Interactions between non-indigenous and indigenous crayfish species.

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ROUNDTABLE SESSION 2B

INTERACTIONS BETWEEN NON-INDIGENOUS AND INDIGENOUS CRAYFISH SPECIES.

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ABSTRACT

The main object of the present essay is to summarise some aspects underlying the interactions between non-indigenous (NICS) and indigenous (ICS) crayfish species. The discussion has been also extended to the effects exercised by NICS on the natural habitats they occupy. While doing research on the dyads NICS/ICS, one starting point is to extrapolate common traits that make NICS good invaders from the analysis of their biology, ecology and ethology and the comparison with indigenous species. A subsequent step is to switch attention to the understanding of the characteristics that make ecosystems less vulnerable to invasions and then to analyse both the complex interactions of invaders and target communities and the negative and positive impacts exerted by NICS on the occupied habitats. Examples from Sweden, Britain, and Italy have shown that NICS can replace the native species by a combination of several interacting mechanisms. Besides the transmission of the crayfish plague fungus, mechanisms into action include mostly competitive interference, but also diverse life history traits, recruitment failure, differential susceptibility to predation, and reproductive interference. It has been claimed that invasion theory is full of rules of thumb that, having no precise predictive powers, are thus useless to guide reliable public policy. The solution of the prediction problem requires an in-depth study of every potential invader and target community, trespassing the boundaries among disciplines and having a look at crayfish as a whole and not a single entity. The expectation is thus the return to precise and clear empirical generalisations that can be most useful to develop management strategies.

INTRODUCTION

In his investigation on Man-related extinctions, DIAMOND (1984, 1989) distinguished four sets of mechanisms inducing the decline of biodiversity, which the author collectively nicknamed the « Evil Quartet ». Besides overkill, habitat destruction and fragmentation, and chains of extinction, a fourth cause has been mediated by non-indigenous species that human intentionally or unintentionally introduced to new environments and that proceeded to exert negative impact into natural habitats.

Since ELTON's (1958) prediction of « huge changes in the natural populations balance of the world », several researchers maintain that Man's continued role in biological introductions may cause irreversible changes to the earth's biota in a relatively short time. In response to the threat from introduced species, biologists are issuing dire warnings. Popular science writers, environmentalists, and several ecologists have vilified non-indigenous species, defining them « malignancies in the environment » (LODGE, 1993). E.O. Wilson speaks of introduced species as « the stealth destroyers of the American environment » (McDONALD, 1999). DiCASTRI (1991) worries that invasive species « are likely to rise progressively to the most widespread and dominant proportion of terrestrial biota ». Many other biologists define those species introduced by humans as: biological

pollution (McKNIGHT, 1993), agents of extinctions (LODGE and HILL, 1994), components of global environmental changes (WILLIAMSON and FITTER, 1996) – perhaps even more significant than global warming (DAEHLER and GORDON, 1997), causes of the Macdonaldization of the biosphere (LÖVEI, 1997) or of a global McEcosystems (ENSERINK, 1999).

The core of the fast growing discipline of biological invasions is the recognition that at present exchanges of biota occur constantly and humans either unintentionally or purposively transfer 10^2-10^4 species per year to other countries (LODGE, 1993). According to the « tens rule » (WILLIAMSON, 1996), one introduced species in ten appears in the wild, one in ten of these become established, and one in ten of established non-indigenous species becomes a pest. Intentional introductions, although made to solve some local problems, may ultimately result in a further case of the Frankenstein Effect, *i.e.* attempts to improve nature may turn out to be a monster (MOYLE *et al.*, 1986).

One paradigm of a non-indigenous species becoming a pest is the zebra mussel, *Dreissena polymorpha*, that hitched a ride in ballast waters from the Caspian and Black Seas into much of Western Europe and then into all the five American Great Lakes. This species provokes economic costs, not simply due to the effects exerted on the invaded habitats: in USA $3.1 billion are spent in 10 years to clear blocked intake pipes (VITOUSEK *et al.*, 1996). In addition, economic resources are required to help affected ecosystems return to their « underlying element of organisation and constancy » (WAGNER, 1993).

The object of this essay is to summarise some aspects underlying the interactions between non-indigenous and indigenous crayfish species (hereafter abbreviated in NICS and ICS, respectively). The discussion will be extended to the effects exercised by NICS on the natural habitats they occupy.

PROPERTIES MAKING NICS GOOD INVADERS

For scientists seeking the ecological principles behind invasions, starting points are (1) the analysis of the biological, ecological and ethological facets of the species under study, (2) the comparison of the properties of a number of dyads non-indigenous/indigenous species, and (3) the deduction of common traits that make non-indigenous species good invaders. These commonalities help understand why certain non-indigenous species overrun natives while others do not (ENSERINK, 1999).

As compared to the ICS, the nearly cosmopolitan distribution of the red swamp crayfish, *Procambarus clarkii*, (HUNER, 1988) has been assigned to its:

1. ability to withstand environmental extremes (HUNER and LINDQVIST, 1995), such as dehydration (GHERARDI *et al.*, 2002a), salinity (HOLDICH *et al.*, 1997), extremes of temperature (GHERARDI and BARBARESI, 2000), and pollutants (GHERARDI *et al.*, 2002b);

2. polytrophism as the result of a generalist and opportunistic feeding behaviour (RENAI *et al.*, 2001);

3. rapid growth (PAGLIANTI *et al.*, 2001);

4. high fecundity (HUNER, 2001);

5. disease resistance (EVANS and EDGERTON, 2001);

6. wide plasticity in the biological cycle (GHERARDI *et al.*, 1999);

7. enlarged breadth of chemical information (HAZLETT *et al.*, 2002);

8. elevated competitive ability (GHERARDI and CIONI, 2002).

As the research goes on, the above list requires a number of comments and modifications. Firstly, NICS are said to be able to construct burrows or burrow systems, where they hide from predators and also hibernate and/or aestivate. The red swamp crayfish is classified a secondary burrower (HOBBS, 1942): its burrows are fairly simple, usually consisting of a subvertical passageway that may slope gently or descend in an irregular spiral, seldom are there more than one opening to the surface and there is rarely a second passageway toward the water table. Questions were addressed as to the extent of burrow occupation and the degree of faithfulness of the crayfish to one single burrow. The first answer was that usually a high percentage of burrows are occupied by one or more individuals - more than 90% in the rice fields of the Lower Guadalquivir (GHERARDI and BARBARESI, 2000). The second was that *P. clarkii* seems not to be faithful to a unique burrow, but occupies the first burrow found empty at the end of its wandering phase or foraging movements, as shown in diversified environmental scenarios (temporary streams in southern Portugal, ILHÉU *et al.*, 2000; irrigation ditches in Italy, S. BARBARESI, pers. obs.). Then, burrowing is not exclusive to NICS, but seems related not much to the ethogram of the species but to the characteristics of the substrate. A number of studies (*e.g.* GROW and MERCHANT, 1979; GROW, 1982; ROGERS and HUNER, 1985; HOBBS and WHITEMAN, 1991; BURRAS *et al.*, 1995) revealed that crayfish are able to construct permanent burrows in soils having appropriate granulometry and free water.

Secondly, ICS are also polytrophic, even if field studies revealed a certain degree of selectivity that reflects the results provided by preference experiments carried out in the laboratory (GHERARDI *et al.*, 2002c). Similarly, the spectrum of the NICS' diet - formerly assumed as decidedly wide - has been viewed as much narrower than expected after more detailed studies on these species' feeding habits (BARBARESI *et al.*, 1998).

A third statement that requires to be in part modified is that NICS can be in some instances agonistically subordinate to ICS. *Cherax destructor* was introduced from the mainland Australia into Tasmania in the 1960s, where it lives in syntopy with the endemic *Astacopsis franklinii* in at least one permanent stream (ELVEY *et al.*, 1996); surveys of this stream showed that the two species did not overlap since *C. destructor* was confined to a single open, slow flowing section, while *A. franklinii* was only found in shaded, rocky, fast-flowing sections. This appears one case of native species outcompeting the non-indigenous one; a further example was provided by GHERARDI and CIONI (2002), who showed in the laboratory that *P. clarkii* was mostly the loser when opposed to the river crab, *P. fluviatile*, reflecting the disjunct distribution of the two decapods recorded in the field.

EFFECTS EXERTED BY NICS ON THE OCCUPIED HABITATS

After any effort paid to describe the features that make a species a good invader, researchers have to switch their attention to the understanding of (1) the characteristics of ecosystems that make them less vulnerable to invasions and (2) the interactions of invaders and target communities.

On the one hand, a long-standing theory is that ecosystems rich in species, with their dense, interconnected webs of ecological relationships, can resist invasions, while those with fewer species usually succumb. For example, islands - which usually have fewer species than comparable areas of mainland - are often also the most heavily invaded. Notwithstanding, the theory of « island biogeography » failed in a number of occasions. For example, sampling 100 plots in nine natural grasslands, national parks and wildlands throughout the Central United States, it was shown that the number of non-indigenous

species was positively correlated with the number of native ones. Circumstances such as light, water and nitrogen favouring the wealth of native species also make the place attractive to newcomers (ENSERINK, 1999).

On the other hand, a variety of novel approaches to paleobiological analyses, microcosm experiments, and modelling studies are suggesting that history, chance and determinism interact to shape ever-changing communities. Together with the complexity of interactions between species and community, these factors make the ability to predict the fate and impact of an introduced species still elusive (LODGE, 1993).

Within the literature on crayfish, no studies have been devoted to the invasibility of ecosystems by NICS, while more interest was concentrated on the impact exercised by NICS on the occupied environments, as reviewed by NYSTRÖM (1999). Such an impact can be mediated both through direct effects (*i.e.* NICS prey on plants and animals and drastically reduce the latter abundance and diversity) and indirect ones (*i.e.* NICS destroy the microhabitats necessary to other species to reproduce and/or shelter). However, due to the system complexity, a clear distinction between direct and indirect effects appears often impossible to be ascertained.

The complex influence exercised by NICS on freshwater communities is exemplified by their action on macrophytes. Water macrophytes are claimed to influence water chemistry (*e.g.* water oxygenation) and biotic interactions within ecosystems. These are the primary source of littoral detritus and an important food source for many invertebrates, including crayfish, and vertebrates, including waterfowl, as well as they constitute the substrate of epiphytic algae that are important food items for many grazing invertebrates. For these reasons, macrophytes influence the distribution and abundance of invertebrates and vertebrates; besides their beds may affect predator-prey interactions, for example reducing fish predation on invertebrates. Thus, any decrease in macrophyte biomass and species richness would be expected to have negative effects on many animal species.

Several crayfish, including ICS, graze on adult macrophytes and feed on seedling stages, thus significantly reducing their biomass. This reduction may also due to non-consumptive cutting of the stems. Because of their selectivity related to easiness to handle, palatability and nutrient content, crayfish may also reduce the number of macrophyte diversity. By consuming macrophytes, crayfish may also affect water transparency, water turbidity increasing due to plankton blooms and resuspended particles. Although a number of studies suggest that NICS may have similar preferences for macrophytes as native crayfish, the former greater consumption and more rapid population development explain a more extensive impact on their biomass. Examples are provided by the studies on *Orconectes rusticus*, which had a higher consumption rate per biomass than the native *O. virilis* and *O. propinquus* (OLSEN *et al.*, 1991), and on *Pacifastacus leniusculus*, which consumed more *Chara* over a wide range of temperature than the native *Astacus astacus* (NYSTRÖM and STRAND, 1996).

To make the story of NICS' impact over the occupied habitats more intriguing, LODGE (1993) observed that the outcome of any introduction into a community not only depends on deterministic interactions of one species with the abiotic and biotic environment. The outcome depends also on the path by which the native community arose. Therefore, predictions about the outcome of colonisations at best will emerge only from focused studies on particular potential invaders and target communities.

While the scientific community appears more prone to negatively evaluate the effects of NICS on freshwater habitats, a number of issues have been raised in favour of the outcomes of these introductions, even if these pertain to a local scale only. Firstly, in the absence of native crayfish, NICS occupy vacant niches, constituting often the unique large macro-consumer within highly « stressed » habitats (GHERARDI *et al.*, 1999) and the

unique macro-grazer in Swedish and Finnish lakes (ACKEFORS, 1999) that help keep water bodies clear from the overgrowth of water plants, as well as recycle energy and inorganic and organic material. The second claim in favour is that either rare or threatened birds and mammals found a new, abundant prey and increased the size of their populations in some areas. Though no quantitative study has been yet made, the appearance of high densities of *P. clarkii*, has been considered responsible for the increase in the number of avian species, like the Ardaeidae *Botarus stellaris*, *Egretta garzetta* and *Ardea purpurea*, together with cormorants, in some European areas, as in the Ebro region (Spain) and Massaciuccoli Lake (Tuscany) (BARBARESI and GHERARDI, 1997). Third, under a socio-economic perspective, the introduction of NICS contributed to (1) the restoration of traditional habits, *e.g.* fishing for crayfish in Sweden, (2) economic benefits for local crayfishermen, *e.g.* Spanish netsmen, (3) diversification of agriculture to include astaciculture, *e.g.* crayfish farmers in Britain and in Spain, and (4) increased trade between countries inside Europe as well as between European countries and countries outside Europe (ACKEFORS, 1999).

REPLACEMENT OF INDIGENOUS SPECIES

Examples from Sweden, Britain, and Italy have shown that NICS can replace the native species by a combination of several interacting mechanisms. On the one hand, some European NICS are the vector of the crayfish plague fungus (they may harbour the fungus within their body in a chronic or latent infection, HUNER and LINDQVIST, 1995). Even when NICS and ICS do not live in syntopy, a high risk of diffusion of this fungus is represented by the movement of fishermen equipment, carrying spores through different streams.

On the other hand, the first direct mechanism of replacement is competitive interference, here defined as the competitive behaviour displayed by the « stronger » species, which actively interferes with the « weaker » species' access to a resource, thus directly decreasing the survivorship of the latter. The advantage of the stronger species could be the faster acquisition of a shelter that constitutes the « principle resource bottleneck » in crayfish populations (HOBBS, 1991). Typically, NICS outcompete native crayfish, as extensively reported in the literature (CAPELLI and MUNJAL, 1982; SÖDERBÄCK, 1991; HAZLETT *et al.*, 1992; GHERARDI and CIONI, 2002), but their dominance is not always size-dependent contrary to the predictions provided by the game theory (at least, in *P. clarkii vs A. pallipes*, GHERARDI and CIONI, 2002; the opposite occurs in *Pacifastacus leniusculus vs Austropotamobius torrentium*, VORBURGER and RIBI, 1999). Notwithstanding, crayfish size is a good indicator of the dimension of their weapons, *i.e.* chelipeds, that act as Resource Holding Potentials (MAYNARD SMITH and PARKER, 1976).

However, competitive interference is not the unique mechanism into action: other equi-probable mechanisms play a relevant role in species replacement, as listed by SÖDERBÄCK (1995). These include diverse life history traits (higher individual growth rates, earlier sexual maturity and higher fecundity) (HUNER and LINDQVIST, 1995; GHERARDI *et al.*, 1999), recruitment failure (SÖDERBÄCK, 1995), differential susceptibility to predation (BUTLER and STEIN, 1985; LODGE *et al.*, 1986; DiDONATO and LODGE, 1993; MATHER and STEIN, 1993; GARVEY *et al.*, 1994), and reproductive interference (CAPELLI and CAPELLI, 1980; BERRILL, 1985; BUTLER and STEIN, 1985; SÖDERBÄCK, 1994; HOLDICH *et al.*, 1995).

And in some instances (LODGE *et al.*, 1986), competition models seem to be inadequate to explain the dynamics of the crayfish assemblage; the outcome of interspecific interactions is variable and probably affected by other community structuring forces such as predation, parasitism, and disturbance.

CONCLUSIVE REMARKS

As underlined by SHRADER-FRECHETTE (2001), invasion theory is full of rules of thumb, such as « non-indigenous species are likely to become invasive and outcompete natives, as evidenced by the degree to which non-indigenous species are implicated as a major cause of extinctions » or « all things being equal, non-indigenous species will be successful colonisers if they have high dispersal rates, or large native ranges, or a broad diet ». Because these rules of thumb do not have precise predictive power, it is impossible to use them to guide reliable public policy.

In accordance to this perspective, the solution of the prediction problem requires an in-depth study of every potential invader and target community (LODGE, 1993). As a consequence, it seems necessary to trespass the boundaries among disciplines and have a look at crayfish not as a physiological or psychological or pharmacological entity but as a whole. To replicate studies on the dyads NICS/ICS would help discover empirical generalisations and, in addition to a top-down account of explanations, a bottom-up approach will be needed for detailed natural history information. The expectation is the return to precise and clear empirical generalisations that can be most useful to develop management strategies.

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