



Recruitment patterns, low cannibalism and reduced interspecific predation contribute to high invasion success of two Pacific crabs in northwestern Europe



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ABSTRACT

Life-history traits and interactions with native species play an important role for the successful establishment of non-native species in new habitats. We investigated the recent successful invasion of the Pacific crabs *Hemigrapsus takanoi* and *H. sanguineus* to the southeastern North Sea coast with respect to their recruitment patterns, as well as interactions of juvenile with sub-adult individuals among the Pacific crabs and with native shore crabs *Carcinus maenas*. A field survey of juvenile native and introduced crab abundances (carapace width 1.4–10 mm) was conducted in the northern Wadden Sea, spanning 24 months from 2014 to 2016. The survey revealed different seasonal recruitment patterns of native *C. maenas* and both introduced *Hemigrapsus* species. Native shore crabs showed a single recruitment peak from June to July, while *Hemigrapsus* spp. mainly recruited from August to early September, but recruits occurred in low densities throughout the winter until the end of the following spring season. Field experiments on the effects of larger crabs on the recruitment intensity showed that recruitment of *H. takanoi* was enhanced by the presence of larger congeners, but remained unaffected by larger *C. maenas*. Recruitment of juvenile *C. maenas*, by contrast, was reduced by the presence of larger *Hemigrapsus* spp. Additional laboratory experiments revealed high rates of cannibalism on newly recruited *C. maenas* by subadult conspecifics as well as strong predation by larger *Hemigrapsus* spp. In contrast, newly recruited *Hemigrapsus* spp. had a much lower risk of being preyed on by subadult conspecifics and native shore crabs. Our results suggest that the timing of recruitment in combination with low intraspecific competition and reduced predation pressure by native shore crabs are crucial for the rapid and ongoing establishment of *Hemigrapsus* spp. in the Wadden Sea.

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1. Introduction

Worldwide, marine ecosystems are invaded by a continuously rising number of non-native species, which is in particular true for coastal and estuarine habitats (Gollasch, 2006; Ruiz et al., 1997; Williams and Grosholz, 2008). The establishment of non-native species can profoundly affect species communities in invaded environments, driven by direct and indirect interactions between native and non-native species (Buschbaum et al., 2016; Edelist et al., 2013; Grosholz et al., 2000; Jensen et al., 2002; Levin et al., 2002; Reise et al., 2017). Life-history traits, especially traits related to

reproduction (Bremner, 2008; Lockwood et al., 2005), and niche allocation processes (Herborg et al., 2007; Peterson, 2003) are assumed to play an important role for the successful establishment and spread of non-native species. Detailed knowledge of the ecology and life-history of non-native species substantially contributes to the understanding of underlying processes of successful bio-invasions, and can also allow projections on possible effects of newly arrived species on native communities. For example, high fecundity and the duration and timing of reproduction periods have been attributed to invasion success in plants (Gerlach and Rice, 2003; Rejmanek and Richardson, 1996) as well as freshwater fish

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(Olden et al., 2006), crayfish (Chucholl, 2012) and gammarids (Grabowski et al., 2007; Pöckl, 2009).

In European coastal waters, the northwestern Pacific Brush-clawed shore crab *Hemigrapsus takanoi* Asakura and Watanabe 2005 and the Asian shore crab *Hemigrapsus sanguineus* (de Haan, 1835), are among the most recent successfully established non-native species. *Hemigrapsus takanoi* was for the first time reported from a ship's hull in Bremerhaven, Germany, in 1993 (Gollasch, 1999) and from the Bay of Biscay coast at La Rochelle, France, in 1994 (Noël et al., 1997). Initially identified as *H. penicillatus*, all populations of Brush-clawed shore crabs in Europe have later been assigned to the newly described *H. takanoi* (Asakura and Watanabe, 2005; Yamasaki et al., 2011). Within two years, this species had extended its range from northern Spain to southern Brittany (Noël et al., 1997). In 1999, it was reported from Le Havre at the French coast of the English Channel (Breton et al., 2002) and in 2000 from the Dutch Delta (Wolff, 2005). In 2006, it was found in the Dutch part of the Wadden Sea (Gittenberger et al., 2010), one year later also on the coast of Lower Saxony, Germany (Obert et al., 2007) and by 2009, it had reached the Sylt-Rømø-Bight between Germany and Denmark in the northern part of the Wadden Sea (Landschoff et al., 2013), thus currently occurring along 2200 km of the European Atlantic and North Sea coastline. Recently, it has also been reported from Great Britain (Ashelby et al., 2017; Wood et al., 2015) and the southwestern Baltic Sea (Geburzi et al., 2015).

Hemigrapsus sanguineus was first recorded at Le Havre and in the Dutch Delta system in 1999 (Breton et al., 2002; Wolff, 2005), spreading along the French, Belgian and Dutch coast of the English Channel and the southern North Sea in the following years (Dauvin and Dufossé, 2011; Gothland et al., 2013; Kerckhof et al., 2007; Wolff, 2005). It reached the Dutch Wadden Sea in 2004 (Gittenberger et al., 2010), German waters in 2006 (Obert et al., 2007) and occurred along the whole German Wadden Sea Coast and on the island of Helgoland in the German Bight by 2009 (Jungblut et al., 2017; Landschoff et al., 2013). In 2012, it was also reported from the Danish Wadden Sea islands Rømø and Fanø (pers. observation) and recently also from Great Britain (Seeley et al., 2015). On the Atlantic coast of North America, *H. sanguineus* was initially reported as an invasive species in 1988 at the mouth of Delaware Bay (McDermott, 1998) and is currently distributed in the United States from South Carolina to Maine (Epifanio, 2013).

The Wadden Sea as the coastal area of the southeastern North Sea is dominated by unstable sediments, and oyster and mussel reefs are the only naturally occurring extensive hard-bottom substrates. While comparatively species-poor, the proportion of non-native species is high, as reflected by over 60 non-native macrobenthic species alone (Buschbaum et al., 2012; Reise et al., 2010). The native decapod crustacean fauna of the Wadden Sea is dominated by the European shore crab *Carcinus maenas*, which is very abundant in benthic communities both inter- and subtidally, and itself a globally successful invader of coastal ecosystems (Carlton and Cohen, 2003). The recent arrival of the two *Hemigrapsus* spp. in this ecosystem allows to simultaneously study interactions between native and invasive and two closely related invasive species, as well as the ongoing establishment process.

Several studies reported detrimental effects of growing *Hemigrapsus* populations on *C. maenas* in North America (Kraemer et al., 2007; O'Connor, 2014) and Europe (van den Brink et al., 2012). These can be connected to apparent advantages of *Hemigrapsus* spp. over *C. maenas* in competition for food and shelter (Gothland et al., 2014; Hobbs et al., 2017; Jensen et al., 2002), but also to reduced recruitment success of *C. maenas* as a consequence of predation on early juveniles by *H. sanguineus* (Lohrer and Whitlatch, 2002). Early juvenile crabs are an especially sensitive

life stage, as they experience high predation pressure (especially from other decapods) and strongly depend on suitable nursery habitats (Lohrer and Whitlatch, 2002; Moksnes et al., 1998). They usually occur in high densities but only for a relatively short time, and all processes influencing crab recruitment are assumed to cause effects on the population level (Moksnes, 2002).

This study aims to investigate temporal dynamics of the recruitment and early juvenile stages of Asian shore crabs in comparison to European shore crabs, as well as possible competitive interactions affecting early juvenile crabs. The first part of the study comprises regular observations of the abundances of *Hemigrapsus* spp. and *C. maenas* in the intertidal of the northern Wadden Sea between 2014 and 2016, with a special focus on size class distributions and the occurrence of recruitment events. Based on observations of several broods per season regularly occurring in *Hemigrapsus* spp. (Fukui, 1988; McDermott, 1998; van den Brink et al., 2013) while only one brood per season is common for *C. maenas* in the North Sea (Crothers, 1967; Klein Breteler, 1976), differences in reproductive cycling of native and non-native species favouring the establishment of *Hemigrapsus* spp. are hypothesised. To the best of our knowledge, the survey data represent the first temporally highly resolved, perennial dataset of *Hemigrapsus* spp. abundances in their invaded European range.

The second part of the study comprises field and laboratory experiments on the influence of subadult and adult crabs on the recruitment success of juveniles, and intra- (e.g. cannibalism) and interspecific predation pressure on newly settled crabs. The latter is a putatively important interaction in crab populations, shaping distribution patterns and abundances of juveniles (Moksnes et al., 1998). We hypothesize differences in the recruitment success of juveniles in response to larger crabs, as well as differential patterns of predation pressure on early juveniles between *C. maenas* and *Hemigrapsus* spp.

2. Material and methods

2.1. Study area

All field investigations and experiments were carried out in the intertidal zone near the northern part of the island of Sylt in the northern Wadden Sea (Fig. 1). This area is dominated by sedimentary soft-bottom habitats with several mixed beds of native blue mussels (*Mytilus edulis*) and introduced Pacific oysters (*Magallana gigas*, Reise et al., 2017), as well as artificial hard structures (boulder groynes), which provide epibenthic hard-bottom habitats in close proximity to each other. It is particularly in these hard-bottom habitats where both *Hemigrapsus* spp. occur in the Wadden Sea. On Sylt, the first specimen of *Hemigrapsus* spp. were found in 2008 close to harbours at the southern and northern tips of the island (J. Landschoff, K. Reise pers. comm.). In 2011, *Hemigrapsus* spp. were already found in hard-bottom habitats at 12 sites all along the east coast of Sylt, occurring sympatrically at 5 of these sites and always co-occurring with *C. maenas* (Landschoff et al., 2013).

We selected an intertidal mixed oyster-mussel-bed at the northern tip of the island (N 55.028° E 8.434°; 'site A'), dominated by *H. takanoi*, and boulder groynes in that area (N 55.013° E 8.432°; 'site B'), dominated by *H. sanguineus*, as sampling sites for the survey (Fig. 1). At site A, also the field experiment was conducted. Both sites are located between 0.3 and 0.5 m above mean low tide level.

2.2. Survey

To gain insight in temporal variations of recruitment and

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