species that live there.

In contrast, the climate in São Pedro, State of São Paulo, southeastern Brazil (latitude 22 °S) is characterized by the alternation of a hot rainy season with a cool dry season (Fig. 2.11b). *Aegla perobae* shows a marked seasonal reproductive period of 5 months (from April to August), with the production of a single egg mass, and a single recruitment pulse per year (Bueno et al. 2014). The reproductive period coincides with the cool dry season, whereby juveniles hatch between July and August when the rainfall and stream flow velocities are at their lowest. The timing of the hatching of juveniles to coincide with the times of the year with low rainfall is a key factor in the life cycle of that aeglid species because it benefits successful local recruitment and guarantees that juveniles will be large enough to withstand the stronger water currents associated with the peak of the following hot rainy season 6 months later. Similar relationships between a marked reproductive

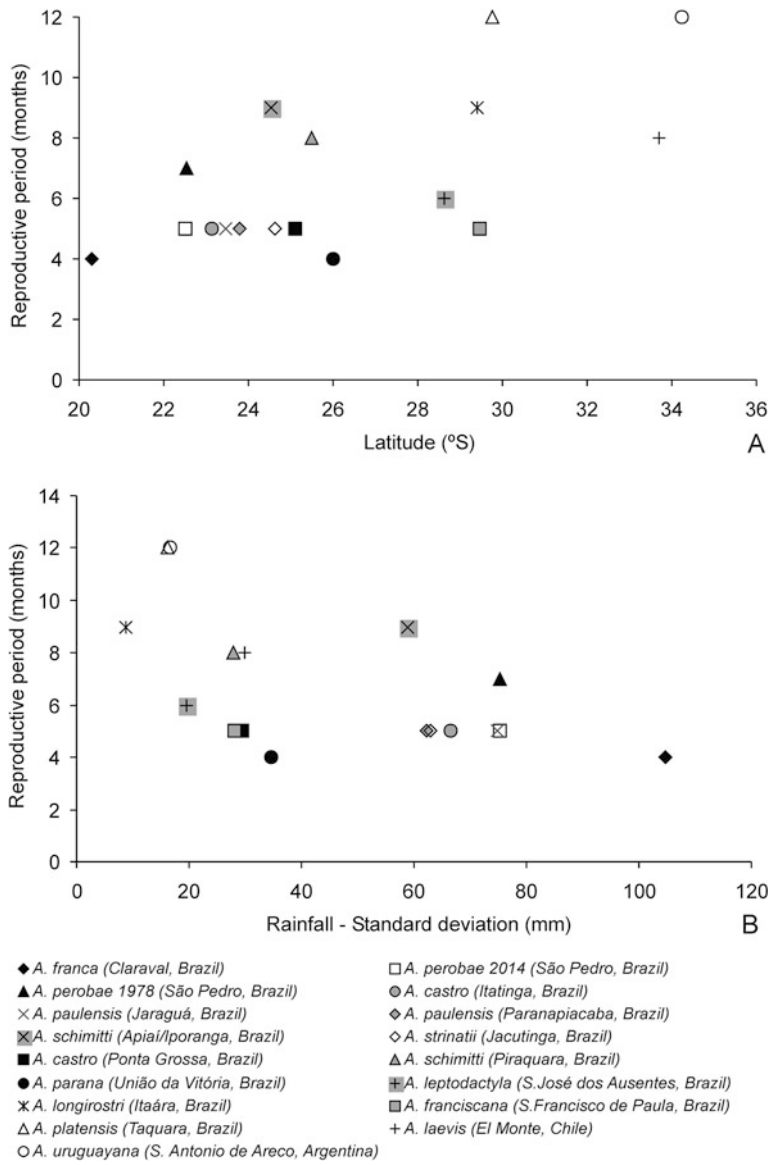
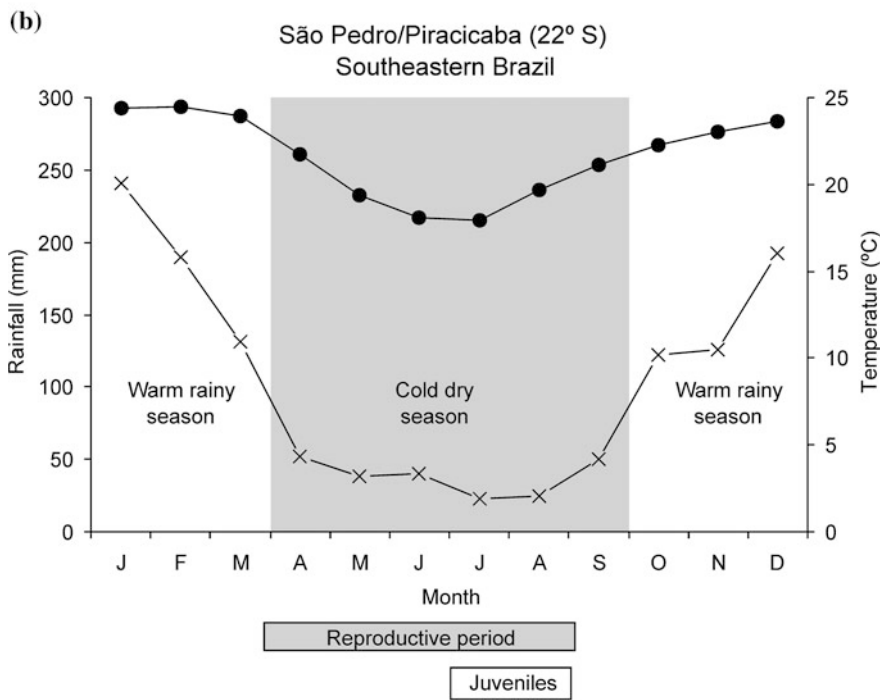
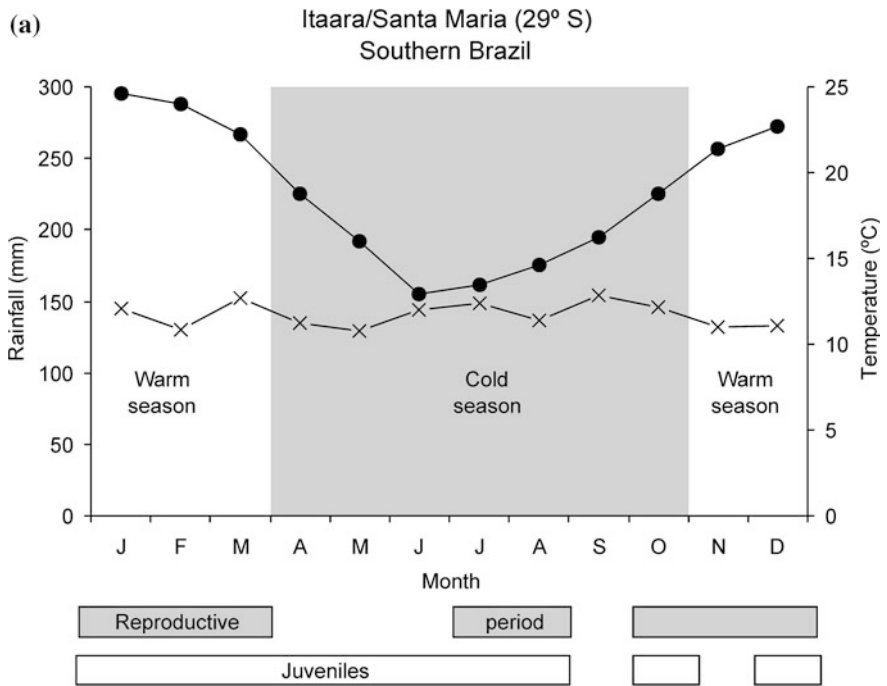


Fig. 2.10 Latitudinal gradient and rainfall effect on reproductive pattern. Variation in length of the reproductive period of aeglid species in relation to latitude (**a**), and rainfall variability (**b**). All species are from lotic habitats. References are the same as those indicated on Table 2.1

period and the regional climate characteristics have also been reported for other aeglid species from localities at low latitudes, such as *A. franca*, *A. strinatii* and *A. paulensis* (Bueno and Shimizu 2008; Rocha et al. 2010; Cohen et al. 2011).



◀ **Fig. 2.11** Contrasting climatic patterns, reproductive pattern and recruitment. Relationship between regional climatic pattern and reproductive pattern/timing of hatching of juveniles of *Aegla longirostri* from Itaára (a) and of *Aegla perobae* from São Pedro (b). Monthly means of rainfall and temperature from Itaára/Santa Maria and from São Pedro/Piracicaba were obtained from daily collection of weather data from each location, available at www.bdclima.cnpm.embrapa.br

These examples suggest the existence of environmental selective pressures at lower latitudes that favour a seasonal reproductive pattern. The increasingly harsh climatic conditions that are found at lower latitudes might have constrained the breeding period progressively as aeglids dispersed from high to low latitudes along the eastern side of South America in ancient times (Bueno and Shimizu 2008).

2.3 Conservation

Freshwater ecosystems are particularly vulnerable to human activities, so much so that they are currently suffering a more dramatic decline in biodiversity than terrestrial ecosystems (Abell 2002; Dudgeon et al. 2006). Freshwater decapods are important macroinvertebrates in benthic communities and their conservation status and global diversity have received a lot of recent attention (Bond-Buckup et al. 2008; Crandall and Buhay 2008; De Grave et al. 2008; Yeo et al. 2008; Cumberlidge et al. 2009; Pérez-Losada et al. 2009; Collen et al. 2014; De Grave et al. 2015).

Table 2.2 shows the conservation status of all 78 species of freshwater aeglids as of 2015. This data compilation is mostly based on the latest official lists from Brazil (Brazil—Ministério do Meio Ambiente 2014; ICMBio—Instituto Chico Mendes de Conservação da Biodiversidade 2014) and Chile (Chile—Ministerio del Medio Ambiente 2014a; Chile—Ministerio del Medio Ambiente 2014b). The conservation status of species not included on those official lists was based on information available in the scientific literature. All categories and criteria were assessed according to IUCN guidelines (IUCN 2013), and most species fall under criterion B, which uses data on geographic range [(extent of occurrence (EOO) and/or area of occupancy (AOO)], distribution patterns (high endemism and/or severe fragmentation in the distributional pattern of highly endemic species resulting in reproductively isolated subpopulations), and habitat quality (continued degradation of environmental conditions and habitat loss).

Aegla is probably the most severely threatened taxon of all decapod crustaceans found in South American freshwaters. More than half (43/78 species, 55.13 %) of freshwater aeglids belong to one of the three threatened categories in the following percentage (Fig. 2.12): Critically Endangered (CR) with twelve species (15.38 %), Endangered (EN) with 22 species (28.21 %), and Vulnerable (VU) with 9 species (11.54 %). The major threats impacting most of the threatened species of aeglids (CR, EN and VU) include the ongoing deterioration of habitat quality that fragments distributional ranges into small disjunct areas of occupancy.

Table 2.2 IUCN categories and criteria, and country of occurrence to all 78 known species and subspecies of *Aegla* as of 2015

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
<i>Critically endangered (CR)</i> , $EOO < 100 \text{ km}^2$; $AOO < 10 \text{ km}^2$				
<i>Aegla affinis</i> Schmitt, 1942	AR CH	B1ab (iii) + 2ab (iii)	Previously suggested category: LC	3, 4, 5
<i>Aegla brevipalma</i> Bond-Buckup and Santos, 2012	BR	B2ab(iii)	Distribution restricted to one location	1, 2, 6
<i>Aegla cavernicola</i> Türkay, 1972	BR	B2ab(iii, v)	Troglobite; one location; Previously suggested category: VU	1, 2, 7, 8
<i>Aegla denticulata lacustris</i> Jara, 1989	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: NT	3, 4, 5
<i>Aegla franca</i> Schmitt, 1942	BR	B2ab(iii)	No longer found in type-locality; fragmented distribution	1, 2, 9
<i>Aegla lata</i> Bond-Buckup and Buckup, 1994	BR	B1ab(i, iii, iv)	No longer found in type-locality; one location	1, 2, 10
<i>Aegla leptochela</i> Bond-Buckup and Buckup, 1994	BR	B2ab(iii, v)	Troglobite; one location; Previously suggested category: VU	1, 2, 8, 11
<i>Aegla ludwigi</i> Santos and Jara, 2013	BR	B1ab(iii)	Distribution restricted to one location	12
<i>Aegla meloi</i> Bond-Buckup and Santos, 2015	BR	B2ab(iii)	Distribution restricted to one location	27
<i>Aegla microphthalmia</i> Bond-Buckup and Buckup, 1994	BR	B2ab(iii, v)	Troglobite; one location	1, 2, 11
<i>Aegla perobae</i> Hebling and Rodrigues, 1977	BR	B2ab(iii)c (iv)	Fragmented distribution; population size fluctuation observed and estimated	1, 2, 13
<i>Aegla renana</i> Bond-Buckup and Santos, 2010	BR	B2ab(iii)	Distribution restricted to one location	1, 2, 14
<i>Endangered (EN)</i> $EOO < 5000 \text{ km}^2$; $AOO < 500 \text{ km}^2$				
<i>Aegla bahamondei</i> Jara, 1982	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: VU	3, 4, 5, 15
<i>Aegla camargoi</i> Buckup and Rossi, 1977	BR	B2ab(iii)	Previously suggested category: LC	1, 2, 16

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
<i>Aegla concepcionensis</i> Schmitt, 1942	CH	B1ab (iii) + 2ab (iii)	Previously suggested category in 1998: VU (ref. 17); reported to be Extinct in the Wild (EX) in 2002 (ref. 5); suggested category in 2009: CR under A2ae + B1ab(I,iii,v) (ref. 16)	3, 4, 5, 15, 16, 17
<i>Aegla expansa</i> Jara, 1992	CH	B1ab (iii) + 2ab (iii)	Previously suggested category in 1998: Data deficient (DD) (ref. 17); reported to be Extinct in the Wild (EX) in 2002 (ref. 5)	3, 4, 5, 15, 17
<i>Aegla georginae</i> Santos and Jara, 2013	BR	B1ab(iii)	Number of locations < 5	12
<i>Aegla inermis</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: VU	1, 2, 16
<i>Aegla itacolomiensis</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
<i>Aegla laevis</i> (Latreille, 1818)	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: CR	3, 4, 5
<i>Aegla lancinhas</i> Bond-Buckup and Buckup, 2015	BR	B1B2ab (iii)	Number of locations = 5	27
<i>Aegla leachi</i> Bond-Buckup and Buckup, 2012	BR	B1ab (iii) + 2ab (iii)	Previously suggested category: VU	1, 2, 6
<i>Aegla loyolai</i> Bond-Buckup and Santos, 2015	BR	B1B2ab (iii)	Number of locations = 5	27
<i>Aegla manuiflata</i> Bond-Buckup and Santos, 2009	BR	B1ab (iii) + 2ab (iii)	Previously suggested category: VU; 3 locations	1, 2, 18
<i>Aegla oblata</i> Bond-Buckup and Santos, 2012	BR	B1ab(iii)	Previously suggested category: VU	1, 2, 6
<i>Aegla obstipa</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: VU	1, 2, 16
<i>Aegla occidentalis</i> Jara et al., 2003	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: LC	3, 4, 16
<i>Aegla papudo</i> Schmitt, 1942	CH	A2ce	Previously suggested category: CR	3, 4, 5

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
<i>Aegla plana</i> Buckup and Rossi, 1977	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
<i>Aegla pomerana</i> Bond-Buckup and Buckup, 2010	BR	B1ab(iii)	Distribution restricted to 2 locations	1, 2, 19
<i>Aegla rossiana</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
<i>Aegla strinatii</i> Türkay, 1972	BR	B2ab(iii)	Troglophile, two locations	1, 2, 20
<i>Aegla talcahuano</i> Schmitt, 1942	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: VU	3, 4, 5, 15, 17
<i>Aegla violacea</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: VU	1, 2, 16
<i>Vulnerable (VU), EOO < 20,000 km²; AOO < 2000 km²</i>				
<i>Aegla cholchol</i> Jara and Palacios, 1999	CH	B1ab (iii) + 2ab (iii)	Possible assemblage of cryptic species	3, 4, 21
<i>Aegla grisella</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)		1, 2
<i>Aegla inconspicua</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
<i>Aegla leptodactyla</i> Buckup and Rossi, 1977	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
<i>Aegla ligulata</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16
<i>Aegla manni</i> Jara, 1980	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: Data Deficient	3, 4, 17
<i>Aegla spectabilis</i> Jara, 1986	CH	B1ab (iii) + 2ab (iii)	Previously suggested category: CR under A2ae + B1ab(I,iii,v)	3, 4, 5
<i>Aegla spinipalma</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2, 16

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
<i>Aegla spinosa</i> Bond-Buckup and Buckup, 1994	BR	B1ab(iii)	Previously suggested category: LC	1, 2
<i>Near threatened (NT)</i>				
<i>Aegla hueicollensis</i> Jara and Palacios, 1999	CH		Previously suggested category: VU	3, 4, 5
<i>Aegla muelleri</i> Bond-Buckup and Buckup, 2010	BR		Category NT suggested by ICMBio/Ministério do Meio Ambiente (Brazil); publication due 2016	22
<i>Aegla prado</i> Schmitt, 1942	BR UR		Previously suggested category: LC; category NT suggested by ICMBio/Ministério do Meio Ambiente (Brazil); publication due 2016	16, 22
<i>Aegla riolimayana</i> Schmitt, 1942	AR CH			16
<i>Least concern (LC)</i>				
<i>Aegla abtao</i> Schmitt, 1942	CH			3, 4
<i>Aegla alacalufi</i> Jara and López, 1981	CH		Previously suggested category: VU	3, 4, 5
<i>Aegla araucaniensis</i> Jara, 1980	CH			3, 4
<i>Aegla castro</i> Schmitt, 1942	BR			16
<i>Aegla denticulata denticulata</i> Nicolet, 1849	CH			3, 4
<i>Aegla franciscana</i> Buckup and Rossi, 1977	BR		Possible assemblage of cryptic species	16, 21
<i>Aegla humahuaca</i> Schmitt, 1942	AR			16
<i>Aegla intercalata</i> Bond-Buckup and Buckup, 1994	AR			16
<i>Aegla jarai</i> Bond-Buckup and Buckup, 1994	BR		Possible assemblage of cryptic species	16, 21
<i>Aegla jujuyana</i> Schmitt, 1942	AR			16
<i>Aegla longirostri</i> Bond-Buckup and Buckup, 1994	BR		Possible assemblage of cryptic species	16, 23

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
<i>Aegla marginata</i> Bond-Buckup and Buckup, 1994	BR		Possible assemblage of cryptic species	16, 21
<i>Aegla neuquensis</i> Schmitt, 1942	CH			3, 4
<i>Aegla odebrechtii</i> Müller, 1876	BR			16
<i>Aegla parana</i> Schmitt, 1942	BR AR		Possible assemblage of cryptic species	16, 21
<i>Aegla parva</i> Bond-Buckup and Buckup, 1994	BR			16
<i>Aegla paulensis</i> Schmitt, 1942	BR		Possible assemblage of cryptic species	16, 24
<i>Aegla pewenchae</i> Jara, 1994	CH			3, 4
<i>Aegla platensis</i> Schmitt, 1942	BR AR UR PA		Possible assemblage of cryptic species	16, 25
<i>Aegla ringueleti</i> Bond-Buckup and Buckup, 1994	AR			16
<i>Aegla rostrata</i> Jara, 1977	CH			3, 4
<i>Aegla sanlorenzo</i> Schmitt, 1942	AR			16
<i>Aegla scamosa</i> Ringuelet, 1948	AR			16
<i>Aegla schmitti</i> Hobbs III, 1978	BR			16
<i>Aegla septentrionalis</i> Bond-Buckup and Buckup, 1994	AR BO			16
<i>Aegla serrana</i> Buckup and Rossi, 1977	BR			16
<i>Aegla singularis</i> Ringuelet, 1948	BR AR			16
<i>Aegla uruguayana</i> Schmitt, 1942	BR AR UR		Possible assemblage of cryptic species	16, 26

(continued)

Table 2.2 (continued)

IUCN categories and aeglid species	Countries	IUCN criteria	Remarks	References
<i>Not evaluated (NE)</i>				
<i>Aegla carinata</i> Bond-Buckup and Loureiro, 2014	UR			
<i>Aegla intermedia</i> Girard, 1855	CH			
<i>Aegla saltensis</i> Bond-Buckup and Jara, 2010	AR			

Key to countries: *AR* Argentina; *BO* Bolivia; *BR* Brazil; *CH* Chile *PA* Paraguay; *UR* Uruguay

Key to Criteria (IUCN 2013)

A2: Population size reduction, observed, estimated, inferred, or suspected in the past where the causes of reduction may not have ceased OR may not be understood or may not be reversible, base on

(c): a decline in area of occupancy (AOO), extent of occurrence (EOO) and/or habitat quality, and

(e): effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites

B1: Extent of occurrence (EOO); B2: Area of occupancy (AOO). Values of EOO and AOO to each threatened category (CR, EN or VU) indicated in the Table

(a) severely fragmented OR number of locations (CR = 1; EN ≤ 5; VU ≤ 10)

(b) continuing decline observed, estimated, inferred or projected in any of

(i) extent of occurrence

(iii) area, extent and/or quality of habitat

(iv) number of locations or subpopulations

(v) number of mature individuals

References: 1 Brazil—Ministério do Meio-Ambiente (2014); 2 ICMBio—Instituto Chico Mendes de Conservação da Biodiversidade (2014); 3 Chile—Ministerio del Medio Ambiente (2014a); 4 Chile—Ministerio del Medio Ambiente (2014b); 5 Pérez-Losada et al. (2002b); 6 Santos et al. (2012); 7 Türkay (1972); 8 Machado et al. (2008); 9 Bueno et al. (2007); 10 Galvês et al. (2007); 11 Bond-Buckup and Buckup (1994); 12 Santos et al. (2013); 13 Bueno et al. (2014); 14 Santos et al. (2010); 15 Jara et al. (2006); 16 Pérez-Losada et al. (2009); 17 Bahamonde et al. (1998); 18 Santos et al. (2009); 19 Bond-Buckup et al. (2010b); 20 Rocha and Bueno (2011); 21 Pérez-Losada et al. (2004); 22 Bueno SLS (personal communication); 23 Marchiori et al. (2014); 24 Moraes et al. (2014); 25 Marchiori et al. (2015); 26 Giri and Collins (2014); 27 Santos et al. (2015)

A few aeglid species were once considered extinct in the wild. The endemic Chilean species *A. conceptionensis* Schmitt, 1942 was initially assessed as vulnerable (VU) by Bahamonde et al. (1998), but a few years later this species, together with *A. expansa* Jara, 1992 from Chile, were both reported to be extinct in the wild (EX) (Pérez-Losada et al. 2002b). Later, in 2006, *A. conceptionensis* and *A. expansa* were rediscovered in a single hydrographic basin outside their previously known area of distribution (Jara et al. 2006; Pérez-Losada et al. 2009), and *A. conceptionensis* was assessed as CR under criteria A2ae + B1ab(i, iii, v) by Pérez-Losada et al. (2009). The most recent evaluation of the conservation status of these two species in 2014 indicates that both *A. conceptionensis* and *A. expansa* are now assessed as endangered (EN) (Chile—Ministerio del Medio Ambiente 2014a; Chile—Ministerio del Medio Ambiente 2014b).

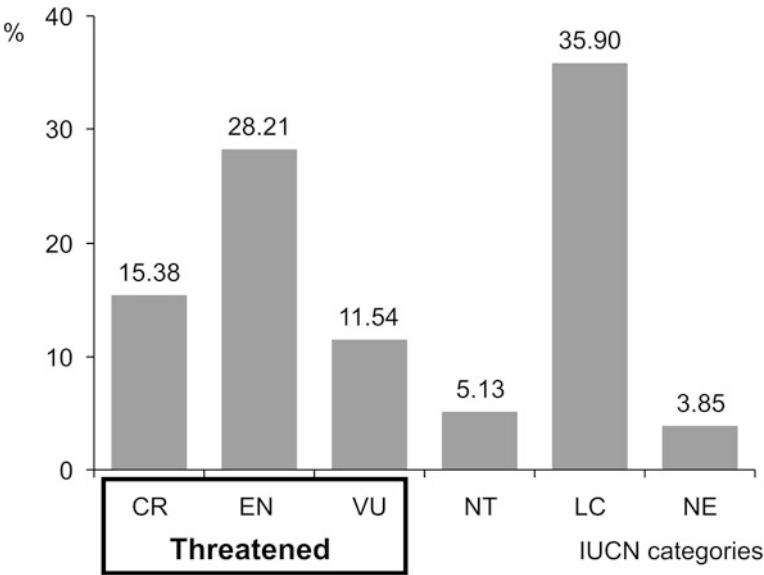


Fig. 2.12 Conservation status. Relative percentage of species and subspecies of *Aegla* (n = 78) according to the IUCN Red List Categories. *Cr* Critically Endangered; *EN* Endangered; *VU* Vulnerable; *NT* Near Threatened; *LC* Least Concern; *NE* Not Evaluated

Similarly, the endemic Brazilian species *A. lata* Bond-Buckup and Buckup 1994, was suspected of being extinct in the wild (EW) because this species was no longer found in the type-locality (then the only known location of the species) (Bond-Buckup and Buckup 1994). Recently, a population of *A. lata* was found in a single location far from its type-locality (Galvez et al. 2007). On the other hand, the Brazilian aeglid *A. brevipalma* Bond-Buckup and Santos 2012 was collected in 2000 from a single location (the type-locality), but has not been seen since then, despite attempts to collect more specimens from that location in 2010 (Santos et al. 2012).

Table 2.3 shows Brazil as the country where most of the 43 threatened species have been reported from (72.09 %, n = 31), followed by Chile (25.58 %, n = 11) and Argentina (2.33 %, n = 1). So far, there are no threatened species reported from Paraguay, Bolivia and Uruguay. In the latter country, however, the recently described *Aegla carinata* Bond-Buckup and Loureiro 2014 is known only from two locations in the northern region (Rivera Department) (Santos et al. 2014) but the conservation status of the species still requires proper evaluation. Of the twelve species which have been assessed or suggested as critically endangered, ten (83.33 %) are country endemics to Brazil (Table 2.3). Most species assessed as endangered (68.18 %) and vulnerable (66.67 %) are also endemic to that country.

All three formally described troglotic species (*A. cavernicola*, *A. leptochela* and *A. microphthalma*) are included in the CR category. These subterranean freshwater aeglids are highly endemic, and the geographic distribution of each one

Table 2.3 Number and percentage of threatened aeglid species per country

IUCN categories	BR + CH + AR	Brazil (BR)		Chile (CH)		Argentina (AR)	
	n	n	%	n	%	n	%
Critically endangered (CR)	12	10	83.33	1	8.33	1	8.33
Endangered (EN)	22	15	68.18	7	31.82	0	0
Vulnerable (VU)	9	6	66.67	3	33.33	0	0
Total	43	31		11		1	
% (CR + EN + VU)/country			72.09		25.58		2.33

Each number of species/country/IUCN category refers to country endemics, except the CR species *Aegla affinis* which occurs in both Argentina and Chile (see Table 2.2). That species is considered here exclusively as an Argentinean species because that is the country from where the species was originally described

is restricted to their respective type-localities. Troglobitic aeglids show allopatric distributions, whereby no two obligate cave-dwelling species are found inhabiting the same cave. Successful colonization of subterranean habitats occurred independently from different epigeic ancestors (Fernandes et al. 2013). Although environmental conditions tend to be fairly stable in the subterranean world cave ecosystems are fragile and highly dependent on nutrients brought in from epigeic habitats (Trajano 2000; Gibert and Deharveng 2002).

Other CR species are single locality endemics that live in epigeic habitats (e.g., *A. renana* Bond-Buckup and Santos 2010, *A. lata*, *A. brevipalma* and *A. meloi* Bond-Buckup and Santos 2015 (Galvez et al. 2007; Santos et al. 2010, 2012, 2015). Other CR species are found in more than one location, but their distributional pattern is severely fragmented and the subpopulations are reproductively isolated from one another. For example, Fig. 2.13 shows all known sites of occurrence of *A. perobae* in São Pedro Cuesta, State of São Paulo, Brazil. The current distributional pattern of this species is highly fragmented (10 locations; combined area of occupancy of 0.02 km²) due to severe and ongoing environmental degradation intrinsically associated with human occupation. In each of these locations a high-gradient stream runs through a steep valley with well-preserved forest cover on the cuesta wall. The plateau and the lowland are highly degraded areas used for cattle grazing and agricultural activities, and the streams in these areas are devoid of riparian vegetation. Both the plateau and lowland areas lack aeglids despite detailed surveys, so gene flow from encounters among individuals from these subpopulations in the lowlands where the streams merge are now unlikely.

Furthermore, due to the landscape characteristics of each location, all subpopulations of *A. perobae* are exposed to unpredictable disturbances on the slopes of the cuesta. Bueno et al. (2014) reported a sharp decrease in the population size of *A. perobae* from the type-locality, which was caused by unseasonal high-intensity flash floods in July 2007 during the dry and cool season that coincided with the period of intense hatching of juveniles (Fig. 2.11b). This adversely affected recruitment of the

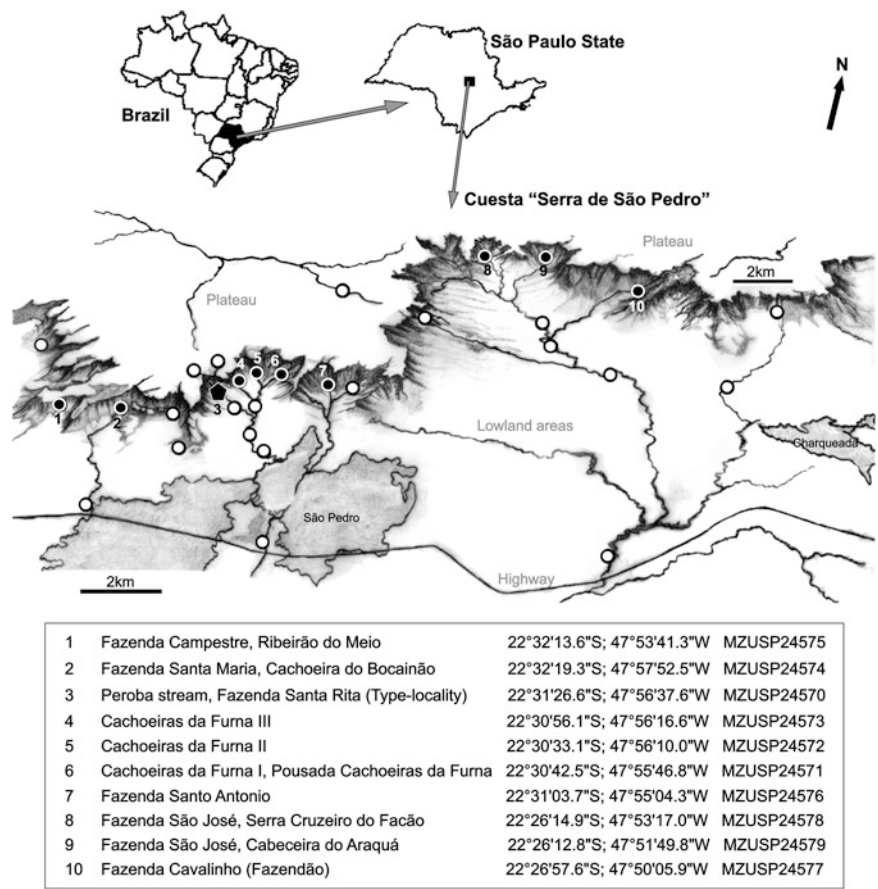


Fig. 2.13 *Aegla perobae*: fragmented distribution. Bird's-eye perspective of São Pedro and Charqueada landscape, state of São Paulo (SP), Brazil, showing partial extension of the cuesta "Serra de São Pedro". Illustration redrawn from satellite view taken from Google Earth. Scales (2 km) vary with perspective. *Black pentagon* type-locality; *black filled circles* sites with positive sampling results; *white filled circles* sites with negative sampling results. See text for details. Names and geographic coordinates of all ten locations where sampling of *Aegla perobae* specimens were positive and their respective number of voucher material deposited in the Museu de Zoologia—University of São Paulo, Brazil (MZUSP) are also provided

cohort produced in that year, causing a severe impact on the size-class structure and on the reproductive output of the population in the years that followed.

Maintaining and encouraging the recovery of the riparian vegetation of the streams in the lowland area could help overcome reproductive isolation among populations of *A. perobae* and greatly diminish the adverse impact caused by unseasonal disturbances. Riparian canopy closure modifies heat and solar radiation received by streams (Gomi et al. 2002), prevents siltation (Magris et al. 2010), and contributes to establish and maintain favorable microhabitats for aeglids. Intact riparian vegetation

along streams acts as an ecological corridor and could increase the area of occupancy of the species by providing viable dispersal routes between connecting sections of streams and thereby re-establishing gene flow among subpopulations.

The number of threatened species of aeglids is expected to increase dramatically in the near future, not only because there are several new and highly endemic species awaiting formal description, but also because species assessed as Least Concern (LC) may actually represent assemblages of cryptic species with limited ranges and small population sizes (Table 2.2). For example, *A. longirostri*, *A. platensis*, *A. marginata* Bond-Buckup and Buckup 1994, *A. franciscana* Buckup and Rossi, 1977, *A. parana* Schmitt, 1942, *A. jarai* Bond-Buckup and Buckup 1994, *A. uruguayana* and *A. paulensis* (Pérez-Losada et al. 2004; Moraes et al. 2014; Giri and Collins 2014; Marchiori et al. 2014, 2015) are all LC species with wide EOOs. Different interpretations of the taxonomic status of any of these species that lead to the recognition of several valid species where once there was one, would require a thorough revision of the conservation status of all taxa. One taxon assessed as LC may end up becoming several restricted range taxa each with the potential for being assessed as either belonging to one of the threatened categories, or to the Data Deficient category.

Aegla paulensis, for example, has a wide distribution over three hydrographic basins: Paraíba do Sul, Tietê, and Ribeira de Iguape (Fig. 2.14), with an extent of occurrence (EOO) of 30,000 km² (shaded area on the EOO map) (Schmitt 1942b;

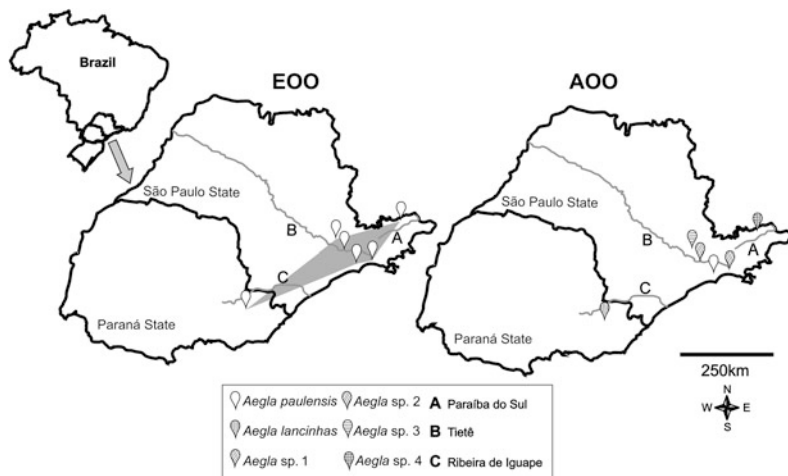


Fig. 2.14 *Aegla paulensis*: from Least Concern to threatened categories. The EOO (extent of occurrence) map shows some of the recorded sites of occurrence of *Aegla paulensis*, as one valid taxon, from three hydrographic basins (A, B and C), totaling an EOO of approximately to 30,000 km². The AOO (area of occupancy) map shows a different possible scenario of *Aegla paulensis* populations as a species complex assemblage, consisting of *A. paulensis* s. str., the recently described new species, *A. lancinhas*, plus several distinct taxonomic units showing distribution restricted to small AOO. See text for details

López 1965; Bond-Buckup and Buckup 1994, 2000; Cohen et al. 2011). However, the 6 locations indicated on the map represent populations that are geographically separated from one another, even those belonging to the same hydrographic basin (Tietê). Although the actual area of occupancy at each location may vary, all populations occupy a small area. Morphological comparisons indicate that the six populations of *A. paulensis* may not be monophyletic (Moraes et al. 2014), and quite recently the population from the Ribeira de Iguape was recognized as a new species, *Aegla lancinhas* Bond-Buckup and Buckup 2015 (Santos et al. 2015).

The continued degradation of freshwater environments has frequently led to habitat loss for aeglids and has contributed to the severely fragmented distribution patterns and the high rates of endemism observed. The discovery of new species, or range extensions of known species are most likely to be made in headwater areas or cryptic habitats. *Aegla* is a bioindicator species whose presence indicates a well-preserved freshwater habitat with clear, well-oxygenated freshwaters (Correa-Araneda et al. 2010). Freshwater aeglids are therefore a desirable target for conservation efforts using either a species-based or ecosystem-based approach.

The Aeglididae is a severely threatened family of South American freshwater decapods. However, aeglids are not charismatic as far as public awareness is concerned and would not make good candidates to raise government and public support for effective conservation actions. On the other hand, the recent IUCN Red List assessment of the extinction risk of aeglids is a solid step toward this goal. We recommend adopting an ecosystem-based conservation strategy with aeglids as flagships or umbrella species because they are a unique and irreplaceable component of the South American freshwater fauna. This is probably the best way to save this highly threatened endemic group of species from extinction.

Any conservation action plan would include an ecosystem-based approach aimed at habitat protection that conserves all native species in situ while maintaining functional ecosystem services (Mace et al. 2007). This approach is illustrated in Pérez-Losada et al. (2002b) for Chilean species of aeglids and in Pérez-Losada et al. (2009) for all species. In the latter work, a multidisciplinary approach based on genetic diversity, conservation status, species richness, distribution patterns, and phylogeny was used to prioritize conservation efforts according to ecoregions as defined by major hydrographic systems.

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