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Moderate establishment success of Pacific oyster, *Crassostrea gigas*, on a sheltered intertidal mussel bed

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ABSTRACT

The Pacific oyster (*Crassostrea gigas* Thunberg 1793) is introduced into marine ecosystems worldwide. In Denmark, *C. gigas* was introduced into the micro tidal Limfjord, around 1972 for aquaculture. This study describes the population structure of *C. gigas* at Agger Tange in 2007, 2009, 2010 and 2011. Here, *C. gigas* use beds of Blue mussels (*Mytilus edulis* L.) as primary habitat. The mean abundance (±1 SD) of *C. gigas* was unchanged during our study (45 ± 2 indv. m^{-2}), while it increased for *M. edulis* from 2010 to 2011 (934 ± 610 to 1434 ± 750 indv. m^{-2}, respectively). In 2009, a newly settled cohort of *C. gigas* was present, but in the succeeding years no or negligible recruitment was recorded. However, age cohort analyses, based on individual shell size at different ages, suggest successful recruitment in three out of seven years. A comparison with the course of the bioinvasion in List Tidal Basin, suggests that the population at Agger Tange is not in the expansion phase of the bioinvasion, despite of frequent settlement, high shell growth rates and relatively high abundance. So far, *C. gigas* has had moderate establishment success. We conclude that *C. gigas* is still in the establishment phase, but that this is prolonged, presumably due to low food availability.

1. Introduction

The Pacific oyster (*Crassostrea gigas* Thunberg 1793) originates from Japan and Southern China, where it inhabits intertidal and shallow subtidal zones in sheltered areas (Nehring, 2006; Miossec et al., 2009). The species has been introduced into many marine ecosystems (Ruesink et al., 2005). In Scandinavia, it has established local populations in Denmark, at the Swedish west coast, and in Norway up to 60° N (Wrange et al., 2010).

C. gigas and the native Blue mussel (*Mytilus edulis* Linnaeus 1758) share some of the same habitat requirements, as both filter feeders inhabit the intertidal and subtidal zone (Troost, 2010), and *C. gigas* are often seen establishing populations on existing mussel beds (Diederich et al., 2005). They might not necessarily compete for food, as they select different species of algae for ingestion (Bougrier et al., 1997), despite having an overlap in the retention spectrum (Bougrier et al., 1997; Zhang et al., 2010). However, the two bivalves could have an effect on each other by reducing the food availability for the other species (Troost, 2010).

With a life history strategy characterised by high growth rate, early sexual maturation, and high fecundity, *C. gigas* displays several of the traits that characterise a successful invasive species (Troost, 2010). It has a large dispersal potential and introduced into new habitats *C. gigas* is, as a bio-engineering species, a strong competitor to a number of other species. At high density, it will significantly modify the invaded habitat by forming stable reef structures (e.g. Markert et al., 2010).

Establishment of feral populations in marine ecosystems, as a result of species introduction, has occurred with varying degrees of success, which seems to depend on different biotic and abiotic factors, such as food availability, predation, competition, salinity, substrate and temperature (Dare et al., 1983; Quayle, 1988; Diederich, 2005; Fabioux et al., 2005; Scheiffarth et al., 2007; Carrasco and Baron, 2010; Troost, 2010).

Reise et al. (2006) defined the phases of a bioinvasion, starting with the arrival of the invasive species to the habitat. This phase is followed by an establishment phase where the species have little or no effects on the recipient biota. The next phase is an expansion phase, where the species increase in abundance and affect the recipient habitat to a certain degree. The final phase is the adjustment phase, where control mechanisms as predators or parasites, may reduce the density of the invasive species. The duration of the establishment and expansion phase, vary from site to site, depending on species and recipient habitat (Diederich et al., 2005; Wrange et al., 2010; Robinson et al., 2011).

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At Agger Tange (AT) in the Limfjord, Denmark *C. gigas* was introduced for aquaculture in 1972 (Jensen and Knudsen, 2005), here it was farmed in concrete ponds on land next to the sea shore, and adjacent to the farming site, it has established populations.

The purpose of this study was to examine if *C. gigas* had been able to establish a permanent reproducing population in this micro tidal area and if so, to determine where in the invasion it was, in order to evaluate whether *C. gigas* would increase in abundance. In other ecosystems where *C. gigas* have successfully established high density populations, it has primarily been confined to mussel beds (e.g. Diederich et al., 2005), and often has an effect on *M. edulis* when it reaches the expansion phase (Eschweiler and Christensen, 2011). Therefore, a *M. edulis* bed in the intertidal zone at the micro tidal area at AT composed the study site for our investigations. We hypothesised that the duration of the establishment phase is dependent on the food availability at the recipient habitat. The hypothesis is tested based on the population structure and condition of the two bivalves at AT contrasted to published data from List Tidal Basin, Wadden Sea. The analysis is supported by information on status of invasions and feeding conditions from other ecosystems. With respect to the invasion phases defined by Reise et al. (2006), a significant effect of the invasive species on the recipient habitat may indicate that it is in the expansion phase, whereas no effect may indicate that the species is in the establishment phase. Hence, the discussion of the invasion phase of *C. gigas* is based on apparent effects on *M. edulis* and the population development of *C. gigas*.

2. Materials and methods

2.1. Study site

The study was conducted at Agger Tange (AT) in the Limfjord, Denmark (the western part of Nissum Bredning, N 56° 43.3′, E 8° 15.4′) (Fig. 1). The study site consisted of a 12,000 m^2 large cluster of bivalve beds inhabited primarily by *M. edulis* and *C. gigas*. The study site is a shallow intertidal area (<1 m), surrounded by extensive sand and mud flats, intersected by relatively deep narrow tidal channels (~2 m). The area is exposed to semidiurnal tide, with a peak-to-peak amplitude of 0.25 m.

2.2. Sample design and data collection

Data was collected during spring of 2007 and the early summer of 2009, 2010, and 2011. In April 2007, only *C. gigas* was included in the sampling programme, as this was considered as a pilot study, and *C. gigas* were collected from a 1 m wide band along two 100 m transects. Transects were placed from the coast line towards south-east, crossing the north-western part of the bivalve bed (Fig. 2a). Data from 2007 were only used for size cohort analysis. In June 2009, individuals of both *C. gigas* and *M. edulis* were collected along five transects each 225 m long (Fig. 2b). On each transect, a ring of 0.25 m^2 was randomly dropped for every 15 m. In the identified sample-circles, all bivalves were collected and the depth of water measured. Furthermore, three smaller fractions of the bivalve bed were sampled with 10 samples at each location. In total, 106 samples were collected. In May–June 2010, the sampling was randomly distributed over the entire study site (Fig. 2c). A virtual grid (cell size 10 × 10 m) was assigned over the study site and within each grid cell two random points were computed using GIS. At each point, the two bivalve species were sampled as in 2009. Furthermore, the three smaller fractions of the bivalve bed sampled in 2009 were re-sampled. In total, 155 samples were collected. In June 2011, sampling points were generated randomly on the bivalve bed (Fig. 2d) and sampled as in 2009–2010. In total 45 samples were collected. In 2010 and 2011, the northernmost part of the study site was excluded from sampling, as it was used for other experimental purposes, hence the lack of sampling points (Fig. 2c, d). During the sampling campaigns, individuals of *C. gigas* and *M. edulis* were removed from the bivalve bed. The sampling during the most intensive year 2010 corresponded to 0.3% of the total area. Furthermore, the position of all samples was determined using GPS, to ensure that no points were sampled twice.

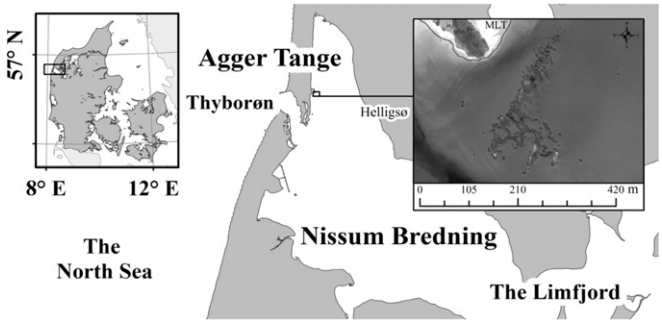

Fig. 1. Overview of the study site at Agger Tange in the Limfjord, Denmark (Orthophoto from June 2010). MLT denotes the approximated mean low tidal line.

2.3. Biomass and condition

Shell lengths of both sampled bivalves (2007–2011) were measured from umbo to the longest diameter (nearest mm) using an electronic pair of callipers. In samples with a high abundance of *M. edulis*, a random subsample of a minimum of 100 mussels was measured, representing the size distribution in that sample. For the quantitative analysis, only samples collected on the bivalve bed were used (N = 79 and N = 41 for 2010 and 2011, respectively) and solitary individuals located outside the bivalve beds were excluded from the analyses. Due to differences in sampling strategies between 2007 and 2009 with the succeeding two years, data from these years were excluded from the quantitative analysis of biomass and density. The individual biomass of *C. gigas* and *M. edulis* was estimated using the relation between shell-free dry weight (DW) (g) and shell length (L) (mm) determined on 180 *C. gigas* (C) and 193 *M. edulis* (M) collected in 2010: ($DW_C = 0.00001\ L^{2.634}$, $R^2 = 0.89$; $DW_M = 0.0001\ L^{2.134}$, $R^2 = 0.86$). The individual biomass was then converted to area specific population biomass (g DW m^{-2}), which was used to calculate the total biomass of the two species at the study site. Condition index (CI) of *C. gigas* was calculated as the ratio between dry weight of the soft tissue and dry weight of the shell (Lucas and Beninger, 1985), based on data from 2010 and 2011. The CI of *M. edulis* was calculated as the ratio between dry weight of soft tissue and shell volume, DW/L^3 (Petersen et al., 2004), based on data from 2010. Dry weight of mussel soft tissue was determined on tissue oven-dried for 24 h at 105 °C (sensu Mo and Nielson, 1994) that was allowed to cool down in a desiccator for 30 min prior to weighing.

2.4. Size cohorts and age determination of C. gigas

The mean shell length of each size cohort was determined using FISAT II version 1.2.2 on all shell length measurements, according to Bhattacharya (1967), using data from 2007, 2009, 2010 and 2011.

Additionally, growth-ring analysis was conducted in 2007, to determine the shell length of different aged *C. gigas* (N = 94), according to Harding and Mann (2006). The lower left shell of each oyster was cut in half at umbo, and the growth-rings were counted independently by two persons. If different estimates were obtained, the mean value was used. In 2011 additional animals (N = 13) were collected for growth-ring analysis of larger animals (>112 mm), which were not sampled in 2007. Combining size cohorts and age determined by the growth-ring analysis, an estimate of size for different age groups was obtained.