



Introduced species in a tidal ecosystem of mud and sand: curse or blessing?

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Abstract

For about a century, biodiversity in the tidal Wadden Sea (North Sea, European Atlantic) has increased by more than one hundred introduced species from overseas. Most originate from warmer waters and could facilitate the transformation of this coastal ecosystem to comply with climate warming. Some introduced species promote sediment stabilization and mud accretion. This could help tidal flats to keep up with sea level rise. Although some introduced species also entail negative effects, introductions have diversified lower food web levels, and may benefit foraging birds. So far, no resident populations have gone extinct because an introduced species had established. Rather than degrading the ecosystem, the establishment of introduced species seems to have raised the capacity to follow environmental change. We support increasing efforts against introductions to avoid risk. However, once species are integrated, the common condemnation attitude against “non-natives” or “aliens” ought to be reconsidered for tidal ecosystems of low biodiversity.

Keywords Biodiversity · Climate change · Species introductions · Macrobenthos · Wadden Sea

Introduction

Coastal ecosystems are susceptible recipients for species introduced from oceans beyond their natural dispersal range (Hedgpeth 1980; Anton et al. 2019; Bailey et al. 2020). These introductions are blending human history with natural history, being part of our cultural heritage while also changing the species composition and functioning of recipient coastal waters. Introduced species have been conventionally condemned as a kind of baneful “biological pollution”, “biocontamination”, “biosecurity risk” and as “threatening” or “degrading” ecosystem services (i.e., Elliott 2003; Olenin

et al. 2007, 2011; Arbačiauskas et al. 2008; Essl et al. 2017; Ojaveer et al. 2018; Anton et al. 2019; Pyšek et al. 2020; Tarkan et al. 2021; Collin and Shucksmith 2022) or as “guilty until proven innocent” (Ruesink et al. 1995). In addition to ecological change, health problems and economic costs may arise (i.e., Cuthbert et al. 2021). Voices demanding more modesty and differentiation with regard to the effects of species introductions (i.e., Davis et al. 2011; Cassini 2020) met fierce opposition (i.e., Simberloff 2011; Ricciardi and Ryan 2018). This conflict is still lingering on, although more and more voices now argue for considering negative effects of introductions in conjunction with positive ones when advising nature

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management (i.e., Schlaepfer et al. 2011; Katsanevakis et al. 2014; Vimercati et al. 2020; García-Díaz et al. 2021; Kourantidou et al. 2022).

A similar situation exists in the European Wadden Sea, an extensive tidal flat ecosystem at the south-eastern coast of the North Sea with a UNESCO world heritage status. For the Danish-German-Dutch Wadden Sea, regular trilateral quality status reports included chapters on introduced species (Reise et al. 2005; Nehring et al. 2009; Buettger et al. 2017, Buettger et al. 2022), and overviews on introductions for sub-regions of the Wadden Sea are given in Nehring and Leuchs (1999), Wolff (2005), Gittenberger et al. (2010) and Lackschewitz et al. (2015, 2022). In a first review on the entire Wadden Sea, Buschbaum et al. (2012) compiled a list of 66 introduced marine-to-brackish macrobenthic species (known until 2010; not included were pelagic and microscopic taxa) which has increased to over 100 benthic and planktonic species recently (Buettger et al. 2022). Twelve percent had arrived in the Wadden Sea directly from overseas, while the majority of introductions arrived in adjacent regions further south, and from there, they spread by secondary introduction and natural dispersal towards the Wadden Sea. In particular, artificial hard substrates attract introduced species, and the share of introduced species is highest in the low salinity, estuarine areas of the Wadden Sea. Although no evidence so far suggests that invading species had expelled resident populations (Buschbaum et al. 2012), the rise of introduced species has sparked numerous discussions in management and conservation circles about the presumably accumulating negative impacts (see Bouma et al. 2011). This has resulted in the request by the UNESCO to develop a trilateral strategic framework for dealing with alien species in the Wadden Sea world heritage site (Buettger et al. 2017).

The major aim of this study is to revisit the discussion around introduced species in the tidal ecosystem of the Wadden Sea by adopting a neutral perspective without prior decision upon whether changes caused by introductions might be good or bad for resident species, the environment or human interests. Instead, we employ species introductions as ‘unplanned experiments’ leading to a better understanding of the functioning of the ecological web, and to wiser nature protection strategies in the Wadden Sea World Heritage Site. Change is an inherent property of coastal ecosystems and is inevitable when newcomers interact with residents and their new environment. We specifically ask (1) Why is the Wadden Sea so susceptible to introductions? (2) Which species have been introduced at what time? (3) Is an end to species introductions in sight? (4) To what extent have introductions transformed food web and habitats? (5) May introductions comply with rapid climate warming? (6) Will introductions homogenize the Wadden Sea ecosystem with those of other sedimentary coasts in the temperate climate zone? Based on the answers to these questions, we finally ask (7) whether introduced

species might be better than their reputation for a tidal ecosystem such as the Wadden Sea.

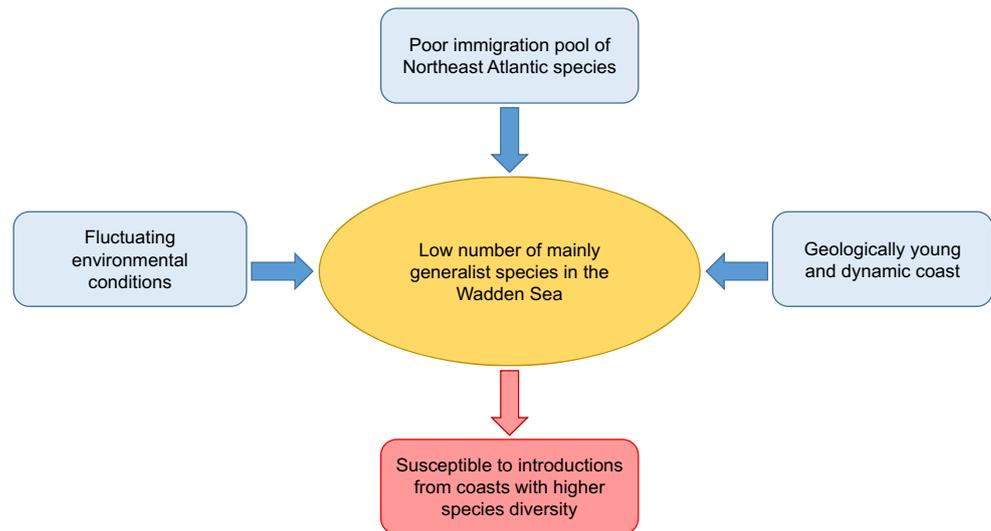
Scope and terminology

In this review, we deliberately focus on introduced macrobenthic species in the Wadden Sea ecosystem, and neglect introductions to its vast but insufficiently known “dark biodiversity” of viral, unicellular, fungal, and meiobenthic organisms. Where appropriate, we consider parasites and diseases affecting macrobenthos. For introduced planktonic and pelagic species, a larger scale than the narrow coastal fringe of the Wadden Sea seems more appropriate, i.e., the entire North Sea or the NE-Atlantic. In our terminology, we prefer the terms introduced species or introductions for taxa that entered the Wadden Sea from outside the European Atlantic region, either by means of human transport or by human-build connections (canals), at some step on the immigration route. Taxa which immigrated by natural dispersal at some time in the past are named residents, and those which spread from adjacent regions in the south in response to climate warming as recent immigrants (corresponding to neonatives as defined by Essl et al. 2019). Not used are the terms alien (non-native, exotic), invasive, and native species because of dubious connotations, depending on context (Larson 2005; Sagoff 2018).

Legacy of past climate

The Wadden Sea is geologically young and highly dynamic. It has high densities of individuals but is poor in species and almost lacks endemics (Fig. 1; Reise et al. 2010). This may be explained by its environmental history and prevailing conditions. Compared to a continuous evolution towards high biotic diversity in the large Pacific region, biota in the North-Atlantic suffered from extreme climatic variability throughout the last millions of years (Vermeij 1991; Briggs 2010). This kept biodiversity at a low level and limited the spectrum of species, which colonized the Wadden Sea when it emerged. Fluctuating physical conditions from tides to multiannual time scales further constrain the number of species, which can survive in this environment. The last major environmental change was a dramatic increase in mean annual temperature by about 8°C after the end of last ice age, followed by sea level rise of more than 100 m. When this rise in sea level finally decelerated and became more or less balanced by the amount of coastal sedimentation, the Wadden Sea gradually emerged less than 8000 years ago (Vos and van Kesteren, 2000; Reise 2013). Among the mix of benthic colonizers into this tidal sea were common cockles *Cerastoderma edule*, expanding from northern refugia (Krakau et al. 2012) and

Fig. 1 Factors contributing to the low species diversity in the Wadden Sea may facilitate the establishment of introduced species from coastal regions with a higher species diversity



common shrimp *Crangon crangon*, immigrating from southern refugia (Luttikhuizen et al. 2008).

Generally, immigrations occurred from more diverse into less diverse ecosystems (Vermeij 1991; Briggs 2010; Fridley and Sax 2014). As a modern analogue to such paleoecological trends, the opening of the Suez Canal in 1869 initiated a massive, still ongoing immigration from the highly diverse Red Sea into the less diverse eastern Mediterranean while almost none migrated in the other direction (Galil 2009; Edelist et al. 2013). Although flow-direction and environmental differences may also be involved, the higher colonization potential of Red Sea and Indo-Pacific immigrants over the Atlantic-derived Mediterranean species spectrum is obvious. A less striking case are brackish-water species from the rich Ponto-Caspian region being introduced as fish food into artificial water reservoirs and immigrating through canals connecting European river systems into the Baltic Sea and North Sea estuaries (Bij de Vaate et al. 2002; Wolff 2005; Leuven et al. 2009). Favored are species combining high environmental tolerance with high agility like some Ponto-Caspian amphipods (see Cuthbert et al. 2020).

The Wadden Sea is a ready receptor for introductions because most other coastal regions are richer in species. We exemplify this by comparing the Wadden Sea with the Korean coast of the Yellow Sea, where climatic conditions and extent of tidal flats are similar (Koh and Khim 2014). Based on macrozoobenthic sampling over the last 40 years, the coastal Yellow Sea harbors 624 macrozoobenthic species (Park et al. 2014), while a corresponding list for the Wadden Sea comprises 436 (compiled from literature until 1979 (Wolff 1983)). Lack of standardized sampling may bias such a comparison, but sampling 30 sites in each region with identical effort and methods supports this difference in species richness (Table 1). However, when considering individual sites (alpha diversity), numbers of species are similar. This

indicates that the two regions do not differ in average species density, while the pool of species in the Yellow Sea is richer than in the North Sea region. This may be primarily a legacy of the different pasts, and suggests a Wadden Sea undersaturated in species and thus open to newcomers.

Accumulating introduced species in the Wadden Sea: who is who?

The rate of species introductions increased since 1900 (Fig. 2). Only few records are known from earlier centuries, but the rate increased particularly strong since 1990 (Buettger et al. 2022). Increasing rates were similar in neighboring coastal regions such as in Belgian, Irish, British, Danish, and French Atlantic waters (i.e., Kerckhof et al. 2007; Minchin 2007; Minchin et al. 2013; Staehr et al. 2020; Pezy et al. 2021), in other aquatic environments (Karatayev et al. 2008; Leuven et al. 2009; Bailey et al. 2020), and globally in major groups of organisms — except intentionally introduced mammals and birds (Seebens et al. 2017). The non-linear increasing trend in the Wadden Sea is typical for mainly unintended introductions, closely linked to increasing global trade (Ojaveer et al. 2018). To some extent, however, regular monitoring programs and alien species inventories may have caused increasing, but probably more realistic rates since the 2000s because inconspicuous arrivals might have gone unnoticed and ports of arrival were rarely sampled in earlier studies. With regard to the total number of introduced species, the Wadden Sea holds an intermediate position (see Table 4 in Buschbaum et al. 2012). Coasts further south with warmer waters and major hubs for overseas traffic have more records of introduced species (i.e., the Normandy coast; Pezy et al. 2021), while colder coasts with brackish waters and minor port destinies further north have less (i.e., Denmark;

Table 1 Yellow Sea and Wadden Sea compared: Species richness of macrofauna (mesh size 1 mm) in intertidal sediments of the Yellow Sea (July 2002) and North Sea (July 2003) obtained from a total sample of 6 m² in each region, composed of 30 sites each with 0.2 m² sample size (20 replicates of 0.01 m² cores; Hong and Reise, unpublished report 2005 to KOSEF/DFG)

Region	Yellow Sea	Wadden Sea
Shore type	Rock and sediment alternate	Sediments only
Coastal length (km)	1000 (Korea)	500
Tidal flat area (km ²)	3800 (Korea)	4700
Semi-diurnal tide range (m)	1–6	1–4
Species in all samples (6 m ²)	119	66
Mean [range] for 30 sites (each 0.2 m ²)	17.8 [9–27]	18.3 [3–31]

Staehr et al. 2020). Artificial hard substrates introduced into the sedimentary environment of the Wadden Sea bear a disproportionally high share of introduced species (Gittenberger et al. 2010; Buschbaum et al. 2012; Lackschewitz et al. 2022). Few residents can utilize this novel habitat, while ship-hull fouling species and those attached to cultured oysters are predestined for establishing there (Wasson et al. 2001; Mineur et al. 2012).

In addition to such generalities, where individual species are treated as numerical equivalents, we provide a narrative description on who is who for the spectrum of introduced species in the Wadden Sea, following the timeline of introductions (Table 2). From each 20-year period, we picked the most prominent representatives in terms of abundance or biomass and/or effects on habitat properties. Buettger et al. (2022) provide a complete list of introduced species. Giving more than one example for the more recent periods reflects the increasing rate of introductions.

Early introductions

The first known arrival is the American clam *Mya arenaria*, introduced with Viking ships to the Kattegat almost 800 years ago (Fig. 2; Petersen et al. 1992; Essink and Oost 2019). In the Wadden Sea, it occurred at least since the fourteenth century (Essink et al. 2016). It is still the largest and deepest burying bivalve in the estuarine dominated areas of the Wadden Sea, without an ecological equivalent among residents (Strasser 1999; Drent et al. 2017). Juveniles are prey to crabs and birds, while adults could attain an age of 20 years or more. Massive shell beds occur alongside tidal channels. Another early arrival of a bivalve is the “shipworm” *Teredo navalis* with a first massive appearance in the Netherlands during 1700 to 1730 (Wolff 2005; Weigelt et al. 2017). It affects artificial wooden structures in the Wadden Sea but not natural habitats because the area is too cold for mangroves.

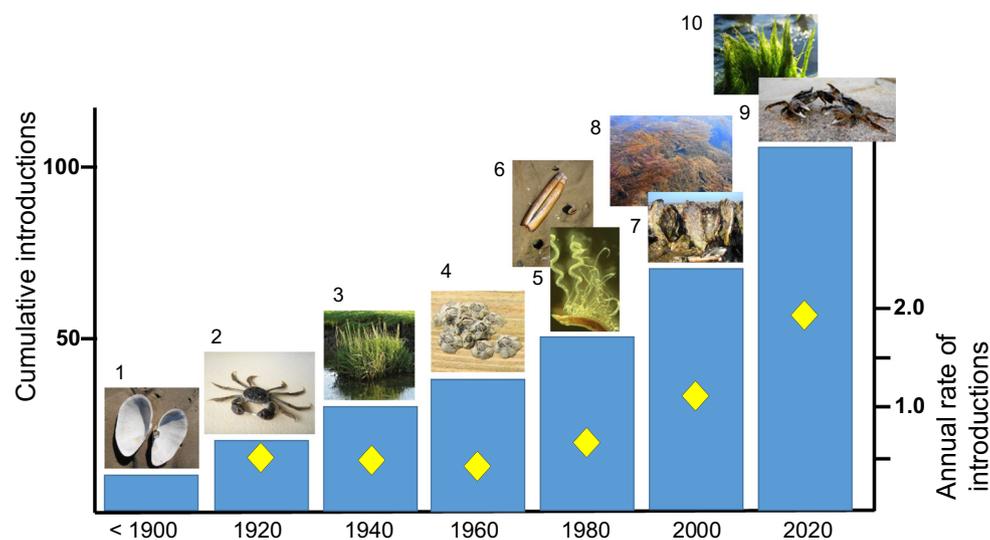


Fig. 2 Accumulated first records for the tidal Wadden Sea of established introduced species, both benthic and pelagic, given in intervals of 20 years since 1900 (axis left). Mean annual rates of new arrivals per period indicated by yellow diamonds (axis right). Not counted are microbial species and terrestrial introductions. Images above columns show representative species for respective periods chosen for further

description (see text): (1) *Mya arenaria*, (2) *Eriocheir sinensis*, (3) *Spartina anglica*, (4) *Austrominius modestus*, (5) *Tharyx maryae*, (6) *Ensis leei*, (7) *Magallana gigas*, (8) *Sargassum muticum*, (9) *Hemigrapsus takanoi* and *H. sanguineus*, (10) *Vaucheria cf. velutina* and *V. longicaulis*. Column heights from data in Buettger et al. (2022)

Table 2 Representative introduced species arranged from early to most recent arrival in the Wadden Sea with traits, habitats, and effects on the recipient environment and its species

Introduced species/origin, pathway and time of arrival	Traits and habitats	Effects
<i>Mya arenaria</i> L. / Atlantic North America / with Viking ships / ~ 1300	Large, deep-dwelling clam in estuarine sediments from lower shore to subtidal zone	Shells used as hideouts and for attachment; only juveniles accessible as prey
<i>Eriocheir sinensis</i> Edwards arrived by ship from China around 1912	Planktonic larvae in the sea, juvenile crabs estuarine, and adults mainly in rivers	Erodes river banks with burrows; no interference with resident crabs
<i>Spartina anglica</i> Hub. fertile hybrid of American with European grass / planted in the 1920–1930s	Perennial tussocks at lower saltmarsh and uppermost tidal flats at sheltered shores	Facilitates mud accretion; monopolizes patches but diversifies habitat structure
<i>Austrominius modestus</i> (Darwin)/Southern Pacific/by ship to England / 1953	Small barnacle, reproduces late summer, benefits from climate warming; intertidal	No effects on resident barnacles, which reproduce in spring and live longer
<i>Tharyx maryae</i> Blake & Gör./origin unknown / 1960s	Small deposit feeding polychaete in muddy sand of intertidal zone	Unknown but often highly abundant
<i>Ensis leei</i> Huber / Atlantic North America / larvae in ballast water / 1978	Deep burrowing razor clam from lower shore to shallow subtidal zone	Important prey to diving ducks, oystercatcher and gulls
<i>Magallana gigas</i> (Thunb.) / NW-Pacific / Imported for culturing / 1980s	Very large oyster; benefits from climate warming; attaches to low intertidal structures and mussel beds	Transforms mussel beds into mixed reefs of large oysters with mussels in between; offers attachment to algae
<i>Sargassum muticum</i> (Yendo) / NW-Pacific / co-introduced with oysters / 1980s	Very large kelp from spring to summer, mainly attached to oysters in shallow subtidal	Kelp beds provide habitat to attached algae, invertebrates and juvenile fish
<i>Hemigrapsus sanguineus</i> and <i>H. takanoi</i> / NW-Pacific / by ship to France / 2000s	Small crabs hiding at stone revetments and in oyster reefs; mainly intertidal	Resident <i>Carcinus maenas</i> juveniles avoid these crabs and prey spectra overlap
<i>Vaucheria</i> cf. <i>velutina</i> and <i>V. longicaulis</i> / origin unknown / 2020s	Grass-like algae rooted in sediment; occur in beds at shallow subtidal zone	Transform rippled sand into bumpy mud flats, expel lugworms but facilitate tube-worms and juvenile clams

Since the beginning of the twentieth century, global maritime trade strongly accelerated and ballast water came into use. This facilitated the introduction of coastal aquatic species from overseas. The Chinese riverine crab *Eriocheir sinensis* (Fig. 2) was first encountered 1912 far inland in the Aller, a tributary of the Weser, which is entering the Wadden Sea. Subsequently, multiple introductions of this crab from China occurred, as genetic population analyses indicate (Wang et al. 2009). Larval development requires marine to brackish salinities (Anger 1991). First mass developments occurred in the Elbe and Weser estuaries in the 1920–1930s (Panning 1938; Peters 1938), and since then *E. sinensis* remained the most common crab in the estuaries of the Wadden Sea. Mitten crabs annoyed trap fishers but now regional Chinese restaurants serve them. Ecological effects on the Wadden Sea ecosystem are negligible because of the transient presence of these primarily limnic crabs.

The American cordgrass *Spartina alterniflora* (Fig. 2) first showed up in France and England in 1803 and 1816, respectively (Ainouche et al. 2009). Five decades later sterile hybrids with resident *S. maritima* occurred. Chromosome doubling in this hybrid gave rise to the novel species *S. anglica*, spreading vigorously in Britain. Plantings in the Wadden Sea in the 1920–1930s in an attempt to accrete more land, did not meet

expectations. However, a wild spread commenced in the 1940s (Nehring and Hesse 2008). This perennial grass established at the pioneer zone of saltmarsh vegetation, with a sprawl of tussocks into resident vegetation and onto bare upper tidal flats. *S. anglica* together with the sterile hybrid diversified the shoreline landscape and the associated species assemblage (Emmerson 2000; Tang and Kristensen 2010; Boestfleisch et al. 2015; Granse et al. 2021a,b).

Introductions from 1950 to 1980

A barnacle, *Austrominius modestus*, described by Darwin in 1854 as *Elminius modestus*, and originating from Australia and New Zealand, had landed in England during World War II. From there, it spreads along the Atlantic coast of Europe, now ranging from Iberia to the Skagerrak (Glennier et al. 2021). As a ship hull fouling species with planktonic larvae, it may have spread secondarily by both means. At the Wadden Sea, it arrived in the 1950s (Fig. 2; Kühl 1963). Compared to resident barnacles, its spatial niche in the tidal waters is wider, mature size smaller, longevity shorter, and reproduction later in the season. Although highly abundant, *A. modestus* did not expel resident barnacles (Witte et al. 2010).

A sudden appearance followed by a massive spread is often characteristic for an introduction. Although the origin is still unknown, this has led to the assumption that the annelid worm *Tharyx maryae*, abundant throughout the Wadden Sea since the 1970s, has arrived from overseas (Lackschewitz et al. 2022). This tiny worm went under several names (i.e., *Cirratulus filiformis*, *Tharyx marioni*, *Chaetozone killariensis*; see Dörjes et al. 1969; Farke 1979; Jensen 1992) because introduced species present a taxonomic challenge when the home region remains undisclosed. While only specialists take notice of such inconspicuous worms, the razor clam *Ensis leei* (formerly *E. directus* or *E. americanus*) quickly became familiar to beachcombers after initial introduction in 1978 into the German Bight (Fig. 2; von Cosel et al. 1982; Mühlenhardt-Siegel et al. 1983). Presumably, larvae from the other side of the Atlantic were released with ballast water. Within a decade, a fast spread occurred throughout the Wadden Sea and beyond (Essink 1985; Armonies and Reise 1999; Vierna et al. 2012). Only young individuals occur in the intertidal, while adults thrive in high numbers and biomass in the shallow subtidal zone. These American razor clams became an important food for oystercatchers and eiders among others (Tulp et al. 2010). Apparently settling in an area scarcely occupied by residents (Armonies and Reise 1999), *E. leei* has not displaced resident bivalves.

Recent introductions

The most spectacular introduction event to the Wadden Sea has been the Pacific oyster *Magallana (Crassostrea) gigas* (Fig. 2). Introduced to France, the Netherlands, and Britain for aquaculture, this large and robust oyster served as an economic substitute for the overharvested European oyster *Ostrea edulis* and an earlier introduced but diseased southern subspecies of *M. gigas* (then referred to as *Crassostrea angulata*; Troost 2010). Feral populations quickly spread along coasts. In the Wadden Sea, it arrived by introduction from the Rhine Delta and with an oyster farm at Sylt in the 1980s (Reise 1998; Moehler et al. 2011). The Pacific oyster settled on hard substrates in the lower intertidal and shallow subtidal zone, particularly on mussel beds. What initially looked like a displacement of resident mussels later turned into co-existence (Reise et al. 2017a). The smaller mussels found shelter underneath a canopy of oysters settling upon each other (Eschweiler and Christensen 2011). These “oyster reefs” accommodate more species than former mussel beds (Markert et al. 2010, 2013). They also attract a wide range of foraging birds, albeit less favored by species preferring mussel prey when these are hiding between and underneath the oysters (Waser et al. 2016).

Prior to the introduction of Pacific oysters, an almost balanced interchange of introductions across the northern Atlantic prevailed between coastal W-Europe and the

Americas. Thereafter, one-way introductions from the Western Pacific represented the majority of introductions. This follows the general trend of introductions proceeding from the more diverse to the less diverse ecosystems (see above). Species associated with Pacific oysters and an increasing number of larger and faster cargo ships commuting between East Asia and Europe are the likely causes for that shift (Wolff and Reise 2002; Dauvin et al. 2019). Particularly, West-Pacific algae spread with oysters and continue to arrive in the Wadden Sea (Lackschewitz et al. 2022). The most conspicuous one is the Pacific brown seaweed *Sargassum muticum* (Fig. 2, Fig. 10), which followed the global oyster trade (Engelen et al. 2015). It arrived in Europe in 1972 and within a decade spread along the entire Atlantic coast of Europe. With up to 8 m long (K. Reise, personal observation measured in a tidal channel near Sylt in July 2021), *S. muticum* became the largest algae in the Wadden Sea, usually anchored on clumps of Pacific oysters and forming seasonal kelp beds in the shallow subtidal zone. These kelp beds are particularly rich in associated epiphytes, adhering invertebrates, and hiding fish (Buschbaum et al. 2006; Polte and Buschbaum 2008; Lang and Buschbaum 2010).

A special case is the tandem introduction of two NW-Pacific predatory crabs, *Hemigrapsus takanoi* and *H. sanguineus*, in the Wadden Sea (Fig. 2; Landschoff et al. 2013). First introduced by ship to the French Atlantic coast in the 1990s, they spread eastward and reached the Wadden Sea in the early 2000s. These agile crabs became highly abundant under exposed (*H. sanguineus*) and sheltered (*H. takanoi*) artificial bolder shores, and both species soon spread to oyster reefs. Comprehensive interference and food competition with juveniles of the resident shore crab *Carcinus maenas* arose (Geburzi et al. 2018; Bouwmeester et al. 2020; Bleile and Thieltges 2021; Cornelius et al. 2021). However, besides prey size overlap, there are differences in prey preferences, and recruitment of the newcomers mainly occurs later in the season than in *C. maenas*. The shore crab grows much larger than the two *Hemigrapsus* species, its adults migrate with the tides, and its depth range is wider than in the Asian species. Therefore, competitive exclusion seems unlikely at the scale of the entire Wadden Sea. Furthermore, as *C. maenas* was introduced to many other coastal regions and ranks among the “100 of the World’s worst invasive alien species” (Lowe et al. 2004), the underlying opportunistic traits make it unlikely that *C. maenas* will suffer from the two new introductions.

Another recent tandem introduction has the capacity to turn rippled sandy flats into bumpy mud flats at the lower shore. This we observed first in 2020 near the island of Sylt in the northern Wadden Sea for two species of *Vaucheria*-algae (Fig. 2; Reise et al. 2022a, b; Rybalka et al. 2022). Their origin is still unknown. One (*V. cf. vellutina*) grows in summer and the other (*V. longicaulis*) at the same sites from autumn to winter. Resident members of this genus in the Wadden Sea are confined

to estuaries and salt marshes, and none occurs at spring low tide level where the two introduced species form dense, green turfs of filaments rooted in the sediment.

This overview shows that introduced species are phylogenetically and functionally diverse, and differ widely in origin, transport route, secondary spread and their interactions with residents and each other (Table 2). Their numbers are increasing, and some achieved high prominence in the benthos of the Wadden Sea. Introduction hot spots are port structures and biogenic hard substrates around spring low tide level. We have not mentioned the majority of imported species that established but were only temporarily or never abundant or remained confined to narrow niches. This pattern of rare or modest occurrence by most species is the same as in resident species. Although displacements may occur, the heterogeneous Wadden Sea environment with a sequence of tidal zones, varying in wave exposure and sediment composition, having interspersed hard substrates and low salinities in estuaries, together hamper competitive exclusion of residents by introduced species. Identical habitat niches are extremely rare. The rich history of introduced species into the tidal Wadden Sea provides evidence that plenty of accommodation space seems available for new arrivals.

Future introductions: three scenarios

Despite of precautionary measures against unintentional introductions, there is not yet an indication that introduction rates begin to fall on a global scale (Pyšek et al. 2020). The underlying transport systems, economic and cultural globalization are increasing in intensity, and ever more regions become globally connected (Sardain et al. 2019; Seebens et al. 2017, 2018, 2021; Cuthbert et al. 2022). Northern European coasts are preferred destinies. New Arctic shipping routes may shorten transport routes between East Asia and Western Europe in the coming decades (Miller and Ruiz 2014). Current global warming will also facilitate immigrations and introductions (see below). What might be the long-term prospects for species richness in the Wadden Sea? Three scenarios seem possible (Fig. 3).

As in the twentieth century, introductions of opportunists will further add ever more species to the resident spectrum dominated already by opportunists without causing concomitant losses in this open and flexible assemblage. Eventually, this trend may level off, either because vector controls become effective or when the global pool of suitable opportunists will become exhausted (scenario A in Fig. 3). Climate warming may facilitate the establishment and population growth of introduced species (see below). Finally, evolutionary processes may consolidate the novel assemblage of species (i.e., Whitney and Gabler 2008).

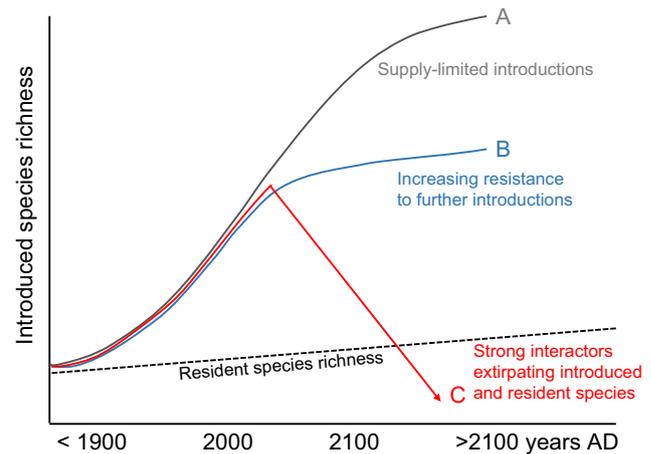


Fig. 3 Future scenarios for species richness when all introductions are additive, and merely limited by a vector driven supply rate and by the global pool of suitable species (A), when biotic resistance increases with each introduction (B), and when strong competitors, predators, parasites and diseases arrive and extirpate more and more species (C). Dotted line indicates resident species richness including immigrants in response to climate warming

Scenario B in Fig. 3 is more modest by entering saturation in the accumulation of introduced species earlier. Although facilitative effects between introduced species are also possible, biotic resistance to newcomers may increase with species richness, and this will decrease the establishment success of further introductions. This process occurred on settling plates of limited size in the marine environment and in other confined ecosystems (Stachowicz et al. 1999; Hooper et al. 2005). However, for the large, open, changeable, and heterogeneous Wadden Sea, we cannot imagine that this process could be effective. Disturbances, directional change, predators, or diseases may always clear enough spaces for the accommodation of new arrivals.

Even more unlikely may be a loss of species richness as depicted by an arrow for scenario C in Fig. 3. Up to now, no strong interactors have arrived among the more than one hundred introductions, which could have expelled residents or earlier introductions. Although theoretically possible, such species have not yet turned up in the Wadden Sea. A possible case affecting a resident non-opportunist could have been the so-called “wasting disease” in seagrasses. However, whether this pathogenic protist *Labyrinthula zosterae* (Muehlstein et al. 1991) was already a resident or introduced in the 1930s, is uncertain. Probably such introductory events will be too rare for reverting or reversing the increasing trend of species richness. Although species loss may not occur, evenness may at least temporarily decline within habitats. Fear that introductions will eliminate species entirely from the Wadden Sea seems unfounded. The persistence of residents in spite of numerous introductions in the past, also suggests that global biological homogenization (sensu Olden et al. 2004) may not be a realistic threat. Dominance by a few hyper-

successful universal invaders is not in sight. Although Pacific oysters with the associated *Sargassum*-kelp or the fouling colonial ascidian *Didemnum vexillum* achieved almost global distribution in the temperate climate zone, their occurrence in the Wadden Sea remained confined to specific habitats in a rather narrow tidal zone.

We suggest the most likely course of further establishment of introduced species may follow scenario A. Only curtailing the global supply of species could end the tide of species introductions. On the other hand, more introductions — if integrated as before — may not threaten the tidal ecosystem to collapse. Instead, increasing species richness may serve as a risk insurance and raises the adaptive capacity in the face of global change (Hooper et al. 2005; Tilman et al. 2014). Introductions affecting resident key species of the food web, such as the cockle *Cerastoderma edule*, or resident key species of habitat engineering, such as the lugworm *Arenicola marina*, may kick off an avalanche of ecological change if not thwarted by introduced equivalents taking over. However, given the Wadden Sea history, introductions leading towards a tipping point or a succession of ecological crashes seem to be an unjustified doom scenario.

Changes in the food web through introduced species

Hunting and fishing as well as coastal transformations over the past millennium have extirpated or decimated charismatic species with top positions in the food web of the Wadden Sea, i.e., grey whale, grey seal, pelican, white egrets, sea eagle, sturgeon, salmon, and rays (Wolff 2000a,b; Lotze 2005; Reise 2013). Nature protection efforts have allowed some of these to return, while others may require re-introduction. Top positions in the Wadden Sea food web are still understaffed. In contrast to losses and returnees at the top of the food web, the many introduced species primarily concern the lower levels of the trophic pyramid (Fig. 4; see also Byrnes et al. 2007). There, shares of introduced species in trophic functional groups are very uneven (Fig. 4, highlighted in red). Both in terms of species as well as in abundance and biomass, the introduced species strengthen the groups of macroalgae and benthic suspension feeders in particular, while other functional groups like herbivores hardly received any introductions. Consequently, the energy flow of the food web has changed considerably (Baird et al. 2012).

Introduced primary producers

Main primary producers in the Wadden Sea are planktonic and benthic microalgae. While a number of introduced species are known from North Sea coastal waters (Gollasch et al. 2008), occurrences in the microphytobenthos are uncertain. In the

1980–1990s, green tides by tubular algae of the genus *Ulva* (formerly *Enteromorpha*) covered tidal flats in masses (Fig. 5; Reise and Siebert 1994; Kolbe et al. 1995). In accordance with other coastal regions (i.e., Smetacek and Zingone 2013; Schreyers et al. 2021; Bermejo et al. 2022), the correlation with high nutrient runoff from land is assumed to be the main cause (van Beusekom et al. 2017, 2019). However, the taxonomy in the genus *Ulva* is like a “nightmare” (Hughes et al. 2022). To what extent introduced species or specific strains (Fort et al. 2020; Steinhagen et al. 2019) have bolstered green tides is still uncertain. Dynamics of green tides are reminiscent of boom-and-bust patterns commonly known from introduced species (Simberloff and Gibbons 2004). A reason for such dynamics may be time lags in the responses of residents to introductions. With regard to introduced brown and red algae, the substrate offered by Pacific oysters around low tide level seems to be key for increasing abundance (Lackschewitz et al. 2022). With the advent of oyster reefs new tide puddles formed. These are often covered with a mixture of introduced and resident algae (Fig. 5; K. Reise, personal observation), but the role of these novel assemblages in the food web is hardly known. In salt marsh vascular plants, merely the introduced cordgrass *Spartina* attains a significant share.

Introduced primary consumers

Among primary consumers, introductions did not supplement the guild of herbivores and relatively few introduced species, mainly annelid worms, are detritivores or grazers on microalgae (i.e., *Tharyx maryae*, *Marenzelleria viridis*, and *Alitta virens*, an omnivore, see Fig. 5). However, diversity of introduced suspension feeders may have surpassed their resident counterparts (Fig. 6). This began with the “archaeozoan” clam *Mya arenaria* centuries ago. At the end of the nineteenth century, the American piddock *Petricola pholadiformis* arrived with American oysters. The latter did not establish while the co-introduced piddock achieved intermittently high abundance but remained rare thereafter. Slipper limpets *Crepidula fornicata* also arrived initially with American oysters, established in the 1930s, and stacks form dense beds in the shallow subtidal zone (Thieltges et al. 2003). The American razor clam *Ensis leei* spread at the same tidal level since the 1980s and achieved high biomass (Schwemmer et al. 2019; Jung et al. 2020). After a slow start in the 1990s, the introduced Pacific oysters took over on mussel beds since the 2000s (Reise et al. 2017b). In the 2010s, the American dwarf surf clam *Mulinia lateralis* spread within four years, and the Pacific Manila clam *Ruditapes philippinarum* established in the northern Wadden Sea (Craeymeersch et al. 2019; Klunder et al. 2019; Lackschewitz et al. 2022). The former arrived with ballast water, and the latter initially by aquacultures in France and Britain. Both clams are expected to boom in the coming years. In upper estuarine reaches, still more introduced bivalve species established (Lackschewitz et al. 2022).

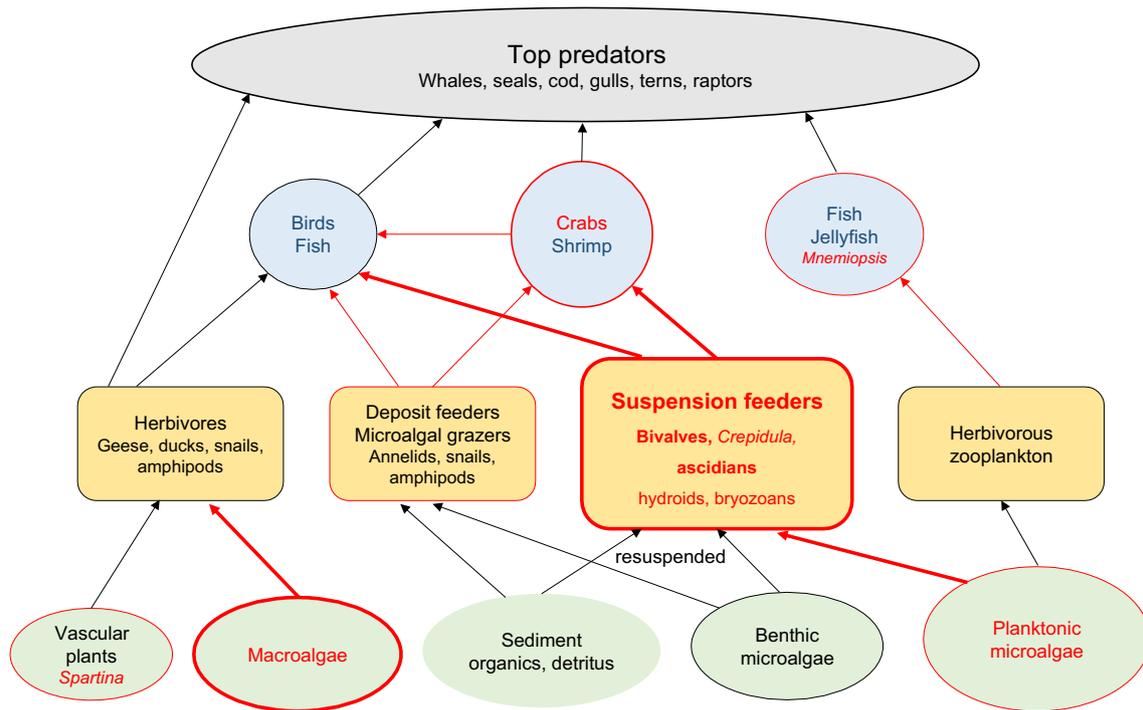


Fig. 4 Simplified Wadden Sea food web with trophic functional groups linked by arrows pointing to consumers. Red indicates high shares of introduced species, simple and bold as well as box sizes indicate their relative importance. Omnivores and parasites are not shown

Introduced ascidians (Tunicata) further add to the suspension feeder guild (Fig. 7). They arrived with ships or with oysters (Lackschewitz et al. 2022). The solitary *Molgula manhattensis* and *Styela clava* often aggregate attached to Pacific oysters in the shallow subtidal zone. At the same habitat, the colonial *Aplidium glabrum*, *Didemnum vexillum*, and *Botryllus schlosseri* expand, while *Botrylloides violaceus* is abundant on port structures. In crowded situations, colonial forms overgrow Pacific oysters and other ascidians. These represent rare cases of lethal competition between introduced suspension feeders.

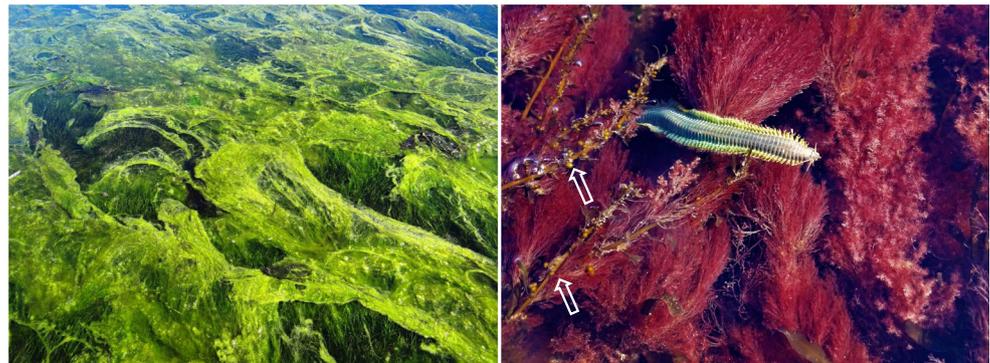
Altogether, introduced species significantly have enriched the functional guild of suspension feeders, raising benthic productivity (Baird et al. 2012; Jung et al. 2020). At high densities, suspension feeders may compete for food and their growth becomes stunted, when phytoplankton availability is temporarily limited (Dekker and Beukema 2012; Reise et al.

2017a,b; Beukema and Dekker 2019). However, predation on spat tends to keep populations of bivalves below current carrying capacity (i.e., Reise 1985; Strasser 2002), and the latter depends on the variable supply of phytoplankton from the North Sea. Although eutrophication in these coastal waters already peaked in the 1990s, it may still exceed carrying capacity for suspension feeders today (van Beusekom 2005; Reise and van Beusekom 2008; Beukema and Dekker 2020).

Introduced secondary consumers

While predation on the introduced ascidians is unknown, some introduced bivalves and slipper limpets are an important food for fish and birds, in particular the population of American razor clams is rich in biomass (i.e., Swennen et al. 1985; Caldow et al. 2007; Tulp et al. 2010; Cervencel et al. 2015; Schwemmer

Fig. 5 Green algae of the genus *Ulva* with suspected immigration background blanketing a seagrass bed (left). Introduced brown algae (*Sargassum muticum*, arrows) growing together with a mix of introduced and resident red algae on clumps of Pacific oysters with the omnivorous polychaete worm *Alitta virens* in between, which originates from Northeast America (right)



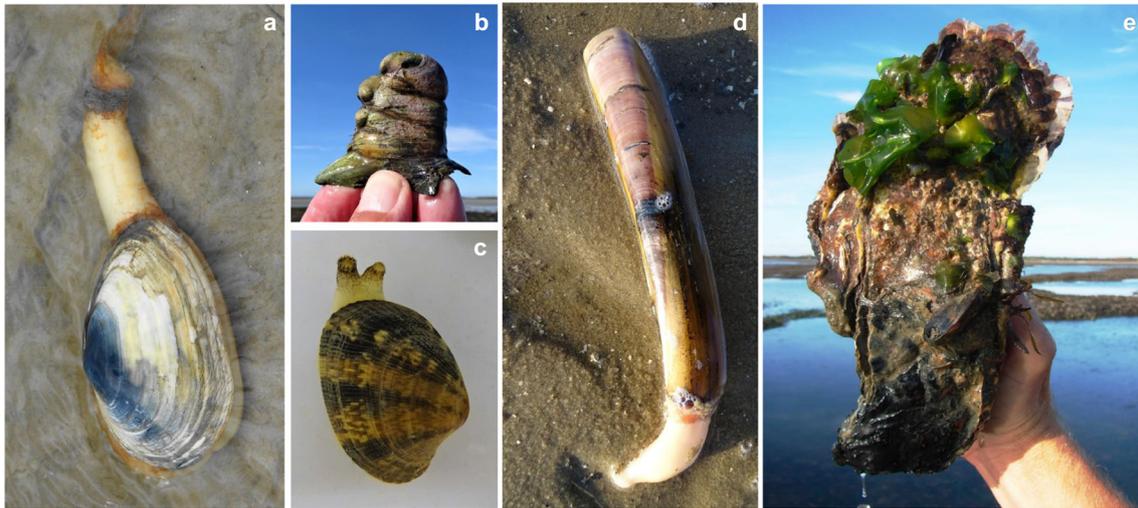


Fig. 6 Introduced suspension feeding mollusks, approximately to scale: **a** American soft shell clam *Mya arenaria*; **b** Stack of American slipper limpets *Crepidula fornicata*; **c** Pacific Manila clam *Ruditapes philippinarum*; **d** American razor clam *Ensis leei*; **e** Pacific oyster

Magallana gigas. All coexisted at spring low tide level in Königshafen near the island of Sylt in the northern Wadden Sea in January 2022, together with the residents *Mytilus edulis*, *Cerastoderma edule*, *Limecola balthica*, and *Venerupis corrugata* (own observation)

et al. 2019). Parasites hijack such links in the food web by using bivalves as intermediate and vertebrates as final hosts (Thieltges et al. 2006). Populations of introduced bivalves carry a lower burden of parasites than populations of residents (Krakau et al. 2006). Causes for this parasite release are small founder populations of hosts as well as the requirement of a specific sequence of hosts by these parasites (Torchin et al. 2003; Goedknecht et al. 2016). On the other hand, introduced suspension feeders may intercept parasite transmissions to resident hosts (Thieltges et al. 2009). In an experiment, American slipper limpets and Pacific

oysters consumed trematode cercariae which otherwise would have infected resident mussels. This dilution effect on infectious parasite stages shows an indirect benefit that introduced species offer to resident suspension feeders. Similarly, introduced Pacific oysters can interfere with parasite infections in resident mussels (Goedknecht et al. 2019; Goedknecht et al. 2020).

Introduced parasites with single host species may have severe effects on naive resident hosts (Fig. 8). In the 1930s, the parasitic copepod *Mytilicola intestinalis* appeared in the gut of mussels (Caspers 1939), followed by mass mortalities of

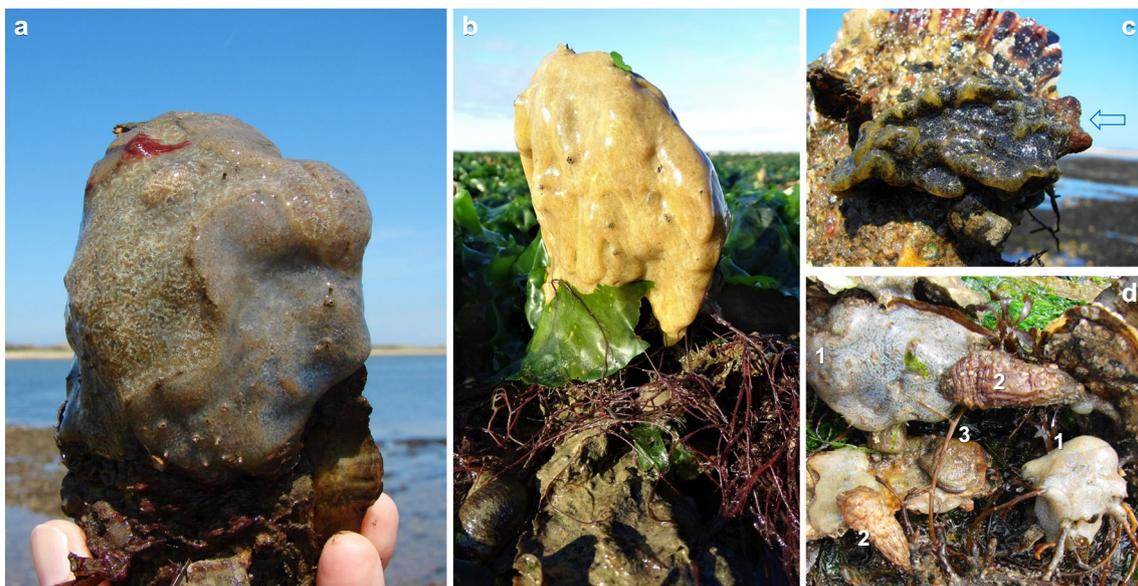


Fig. 7 Introduced ascidians in reefs of Pacific oysters: **a** Two competing colonies of *Aplidium glabrum* killed an oyster by overgrowing its aperture; between the panels; **b** Colony of *Didemnum vexillum* doing the same; between the panels; **c** Colony of *Botryllus schlosseri* overgrowing *Styela*

clava, of which merely the apertures remained free (arrow); between the panels; **d** Assembly of ascidians: Colonies of *A. glabrum* (1) with solitary *S. clava* (2) and *Molgula manhattensis* (3)

Fig. 8 Introduced parasitic copepods dwelling in the gut of bivalve hosts. While *Mytilicola intestinalis* is specific to its mytilid host, *M. orientalis* infests besides its main host *Magallana gigas* also *Mytilus edulis* and, to a lesser degree, other bivalves. Females of about 8 mm in length, the right one with egg sacs



heavily infected *Mytilus edulis* (Korringa 1968). However, in recent years, no such mortalities were observed, suggesting that early mass mortalities might rather have been caused by secondary infestations (e.g., *Vibrio* bacteria, Demann and Wegner 2018). Furthermore, reciprocal adaptations of hosts and parasites may have reduced the parasite's virulence without losing its infectivity (Feis et al. 2016). The congeneric *M. orientalis* arrived with cultured Pacific oysters and then infected some resident hosts including mussels (Goedknecht et al. 2017). While effects on the newly acquired mussel host are minor, *M. orientalis* can interfere with the host choice behavior of *M. intestinalis*, which lead to a strong decline of *M. intestinalis* in some populations (Feis et al. 2022). The decline of *M. intestinalis* went hand in hand with an overall reduction of infection rates in the shared mussel host (Feis et al. 2022). This demonstrates that negative effects of an introduced species on another (new parasite–old parasite) can at the same time have unexpected beneficial effects on residents (i.e., mussel hosts). Mortalities of resident and introduced species are more frequently caused by bacterial or viral pathogens. Population specific mortalities of Pacific oysters in the Wadden Sea are for example a result of rapid local adaptation to resident pathogenic strains of *Vibrio*-bacteria (Wendling and Wegner 2015). These disease agents stem from the recipient environment and have the potential to keep the introduced oyster population within limits (Wendling et al. 2014). In contrast, infections with ostreid herpes virus OsHv-1 spread globally with the aquaculture of Pacific oysters (Mineur et al. 2014). In combination with opportunistic bacterial infections, OsHv-1 can cause mass mortalities (de Logeril et al. 2018), and the virus was also found in resident species in

contact with introduced Pacific oysters (O'Reilly et al. 2018; Morga et al. 2021). Introduced ascidians can serve as a reservoir for such diseases (Costello et al. 2021).

So far, introduced predators seem to have no striking impacts on the food web in the Wadden Sea. In the plankton, the presence of the introduced ctenophore *Mnemiopsis leidyi* is highly variable from year to year but seasonally reaches high peak densities in the Wadden waters (van Walraven et al. 2013; own observations). Effects on fish larvae may remain low because of seasonal mismatch. In the Skagerrak region, endoparasitic larvae of a sea anemone (*Edwardsiella* sp.) infect *M. leidyi* at high rates, probably controlling the host population there (Selander et al. 2010) but has not yet been observed in the Wadden Sea. In the benthos, effects of the two introduced Pacific crabs, *Hemigrapsus sanguineus* and *H. takanoi*, may amplify the predation pressure imposed by the resident crab *Carcinus maenas* and the resident shrimp *Crangon crangon* on early benthic stages of bivalves and other groups (Bleile and Thielges 2021; Cornelius et al. 2021). However, the dynamics of other introduced populations have taught us to wait for more years until evaluating impacts on the food web. In view of the introduced bivalves and barnacles, being potential prey of the introduced crabs, an increased predation pressure may not endanger the food web but rather could dampen prey dynamics — similar as outlined above for the effects of parasites and diseases on introduced species.

In conclusion, rather than weakening the Wadden Sea food web, introduced species added several new links to the guilds of primary producers and suspension feeders, entailed by complex interactions with introduced predators, parasites, and diseases. The latter may exert control on introduced populations, but also spread to some resident species. The many

introduced species may oblige coastal birds as the flagship top consumers in the Wadden Sea to switch prey preferences. For example, large not consumable Pacific oysters may sometimes limit predator access to the preferred mussels, prompting birds to switch to American razor clams. Rather than suffering, birds are more likely to benefit. Overall, production and functional redundancy increased with species introductions, and this begets ecosystem stability — contrary to ecosystem degradations which have been assumed so often (i.e., Pyšek et al. 2020).

Increased habitat stability and complexity through introduced species

Introduced species that modify or transform habitat structure may have cascading effects on the entire ecosystem (Crooks 2002; Ruesink et al. 2006; Wallentinus and Nyberg 2007; Guy-Haim et al. 2018). In the Wadden Sea, most introduced ecosystem engineers have contributed to habitat complexity. In particular, empty shells of introduced bivalves not only accumulate large amounts of calcimass but also provide habitat to epibionts as well as hiding spaces (see Gutiérrez et al., 2003). Upright plants or reefs of Pacific oysters intercept and deflect tidal currents. In the sedimentary environment, the main effect of introduced species seems to be stabilization and sediment accretion (Fig. 9).

At the seaward edge of salt marshes, perennial *Spartina*-grasses often have established a belt of almost monospecific tussocks with higher growth and deeper roots than the resident annual glasswort *Salicornia*. Resident saltmarsh plants are displaced at the scale of tussocks; however, diversity is increased on a landscape scale. *Spartina*

facilitates sediment accretion and cushions erosion scarps at the edge of resident vegetation (Fig. 9; van Wesenbeeck et al. 2008; Balke et al. 2012; Granse et al. 2021a). This is beneficial for coping with accelerating sea level rise and constitutes a strengthening of the resident pioneer vegetation. Seaward, tussocks of *Spartina* either displace intertidal seagrass or get into spatial competition with resident sediment-destabilizing lugworms in a narrow zone of uppermost tidal flats.

Near low tide level, resident mussel beds stabilize and accrete sediment. By means of their byssal mesh, mussels form a coherent carpet upon the sediment, which storm surges or scouring ice shoals may uplift during rough season (Nehls and Thiel 1993; Donker et al. 2015). This seems to have changed since Pacific oysters became dominant on mussel beds (Fig. 9; Walles et al. 2015; Reise et al. 2017a,b; Bungenstock et al. 2021). Multi-generational towers of oysters anchor deeply in the accumulated mud and mussels intermesh with these vertical structures at the sediment-water interface (van der Meer et al. 2019). The composite structure, named oyssel reef, is more stable than a pure mussel bed, reaching further into and out of the sediment. Dominance of mussels persists where tidal exposure is too long for the oysters. Sterile wrack *Fucus vesiculosus*, anchored by byssal threads, often covers mussels, while this brown alga vanishes where oysters achieve prominence. Then other algae may take over if not prevented by grazing periwinkles. Dislodged clumps of Pacific oysters scatter over vast areas of intertidal and subtidal flats. These are rich in algal and invertebrate epibionts and serve as hideouts (Fig. 10). At sheltered sites in the shallow subtidal zone, these clumps provide anchorage to introduced *S. muticum*, forming seasonal kelp beds, reminiscent of former subtidal seagrass beds, which went extinct in the 1930s.

Fig. 9 Although large intertidal flats remain dominated by resident species (*Arenicola marina* and *Cerastoderma edule*), introduced species stabilize habitats at upper and lower shore in the Wadden Sea at Sylt: a belt of tussocks with *Spartina anglica* protects resident saltmarsh vegetation against wave erosion at mean high tide level (HW). Large oysters *Magallana gigas* associate with small resident mussels, and dislodged clumps scatter widely. Turfs of *Vaucheria*-algae convert rippled sand flats into bumpy mud flats at spring low tide level (LW)

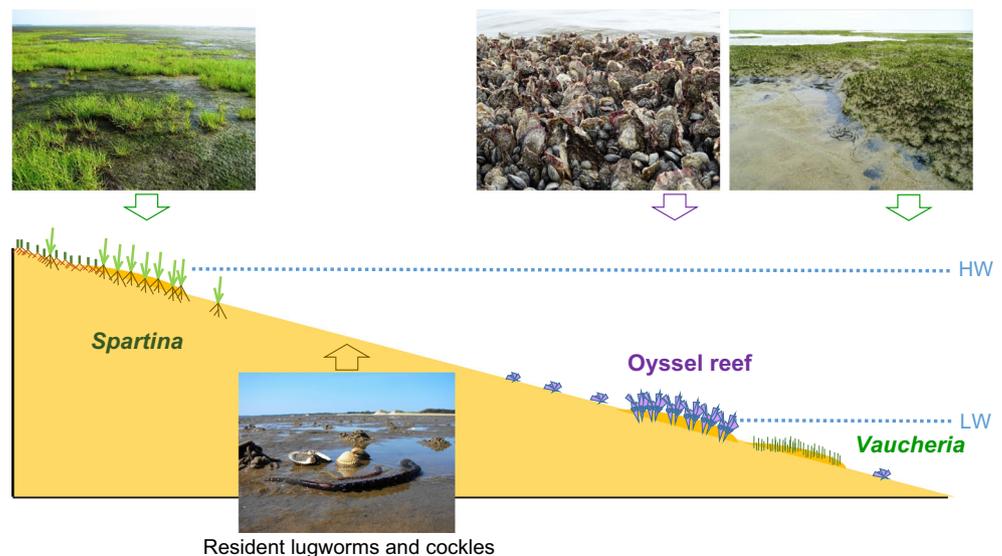




Fig. 10 Introduced mollusks as habitats: **a** clump of Pacific oysters with attached *Sargassum muticum*; **b** Shell of American razor clam sticking out of sediment and fouled by ascidians and barnacles; **c** *Hemigrapsus*

takanoi hiding in Pacific oyster valve; **d** Pacific oysters with attached mussels, barnacles and algae; **e** bed with stacks of American slipper limpets poor in epibionts because covered by silt

The recently developed turfs of the introduced, siphonous algae *Vaucheria* cf. *velutina* and *V. longicaulis* accrete fine sediment up to 20 cm higher than ambient tidal flat surface (Fig. 9; Reise et al. 2022a, b). This renders the habitat unsuitable for resident lugworms but facilitates small tube-building worms. Turfs also serve as nursery to transient early settlement stages of the tidal flat macrofauna. The tiny slug *Alderia modesta*, formerly confined to salt marshes where resident *Vaucheria* grow, is now also common at spring low tide level. It is specialized on *Vaucheria* as food and reproduces in the novel algal turf.

In conclusion, some introduced species in the Wadden Sea are important habitat transformers and habitat providers. Resident species may be expelled on a small spatial scale; however, they persist at larger scale across tidal zones. Most introduced species stabilize the sedimentary environment and facilitate mud accretion. Introduced epibenthic mollusks supply additional substrates for epibionts, and together with algae offer more hiding spaces than there were before. The overall effect is an increase of habitat and species diversity in the Wadden Sea.

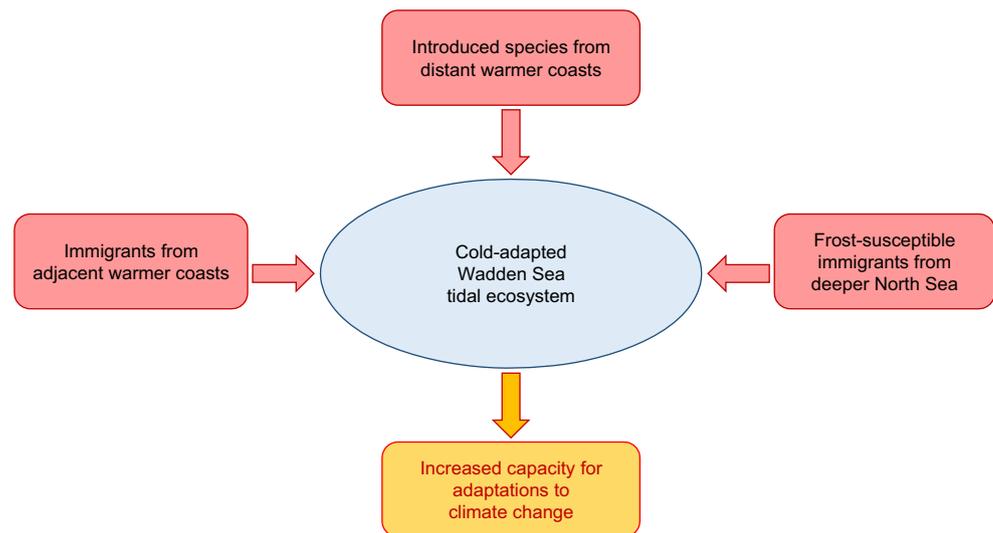
Preadapted for a warmer Wadden Sea

Human-caused climate warming entailed mean annual air and water temperatures increasing by more than 1°C in the

Wadden Sea since the 1980s, with rare sea ice in winter and more heat waves in summer (Oost et al. 2017; Rick et al. 2022). This trend may continue and extreme temperatures may affect marine biota more than annual means (Wetthey et al. 2011). Biological support for the heat-challenged but cold-adapted tidal ecosystem of the Wadden Sea may come from three different sources (Fig. 11).

Recently, some cold-intolerant species managed to extend their biogeographic ranges northward along the European Atlantic coasts (i.e., Beare et al. 2004; Türkay 2014; Philippart et al. 2017), while few populations of heat-intolerant species moved out of the North Sea region (Engelhard et al. 2014). Also, some frost-intolerant North Sea species have entered the intertidal zone of the Wadden Sea (i.e., Beukema and Dekker 2011; Kröncke et al. 2013; own observations). Long-distance migrants among wading birds declined (van Gils et al. 2016; Rakhimberdiev et al. 2018). These are feeding in the Wadden Sea in spring and autumn for doubling their weight to accomplish the second half of their seasonal flyway. Rapid warming in the Arctic entailed a cascade of mismatches. Chicks miss the peak abundance of their main prey (dipteran larvae) before hatching. As a consequence, their beaks remain too short for reaching preferred clams buried in mud flats of their wintering grounds (van Gils et al. 2016). This may eventually cause birds to

Fig. 11 Dominant contribution of introductions to species preadapted to climate warming in the Wadden Sea



cancel their long flight to Africa and stay in the Wadden Sea over winter as conspecifics breeding elsewhere already do. In that case, foraging birds may diminish food supplies if prey populations will not increase concomitantly.

What has been and will be the response of introduced species to climate warming in the Wadden Sea? Species arriving with global shipping usually embarked at ports located in warmer coastal regions than the Wadden Sea, because that is where major ports of departure are located (see Seebens et al. 2013; Sardain et al. 2019). Species introduced for aquaculture together with unintended co-introductions also mostly stem from warmer coasts. Once introduced, these species may quickly establish and spread, while immigrants from adjacent southern coasts may need more time to arrive. Thus, introductions have a head start advantage compared to range expansions (Wiens et al. 2019). Most of the one hundred species already introduced into the Wadden Sea seem to be preadapted to a warmer Wadden Sea. Probably, severe winter conditions have often prevented the establishment of many more introduced species in the past. In the case of the Pacific oysters, severe winters have delayed establishment (Reise et al. 2017b). This hurdle may become less significant with continued warming.

Several introduced species have responded with increasing abundance to recent warming (Pederson et al. 2011). Examples from the Wadden Sea are cordgrass *Spartina anglica* (Loebl et al. 2006), American slipper limpets *Crepidula fornicata* (Thieltges et al. 2004; Nehls et al. 2006), the Australian barnacle *Austrominius modestus* (Witte et al. 2010), and Pacific oysters *Magallana gigas* (Diederich et al. 2005; Reise et al. 2017b). Introduced prior to current warming, these species were on stand-by as so-called “sleepers” (sensu Spear et al. 2021). Of the more recently or newly introduced species, extremely warm summers could explain their rapid population expansion, for example, the

Pacific tube-building worm *Ficopomatus enigmaticus* in summer 2020 (Hille et al. 2021; Lackschewitz et al. 2022), the shell-boring worm *Polydora websteri* (Waser et al. 2020) or the Manila clam *Ruditapes philippinarum*, and two *Vaucheria* algae (personal observation). The latter had a poor performance in the northern Wadden Sea in the relatively cold summer of 2021 compared to the summer of 2020.

In conclusion, introduced species may raise the adaptive capacity of the Wadden Sea ecosystem facing global warming. The same should apply to warm-temperate species of the European Atlantic. However, these seem to expand more slowly. The success of introductions facilitated by warming could provide additional food to migrant wader populations, otherwise threatened by global warming. One cannot reject the possibility that some newcomers may facilitate a decline of resident populations in response to climate change. Recruitment failure in mussels (*Mytilus edulis*) during recent years should be investigated under this hypothesis (own observation, Troost 2010).

Comparisons with other coasts

With respect to effects from introductions, the Wadden Sea ecosystem is not unique in European coastal waters (i.e., see Katsanevakis et al. 2014). At the long and species-rich coast of South Africa, less introductions have established than in the Wadden Sea. However, local rocky shores may have low biodiversity, and there the introduced Mediterranean mussel *Mytilus galloprovincialis* exerted similar effects to those of Pacific oysters in the Wadden Sea (Sadchatheeswaran et al. 2018). The introduced mussels took over and displaced a native mussel species. However, the biotic zonation along the tidal gradient moderates that effect, and many other species took advantage of the complex structure of the new mussel

beds. As in the Wadden Sea, further introductions (a Pacific barnacle and a South American mussel) enriched the species spectrum at this rocky shore.

Willapa Bay and Wadden Sea

Sedimentary lagoons at the cool-temperate Pacific coast of North America accommodate a similar number of introduced species compared to the Wadden Sea (Wonham and Carlton 2005). Resident biota of the two regions share few species. However, introductions have established similarities, although the introductions occurred independently and at different times (Fig. 12; see Ruesink et al. 2006). The introduced oyster *Magallana (Crassostrea) gigas* and the Manila clam *Ruditapes philippinarum* now thrive in both regions. Ecologically, the introduced cordgrasses *Spartina alterniflora* and *S. anglica* are very similar as are the two dwarf eelgrasses, the resident *Zostera noltei* in the Wadden Sea and the introduced *Z. japonica* at Willapa Bay.

Nevertheless, the singular ecological histories of the two regions retained conspicuous differences. In the Wadden Sea, diseased subtidal beds of *Z. marina* never recovered, except for a small growth form in the intertidal. At Willapa Bay, this eelgrass remained in place. Fishery overharvested resident oysters in both regions. However, the Northeast Pacific *Ostrea lurida* survived at decimated state, while the European *O. edulis* vanished from the Wadden Sea. Here, mussel beds turned into oyster reefs by the introduced Pacific oysters (see above), while Pacific bay mussels (*M. trossulus*) occur only in rare habitats inaccessible to predators in Willapa Bay, so no analogue to an oyster reef occurs (J. Ruesink, personal communication). The introduced

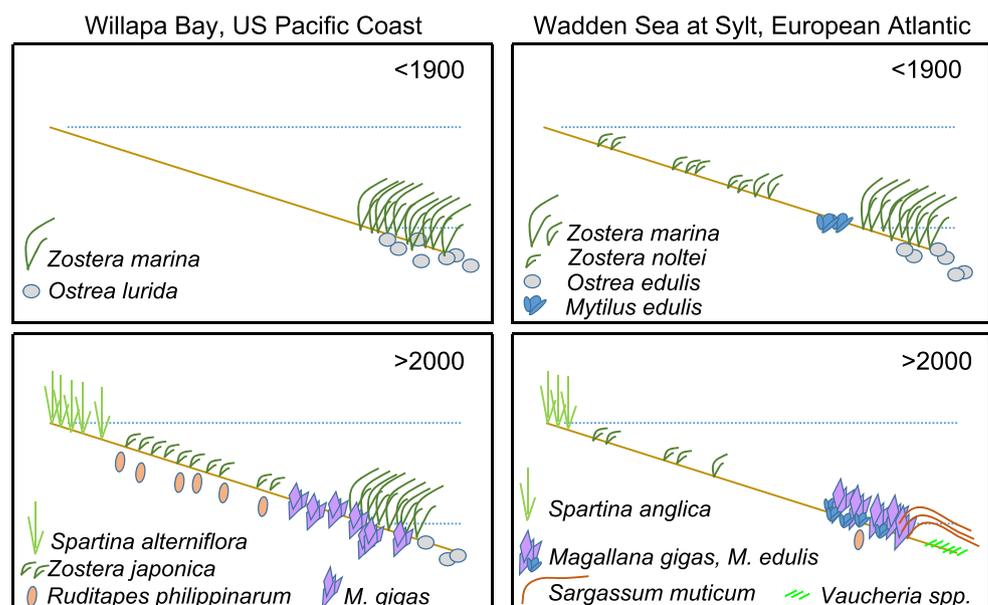
Vaucheria-algae below low tide level in the Wadden Sea has no analogue in Willapa Bay, while the kelp *Sargassum muticum* established in both regions. Intermittently it was abundant but is not conspicuous anymore in Willapa Bay (Kincaid 1968; J. Ruesink personal communication). The two regions also differ in resident sediment bioturbators, the Pacific shrimp *Neotrypaea (Callinassa) californiensis* in Willapa Bay and the Atlantic lugworm *Arenicola marina* in the Wadden Sea.

In addition to ecological differences, shellfish farming and environmental management follow different strategies. At Willapa Bay, Pacific oysters and Manila clams are primarily grown on or in sediment, and both planted and feral populations are harvested. In part of the Wadden Sea at Sylt, bottom cultures are in use for harvesting resident mussels, while Pacific oysters grow in net bags on trestles. Feral populations remain more or less untouched. At Willapa Bay, introduced cordgrass was controlled with herbicides, while such measures are not allowed — and not necessary — in the protected Wadden Sea. In spite of some parallel developments and profound ecological change caused by introductions, convergence of the two ecosystems will remain limited, not leading to ecological homogenization, mainly because residents remain in place and not all introductions are shared.

Limits to biotic homogenization

Similar coastal ecosystems neighboring the Wadden Sea have received similar introductions. Only the timelines differ. The Dutch Rhine Delta includes with the Oosterschelde a hotspot of shellfish farming and with Rotterdam and Antwerp Europe's most important port facilities. Not surprisingly,

Fig. 12 Long-term change (before 1900 and after 2000) in space-occupying species on tidal flats of Willapa Bay, Washington, USA (redrawn after Ruesink et al. 2006) and in the Wadden Sea at Sylt, showing losses (overharvested *O. lurida* and *O. edulis*, diseased European *Z. marina*), and species introductions: *S. alterniflora/anglica* and *Z. japonica* occupy similar niches, respectively. *M. gigas* and *R. philippinarum* arrived decades later in the Wadden Sea. Slopes are exaggerated; stippled lines show mean high and low water levels of similar tide ranges



many introductions first occurred in the Rhine Delta before they have spread further to the Wadden Sea. Although smaller than the Wadden Sea, the Rhine Delta has a record of 137 introduced species (Gittenberger et al. 2017) compared to 113 in the Wadden Sea (Buettger et al. 2022). Differences in the spectrum of introduced species usually do not last long.

A look beyond the Wadden Sea shows that also ecosystems in other coastal regions changed profoundly in the wake of biological globalization, often more than by other anthropogenic effects, although these always interact (Anton et al. 2019; Byrnes et al. 2007; Cuthbert et al. 2021; Dauvin et al. 2019; Hewitt et al. 2004; Kerckhof et al. 2007; Occhipinti-Ambrogi et al. 2011; Pezy et al. 2021; Staehr et al. 2020; Wasson et al. 2005). Common to all is species enrichment at the lower levels of the trophic pyramid and novel biogenic habitats. Coastal ecosystems of distant regions but similar climate have converged to some extent. However, they will most likely not become the same because the different residents remain, timelines of introductions differ, and interactions between resident and introduced species launch different co-evolutionary trajectories (Feis et al. 2016). Although aquafarming or planting promoted a few universal “winners”, our conclusion contradicts the expectation of McKinney and Lockwood (1999) because residents are not generally the “losers” in coastal ecosystems. They are not the ecological specialists replaced by “broadly adapted ecological generalists”, but more often, they intermix and ecosystems become more complex rather than simpler. To quantitatively investigate generalities and specificities, a more comprehensive meta-analysis using a broad database of coastal ecosystems is desirable.

A blessing rather than a curse?

Readers familiar with the dogma that introduced species are threatening biodiversity and ecosystem functions, may accuse us of romanticizing virulent introductions into felicitous ecological complements, like stylizing a criminal like “Billy the kid” into a “Robin Hood” of the wild west. The reason for our deviant position is that the Wadden Sea is neither a remote oceanic island nor an isolated continental lake with a high degree of vulnerable endemism and low predator diversity. Furthermore, it is not a landscape with fragmented and transformed natural habitats nor with a sprawl of human residence and infrastructures. Instead, the Wadden Sea is a large protected nature area where humans are supposed to be merely visitors. Low diversity of benthic biota in this northern coastal sea is the result of a changeable geological and ecological history. Natural immigrants have been few because strongly fluctuating environmental conditions constitute a barrier. The fall of biogeographic boundaries in the wake of transoceanic shipping and aquaculture has made this region accessible to

more species adapted to this kind of environment. These newcomers particularly enlarged the guilds of suspension feeders, habitat stabilizers, and genotypes preadapted to a Wadden Sea now subject to global warming. More than one hundred introduced species have raised biodiversity and boosted ecosystem functioning. Admittedly, introductions can also affect other species negatively. However, our review shows that these negative effects are comparatively rare and context dependent. It would thus be a distortion when only focusing on those and neglecting beneficial effects (Katsanevakis et al. 2014; Kourantidou et al. 2022).

If we regard well-integrated introduced species as natural components of an ecosystem responding to change, then these do not violate the guiding principle for the protected Wadden Sea (Common Wadden Sea Secretariat 2010): “... to achieve, as far as possible, a natural and sustainable ecosystem in which natural processes proceed in an undisturbed way”. There is no strict definition for natural. Since the omnipresence of human impacts in the planetary biosphere, the term natural can no longer stand for the irreversibly lost pristine conditions. The aim can only be an absence of direct human interferences in the ecological processes. This certainly also includes introductions. However, introduced species after centuries or decades of integration should not anymore regarded as a direct human impact. Their origin has no implications on their present role in the ecological web. They contribute to ecosystem sustainability just as other resident species do.

The Wadden Sea is not an outstanding hot spot of species introductions relative to other coastal regions and, similar to these, newcomers have not fundamentally transformed this ecosystem. Together with climate change, sea level rise, coastal protection, and other human impacts, species introductions have nevertheless accumulated irreversible ecological change within human lifetime that once occurred at the scale of millennia. Such developments challenge traditional conservation goals (Carroll 2011; Schuurman et al. 2022). If they ever applied, concepts of maintaining or restoring pristine conditions, of resilience and ecological integrity, they no longer help in this nonstationary world. Especially in the context of introduced species often being characterized as abrupt ecological dynamics, we need concepts for stewarding change by quality indicators that are rate-based rather than state-based (Williams et al. 2021). This is the aim of our appraisal on the effects of introduced species in the tidal ecosystem of the Wadden Sea.

The high integrative capacity of the Wadden Sea ecosystem is a legacy of its nature. So far, biological newcomers have supplemented the ecosystem without expelling residents. Biodiversity increased and this mitigates effects of other consequences of human dominance in the biosphere which do not stop at boundaries of protected areas for nature. Universally outstanding values of the Wadden Sea World Heritage Site are large expanses of tidal flats and spectacular flocks of foraging

migratory birds. Chances to protect the inherited poor benthic diversity from further introductions in an era of globalization are extremely low. Furthermore, eradications of established populations in marine environments are almost impossible (i.e., Cheng et al. 2022; but see Williams and Grosholz 2008). Some introduced populations only unfold decades after their initial introduction (Spear et al. 2021). Early introductions might have already initiated co-evolutionary adaptations with residents, and evolved specific adaptations to their new environment (Strayer et al. 2006). Facing rapid warming and accelerating sea level rise, we may even ask how desirable eradications would be. Introduced species often attained valuable positions in ecological webs. As long as excessive global trade is at the root of increasing biotic globalization, this can at best be mitigated but not stopped unless economic degrowth leads to a post-capitalistic global economy.

Our review is confined to the aquatic realm of the Wadden Sea, but the situation with introduced species seems to be rather similar at many other coasts. On adjacent land with salt marsh and sand dune habitats; however, our conclusions may not apply (Buettger et al. 2022). These habitats have a more intricate cultural history, biosecurity and aesthetic values are involved, and human uses are more intense than under tidal waters. In salt marshes and dunes, policies and nature management have to consider more specific human interests. Handling of introduced species should be part of that. Eco-evolutionary dynamics of interactions between resident and introduced species may be attended with conciliatory strategies (Carroll 2011). In contrast to an adverse attitude against introduced species in general, we advocate a species and ecosystem specific evaluation.

Recommendations

We do not recommend continuing with unabated introductions because these always bear a risk of introducing devastating diseases or predators with ecosystem-wide effects (Gurevitch and Padilla 2004). The competitive race between the resident shore crab *Carcinus maenas* and the two introduced *Hemigrapsus* species is certainly still open in the Wadden Sea and fouling ascidians can smother their basibionts (see above). Furthermore, there always may remain a residual risk that in the very long term, the once introduced and then well integrated species may expel others when new circumstances arise. On the other hand, it would be shortsighted to demand for more biosecurity with false substantiations on threatened biodiversity and potential malfunctions of the Wadden Sea ecosystem. With this review on the effects of species introductions in the Wadden Sea, we admonish honesty and realism. Nature management should continue elaborating on pre-entry precautionary measures against introductions at the scale of the European Atlantic coasts. In the

Wadden Sea, however, we should overcome mental reservations against “alien species”, often fueled by overgeneralizing and alarming scientific literature on “severe impacts of biological invasions” when no more than ecological change in species interactions is at stake. Warnings may be appropriate for many ecosystems (i.e., Pyšek et al. 2020). However, in the case of the tidal Wadden Sea and other coastal regions, we should recognize the special legacy of the past and the outstanding integrative capacity of such ecosystems. In the Wadden Sea, the overall result of more than one hundred integrations of introduced species is not a degenerated ecosystem but rather one of increased adaptability by a unique mixture of resident species with those from overseas. We recommend assessing the balance between negative and beneficial effects of introductions in other coastal ecosystems in view of ongoing other global change processes which require novel adaptations.

Instead of worrying about decreasing naturalness when lists of “alien species” become longer and longer, we should better turn to an appreciation of what has happened to this sea of immigrants in terms of ecological diversity and complexity. The entertaining and often fascinating narratives behind individual introductions, entailed by ecological cascades that research can reveal, constitute both, a cultural as well as natural enrichment. These species introductions may even serve to bridge the traditional dichotomy between nature and culture in our human-nature relationship. We could admire the unfolding novel nature.

Although replacing words can only be a minor step when complex attitudes towards values and norms are concerned, we recommend accepting introduced species as new or novel residents once established, and not continue calling them aliens or invasive species. From an ecological or evolutionary perspective, introduced species are a similar challenge to the recipient ecosystem than are recent immigrants from adjacent regions, which respond to human-caused climate warming by extending their biogeographic range into the Wadden Sea. Different appraisal may not be justified. We may compare our attitude towards introduced species with our use of words from other languages. Most are not necessary, but some are inescapable. By prolonged usage, these words become an integral part of our daily language and we forget about their origin. Nevertheless, research on their etymology may offer interesting insights to our cultural history. The same applies to ecological research on introduced species improving our knowledge on ecosystem functioning.

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References

- Ainouche ML, Fortune PM, Salmon A, Parisod C, Grandbastien M-A et al (2009) Hybridization, polyploidy and invasion: lessons from *Spartina* (Poaceae). *Biol Invasions* 11:1159–1173. <https://doi.org/10.1007/s10530-008-9383-2>
- Anger K (1991) Effects of temperature and salinity on the larval development of the Chinese mitten crab *Eriocheir sinensis* (Decapoda, Grapsidae). *Mar Ecol Prog Ser* 72:103–110
- Anton A, Geraldi NR, Lovelock CE, Apostolaki ET, Bennett S, Cebrian J et al (2019) Global ecological impacts of marine exotic species. *Nat Ecol Evol* 3:787–800. <https://doi.org/10.1038/s41559-019-0851-0>
- Arbačiauskas K, Semenchenko V, Grabowski M, Leuven RSEW, Paunović M et al (2008) Assessment of biocontamination of benthic macroinvertebrate communities in European inland waterways. *Aquat Invasions* 3:211–230. <https://doi.org/10.3391/ai.2008.3.2.12>
- Armonies W, Reise K (1999) On the population development of the introduced razor clam *Ensis americanus* near the island of Sylt (North Sea). *Helgol Mar Res* 52:291–300. <https://doi.org/10.1007/BF02908903>
- Bailey SA, Brown L, Campbell ML, Canning-Clode J, Carlton JT et al (2020) Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: a 50-year perspective. *Divers Distrib* 26:1780–1797. <https://doi.org/10.1111/ddi.13167>
- Baird D, Asmus H, Asmus R (2012) Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. *Mar Ecol Prog Ser* 462:143–162. <https://doi.org/10.3354/meps09837>
- Balke T, Klaasen PC, Garbutt A, van der Wal D, Herman PJM, Bouma TJ (2012) Conditional outcome of ecosystem engineering: a case study on tussocks of the salt marsh pioneer *Spartina anglica*. *Geomorphology* 153–154:232–238. <https://doi.org/10.1016/j.geomorph.2012.03.002>
- Beare DJ, Burns F, Greig A, Jones EG, Peach K et al (2004) Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. *Mar Ecol Prog Ser* 284:269–278
- Bermejo R, Golden N, Schrofner E, Knöller K, Fenton O et al (2022) Biomass and nutrient dynamics of major green tides in Ireland: implications for biomonitoring. *Mar Pollut Bull* 175:113318. <https://doi.org/10.1016/j.marpolbul.2021.113318>
- Beukema JJ, Dekker R (2011) Increasing species richness of the macrozoobenthic fauna on tidal flats of the Wadden Sea by local range expansion and invasion of exotic species. *Helgol Mar Res* 65:155–164. <https://doi.org/10.1007/s10152-010-0210-7>
- Beukema JJ, Dekker R (2019) The carrying capacity of a tidal flat area for suspension-feeding bivalves. *Mar Ecol Prog Ser* 629:55–65. <https://doi.org/10.3354/meps13099>
- Beukema JJ, Dekker R (2020) Half century of monitoring microbenthic animals on tidal flats in the Dutch Wadden Sea. *Mar Ecol Prog Ser* 656:1–18. <https://doi.org/10.3354/meps13555>
- Bij de Vaate A, Jazdzewski K, Ketelaars HAM, Gollasch S, van der Velde G (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Can J Fish Aquat Sci* 59:1159–1174. <https://doi.org/10.1139/F02-098>
- Bleile N, Thielges DW (2021) Prey preferences of invasive (*Hemigrapsus sanguineus*, *H. takanoi*) and native (*Carcinus maenas*) intertidal crabs in the European Wadden Sea. *J Mar Biol Assoc UK* 101:811–817. <https://doi.org/10.1017/S0025315421000655>
- Boestfleisch C, Drotleff AM, Ternes W, Nehring S, Pažzoutová S, Papenbrock J (2015) The invasive ergot *Claviceps purpurea* var. *spartinae* recently established in the European Wadden Sea on common cord grass is genetically homogenous and the sclerotia contain high amounts of ergot alkaloids. *Eur J Plant Pathol* 141:445–461. <https://doi.org/10.1007/s10658-014-0555-x>
- Bouma S, Gollasch S, Lengkeek W (2011) Neobiota in the Wadden Sea including recommendations for a trilateral strategy. Report nr 11-097. Prepared for Programma Rijke Waddenzee and the Common Wadden Sea Secretariat, Wilhelmshaven, Germany. 80 p
- Bouwmeester MM, Waser AM, van der Meer J, Thielges DW (2020) Prey size selection in invasive (*Hemigrapsus sanguineus* and *H. takanoi*) compared with native (*Carcinus maenas*) marine crabs. *J Mar Biol Assoc UK* 100:73–77. <https://doi.org/10.1017/S0025315419000985>
- Briggs JC (2010) Marine biology: the role of accommodation in shaping marine biodiversity. *Mar Biol* 157:2117–2126. <https://doi.org/10.1007/s00227-010-1490-9>
- Buettger H, Buschbaum C, Dolmer P, Gittenberger A, Jensen K, Kabuta S, Lackschewitz D, Troost K (2017) Alien species. In: Kloepper S et al (eds) Common Wadden Sea Secretariat. Wilhelmshaven, Germany [qsr.waddensea-worldheritage.org/reports/alien-species](https://www.qsr.waddensea-worldheritage.org/reports/alien-species)
- Buettger H, Christoph S, Buschbaum C, Gittenberger A, Jensen K, Kabuta S, Lackschewitz D (2022) Alien species. In: Kloepper S et al (eds) Common Wadden Sea Secretariat. Wilhelmshaven, Germany [qsr.waddensea-worldheritage.org/reports/alien-species](https://www.qsr.waddensea-worldheritage.org/reports/alien-species)
- Bungenstock F, Hertweck G, Hochstein ML, Wehrmann A (2021) Distribution pattern and controls of biosedimentary facies in backbarrier tidal flats of the central Wadden Sea (North Sea). *Z Dt*

- Ges Geowiss 172:409–428. <https://doi.org/10.1127/zdgg/2021/0248>
- Buschbaum C, Chapman AS, Saier B (2006) How an introduced seaweed can affect epibiota diversity in different coastal systems. *Mar Biol* 148:743–754. <https://doi.org/10.1007/s00227-005-0128-9>
- Buschbaum C, Lackschewitz D, Reise K (2012) Nonnative macrobenthos in the Wadden Sea ecosystem. *Ocean Coast Manag* 68:89–101. <https://doi.org/10.1016/j.ocecoaman.2011.12.011>
- Byrnes JE, Reynolds PL, Stachowicz JJ (2007) Invasions and extinctions reshape coastal marine food webs. *PLoS ONE* 3:e295. <https://doi.org/10.1371/journal.pone.0000295>
- Caldow RWG, Stillman RA, Durell SEA, West AD, McGroarty JD et al (2007) Benefits to shorebirds from invasion of a non-native shellfish. *Proc R Soc B* 274:1449–1455. <https://doi.org/10.1098/rspb.2007.0072>
- Carroll SP (2011) Conciliation biology: the eco-evolutionary management of permanently invaded biotic systems. *Evol Appl* 4:184–199. <https://doi.org/10.1111/j.1752-4571.2010.00180.x>
- Caspers H (1939) Über Vorkommen und Metamorphose von *Mytilicola intestinalis* Steuer (Copepoda paras.) in der südlichen Nordsee. *Zool Anz* 126:161–171
- Cassini MH (2020) A review of the critics of invasion biology. *Biol Rev* 95:1467–1478. <https://doi.org/10.1111/brv.12624>
- Cervencel A, Troost K, Dijkman E, de Jong M, Smit CJ et al (2015) Distribution of wintering common Eider *Somateria mollissima* in the Dutch Wadden Sea. *Mar Biol* 162:153–168. <https://doi.org/10.1007/s00227-014-2594-4>
- Cheng BS, Blumenthal J, Chang AL, Barley J, Ferner MC et al (2022) Severe introduced predator impacts despite attempted functional eradication. *Biol Invasions* 24:725–739. <https://doi.org/10.1007/s10530-021-02677-3>
- Collin SB, Shucksmith RJ (2022) Developing biosecurity plans for non-native species in marine dependent areas: the role of legislation, risk management and stakeholder engagement. *Manag Biol Invasions* 13:1–23. <https://doi.org/10.3391/mbi.2022.13.1.01>
- Common Wadden Sea Secretariat (2010) Sylt Declaration. Ministerial Council Declaration of the Eleventh Trilateral Governmental Conference on the Protection of the Wadden Sea. Common Wadden Sea Secretariat, Wilhelmshaven, Germany
- Cornelius A, Wagner K, Buschbaum C (2021) Prey preferences, consumption rates and predation effects of Asian shore crabs (*Hemigrapsus takanoi*) in comparison to native shore crabs (*Carcinus maenas*) in northwestern Europe. *Mar Biodivers* 51:75. <https://doi.org/10.1007/s12526-021-01207-7>
- Costello KE, Lynch SA, McAllen R, O’Riordan RM, Culloty SC (2021) The role of invasive tunicates as reservoirs of molluscan pathogens. *Biol Invasions* 23:641–655. <https://doi.org/10.1007/s10530-020-02392-5>
- Craeymeersch JA, Faasse MA, Gheerardyn H, Troost K, Nijland R et al (2019) First records of the dwarf surf clam *Mulinia lateralis* (Say, 1822) in Europe. *Mar Biodiv Records* 12:5. <https://doi.org/10.1186/s41200-019-0164-7>
- Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166. <https://doi.org/10.1034/j.1600-0706.2002.970201.x>
- Cuthbert RN, Kotronaki SG, Carlton JT, Ruiz GM, Fofonoff P, Briski E (2022) Aquatic invasion patterns across the North Atlantic. *Glob Chang Biol* 28:1376–1387. <https://doi.org/10.1111/gcb.16016>
- Cuthbert RN, Kotronaki SG, Dick JTA, Briski E (2020) Salinity tolerance and geographical origin predict global alien amphipod invasions. *Biol Lett* 16:20200354. <https://doi.org/10.1098/rsbl.2020.0354>
- Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Daigne C et al (2021) Global economic costs of aquatic invasive alien species. *Sci Total Environ* 775:145238. <https://doi.org/10.1016/j.scitotenv.2021.145238>
- Dauvin J-C, Pezy J-P, Baffreau A (2019) The english channel: becoming like the seas around Japan. In: Komatsu T et al (eds) *Oceanography challenges to future earth*. https://doi.org/10.1007/978-3-030-00138-4_9
- Davis M, Chew MK, Hobbs RJ, Lugo AE, Ewel JJ et al (2011) Don’t judge species on their origin. *Nature* 474:153–154
- de Logeril J, Lucasson A, Petton B, Toulza E, Montagnani C et al (2018) Immune-suppression by OsHV-1 viral infection causes fatal bacteraemia in Pacific oysters. *Nat Commun* 9:4215. <https://doi.org/10.1038/s41467-018-06659-3>
- Dekker R, Beukema JJ (2012) Long-term dynamics and productivity of a successful invader: The first three decades of the bivalve *Ensis directus* in the western Wadden Sea. *J Sea Res* 71:31–40. <https://doi.org/10.1016/j.seares.2012.04.004>
- Demann F, Wegner KM (2018) Infection by invasive parasites increases susceptibility of native hosts to secondary infection via modulation of cellular immunity. *J Anim Ecol* 88:427–436. <https://doi.org/10.1111/1365-2656.12939>
- Diederich S, Nehls G, van Beusekom JEE, Reise K (2005) Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? *Helgol Mar Res* 59:97–106. <https://doi.org/10.1007/s10152-004-0195-1>
- Donker JJA, van der Vegt M, Hoekstra P (2015) Erosion of an intertidal mussel bed by ice- and wave-action. *Cont Shelf Res* 106:60–69
- Dörjes J, Gadow S, Reineck H-E, Bir Sing I (1969) Die Rinnen der Jade (Südliche Nordsee). *Sedimente und Makrobenthos*. Senckenberg Marit 50:5–62
- Drent J, Bijkerk R, Herlyn M, Grotjahn M, Voß J et al. (2017) Macrozoobenthos. In: Wadden Sea Quality Status Report 2017. Klopper S et al. (eds). Common Wadden Sea Secretariat, Wilhelmshaven, Germany
- Edelist D, Rilov G, Golani D, Carlton JT, Spanier E (2013) Restructuring the sea: profound shifts in the world’s most invaded ecosystem. *Divers Distrib* 19:69–77. <https://doi.org/10.1111/ddi.12002>
- Elliott M (2003) Biological pollutants and biological pollution – an increasing cause for concern. *Mar Pollut Bull* 46:275–280. [https://doi.org/10.1016/S0025-326X\(02\)00423-X](https://doi.org/10.1016/S0025-326X(02)00423-X)
- Emmerson M (2000) Remedial habitat creation: does *Nereis diversicolor* play a confounding role in the colonization and establishment of the pioneering saltmarsh plant, *Spartina anglica*? *Helgol Mar Res* 54:110–116. <https://doi.org/10.1007/s101520050009>
- Engelen AH, Serebryakova A, Ang P, Britton-Simmons K, Mineur F et al (2015) Circumglobal invasion by the brown seaweed *Sargassum muticum*. *Oceanogr Mar Biol Annu Rev* 53:81–126
- Engelhard GH, Righton DA, Pinnegar JK (2014) Climate change and fishing: a century of shifting distribution in North Sea cod. *Glob Chang Biol* 20:2473–2483. <https://doi.org/10.1111/gcb.12513>
- Eschweiler N, Christensen HT (2011) Trade-off between increased survival and reduced growth for blue mussels living on Pacific oyster reefs. *J Exp Mar Biol Ecol* 403:90–95. <https://doi.org/10.1016/j.jembe.2011.04.010>
- Essink K (1985) On the occurrence of the American jack-knife clam *Ensis directus* (Conrad, 1843) (Bivalvia, Cultellidae) in the Dutch Wadden Sea. *Basteria* 49:73–80
- Essink K, Oost AP (2019) How did *Mya arenaria* (Mollusca; Bivalvia) repopulate European waters in medieval times? *Mar Biodivers* 49:1–10. <https://doi.org/10.1007/s12526-017-0816-y>
- Essink K, Oost AP, Streurman HJ, van der Plicht J (2016) Are medieval *Mya arenaria* (Mollusca; Bivalvia) in the Netherlands also clams before Columbus? *Neth J Geosci*:1–8. <https://doi.org/10.1017/njg.2016.17>
- Essl F, Dullinger S, Genovesi P, Hulme PE, Jeschke JM et al (2019) A conceptual framework for range-expanding species that track human-induced environmental change. *BioScience* 69:908–919. <https://doi.org/10.1093/biosci/biz101>

- Essl F, Hulme PE, Jeschke JM, Keller R, Pyšek P et al (2017) Scientific and normative foundations for the valuation of alien-species impacts: Thirteen core principles. *BioScience* 67:166–178. <https://doi.org/10.1093/biosci/biw160>
- Farke H (1979) Population dynamics, reproduction and early development of *Tharyx marioni* (Polychaeta, Cirratulidae) on tidal flats in the German Bight. *Veröff Inst Meeresforsch Bremerhaven* 18:69–99
- Feis ME, Goedknecht MA, Thielges DW, Buschbaum C, Wegner KM (2016) Biological invasions and host-parasite coevolution: different coevolutionary trajectories along parasite invasion fronts. *Zoology* 119:366–374. <https://doi.org/10.1016/j.zool.201.05.012>
- Feis ME, Gottschalck L, Ruf LC, Theising F, Demann F, Wegner KM (2022) Invading the occupied niche: how a parasitic copepod of introduced oysters can expel a congener from native mussels. *Front Mar Sci* 9:915841. <https://doi.org/10.3389/fmars.2022.915841>
- Fort A, Manion C, Fariñas-Franco JM, Sulpice R (2020) Green tides select for fast expanding *Ulva* strains. *Sci Total Environ* 698:134337. <https://doi.org/10.1016/j.scitotenv.2019.134337>
- Fridley JD, Sax DF (2014) The imbalance of nature: revisiting a Darwinian framework for invasion biology. *Glob Ecol Biogeogr* 23:1157–1166. <https://doi.org/10.1111/geb.12221>
- Galil BS (2009) Taking stock: inventory of alien species in the Mediterranean Sea. *Biol Invasions* 11:359–372. <https://doi.org/10.1007/s10530-008-9253-y>
- García-Díaz P, Cassey P, Norbury G, Lambin X, Montti L et al (2021) Management policies for invasive alien species: addressing the impacts rather than the species. *BioScience* 71:174–185. <https://doi.org/10.1093/biosci/biaa139>
- Geburzi JC, Brandis D, Buschbaum C (2018) Recruitment patterns, low cannibalism and reduced interspecific predation contribute to high invasion success of two Pacific crabs in northwestern Europe. *Estuar Coast Shelf Sci* 200:460–472. <https://doi.org/10.1016/j.ecss.2017.11.032>
- Gittenberger A, Rensing M, Stegenga H, Hoeksema B (2010) Native and non-native species of hard substrata in the Dutch Wadden Sea. *Nederlands Faunistische Mededelingen* 33:21–75
- Gittenberger A, Rensing M, Wesdorp KH (2017) Non-indigenous marine species in the Netherlands. GiMaRIS report 2017-13, pp 39
- Glenner H, Lützen J, Pacheco-Riáño LC, Noever C (2021) Expansion of the barnacle *Austrominius modestus* (Darwin, 1854) (Cirripedia, Thoracia, Balanidae) into Scandinavian waters based on collection data and niche distribution modeling. *Aquat Invasions* 4:675–689. <https://doi.org/10.3391/ai.2021.16.04.06>
- Goedknecht MA, Buschbaum C, van der Meer J, Wegner KM, Thielges DW (2020) Introduced marine ecosystem engineer indirectly affects parasitism in native mussel hosts. *Biol Invasions* 22:3223–3237. <https://doi.org/10.1007/s10530-020-02318-1>
- Goedknecht MA, Feis ME, Wegner KM, Luttkhuizen PC, Buschbaum C et al (2016) Parasites and marine invasions: ecological and evolutionary perspectives. *J Sea Res* 113:11–27. <https://doi.org/10.1016/j.seares.2015.12.003>
- Goedknecht MA, Nauta R, Markovic M, Buschbaum C, Folmer EO, Luttkhuizen PC et al (2019) How invasive oysters can affect parasite infection patterns in native mussels on a large spatial scale. *Oecologia* 190:99–113. <https://doi.org/10.1007/s00442-019-04408-x>
- Goedknecht MA, Schuster A-K, Buschbaum C, Gergs R, Jung AS et al (2017) Spillover but no spillback of two invasive parasitic copepods from invasive Pacific oysters (*Crassostrea gigas*) to native hosts. *Biol Invasions* 19:365–379. <https://doi.org/10.1007/s10530-016-1285-0>
- Gollasch S, Haydar D, Minchin D, Reise K, Wolff WJ (2008) Introduced aquatic species of the North Sea coasts and adjacent brackish waters. In: Rilov G, Crooks JA (eds) *Biological invasions in marine ecosystems: ecological, management, and geographic perspectives*. Springer, Berlin, pp 507–528
- Granse D, Suchrow S, Jensen K (2021a) Long-term invasion dynamics of *Spartina* increase vegetation diversity and geomorphological resistance of salt marshes against sea level rise. *Biol Invasions* 23:871–883. <https://doi.org/10.1007/s10530-020-02408-0>
- Granse D, Motta MR, Suchrow S, von Schwartzberg K, Schnittger A, Jensen K (2021b) The overlooked hybrid: geographic distribution and niche differentiation between *Spartina* cytotypes (Poaceae) in Wadden Sea salt marshes. *Estuar Coasts*. <https://doi.org/10.1007/s12237-021-00985-4>
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends Ecol Evol* 19:470–474. <https://doi.org/10.1016/j.tree.2004.07.005>
- Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101:79–90
- Guy-Haim T, Lyons D, Kotta J, Ojaveer H, Queirós AM et al (2018) Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: a global review and meta-analysis. *Glob Chang Biol* 24:906–924. <https://doi.org/10.1111/gcb.14007>
- Hedgpeth JW (1980) The problem of introduced species in management and mitigation. *Helgoländer Meeresun* 33:662–673
- Hewitt CL, Campbell ML, Thresher RE, Martin RB, Boyd S et al (2004) Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. *Mar Biol* 144:183–202. <https://doi.org/10.1007/s00227-003-1173-x>
- Hille S, Kunz F, Markfort G, Rizhofen L, Zettler ML (2021) First record of mass occurrence of the tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923) (Serpulidae: Polychaeta) in coastal waters of the Baltic Sea. *Biol Invasions Records* 10:859–868. <https://doi.org/10.3391/bir.2021.10.4.10>
- Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35. <https://doi.org/10.1890/04-0922>
- Hughey JR, Gabrielson PW, Mags CA, Mineur F (2022) Genomic analysis of the lectotype specimens of European *Ulva rigida* and *Ulva lacimulata* (Ulvaceae, Chlorophyta) reveals the ongoing misapplication of names. *Eur J Phycol* 57:143–153. <https://doi.org/10.1080/09670262.2021.1914862>
- Jensen KT (1992) Macrobenthos on an intertidal mudflat in the Danish Wadden Sea: comparisons of surveys made in the 1930s, 1940s and 1980s. *Helgoländer Meeresun* 46:363–376
- Jung AS, van der Veen HW, Philippart CJM, Waser AM, Ens BJ et al (2020) Impacts of macrozoobenthic invasions on a temperate coastal food web. *Mar Ecol Prog Ser* 653:19–39. <https://doi.org/10.3354/meps13499>
- Karatayev AY, Mastitsky SE, Burlakova LE, Olenin S (2008) Past, current, and future of the central European corridor for aquatic invasions in Belarus. *Biol Invasions* 10:215–232. <https://doi.org/10.1007/s10530-007-9124-y>
- Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Cinar ME et al (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquat Invasions* 9:391–423. <https://doi.org/10.3391/ai.2014.9.4.01>
- Kerckhof F, Haelters J, Gollasch S (2007) Alien species in the marine and brackish ecosystem: the situation in Belgian waters. *Aquat Invasions* 2:243–257. <https://doi.org/10.3391/ai.2007.2.3.9>
- Kincaid T (1968) The ecology of Willapa Bay, Washington, in relation to the oyster industry. Kincaid (self-published), Seattle, WA
- Klunder L, Lavaleye M, Schaars LK, Dekker R, Holthuisen S, van der Veer H (2019) Distribution of the dwarf surf clam *Mulinia lateralis* (Say, 1822) in the Wadden Sea after first introduction. *Biol Invasions Records* 8:818–827. <https://doi.org/10.3391/bir.2019.8.4.10>

- Koh C-H, Khim JS (2014) The Korean tidal flat of the Yellow Sea: physical setting, ecosystem and management. *Ocean Coast Manag* 102:398–414. <https://doi.org/10.1016/j.ocecoaman.2014.07.008>
- Kolbe K, Kaminski E, Michaelis H, Obert B, Rahmel J (1995) Macroalgal mass development in the Wadden Sea: first experiences with a monitoring system. *Helgoländer Meeresun* 49:519–528
- Korringa P (1968) On the ecology and distribution of the parasitic copepod *Mytilicola intestinalis* Steuer. *Bijdr Dierkd* 38:47–57
- Kourantidou M, Haubrock PJ, Cuthbert RN, Bodey TW, Lenzner B et al (2022) Invasive alien species as simultaneous benefits and burdens: trends, stakeholder perceptions and management. *Biol Invasions* 24: 1905–1926. <https://doi.org/10.1007/s10530-021-02727-w>
- Krakau M, Jacobsen S, Jensen KT, Reise K (2012) The cockle *Cerastoderma edule* at Northeast Atlantic shores: genetic signatures of glacial refugia. *Mar Biol* 159:221–230. <https://doi.org/10.1007/s00227-011-1802-8>
- Krakau M, Thielges DW, Reise K (2006) Native parasites adopt introduced bivalves of the North Sea. *Biol Invasions* 8:919–925. <https://doi.org/10.1007/s10530-005-4734-8>
- Kröncke I, Reiss H, Dippner JW (2013) Effects of cold winters and regime shifts on macrofauna communities in shallow coastal regions. *Estuar Coast Shelf Sci* 119:79–90. <https://doi.org/10.1016/j.ecss.2012.12.024>
- Kühl H (1963) Die Verbreitung von *Elminius modestus* Darwin (Cirripedia Thoracia) an der deutschen Küste. *Crustaceana* 5:99–111
- Lackschewitz D, Reise K, Buschbaum C, Karez R (2015) Neobiota in deutschen Küstengewässern. LLUR SH – Gewässer D25, Flintbek, Germany
- Lackschewitz D, Reise K, Buschbaum C, Karez R (2022) Neobiota der deutschen Nord- und Ostseeküste. LLUR SH – Flintbek, Germany (in press)
- Landschoff J, Lackschewitz KK, Reise K (2013) Globalization pressure and habitat change: Pacific rocky shore crabs invade armored shorelines in the Atlantic Wadden Sea. *Aquat Invasions* 8:77–87. <https://doi.org/10.3391/ai.2013.8.1.09>
- Lang AC, Buschbaum C (2010) Facilitative effects of introduced Pacific oysters on native macroalgae are limited by a secondary invader, the seaweed *Sargassum muticum*. *J Sea Res* 63:119–128. <https://doi.org/10.1016/j.seares.2009.11.002>
- Larson BMH (2005) The war of the roses: demilitarizing invasion biology. *Front Ecol Environ* 3:495–500. <https://doi.org/10.2307/3868637>
- Leuven RSEW, van der Velde G, Baijens I, Snijders J, van der Zwart C et al (2009) The river Rhine: a global highway for dispersal of aquatic invasive species. *Biol Invasions* 11:1989–2008. <https://doi.org/10.1007/s10530-009-9491-7>
- Loebl M, van Beusekom JEE, Reise K (2006) Is spread of the neophyte *Spartina anglica* recently enhanced by increasing temperature? *Aquat Ecol* 40:315–324. <https://doi.org/10.1007/s10452-006-9029-3>
- Lotze HK (2005) Radical changes in the Wadden Sea fauna and flora over the last 2,000 years. *Helgol Mar Res* 59:71–83. <https://doi.org/10.1007/s10152-004-0208-0>
- Lowe S, Browne M, Boudjelas S, De Poorter M (2004) 100 of the World's worst invasive alien species. A selection from the Global Invasive Species Database. IUCN www.issg.org/booklet.pdf
- Luttikhuisen PC, Campos J, van Bleijswijk J, Peijnenburg K, van der Veer HW (2008) Phylogeography of the common shrimp, *Crangon crangon* (L.) across its distribution range. *Mol Phylogenies Evol* 46:1015–1030. <https://doi.org/10.1016/j.ympev.2007.11.011>
- Markert A, Esser W, Frank D, Wehrmann A (2013) Habitat change by the formation of alien *Crassostrea*-reefs in the Wadden Sea and its role as feeding sites for waterbirds. *Estuar Coast Shelf Sci* 131:41–51. <https://doi.org/10.1016/j.ecss.2013.08.003>
- Markert A, Wehrmann A, Kröncke I (2010) Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biol Invasions* 12:15–32. <https://doi.org/10.1007/s10530-009-9425-4>
- McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 14:450–453
- Miller AW, Ruiz GM (2014) Arctic shipping and marine invaders. *Nat Clim Chang* 4:413–416. <https://doi.org/10.1038/nclimate2244>
- Minchin D (2007) A checklist of alien and cryptogenic aquatic species in Ireland. *Aquat Invasions* 2:341–366. <https://doi.org/10.3391/ai.2007.2.4.4>
- Minchin D, Cool EJ, Clark PF (2013) Alien species in British brackish and marine waters. *Aquat Invasions* 8:3–19. <https://doi.org/10.3391/ai.2013.8.1.02>
- Mineur F, Cook EJ, Minchin D, Bohn K, MacLeod A, Maggs CA (2012) Changing coasts: marine aliens and artificial structures. *Oceanogr Mar Biol Annu Rev* 50:189–234
- Mineur F, Le Roux A, Maggs CA, Verlaque (2014) Positive feedback loop between introductions of non-native marine species and cultivation of oysters in Europe. *Conserv Biol* 28:1667–1676. <https://doi.org/10.1111/cobi.12363>
- Moehler J, Wegner KM, Reise K, Jacobsen S (2011) Invasion genetics of Pacific oyster *Crassostrea gigas* shaped by aquaculture stocking practices. *J Sea Res* 66:256–262. <https://doi.org/10.1016/j.seares.2011.08.004>
- Morga B, Jacquot M, Pelletier C, Chevignon G, Degremont L, Biétry A et al (2021) Genetic diversity of the ostreid herpesvirus type 1 across time and location and among host species. *Front Microbiol* 12:711377. <https://doi.org/10.3389/fmicb.2021.711377>
- Muehlstein L, Porter D, Short FT (1991) *Labyrinthula zosterae* sp. nov., the causative agent of wasting disease of eelgrass, *Zostera marina*. *Mycologia* 83:180–191. <https://doi.org/10.1080/00275514.1991.12025994>
- Mühlenhardt-Siegel U, Dörjes J, von Cosel R (1983) Die amerikanische Schwertmuschel *Ensis directus* (Conrad) in der Deutschen Bucht. II. Populationsdynamik. *Senckenberg Marit* 15:93–110
- Nehls G, Diederich S, Thielges DW, Strasser M (2006) Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? *Helgol Mar Res* 60:135–143. <https://doi.org/10.1007/s10152-006-0032-9>
- Nehls G, Thiel M (1993) Large-scale distribution patterns of the mussel *Mytilus edulis* in the Wadden Sea of Schleswig-Holstein: do storms structure the ecosystem? *Neth J Sea Res* 31:181–187
- Nehring S, Hesse K (2008) Invasive alien plants in marine protected areas: the *Spartina anglica* affair in the European Wadden Sea. *Biol Invasions* 10:937–950. <https://doi.org/10.1007/s10530-008-9244-z>
- Nehring S, Leuchs H (1999) Neozoa (Makrobenthos) an der deutschen Nordseeküste. Eine Übersicht. Bundesanstalt für Gewässerkunde, Koblenz, pp 131
- Nehring S, Reise K, Dankers N, Kristensen PS (2009) Alien species. Thematic Report 7. In: Marencic H, de Vlas J (eds) Quality Status Report 2009. Wadden Sea Ecosystem No. 25. Common Wadden Sea Secretariat, Wilhelmshaven, Germany, pp 28
- O'Reilly AJ, Laide C, Maloy A, Hutton S, Bookelaar B, O'Sullivan K et al (2018) The role of the mussel *Mytilus* spp. in the transmission of ostreid herpesvirus-1 microVar. *Parasitology* 145:1095–1104. <https://doi.org/10.1017/s0031182017002244>
- Occhipinti-Ambrogi A, Marchini A, Cantone G, Castelli A, Chimenz C et al (2011) Alien species along the Italian coasts: an overview. *Biol Invasions* 13:215–237. <https://doi.org/10.1007/s10530-010-9803-y>
- Ojaveer H, Galil BS, Carlton JT, Alleway H, Gouilletquer P et al (2018) Historical baselines in marine bioinvasions: implications for policy

- and management. *PLoS ONE* 13(8):e0202383. <https://doi.org/10.1371/journal.pone.0202383>
- Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol Evol* 19:18–24. <https://doi.org/10.1016/j.tree.2003.09.010>
- Olenin S, Elliott M, Bysveen I, Culverhouse PF, Daunys D et al (2011) Recommendations on methods for the detection and control of biological pollution in marine coastal waters. *Mar Pollut Bull* 62:2598–2604. <https://doi.org/10.1016/j.marpolbul.2011.08.011>
- Olenin S, Minchin D, Daunys D (2007) Assessment of biopollution in aquatic ecosystems. *Biol Poll Bull* 55:379–394. <https://doi.org/10.1016/j.marpolbul.2007.01.010>
- Oost AP, Hofstede J, Weisse R, Baart F, Janssen G, Zijlstra R (2017) Climate change. In: Klopper S et al. (eds) Wadden Sea quality status report 2017. Common Wadden Sea Secretariat, Wilhelmshaven, Germany
- Panning A (1938) Die Verteilung der Wollhandkrabbe über das Flußgebiet der Elbe nach Jahrgängen. *Mitt Hamb Zool Mus Inst* 47:65–82
- Park J, Song SJ, Ryu J, Kwon B-O, Hong S et al (2014) Macrozoobenthos of Korean tidal flats: a review on species assemblages and distribution. *Ocean Coast Manag* 102:483–492. <https://doi.org/10.1016/j.ocecoaman.2014.07.019>
- Pederson J, Mieszkowska N, Carlton JT, Gollasch S, Jelmet A et al. (2011) Climate change and non-native species in the North Atlantic. Chap. 11. In: Reid PC, Valdés L (eds) ICES status report on climate change in the North Atlantic. ICES Cooperative Research Report 310:174–190
- Peters N (1938) Ausbreitung und Verbreitung der chinesischen Wollhandkrabbe (*Eriocheir sinensis* H.M.-Edw.) in Europa im Jahre 1933 bis 1935. *Mitt Hamb Zool Mus Inst* 47:1–31
- Petersen KS, Rasmussen KL, Heinemeier J, Rudd N (1992) Clams before Columbus? *Nature* 359:679
- Pezy J-P, Baffreau A, Raoux A, Rusig A-M, Mussio I, Dauvin J-C (2021) Non-indigenous species in marine and brackish waters along the Normandy coast. *BioInvasions Rec* 10:755–774. <https://doi.org/10.3391/bir.2021.10.4.01>
- Philippart CJM, Mekkes L, Buschbaum C, Wegner KM, Laursen K (2017) Climate ecosystems. In: Klopper S et al. (eds) Wadden Sea Quality Status Report 2017. Common Wadden Sea Secretariat, Wilhelmshaven, Germany
- Polte P, Buschbaum C (2008) Native pipefish *Entelurus aequoreus* are promoted by the introduced seaweed *Sargassum muticum* in the northern Wadden Sea, North Sea. *Aquat Biol* 3:11–18. <https://doi.org/10.3354/ab00071>
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM et al (2020) Scientists' warning on invasive alien species. *Biol Rev* 95:1511–1534. <https://doi.org/10.1111/brv.12627>
- Rakhimberdiev E, Duijns S, Karagicheva J, Camphuysen CJ, Castricum VRS et al (2018) Fuelling conditions at staging sites can mitigate Arctic warming effects in a migratory bird. *Nat Commun* 9:4263. <https://doi.org/10.1038/s41467-018-06673-5>
- Reise K (1985) Tidal flat ecology. Springer-Verlag, Berlin
- Reise K (1998) Pacific oysters invade mussel beds in the European Wadden Sea. *Senckenberg Marit* 28:167–175
- Reise K (2013) A natural history of the Wadden Sea. Wadden Academy and Common, Leeuwarden, Wadden Sea Secretariat, Wilhelmshaven, pp 94
- Reise K, Baptist M, Burbridge P, Dankers N, Fischer L, Flemming B, Oost AP, Smit C (2010) The Wadden Sea – a universally outstanding tidal wetland. *Wadden Sea Ecosystem* 29. Common Wadden Sea Secretariat, Wilhelmshaven, Germany, pp 7–24
- Reise K, Buschbaum C, Büttger H, Wegner KM (2017a) Invading oysters and native mussels: from hostile takeover to compatible bedfellows. *Ecosphere* 8(9):e01949. <https://doi.org/10.1002/ecs2.1949>
- Reise K, Buschbaum C, Büttger H, Rick J, Wegner KM (2017b) Invasion trajectory of Pacific oysters in the northern Wadden Sea. *Mar Biol* 164:68. <https://doi.org/10.1007/s00227-017-3104-2>
- Reise K, Dankers N, Essink K (2005) Introduced species. In: Essink K et al. (eds) Wadden Sea Quality Status Report 2004. Wadden Sea Ecosystem No. 19. Common Wadden Sea Secretariat, Wilhelmshaven, Germany, pp 155–161
- Reise K, Lackschewitz D, Wegner KM (2022a) Marine turf of an invasive alga expels lugworms from the lower shore. *Mar Biol* 169:16. <https://doi.org/10.1007/s00227-021-04004-9>
- Reise K, Michaelis R, Rybalka N (2022b) Invading grass-like alga transforms rippled sand bars into bumpy muddy flats: arrival of a game changer in the Wadden Sea? *Aquat Invasions* 17:1–20. <https://doi.org/10.3391/ai.2022.17.1.01>
- Reise K, Siebert I (1994) Mass occurrence of green algae in the German Wadden Sea. *Dtsch Hydrogr Zeitschrift, Supplement* 1:171–180
- Reise K, van Beusekom JEE (2008) Interactive effects of global and regional change on a coastal ecosystem. *Helgol Mar Res* 62:85–91. <https://doi.org/10.1007/s10152-007-0102-7>
- Ricciardi A, Ryan R (2018) The exponential growth of invasive species denialism. *Biol Invasions* 20:549–553. <https://doi.org/10.1007/s10530-017-1561-7>
- Rick JJ, Scharfe M, Romanova T, van Beusekom JEE et al (2022) An evaluation of long-term physical and hydrochemical measurements at the Sylt roads marine observatory (1973–2019). *Wadden Sea, North Sea. Earth Syst Sci Data* (preview). <https://doi.org/10.5194/essd-2020-263>
- Ruesink JL, Feist BE, Harvey CJ, Hong JS et al (2006) Changes in productivity associated with four introduced species: ecosystem transformation of a 'pristine' estuary. *Mar Ecol Prog Ser* 311:203–215. <https://doi.org/10.3354/meps311203>
- Ruesink JL, Parker IM, Groom MJ, Kareiva PM (1995) Reducing the risks of nonindigenous species introductions. *BioScience* 45:465–477
- Rybalka N, Epkes S, Wegner KM, Michaelis R, Reise K (2022) Invasive *Vaucheria* (Xanthophyceae) at the lower shore of the Wadden Sea. *Phycologia* 61:274–283. <https://doi.org/10.1080/00318884.2022.2035532>
- Sadchatheeswaran S, Branch GM, Moloney CL, Robinson TB (2018) Impacts of alien 'ecosystem engineers' overwhelm interannual and seasonal shifts in rocky-shore community composition on Marcus Island, South Africa. *Afr J Mar Sci* 40:137–147. <https://doi.org/10.2989/1814232X.2018.1462729>
- Sagoff M (2018) Invasive species denialism: a reply to Ricciardi and Ryan. *Biol Invasions* 20:2723–2729. <https://doi.org/10.1007/s10530-018-1752-x>
- Sardain A, Sardain E, Leung B (2019) Global forecasts of shipping traffic and biological invasions to 2050. *Nature Sustainability* 2:274–282. <https://doi.org/10.1038/s41893-019-0245-y>
- Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native species. *Conserv Biol* 25:428–437. <https://doi.org/10.1111/j.1523-1739.2010.01646.x>
- Schreyers L, van Emmerik T, Biermann L, Le Lay Y-F (2021) Spotting green tides over Brittany from space: three decades of monitoring with Landsat imagery. *Remote Sens* 13:1408. <https://doi.org/10.3390/rs13081408>
- Schuurman GW, Cole DN, Cravens AE, Covington S, Crausbay SD et al (2022) Navigating ecological transformation: resist-accept-direct as a path to a new resource management paradigm. *BioScience* 72:16–29. <https://doi.org/10.1093/biosci/biab067>
- Schwemmer P, Volmer H, Enners L, Reimers H-C, Binder K et al (2019) Modelling distribution of common scoter (*Melanitta nigra*) by its predominant prey, the American razor clam (*Ensis leei*) and hydrodynamic parameters. *Estuar Coast Shelf Sci* 225:106260. <https://doi.org/10.1016/j.ecss.2019.106260>

- Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W et al (2021) Projecting the continental accumulation of alien species through to 2050. *Glob Chang Biol* 27:970–982. <https://doi.org/10.1111/gcb.15333>
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE et al (2017) No saturation in the accumulation of alien species worldwide. *Nat Commun* 8:14435. <https://doi.org/10.1038/ncomms14435>
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE et al (2018) Global rise in emerging alien species results from increased accessibility of new source pools. *PNAS* 115:E2264–E2273. <https://doi.org/10.1073/pnas.1719429115>
- Seebens H, Gastner MT, Blasius B (2013) The risk of marine bioinvasion caused by global shipping. *Ecol Lett* 16:782–790. <https://doi.org/10.1111/ele.12111>
- Selander E, Møller LF, Sundberg P, Tiselius P (2010) Parasitic anemone infects the invasive ctenophore *Mnemiopsis leidyi* in the North East Atlantic. *Biol Invasions* 12:103–1009. <https://doi.org/10.1007/s10530-009-9552-y>
- Simberloff D (2011) Non-natives: 141 scientists object. *Nature* 475:36. <https://doi.org/10.1038/475036a>
- Simberloff D, Gibbons L (2004) Now you see them, now you don't! – population crashes of established introduced species. *Biol Invasions* 6:161–172. <https://doi.org/10.1023/B:BINV.0000022133.49752.46>
- Smetacek V, Zingone A (2013) Green and golden seaweed tides on the rise. *Nature* 504:84–88. <https://doi.org/10.1038/nature12860>
- Spear MJ, Walsh JR, Ricciardi A, vander Zanden MJ (2021) The invasion ecology of sleeper populations: prevalence, persistence, and abrupt shifts. *BioScience* 71:357–369. <https://doi.org/10.1093/biosci/biaa168>
- Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577–1579
- Staehr PA, Jakobsen HH, Hansen JLS, Andersen P, Christensen J et al (2020) Trends in records and contribution of non-indigenous and cryptogenic species to marine communities in Danish waters: potential indicators for assessing impact. *Aquat Invasions* 15:217–244. <https://doi.org/10.3391/ai.2020.15.2.02>
- Steinhagen S, Karez R, Weinberger F (2019) Cryptic, alien and lost species: molecular diversity of *Ulva sensu lato* along the German coasts of the North and Baltic Sea. *Eur J Phycol*. <https://doi.org/10.1080/09670262.2019.1597925>
- Strasser M (1999) *Mya arenaria* – an ancient invader of the North Sea coast. *Helgoländer Meeresun* 52:309–324. <https://doi.org/10.1007/BF02908905>
- Strasser M (2002) Reduced epibenthic predation on intertidal bivalves after a severe winter in the European Wadden Sea. *Mar Ecol Prog Ser* 241:113–123
- Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. *Trends Ecol Evol* 21:645–651. <https://doi.org/10.1016/j.tree.2006.07.007>
- Swennen C, Leopold MF, Stock M (1985) Notes on growth and behavior of the American razor clam *Ensis directus* in the Wadden Sea and the predation on it by birds. *Helgoländer Meeresun* 39:255–261
- Tang M, Kristensen E (2010) Associations between macrobenthos and invasive cordgrass, *Spartina anglica*, in the Danish Wadden Sea. *Helgol Mar Res* 64:321–329. <https://doi.org/10.1007/s10152-009-0187-2>
- Tarkan AS, Yoğurtuoğlu B, Karachle PK, Kalogianni E, Karakuş NT, Tricarico E (2021) Editorial: understanding the impact and invasion success of aquatic non-native species: How they interact with novel environments and native biota. *Front Ecol Evol* 9:790540. <https://doi.org/10.3389/fevo.2021.790540>
- Thieltges DW, Krakau M, Andresen H, Fottner S, Reise K (2006) Macroparasite community in molluscs of a tidal basin in the Wadden Sea. *Helgol Mar Res* 60:307–316. <https://doi.org/10.1007/s10152-006-0046-3>
- Thieltges DW, Reise K, Prinz K, Jensen KT (2009) Invaders interfere with native-parasite host interactions. *Biol Invasions* 11:1421–1429. <https://doi.org/10.1007/s10530-008-9350-y>
- Thieltges DW, Strasser M, Reise K (2003) The American slipper limpet *Crepidula fornicata* (L.) in the northern Wadden Sea 70 years after its introduction. *Helgol Mar Res* 57:27–33. <https://doi.org/10.1007/s10152-002-0119-x>
- Thieltges DW, Strasser M, van Beusekom RK (2004) Too cold to prosper – winter mortality prevents population increase of the introduced American slipper limpet *Crepidula fornicata* in northern Europe. *J Exp Mar Biol Ecol* 311:375–391. <https://doi.org/10.1016/j.jembe.2004.05.018>
- Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. *Annu Rev Ecol Syst* 45:471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421:628–630
- Troost K (2010) Causes and effects of a highly successful invasion: case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *J Sea Res* 64:145–165. <https://doi.org/10.1016/j.seares.2010.02.004>
- Tulp I, Craeymeersch J, Leopold M, van Damme C, Fey F, Verdaat (2010) The role of the invasive bivalve *Ensis directus* as food source for fish and birds in the Dutch coastal zone. *Estuar Coast Shelf Sci* 90:116–128. <https://doi.org/10.1016/j.ecss.2010.07.008>
- Türkay M (2014) On the occurrence of *Diogenes pugilator* in the German Bight (Crustacea, Decapoda, Diogenidae). *Helgol Mar Res* 68:281–287. <https://doi.org/10.1007/s10152-014-0388-1>
- van Beusekom JEE, Bot P, Carstensen J, Grage A, Kolbe K et al. (2017) Eutrophication. In: Kloepper S et al. (eds) Wadden sea quality status report. Common Wadden Sea Secretariat, Wilhelmshaven
- van Beusekom JEE, Carstensen J, Dolch T, Grage A, Hofmeister R et al (2019) Wadden Sea eutrophication: long-term trends and regional differences. *Front Mar Sci* 6:370. <https://doi.org/10.3389/fmars.2019.00370>
- van Beusekom JJE (2005) A historic perspective on Wadden Sea eutrophication. *Helgol Mar Res* 59:45–54. <https://doi.org/10.1007/s10152-004-0206-2>
- van der Meer J, Dankers N, Ens BJ et al (2019) The birth, growth and death of intertidal soft-sediment bivalve beds: no need for large-scale restoration programs in the Dutch Wadden Sea. *Ecosystems* 22:1024–1034. <https://doi.org/10.1007/s10021-018-0320-7>
- van Gils JA, Lisovski S, Lock T, Meissner W, Ożarowska A et al (2016) Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science* 352:819–821
- van Walraven L, Langenberg VT, van der Veer HW (2013) Seasonal occurrence of the invasive ctenophore *Mnemiopsis leidyi* in the western Dutch Wadden Sea. *J Sea Res* 82:86–92. <https://doi.org/10.1016/j.seares.2013.02.003>
- van Wesenbeeck BK, van de Koppel J, Herman PMJ, Bertness MD, van der Wal D et al (2008) Potential for sudden shifts in transient systems: Between local and landscape-scale processes. *Ecosystems* 11:1133–1141. <https://doi.org/10.1007/s10021-008-9184-6>
- Vermeij GJ (1991) When biotas meet: Understanding biotic interchange. *Science* 253:1099–1104
- Vierna J, Jensen KT, González-Tizón AM, Martínez-Lage A (2012) Population genetic analysis of *Ensis directus* unveils high genetic variation in the introduced range and reveals a new species from the NW Atlantic. *Mar Biol* 159:2209–2227. <https://doi.org/10.1007/s00227-012-2006-6>
- Vimercati G, Kumschick S, Probert AF, Volery L, Bacher S (2020) The importance of assessing positive and beneficial impacts of alien species. *NeoBiota* 62:525–545. <https://doi.org/10.3897/neobiota.62.52793>
- von Cosel R, Dörjes J, Mühlenthal-Siegel U (1982) Die amerikanische Schwertmuschel *Ensis directus* (Conrad) in der deutschen Bucht. I.

- Zoogeographie und Taxonomie im Vergleich mit den einheimischen Schwertmuschel-Arten. *Senckenberiana Maritima* 14:147–173
- Vos PC, van Kesteren WP (2000) The long-term evolution of intertidal mudflats in the northern Netherlands during the Holocene; natural and anthropogenic processes. *Cont Shelf Res* 20:1687–1710
- Wallentinus I, Nyberg CD (2007) Introduced marine organisms as habitat modifiers. *Mar Pollut Bull* 55:323–332. <https://doi.org/10.1016/j.marpolbul.2006.11.010>
- Wallis B, Mann R, Ysebaert T, Troost K, Herman PMJ, Smaal AC (2015) Demography of the ecosystem engineer *Crassostrea gigas*, related to vertical reef accretion and reef persistence. *Estuar Coast Shelf Sci* 154:224–233. <https://doi.org/10.1016/j.ecss.2015.01.006>
- Wang C, Sifa L, Fu C, Gong X et al (2009) Molecular genetic structure and evolution in native and colonized populations of the Chinese mitten crab, *Eriocheir sinensis*. *Biol Invasions* 11:389–399. <https://doi.org/10.1007/s10530-008-9256-8>
- Waser AM, Deuzeman S, van Kangeri AK, van Winden E, Postma J et al (2016) Impact on bird fauna of a non-native oyster expanding into blue mussel beds in the Dutch Wadden Sea. *Biol Conserv* 202:39–49. <https://doi.org/10.1016/j.biocon.2016.08.007>
- Waser AM, Lackschewitz D, Knol J, Reise K, Wegner KM, Thielges DW (2020) Spread of the invasive shell-boring annelid *Polydora websteri* (Polychaeta, Spionidae) into naturalized oyster reefs in the European Wadden Sea. *Mar Biodivers* 50:63. <https://doi.org/10.1007/s12526-020-01092-6>
- Wasson K, Fenn K, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. *Biol Conserv* 102:143–153. [https://doi.org/10.1016/S0006-3207\(01\)00098-2](https://doi.org/10.1016/S0006-3207(01)00098-2)
- Wasson K, Fenn K, Pearse JS (2005) Habitat differences in marine invasions of central California. *Biol Invasions* 7:935–948. <https://doi.org/10.1007/s10530-004-2995-2>
- Weigelt R, Lippert H, Karsten U, Bastrop R (2017) Genetic population structure and demographic history of the widespread common shipworm *Teredo navalis* Linnaeus 1758 (Mollusca: Teredinidae) in European waters inferred from mitochondrial COI sequence data. *Front Mar Sci* 4:196. <https://doi.org/10.3389/fmars.2017.00196>
- Wendling CC, Batista FM, Wegner KM (2014) Persistence, seasonal dynamics and pathogenic potential of *Vibrio* communities from Pacific oyster hemolymph. *PLoS ONE* 9(4):e94256. <https://doi.org/10.1371/journal.pone.0094256>
- Wendling CC, Wegner KM (2015) Adaptation to enemy shifts: rapid resistance evolution to local *Vibrio* spp. in invasive Pacific oysters. *Proc Royal Soc B-Biol Sci* 282(1804):e20142244. <https://doi.org/10.1098/rspb.2014.2244>
- Wetthey DS, Woodin SA, Hilbish TJ, Jones SJ, Lima FP, Brannock PM (2011) Response of intertidal populations to climate: effects of extreme events versus long term change. *J Exp Mar Biol Ecol* 400:132–144. <https://doi.org/10.1016/j.jembe.2011.02.008>
- Whitney K, Gabler C (2008) Rapid evolution in introduced species, ‘invasive traits’ and recipient communities: challenges for predicting invasive potential. *Divers Distrib* 14:569–580. <https://doi.org/10.1111/j.1472-4642.2008.004373.x>
- Wiens JJ, Litvinenko Y, Harris L, Jeskova T (2019) Rapid niche shifts in introduced species can be a million times faster than changes among native species and ten times faster than climate change. *J Biogeogr* 46:2115–2125. <https://doi.org/10.1111/jbi.13649>
- Williams JW, Ordonez A, Svenning JC (2021) A unifying framework for studying and managing climate-driven rates of ecological change. *Nat Ecol Evol* 5:17–26. <https://doi.org/10.1038/s41559-020-01344-5>
- Williams SL, Grosholz ED (2008) The invasive species challenge in estuarine and coastal environments: marrying management and science. *Estuaries and Coasts J CERF* 31:3–20. <https://doi.org/10.1007/s12237-007-9031-6>
- Witte S, Buschbaum C, van Beusekom JEE, Reise K (2010) Does climatic warming explain why an introduced barnacle finally takes over after a lag of more than 50 years? *Biol Invasions* 12:3579–3589. <https://doi.org/10.1007/s10530-010-9752-5>
- Wolff WJ (2000a) Causes of extirpations in the Wadden Sea, an estuarine area in the Netherlands. *Conserv Biol* 14:876–885. <https://doi.org/10.1046/j.1523-1739.2000.98203.x>
- Wolff WJ (2000b) The south-eastern North Sea: losses of vertebrate fauna during the past 2000 years. *Biol Conserv* 95:209–217
- Wolff WJ (2005) Non-indigenous marine and estuarine species in the Netherlands. *Zoologische Mededelingen* 79(1):1–116
- Wolff WJ (1983) Ecology of the Wadden Sea. *Balkema, Rotterdam* 1/4:12–60
- Wolff WJ, Reise K (2002) Oyster imports as a vector for the introduction of alien species into northern and western European coastal waters. In: Leppäkoski E et al (eds) *Invasive aquatic species of Europe*. Kluwer Acad Publ, pp 193–205. https://doi.org/10.1007/978-94-015-9956-6_21
- Wonham MJ, Carlton JT (2005) Trends in marine ecological invasions at local and regional scales: the Northeast Pacific Ocean as a model system. *Biol Invasions* 7:369–392. <https://doi.org/10.1007/s10530-004-2581-7>

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