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High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea

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Abstract

Pacific oysters *Crassostrea gigas* (Thunberg, 1793) were introduced to the northern Wadden Sea (North Sea, Germany) by aquaculture in 1986 and finally became established. Even though at first recruitment success was rare, three consecutive warm summers led to a massive increase in oyster abundances and to the overgrowth of native mussel beds (*Mytilus edulis* L.). These mussels constitute biogenic reefs on the sand and mud flats in this area. Survival and growth of the invading *C. gigas* were investigated and compared with the native mussels in order to predict the further development of the oyster population and the scope for coexistence of both species. Field experiments revealed high survival of juvenile *C. gigas* (approximately 70%) during the first three months after settlement. Survival during the first winter varied between >90% during a mild and 25% during a cold winter and was independent of substrate (i.e., mussels or oysters) and tide level. Within their first year *C. gigas* reached a mean length of 35–53 mm, and within two years they grew to 68–82 mm, which is about twice the size native mussels would attain during that time. Growth of juvenile oysters was not affected by substrate (i.e., sand, mussels, and other oysters), barnacle epibionts and tide level, but was facilitated by fucoid algae. By contrast, growth of juvenile mussels was significantly higher on sand flats than on mussel or oyster beds and higher in the subtidal compared to intertidal locations. Cover with fucoid algae increased mussel growth but decreased their condition expressed as dry flesh weight versus shell weight. High survival and growth rates may compensate for years with low recruitment, and may therefore allow a fast population increase. This may lead to restrictions on habitat use by native mussels in the Wadden Sea.
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Keywords: *Crassostrea gigas*; Growth; Introduced species; *Mytilus edulis*; Survival; Wadden Sea

1. Introduction

The accidental or deliberate release of 'exotic' (non-native) species into new habitats by shipping and aquaculture activities is an increasing phenom-

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enon in coastal ecosystems all over the world (Carlton and Geller, 1993; Reise et al., 1999; Ruiz et al., 2000; Naylor et al., 2001). Most introductions fail to produce self-sustaining populations or develop only a limited population growth (Williamson and Fitter, 1996). Nevertheless, there are numerous examples of invasive exotics that profoundly changed the recipient ecosystem (Nichols et al., 1990; Grosholz and Ruiz, 1996; Kideys, 2002). The Pacific or Japanese oyster (*Crassostrea gigas*) is an example of an invasive species that has been introduced to various coastal areas through aquaculture activities and subsequently established in the wild (Andrews, 1980; Chew, 1990). Examples include introduced oyster populations in British Columbia (Quayle, 1988), California (Span, 1978), South Africa (C. Griffith, pers. comm.), Australia (Ayres, 1991), New Zealand (Dinamani, 1991), France (Grizel and Héral, 1991), The Netherlands (Drinkwaard, 1999), and Germany (Reise, 1998).

Recently a dramatic increase in oyster abundances has been observed in the Dutch and German Wadden Sea (Dankers et al., 2004; Diederich et al., 2005). As this area is characterised by extensive intertidal mud and sand flats, it lacks primary hard substrata for oyster settlement. However, epibenthic mussel beds (*Mytilus edulis*) and dead shell material provide secondary hard substrata, which the oysters use as settlement surfaces. In the German Wadden Sea, oysters are therefore mainly found as epibionts on intertidal mussel beds and are at present turning some mussel beds into oyster reefs (Diederich et al., 2005). Since mussel beds take a prominent position in the Wadden Sea and generally constitute hot spots with respect to productivity and filtering-capacity (Asmus, 1987; Asmus et al., 1992; Dankers and Zuidema, 1995), biodiversity (Riesen and Reise, 1982; Tsuchiya and Nishihira, 1986; Dittmann, 1990), and as a food resource for various crustaceans, fish, birds and man (Seed and Suchanek, 1992; Nehls et al., 1997; Saier, 2001), their overgrowth or possible displacement by oysters might profoundly change the entire ecosystem. Up to now, recruitment of *C. gigas* in the northern Wadden Sea was sporadic depending on years with high summer water temperatures. However, three consecutive warm summers (2001–2003) and a positive feedback of adult oysters on recruitment of juveniles, strongly increased oyster abundance and expansion of the population (Diederich, 2005; Diederich et al., 2005). Thus, abundance may be high enough, by now, to ensure some recruitment even during 'cool' summers. Provided these recruits suffer a low mortality and adults achieve high longevity, this might guarantee population persistence and facilitate a further increase in the Wadden Sea. As a consequence, oysters might permanently restrict the local mussels to less favourable habitats, especially if they show higher growth and survival rates than the natives. However, no information is available on survival and growth of *C. gigas* in the Wadden Sea. The present study aims to fill that gap and attempts to find out whether oyster reefs may be regarded as a temporary phenomenon or are likely to be habitat structures superseding mussel beds in the Wadden Sea.

Generally, survival or mortality of benthic bivalves is described as a change in abundance of individuals or year classes present in a population over some period of time. In addition to physical stress and competition, predation is often a major cause of natural mortality in bivalves (Walne and Davies, 1977; Reise, 1985; McGrorty et al., 1990; Strasser, 2002). As predation is especially effective on juveniles and under conditions of extended submersion, survival largely depends on size and tide level (Theisen, 1968; Seed, 1969, 1993). Fast growing species may rapidly outgrow predation pressure. Therefore, it is assumed that Pacific oysters, which grow to about 30 cm in their native habitat as well as in the Dutch Wadden Sea (Korringa, 1976; Dankers et al., 2004) might have an advantage over the much smaller native mussels (*M. edulis*), which attain a maximum size of about 7 cm in the northern Wadden Sea (Nehls, 2003). The growth rates of both, mussels and oysters may depend on various factors, including tidal exposure (Quayle, 1988; Buschbaum and Saier, 2001), interspecific competition (Bertness and Grosholz, 1985; Okamura, 1986) and epibionts on the shells like algae or barnacles (Arakawa, 1990; Dittman and Robles, 1991; Buschbaum and Saier, 2001).

In the study at hand, survival of *C. gigas* and growth of both, *C. gigas* and *M. edulis,* were investigated in relation to tide level, substrate, barnacle epigrowth and algal cover, in order to assess whether habitat requirements are the same or whether there might be species specific refuges from potential competition. Information on mussel survival and growth

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