

Research Article

Expansion of the barnacle *Austrominius modestus* (Darwin, 1854) (Cirripedia, Thoracica, Balanidae) into Scandinavian waters based on collection data and niche distribution modeling

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Abstract

The barnacle *Austrominius modestus*, native of New Zealand and Australia was introduced to the South of England around 1943 and has since spread to most coastal waters in Western Europe, including the southern North Sea. Apart from an ephemeral incursion into the Danish Wadden Sea in 1978, since 2010 it has established permanent populations capable of reproduction along the North Sea coast of the Jutland peninsula, the Limfjord, the north-western Kattegat, and the Skagerrak. It has probably invaded Danish waters by pelagic larvae originating in the German Wadden Sea. The species has since spread to other Danish localities, likely following the prevailing currents, but other means, as for instance transport by vessels, are possible. The barnacle inhabits stones, stone-reefs, mollusk shells, and live shore crabs in shallow waters. Based on hydrographical data from its native and recently invaded areas, we predict its future distribution to extend to most coasts of continental Europe except for brackish waters (< 20 PSU), and the Arctic seas. The northernmost distribution limit may include the Lofoten Islands of Norway.

Key words: species distribution, Wadden Sea, Limfjord, Kattegat, Skagerrak, marine invasive species

Introduction

The barnacle *Austrominius modestus* (Darwin, 1854) (earlier and more widely known as *Elminius modestus*) is invasive to European waters. From its native range, New Zealand and southern Australia, it has spread to England in 1943 through ship hull fouling (Stubbings 1950). Soon afterwards, it invaded all coasts of the British Isles, including the Shetland Islands (Hiscock et al. 1978), Ireland, the Atlantic and Channel coasts of France, and the Iberian Peninsula (Crisp 1958; Harms 1998). It has also spread along the North Sea coasts of the Netherlands and Germany (den Hartog 1953; Kühl 1954, 1963; Harms and Anger 1983; Gollasch 2002; O’Riordan et al. 2020).

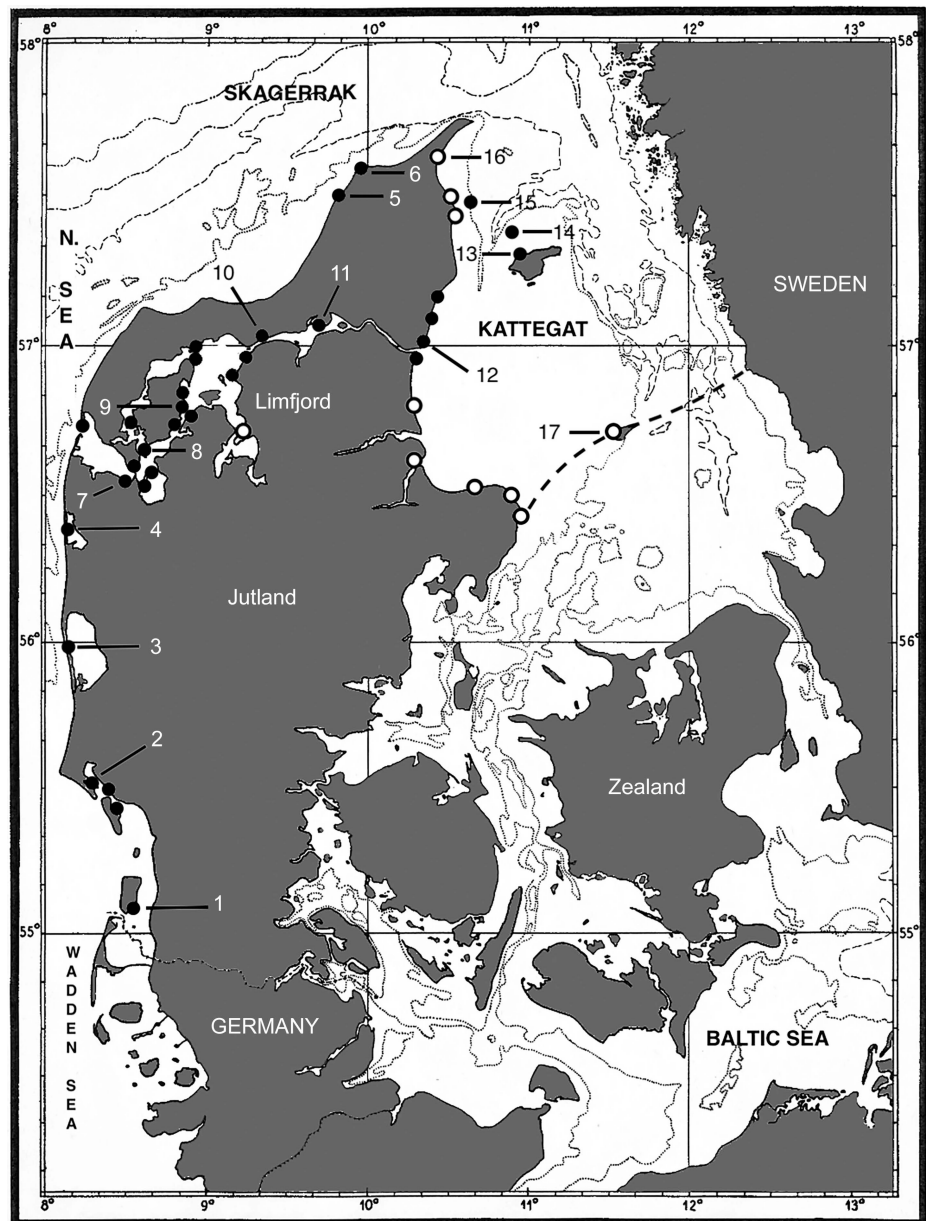


Figure 1. Presences (filled circles) and presumed absences (open circles) of *A. modestus* in Danish waters. The dashed line indicates the approximate position of the 20 PSU surface isohaline in the Kattegat. Sites occupied by *A. modestus* south of the Danish-German border are not shown. Numbers (1–17) refer to localities mentioned in the text (Rømø harbour 1; Ho Bay 2; Hvidesande 3; Thorsminde, Nissum Fjord 4; Lønstrup 5; Hirtshals 6; Oddesund West 7; Jegindø Tap 8; Nykøbing Mors harbour 9; Aggersund 10; Gjøl 11; Hals 12; Læsø 13; Nordre Rønner 14; Hirtsholmene 15; Ålbæk 16; Anholt 17).

The German North Sea populations were expected to spread further to the waters of Jutland, Denmark. There is a first, unconfirmed record from the west coast of Jutland by Nilsson-Cantell (1978). The species made a short-lived intrusion in 1978 into the Danish Wadden Sea, South of Esbjerg (Theisen 1980) (Figure 1: 1 and 2), and an isolated record was made at the eastern exit of the Limfjord into the Kattegat (Jensen 2009) (Figure 1: 12). Since 2010 we have noted the presence of *A. modestus* in the Danish Wadden Sea, and from 2011 its permanent presence in the western part of the Limfjord (Lützen and Glenner 2015). In the present paper we report on

its permanent occurrence not only in the other parts of this fjord, but also along the western coast of Jutland, and along the north-western coast of the Kattegat.

The purpose of the present investigation is to examine the invasive pathway of *A. modestus* from its presence in the southern parts of the German North Sea into Danish waters. Using ecological niche modeling we aim to identify the limits of the worldwide distribution of the species and predict its future distribution along the coasts of continental Europe.

Materials and methods

Species identification

Austrominius modestus might be confused with *Semibalanus balanoides* (Linnaeus, 1767) which is also inhabiting the upper intertidal zone (Southward 2008). Both species have membranous, uncalcified bases. The best distinctive trait of *A. modestus* is that it has four compartmental plates (carina, two laterals and fused rostrilaterals), whereas all other thoracican barnacles occurring in Europe have six plates (Figure 2), except for a very short period following larval settlement (Glenner and Høeg 1993). The separation of the four plates is very distinctive, although in smaller specimens it often needs verification with a magnifying glass. Another characteristic of *A. modestus* is that each of the four plates usually have bulging ridges extending slightly outward over the substrate, giving the animal as viewed from above a star-shaped or wavy outline. Similar structures may occur in *S. balanoides*, but here they are more irregular in number, size and shape.

Study sites were investigated for the presence of *A. modestus* between 2010 and 2020. At most sampling sites we investigated several individuals for their reproductive status. Measurements were taken from several hundred individuals attached to crabs and stones. Sizes were measured as rostro-carinal length. The material was observed and partially dissected in the field and the material has therefore only been stored to a limited extent. All examined localities in Denmark and Norway are presented in Supplementary material Table S1. The investigated Danish sites are shown in Figure 1.

Areas inspected.

Denmark.

The Danish coasts host only few rocky stretches, but there are many mixed sand-rock beaches and scattered shore-based or subtidal stone-reefs that provide a suitable substrate for *A. modestus* and other barnacles. Besides these, we also surveyed many stony jetties around harbours. Since *A. modestus*, when it occurs, is clearly restricted to near-surface substrata, we have concentrated our efforts on the upper one meter. However, the barnacle may



Figure 2. Native and invasive barnacles on the dorsal carapace of the European shore crab, *Carcinus maenas*. A. Crab with solitary *A. modestus*. Crab with solitary *Balanus crenatus*. C. Two *A. modestus* specimens at mating distance. D. Two *Amphibalanus improvisus* specimens at mating distance and one solitary *A. modestus* specimen (green arrow). E. Mating group of *B. crenatus* (red arrow) and several mating groups of *A. modestus* (green arrow) on the same crab host. Photographs by Henrik Glenner.

also occur as epifauna on shore crabs (*Carcinus maenas* (Linnaeus, 1758)) (Lützen and Glenner 2015) in the Limfjord and descend several meters with the host. A special study was conducted on the frequency of *A. modestus* compared to other epibiontic barnacle species on shore crabs in the area. In the Danish Wadden Sea, as well as elsewhere along the Danish coasts,

the tide amplitude is restricted to around one meter, and sea level variations above this value have mostly atmospheric causes.

Austrominius modestus predominantly settles on objects at or near the sea surface (Rainbow 1984; Harms 1998) and is therefore relatively easy to record. Because at northern European latitudes the larvae's settling period lasts throughout the summer and autumn (Harms and Anger 1989), the sea surface summer-autumn temperatures, and a PSU above 20, required for larval release and survival (Harms 1998; Cawthorne and Davenport 1980), will expectedly define the area suitable for successful settling, breeding and growth of the species. In the Danish waters this includes the west coast of Jutland, the entire Limfjord, and the north-western part of Kattegat (dashed line shown in Figure 1). This includes the islands of Læsø (Figure 1: 13) and Anholt (Figure 1: 17). The presence of *A. modestus* was surveyed within these limits. To determine when *A. modestus* reproduces in Danish waters the size of several hundred specimens were measured to identify the smaller (and supposedly youngest) specimens. This was combined with dissections of a few individuals to determine the status of any progeny in the mantle cavity.

Norway and Sweden

The upper littoral barnacle-rich tidal zones of south-western fjords of Norway and of the inner and outer part of the Oslo fjord (including the Koster islands, Swedish) were monitored, but *A. modestus* was apparently absent everywhere (see Table S1). Personal communication from Dr. Malin Werner, Swedish University of Agricultural Sciences and Dr. Matz Berggren, the Sven Lovén Center, Fiskebäckskil, Sweden provided information on the non-presence of the species in the remaining south-western part of the Swedish waters. The coasts of these sites are all rocky, and their salinities and temperatures are within the values adequate for the survival of *A. modestus*.

Ecological niche modeling

To model the suitability distribution for *A. modestus*, we downloaded the occurrence data from the Global Biodiversity Information Facility – GBIF (GBIF 2019). The data was subset into two parts, one only with the occurrences of the species' native range (Australia and New Zealand) and one with the invaded occurrences in European locations. For the native range subset, duplicated records were eliminated and effects of spatial autocorrelation were reduced by thinning records with a distance of 1 km radius, using the *spThin* package (Aiello-Lammens et al. 2015). In total there were 127 presence records. Consequently, the occurrences were split randomly into 75–25% subsets for model calibration and internal testing, respectively.

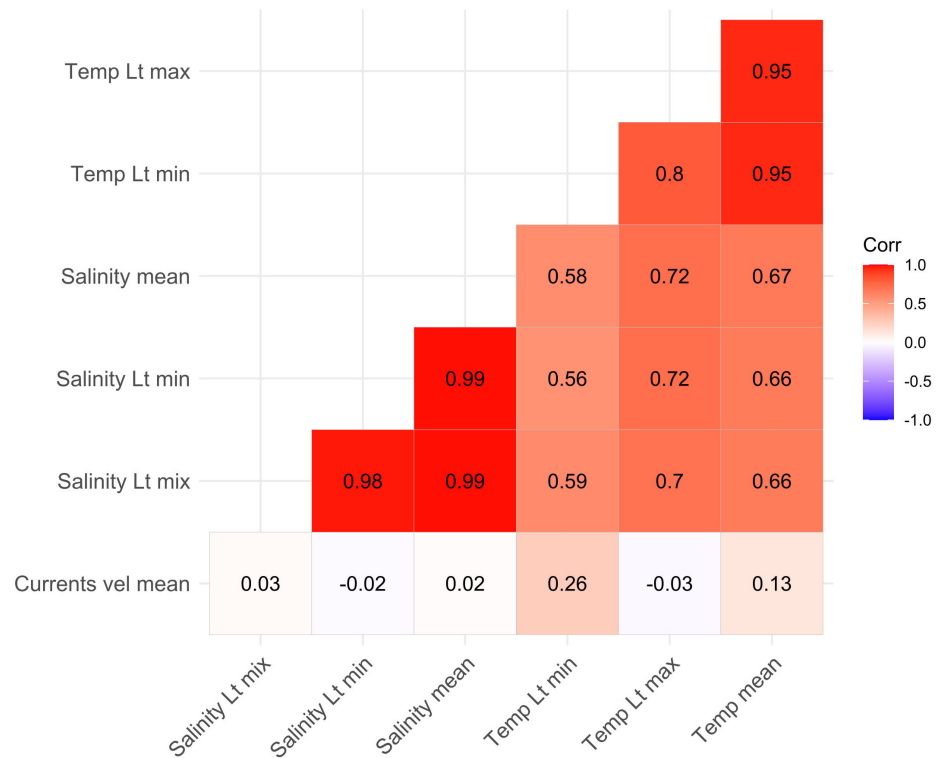


Figure 3. Pearson correlations between environmental variables.

As environmental predictors we used 5 variables, cloud cover, mean current velocity, long term minimum temperature, long term maximum temperature, long term maximum sea surface salinity from the Bio-ORACLE dataset version 2.1 (Tyberghein et al. 2012).

The environmental variables were selected based on the environmental data availability and we considered the most relevant variables that will limit the species distribution based on the literature. Pairwise Pearson correlations between used environmental variables was less than 0.85 (Figure 3). Initially we considered including mean salinity and temperature. However, these two variables were highly correlated with the minimum and maximum long-term variables (Figure 3). The environmental predictors layers were clipped to the barnacle’s native ranges areas in the Tasman and Coral Sea. As *A. modestus* occurs in intertidal and shallow subtidal sites, we also clipped the layers with a buffer of 10 km distance to the shore using the layer distance to shore from MARSPEC dataset (Sbrocco and Barber 2013). The same process was repeated with the environmental variables for Europe’s marine areas to used them as projected layers. Environmental predictors were obtained at spatial resolution of 5 arcmin (approximately 9.2 km at the equator).

We used MaxEnt 3.4.0 (Phillips et al. 2006) for estimating the climatic niche of *A. modestus* across marine areas of Australia and New Zealand, following the modelled protocol in Muscarella et al. (2014).

1054 candidate models were evaluated under varying combinations of model response types (i.e., all potential combinations of linear, quadratic,

product, threshold, and hinge, responses), 17 regularization multiplier values (0.1–1 with intervals of 0.1; 1–6 with intervals of 1; 8 and 10), and 2 sets of environmental variables, one set including cloud cover and one set without.

We then filtered the candidate models by (1) significant models with (partial ROC) (2) omission rates $\leq 5\%$ and (3) by lowest values of the Akaike Information Criterion corrected for small sample sizes (AICc) (less complex) and those with delta AICc values of ≤ 2 were chosen. A final model was created using the selected parameter settings and performing 10 replicates; models were then transferred to European coastal areas under present-day conditions, allowing extrapolation with clamping in predictions.

The mobility-oriented parity (MOP) metric (Owens et al. 2013) was used to analyze the projected conditions relative to European coastlines. This analysis facilitates determine transfer areas with values outside the range of climates in the calibration areas (extrapolation risk). Areas with low similar values indicate higher uncertainty; and caution is required when interpreting likelihood of the species presence in such areas. The candidate model creation evaluation and best model selection and MOP analyses were done using the *kuenm* package (Cobos et al. 2019). All of our analyses were performed in R version 3.6.1 (R Core Team 2019).

To obtain the final suitability map (Figure 4), we reclassified the resulting species suitability model previously obtained. Areas below 20 PSU and outside the minimum long-term temperature of 6 °C and maximum long term of 36 °C were reclassified to 0 since these areas appear outside of the survival water salinity and temperature tolerance of larvae release and survival (Cawthorne and Davenport 1980; Harms 1984). This procedure was done in ArcGIS (vs.10.7.1).

Results

Status of the distribution in Denmark 1978–2020

Figure 1 summarizes the up-to-date distribution of *A. modestus* in Danish waters, with some of the localities numbered (in brackets). In the Danish Wadden Sea the species was first recorded in 1978 at two localities (Figure 1: 1 and 2) from where it disappeared shortly afterwards (Theisen 1980). It has since been re-found in 2010 in 2015 and 2018 at two further localities (Figure 1: Fanø at Sønderho and Nordby). According to E. Vestager (Danish Wadden Sea Center), it presently occurs regularly and permanently on suitable substrates, especially on shell-banks, attaching mostly to live or dead blue mussels (*Mytilus edulis* Linnaeus, 1758), and less often to the introduced Japanese oyster, *Crassostrea gigas* (Thunberg, 1793). Along the non-tidal part of the western coast of Jutland, *A. modestus* has been found at four sites in the North Sea (Figure 1: 3, 4) and in the Skagerrak (Figure 1: 5, 6) either within harbours or on breakwaters. Hirtshals (6) represents the species' northernmost record in Scandinavia (57°35'N).

In the Limfjord, an isolated record of *A. modestus* was reported by Hals in 2009, at the eastern entrance to the fjord (Jensen 2009; Figure 1: 12). This may indicate an earlier unnoticed invasion along the Jutland western coast and through the Limfjord than reported by Lützen and Glenner (2015). The species has occurred in the fjord in every year monitored (2011–2020) on shore crabs, bivalve shells, stone reefs and stone piers. It probably occurs throughout the entire fjord in suitable places, except for some of the blind fjord branches. It is most common in the western Limfjord, with high densities in the narrow of Oddesund (Figure 1: 7), where it was recorded with a maximum length of 11 mm, at Jegindø Tap (Figure 1: 8) and Nykøping Bay (Figure 1: 9). It is also present in the less saline eastern part of the fjord at mean PSU values of 22 (Figure 1: 10, 11).

In the north-western Kattegat *A. modestus* occurs from the eastern mouth of the Limfjord (Figure 1: 12) along the Jutland coast to the islands of Læsø (Figure 1: 13) and Nordre Rønner (Figure 1: 14), where it is very common. The northernmost site of occurrence in the Kattegat is at the Hirsholmene islands (Figure 1: 15), where in the summer of 2016 specimens 6–7 mm in size contained developing eggs or nauplii. We have searched for the species from 2015 to 2017 in Aalbæk Bay (Figure 1: 16) and at six sites south of the eastern entrance to the Limfjord, including the island of Anholt (Figure 1: 17) without success.

Reproduction and growth in Danish waters

Breeding of *A. modestus* may begin when the water temperature exceeds 6 °C (Harms 1984). The presence of 1–3 mm individuals in the months of June to November with maxima from July to September indicates a continuous breeding season throughout most of summer and autumn. This agrees with the information by Kühl (1963) from the German North Sea coast, who reported that settling of *A. modestus* lasts from May–June until October–November, and that it takes the species two months to reach sexual maturity (above 6–7 mm; Rainbow 1984). Most findings from Denmark suggest the presence of two cohorts, one consisting of individuals settled from June to late autumn and attaining a maximum length of 7–8 mm, and another, older generation, that reaches lengths of 9–11 mm, with the two overlapping in June–August (11 mm were the maximal size measured in the study). This suggests that the older generation is mainly responsible for the production of larvae initiating the breeding season, while the other one produces the larvae of the second period. It also indicates a life-span of not more than ca. fourteen months in Danish waters. In late June and July, 6–8 mm specimens located within fertilization distance had paired ovisacs in the mantle cavity and specimens collected as late as October 30, still produced live nauplii.

Table 1. Number of individuals and percentages of *A. modestus* of all barnacles fouling *Carcinus maenas* (male crabs in red colour phase) in the Limfjord.

	Total no. of barnacles	No. <i>A.modestus</i>	% <i>A.modestus</i>
2012 autumn (Sep)	35	2	5.7
2013 autumn (Sep/Oct)	410	32	7.8
2019 autumn (Oct)	107	51	47.7

Habitat and species interaction; growth of the population

In intertidal beaches, *A. modestus* does not occur on boulders exposed to wave action, where *S. balanoides* is dominant. On less exposed sites, however, *A. modestus* seems to be able to compete for space on hard substrates. Along the western coast of northern Jutland it is common to find adults of *A. modestus* side by side with *S. balanoides*. Although we did not quantify this relationship, it appears that in these recently invaded areas *A. modestus* is highly competitive on protected, high intertidal locations. In contrast to *S. balanoides*, *A. modestus* also occurs in the subtidal zone, where we registered an increasing settlement of specimens on typical subtidal dwelling animals like blue mussels, *Mytilus edulis*, and on the common shore crab, *Carcinus maenas*, at most study sites in the Limfjord during our ten years long monitoring of the species' invasion.

The successful colonization of Danish waters by *A. modestus* is well illustrated by the fact that a few years ago it occurred on only a few shore crabs, which are commonly fouled by barnacles (mainly *Balanus crenatus* (Bruguère, 1789), *Amphibalanus improvisus* (Darwin, 1854), and more rarely *B. balanus* (Linnaeus, 1758)). By 2019 it had become almost equally common on crabs as the aforementioned barnacle species (Table 1). *Austrominius modestus* settles either alone or side-by-side with *A. improvisus*, *B. crenatus* and *B. balanus* (Figure 2). These observations indicate that, in the newly invaded areas, the realized niche of *A. modestus* is extremely broad, and it is able to compete with the indigenous barnacle species in wave-protected high intertidal, as well as in the sub-intertidal habitats.

Ecological niche modelling

The native range of *A. modestus* in Australia and New Zealand coincides with the predicted one (Figure 4A). Figure 4B indicates that the species distribution in Europe might extend to cover most of the western coast of Sweden, and the coast of Norway up to and including Lofoten (ca. 68 °N). With rising sea temperatures there is a potential risk for this barnacle species to spread even further north, possibly reaching arctic-boreal areas. In addition, it will probably also be a natural member of the fauna of the Mediterranean Sea.

In model calibration, we assessed 1054 models, 1050 of which were statistically significant as compared with a null model of random prediction. Of these significant models, 7 (0.6%) met the omission criterion of 5%. Finally, of the significant, low-omission model (0.03), the model with the minimum AICc value (2043.8) was one with a regularization parameter value of 0.9

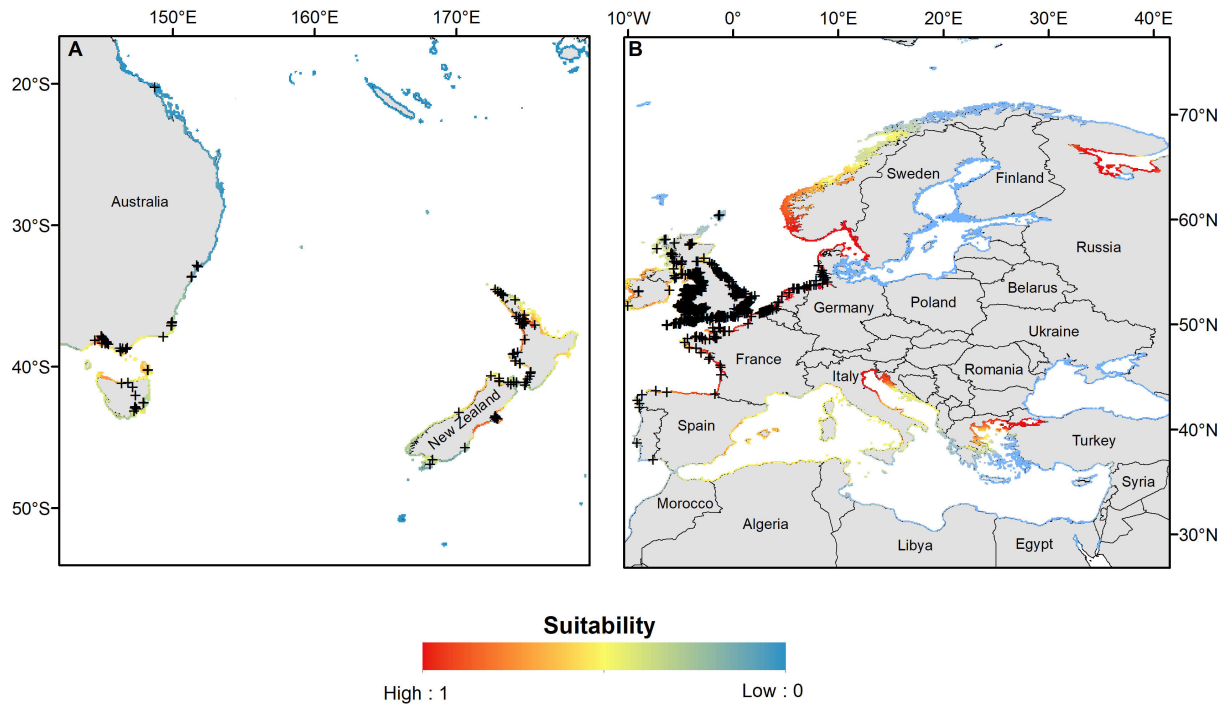


Figure 4. Climatologically suitable areas for *A. modestus* (A) in Australia and New Zealand resulting from Maxent climatic modeling using occurrence records within the species native range; (B) Projection map for the potential future distribution of *A. modestus* in Europe. Occurrences of the species are represented by black crosses. Reddish colors have a high probability of presence, blue colors have a low probability of presence.

(Mean AUC = 0.84, Partial ROC = 0); linear and quadratic features; and the second set of environmental variables.

The median of the selected model (Figure 4A) identified areas with different levels of suitability for *A. modestus* its native range of the coasts of Australia and New Zealand. The MOP analysis for the projected model indicated that model predictions for of European coasts were based on extrapolative conditions of the native range (Figure 5).

The projection of the native range distribution model onto European coasts showed that predicted occurrence included the actual invaded range of *A. modestus* along the coasts of United Kingdom, Ireland, North of France, Spain, Portugal, and Germany (Figure 4B). Based on the projected distribution it seems that the barnacle species can spread far to the north along the coast of Denmark, Sweden, and Norway, and to the south towards the south coast of Spain until reaching the Mediterranean Sea, where *A. modestus* has been observed (O’Riordan and Ramsay 1999; Casellato et al. 2007), but not yet is widespread. The isohaline that divides the Kattegat from the Djursland peninsula (Jutland) via the Island of Anholt to the Swedish coast acts as a barrier for the species to invade further into the Baltic Sea.

Discussion

The impact of low winter temperatures

The only area of the current European distribution of *A. modestus* where low temperatures may seriously restrict its occurrence are the coasts of the

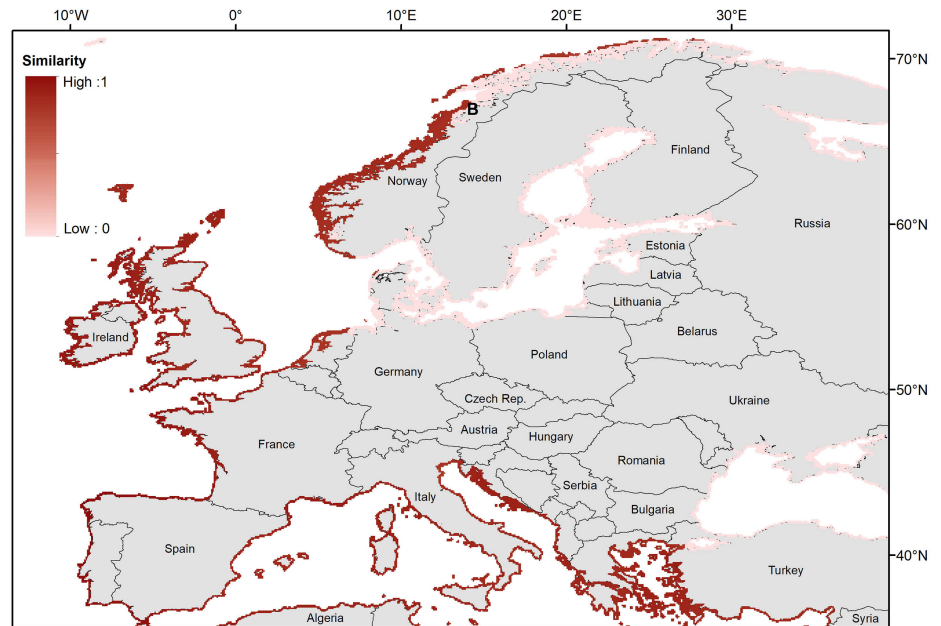


Figure 5. Extrapolation risk in model transfers via mobility-oriented parity (MOP) results on the European coast final model projection.

southern North Sea, the Limfjord and the Kattegat. Kühl (1963) pointed out that the species would survive only in the tidal zone of the German Wadden Sea if air temperatures are not too low. In the fall of 1978, a vigorous population of *A. modestus* in the Danish Wadden Sea was exterminated by a long period of sub-zero temperatures when the animals were out of the water during low tide periods (Theisen 1980). Adult populations were visibly decimated during the same winter in the German Bight (Helgoland), but had already recovered by 1981 (Harms and Anger 1989). The single isolated record of *A. modestus* by Hals in 2009 (eastern entrance to the Limfjord, Figure 1: 12) preceded one of the severest ice winters in Denmark (2009–2010), with a continuous two months ice coverage in the Limfjord, but the species had obviously recovered since it was found again in 2011. The fact that the sub-tidal occurrence of *A. modestus* on shore crabs and mussels in the Limfjord, might indicate that these substrates can act as a reservoir in years where tidal inhabiting specimens are exterminated during cold winters. The increased presence of *A. modestus* throughout 2010 to 2019 in Danish waters coincided with average winter temperatures and fits well with the perception of *A. modestus* as a warm water adapted species (Gallagher et al. 2017), which is increasingly able to realize its ecological and spatial niche (Witte et al. 2010).

Probable ways of invasion of Danish waters

Apart from an ephemeral occurrence in the Danish Wadden Sea (Theisen 1980), a permanent presence of *A. modestus* occurred in the same area from at least 2010, with wider distributions in 2015 and 2018, presumably as a result of the spread from populations in the German Wadden Sea or

the island of Helgoland. Although its further spread to North Jutland by ships cannot be ruled out (den Hartog 1953; Gollasch 2002), it is more likely that the species' larvae released in the Wadden Sea have been transported by the predominantly north-bound Jutland Current. This is a slow (ca. 2 km/day) surface current along the North Sea and the Skagerrak coasts of Jutland, but it may be more rapid during periods of strong south-south-western winds (M.H. Nielsen *pers. comm.*). A nearly 350 km stretch along the sandy North Sea coast of Jutland presents few natural habitats for settling of the species' larvae, but there are many artificial hard substrata, including many breakwaters and four major harbours: Hvide Sande (Figure 1: 3), Thorsminde (Figure 1: 4), Hanstholm (not examined), and Hirtshals (Figure 1: 6), as well as many breakwaters off exposed places (e.g. Lønstrup, Figure 1: 5). These sites may serve as suitable stepping stones from the Wadden Sea to the Limfjord, and *A. modestus* is present at all of four sites surveyed. Its larval development, excluding the cypris stage, requires from 40 days at 6 °C, to 10 days at 18 °C (Harms 1984), which allows the larvae to drift from the Wadden Sea to the nearest harbour (Hvide Sande), especially under favourable wind conditions. Having reached the narrow western entrance into the Limfjord, the larvae may drift eastwards along the fjord as the net currents through the various passages and straits are generated by the prevailing westerly winds (NOVANA 2005). The beaches and the sub-littoral of the fjord are often stony, which favors the settlement of *A. modestus*. The barnacle forms populations capable of reproducing throughout the fjord and larvae produced there may easily spread along its length (150 km) before they exit into the Kattegat. Larvae that evade drifting into the Limfjord are obviously displaced further north and northeast along the coast of N. Jutland, reaching as far as Hirtshals (Figure 1: 6).

In the north-western part of the Kattegat currents often change, but for most of the year (72–87% of the time) they flow northwards due to a surplus amount of freshwater originating in the Baltic Sea (Sparre 1982). This may explain the species' recent distribution in the Kattegat, where until now it has not been recorded from areas to the south of the eastern mouth of the Limfjord, while it does occur at a number of sites in the northern part. There are many examples suggesting that the Limfjord is an invasion hub for invasive species arriving from the North Sea, which after a period of adaptation and consolidation, spread to the neighbouring Kattegat to eventually invade other locations (Petersen et al. 2017).

Prediction of future spread in Danish waters

In the Kattegat, *A. modestus* is yet absent from Aalbæk Bay (Figure 1: 16), and the coast of Jutland south of the mouth of the Limfjord, including the island of Anholt in the central Kattegat. Even if the prevailing currents in the Kattegat favour its recent distribution, it will certainly sooner or later

spread towards the south until the surface water becomes intolerably brackish. The Kattegat is characterized by a north-south gradient of decreasing salinity due to the input of low salinity surface water from the Baltic. The salinity tolerance of adult *A. modestus* is not known (but see Foster 1970), but the liberation of larvae ceases at salinities of approximately 21 PSU (Cawthorne and Davenport 1980), while larval development occurs at values down to 16 PSU (Harms 1984). The average 20 PSU isohaline bisects the middle of Kattegat roughly from mid E. Jutland across the island of Anholt to the Swedish west coast (Figure 1). It is very likely that *A. modestus* will eventually colonize the littoral of all suitable coasts of North Jutland.

Prediction of future spread in European waters

The projection of the native range distribution model of south-eastern Australia and New Zealand include all local records of *A. modestus* (Figure 4A). Figure 4B shows that the predicted occurrence also includes the actual invaded range of *A. modestus* in Europe. Based on the projected distribution, the barnacle will very likely spread further north along the rocky coasts of Sweden and Norway. Its early establishment in the Shetland Isles (Hiscock et al. 1978) may suggest that this might become the source of its populations along the relatively nearby coast of Norway, but this apparently has not happened yet. Until now, the species has not been recorded from any Norwegian locality (Table S1). Presently, it also seems to be absent from the Swedish coasts (see Table S1 and *pers. comm.* from Malin Werner and Matz Berggren), although it is on the Swedish alert list (Främmande Arter 2008). From its populations in Southern Portugal, the barnacle may colonize the Mediterranean Sea. The two major European brackish water basins, the Baltic Sea and the Black Sea, however, are unlikely to be invaded by *A. modestus*, except for stray individuals that may settle but unable to reproduce because of the low salinity and temperature.

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References

- Aiello-Lammens MÉ, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38: 541–545, <https://doi.org/10.1111/ecog.01132>

- Casellato S, Masiero L, Sichirollo E, Soresi S (2007) Hidden secrets of the Northern Adriatic: “Tegnùe,” peculiar reefs. *Open Life Sciences* 2: 122–136, <https://doi.org/10.2478/s11535-007-0004-3>
- Cawthorne DF, Davenport J (1980) The effect of fluctuating temperature, salinity and aerial exposure upon larval release of *Balanus balanoides* and *Elminius modestus*. *Journal of the Marine Biological Association of the United Kingdom* 60: 367–377, <https://doi.org/10.1017/S0025315400028393>
- Cobos ME, Townsend Peterson A, Barve N, Osorio-Olvera L (2019) Kuenm: An R package for detailed development of ecological niche models using Maxent. *PeerJ* 7: e6281, <https://doi.org/10.7717/peerj.6281>
- Crisp DJ (1958) The spread of *Elminius modestus* Darwin in North-West Europe. *Journal of the Marine Biological Association of the United Kingdom* 37: 483–520, <https://doi.org/10.1017/S0025315400023833>
- den Hartog C (1953) Immigration, dissemination and ecology of *Elminius modestus* Darwin in the North Sea, especially along the Dutch coast. *Beaufortia* 4(33): 9–20
- Foster BA (1970) Responses and acclimation to salinity in the adults of some balanomorph barnacles. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 256: 377–400, <https://doi.org/10.1098/rstb.1970.0001>
- Främmande Arter (2008) Havstulpan (*Elminius modestus*). Fact-sheet. <http://www.främmandearter.se/5arter/pdf/Elminius-modestus.pdf>
- Gallagher MC, Culloty SC, Davenport J, Harman L, Jessopp MJ, Kerrigan C, Murray C, O’Riordan RM, McAllen R (2017) Short-term losses and long-term gains: The non-native species *Austrominius modestus* in Lough Hyne Marine Nature Reserve. *Estuarine, Coastal and Shelf Science* 191: 96–105, <https://doi.org/10.1016/j.ecss.2017.04.020>
- Glenner H, Høeg JT (1993) Scanning electron microscopy of metamorphosis in four species of barnacles (Cirripedia Thoracica Balanomorpha). *Marine Biology* 117: 431–439, <https://doi.org/10.1163/193724095X00514>
- GBIF (2019) Global Biodiversity Information Facility. Occurrence download, <https://doi.org/10.15468/dl.doaqyp> (19 November 2020)
- Gollasch JB (2002) The importance of ship hull fouling as a vector of species introductions into the North Sea. *Biofouling* 18: 105–121, <https://doi.org/10.1080/08927010290011361>
- Harms J (1984) Influence of water temperature on larval development of *Elminius modestus* and *Semibalanus balanoides* (Crustacea, Cirripedia). *Helgoländer Meeresuntersuchungen* 38: 123–134
- Harms J (1998) The neozoon *Elminius modestus* Darwin (Crustacean, Cirripedia): Possible explanations for its successful invasion in European water. *Helgoländer Meeresuntersuchungen* 52: 337–345, <https://doi.org/10.1007/BF02908907>
- Harms J, Anger K (1983) Seasonal, annual, and spatial variation in the development of hard bottom communities. *Helgoländer Meeresuntersuchungen* 36: 137–150, <https://doi.org/10.1007/BF01983853>
- Harms J, Anger K (1989) Settlement of the barnacle *Elminius modestus* Darwin on test panels at Helgoland (North Sea): A ten year study. *Topics in Marine Biology. Scientia Marina* 53: 417–421
- Hiscock K, Hiscock S, Baker JM (1978) The occurrence of the barnacle *Elminius modestus* Darwin in Shetland. *Journal of the Marine Biological Association of the United Kingdom* 58: 627–629, <https://doi.org/10.1017/S0025315400041278>
- Jensen KR (2009) National Report Demark, 2008. In: ICES. Report of the Working Group on Introduction and Transfers of Marine Organisms (WGITMO), 11–13 March 2001, Washington D.C., USA, pp 41–63
- Kühl H (1954) Über des Auftreten von *Elminius modestus* Darwin in der Elbmündung. *Helgoländer wissenschaftliche Meeresuntersuchungen* 5: 53–56, <https://doi.org/10.1007/BF01609108>
- Kühl H (1963) Die Verbreitung von *Elminius modestus* Darwin (Cirripedia Thoracica) an der Deutschen Küste. *Crustaceana* 5: 99–111, <https://doi.org/10.1163/156854063X00372>
- Lützen J, Glenner H (2015) Firepladet rur (*Austrominius modestus*) i Limfjorden. *Flora og Fauna* 121: 30–35 [in Danish]
- Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution* 5: 1198–1205, <https://doi.org/10.1111/2041-210X.12261>
- Nilsson-Cantell C-A (1978) Cirripedia Thoracica and Acrothoracica. *Marine Invertebrates of Scandinavia* 5. Universitetsforlaget, Oslo, 133 pp
- NOVANA (2005) Marin overvågning 2004–2009. Vandmiljø i Limfjorden 2005. Limfjordsovervågningen, Viborg, Denmark, 50 pp [in Danish]
- O’Riordan RM, Ramsay NF (1999) The current distribution and abundance of the Australasian barnacle *Elminius modestus* in Portugal. *Journal of the Marine Biological Association of the United Kingdom* 79: 937–939, <https://doi.org/10.1017/S0025315498001118>

- O’Riordan RM, Culloty SC, Mcallen R, Gallagher MC (2020) Chapter 1. The biology of *Austrominius modestus* (Darwin) in its native and invasive range. In: Hawkins SJ, Allcock AL, Bates AE, Evans AJ, Firth LB, McQuaid CD, Russell BD, Smith IP, Swearer SE, Todd PA (eds), *Oceanography and Marine Biology. An Annual Review*. Vol. 58. CRC Press, 1–78, <https://doi.org/10.1201/9780429351495-1>
- Owens HL, Campbell LP, Dornak LL, Saupé EE, Barve N, Soberón J, Ingenloff K, Lira-Noriega A, Hensz CM, Myers CE, Peterson AT (2013) Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling* 263: 10–18, <https://doi.org/10.1016/j.ecolmodel.2013.04.011>
- Petersen JK, Glenner H, Nielsen P, Lützen J (2017) Invasive skaldyr i Limfjorden. *Kasketot* 215: 36–39 [In Danish]
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distribution. *Ecological Modeling* 190: 231–259, <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Rainbow PS (1984) An introduction to the biology of British littoral barnacles. *Field Studies* 6: 1–51
- R Core Team (2019) The R Stats Package. R Foundation for Statistical Computing. Vienna
- Southward AJ (2008) Barnacles. *Synopses of the British Fauna (New Series)*, No. 57. Field Studies Council, Shrewsbury, 140 pp
- Sbrocco EJ, Barber PH (2013) MARSPEC: ocean climate layers for marine spatial ecology. *Ecology* 94: 979–979, <https://doi.org/10.1890/12-1358.1>
- Sparre A (1982) *Klimatologiske Meddelelser*. Danish Meteorological Papers No.9. The Danish Meteorological Institute, Copenhagen, technical report
- Stubbings HG (1950) Earlier Records of *Elminius modestus* Darwin in British Waters. *Nature* 166: 277–278, <https://doi.org/10.1038/166277a0>
- Theisen BF (1980) *Elminius modestus* Darwin i Danmark. *Flora og Fauna* 86: 17–19 [in Danish]
- Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography* 21: 272–281, <https://doi.org/10.1111/j.1466-8238.2011.00656.x>
- Witte S, Buschbaum C, van Beusekom JE, Reise K (2010) Does climatic warming explain why an introduced barnacle finally takes over after a lag of more than 50 years? *Biological Invasions* 12: 3579–3589, <https://doi.org/10.1007/s10530-010-9752-5>

Supplementary material

The following supplementary material is available for this article:

Table S1. Dates and coordinates for all collection locations.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Glenner_etal_SupplementaryMaterial.xlsx