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Are aliens threatening European aquatic coastal ecosystems?

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Abstract Inshore waters of European coasts have accumulated a high share of non-indigenous species, where a changeable palaeoenvironment has caused low diversity in indigenous biota. Also strongly transformed modern coastal ecosystems seem to assimilate whatever species have been introduced and tolerate the physical regime. Adding non-native species does not have any directional predetermined effects on recipient coastal ecosystems. The status of being a non-native rather refers to a position in evolutionary history than qualify as an ecological category with distinct and consistent properties. Effects of invaders vary between habitats and with the phase of invasion and also with shifting ambient conditions. Although aliens accelerate change in European coastal biota, we found no evidence that they generally impair biodiversity and ecosystem functioning. More often, invaders expand ecosystem functioning by adding new ecological traits, intensifying existing ones and increasing functional redundancy.

Keywords Biodiversity · Non-indigenous species · Invasive species · Introduced species · Coastal waters · Ecosystem functioning · Xenodiversity

Introduction

Public media reported on ‘killer algae’ spreading through the Mediterranean or on ‘horrific’ giant Kamchatka crabs invading northern European coasts. Since

the book *Ecological Imperialism* (Crosby 1986) opened the gate, the treacherous ground between objective ecological science, ethics and hostility to foreigners is widely discussed (Simberloff 2003). From an ecological perspective, many questions arise: are European coastlines also facing the disasters that introduced species have inflicted on island ecosystems? How do introductions of species change coastal biodiversity and ecosystem functioning? Are aliens threatening European coastal ecosystems or do they strengthen ecological functions? Do they impair or improve the ecological goods and services to coastal societies? How to weigh the good, bad and ugly impacts of aliens? How much effort to stem the tide of exotic immigrants is justified?

Although precaution is the obvious choice in the face of uncertainty, science is asked to provide a comprehensive scientific basis on the effects of alien species at European coasts. However, a consensus view on these questions is not yet in sight. We are still primarily in a phase of assessment (Leppäkoski et al. 2002) rather than measuring and evaluating the effects of species introductions in the ecological web of European coastal ecosystems. The aim of this paper is to conceptually advance our research efforts on the effects of species introductions, and to stress that we have to keep this research free of hidden assumptions. In the following, we first summarize the invasibility of European coastal habitats and then discuss the multiple effects that invaders can have on recipient biota, and finally conclude with what we think is the most appropriate perspective on the effects of introduced species on European aquatic coastal ecosystems based on current knowledge.

The study of bioinvasions is a rapidly expanding field, which intensively interacts with the public and thus terms often shift their meaning or get blurred. The relevant terminology was discussed in several recent papers (Boudouresque and Verlaque 2002; Elliott 2003; Colautti and MacIsaac 2004; Occhipinti-Ambrogi and Galil 2004) which we used to define the technical terms in this text: ‘Introduction’ refers to a deliberate or accidental transfer or release of organisms into the open environ-

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ment by human activities across natural barriers of dispersal, while ‘Invasion’ is used for any process of colonization and establishment beyond a former range, particularly in which a species plays a conspicuous role in the recipient ecosystems. While introduction refers to the movement of organisms, invasion addresses to the occupation process with ecological interactions and evolutionary changes. In the ecological context we study the *effects* that invaders may have on recipient biota and habitats, while we avoid the term *impact* unless the consequences for human interests are considered. Taxa are regarded as *non-indigenous* (non-native, introduced, alien or exotic) when their arrival in a region since the Neolithic (6,000 BP) has been mediated or facilitated by humans.

Hostile or hospitable coasts?

Approximately 450–600 species (numbers vary in particular because of uncertainty with regard to establishment of introduced non-indigenous species; Streftaris et al. 2005; Gollasch 2006, in press) known to have been added to the European coastal aquatic flora and fauna through shipping, canals, aquaculture and aquaria have generally increased species richness, particularly in the previously species-poor brackish water seas and estuaries (Paavola et al. 2005; Wolff 2005; Nehring 2006). On the other hand, species compositions in coastal biota within Europe and all around the globe are becoming more similar. The net effect is an increasing diversity or *xenodiversity* (i.e. structural and functional diversity caused by non-native species, *sensu*; Leppäkoski and Olenin 2000) of the European coastal waters, which may be traced at all levels of biological organization from genes to communities and biotopes (Table 1). The increasing xenodiversity leads to an advancing sameness and a global sprawl of universal species, a phenomenon termed anthropogenic homogenization (McKinney and Lockwood 1999; Olden et al. 2004; Olden and Poff 2004).

Compared with the almost 30,000 listed in the register of European marine species (Costello et al. 2001), the share of aliens is 2%, or 2.5% when taxonomic groups not covered consistently are left out. Numerically this may seem almost negligible. However, while from off-

shore species-rich benthos almost no introduced species are known, their numbers increase towards the shore and attain a maximum in estuaries, lagoons, harbours and canals where species richness tends to be low. Roughly, ratios for non-native to native species may be 1:40 in European marine waters, 1:20 at open coasts and 1:5 in estuaries or lagoons (see Reise et al. 1999; Wolff 2005; Nehring 2006). More than half of all alien species are benthic invertebrates and macroalgae rank second in numbers (Streftaris et al. 2005; Gollasch 2006).

However, we should keep in mind that any such numbers and ratios are biased by our incomplete knowledge of the small meiobenthic organisms. Of these we usually do not know how many species there are, what geographical ranges they have and whether we can extrapolate from the better known larger organisms to the little ones. Further, transoceanic seafaring started much earlier than biological science, and a reconstruction of introductions during the distant past still needs to be done.

Compared with the northern Pacific, European coastal waters have fewer species (see Vermeij 1991). Presumably this is the outcome of a relatively turbulent environmental history. The Mediterranean Sea dried up in the late Miocene. Several glacial periods severely struck Europe in the last 2 million years. Sea level was up to 150 m lower than today at the last glacial maximum 18 ka BP. Mediterranean waters began to enter the freshwater Black Sea 9–7.5 ka BP (Kaplin and Selivanov 2004), and the Baltic Sea turned brackish 7 ka BP (Harff et al. 1995). A medieval climate optimum from 950 to 1310 A.D. and a cooling phase from 1450 to 1850 A.D. are now followed by a warming Anthropocene and decadal North Atlantic climate oscillations preclude environmental stability (Meincke et al. 2003). Recovery from such past disturbances is still ongoing; many species shift their ranges and community compositions change accordingly. In this process it makes no difference whether immigrants stem from adjacent waters, have crossed oceans with ships or continents through canals. In the wake of this overall immigration and emigration process, immigrants that stem from adjacent waters and those that have been introduced from distant waters may be assimilated likewise by the recipient biota without any general difference.

Table 1 Xenodiversity at different levels of biological organization

Level	Effect	Example
Genetic	Hybridization and addition of genetically modified organisms	<i>Crassostrea virginica</i> (Lyu and Allen 1999); <i>Fucus evanescens</i> (Coyer et al. 2002)
Species	Addition of alien species, elimination of native species	<i>Caulerpa taxifolia</i> (Verlaque and Fritayre 1994); <i>Cercopagis pengoi</i> (Antsulevich and Valipakka 2000)
Functional community	Emergence of novel or unusual functions, changes in community structure, alterations of food webs and ecosystem functioning	<i>Marenzelleria neglecta</i> (Olenin and Leppäkoski 1999); <i>Mnemiopsis leidyi</i> (Volovik 2000)
Biotope	Habitat engineering, encrusting of solid objects, changes in bottom microtopography, alteration of biotope	<i>Dreissena polymorpha</i> (Karatayev et al. 2002); <i>Crepidula fornicata</i> (Montaudouin and Sauriau 1999)

In estuaries, embayments and closed seas many anthropogenic changes (i.e. nutrient enrichment, habitat transformations, loss of top consumers) may come together creating novel conditions where indigenous species barely have any adaptive advantage over introduced aliens. Here the terminology of native and non-native species has partly lost its meaning. All are strangers in a strange environment, and little resistance to invaders can be expected. We assume that the invasibility of European inshore aquatic biota is high because of low species richness combined with strong anthropogenic change. High invasibility applies to ‘native’ species (e.g. massive developments of several green algal taxa in eutrophicated lagoons; Fletcher 1996) and to aliens (Occhipinti-Ambrogi and Savini 2003) likewise.

The more invasions that have already occurred in a habitat the more chances there are provided to make a living to further immigrants (invasional meltdown *sensu*; Simberloff and von Holle 1999; Riccardi 2001). For example, the parasitic rhizocephalan *Heterosaccus dollfusii* could only become established after its host, the swimming crab *Charybdis longicollis*, had pathed through the Suez Canal and became abundant in the eastern Mediterranean (Galil and Zenetos 2002). Most invaders are less specific in their requirements. Invading suspension feeders may share resources with natives and differences between intra- and interspecific competition for food may not arise (Olenin and Daunys 2005). In the North Sea, introduced Pacific oysters *Crassostrea gigas* managed to establish by settling on top of highly crowded mussel beds (Reise 1998). Apparently food was not limiting and it only counted who was above. Whether oysters will eventually displace the mussel *Mytilus edulis* will probably depend on differential recruitment success rather than resources (Diederich et al. 2005; Nehls et al. 2006). Resistance of native biota against introduced species may be confined to direct interference competition or predaceous interactions. However, only reverse cases where non-natives displace natives have been reported (e.g. the displacement of two native by four non-native gammarid amphipods in Vistula lagoon in the southern Baltic; Grabowski et al. 2006, in press). It may be concluded that European inshore habitats are generally hospitable and readily assimilate invaders because (1) past and ongoing disturbances keep species assemblages open and (2) native species are relatively few.

Phases and places of invasion

Invasions begin with one or more incidences of arrival, and then an establishment of a small group of successfully reproducing individuals, and these may proceed into an expansive phase, which eventually will turn into a phase of adjustments (Fig. 1). It is important to know in which phase of an invasion process an evaluation of effects is attempted, particularly in comparisons with the same invader in other regions or vice versa. Research

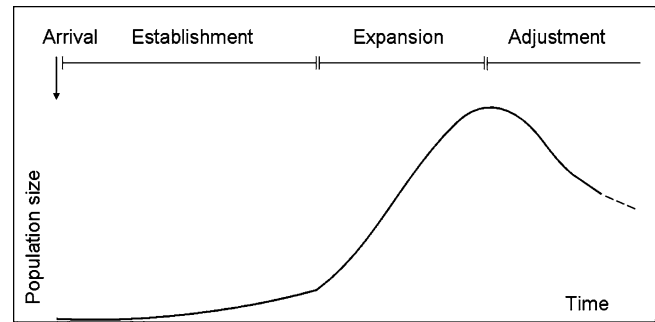


Fig. 1 Phases of invasion

should focus on initial phases to identify limiting factors, which prevent an introduced species from entering expansion phase. This may help to make predictions. Comparisons with a species’ performance in its native region and in other recipient regions are particularly elucidating (Grosholz and Ruiz 1996; Parker et al. 1999).

In the course of an expansion phase, effects on recipient biota and habitats will transcend from weak to moderate to strong. Proxies for effects of invaders on native biota may be changes in the abundance and biomass of other species, the proportion of shared resources and displacement or attraction of other species including introduced ones. The latter may enter expansion phases almost immediately after arrival, for example, in the case of the razor clam *Ensis americanus* in the coastal North Sea which has built up high population stocks along the coast during just a few years following initial arrival (Armonies 2001). Other invaders may be ‘sleepers’ for decades and then expand after changes in conditions have occurred. For example, the American slipper limpet *Crepidula fornicata* arrived with introduced oysters in the North Sea in 1887, remained of moderate abundance for long and now is proliferating because of milder winters (Thieltges et al. 2004).

An expansion phase sooner or later comes to an end, followed by a phase of stasis or decline, which may be termed adjustment phase. There are numerous examples for such “boom and bust” phenomena in invasions but often the actual cause of decline has not been investigated (Table 2). Either the resources that allowed for a rapid population expansion are fading away or more

Table 2 Boom and bust of invaders in European coastal waters

<i>Marenzelleria viridis</i>	Wadden Sea	Essink and Dekker (2002)
Polychaeta		
<i>Marenzelleria neglecta</i>	Baltic Sea	Zettler et al. (2002)
Polychaeta		
<i>Rapana venosa</i>	Black Sea	Gomoiu et al. (2002)
Gastropoda		
<i>Mnemiopsis leidyi</i>	Black Sea	Gomoiu et al. (2002)
Ctenophora		
<i>Dyspanopeus sayi</i>	Venice lagoon	Occhipinti-Ambrogi (2002)
Decapoda		
<i>Tricellia inopinata</i>	Venice lagoon	Occhipinti-Ambrogi (2002)
Bryozoa		

and more consumers and pathogens become focussed on the invading population. Also evolutionary responses to the invader may soon take place in a recipient community (Cox 2004).

In addition to the temporal phase of an invasion, effects on recipient biota also vary with location. Epibiota which colonized the Japanese seaweed *Sargassum muticum* in the North Sea were very much alike to that on the structurally similar native *Halydris siliquosa* on a rocky shore, while on a sandy shore the epibiota on *S. muticum* were more diverse and different from that of *Fucus vesiculosus*, the only other habitat providing but structurally simpler algae at that site (Buschbaum et al. 2005). Although total species richness of epibiota on the introduced seaweed was equivalent in both the locations, the effect on biodiversity was redundant on the rocky shore but facilitative in the sedimentary environment.

The American slipper limpet, referred earlier, has formed dense carpets in the shallow subtidal of the French Atlantic coast with cascading effects on other species and the food web (Blanchard 1997; Chauvaud et al. 2000; Montaudouin and Sauriau 1999), while in the German North Sea occasional cold winters have limited such a development until recently (Thieltges et al. 2004). Thus, the effects of an invader cannot be generalized but depend on the phase of invasion, the recipient biota and current habitat conditions.

Practice and prejudice

Identifying the manifold effects that alien invaders have or may have on recipient biota and habitat properties is a challenging task and more complex than it may seem at first glance. In addition to the problems related to invasion phase and place discussed previously, effects of invaders on other species may be more complex than generally assumed since they may not only be negative but also positive for native biota. Proceeding with the example of the American slipper limpet, experiments showed a negative effect of *C. fornicata* epigrowth on mussel growth and survival (Thieltges 2005a) while at the same time, the attached slipper limpets reduce star fish predation by enhancing predation effort (Thieltges 2005b). There are also other positive effects known from this species (Thieltges et al. 2006, in press).

Another pitfall in invasive species research can be exemplified with this introduced species. Ever since, slipper limpets had a very bad reputation. Oyster farmers in Europe regarded them as an 'oyster pest' and spent much effort to get rid of them (e.g. Orton 1927; Korringa 1951). However, when Montaudouin et al. (1999) conducted experiments they found no evidence for *C. fornicata* to impair growth of oysters, although it cannot be excluded that in dense assemblages siltation and other indirect inhibitions may occur. The example of the slipper limpet highlights the complexity of assessing and evaluating effects of an introduced species

on recipient biota and the problem that current evaluations often rest on prejudice and not on science. Non-natives may have negative effects but also neutral ones or may even be beneficial to native species in that they do not differ from the multiple interactions native species exert on each other in their communities.

A further complication arises because invaders cannot be regarded as stable genetic entities nor does this apply to the native biota they are interacting with. Invasions may speed up the evolutionary play for example by hybridizing with related natives (Cox 2004). A spectacular example occurred in a British salt marsh where the cordgrass *Spartina alterniflora* was accidentally introduced from North America. It hybridized with *S. maritima*, which either is a European native or itself introduced earlier from Africa. Initially the hybrid was sterile but it became fertile by autogenic chromosome doubling. The new separate species named *S. anglica* began to spread rapidly and partly displaced *S. maritima* (Gray et al. 1991; Thompson 1991). It also colonized bare mud flats and therefore was welcomed as a pioneer plant facilitating sediment accretion. To help in land reclamation *S. anglica* became intentionally introduced to other coasts in Europe and beyond. *S. anglica* profoundly altered native saltmarsh vegetation, invaded seagrass beds and altered the composition of macrobenthic fauna. Often a monotypic belt of cordgrass was formed but dynamic mosaics with the native vegetation also developed in late succession (Reise et al. 1999). When in the wake of nature conservation, draining and grazing of salt marshes was banned, *S. anglica* began to spread again (Stock et al. 2005). More than a century after the introduction of *S. alternifolia*, the invasion is still in progress at its northern range, possibly promoted by warmer temperatures in spring (Loebl et al. 2006, in press). This sequence of contingent events of accidental introduction, hybridization and genomic doubling, intentional introductions, nature conservation and climate change demonstrate the limited value of a snapshot analysis on the effects that invaders may have on recipient coastal ecosystems.

In addition to ecological and evolutionary effects, the implications for the goods and services also need to be considered, which may not be the same for all societal groups. For example, the recent invasion of Pacific oysters in the European Wadden Sea turns into a disaster for the mussel fishery, impedes touristic bare-foot walking across tidal flats because of razor-sharp shells but may give rise to more intensive oyster farming.

Ecosystem functions and fictions

There is no question that alien invaders have profoundly altered coastal water ecosystems in Europe and are displacing native species. However, there is no evidence yet that aliens have caused large-scale extinctions in recipient coastal biota (see Leppäkoski et al. 2002; Wolff

2000), and more research is needed to clarify this crucial relation (Gurevitch and Padilla 2004). Particularly in coastal aquatic ecosystems, an equilibrium perspective in the sense that if some species come in then others have to get out, finds no support.

Contrary to the general assumption of invaders negatively affecting native biota, aliens in coastal waters often seem to play a beneficial role in ecosystem functioning. Non-native species may often be complementary to natives in their patterns of resource use. For example, the often observed establishment of alien suspension feeders is strengthening the coastal biofilter and increases benthic biomass production, for example, *Dreissena polymorpha* in brackish lagoons (Daunys et al. 2006, in press; Orlova et al. 2006, in press) and *Ensis americanus* along coasts of the North Sea (Armonies and Reise 1998). Non-native species may be also complementary to natives in their responses to environmental change. The alien barnacles *Balanus improvisus* and *Elminius modestus* supplement and extend the native barnacle range into brackish water where none occurred before (Lawson et al. 2004; Kotta et al. 2006).

New ecological functions have also been introduced to European coastal ecosystems with alien species (Olenin and Leppäkoski 1999). Before the Chinese mitten crab *Eriocheir sinensis* arrived, there was no crab migrating upstream in European rivers and then back into the sea to shed their larvae (Gollasch 1999). The American slipper limpet is the first suspension feeding gastropod in Europe employing a mucus net (Werner 1953). Only the Japanese seaweed *S. muticum* began to provide a structurally complex habitat to an epibiotic assemblage in the shallow subtidal sedimentary bottoms of the North Sea (see earlier para).

With many other non-natives, which became established but never attained high abundances, it may be attributed to our limited knowledge that we categorize these as functionally redundant because of an assumed similarity to some natives. Taken together, complementarity, novelty and redundancy all may contribute to functional diversity of recipient ecosystems. Functional diversification has been suggested to improve adaptability to environmental change (Hooper et al. 2005). However, the species-specific functional characteristics of invaders may have more influence on recipient ecosystem properties than any numerical aspect of xenodiversity. Introduced species as such do not constitute a threat but to predict which species among the immense spectrum of potential introductions may become problematic is an endless and non-promising task. Therefore, precaution is advised as species introductions are irreversible and accumulate over time.

In coastal waters, no control on aliens is feasible which would not also harm other components of the biota once an invasion process is underway. Policy and management should focus on vectors of introduction and prevent immigrations of species, which are suspected to impair the goods and services that the European coastal biota could provide.

Conclusions

European continental coastal waters are natural corridors of dispersal with continuously changing species assemblages. Further, European inshore environments tend to have a long history of human interferences, which have caused changes in habitats and biotic composition. Adding non-native species to the resultant fortuitous assemblages of the so-called natives may not have any directional predetermined effects on recipient coastal ecosystems. The status of being a non-native refers to a position in evolutionary history but does not qualify as an ecological category with distinct and consistent properties. However, the next invasion may be the first with profound consequences on coastal ecosystems and precautionary measures should be taken.

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