Endemism in the Ponto-Caspian Fauna, with Special Emphasis on the Onychopoda (Crustacea)

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The Caspian Lake originated in the Miocene as the eastern half of the Ponto-Caspian basin. During the Pliocene, this water body sometimes merged with the Black Sea, also engulfing the Aral Lake and during its > 5 My existence has experienced strong and repeated fluctuations in salinity. These salinity changes have had important repercussions for the colonization of the lake and the evolution of its fauna.

Speciation in the lake has produced an overall level of endemism of c. 42%, somewhat lower than that of Lake Baikal (c. 54%). In both lakes endemism has reached the genus level, and in some faunal groups subject to adaptive radiation, levels of endemism close to 100% are seen. The main difference between these lakes is in absolute species richness and in the nature of the groups that radiated. In the Caspian Lake, selection systematically favoured groups with wide salinity tolerances. Among the Crustacea, this produced species flocks in the Mysidacea, Cumacea, the corophiid amphipods and the cytherid ostracods, while in the Onychopoda a unique pelagic speciation event occurred. The ancestors of all of these taxa were probably either estuarine (living in estuaries that flowed into the Tethys or Paratethys Seas) or freshwater animals. It is postulated that the Onychopoda are monophyletic and evolved in situ from the Sarmatian onwards.

Of the pelagic onychopods, seven species expanded into the oceans, and only two (possibly three) species are almost exclusively freshwater forms. In recent decades, however, the two freshwater species, and Caspian species tolerant of freshwater, have expanded their ranges to outside the Caspian. Artificial constructions (reservoirs, canals) as well as transport facilities (ships: ballast water) and incidental introduction with other, intentionally displaced Caspian species are believed to have facilitated these range expansions. Caspian onychopods are now found in the Laurentian Great Lakes of North America, the Baltic Gulf, lakes in Siberia and Central Asia, and drinking-water reservoirs in Western Europe. At least one "marine" species reinvaded the Caspian Lake.

It is known that speciation of the Onychopoda took place within the Ponto-Caspian. yet more "species" co-occur in the open water at any one time than ecological theory can
explain. This unusual situation is loaned added interest by the fact that these excellent swimmers do not utilize the water column beyond 50 m depth (maximum recorded depth = 100 m), a consequence of the risk of anoxic conditions that may occur at greater depths about twice per century. In addition to detailed ecological investigations, a taxonomic revision of the speciose genera *Corniger* and *Cercopagis* is recommended.

Adaptations to the risk of anoxia in deeper waters seem to be of two kinds: living in littoral bays, such that resting eggs do not sink too deep and are able to reach an oxygenated bottom or, alternatively, abandoning sexual reproduction altogether. The latter adaptation is most unusual and evolutionarily hazardous, and merits further study.

**INTRODUCTION**

The origin and geological history of the Ponto-Caspian basin is both long and involved. During the Miocene, the Arabian subcontinent collided with western Asia, pushing up the Caucasus and Elburz mountains and severing the pre-existing marine waterway between the Atlantic and Indian Oceans. At the same time, the Tethys Sea gave way to the Sarmatian Lake, filling up the Ponto-Caspian basin, including most of the present Black and Caspian Sea areas.

Although it is possible that there was an occasional connection between this giant brackish water body and the ocean (Zaitsev and Mamaev, 1997), the Ponto-Caspian basin has existed as a lacustrine body for at least the past 5 My. This explains why true marine groups like the Echinodermata and the Chaetognatha were unable to colonize the Pontocaspian until the Holocene, when the connection between the Black Sea and the Mediterranean Sea transformed the former from a lake to a true hybrid between lake and sea. Following this event, salinity in the Black Sea rose to a level sufficient to permit invasion by exclusively marine faunas, although even to the present day, this invasion has remained quite selective. At the same time, the increasing salinity levels forced most of the exclusively freshwater species among the Onychopoda (Crustacea) out of the pelagic and into estuarine and marginal freshened zones, such as the north-west area of the lake and the Sea of Azov.

By the early Pliocene, a deep regression, coupled to continued crustal movements, had separated the western (Black) and the eastern (Caspian) sub-basins. This long regressive phase, corresponding to an increase in salinity from an almost fresh to a moderately saline water body, only reversed at the Pliocene–Pleistocene transition, when two high lake stands of long duration (the Akchagylian and the Apsheronian), the second lasting until c 700,000 years ago, reunited the Black, Caspian and Aral Lakes into a single gigantic brackish-water lake (Figure 1). During the intervening regressions, separate saline-water lakes were formed again (Dumont, 1998a).
Fluctuations in the level of the Caspian have continued to the present (for details, see Kaplin, 1997), with the lake surface first sinking below world ocean level possibly not later than c. 40 000 years ago. After that, it continued sinking to an absolute low of c. -40 m. In historical times, the lake level has never exceeded the -20 m mark, and has averaged c. -27 m. During the twentieth century, the amplitude of variation has been about 4 m, with minimum levels reached in 1977 and a rapid rise thereafter. As noted later, lake levels exceeding the -26 m mark are likely to be of considerable significance for the fauna of Caspian Lake.

CASPIAN SPECIES RICHNESS AND LEVEL OF ENDEMSM

Ignoring Protista, the total species richness of the Caspian is currently estimated at c. 950 species (Kasymov, 1987), with about 400 species endemic to the lake. This is less than the species richness of Lake Baikal, presently standing at 1874 species (Kozhova and Izmost'eva, 1998). However, these recent estimates for Lake Baikal are themselves considerably higher than former estimates. Around 1960, only 902 species, of which 618 were endemic, had been counted in Baikal (Kozhov, 1963). Further studies of the
Caspian fauna might also result in a large increase in the number of species described from this lake. As noted below, for certain faunal groups in the Caspian, estimates of species diversity differ greatly.

Although the overall level of endemism in the Caspian appears to be lower than that of Lake Baikal, there are several reasons why such a direct comparison might be misleading and of little value.

First, it may be argued that all faunal elements shared between the Caspian, the Black Sea and Lake Aral should be classed as endemics of a single water body: the Ponto-Caspian.

Secondly, the Caspian has a steep north-south gradient in salinity, from the shallow fresh waters of the Volga and Ural in the northern third of the lake, to the deep brackish basins of the center and the south, where salinity may sometimes exceed 13%. In the northern third, a freshwater fauna of wide biogeographic distribution is found, together with only few true Caspian elements. Including this fauna as Caspian increases total species richness, but decreases percentage endemism. For example, the delta region of the Volga River, which enters the Caspian, harbours 226 species of rotifers, 110 species of cladocerans s.l. (including onychopods) and 75 species of copepods (Chuikov, 1994). In comparison, the Caspian is home to 78 species of rotifers, 55 species of cladocerans and 41 species of copepods (Kasymov, 1987). These differences are large, and reflect the wide variety of wetlands and shallow, enclosed lakes of the deltaic zone, which contain a rich but wide-ranging fauna. However, exactly the same is true of the marginal bays (sors) and shallows of Lake Baikal (see Sideleva; Kozhova et al.; Takhteev, this volume). Much of the discrepancy between the 1960s and the 1990s faunal estimates for Baikal is due to the inclusion in the most recent list of biota from the sors. After including the sors biota, apparent endemism in Lake Baikal decreased from over 80% to 54%, a figure comparable with that for the Caspian (42%, using Kasymov's 1987 figures).

Thirdly, it should also be stressed that, as the Ponto-Caspian graben formed, mountain ranges were pushed up, creating rivers that have the same age as the lake. These rivers (e.g. the western Rivers Kura, Samur, Sulak and Terek, all draining the Caucasus mountains) all have an endemic species component in their mollusc, insect and fish faunas. It is debatable whether these should be included with the fauna of the Caspian proper or not, but they are indisputably part of the fauna of the basin.

An extreme example is that of the Amu and Syr Darja Rivers, in the eastern Caspian basin. Both currently drain the Tiyan Shan and Pamir mountains towards Lake Aral in the north. However, the Amu Darja is noted for changing the direction of its flow: even in historical times, it has drained alternatively to the Caspian, either directly or via the Sarykamish depression, or to Lake Aral (Aladin, 1996). Both rivers are home to unusual (presently endangered) sturgeon fish of the genus *Pseudoscaphyrhynchus* (Acipenseridae, Subfamily Scaphyrhynchinae). The three
species in this genus are restricted to the Lake Aral basin. The closest relatives to these sturgeons are the three species of the genus *Scaphyrhynchus* (also subfamily *Scaphyrhynchinae*), which live in the Mississippi basin in North America. Evidence suggests that ancestors of these currently land-locked species lived in rivers that drained central Asia to the Indian Ocean before the uprise of the Himalayas (Bemish and Kynard, 1997). These ancestors may have been anadromous (as are many acipenserids today) and inhabited the Tethys Sea, extending as far west as the North American shores of the Atlantic.

In conclusion, if one were to compare basins and not strictly lakes, endemism within the Ponto-Caspian fauna would perhaps turn out to be even higher than that of the (comparatively small) Baikal basin. Such comparisons are best made on taxa which are well represented in both lakes, such as molluscs, crustaceans and fishes (Table 1). In details, these figures may be subject to future change, yet they eloquently show that in several families of gastropods and fish, and in several crustacean orders, in both lakes the level of endemism may approach 100%. Endemism in these lakes reaches at least the genus level, and sometimes higher. From Table 1 it is also evident that the differences between these lakes resides not in the degree of endemism, but in the nature of the taxa that underwent adaptive radiation.

**THE NATURE OF SPECIATION IN THE CASPIAN**

Taking, henceforth, the Crustacea as an example (but the same trends apply also to other groups), it is clear that speciation in the Ponto-Caspian proceeded along a different path from that in Lake Baikal. All Caspian groups that radiated are typical of estuarine environments. Some of these are marine groups with few (Mysidacea) or no (Cumacea) representatives in limnic ecosystems. Others, such as the Ostracoda and the Amphipoda, have a more balanced distribution between marine and continental waters, yet their Caspian representatives (the Cytheridae and Corophiidae, respectively) are, at least in part, related to marine or brackish-water families. Even the sole Caspian cnidarian possessing a medusa phase, *Moerisia pallasi*, belongs to a family and genus whose species occur mainly in estuarine environments (Dumont, 1994a).

This intriguing phenomenon has not been well analysed in the literature and calls for more investigation. It reflects a history of repeated changes in salinity of the lake(s), whereby natural selection was invariably picking out taxa for their euryhalinity and broad capacity for osmoregulation (Aladin, 1996).

However, whether the ancestors of the current Caspian endemics were of marine or freshwater origin is a different matter. There are probably no true marine-derived species in the Caspian, and thus the term "Tethyan relicts" strictly does not apply (contra Dumont, 1998b). The ancestral forms of the Moerisiidae, Cumacea, Corophiidae, Gobiidae,
Clupeidae, etc., of the modern Caspian Lake probably lived in the estuaries and tidal zones of rivers that emptied into the Tethys before the closing of the Sarmatian basin. Their osmoregulatory abilities meant they were preadapted for life in the brackish Sarmatian lake. All other Caspian biota must be considered to have been derived from freshwater stock.

THE CASE OF THE ONYCHOPOD CRUSTACEA

The order Onychopoda represents the only case of adaptive radiation among the branchiopod crustaceans. Formerly classified with the Cladocera, and still often indicated by that name, they were separated in a specific order by Fryer (1987). Ongoing molecular work, using the full sequence of the 18S rDNA nuclear gene, has not only confirmed this position, but also suggests that the Onychopoda might even be more closely related to the Anostraca than with the cladoceran orders Ctenopoda and Anomopoda (Weekers et al., unpublished).

That the Onychopoda and Anostraca might share a common ancestry is indeed revealing, because they are clearly primarily freshwater animals. Yet some extant genera, and even families, of the Anostraca (the Artemiidae and Pararemiidae, as well as some Branchinecta species) have a

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<td>Total spp.</td>
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<td>Ostracoda</td>
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<sup>a</sup>23, and <sup>b</sup>69, according to Mordukhai-Boltovskoy (1979).
<sup>c</sup>Based on data in Kohzov (1963).

Clupeidae, etc., of the modern Caspian Lake probably lived in the estuaries and tidal zones of rivers that emptied into the Tethys before the closing of the Sarmatian basin. Their osmoregulatory abilities meant they were preadapted for life in the brackish Sarmatian lake. All other Caspian biota must be considered to have been derived from freshwater stock.
capacity for osmoregulation that permits them to inhabit saline waters, from slightly brackish to almost saturated brines. If such a capacity was already present in the ancestor, which appears a reasonable supposition, this ancestor was preadapted to the nascent Ponto-Caspian. This hypothesis assumes a monophyletic origin of the Onychopoda, in the Ponto-Caspian basin itself. Their radiation must have started as soon as marine conditions had been replaced by a lacustrine environment, i.e. in the early Sarmatian, although the ancestral form itself might be significantly older.

This evolutionary scenario runs counter to the opinion of Rivier (1998), who postulates a far more complex, possibly diphyletic, origin for the Onychopoda, with the podonids (one of the three onychopod families) derived from a pure marine ancestry. The podonids have seven marine species, in addition to nine Ponto-Caspian species (Table 2); a situation which lends some support to the diphyletic origin hypothesis. However, several other points argue strongly against Rivier's position.

First, even the so-called marine species often thrive best at below-seawater salinities and several reach maximum abundance in the lower zones of estuaries, or in marine lagoons diluted with inflowing freshwater, or in brackish-water seas such as the Baltic. Moreover, except for *Evadne spinifera* and the tropical *Pleopis schmackeri*, all of the marine species are restricted to coastal or near-coastal zones.

Secondly, of the seven marine onychopods, five approach a world-wide distribution or are widely distributed in the northern hemisphere. All but *P. schmackeri* are present in the Black Sea, and none of the other six species shows signs of speciation or subspeciation in restricted marine zones. This absence of incipient speciation is a feature strongly suggestive of a recent conquest of the ocean. Their entry to the ocean may be as recent as the Holocene, when the Black Sea became connected to the Mediterranean. This event also provided an entry route for true marine elements to the Black Sea, as an exit for those Ponto-Caspian species with a high salinity tolerance. Some of these species may have gone extinct in the Caspian itself, at a time when local salinity was too low for them to survive. That this is currently no longer the case was demonstrated by the successful reinvasion of the Caspian by *Pleopis polyphemoides* after 1957.

Evidence of the inability of some onychopods to tolerate high salinity levels is provided by the rapid salinization of the drying out Aral Lake, where at 24‰ salinity *Podonevadne camptonyx* was the only one of four onychopod species to survive into the 1990s (Aladin, 1995). In the Black Sea also, and for the same reason (salinity of the open water becoming too high after the inflow of Mediterranean water), several species survive under precarious conditions by colonizing marginal habitats, in coastal wetlands and limans (coastal lagoons) (Wilson and Moser, 1994), estuaries and the fresher Azov Sea (Table 2).
From the varied sources of evidence, the marine onychopods may be best considered as salt-tolerant Ponto-Caspian animals that recently expanded from the Black Sea to the ocean, via the Mediterranean Sea. More examples of recent range expansions are given later.

Studies of the marine onychopods in Chesapeake Bay demonstrated that they partition ecological space by living at specific salinity-temperature combinations, and thereby reduce or avoid niche overlap (Bryan and Grant, 1974). A similar strategy appears to be present in Caspian species (Rivier, 1998), with the sole difference that each occupies a specific range of below-marine salinities. Several of these taxa (*Podonevadne trigona*, *Cernigerius maeticus*, *Cercopagis pengoi*) are perfectly capable of surviving in true freshwater, although tolerant of salinities of up to 13%, the current maximum in the south-east Caspian. An isolated population of *P. trigona* in the freshwater Lake Chalkar (Behning, 1928; Rivier, 1998) is believed to be a relict of a former lake transgression into the valley of the Ural River. Both other species migrate up rivers, either actively (which seems improbable), or as resting eggs.
transported in the intestine of fish, with birds or by other means. If stagnant water bodies are encountered en route, this upstream migration can be effective and rapid. This is evinced by the upstream expansion of the three above-cited species in several rivers feeding the Black and Caspian Lakes (the Danube, Don, Dniepr and Ural Rivers) after reservoirs had been constructed across their valleys. The most spectacular case is that of the Volga River, dammed in cascade since the 1930s, and where at least three former exclusively Caspian onychopods have now colonized all these artificial reservoirs.

There are two (or three, if Cornigerius lacustris is indeed a valid species; see below) true freshwater species. *Bythotrephes longimanus* is capable of surviving in slightly brackish water. The haloxenic Caspian species *Polyphemus exiguis* is not universally accepted as specifically distinct from the widespread, freshwater *Polyphemus pediculus*. This, the only onychopod known to live in temporary waters and to have a resting egg that is drought resistant does, however, also occur in the brackish Baltic Sea. Both are thus so closely related to typical Caspian species that a recent common ancestor is obvious, and both have also maintained a capacity for euryhalinity.

In their expansion outside the lake, these two species have managed to cover a Holarctic or north Eurasian range and, more recently, both have begun expanding their ranges even further. It has become clear that the ability of large *B. longimanus* to colonize new biotopes is restricted mainly by the nature and depth of the new habitat: it requires stagnant waters with a minimum depth of c. 5-10 m. Consequently, while it may occur as isolated specimens in river water, in the newly created reservoirs of the Volga it has flourished, and now coexists there with the two or three aforementioned Caspian species. In the course of the twentieth century, no doubt aided by human activity (ships carrying ballast water), it reached North America, where its populations increased greatly during the late 1980s (Bur et al., 1986; Lehman, 1987; Sprules et al., 1990). Recently, it expanded from the north of Europe to The Netherlands and Belgium (Ketelaars and van Breemen, 1993). Ketelaars and Gille (1994) state that this invasion was facilitated by the construction of large, deep (up to 15 m) drinking-water reservoirs in an area that used to consist of swamps and shallow lakes, but also note the close proximity of several major ports, suggesting that shipping might also have played a role. Possibly, the invasion proceeded in a sequence of small steps, with Antwerp currently its southern border of distribution in Atlantic western Europe.

In 1992, *Cercopagis pengoi* was first recorded from the Gulf of Riga, but soon was found across the whole brackish-water Baltic Sea (Krylov and Parrot, 1998). Gorokhova et al. (2000) believe that it may have been present here much longer, but either was ignored or misidentified as *Bythotrephes*, and that the morphological variation in the Baltic populations overlaps with that of at least two other *Cercopagis* species, and even with that of *Apagis* (see below). Intentional introductions of Caspian animals to
other parts of the Soviet Union were common, especially in
the 1960s and 1970s (Mordukhai-Boltovskoy, 1979), and the
earlier, undocumented presence of this species at low
densities is thus a strong possibility. Mysids were a
popular object for such "acclimatizations", as were
amphipods, polychaetes, molluscs and fish. In the 1960s,
large water containers with live mysids (and probably also
onychopods) were transported to some reservoirs on the
Baltic rivers Daugava and Neman. Zjuravel (1965) explicitly
called these nuclei ("otchagi") of further dispersal. Over
30 years later, the facts show him to have been correct.

The introduction of two species of the cercopagid
subgenus *Apagis* (*A. cylindrata* and *A. longicaudata*; Table 2)
into the large, fluctuating, saline Lake Chany, west of
Novosibirsk in Siberia, may have taken place by the same
means (large water containers) (Vizen, 1986). In *Apagis*, no
resting stages are known (see below), and provided the Lake
Chany populations indeed belong to this subgenus, live
transport is here an even more probable scenario.

In conclusion, given a suitable means of
transportation, the considerable osmotic tolerance of the
Ponto-Caspian onychopods makes them ideally preadapted to
invade new environments, whether the ocean (for the most
salt-tolerant species) or fresh water (for the least salt-
tolerant species). Their range expansion has been slowed
down more by a scarcity of easily accessible deep, pelagic
biotopes than by salinity. That until recently so few of
them had been able to expand beyond the Ponto-Caspian also
testifies to the relative isolation of that region and to a
rather recent origin of the group. Current range expansions
seem almost exclusively due to humans, either intentional,
or facilitated by constructions (reservoirs, canals) or
vehicles (ships).

**WHY SO MANY PELAGIC ONYCHOPODS IN THE CASPIAN?**

In an earlier paper on the zooplankton of ancient
(pre-Pleistocene) lakes, the present author argued that,
with time, a simplification of the pelagic foodweb structure
should occur (Dumont, 1994b). This process would eventually
result in a single efficient filter-feeding algivore,
usually a calanoid copepod, becoming dominant, while
Cladocera, in spite of possible attempts at reinvasion,
would be consistently barred from success in the limnetic
environment (Dumont, 1994b).

The Caspian was not included in the list of lakes
examined at that time. Indeed, relative to other ancient
lakes, its pelagic presents several complications: the
shallow, freshwater north area of the lake is very different
from the saline centre and south. The north freezes in
winter, the centre partly freezes and turns over, yet the
surface water temperature in the south never drops below
10°C. Circulation here is driven by salinity increases at
the surface as water evaporates, and is extremely slow
(Kosarev and Yablonskaya, 1994; Dumont, 1998b). This
physical heterogeneity, and immigration waves of northern
animals that arrived via the Volga following deglaciation in Russia and through the artificial Volga-Don canal in the twentieth century, have made it possible for five or six species of pelagic calanoid to become established in the lake, partitioning its ecological space in several salinity-temperature compartments.

Cladocerans (anomopods and ctenopods) seldom occur in the centre and south, but at least 23 species of Onychopoda have been claimed to inhabit the lake. They are partly or entirely predacious and therefore may not compete with the calanoids. As stated earlier, they, too, partition lake space in temperature-salinity zones. In addition, some are more littoral in habitat choice and others more strictly pelagic. In spite of this, four or more congeners may co-occur at any one time. All of these fall into two groups, similar in shape and size, and show no evidence for partitioning of food items (Dumont, 1998a, b).

This assemblage of closely related, similar species seems to defy one of ecology's basic tenets: Gause's rule. Indeed, the coexistence of so many species, with little evidence of niche partitioning, leads one to question whether the number of "species" has not been grossly exaggerated. For example, the four small-sized species of the genus Cornigerius (including C. lacustris, the "endemic" of the East-Anatolian freshwater Lake Hazar) only differ in details of body form and in the shape of the horn(s) on their heads. The latter, perhaps antipredator devices, may be transient (predator triggered) morphologies, or represent cyclomorphic traits such that, in reality, there is perhaps only a single species (cf. Mourguiart, this volume). How the Anatolian "species" reached Lake Hazar is unknown. This elongated lake lies isolated between mountain ranges and therefore phoretic transport by birds seems the most plausible mechanism.

Similar concerns apply to the large-sized species of the genus Cercopagis (s.l.) (13 named species). The pointed brood pouch in the C pengoi group, for example, may be an environmentally introduced antipredator morphology without taxonomical meaning. The same is true of the presence or absence of spinules on the cauda, the length of the cauda and even the presence or absence of a loop in the cauda (the main distinctive character between Cercopagis s.s. and Apagis). Although the distinction of two subgenera on morphological grounds is supported by ecological differences (see below), a taxonomic revision, based on a two-track approach utilizing morphology and molecular information, is needed to resolve this question.

One obvious mechanism for reducing interspecific competition in situations where congeners co-occur is via a different vertical distribution within the water column, but this is not present in the onychopods. All onychopods are eyed animals that hunt visually, and had they coexisted for a long time, specializations would inevitably have been selected for, one of which could involve a vertical segregation. Yet these excellent swimmers and vertical migrants do not extend beyond a zone reaching from the surface to a depth of 50 m, with only the occasional
solitary specimen venturing down to a maximum depth of 100 m (Mordukhai-Boltovskoy and Rivier, 1987). As such, c. 800 m of the 900 m water column in the lake is not being used, except by the occasional specimen of Apagis (Rivier, 1998).

The reason why these animals utilize only a limited depth range is perhaps the same as for the absence of a true deep-water benthos (Dumont, 1998b): at high stands of the Caspian, when more fresh water flows in than evaporates, the density-driven circulation of the deep basins breaks down and meromictic conditions develop. Anoxia in the deeper waters was observed during the high lake levels of the 1930s, with meromixis setting in at near the −26 m mark. Since that mark may be reached or exceeded about twice per century, it is clear that the low oxygen content of the deep waters of the Caspian, and possibly the entire water mass below 200 m (an analogy with Lake Tanganyika is obvious here), with unpredictable anoxic pulses, has been impossible for animals to adapt to. In all probability, mass mortalities in the hypolimnion have been a recurrent phenomenon and plankton has been selected not to migrate beyond a critical depth. This extreme compression of the pelagic space to the upper 50 m has important ecological consequences in that competition here is exacerbated. This, in turn, makes the indefinite coexistence of so many similar species all the more improbable (see Simm and Ojaveer, 1999).

WHY RESTING EGGS?

The capacity to produce eggs (more correctly, encysted gastrulas) resistant to adverse conditions and with a long dormant period is an asset in circumstances where the environment may present sudden changes of undetermined duration. Thus, as an adaptation to life in temporary waters anostracans routinely produce cysts that are drought resistant (Polyphemus pediculus being the only onychopod known to be capable of the same). Many anomopods and Artemia, living in (sometimes deep) lakes, produce resting stages that float to the surface. As a rule, cysts are produced shortly before the temporary disappearance of active populations. In contrast, all onychopods with cyclical parthenogenesis produce resting eggs that sink to the bottom (Rivier, 1998).

What might be the adaptive significance of this life tactic in a lake with an episodic anoxic hypolimnion? Even if the hypolimnion was well oxygenated, it seems unlikely that environmental cues to trigger hatching would be perceived by sedimented cysts, this environment being too cold and too dark. It is known (pers. obs.) that in low-salinity environments Artemia cysts sink, and will become suspended and float only after evaporation results in an increased salinity (and density) of the water. Perhaps, cysts in a monimolimnion becoming more saline might be floated to the top of the anoxic layer (if sufficiently long lived and still viable after immersion in anoxic waters), but this certainly does not appear to be an efficient mechanism for survival.
Avoidance of the deepest basins, and selecting bays or shallows in which to live would seem a more rewarding strategy, and this is exactly what seems to be happening in several species. However, in a significant number of other species (seven in all, the marine Pleopis schmackeri, the Caspian Evadne prolongata, Caspievadne maximowitchi, and all four Apagis species), a different avenue has been explored. All of these species seem to have completely abandoned sexual reproduction, thereby eliminating the risk of losing an investment in a sexually produced cyst. The cost of this solution is considerable: risk of accumulating a genetic load, as well as the need for an active population to be present throughout the year. Yet, in light of the history and conditions in the Caspian, this solution is more appropriate and seems to have arisen three times independently. In view of the rarity of animals completely abandoning sex, even under severe selective pressure, further research on the crustacean fauna of the Caspian Lake is clearly warranted.

REFERENCES


