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Neozoans in European waters – Exemplifying the worldwide process of invasion and species mixing

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Abstract. The loss of biodiversity – the tendency of the world's fauna to become more and more homogeneous – is widely acknowledged as a problem. Biodiversity is threatened by neozoism and acculturation as much as the extinction of species, but these dangers are less well known. Neozoism and acculturation have an effect on two levels; they lead 1) to an equalisation of the faunal regions and their originally different, specially adapted biocenoses, and 2) to a reduction of genetic diversity below the species level. These processes develop very rapidly in the European waters, particularly in the lowland river systems. The present contribution gives a brief review on neozoans in European inland waters.
Key words. Neozoans; invasions; Europe; Rhine river; aquatic fauna; conservation strategies.

1. Introduction

Worldwide biodiversity is endangered by three important types of faunal change which threaten the natural environment itself, as well the human ability to use and preserve natural resources. These changes are:

- the loss of species on a local or global base ('extinction'). It results in the survival of only a relict of the original fauna, including chance survivor and opportunistic species;
- worldwide faunal exchange by introduction of allochthonous species, homogenising faunas ('neozoism');
- the genetic change of wild populations by adaptation to human environments, by domestication, or by interbreeding with already domesticated stocks ('acculturation').

All three have significantly contributed to the contemporary fauna, which is a product of human impact on the global ecosystem. They have strongly influenced the ecosystem during the 160 years of the industrial epoch, parallel to the growing human population density and activity. But they have not received an equal share of public awareness, even within the scientific community. Meanwhile the diminution of biodiversity, above all the total loss of species, is widely accepted as a problem. It is subject of intense discussion, although treatment of the problem and remedies are still controversial. This is not the case for neozoism and acculturation, which both describe a homogenisation of the world's wildlife which is threatening biodiversity as much as the extinction of species. There are two levels: 1) mixing of faunal regions and their originally different, specially adapted biocenoses, and 2) reduction of genetic diversity below the species level. There are three reasons for this difference in perception:

First, the scientific interest in faunistics and zoogeography is low. The British hydrobiologist H. B. N. Hynes expressed the hope that field observations on distribution of animals would not be ignored and discouraged by 'official' zoology[40].

Second, loss of diversity due to faunal exchange, although found worldwide, can only be experienced regionally. Compared with biodiversity as a whole the problem has few general aspects, the regions, indigenous faunas and invading species being always different, using different strategies and suffering different fates. Expanding animals are noticed only by regional observers in the context of a local fauna. Thus, their meaning is frequently overlooked for a long time.

Third, the invading organisms are treated as curiosities, suitable for the weekend magazine of your newspaper, with the 'message': how funny, this exotic turtle (frog, butterfly, clam ...) is now found here. Or, 'all mallards in the river park now show this broad white breast patch, instead of the narrow white collar they used to have before'. It is just something to chat about. Only when economic interests are threatened does this phenomenon attract some worldwide publicity.

Is faunal exchange not a natural fate? Do not all faunae tend naturally to spread out and mix? According to the famous microbiologist R. Koch "the milieu is all, the bacterium nothing". This means that distribution is solely determined by the availability of suitable substrates or habitats. This is true for the ubiquitous bacteria. For higher organisms, it is true only over long periods, allowing dispersal over all parts of the globe which are suitable for the species under consideration. Distribution depends on limited means of dispersal and on the grade of difficulty of the natural obstacles.

Neozoism and acculturation refer to all species and ecotypes of organisms. For example, game species were brought from England to New Zealand. Acclimatization of useful animals was the norm at the end of the

19th century[30]. From then on, America's fur-bearing muskrats and coypus roamed in European lowlands[80,85]; hundreds of bird species were spread all over the world[76]; dozens of fish species were domesticated for fish farming and now, as escapees, ruin the genetic properties of wild populations[75].

Case studies are also numerous in the marine environment. Worldwide ship traffic has changed the fauna of harbours, and of adjoining bights and shelf seas, beginning with the early import of the mussel *Mya arenaria* to Europe by the Vikings[38]. Far more species were transported by cargo ships from the 19th century on. Mussel farming imported the bivalves *Crassostrea virginica* and *Petricola pholadiformis*, and the gastropods *Rapana venosa*[66], *Crepidula fornicata*, *Urosalpinx cinerea* to European coastal waters. Science inadvertently released the 'killer weed' *Caulerpa prolifera* into the Mediterranean Sea. Finally, there is a gigantic ecological experiment which started as a by-product in 1869 with the opening of the Suez Canal, allowing several hundred indo-pacific species access into the Mediterranean Sea by 'Lessepsian Migration'[29,101,134].

Faunal change is most striking in freshwater, mainly in big rivers (potamocenosis)[59–61,73,115,122]. There the pace can be breathtaking: in the northern upper Rhine alone during the last 10 years, eight additional species of crustaceans and molluscs have arrived[17,33,37,39,43,70,71,94–100,132].

River catchment basins under natural conditions are usually well separated for relatively long geological periods. They are less coherent than terrestrial or marine biota. Only under special conditions, due to human activity, are animals able to invade new areas.

2. Anthropogenous area dynamics

2.1. Typology and general characteristics

The process of invasion or expansion takes place at the level of individuals, populations, species, and biocenoses. The most striking feature is the change in size and shape of the distribution area, which is easily recorded, and the first – if not only – character studied. However, in natural inland water habitats, the dynamics of faunal changes due to immigration is different. In the biocenosis of brooks and streams (rhithrocenosis) the rate of change is low, while in lowland rivers (potamocenosis) it is high. In stagnant water highest immigration rates occur in shallow, medium sized, and eutrophic ponds. The immigration rate is low in waters demanding special adaptations to severe ecological factors (e.g. current, cold, low oxygen, salinity), in those harbouring intact autochthonous biocenoses, and in waters whose catchment basins are defined by strict, longlasting barriers which are not easily overcome by natural means of distribution.

As mentioned above, humans are increasingly involved in the introduction of new fauna into a region or ecosystem. This may be directly or indirectly, deliberately or inadvertently, and may initiate the process, provide the means of transportation, or just speed up natural processes. Human activity superimposes on the natural dynamics of biocenoses and, in a holostic view, may be considered only as a vehicle for change, like a vector species. So, neozoism is better understood as a part of the whole process of faunal and floral change in Europe north of the Pyreneo-Alpine-Karpathian barrier after the last Pleistocene glaciation. The following periods can be differentiated:

1) The postglacial period saw the migration of plants (e.g. forest) and animals from Mediterranean refuges[20] into now suitable areas in the north. The high mountain chains in east-west direction were frequently by-passed. In this way the typical pattern for central Europe of twin taxa, genetically separated in different levels, originated. The western and – more complex – eastern populations of the white stork (*Ciconia ciconia*) and probably the pond turtle (*Emys orbicularis*)[68] differ only slightly, e.g. in hibernation areas. Longtail tits (*Aegithalus caudatus*) differ in eastern and western subspecies, as do the carrion crow and hooded crow (*Corvus c. corone* and *C. c. cornix*), and the salamander (*Salamandra s. salamandra* and *S. s. quadrivirgata*). Differences are also seen at the species level, e.g. with the creeper (*Certhia familiaris*, *C. brachydactyla*).

These remigrants (together with persisting parts of the periglacial and subglacial fauna) represent the 'autochthonous fauna' (analogous to the flora). Neozoism partly fits into this remigration, as far as species of Pontian or Mediterranean origin are involved. Human activity speeds up the migration process, which is slower in inland waters due to the inhibiting watersheds, and the limited means of distribution of many water animals.

2) A wealth of plant species moved to the north following the agriculture of the Neolithic Revolution. They

Table 1. The ten great environmental changes in European lowland rivers (after Kinzelbach, 1978, cf. ref. 60).

1	Correction
2	Construction of normed riverbeds
3	Construction of dams and reservoirs
4	Cutting-off of lowlands and inundation areas
5	Connection to neighbouring river systems by ship- or irrigation-canals
6	Pollution by organic matter
7	Pollution by natural matter (salt, mineral turbidity)
8	Pollution by toxic or subtoxic waste
9	Discharge of warm water by power stations
10	General intensity of use (boat traffic, sports, fishing, recreation)

Table 2. List of the neozoans of inland waters in central western Europe.

	Success[a]	Means of immigration[b] (several possible)	Origin[c]
Coelenterata			
Cordylophora caspica	++	S	PK
Craspedacusta sowerbyi	++	S V K	?AS
Turbellaria			
Dugesia tigrina	++	P K A	NA
Trematoda			
Bucephalus polymorphus	+	K	PK
Kamptozoa			
Barentsia ramosa	–	S	PK
Urnatella gracilis	+	S	?PK
Annelida			
Branchiura sowerbyi	+	P S	?AS
Helobdella punctatolineata	>Egypt	P	NA
Crustacea			
Balanus improvisus	+	S	MA
Atyaephyra desmaresti	+	I K	ME
Palaemon longirostris	+	A	MA
Pontastacus leptodactylus	+	P	PK
Pacifastacus leniusculus	+	P	NA
Procambarus clarkii	>Spain, E-Europe	P	NA
Orconectes limosus	++	P A	NA
Eriocheir sinensis	+	P A K	AS
Rhithropanopeus harrisi	+	P A	NA
Callinectes sapidus	+	P	NA
Corophium curvispinum	+	K	PK
Crangonyx pseudogracilis	++	S	PK
Orchestia cavimana	+++	K I	ME
Gammarus tigrinus	++	P A	NA
Gammarus ischnus	+	K	PK
Echinogammarus berilloni	++	I K	ME
Dikerogammarus haemobaphes	+	K	PK
Asellus meridianus	+	K I	ME
Asellus coxalis	+	P A K	ME
Asellus communis	–	P	NA
Mollusca			
Viviparus viviparus	++	S A	PK
Viviparus ater	+	P	ME
Lithoglyphus naticoides	+	K S	PK
Potamopyrgus antipodarum	++	P A V	AU
Melanoides tuberculata	+	P	VO/AS
Physella acuta	++	P K	ME
Physa heterostropha	+	P	NA
Ferrissia wautieri (*)	++	K I	ME
Gyraulus parvus	+	P	NA
Helisoma sp.	>Egypt, Israel	P	NA
Lymnaea catascopium	+	P	NA
Corbicula fluminea	+++	P S	NA/AS
Corbicula fluviatilis	+++	P S	NA/AS
Dreissena polymorpha	+++	K S	PK
Mytilopsis leucophaeata	+	P	AF
Teleostei			
Parasalmo gairdneri	++	P A	NA
Hucho hucho	+	P	PK
Oncorhynchus tschawytscha	+	P	EA
Salvelinus fontinalis	+	P	NA
Aspius aspius	+	P	EU
Carassius auratus gibelio	+	P	EA
Idus idus var.	+	P	?AS
Cyprinus carpio	+	P	?PK
Vimba vimba	+	P	EU
Ctenopharyngodon idella	+	P	EA
Hypophthalmichthys molitrix	+	P	EA
Astronotus occellatus	–	P	AF
Gambusia holbrooki	+	P	NA

Table 2. (contd.)

	Success[a]	Means of immigration[b] (several possible)	Origin[c]
Umbra pygmaea	+	P	NA
Lebistes reticulatus	+	P	NA
Silurus glanis (*)	+	P	EE
Ictalurus nebulosus	+	P	NA
Lepomis cyanellus	+	P	NA
Lepomis gibbosus	++	P A	NA
Micropterus salmoides	+	P	NA
Micropterus dolomieu	+	P	NA
Stizostedion lucioperca	+++	P A	PK
Zoarces viviparus	+	P	MA
Platichthys flesus	+	P	MA
Amphibia			
Rana catesbeiana	>Italy	P	NA
Reptilia			
Mauremys caspia	–		ME
Chryemys scripta	+	P	NA
Aves			
Cygnus olor immutabilis (*)	++	P A	EU
Cygnus atratus	++	P	AU
Tadorna ferruginea	+	P A	PK
Alopochen aegyptiacus	++	P	AF
Anser indicus	+	P	AS
Branta canadensis	+	P A	NA
Anas platyrhynchus var. (*)	++	P A	EU
Aix galericulata	+	P	E-AS
Aix sponsa	+	P	NA
Oxyura jamaicensis	+	P	NA
Mammalia			
Fiber zibethicus	++	P A	NA
Myocastor coypus	+	P A	SA
Castor fiber (*)	+	P	EU/NA

[a] > = Not yet recorded, expected from neighborhood or by import. – = Import failed. * = No reproduction, stabilised by repeated import. + = Successful, local populations. ++ = Successful, widely distributed. +++ = extremely successful.
[b] P = local import by fishermen, aquarists, botanical and zoological gardens. K = canal connections. S = transport by ships. V = transport by birds. A = active migration following import.
[c] CE = Central West Europe, (*) locally autochthonous there, expansion supported by humans. EE = Eastern Europe. ME = Mediterranean Europe. PK = Pontocaspian region. AF = Africa. AS = South and Southeast Asia. EA = Central and East Asia. AU = Australia, New Zealand. NA = North America. SA = South America. MA = marine origin. ? = unknown.

are still present as the plants of the 'agriculture-steppe', as weeds, and as wild herb communities. At the same time animals invaded: the human commensals or the agriculture followers such as the cockroach (*Blatta orientalis*) and the house- and Norwegian rat (*Rattus rattus*, *Rattus norvegicus*). Birds like the house sparrow (*Passer domesticus*), swift (*Apus apus*), and the house redstart (*Phoenicurus ochruros*) were favoured[10]. The last traces of this type of expansion are some immigrations north of the Alps in the late Roman or early medieval periods: the carp (*Cyprinus carpio*), pheasant (*Phasianus colchicus*), the rabbit (*Oryctolagus cuniculus*). A very similar process can be observed today in Siberia, where the fauna is adapting in the wake of the introduction of agriculture in the north. This flora, the 'early human-supported immigrants', is named the 'Archaeophyta'[77]. The equivalent for animals, 'Archaeozoa', is not in use.

3) Import of plants for agriculture or gardens and animals for husbandry and menageries from all over the world to Europe (and later, world-wide) by human activities during the age of discoveries, from the 16th century onwards, continued during the age of colonialism. Imports showed a staggering expansion in the 19th and 20th centuries, in the wake of the Industrial Revolution and its manifold secondary effects on habitats. Again human activity became a determining factor in the change of flora and fauna. These last additions to flora and fauna include the recent immigrants, the 'neozoa' or neophyta (agriophyta, cf. ref. 77). The term 'neozoa' was introduced in 1972[59] in analogy to neophyta, to avoid the usually unfriendly and warlike terms such as newcomers, invaders, intruders, immigrants, strange animals . . .

This last development is especially important for the inland waters. They experienced incisive habitat changes (table 1), which initiated or fostered the immigration of water- or lowland plants as *Impatiens glanduligera*, *Reynoutria* spp., *Elodea* spp., *Azolla* spp. The aquatic neozoan fauna comprises some 80 species in central and western Europe (table 2).

Table 3. The general types of neozoism. Categories of human-induced or supported positive areal change by translocation. Adapted after Niethammer[85] and Nowak[87].

(1) Expansion. Not directly influenced by humans, frequently by habitat change. The subsequent categories are frequently followed by this type.

(2) Translocation. Non-intentional displacement of animals. E.g. *Craspedacusta sowerbyi.*

(3) Intended import. A species is brought purposedly into an area where it was never found before. The intention is to establish a free-living, self sustaining population. E.g. carp, rainbow trout, grass carp.

(4) Unintended import. A species is brought into areas where it was never found before, e.g. as a pet, as a farm animal, but the establishment of a free-living population was not intended. This was founded by escapees or by unintentionally or carelessly released specimens. E.g. domestic pigeon (*Columba livia*), coypu, muskrat.

(5) Re-introduction. Where a wild species has become locally extinct and the reasons for its disappearance, usually persecution and/or change of habitat, have been removed, it may be re-introduced. The intention is to regain the former original habitat which has been lost or 'thinned out'. There are many obstacles: the stock from which the new founders are taken should not be weakened; genetic conformity with the original population should be as close as possible; a success should be very likely. E.g. sea trout (*Salmo t. trutta*), stork (*Ciconia ciconia*), beaver (*Castor fiber*).

(6) Re-introduction for support of a weak autochthonous population, as (5), used by protectionists. The intention is to strengthen a local population or provide mates for single individuals, either relicts or occasionally solitary immigrants. E.g. European sturgeon (*Acipenser sturio*), pond turtle (*Emys orbicularis*).
A re-introduction is always an introduction if:
- there passed several generations, during which the species continued in its process of genetic adaptation.
- the stock for resettlement is taken far from the region which is intended to be re-settled. 'Far' means far enough to suspect a different genetic composition in the sense of a subspecies or local differently adapted population. In mammals like the bear, this distance may be 500 km or more; in invertebrates it may happen that the population of the next minor affluent is significantly different (e.g. populations of the mussel *Unio crassus*).

(7) Supporting natural migrations by active transport, e.g. eel (*Anguilla anguilla*), or by providing means such as fish ladders, e.g. salmon (*Salmo solar*). Guarding natural migration as in the American whooper crane.

(8) Dislocation of plant or animal populations within the natural area of a species to new, more suitable, less threatened places.

2.2. Neozoans of the European inland waters

Neozoans of the inland waters must be able to take advantage of humans as either active or passive vectors. They must also be able to take advantage of new or changed human habitats for settlement. Among the biocenotic changes caused by altered aquatic habitats are:
- Extinction of many species. Some prominent ones in central Europe are *Prosopistoma foliaceum* (Ephemeroptera), *Pseudunio sinuatus* (Bivalvia), the pond turtle *Emys orbicularis*, the European sturgeon *Acipenser sturio*[67,68].
- Introduction of opportunistic species which find suitable conditions after the environmental changes and take advantage of them, e.g. many filter feeders exploit the increased availability of solid substrate or food (bacterial suspensions, detritrus)[31].
- Immigration, neozoans (see below).
- Acculturation (see section 4).

2.2.1. Facts

Typology of neozoans. There are several categories of faunal change caused by human beings (table 3).

Origins and pathways. The inland waters of Europe have been invaded by animals from many other parts of the world (table 2). Origins, places, velocity, and geographical pathways of expansion are quite different, depending on the specific strategies of the species under consideration. An original human introduction was usually followed by an expansion of the species. Failures are frequent.

There are several zoogeographical categories:

1) Mediterranean fauna expanding to the north, mainly from southwestern Europe where the relatively dense hydrographical net of the French plains, connected since the 18th century by canals, provides an easy pathway to the Netherlands and to central Europe. There is also the Rhine-Rhône canal as a possible artificial pathway.

Examples: The amphipods *Orchestia cavimana*[57], *Echinogammarus berilloni*, the prawn *Atyaephyra desmaresti*[9,12,34,102,114,126], the snails *Physella acuta*[125], *Ferrissia wautieri*[62,63,103,109,129,131]. Some of them may already have passed by natural routes from the Mediterranean basin to the North Sea catchment basin, from the Rhône and Doubs to the Ill and Rhine by the Gates of Burgundy, making use of the changes of watersheds in the early Pleistocene[105]. This pathway has been documented for old natural immigrants such as the mussels *Unio mancus* and *Pseudunio sinuatus*, and the southern barbel *Barbus meridionalis*[69,83].

2) Species of the Pontoaralocaspian fauna, expanding by human activity from the tributaries of the northern Black Sea to the west, by way of the rivers Dniepr, Pripiet, Bug, Vistula, and Oder, and from there to the Midland Canal (Mittelland-Kanal), which gives access to the whole waterway system of central and western Europe[55,120].

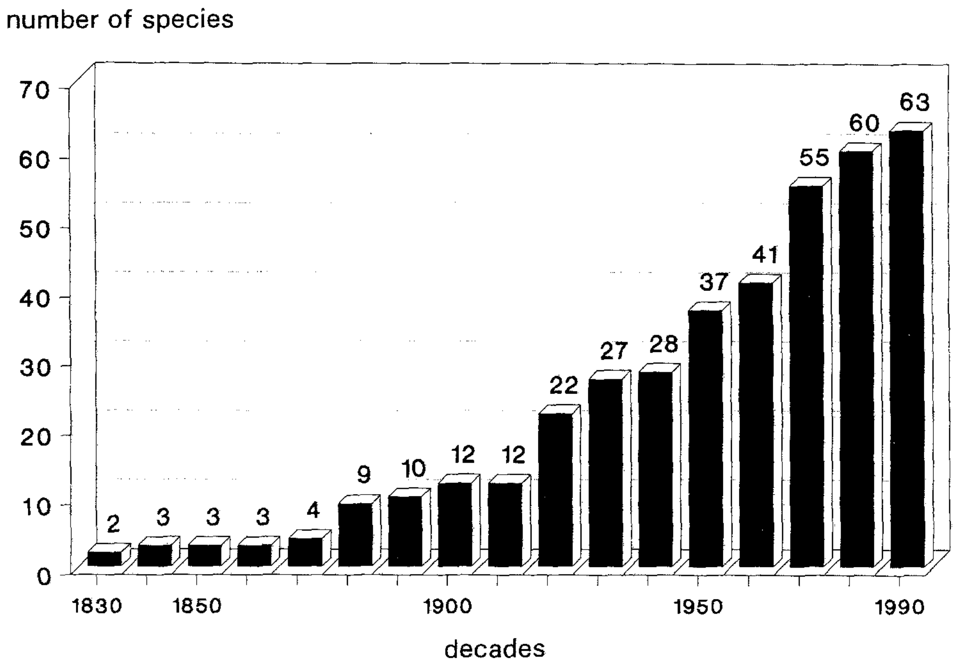

Figure. Increase in neozoan species in the Rhine shipway. The increase of species numbers is correlated to the growing human population density in the area taken into consideration. The visible steps are correlated to:
- Correction of rivers.
- Period of the acclimatisation mode 1880–1910.
- Change of riverbed by canalisation of the Upper Rhine after World War I.
- Transports from other continents during and after World War II.
- Increasing pollution with a maximum around 1970.
- Increase of imports by ship traffic, tourism, pet-trade.

Examples: the zebra mussel *Dreissena polymorpha*[72], the snails *Lithoglyphus naticoides*, *Viviparus viviparus*, the amphipods *Chaetogammarus ischnus*[33,43,54,55,113], *Corophium curvispinum*[11,49,50,81,112,128,130,132], the hydrozoan *Cordylophora caspia*[32], and the trematod *Bucephalus polymorphus*[18,19].

3) Imports from overseas to harbors, into estuaries or into brackish coastal waters.

Examples: the clams *Corbicula fluviatilis*, *Corbicula fluminea*[4,70,71], the crabs *Eriocheir sinensis*[45,88,89,91,92,124], *Rhithropanopeus harrisii*[7,79,90,121,123] and *Callinectes sapidus*[21,29,41,46,58,133].

4) Brackish water species invading inland waters, even pure freshwater basins.

Examples: the barnacle *Balanus improvisus*[78], the prawn *Palaemon longirostris*[127], the amphipod *Gammarus tigrinus*[8,14,35,37,94–100,110].

5) Deliberate import in many places, usually of animals for human use.

Examples: freshwater fish[75] such as rainbow trout (*Oncorhynchus mykiss*), carp (*Cyprinus carpio*), tilapia (*Tilapia zillii*), mosquito fish (*Gambusia holbrooki*)[6]; crayfish such as *Pontastacus leptodactylus*, *Orconectes limosus*, *Pacifastacus leniusculus*, *Cambaroides clarkii*[1,13]; fish food, such as the amphipod *Gammarus tiginus*; fur-producing mammals, such as muskrat *Fiber zibethicus* and coypu *Myocastor coypus*[85,86]. Most of these species came from the Arctic region, either in America or eastern Asia, which may explain their success in the western Palearctic Region.

6) Unintentional import in many places by aquaria, the animal trade, zoological and botanical gardens, establishing inadvertent centres of 'infection'.

Examples: the hydrozoan *Craspedacusta sowerbyi*[28]; the planarian *Dugesia tigrina*[42]; the leech *Hirudo medicinalis* (sometimes also the African *Limnatis nilotica*), which after the exhaustion of natural populations were imported from southeast Europe; the snails *Physella acuta* and *Potamopyrgus antipodarum*[104].

Events and chances. Some specific human events destroyed distribution barriers, and triggered a whole series of immigrations. Most famous is the Suez canal (1868). Less known, but nevertheless important for freshwater animals, is the Pripiet-Bug canal (1780), starting a wave of east-west expansions. The Rhine-Marne and Rhine-Rhône canals introduced Mediterranean fauna to central Europe. By way of the Main-Danube canal, the danubian amphipod *Dikerogammarus haemobaphes* recently invaded the Main river[108].

Increased human transport activities, e.g. during or immediately after wars, favoured immigration (fig.).

The first record of an immigrant at a specific locality is not necessarily the date of its first arrival. Except for intentional imports, the date of arrival has to be inferred. In many cases this is not identifiable. Thus, there are aquatic animals which may or may not be such early neozoans: e.g. the hydrozoan *Craspedacusta sowerbyi* and the kamptozoan *Urnatella gracilis*[28]. Only in recent years has the network of monitoring by science and water administration been sufficiently dense in central Europe to determine the time of arrival reliably.

Suitability and success. Most species displacements remain unnoticed since most of them fail. Successes may be estimated at 10%, the really successful and hence dangerous species may be 1%. The literature accords relatively scant notice to the great number of failures, immediate or deferred, or to the faltering successes, although these merit equal study[44]. Success is influenced at different levels and by different circumstances:

1) Autecology. Casual and intentional introductions involve quite different types of animals, the latter in freshwater being confined mainly to waterfowl, fish and a few species of edible crustaceans. In the invertebrates, successful neozoans are frequently characterised by:

a) small body size, suitable for phoresy. Transport by birds occurs frequently for very small, planctonic water animals; since most of them are widely distributed there is no proof of it. In macrozoobenthic neozoans there is evidence that *Potamopyrgus antipodarum* may be transported by waterfowl, besides other mechanisms of dispersal[104].

b) the presence of suitable asexual dispersal mechanisms or stages, e.g. body fragments in the hydrozoan *Cordylophora caspia*, the tiny polyp of the freshwater meduse *Craspedacusta sowerbyi*, or the planctonic veliger larvae of the mussels *Corbicula* spp. and *Dreissena polymorpha*.

c) parthenogenesis, e.g. in the snails *Melanoides tuberculata*[27,48,51,82,118] and *Potamopyrgus antipodarum* (cf. ref. 116).

d) a euryecous nature for some of the basic properties of waters, such as salinity, temperature, availability of oxygen[22–25,106,111]. Their reactions to pollutants are also important[117].

e) strong competition for substrate and sustenance.

f) rapid propagation (r-strategy); many have several generations per annual cycle, e.g. *Gammarus tigrinus*[36], *Corophium curvispinum*.

2) Population. The founding population is initially much smaller numerically than is ever found in its original environment. Population growth will start at a much lower number and is usually accompanied by expansion of range. Population growth and expansion continue, with high velocity. There is a common pattern to the population dynamics: an original mass distribution is followed by regulation to a lower population density.

3) Area. As the population starts with small numbers, so the new area is initially occupied only to a very small degree or at several spots which may then grow together. Natural habitats frequently have similar patterns for many species, due to a shared paleogeography or ecology. Newcomers may, in contrast, be identified by the fact that they occupy 'unnatural' areas, indicating that the process of settlement in all the potential habitats within a zoogeographical unit is not yet complete[120]. The potential area filled is a function of the time available.

4) Habitats. Waters with particular environmental stress, e.g. fast flow, low temperature, or voluminous water bodies (pelagial lakes) are less likely to be settled. Further obstacles are stable abiotic factors and the degree of geographic isolation.

In contrast, waters with unstable conditions and a rich variety of biochoriocenoses (e.g. potamocenosis) are more suitable for successful invasion. In riverine invertebrates, the immigrants usually succeed only if the autochtonous species are weakened or absent[26]. As an example, the recent expansion of the amphipods *Gammarus tigrinus*, *Gammarus ischnus*, *Corophium curvispinum*, and *Crangonyx pseudogracilis* into the Upper Rhine may be mentioned: after the chemical accident at Schweizerhalle in 1986, the populations of four autochthonous amphipod species disappeared from the main courses of the Upper Rhine. The newcomers, in the sequence in which they are listed above, took advantage of this situation, and now occupy most of the Rhine waterway sometimes in extremely dense populations.

5) Community ecology. Invaders usually have no chance to establish themselves in an intact biocenosis. This may be one of the reasons that in Europe the small rivers, rhithocenoses, are usually less settled by neozoans. Schellenberg[107] postulated that after the last glaciation, central Europe was deprived of many taxa of crustaceans. It was in this respect an unsaturated biocenosis. This made it easier for neozoans to succeed. The same may be the case with rivers deprived of part of their faunas by pollution: 'empty' Eltonian niches may then be occupied by newcomers.

2.2.2. Significance

Impact on the ecosystem. Whether or not we are happy about it, virtually all habitats in central Europe except for Alpine peaks are subject to intense human influence. This is especially true for the ecosystem of the lowland rivers (potamocenosis). The riverine biocenosis was altered by human activity during approximately the last 150 years more than by any other environmental impact since the end of the last glaciation some 10,000 years ago.

In Europe, the Rhine is, in this respect, the most international river. It harbors approximately 80 more or less successful imported species. About 50 of them are constantly found in the catchment area. In 1986 12% of the benthic animal species of the 850 km Rhine shipway were neozoans[73].

In terms of biomass, these species are even more important. The zebra mussel *Dreissena polymorpha* had the highest production rate among the neozoans in 1986, followed by the snail *Potamopyrgus antipodarum*, the amphipods *Gammarus tigrinus* and *Orchestia cavimana*. This range has since changed. In 1994, the clams *Corbicula fluminea* and *Corbicula fluviatilis* are on top, followed by the amphipods *Corophium curvispinum*, *Gammarus tigrinus*, and *Gammarus ischnus*.

Biocenotic effects are diverse. The neozoans feed on all types of organic matter, as grazers, filter feeders, scavengers, predators, parasites, etc.; they serve as vectors, substrates, and shelters; they provide food for fish, birds, and mammals. Prominent examples are:

The zebra mussel, *Dreissena polymorpha*, which is considered by some authors to be the most characteristic animal of central European river ecosystems, is, together with the snail *Potamopyrgus antipodarum*, an important food source for wintering and resting waterbirds on the northwestern pre-Alpine lakes[15,53,119]. *Dreissena* is now diminished by competition, mainly from the amphipod *Corophium curvispinum*[130].

In addition to single species the immigration of an organism complex has been also observed. *Dreissena polymorpha* arrived from eastern Europe in the Upper Rhine around 1840; it was followed by the pike perch (*Lucioperca lucioperca*) which was also imported from eastern Europe in 1888. Since 1960, a trematod (*Bucephalus polymorphus*) using the mussel as intermediary host was observed in the upper Seine and in parts of the Rhine catchment basin[18,19]. Another immigrating organism complex has been studied carefully in the brackish water of San Francisco Bay[16,84].

Practical meaning. Living resources sometimes need to be managed and protected, but an invader, qua invader, is neutral in nature; it is problematic only if it threatens human consumption of a resource, or the human desire to protect a certain autochthonous species or ecosystem.

Benefits from species' introduction. As human beings extended over the earth, so did the associated livestock, crop seeds, diseases and parasites. Humans are part of an 'organism complex'. Species which can provide food, forage, fibers, ornament, recreation and medical benefits have very often been deliberately introduced into new places.

Introduced species may be of direct use as mentioned above, or they may control crop insects, disease vectors, weeds and other organisms harmful to man. Imported plants may enrich or protect devastated habitats. In freshwater, by deliberately mixing up fish faunas, we enhance the possibilities for sport and food. We achieved an internationalised, degraded, uniform, but at least working, animal community in most lowland rivers.

In many cases benefits did not meet expectations. The fur of muskrats imported into Europe is less valuable than the same product of the original populations in America[85]. The mosquito fish (*Gambusia holbrooki*) in Europe turned out to prefer other foood to mosquito larvae, and became a strong food competitor for wild or cultivated fish stocks[6,72a].

There are some possibilities for pest control which have to be explored. The water lily *Eichornia crassipes*, a pest in many tropical waters, may be destroyed by Palearctic amphipods, which have no functional equivalent in the tropics[64].

Dangers of species' introduction. Translocations of species must be recognised as always having an element of risk. Newly arrived species may carry parasites and disease, prey upon autochthonous organisms, display toxic reactions, be highly competitive or may otherwise adversely affect native species or communities. They may be scientifically or esthetically undesirable. Some have been a nuisance through sheer overabundance.

Immigrants may adapt genetically to the new environment and develop properties different from those of their origin populations. New feeding habits may cause irreversible damage in areas into which they have been introduced. Dangers are not always predictable and problems have been common, especially with agricultural pests. On the other hand, complete extinction of autochthonous animals by imported competitors or predators is comparatively rare. It is frequently found only in island faunas, which suffered considerably from imported rats, pigs or goats.

In aquatic animals of inland waters negative effects are mostly negligible, except in the case of some powerful competitors, predators or diseases. Examples are mosquito fish (*Gambusia holbrooki*), sunfish (*Lepomis gibbosus*, *L. cyanellus*), trout perch (*Micropterus salmoides*) and grass carp (*Ctenopharyngodon idella*), but also autochthonous species, e.g. introduced sticklebacks (*Gasterosteus aculeatus*) may cause losses in breeding sites of Amphibia. In Switzerland, the lake frog (*Rana ridibunda*) expands at the cost of the pond frog (*Rana lessonae*) and their hybrid, the common green frog (*Rana esculenta*). The American bullfrog (*Rana catesbiana*) and the crayfish *Cambaroides clarkii* are considered to be undesirable in southern Europe, where they occur in rice plantations. The fungus *Aphanomyces* sp., introduced in the late 19th century from North America, perhaps together with a host, the crayfish *Orconectes limosus*[1,13], expanded from northern Italy to France and Germany; in 1928 it found its way to Scandinavia, 1979 to Spain, and between 1981 and 1991 it conquered the crayfish stocks in Turkey. This disease destroyed a large part of the European population of the common crayfish (*Astacus astacus*), and of the Pontian crayfish (*Astacus leptodactylus*) in eastern Europe and recently in Anatolia[65].

More than 150 years ago[74] the lamprey *Petromyzon marinus* invaded the Great Lakes in North America, causing losses in the populations of commercially valuable fish. The zebra mussel *Dreissena polymorpha* is well known as an obstacle in manmade canals, tubs and basins. The Chinese mitten crab *Eriocheir chinensis* threatens fisheries, especially in the Elbe river. But the latter examples also teach us that sometimes the influence and damage was initially overestimated. Recently, populations have decreased, and the view of the immigrant as a threat has changed.

Theoretical interest. The newcomers offer large-scale field experiments in many basic scientific problems of genetics and of population and community ecology. This opportunity has not been sufficiently used, although many scientists point to it. Most of the published work on immigration biology in the focal points of New Zealand, Hawaii, the eastern Mediterranean, and in European rivers to date is more descriptive than investigative.

3. Aquatic neozoans in other faunal regions

The import of allochthonous plant and animal species into river ecosystems is a world-wide phenomenon. Only a few examples are mentioned here.

In North America, scientific work on aquatic neozoans focusses on the Great Lakes area, where – compared with Europe – a small number of very successful animals is subject to intense study, e.g. *Dreissena polymorpha*, *Mytilopsis* sp., *Petromyzon marinus*. Florida has many newcomers, which have yet to be carefully studied.

In Africa, three of the most characteristic and commonest organisms of the Lower Nile are newcomers: the water hyacinth (*Eichornia crassipes*), the mosquito fish (*Gambusia holbrooki*), and the cattle heron (*Bubulcus ibis*). Recently the leech *Helobdella punctatolineata* and the snail *Helisoma* sp. were found near Cairo, probably escapees of scientific experiments[52].

Seawater animals were brought into inland brackish water in Iraq, e.g. the prawn *Palaemon elegans* from the Mediterranean Sea[47]. In Egypt, in the increasingly saline Lake of Qarun in the Fayum Basin, an artificial fauna was created by importing some 20 species of molluscs, crustaceans and fish from the Mediterranean Sea[56].

In Asia, even remote regions as Lake Baikal are infested with neozoans: on shallow banks everywhere shoots of the water pest (*Elodea* sp.) are found, imported from America, as well as the muskrat (*Ondatra zibethica*). Mainly by eutrophication of the upper water-layer of some bights, euryecous species (e.g. snails, leech) of the widespread siberian aquatic fauna supplant the autochthonous, and in this case also endemic, aquatic animals.

4. Acculturation

There is an overlap between the spreading out of neozoans and the genetic change of wild populations ('acculturation'), since neozoans tend to adapt genetically to their new environment and to become different from the original populations.

Frequently, animals which are imported deliberately into new environments originate from a domestic or artificially selected or raised stock. This applies to most of the fish species in table 2. In addition, the wild populations of these and many other fish species are artificially supported by broods from hatcheries, for example the green tench (*Tinca tinca*), gold fish (*Carassius auratus*), carp (*Cyprinus carpio*), pike (*Esox lucius*), trout (*Salmo trutta*), and also salmon; the latter in the state-promoted programme for the re-introduction of *Salmo salar*[3]. The frequent escapes from hatcheries have the same effect. This applies also to animals that rarely or never reproduce in Europe such as the rainbow trout and grass carp, and the non-fertile hybrids of sturgeon species.

Little is known about the effects of the permanent, uncontrolled introduction by sport fishermen or their organisations of fish species, which are indigenous but from different regions and belonging to different subspecies. This occurred on a large scale e.g. in Germany, where unsorted fish from the Danube and Balkan countries were imported for resettlement of artificial waters or as additional food for the predatory fish stocks.

Recently this change of fauna has been regulated by law. Most of these animals were accumulated in the large rivers, because these are the main drainages and provide a high habitat diversity. They are now genetic melting pots and experimental fields.

Wild populations in many cases are already endangered by interbreeding with (semi-)domesticated animals. Some examples are:

- the trout (*Salmo trutta fario*), mixing with escapees from fish farms, which differ very much in their ecophysiology from their wild ancestors.
- the mallard (*Anas platyrhynchus*) threatens to become a hybrid of domestic duck, by breeding with artificially raised and released game birds.
- the mute swan (*Cygnus olor*), which settles in increasing numbers on all types of stagnant waters in central Europe, and is for lay persons a symbol of nature and wilderness, descends in fact from semidomesticated park animals. In many cases it belongs to a genetic variety ('immutabilis') whose immature plumage is already white, instead of grey as in the wild population.

5. How to cope with the problem?

Faunal change by expansion of species into new territories cannot be undone. Its continuation and increase cannot be prevented, except in special cases. So, as in some diseases, there is no solution to the problem. There are only some ways and strategies to cope with it[80,93,116].

1) First, it should be considered to be a problem. Education of fishermen, hunters, farmers, foresters and animal lovers has to be focussed on the objective of keeping their pets, game or domestic stocks separate from wildlife.

2) Introduction of usable plants and animals (and their diseases) should basically be prohibited. This is not only a matter for customs or agricultural protection authorities; once in a country, these plants and animals should be subject to continued technical and scientific control and management.

3) Many species are brought in inadvertently. This is true for most of the modern immigrants into European waters. We cannot get rid of them, nor can we avoid a continuation of this migration. Some of them are even welcome as parts of the food chain (cf. *Dreissena polymorpha*). So it will be necessary to give up a defensive point of view, accept change and observe it. The fauna of the future will not just be influenced by human beings as it is today, but will be totally managed by them, and dependent on them.

4) No panics about neozoans. In the USA the freshwater clams *Corbicula* spp. from time to time cause apocalyptic headlines in the newspapers: 'Here come the clams'. The immigrating animals should not be stigmatised by defending a 'pure' autochthonous fauna; just as in society, this viewpoint is destructive.

5) Conservation strategies, aimed at optimising the protection of genetic resources, have to include an additional viewpoint. Up to now they have mainly protected the inventory of the ecological process, e.g. fauna, flora, habitats, but tend to ignore the process itself. They try, with a lot of energy input, to stabilise arbitrarily selected states of a local ecosystem, instead of enabling its further development and succession. This can only be accepted in special cases, but not as a general strategy. New concepts and goals have to be found, and a balance between allowing free struggle for life, and administrating and managing 'unadministrable' nature. Faunal exchange must be accepted as an inevitable part of the adaptation of the whole ecosystem to the increasing number and increasing activity of the human species. Thus, faunal exchange proves that ecosystems work.

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