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Low mortality rates of juvenile Pacific oysters in the German Wadden Sea are characteristic for invasive species: a reply to Beukema and Dekker

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Many marine invertebrate species have decreasing mortality rates with age (Gosselin and Qian 1997), which raised a question (Beukema and Decker 2009) on the low mortality we reported for juvenile Pacific oysters in the East Frisian Wadden Sea (Schmidt et al. 2008). High fecundity is traditionally interpreted as a life history strategy to counteract high mortalities during early life stages, when unfavourable environmental conditions, competition or high predation can lead to a low recruitment success (Olafsson et al. 1994; Hunt and Mullineaux 2002). Beukema and Decker (2009) may therefore not be alone in doubting our values and we welcome the opportunity to clarify that such low juvenile mortalities are indeed a trait observable in the early stages of the invasion of marine invertebrates. Furthermore, as Gosselin and Qian (1997) also highlight, survival rates vary throughout the first year which may necessitate differentiation in future studies.

Prior to any evaluation of mortality, correct assessment of population parameters has to be assured. This can be confounded by sampling design and sampling errors, in particular where investigations are primarily field based, early life stages difficult to detect, or where high mobility of

juveniles can lead to import and export of individuals (Gosselin and Qian 1997). In our study, the establishment of Pacific oysters (*Crassostrea gigas*) was studied along a 160 km stretch of intertidal coastline, with a dense net of sampling stations and a high rate of replication, yielding about 1,500 quadrat counts at each annual sampling occasion. All shell material found on the quadrates was visually examined for oyster spat in the field, carefully lifting the material off the sediment, cleaning it from attached sediment and checking all sides of the shells. Even oysters as small as 1 mm could be identified, as they differ in their colouration and structure from other epibionts (e.g. barnacles) or byssus thread attachments. We are thus confident that we accurately estimated the small oysters in the field. Retrieving material for cross-checks in the laboratory would not have been feasible as the overall goal of the monitoring scheme was to establish a long-term/large-scale data series on the population development of Pacific oysters in this region. Therefore, fixed GPS positions marked with bamboo stakes in the field were used to relocate the study sites. Beukema and Decker (2009) are concerned that morphological changes in mussel beds could account for variation in settlement substrates between years. Only well-established mussel beds with a stable topography were used for our surveys, documented through mussel monitoring (Herlyn and Millat 2004) and own assessment of the perimeter in 2003 and 2006 (Schmidt 2009; Wehrmann et al. 2009).

Beukema and Decker (2009) are further concerned about the allocation to cohorts based on size-frequency distributions, yet the program FISAT II allows for potential overlap, applying standard procedures to differentiate cohorts using Bhattacharya's method (Gayani et al. 2005).

To corroborate the mortality rate based on the annual monitoring, we calculated mortality for the first year from spatfall collectors deployed in the field (Schmidt 2009).

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Table 1 Comparison of mortality and survival rates recorded for various time intervals of juvenile bivalves and for settlement on different substrate

Species	Timeframe	Z (days ⁻¹)	Z (years ⁻¹)	Survival (%)	Comment	References
<i>Crassostrea gigas</i>	89 days	0.004 ± 0.001		70	Ceramic tiles; August 2002–November 2002	Diederich (2006)
	314 days	0.003	1.136	38	Shell collectors (oyster shells); September 2004–August 2005, near Mellum	This paper
	314 days	0.002	0.612	59	Shell collectors (<i>Mytilus</i> shells); September 2004–August 2005, near Mellum	This paper
	314 days	0.004	1.599	25	Shell collectors (<i>Mya</i> shells); September 2004–August 2005, near Mellum	This paper
	314 days	0.003	1.026	41	Shell collectors (<i>Cerastoderma</i> shells); September 2004–August 2005, near Mellum	This paper
	86 days	0.005 ± 0.001	1.914	63.7 ± 7.1	Shell collectors (oyster shells); November 2002–February 2003	Diederich (2006)
	224 days	0.004 ± 0.0004	1.39	42.6 ± 3.9	Shell collectors (oyster shells); November 2002–July 2003	Diederich (2006)
	213 days	0.0003	0.104	94.1	Oyster plots November 2001–May 2002	Diederich (2006)
	578 days	0.003	0.90	23.9	Oyster plots November 2001–May 2003	Diederich (2006)
	323/393 days		0.03/0.13	97/88	Based on annual surveys for population dynamics May/July 2003–June 2004, near Borkum/Juist	Schmidt et al. (2008)
	19 months	0.0003	0.107	84	River Exe crab tiles November 1991–June 1993	Spencer et al. (1994)
	12 months			96	River Teigh, naturally set oyster spat on poches October 1991–October 1992	Spencer et al. (1994)
	<i>Ensis directus</i> (cf. <i>americanus</i>)	9 months	0.0145	5.307	1	Shallow water, high abundances
9 months		0.002	0.717	55	Deeper water, low abundances	Mühlenhardt-Siegel et al. (1983)

Oyster spatfalls occurred around August in the northern and western Wadden Sea, thus recordings starting several months later could have missed initial mortality. Exact dates for spatfall were not available in most cases, therefore the timeframe of exposure is given in days or months instead of the age. In some cases recording preceded the spatfalls and actual sampling months are given in ‘comments’

Collectors composed of numerous shells of various bivalve species suitable as initial settlement substrate were attached to the ground within a mussel bed near Mellum in April 2004 and the first collector set of each shell type retrieved on 30 September 2004, about 4–6 weeks after spatfall, and the second 1 year later on 10 August 2005. These shells were analysed in the laboratory for oyster spat, which was counted and measured under the microscope. The data provide us with an assessment of the population size at N_1 and N_0 , and calculation of mortality using the same formula as in Schmidt et al. (2008).

The mortality rates obtained are comparable to those found on various collectors by Diederich (2006), and furthermore indicate different mortalities subject to the shell type used for settlement, with the lowest mortality recorded on blue mussel and the highest on *Mya* shells (Table 1). The comparison presented in Table 1, including further studies on early stages of the oysters invasion in the UK

and of the American razor shell into the North Sea, reveals quite similar daily mortality rates. These low values vary with the duration of a study and the timing of the study period in relation to the spatfall, which leads to differences in the calculated annual mortality rates. Furthermore, the table shows that juvenile survival rates appear to decrease during the early years of invasion, and also differ between locations subject to site-specific commencement of invasion. A critical appraisal of the temporal study design is therefore needed prior to any evaluation of juvenile mortalities. The values compiled in Table 1 are further corroborated by the review of Gosselin and Qian (1997; Fig. 1) who showed that mortality decreases strongly in the time range of 120–180 days after settlement and remained low thereafter.

In our paper (Schmidt et al. 2008) we had stated clearly that the early mortality directly after settlement was not included in the calculation due to the sampling strategy

used, and that we determined N_0 about 6 months after settlement. Our values are comparatively low (Table 1), yet similar to mortality rates found during the early stages in the invasion of *C. gigas* in estuaries of the UK (Spencer et al. 1994) and by Diederich (2006) for oysters surviving the winter 2001–2002. Hence, the question is what could make high survival of juvenile invasive organisms possible.

Low juvenile mortality of recently introduced alien species, can be explained by various factors and processes. Predators may not have adapted to the new prey items available and competition may be negligible as densities are low. Furthermore, environmental conditions may be favourable. For example, high water temperatures ($>20^\circ\text{C}$) during spawning over summer could have reduced the energy expenditures of the larvae, leaving higher energy reserves for early juvenile stages (Gosselin and Qian 1997). Future research should address the relevance of high juvenile survival which could explain the exponential growth observed for many invasive species.

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