predation by *Pseudopallene* spp. Ryland (1976) is of the opinion that pycnogonids are the most important consumers of bryozoans.

Important references

For comprehensive reviews of the group, readers are referred to Arnaud and Bamber (1987) and Cadien (1997).

Insecta (insects)

Kirsten Jensen and Ricardo L Palma

Introduction

The Insecta is the most diverse group of metazoan animals on land, possibly including over one million species (most of them not yet described). Few free-living species have invaded marine habitats, but many are parasitic on marine mammals and birds, often causing considerable harm to their hosts. Only five of the over 12 000 species of caddisflies are marine, and only one of these is known to be a larval parasite of starfish.

Phthiraptera

Phthiraptera (lice) are wingless, dorso-ventrally flattened, ectoparasitic insects with single host life cycles, completing their life cycle in or on the feathers, hair or skin of vertebrates. They are hemimetabolous and their developmental stages consist of the egg, three nymphal stages and adult. Four suborders are recognised in the order (Barker *et al*. 2003), three of which are known to parasitise marine vertebrates: the Amblycera (Fig. 5.32A) and Ischnocera (Fig. 5.32B), both known as chewing lice, and the Anoplura (Fig. 5.32C), known as sucking lice. Amblycera and Ischnocera are ectoparasites of birds and mammals. The Anoplura exclusively parasitise mammals.

Chewing lice of marine birds (Amblycera and Ischnocera)

Over 4460 valid species of amblycerans and ischnocerans are recognised (Price *et al.* 2003), 88% parasitising birds, and the rest mammals. In marine ecosystems, amblycerans and ischnocerans are restricted to birds. This section is focused on amblyceran and ischnoceran lice that are associated with bird families that consist entirely or largely of marine species (e.g. Diomedeidae and Laridae, respectively).

Amblycera and Ischnocera possess mandibulate chewing mouthparts and a head that is as wide as or wider than the prothorax. Two characters used to distinguish between these groups are the presence or absence of maxillary palps and form of the antennae. Amblycerans possess maxillary papillae and have four-segmented antennae concealed in lateral grooves. Ischnocerans lack maxillary papillae and possess filiform antennae that are fully visible (Johnson and Clayton 2003). Amblycerans feed mainly on feathers, host skin products and blood, as well as on eggs and moulting nymphs of conspecifics or lice of other species. In contrast, most ischnocerans feed on feathers and dead skin (see Murray 1976, Johnson and Clayton 2003). In general, amblycerans are less site-specific than are ischnocerans (see Marshall 1981), but some degree of site specificity is exhibited by most taxa. For example, *Saemundssonia* species parasitise the heads of their hosts (see Marshall 1981), *Naubates* primarily the wing feathers (see Palma and Pilgrim 2002), and adults of *Piagetiella* the throat pouch (see Marshall 1981). The major mode of transmission of these lice between hosts is via direct contact of individual birds (Johnson and Clayton 2003).

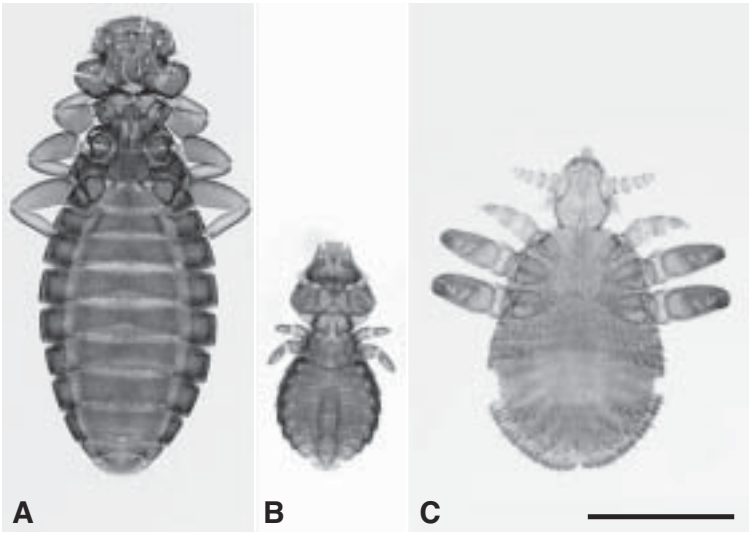

Figure 5.32 Examples of Phthiraptera known to parasitise marine vertebrates. **A**. Female *Actornithophilus piceus lari* (Phthiraptera: Amblycera: Menoponidae) from the California gull, *Larus californicus*. **B**. Male *Saemundssonia* (*Saemundssonia*) *lari* (Phthiraptera: Ischnocera: Philopteridae) from the glaucous-winged gull, *Larus glaucescens*. **C**. Nymph (pharate) *Antarctophthirus trichechi* (Anoplura: Echinophthiriidae) from the walrus, *Odobenus rosmarus*. Scale bar = 1 mm. Figures **A**.–**C**. are depicted to same scale.

Lice of marine birds, in general, do not possess adaptations to cope with the marine environment since they essentially lead a terrestrial life style, including lice parasitising penguins, which live in a pocket of air among the water repellent feathers, without contact with the marine environment.

Sucking lice of marine mammals (Anoplura)

Over 532 species of anoplurans in 15 families are known (Durden and Musser 1994). Echinophthiriidae is the only anopluran family reported from marine mammals. Anoplurans possess a head that is narrower than the prothorax, and piercing–sucking mouthparts. They feed on host blood by inserting their mouthparts directly into the host blood vessels.

Lice of hair seals (Phocidae) live exposed to the marine environment among sparse, scale-like hair on regions of the body used in heat dissipation (e.g. flippers, tail, genital and anal orifices), and thus are required to spend prolonged periods of time submersed (see Marshall 1981). These lice require adaptations to cold-water temperatures, and submersion. Lice of fur seals (Otariidae) either parasitise the pelage and therefore live in the air space created by the fur, not exposed to the marine environment, or, like lice of hair seals, live on the exposed/naked areas of the body (e.g. fins, nostrils and eyelids). Adaptations include unusually well-developed musculature and valves of the atria of the thoracic and abdominal spiracles, presumably to prevent water from entering during prolonged dives (Marshall 1981). In addition, modified scale-like setae on the abdomen are thought to trap air to allow for gaseous diffusion through the cuticle when submersed (see Murray 1976, Mehlhorn *et al*. 2002).

Host associations and specificity

Eight genera of Amblycera have been reported from marine bird families (Table 5.3), but five of them also include species parasitic on non-marine birds: species of *Colpocephalum* and

Austromenopon parasitise birds in 11 and four avian orders, respectively; species of *Actornithophilus* parasitise birds in 11 families of Charadriiformes, but only three of them are exclusively marine; and *Eidmanniella* and *Piagetiella* include a few species parasitic on freshwater species of cormorants and pelicans. Therefore, only three amblyceran genera are restricted to exclusively marine bird families: *Ancistrona* and *Longimenopon* with species parasitic on petrels, and *Fregatiella* unique to the frigatebirds.

Based on the index of host specificity as defined by Caira *et al.* (2003) and the data from (Price *et al.* 2003), specificity index values were calculated for 22 species of amblycerans in five genera (i.e. genera parasitising bird groups in which all or most of the species are marine). Five of the six species of *Longimenopon* are oioxenous (only found in one species of host), and one species is euryxenous (parasitising hosts in more than one family). All nine species of *Piagetiella* are either oioxenous or mesostenoxenous (restricted to a number of species in one genus). Four of the five species of *Eidmanniella* are mesostenoxenous, and one species is metastenoxenous (parasitising hosts in one family, but more than one genus). The single species of *Fregatiella* is mesostenoxenous. *Ancistrona vagelli* is euryxenous.

Ischnoceran lice of marine birds are more diverse than amblycerans. Eighteen genera have been reported from marine birds (Table 5.3). Fifteen of these are restricted to exclusively marine birds, whereas most species of *Quadraceps* and *Saemundssonia*, but only a few species of *Pectinopygus*, are found also on non-marine birds. Specificity of these lice at the generic level is pronounced. Eleven of the 18 genera are each unique to a single bird family. These are: *Austrogoniodes* and *Nesiotinus* on penguins (although see Mey *et al.* 2002), *Bedfordiella*, *Pseudonirmus*, *Naubates* and *Trabeculus* on petrels, *Episbates* and *Harrisoniella* on albatrosses, *Haffneria* on skuas and jaegers, *Pelmatocerandra* on diving petrels and *Philoceanus* on storm petrels. Five genera (*Pectinopygus*, *Docophoroides*, *Paraclisis*, *Halipeurus* and *Perineus*) are each reported from two or more families within one order.

Host specificity index values (*sensu* Caira *et al.* 2003) based on data from Price *et al.* (2003) and Banks and Palma (2003) were calculated for 140 species of ischnocerans in 16 genera which parasitise only marine birds. By this analysis, 66 species are oioxenous, 59 are mesostenoxenous, 14 are metastenoxenous and one is euryxenous.

Because of their narrow specificity (89% of the 162 amblyceran and ischnoceran species analysed parasitise one or more species within a single genus), lice of marine birds have been used in cophylogenetic studies, mainly comparing louse and host phylogenies using a variety of methods (Paterson *et al.* 2000, Paterson and Banks 2001, Banks and Paterson 2004, Page *et al.* 2004). Evidence of cospeciation is not consistently unequivocal.

Marine mammals serving as hosts for sucking lice are pinnipeds, belonging to the carnivore families Odobenidae (walruses), Otariidae (eared seals, fur seals and sea lions) and Phocidae (true, earless or hair seals). The sucking louse family Echinophthiriidae consists of five genera, four of which (*Antarctophthirus*, *Echinophthirius*, *Lepidophthirus* and *Proechinophthirus*) are restricted to pinnipeds. While *Antarctophthirus* parasitises all three pinniped families, *Echinophthirius* and *Lepidophthirus* parasitise only phocids, and *Proechinophthirus* is restricted to otariids (Durden and Musser 1994). A total of 11 species of sucking lice have been reported from 21 of the 33 species of pinnipeds. Seven of the 11 species are oioxenous (also Kim 1985). Among the species that parasitise more than one species of host, none parasitise hosts from more than one family (i.e. are mesostenoxenous or metastenoxenous).

Effects on hosts

Studies on the effect of chewing lice on marine birds are few (see Johnson and Clayton 2003) and little is known overall.

Table 5.3 Distribution of louse genera in families of birds which include marine species exclusively or as a majority

Avian family	PHTHIRAPTERA	
	Amblycera	**Ischnocera**
Spheniscidae	–	*Austrogoniodes; Nesiotinus*
Diomedeidae	*Austromenopon*[A]	*Docophoroides; Episbates; Harrisoniella; Paraclisis; Perineus; Saemundssonia*[A]
Procellariidae	*Ancistrona; Austromenopon; Longimenopon*	*Bedfordiella; Docophoroides; Halipeurus; Naubates; Paraclisis; Perineus; Pseudonirmus; Saemundssonia; Trabeculus*
Hydrobatidae	*Ancistrona; Austromenopon; Longimenopon*	*Halipeurus; Philoceanus; Saemundssonia*
Pelecanoididae	*Austromenopon*	*Halipeurus; Pelmatocerandra*
Fregatidae	*Colpocephalum*[A]*; Fregatiella*	*Pectinopygus*
Phaethontidae	*Austromenopon*	*Saemundssonia*
Pelecanidae	*Colpocephalum; Piagetiella*	*Pectinopygus*
Sulidae	*Eidmanniella*	*Pectinopygus*
Phalacrocoracidae	*Eidmanniella; Piagetiella*	*Pectinopygus*
Stercorariidae	*Austromenopon*	*Saemundssonia; Haffneria; Quadraceps*[A]
Laridae	*Actornithophilus*[A]*; Austromenopon*	*Saemundssonia; Quadraceps*
Chionididae	*Actornithophilus*	*Saemundssonia; Quadraceps*
Alcidae	*Austromenopon*	*Saemundssonia; Quadraceps*

[A] Specificity index values were not calculated for species in these genera since most species parasitise non-marine birds.

Direct and indirect effects on the health of their marine mammal hosts by anopluran lice have been suggested. During times of decreased food availability, high burdens of the louse *Echinophthirius horridus* on harbour seals, *Phoca vitulina*, may ultimately contribute to a reduction in the survival of young seals (Thompson *et al.* 1998). In addition, *E. horridus* is the intermediate host of the seal heartworm, *Dipetalonema spirocauda*. Infection by this nematode impairs the host's blood circulation (Geraci and Lounsbury 2002).

Siphonaptera

Siphonaptera (fleas) are wingless, bilaterally flattened, ectoparasitic insects on warm-blooded vertebrates. Fleas are holometabolous and their developmental stages consist of the egg, usually three larval stages, pupa and adult. With two exceptions, the adult is the only parasitic stage. Adult fleas possess piercing–sucking mouth parts and feed exclusively on host blood. When the adults reproduce and oviposit on the host, the eggs are not attached and drop off, commonly into the nest of their hosts or the surroundings. Consequently, development from egg to pupae occurs away from the host, with the larvae feeding on debris, including the faeces of the adult fleas.

The order Siphonaptera consists of almost 2000 species (not including subspecies) in 15 families (Lewis 1998), most of which parasitise mammals; however, some species are found

parasitising birds. There are no records of fleas from marine mammals. According to Lewis (1998), 106 species of fleas in 16 genera parasitise birds. At least 30 species of fleas in 10 genera (i.e. *Actenopsylla*, *Ceratophyllus*, *Dasypsyllus*, *Glaciopsyllus*, *Listronius*, *Megabothris*, *Mioctenopsylla*, *Notiopsylla*, *Parapsyllus* and *Xenopsylla*) belonging to four families (Ceratophyllidae, Pulicidae, Pygiopsyllidae and Rhopalopsyllidae), parasitise marine birds as their primary host (Johnson 1957, Smit 1979, Hoberg and Wehle 1982, Traub *et al.* 1983, Smit 1984, Holland 1985). A marine bird is considered the primary host if the bird shows the highest prevalence of infection with this flea as compared to other non-marine birds, and if the flea breeds in the marine bird's nest. One species of flea with a most unusual life history is *Glaciopsyllus antarcticus* (Ceratophyllidae), a species parasitising two petrel species breeding in Antarctica. This species is one of only two flea species in which the larvae are also parasitic on the host, feeding on blood, and pupating on the host, instead of in the nest (Bell *et al.* 1988).

While there are few studies in which the effects of fleas on marine bird populations have been measured (see e.g. Merino *et al.* 1999), effects similar to those of ticks and mites (i.e. nestling mortality and nest abandonment) can be speculated with high intensities of infestation (Merino *et al.* 1999).

Trichoptera

Though poorly known, one species of caddisfly is intriguing because of its apparent parasitic association with starfish. While all of the about 12 000 caddisfly species (order Trichoptera) develop in freshwater, only the five species in the family Chathamiidae are known to have marine larvae. One of these five species (*Philanisus plebeius*) is unique among caddisflies in that females may oviposit individual, small clusters or strings of eggs in the coelomic cavity of starfish of the genus *Patiriella* (Asteroidea, Asterinidae), where they hatch. The larvae subsequently leave the starfish and become free living in the intertidal zone. *Philanisus plebeius* occurs in coastal south-eastern Australia and New Zealand. Anderson *et al.* (1976) reported caddisfly eggs from the starfish *Patiriella exigua* in Australia, while Winterbourn and Anderson (1980) reported them from *Patiriella regularis* in New Zealand. Eggs of *Philanisus plebeius* are not surrounded by a protective gelatinous or cement-like matrix common among other trichopterans (Anderson and Lawson-Kerr 1977). Unfortunately, oviposition and escape of larvae from the starfish have not been observed in nature.

Important references

An important contribution on insect parasites of marine birds and mammals is by Murray (1976). Extensive accounts of parasitic insects were given by Marshall (1981), who published a monograph, and Durden and Musser (1994) and Price et al. (2003), who published checklists of parasitic insects. Johnson and Clayton (2003) reviewed the biology, ecology and evolution of chewing lice; Holland (1985) gave an account of the fleas of Canada, Alaska and Greenland, and Smit (1979) of the fleas of New Zealand. Geraci and Lounsbury (2002) discussed the impact of parsitic insects on marine mammal health. Studies on a marine parasitic caddisfly are by Anderson *et al.* (1976) and Anderson and Lawton-Kerr (1977).

Tardigrada (water bears)

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Introduction

The phylum Tardigrada (water bears) consists of microscopic, multicellular coelomates with four pairs of segmented legs. Tardigrades belong to the Panarthropoda group, together with fossil lobopodians, onychophorans (velvet worms) and arthropods (Nielsen 2001). Recent