PERSPECTIVE

WHY ARE THERE NO INSECTS IN THE OPEN SEA?

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Summary

The air-filled tracheal respiratory system of insects prevents them from diving deeply in water. It is argued that this is the major factor in preventing insects from colonizing the open sea: they cannot descend sufficiently deeply in the daytime to escape being eaten by fish.

Key words: insect, sea, tracheal system, crustacean, competition, predation.

Judged by the number of species, insects are the most successful group of animals on earth. However, this disguises the striking fact that, while they vastly outnumber other animals on land, they are virtually absent from the sea. It is supposed that there are some 5–10 million species of insects on land (Wilson, 1992) and some estimates run as high as 20 million species (Foster, 1986). While some species of insect thrive on the surface of the sea and in and around the margins of the sea (Cheng, 1976), not a single insect species can be said to live in the open sea (Foster, 1986). It cannot easily be argued that there are physiological reasons for the absence of insects from the sea; the larvae of many insects can easily be reared in sea water and thrive in nature in waters that are osmotically and/or ionically much more challenging (Scudder, 1969; Phillips and Maddrell, 1974).

It might be argued that insects are poor competitors and so are outcompeted in the marine environment, perhaps by crustaceans, their close relatives. And since crustaceans have been there since long before insects evolved and their environment has been more stable than that on land, they have been difficult to displace. However, this is an unsatisfying explanation unless it can be said why this should be so. The central claim of the present paper is that insects fail in the open sea largely because of the presence there of predators, namely fish. The crustaceans have developed successful strategies to avoid predation from fish, in particular they descend during the day to the depths. Insects, encumbered by their air-filled respiratory system, cannot follow.

In the arguments developed in this paper, the proper but cumbersome way of describing change by evolutionary adaptation has been substituted by shorter overtly teleological statements. This should not be taken to imply that evolution proceeds by anything other than from mutations arising by chance, with those that impart an advantage being retained by natural selection.

In the open sea, the only escape routes from fish predation that might be available to insects are likely to be those used by crustaceans. Crustaceans make extensive diurnal vertical migrations that remove them from the upper reaches of the sea in the daytime when they are visible and so at risk. Of course, there may be other reasons for this migration, but several studies have shown that a key reason is that it makes it more difficult for their predators (Pearre, 1979; Wright *et al.* 1980; Gliwicz, 1986a; Lampert, 1989). Insects cannot adopt the same strategy because, for virtually all of them, their tracheal method of respiration depends on the presence of gaseous air in at least parts of the body (Wigglesworth, 1972; Thorpe, 1950). At 100 m depth, for example, the total pressure is above 10 atmospheres (1013 kPa), and this would so reduce the volume of air in the system that it fails. In addition, the use of a surface film of air as a physical gill, the plastron (Thorpe, 1950), by which many freshwater insects can live for prolonged periods under water without requiring access to the surface, fails at depths below approximately 30–40 m because the pressure causes bending of the supporting hairs and the collapse of the air film (Thorpe and Crisp, 1947). So insects could only survive in the sea if they stayed in the depth range of the top few tens of metres. Unfortunately for them, there is no escape there from daytime predation by fish. They cannot, for example, reduce predation by becoming transparent, an adaptation of some small crustaceans. That would merely reveal their glistening air-filled tracheal system which is so obvious in any insect dissection. Neither could they become sufficiently unpalatable to ward off predators. If this were possible, then the same adaptation would have been selected for in crustaceans.

While it can perhaps be admitted that insects fail in the open sea because they cannot escape fish predation is logically sound, it is of less value if it cannot be tested. Since it is not easy except in the mind to remove fish from the sea, one must look elsewhere for a test. By an extension of the ideas presented here, it can be argued that insects should not survive predation from fish in other bodies of open water, such as freshwater lakes and large rivers, for example. It is significant, therefore, that freshwater insects mostly live either on the surface or at least for part of the time in or on the solid bottom of lakes and rivers. Insects that elsewhere live free in the water are conspicuously absent from waters that contain fish; insects are very rare in the open waters of lakes (J. Green, personal communication).

A major but apparently solitary exception to this is found with larvae of the midge *Chaoborus*, which can occur in enormous numbers in very large lakes. However, this hides the facts that it avoids predation exactly as advocated above, i.e. it dives, down to 70 m in this case (Green *et al.* 1973), and that it is a highly unusual insect. It can avoid the limitation that its tracheal system must fail at these depths from the fact that it is reduced to two pairs of gas-filled spherical sacs used to provide variable buoyancy (Wigglesworth, 1972). It survives well in Lake Barombi Mbo (West Cameroon), although there is essentially no oxygen below 20 m. The cichlid fish that is the major predator of *Chaoborus*, *Konia dikume*, has blood with an extraordinarily high haemoglobin content, presumably to allow it better to prey on *Chaoborus* larvae in anoxic water as these dive at dawn and ascend at dusk. It seems that larval *Chaoborus* are uniquely adapted to avoid asphyxiation by using an anaerobic malate cycle to generate ATP (Gäde, 1985). In addition, they are able to migrate vertically using a buoyancy control mechanism in which the cuticular walls of the tracheal sacs are made to swell or shrink, presumably under the control of the underlying epidermal cells (Wigglesworth, 1972) and presumably by shifts in intracuticular pH that cause cuticular proteins to swell or shrink (Reynolds, 1975). Their success has been achieved by evading predation in this unique way.

Mosquito larvae are only found in relatively temporary pools or ponds where there are no fish or in more established bodies of water that are so physiologically stressful as to exclude fish, for example in alkaline and hypersaline lakes (Scudder, 1969; Nayar, 1969; Phillips and Maddrell, 1974). A very effective way of controlling mosquitoes in small ponds and casual water is to introduce fish into the waters where they live. However, there is evidence of very large numbers of insects in fish-free ponds or lakes. Mono Lake (California, USA) supports extraordinary numbers of larvae of the alkali fly *Ephydra hians* that feed there on diatoms and filamentous cyanobacteria. The lake has only a restricted volume (its feed waters have been diverted to help supply Los Angeles), which makes it so osmotically and ionically concentrated that no fish live there. As a result, the alkali fly thrives to such an extent that the edges of the lake (see Fig. 1) are black with countless numbers of pupae. Similarly, ephydrid pupae were present in such

quantities in the Great Salt Lake of Utah, also too salty for fish, that they were able to provide a food source for the Indians of the area. It appears that there is indeed a strong correlation between the presence or absence of fish and the ability of insects to thrive in natural bodies of open water.

Other studies have shown that the numbers of crustaceans in open waters are similarly reduced following the introduction of fish. For example, larger crustaceans were eliminated from the zooplankton in Crystal Lake in Connecticut when fish of the species *Alosa aestivalis*, the glut herring, were accidentally introduced there in 1942. Before this, the modal length of the cladocerans and copepods living there had been 0.8 mm. When the lake was studied some years later, the species composition had changed, and now the modal length of the surviving cladocerans and copepods was only 0.3 mm (Brooks and Dodson, 1965).

For freshwater crustaceans, diving is an important strategy to avoid predation by fish. This has been shown in studies on two similar species of *Daphnia*, 1.7–2.0 mm long, found in Lake Constance in Germany. *D. galeata* lives all the time in

Fig. 1. A view of the shore of Mono Lake in California, USA. Countless numbers of ephydrid pupae and adult flies form the wide black layer at the edge of the blue water.

the top few metres of water, while *D. hyalina* dives to 35 m during the day in summer. Although *D. galeata* has a much higher birth rate than *D. hyalina*, whitefish and perch eat nine times as many of them and, as a result, they are less numerous during most of the year (Stich and Lampert, 1981).

The most striking and beautiful demonstration of the importance of visual predation by fish to the density of aquatic zooplankton comes from work by Gliwicz (1986*b*) on predation by sardines on six species of crustaceans in a freshwater lake in southeast Africa. He showed that cycles of zooplankton density that fluctuated in phase with the moon were clearly linked to increased mortality caused by more intensive nocturnal feeding by fish during the phase of the full moon when they could see their prey better. On nights when a nearly full moon rose, some hours after sunset, zooplankton were caught in a 'moon trap' in which they suffered very high predation when the moon rose suddenly in a previously dark night. Once zooplankton become visible to fish, even if only by moonlight, they are slaughtered. The ability of fish to lord it over both crustaceans and insects in surface waters may come from their much superior locomotion that in turn derives from that characteristic vertebrate feature the spinal column.

In another environment, the air, the distribution and behaviour of insects is consistent with the ideas discussed here. To avoid predators, largely birds in this case, the aerial adults of many species of insect only fly at dawn and dusk; only the most manoeuvrable and/or unpalatable insects fly during the day. During the daytime, most flighted insects hide themselves. Were there flighted insects feeding in the upper waters of the sea at night that retreated into the air in the day, they would presumably escape fish only to fall into the throats of birds.

The above considerations provide an explanation for the absence of insects from much of the sea. There are, of course, insects in parts of the marine environment other than the open sea (Cheng, 1976), but even there they are under-represented. Why, for example, are there so few insects at the sea edge below the high water mark? Since insects are often abundant in the bottoms of or among plant life in shallow bodies of freshwater and inland saline lakes, they ought to be able to escape predation from fish in shallow sea water. Conceivably, they could escape fish there but are outcompeted by crustaceans. Why should this be? A characterizing feature of insects is their ability to cope with high degrees of osmotic and ionic stress (Maddrell, 1981, 1982). But marine crustaceans face no osmoregulatory problems as they have internal ionic and osmotic compositions very similar to that of sea water, so this potential advantage for insects counts for naught. And, indeed, since insects have internal ionic concentrations much lower than that of sea water, their running costs in this respect are higher than those of crustaceans. So one can see why insects might better compete with crustaceans in osmotically challenging environments (such as freshwater and hypersaline lakes) but at the same time fail in sea water, where such stresses are virtually non-existent for crustaceans. Further than this, other features of insects, particularly their waterproofing, strong yet light cuticle, metamorphosis and flight are either irrelevant or positive disadvantages for marine organisms (Foster, 1986). A related point arises here: if fish outcompete both crustaceans and insects in the open sea, why do they not do so in shallow waters at the edges of seas? In other words, why are there any crustaceans in such environments? A possible explanation comes from the fact that all fish, with the single exception of the hagfish, have internal ionic concentrations that are much lower than that of sea water. In addition, all bony fish face the additional expense of osmoregulation from the fact that their internal osmotic concentration is also much lower than that of sea water. Both these problems become steadily more severe as size decreases as the surface area/volume ratio increases. Crustaceans, as noted above, face neither problem and so may be better able to survive competition from small fish (and small insects) because of their much lower osmoregulatory costs.

The available evidence encourages the idea that insects and fish cannot co-exist in natural bodies of deep water because the fish eat the insects. Apparently, the only successful strategy for escaping predation there is to dive, and the respiratory system of insects makes that uniquely difficult for them. In shallow sea water, crustaceans are dominant. It seems that insects have had no success in colonizing the sea because the predation and competitive pressures there are too great. It is even more impressive then that insects are so enormously successful on land.

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