Minute exceptions: insects that live in the sea

RESEARCH SPOTLIGHT

> ***"It has frequently been said that no true insect is marine; and though this is not literally true, the minuteness of the exception makes the rule even more striking than it would have been if absolutely universal"***
>
> **Philip Henry Gosse (1855)**

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It is well known that few insects live in the sea. Why is this so? Life originated in oceans, and arthropods were among the first animals to make the transition from marine to terrestrial life (van Straalen, 2021; Buatois *et al.*, 2022). As entomologists, we never tire of hearing that insects and their wingless relatives (*i.e.*, hexapods) are the most successful of those animal groups, and this is reflected today in their fabulous land-based diversity. Insects are everywhere – but only on land. They are less diverse in freshwater (Vermeij, 2020), but as we shall see, very few insects live on the seashore, and only a handful of species can realistically be said to live their entire lives at sea. Even then, they actually live on top of the sea, rather than in it. In failing to colonise the oceans, it seems that despite their prodigious capacity for diversification, insects have not adapted well to marine environments. This is the consequence of a general pattern seen throughout the Arthropoda, in which there is a strong tendency towards diversification but relatively few transitions between sea and land (Vermeij, 2020). This is in marked contrast to the phylum Nematoda, the other major hyperdiverse metazoan group (Blaxter, 2016), in which there is evidence that numerous transitions have taken place in both directions between marine and terrestrial ecosystems, but only a moderate

Fig. 1. Curtis's illustration of *Aepus marinus.* The accompanying plant is *Lobelia dortmanna*, incorrectly associated with the insect. From Curtis (1828).

degree of diversification (Holterman *et al*., 2019).

Why have so few hexapods made the return journey to the sea? Such questions are hard to answer, but the first step is to know which kinds of insects actually occupy marine niches. This will then enable us to look for macroevolutionary patterns.

Insects that live in the sea

According to Miall (1895), early entomologists thought that there were no insects at all in the sea. The falsity of this prejudice was uncovered in the late 18th century, when the small carabid beetle *Aepus marinus* was discovered living on the seashore by the Norwegian naturalist Hans Strøm who described it in 1783 (see Plateau, 1890). It was immediately evident that this insect, widely distributed on European rocky shores, survived regular inundation by the tide. The discovery attracted much attention from entomologists, including the incomparable John Curtis (1828), who illustrated it in his beautiful book 'Insects of Britain and Ireland' (Fig. 1). But Curtis evidently couldn't believe that this was really a marine insect, and he incorrectly coupled it with a drawing of a freshwater plant, *Lobelia dortmanna*, instead of the intertidal seaweeds on which it is actually found.

Subsequently, it turned out that although they are generally not plentiful, plenty of other insect species can be found living closely associated with the sea. The question 'how many marine insects are there?' was addressed by the Belgian, Félix Plateau (1890), who included *A. marinus* in the first comprehensive catalogue of marine insects. There were remarkably few of them, the list including only 53 species from 24 genera. Most were predatory beetles. A further six species were wingless Collembola, then considered to be proper insects (although they aren't now); the most well-known being the tiny but beautiful deep-blue springtail *Anurida maritima* (Fig. 2), widespread on rocky shores around Europe and often seen floating on the surface of rock pools.

But there were unaccountable blanks in Plateau's list, including the notable omission of the whole of the order Diptera; Plateau asserted that he didn't believe that there were any flies that could survive immersion in the adult state (as if their corresponding larvae didn't matter!). Plateau specifically mentioned the acalyptrate fly *Helcomyza ustulata* and also referred to the work of Packard (1869) on the chironomid midge *Halocladius variabilis*. Larvae of both of these insects were even then known to live totally immersed in sea water. Astonishingly, Plateau nevertheless concluded "it is obvious that [these species] do not fall into the category of animals which I am trying to catalogue"!

Nowadays, we recognise that the order Diptera is the most strongly represented among marine insects, with many examples within six nematoceran and 4 brachyceran families. In almost all these cases, it is the larvae that actually live totally or partially in sea water, and the adults emerge from the sea in order to reproduce. Among the most familiar insects on the seashore, members of two dipteran genera, *Coelopa* (Coelopidae) and *Fucellia* (Anthomyiidae) are found in huge numbers inhabiting the linear piles of wrack seaweed so commonly found along the high tide mark (Fig. 3).

Fig. 2. *Anurida maritima*. Photo by Gustav Paulay, eol.org, CC-BY-NC 4.0 https://eol.org/media/3313448.

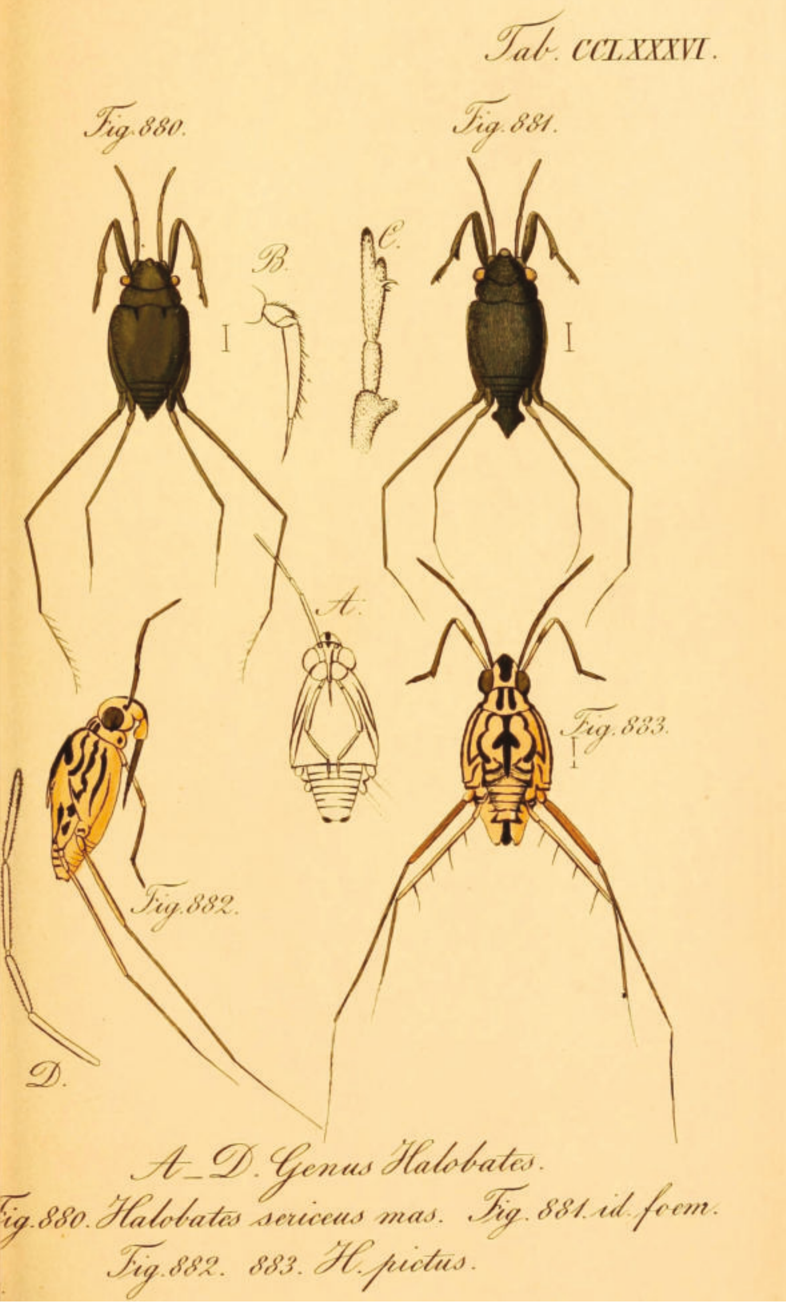

Fig. 4. *Halobates micans* Eschscholz. Male, body length 4.4 mm. From White, 1883 https://upload.wikimedia.org/wikipedia/commons/8/8a/Die_wanzenartigen_Insecten_%28Tab._CCLXXXVI%29_%287746553968%29.jpg

Fig. 3. *Coelopa frigida*. Photo by Janet Graham CC-BY-2.0 https://en.wikipedia.org/wiki/Coelopa_frigida#/media/File:Coelopa_frigida_(by_Janet_Graham).jpg

Fig. 5. *Bledius spectabilis*. Photo from ukbeetles.co.uk, image unattributed, CC-BY 4.0. https://eol.org/pages/1038239

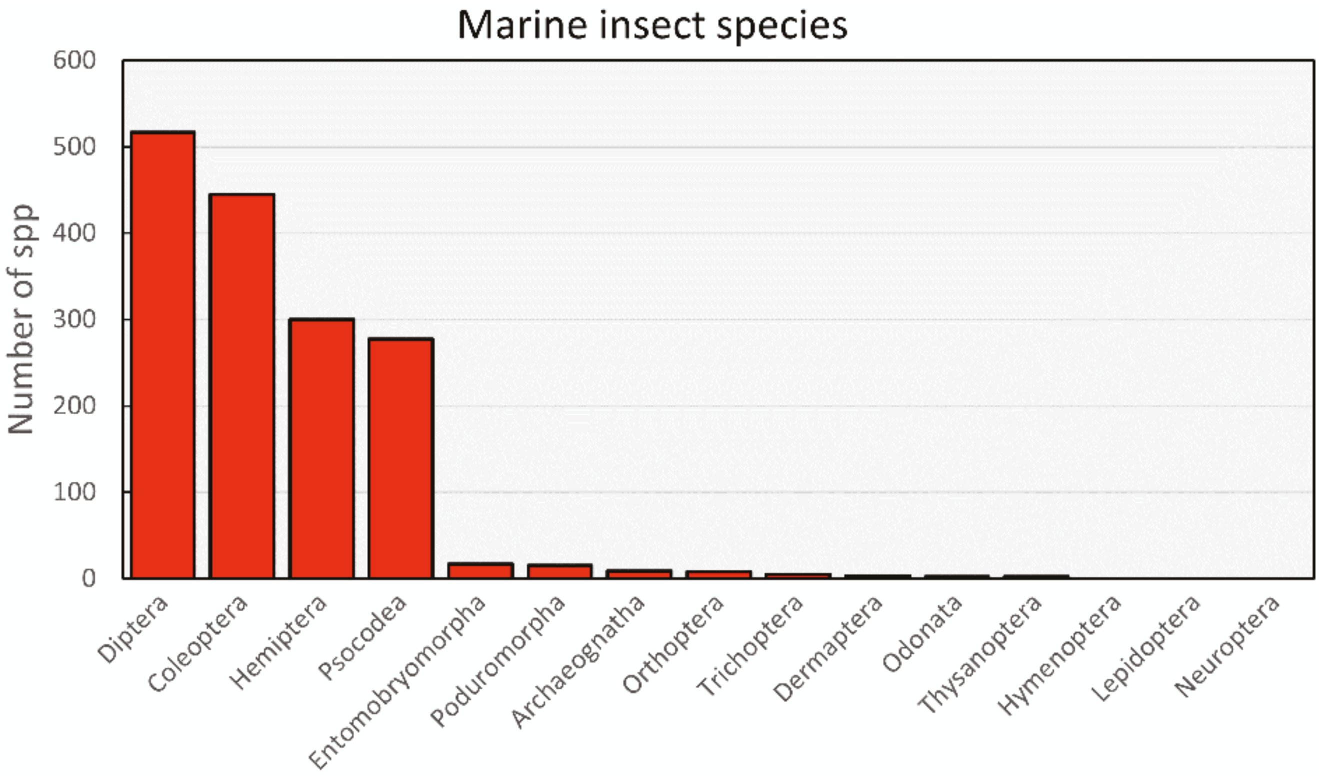

Fig. 6. Numbers of marine hexapod species according to order. Data taken from the WoRMS database. Original figure.

Another important limitation of Plateau's list is that it mentions only a single hemipteran species, *Aepophilus bonnairei*, a predatory bug of the family Aepophiliidae characteristically found skulking among rocks in the low intertidal zone. Many more marine Hemiptera are known today, and in particular Plateau was apparently completely unaware of the several species of ocean-going water striders (Family Gerridae) belonging to the genus *Halobates* (Fig. 4), which are almost certainly the only marine insects to live their entire lives on the open sea. *Halobates* is so extensively adapted to a life on the ocean wave that I'll return to it later in this article.

Plateau's attention was directed to the seashore, but this is not the only habitat that can justifiably be called 'marine'. Many saltmarsh insects live in burrows in the muddy substrate and are frequently inundated by seawater at high tide, so justifying the appellation 'marine'. Some well-known insect species found only on salt marshes are listed by Foster *et al*. (1976) including the staphylinid beetle *Bledius spectabilis* (Fig. 5) which lives in burrows that are regularly submerged by sea water.

Plateau's list updated: which kinds of insect are most common in the sea?

More than 130 years have elapsed since Plateau compiled his list. Although many additional species are now known from all around the world, there are still remarkably few of them. A remarkable database, the World Register of Marine Species (WoRMS), attempts to list all marine organisms, including information on synonymy (WoRMS Editorial Board, 2021). Appeltans *et al*. (2012) used WoRMS to count 2,037 species of insect and their six-legged relatives living in or close to the sea. This represents only about 0.2% of an estimated 1,013,825 described hexapod species (Stork, 2017). On both land and in freshwater, insects are notably adaptable, but considering that 71% of the Earth's surface area is covered by the oceans, surely there should be more marine species than this?

My own list of marine insects from WoRMS of 1,600 seagoing hexapod species is 21.5% smaller than that of Appeltans *et al*., probably because I excluded records where the database entry gave no positive assurance of marine-associated status. I'm sure that this list is not complete; I identified a number of omissions of known species, and anyway, how could it be complete when so many insect species are as yet undescribed? But this is probably as good as we are going to get at the moment.

Most of the confirmed marine species (79% of the total) are members of just three insect orders, Diptera, Coleoptera and Hemiptera (Fig. 6). We'd expect these groups to be strongly represented simply because they are all extremely diverse; beetles, flies and bugs together represent more than 60% of insect species as a whole (Stork, 2017). A surprise for me was the realisation that the order Psocodea (bark and book lice as well as parasitic lice) is also extremely well represented among marine insects, accounting for 17% of all marine hexapods. On the other hand, the remaining hexapod orders are mostly either represented in single figures or are completely absent.

There's little doubt that hexapods evolved on land, perhaps having passed through an association with fresh water (van Straalen, 2021). The adoption of a sea-going lifestyle by a formerly terrestrial insect implies a process like a biological invasion of the ocean, the colonisation of a new niche presumably involving an initially opportunistic exploitation of abundant food sources of marine origin, possibly combined with relief from the attentions of land-based natural enemies, followed by a period of genetic adaptation (Sherpa *et al*., 2021). The greater the contrast between the original land-based niche and the new marine one, the less the likelihood of a successful transition.

Marine-associated species are widely distributed within the

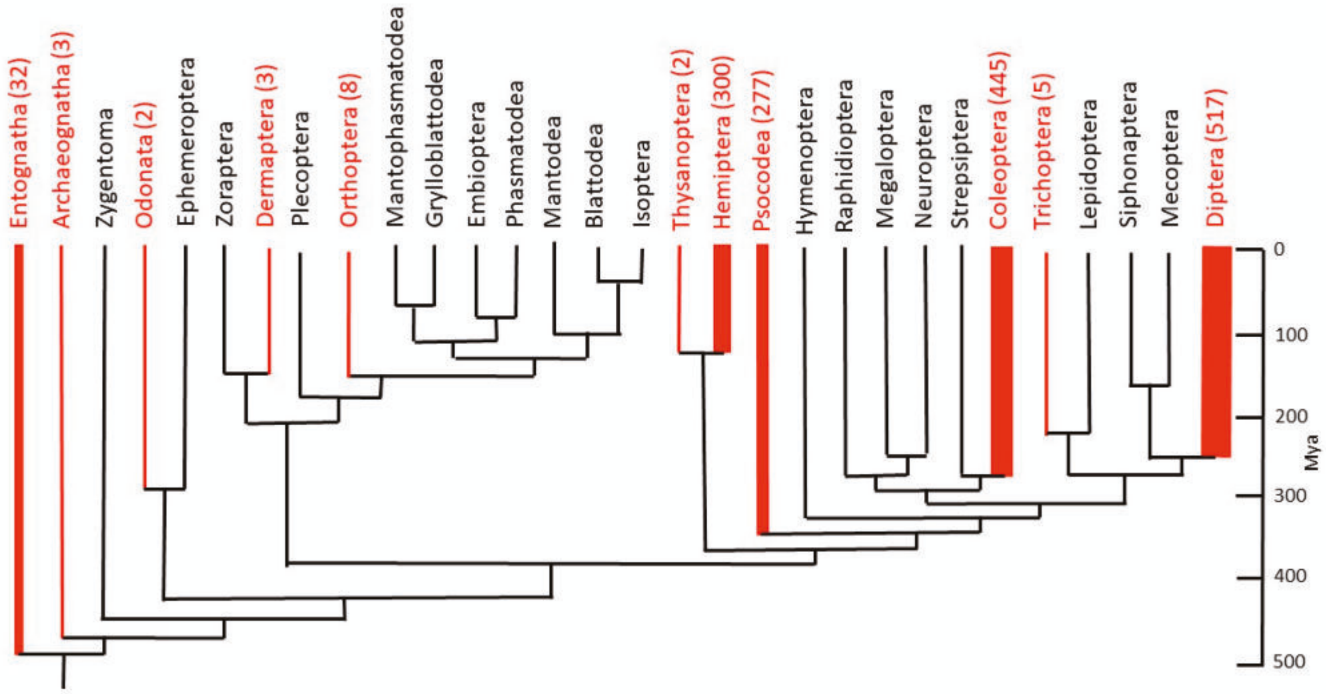

Fig. 7. Hexapod phylogenetic tree (data from Misof *et al.*, 2014). Those orders in which marine species occur are shown in red, the number of marine species being shown in parenthesis. Original figure.

hexapod phylogenetic tree (Fig. 7) indicating that invasions of marine habitats have occurred on multiple occasions and within well-separated clades. This implies that the challenge of recolonising the sea does not require the reinvention of an improbable trait. Consistent with this, Pak *et al*. (2021) concluded from a similar but deeper analysis restricted to marine-dwelling Diptera, that colonisation of the sea by insects of this order is likely to have arisen on at least 20 occasions.

It is immediately obvious that these insect invasions of the sea have occurred very unevenly; the third and fourth largest insect orders, Lepidoptera and Hymenoptera, are completely missing from the WoRMS list of marine insect species. To some extent, the absence of eusocial Hymenoptera is understandable: their societies depend heavily on chemical communication through surface deposits, and this would be hard to maintain underwater. Moreover, species that make a living as pollinators of flowering plants are unlikely to prosper in marine environments, and while some species of ant have been recorded to forage on the shore, they don't do so to the exclusion of other environments away from the sea. But a sizeable fraction of this order is made up of parasitoid wasps, some of which parasitise shore-dwelling insect hosts. For example, Hodge *et al.* (2016) found 19 species from six hymenopteran families parasitising various seaweed flies (Coelopidae) on beaches in New Zealand, while Yamazaki (2012) reported nine parasitoid species from two families parasitising the very numerous seaweed flies *Coelopa frigida* and *Fucellia* spp. on beaches in central Japan. The rate of parasitism in the Japanese study approached 15% of the fly larvae examined from one locality. The platygastroid wasp *Echthrodesis lamorali* is found in the intertidal zone of the Cape Pensinsula, South Africa, where it parasitises spider eggs (van Noort *et al*., 2014). Extrapolating these findings to the rest of the world suggests that there must be a considerable number of marine parasitoids, and yet not a single species has been registered on the WoRMS database. Since wrack seaweed is thrown up in huge quantities on beaches all over the world (Hyndes *et al.,* 2022) and is associated with diverse and numerous dipteran and coleopteran populations, it is clear that parasitic Hymenoptera have probably been underestimated as components of marine insect communities. Although a review of the existing literature on host relations of hymenopteran parasitoids would yield additional candidates for the marine list, what is really needed is a dedicated empirical study of the parasitoids of marine insects.

By contrast, the complete absence of butterflies and moths from the list of marine insects is probably a real phenomenon. The total number of species may not be zero; the lepidopteran family Crambidae includes many species that have freshwater aquatic larvae, and at least one, the antipodean *Hygraula nitens*, has been found in the brackish waters of estuaries, where it eats eelgrass (*Zostera* spp.) (Habeck *et al.,* 2005). But many adult butterflies and moths are only passing visitors to the seaside; a few lepidopteran species are associated with salt marsh plants (Foster *et al*., 1976) but these species may also occur in fully terrestrial habitats and so cannot be regarded as marine specialists. One possible explanation for the absence of dedicated marine Lepidoptera is that these insects do not thrive in contact with water due to the delicacy of their scaly adult cuticle. Although the larvae of a few members of at least some lepidopteran families do live under the surface of still, fresh waters (Pabis, 2018), they are not numerous, and it may be that they cannot cope with the mechanically rough conditions that typically occur in the sea. But it is likely that a more important factor is that lepidopteran larvae are virtually all specialist herbivores, the order owing its evolutionary success almost entirely to the adaptative abilities of individual species to overcome the chemical antiherbivore defences of living angiosperm land plants (Janz, 2011). Moreover, many adult Lepidoptera are nectivores that possess specially modified mouthparts for the purpose, and it would not be easy for insects with this dual feeding strategy to make a living in a marine environment. Although some angiosperms are plentiful in the sea (Heck *et al.*, 2006), their secondary chemistry is entirely different from that of terrestrial angiosperms (Zidorn, 2016), their flowers do not secrete nectar, and there are no known specialist pollinators in the sea.

Marine lice and other parasites

One group of insects that has been conspicuously successful in colonising the sea is the parasitic lice (Phthiraptera) found within the order Psocodea. The WoRMS database lists no fewer than 277 marine species of lice. Although Phthiraptera are indeed diverse, whether on land or at sea, the order Psocodea represents less than 1% of all described insects (Stork, 2017), so that lice appear to be overrepresented among marine hexapods by almost twenty-fold. There are three major superfamilies of parasitic lice: Ichnocera, made up mostly of specialist parasites of birds; another, Anoplura, found only on mammals, while a third group, Amblycera, comprises parasites of both birds and mammals (Johnson *et al.*, 2018). In general, bird lice eat feathers, but mammalian lice drink their hosts' blood. Parasitic lice in general have narrow host ranges, and those parasitising sea-going birds and mammals are not found on non-marine hosts (Murray, 1976). Although lice have diversified at a greater rate than other animals, including the vertebrate hosts they parasitise (Johnson, 2022), the large number of marine psocodean species is due to the fact that there are so many different kinds of sea-going birds and mammals. There are more than 550 species of seabirds in 30 families (Hackett *et al.*, 2008) all of which come on shore to breed (many in large, closely packed colonies), where they are particularly subject to parasitism by insects, especially lice. There are fewer marine mammals but there are nevertheless 134 species in 21 families (Society for Marine Mammalogy, 2022); while most of these are whales, dolphins *etc.* (cetaceans) living entirely in the sea and therefore free of psocodean ectoparasites, there are still 35 species of pinniped in three families (seals, sea lions and walruses), all of which haul out of the sea to breed, when they acquire and exchange specialised siphonapteran ectoparasites.

Interestingly, like their hosts, marine lice do not reproduce in the sea, but synchronise their reproduction with that of their hosts, so that their eggs and immature stages are not exposed to immersion in sea water at all during the period while their hosts are out of the water. Phylogenetic analysis shows that repeated host switching has occurred frequently during the evolution of bird lice, but there is less evidence for this in lice parasitising mammalian hosts. Interestingly, lice that infest pinnipeds (seals) appear to have co-evolved with their hosts (Leonardi *et al.*, 2019), presumably because they are mostly vertically transmitted from the mother, with only very limited opportunities for the parasite to come into contact with other potential host species (Leonardi *et al.*, 2013).

Sea-going lice have special adaptations to enable their parasitic lifestyle. Obviously, they must be able to cling onto the feathers or fur of their hosts under mechanically challenging circumstances, and like all other lice they have developed specially modified appendages for this purpose. Like other insects, lice need to moult their exoskeleton as they grow and develop (and I for one would like to know how they manage this). But a greater challenge must be to survive immersion in seawater. The deepest pinniped dives are those of Southern Elephant Seals (*Mirounga leonina*), which dive to 2,000 m (20.31 MPa) and may remain underwater for up to two hours (McIntyre *et al.*, 2010). Clearly, their specialised lice, *Lepidophthirus macrorhini* (Fig. 8), must also be able to tolerate such pressures and Leonardi *et al.* (2020; 2022) have shown experimentally that this is the case.

Lice are not the only hexapods associated with the sea through parasitism, or some other kind of phoretic relationship with larger vertebrate seagoing animals. Aboard HMS Beagle, on February 16th 1832, Charles Darwin put ashore on the remote St Paul's Rocks, a tiny Atlantic archipelago (0° 58' N, 29° 15' W) 870 km from the coast of S. America and 560 km from the nearest island. There he found a "vast multitude" of nesting seabirds. He noted (Darwin, 1845, p10): "*Not a single plant, not even a lichen, grows on this islet; yet it is inhabited by several insects and spiders*". Among the several kinds of insect he found in and around the nests of Brown Boobies (*Sula leucogaster*) was an ectoparasitic hippoboscid (often called a 'louse fly'); probably it was *Olfersia aenescens* (see Smith, 1987). This biting insect occurs widely at low latitudes and is frequently associated with seabirds. Although it has functional wings, it rarely flies or indeed leaves its host at all. Darwin also found a tick at the same site, also associated with seabird nests. Unfortunately, the tick specimen that Darwin collected has not survived; it might have been the hard tick *Ixodes uriae*, but a more likely candidate is the soft tick *Carios capensis*, which has since been recorded from the location. Both of these ticks specialise in parasitising seabirds and use the Brown Booby as a host (Dietrich *et al.,* 2011).

Okamura *et al.* (2022) have observed that evolutionary transitions between freshwater and marine environments are particularly common among endoparasites. The data from marine lice, however, imply that such transitions between the realms of life may also occur frequently in ectoparasites. If this is so, then is it of ecological significance? Although marine lice and other arthropod ectoparasites come in many different kinds, I suggest that they probably contribute little to marine ecosystems, either in terms of their absolute numbers and biomass, or the flow of materials and energy through them. On the other hand, it is possible that that lice and other arthropod ectoparasites may exert significant indirect effects on seabird and sea mammal populations by acting as disease vectors (Hirzmann *et al.*, 2021; Ebmer *et al.*, 2022).

Halobates: ocean going water striders

If there is a convincing exception to Gosse's 'rule' that insects don't live

Fig. 8. The Elephant Seal Louse, *Lepidophthirus macrorhini*. Photo from Frost Entomological Museum, CC-BY-2.0 https://commons.wikimedia.org/wiki/File:Lepidophthirus_macrorhini.jpg

in the sea, then surely it is the genus *Halobates*. There are numerous estuarine representatives of this genus, all of which live on the surface of the water during all of their lives. But five species have colonised the open sea and never return to the land at all, even to reproduce (Andersen *et al.*, 1999; Cheng *et al.*, 2022). Although discovered and described in the first quarter of the 19th century (Eschscholz, 1822), the first report of a *Halobates* species (now designated *H. micans*) in an English journal was that of Templeton (1835). But no proper account of the biology of *Halobates* as a permanent resident of the ocean surface was given until more than 50 years after its discovery, when White (1883) described the entomological findings of the 1872 global scientific expedition of HMS *Challenger* (Fig. 4).

This raises the question of why Charles Darwin, who spent 5 years at sea (1831–1836), and was a keen entomologist, failed to notice *Halobates*. Had he seen this charismatic insect, he would certainly have mentioned it in *The Voyage of the Beagle* (Darwin, 1845). Cheng *et al.* (2011) have pointed out that Darwin did not systematically sample the ocean surface with a net. As for spotting it visually on the surface, why would he have looked for it there if he did not already know about it? And anyway, *Halobates* is tiny, inconspicuous and patchily distributed, fast-moving and readily submerging when alarmed. Had Darwin been aware of Templeton's paper (published during the Beagle's voyage), he would doubtless have looked for *Halobates*. It must originally have been hard for entomologists of the time to overcome the prejudice that insects do not belong on the surface of the ocean. Even Templeton himself believed that *Halobates* was not really an open-sea insect, suggesting that the insects that he had captured in mid-Atlantic may have been driven away from the shore of Africa by a south-easterly gale.

We now know that ocean-going species of *Halobates* have a worldwide distribution across all tropical oceans. Their populations are not numerous compared with the most successful terrestrial insects; according to Nakajo *et al.* (2013), *Halobates* spp. may reach densities of 86,000 adults km^{-2}, which sounds like a lot, but this actually represents less than one insect in a sea area of 100 m^2. Nevertheless, with such a large area of habitat to exploit (total tropical ocean area is in the order of 170 x 10^6 km^2), there are probably billions of individual *Halobates*.

The unexceptional: why are most insects excluded from the oceans?

Ever since the existence of insects living in or close to the sea was first discovered, their scanty diversity has been a popular topic for speculation by both entomologists and marine biologists. Are these insects really 'exceptional' as Gosse (1855) suggested? The issue came into sharp focus in 1976 with the publication of what remains the only monograph on the subject, *Marine Insects*, edited by Lanna Cheng of the Scripps Institution of Oceanography in La Jolla, California. The question of why most insects (presumably the 'unexceptional' ones) fail to prosper in the sea recurs repeatedly in the book's 19 chapters. Its title begs the question, are there any truly marine insects at all? Even Cheng, still the doyenne of those who study marine insects, admitted in her Introduction that "*as far as we know, no marine insects remain submerged throughout their lives*" (Cheng, 1976). Even the five *Halobates* spp. that manage to live full time in the open ocean avoid becoming immersed and can only lay their eggs on floating materials (Andersen *et al.*, 1976). It was once claimed that the four species of the marine chironomid genus *Pontomyia* lived and reproduced entirely under the surface of the sea (Edwards, 1926), but it is now known that the adult flies leave the water to mate and lay their eggs (Huang *et al.*, 2011). Thus, not a single one of those usually described as a 'marine insect' occupies a niche that is fully immersed. Marine insects may survive occasional or even regular prolonged submersion in seawater, but sooner or later it seems that almost all of them must leave it, either to complete their development or to reproduce. In this sense, insects appear to have failed where other essentially terrestrial animal classes such reptiles (sea-snakes) and mammals (dolphins and whales) have succeeded in returning at least some representatives full-time to the ocean.

Many commentators have attempted to 'explain' the comparative lack of success of insects in exploiting the oceans in adaptive terms; in other words, they consider the problem in terms of the physiological, ecological or developmental problems faced by hexapods attempting to live in the sea. The continuing interest in this topic is quite natural if we are interested in insect evolution. If we can identify the adaptations that have enabled just a few exceptional insects to colonise the sea, then we will have made significant progress towards understanding why the vast majority of hexapods have failed to do so.

I won't look here in any detail at particular hypothetical adaptive traits, but I will list a few of them. Evans *et al.* (1971) showed experimentally that when saltmarsh beetles are submerged by the tide and thus deprived of oxygen, they react by ceasing to move, but nevertheless incur an oxygen debt; but some marine insects overcome this limitation in the same way as scuba divers, and as early as 1835 the pioneering entomologist William Spence drew attention to the fact that some marine beetles carry down air bubbles when they are submerged, commenting that they "*alternately decompose and renew the small bubble of air*". Carpenter (1928, p282) commented on the small size and winglessness of many marine insects; Mahadik *et al.* (2020) drew attention to the extreme hydrophobicity of some marine insect cuticles, as well as the presence of comb-like assemblages of long cuticular hairs to support the insect on the surface; Hinton (1966) documented the use by many marine insects of arrays of short cuticular hairs that allow plastron respiration; while Bradley *et al.* (2009) noted salt transport across the wall of the hindgut. As well as adaptation to physical aspects of the environment, biotic interactions may also be important. Buxton (1926) and Van der Hage (1996) proposed that a lack of angiosperm plants in the sea was a limitation, although this idea was criticised by Ollerton *et al.* (1998) on the ground that angiosperms are evolutionary newcomers compared to the Hexapoda. Nevertheless, I suggest that this factor may have been particularly important in preventing the adaptation of Lepidoptera to enter the sea. One of the strongest cases for a single limiting factor was made by Maddrell (1998), who argued that the air-filled tracheal system of insects imposes a serious limitation on their ability to dive and thus avoid predators; although the physiological problems of a tracheal system are undoubtedly present, Ruxton *et al.* (2007) subsequently pointed out that there are many alternative antipredator strategies available to aspiring colonists of marine habitats.

I concur with Ruxton *et al.* (2007) in their conclusion that no single adaptive explanation is completely satisfactory, and the existence of obvious exceptions implies that each of the suggested, supposedly insuperable, difficulties can in fact be overcome.

Irreversible evolution? Marine insects as exceptions to the rule?

If we can agree that for a present-day insect or apterygote to recolonise the sea must require it to recover at least some of the adaptive traits that allowed its remote ancestors to live in the ocean, then we face a problem. Can evolution ever be 'reversed' in order to adapt to a habitat previously abandoned?

In 1893, the Belgian biologist Louis Dollo (1893) proposed that "*an organism cannot return, even partially, to an anterior state already realised in the series of its ancestors*" (my translation). It is now generally agreed that to be seriously considered, Dollo's Law must be modified to refer only to 'sufficiently complex traits' (Gould, 1970; Goldberg *et al.*, 2008). The real issue is one of homology (Collin *et al.*, 2008). If an ancestor and a descendent both possess the ability to live in the sea, but are separated in the phylogenetic tree that connects them by at least one organism that did not possess that adaptive trait, then is it the case that evolution has recreated the original (*i.e.*, homologous) trait in the way that Dollo's Law prohibits? Or is the resumption of the ancestral marine condition merely the result of convergent evolution? The assumption behind the modern version of Dollo's Law is that a newly emergent 'sufficiently complex trait' could not be identical to the original on statistical grounds.

Collin *et al.* (2008), however, suggest that identity does not need to extend to every last codon of the relevant genes, and that re-evolved adaptive traits may be said to be homologous if their expression is governed by the same regulatory gene network (RGN) as the ancestral character. RGNs preserve their function despite differing in detail between species (Davidson *et al.*, 2005). It is not unlikely that modern hexapods might well retain RGNs with the same function as were originally present in their crustacean ancestors to preside over the suite of adaptive responses to, *e.g.*, salinity; these would have been preserved because the network's genes were always required, *e.g.*, when living in periodically dry environments, as experienced by a large fraction of terrestrial species. In that case, it would indeed be true that in regaining the ability to live in the sea, a formerly terrestrial insect might be 'reversing evolution' and would thus be an exception to Dollo's Conjecture, which could no longer claim the status of a 'law'.

Nevertheless, we might still consider that it is at least less likely that the RGN governing a highly-derived trait that is adaptive in one realm of the biosphere could be successfully transformed so that it is adaptive in another realm of the biosphere. This would mean that evolutionary transitions from one realm to another occur less frequently. This general approach to investigating the evolution of marine insects seems to me to be interesting but challenging, as we don't yet have much information about the RGNs that govern the relevant traits.

Ecological explanations

The difficulty or cost of adapting to physical conditions may in any case not be relevant to the question of how a few 'exceptional' insects have recolonised the sea. In two closely argued but perhaps rather speculative essays on the subject, Vermeij *et al.* (2000) and Vermeij (2020) shrug off most previous speculation about such traits to put forward two mainly ecological explanations for the paucity of the marine insect fauna. First, they reiterate what they call the 'incumbency hypothesis', which suggests that it is difficult for colonists in a new habitat to displace those species that are already well adapted to it. This is in effect the other side of the coin of the 'empty niche' hypothesis of biological invasions. Second, they compare the diversity of marine and freshwater insects, pointing out that the latter are at least ten times more speciose than those in the sea. They attribute this largely to the greater possibility of escaping predation in small bodies of fresh water, speculating that the greater diversity of ecological conditions in freshwater may be responsible for this disparity. To some extent this may be the result of the 'island' nature of small lakes and streams, which may not be large enough to support resident populations of predators, and it is true that aquatic insects do much less well in large lakes than in small ones.

Vermeij (2020) goes on to propose that the functional roles played by insects and other small terrestrial arthropods in terrestrial ecosystems may place them in a disadvantageous starting position from which to invade marine habitats; these roles "*emphasise high locomotor performance and long-distance communication, traits that work less well in the denser, more viscous medium of water*". One can hardly challenge the first part of this statement as a concise and percipient summary of why insects have been successful on land, but is it really true that these traits are less useful in marine habitats? Perhaps.

Competitiveness thus emerges as a central issue in understanding the apparent exclusion of insects from the oceans. Vermeij (2020) observes that "*Unlike the spread of species into physically similar but previously unoccupied geographical regions, transitions among realms generally involve species that were not powerful competitors in their ancestral realm… High competitive status in any one realm, therefore, evolves in that realm and is not the direct consequence of colonization.*"

But how could this essentially qualitative argument be turned into a testable hypothesis? There is little consensus on how to measure competitiveness between species in natural environments (Hart *et al.*, 2018). An indirect approach would be to compare speciation rates in marine, freshwater and terrestrial hexapods, as did Davis *et al.* (2022) for Crustacea, finding that speciation rate in terrestrial lineages is significantly greater than in freshwater or marine habitats. I hope that someone will attempt a similar project for hexapods. But even this approach would still have to infer competitiveness from a different parameter.

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References

Andersen N.M. *et al.* (1976) pp 187–224. In Cheng, L. [Ed] *Marine Insects*. Amsterdam, North-Holland Publ.
Andersen, N.M. *et al.* (1999) *Ecography* **22**, 98–111.
Appeltans, W. *et al.* (2012) *Current Biology* **22**, 2189–2202.
Blaxter, M. (2016) *Philosophical Transactions of the Royal Society of London B* **371**, 20150329.
Bradley, T. *et al.* (2009) *Integrative and Comparative Biology* **49**, 590–606.
Buatois, L.A. *et al.* (2022) *Integrative and Comparative Biology* **62**, 297–331.
Buxton, P.A. (1926*) Proceedings of the Zoological Society of London* **53**, 807–814.
Carpenter, G.H. (1928) *The Biology of Insects*. pp473. London, Sidgwick & Jackson Ltd.
Cheng, L. (1976) *Marine Insects*. pp581. Amsterdam, North-Holland Publishing Co.
Cheng, L. *et al.* (2011) *Antenna* **35**, 36–42.
Cheng L, *et al.* (2022) *PLoS Biology* **20**, e3001570.
Collin, R. *et al.* (2008) *Trends in Ecology and Evolution* **23**, 602–609.
Curtis, J. (1828) *British Entomology*, vol. 1. Plate 39. London, printed for the author. https://www.biodiversitylibrary.org/item/230993 (accessed 30 December 2022).
Darwin, C.R. (184). *Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world, under the Command of Capt. Fitz Roy, R.N.* 2d ed. London: John Murray.
Davidson, E. *et al.* (2005) *Proceedings of the National Academy of Sciences USA* **102**, 4935.
Davis, K. *et al.* (2022*) Integrative and Comparative Biology* **62**, 332–344.
Dietrich *et al.* (2011) *Vector-borne and Zoonotic Diseases* **11**, 453–470.
Dollo, L. (1893) *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* **7**, 164–166.
Ebmer, D. *et al.* (2022) *Scientific Reports* **12**, 14078.
Edwards, F.W. (1926) *Proceedings of the Zoological Society of London* **96**, 779–806.
Eschscholz, J.F. (1822). *Entomographien*. Vol. 1. 128 pp. Berlin, G. Reimer. https://www.biodiversitylibrary.org/bibliography/65315 (accessed 30 December 2022).
Evans, P.D. *et al.*, (1971) *Journal of the Marine Biological Association of the United Kingdom* **51**, 75–386.
Foster, W.A. *et al.* (1976) pp 5–42. In Cheng, L. [Ed] *Marine Insects*. Amsterdam, North-Holland Publishing Co.
Goldberg, E.E. *et al.* (2008) *Evolution* **62**, 2727–2741.
Gosse, P.H. (1855) *A Manual of Marine Zoology of the British Isles* Part I, p 178, London, J. van Voorst.
Gould, S.J. (1970) *Journal of the History of Biology* **3**, 189–212.
Habeck, D.H. *et al.* (2005) *Australian Journal of Entomology* **44**, 354–363.
Hackett, S.J. *et al.* (2008) *Science* **320**, 1763–1768.
Hart, S.P. *et al.* (2018*) Journal of Ecology* **106**, 1902–1909
Heck, K.L. *et al.* (2006) *Journal of Experimental Marine Biology and Ecology* **330**, 420–436.
Hinton, H.E. (1966) *Nature* **209**, 220–221.
Hirzmann, J. *et al.* (2021) *Parasites & Vectors* **14**, 96.
Hodge, S. *et al.* (2016) *New Zealand Entomologist* **39**, 117–128.
Holterman, M. *et al.* (2019) *Biological Journal of the Linnean Society* **128**, 756–767.
Huang, D. *et al.* (2011*) Zoological Journal of the Linnean Society* **162**, 443–456.
Hyndes, G.A. *et al.* (2022) *Biological Reviews* **97**, 2127–2161.
Janz, N. (2011) *Annual Review of Ecology, Evolution and Systematics* **42**, 71–89.
Johnson, K.P. *et al.* (2018) *Biology Letters* **14**, 20180141.
Johnson, K.P. (2022) *Life* **12**, 1442.
Leonardi, M.S. *et al.* (2013) *Parasitology Research* **112**, 3315–3323.
Leonardi, M.S. *et al.* (2019) *Systematic Entomology* **44**, 699–708.
Leonardi, M.S. *et al.* (2020*) Journal of Experimental Biology* **223**, 226811.
Leonardi, M.S. *et al.* (2022) *Insects* **13**, 46.
Maddrell, S.H.P. (1998) *Journal of Experimental Biology* **201**, 2461–2464.
Mahadik G.A. *et al.* (2020) *Scientific Reports* **10**, 7785.
McIntyre, T. *et al.* (2010) *Polar Biology* **33**, 1037–1048.
Miall, L.C. (1895) *The Natural History of Aquatic Insects*. Ch. XII. London, Macmillan & Co.
Misof, B. *et al.* (2014) *Science* **346**, 763–767.
Murray, M.D. (1976) pp 79–96. in Cheng, L. [Ed] *Marine Insects*. Amsterdam, North-Holland Publishing Co.
Nakajo, M. *et al.* (2013) *Scientific Research* **5** (12A) 9–15.
Okamura, B. *et al.* (2022) *Integrative and Comparative Biology* **62**, 345–356.
Ollerton J. *et al.* (1998) *Functional Ecology* **12**, 976–977.
Pabis, K. (2018) *Knowledge and Management of Aquatic Ecosystems* **419**, 42.
Packard, A.S (1869) *Annals and Magazine of Natural History* **7**, 230–240.
Pak, N. *et al.* (2021) *Ecology and Evolution* **11**, 11440–11448.
Plateau, F. (1890) *Journal de l'Anatomie* **26**, 236–269. [https://www.biodiversitylibrary.org/item/178223#page/246/mode/1up] (accessed 30 December 2022).
Ruxton, G.D. *et al.* (2007) *Marine Ecology* **29**, 72–75.
Sherpa, S. *et al.* (2021) *Evolutionary Applications* **14**, 1463–1484.
Smith, K.G.V. (1987) *Bulletin of the British Museum (Natural History) Historical Series* **14** , 1–143.
Society for Marine Mammalogy (2022) [https://marinemammalscience.org/science-and-publications/list-marine-mammal-species-subspecies/] (accessed 30 December 2022).
Spence W. (1835) *Transactions of the Royal Entomological Society of London* **1**, 179–181.
Stork, N.E. (2017) *Annual Review of Entomology* **63**, 31–45.
Templeton R. (1835) *Transactions of the Royal Entomological Society of London* **1**, 230–231.
Van der Hage, J.C.H. (1996) *Functional Ecology* **10**, 546–547.
van Noort, S. *et al.* (2014*) Invertebrate Systematics* **28**, 1–16.
van Straalen, N.M. (2021) *Pedobiologia – Journal of Soil Ecology* **87–88**, 150753.
Vermeij, G.J. (2020) *Arthropod Structure and Development* **56**, 100930.
Vermeij, G.J. *et al.* (2000) *Biological Journal of the Linnean Society* **70**, 541–554.
White, F.B. (1883) *HMS Challenger Reports* **7**, 1–82. [https://www.biodiversitylibrary.org/part/78293] (accessed 30 December 2022)
WoRMS Editorial Board (2021) http://www.marinespecies.org. (accessed 03 October 2022).
Yamazaki, K. (2012) *Entomological Science* **15**, 28–34.
Zidorn, C. (2016) *Phytochemistry* **124**, 5–28.