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ScienceDirect
Marine Pollution Bulletin 55 (2007) 323–332
MARINE POLLUTION BULLETIN
www.elsevier.com/locate/marpolbul

Introduced marine organisms as habitat modifiers

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Abstract

Introductions of non-indigenous species (NIS) are mostly discussed through their impact on biodiversity. However, NIS can also act as ecosystem engineers, influencing the habitat itself, positively or negatively, directly or indirectly, which should be included when making risk assessments. Special concern should be given to changes in ecological services provided by the ecosystem. Physically, NIS may affect the substrate itself, or alter habitat architecture, indirectly influencing water movements, sediment accumulation, and light conditions. Chemical changes brought upon by NIS occur both on small and large scales, some having positive effects on ecosystem services, others can perturb epibionts. Furthermore, NIS may negatively affect natural resources, aquaculture or create fouling communities, all resulting in a negative impact on economics. However, if removed, already established NIS can be used as bioremediators, having a positive effect on different ecosystems. Using NIS for habitat management may be economically profitable, but could affect the habitat adversely.

Keywords: Aliens; Ecosystem engineers; Foundation species; Habitat architecture; Ecosystem services; Management

1. Introduction

1.1. General background

Non-indigenous species (NIS), once having become established, have caused much concern, since they are almost impossible to eradicate, especially when occurring submersed, and even worse when present as only small, viable algal fragments or microscopic stages (e.g. Ceccherelli and Piazzi, 2005; Conklin and Smith, 2005; Glasby et al., 2005; Hewitt et al., 2005; Nyberg and Wallentinus, 2006). The reason for concern is the ability of NIS to change adversely the ecosystem they arrive in. The consequences often are due to ecological interactions through e.g. competition for resources, including place to settle and spawning grounds, grazing or predation, trophic cascading effects, or filling up empty niches. However, many NIS can also have a severe impact by changing the habitat itself, physically or chemically, directly or indirectly. In such cases, it is even more difficult for the native inhabitants to survive and flourish, especially if NIS will more or less monopolize the area. Many marine plants and macroalgae, but also several sessile invertebrates, have a profound architectural importance for the ecosystem structure. Hence, unintentional or intentional introductions of such species may play a fundamental role, especially when they establish in high abundances. In fact, they may also have a positive impact, by providing places for shelter in previously barren areas or increasing habitat diversity and spatial heterogeneity. In this review, we will give examples of different scenarios, where marine and brackish introduced organisms have been involved in habitat modifications. The speed, with which a habitat is changed, is also coupled to the stability and resilience of the ecosystem, and the impact can also be on different scales in space and time. It should also be remembered that an ecosystem may have more than one phase of equilibrium (Holling et al., 1995; Folke et al., 2004), and if reaching a new phase (either brought upon by a NIS or by other processes), return to the former state may be almost impossible. In this paper we will also incor-

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0025-326X/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.marpolbul.2006.11.010

porate scenarios, when organisms, through habitat modifications, could directly influence economics, mostly negatively, while effects of intentional introductions for aquaculture and fisheries will not be discussed (as assumed by definition economically positive).

1.2. Biodiversity aspects and ecosystem engineers

The impact of NIS on biodiversity has been recognized since long. Although, at a first glance, one could argue that NIS establishment would increase species richness, the opposite effect is mostly the case, resulting in what can be called biological pollution. That is because many NIS tend to become invasive, in the sense of having negative ecological and/or economical impact (e.g. Boudouresque and Verlaque, 2002). In the wider definition of biodiversity (i.e. including the relative abundances of different species), this would mean decreased diversity and evenness of the system. Such impact, for which there are copious amounts of references, is often reached by being a superior competitor for resources, or by being an efficient predator/grazer, resulting in decreased populations of prey species.

However, also influences on the habitat itself, either directly or indirectly, could in a longer perspective drastically decrease the biodiversity. Such species, termed ecosystem engineers, have been considered keystone species for the ecosystem (e.g. Jones et al., 1994, 1997; Crooks, 2002; Cuddington and Hastings, 2004; Wright and Jones, 2006). This has mainly been discussed when such species, which also have the ability to create more complex ecosystems, decrease drastically, e.g. by over-fishing (Coleman and Williams, 2002). However, the establishment of a NIS, acting as an ecosystem engineer, could imply a significant impact on the ecosystem. Thus, habitat modifications, and the processes driving them, also must be considered in management and control efforts. Bruno et al. (2003) used "foundation species" for organisms that change the habitat by facilitating establishment of other species, and pointed to their importance in restoration, with *Spartina alterniflora* Loisel. as an example, which elsewhere is an invasive species.

1.3. Ecosystem services

Many recent studies in ecosystem ecology have focused on the importance of the ecological services and goods provided by the ecosystems studied (e.g. Folke et al., 1996, 2004; de Groot et al., 2002; Chee, 2004; Eamus et al., 2005). The terms are used mainly for the benefit they provide to humans, and thus these aspects also need to be considered, when managing a coastal area. Many attempts have been made to evaluate those processes in monetary terms (e.g. Costanza et al., 1997; Farber et al., 2002). However, Chee (2004) in a review paper criticized the methods used in economics to achieve those values, since the complexity and dynamics of the ecosystems were not taken into account, nor were the couplings between ecosystems. He especially emphasized the difficulty in evaluating resilience of ecosystems, incorporating irreversibility and uncertainties, and techniques other than those commonly applied were presented, the discussion of these, however, are outside the scope of this paper.

Goods provided by an ecosystem largely depend on which species are present, and although NIS may affect those, both positively (e.g. harvestable NIS replace non-harvestable, native species) or negatively (e.g. non-harvestable NIS replace harvestable, native species), this may or may not be coupled to habitat modifications. Ruesink et al. (2006) described how a "pristine" area, after being invaded by four important NIS, increased primary productivity (>50%) (through the introductions of *Zostera japonica* Aschers. and Graebn. and *S. alterniflora*) as well as secondary productivity (250%) (through the introductions of *Crassostrea gigas* (Thunberg 1793) and *Ruditapes* (= *Venerupis* = *Tapes*) *philippinarum* (Adams and Reeve, 1850)), in comparison to when native mussels were harvested. Furthermore, also water filtration, detritus passways and biogenic structure were changed and the ecological character of this estuary was reshaped. Thus changes in the ecological services could be connected to induced habitat changes, since the NIS partly occupied areas with no similar native species. Of course, also many other processes such as eutrophication, overexploitation of natural resources, biotope fragmentations could lead to altered ecosystem services. Examples of changeable ecosystem services are given in Table 1, and some modifications caused by NIS are highlighted below.

1.4. Aims of the paper

The aims of this review were not to give a complete account for all NIS causing habitat modifications. We wanted to elucidate these processes as such, which are less often discussed in invasion literature (but see e.g. Crooks, 2002; Cuddington and Hastings, 2004), by describing whether the impact has been positive or negative, mainly from an ecosystem perspective. Not included are effects on man-made structures caused by NIS, such as fouling on artificial surfaces by algae and sessile invertebrates (e.g. the main ship-fouling organism in the Baltic Sea is the introduced barnacle *Balanus improvisus* (Darwin, 1854), nor organisms boring in wooden structures such as the introduced ship-worms of several genera and, the isopods *Sphaeroma* and *Limnoria*.

Many of the examples quoted below have come from direct field observations, while others are results from experimental work or from modelling. For instance, Cuddington and Hastings (2004) developed a model quantifying the effects of an invasive species, using the saltmarsh grass *S. alterniflora* as model organism, which has been shown to increase sedimentation rates and reduce water movements, resulting in elevated bottoms and marshlands, replacing previous mudflats. Their main conclusions from the simulations were that invasive species, which modify their envi-