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Cotula coronopifolia
- Invasive or just another alien species?

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Abstract

It is known that alien species can become invasive in a new environment and in new geographic areas. The recent and rapid expansion of *Cotula coronopifolia* (cotula) on the island of Öland in Sweden has raised questions about its potential invasiveness. The lack of information about the species ecology and behavior lead to this study which focuses on cotula's history of expansion, dispersal mechanisms and potential vectors, expansion speed and habitat preferences, and if there is any spatial competition between cotula and native species.

A literature review, a field study and a couple of floating experiments indicates that the main dispersal mechanism of cotula is its good floating ability regarding both plants and seeds. The present population in Sweden is most likely a result of secondary spread by water across the Baltic Sea around 2002. A mapping survey done over two seasons, 2018 and 2019, of two populations on the island of Öland and a demographic study showed a high dispersal potential, with 2.4 million seeds produced per m^2, and an expansion speed of, at least, 380 m per year. The field study, in combination with the mapping survey, showed that cotula has a broader niche in terms of habitat preferences than the literature indicated. I also found that the adult plants were able to endure much more frost and ice than previously known. A survey of 290 vegetation plots (0.0625 m^2) with cotula present showed that there is a negative correlation between the cover of cotula and the native species and also with species number. This indicates spatial competition between cotula and the native species. The present populations will likely continue to grow and spread since there is plenty of uncolonized habitat available along the coasts of the Baltic Sea. Hence, there is a need for an action plan to prevent further establishment and a readiness for rapid eradication once the species reaches new areas.

Keywords: Cotula coronopifolia, Baltic Sea, dispersal mechanism, invasive species, salt marsh

Sammanfattning

I samband med den nyliga och hastiga spridningen av kotula, *Cotula coronopifolia* i Sverige har det väckts frågor kring dess potentiella invasivitet. Eftersom litteraturen kring kotulans ekologi och historia är mycket sparsam så initierades denna studie som fokuserar på kotulans historiska spridningsvägar, dess spridningsmekanismer och potentiella vektorer, dess expansionshastighet, habitatpreferenser, och om det finns någon indikation på spatial/rumslig konkurrens mellan kotulan och inhemska arter.

Litteraturstudien, fältstudien och flytexperimenten indikerar att den huvudsakliga spridningsmekanismen är dess goda flytförmåga, av både plantor och frön. Dagens svenska population är troligen ett resultat av sekundär spridning och kom troligen vattenvägen över Östersjön kring år 2002. Kartläggningen som gjordes av två populationer på Öland, år 2018 och 2019, tillsammans med en demografistudie visar på kotulans höga spridningspotential, en fröproduktion av 2,4 miljoner frön per kvadratmeter och en expansionshastighet på minst 380 meter per år. Denna studie visade också att kotulan har en bredare habitatnisch och uthärdar mer kyla och frost än vad litteraturen indikerar. En täckningsgradsinventering utfördes i 290 stycken 0,0625 m^2 vegetationsrutor där kotula fanns närvarande, vilket visade på att det fanns en negativ korrelation mellan kotulas täckningsgrad och de inhemska arternas och även med antalet arter. Detta indikerar att det förekommer spatial konkurrens mellan kotula och de inhemska arterna. Den befintliga populationen i Sverige kommer troligtvis att fortsätta expandera och sprida sig då det finns gott om potentiellt habitat längs Östersjöns kuster. Därav behövs det en handlingsplan som avser att hindra vidare spridning och en beredskap för utrotning av kotula när den etablerar sig på nya lokaler.

Nyckelord: havsstrandäng, expansionshastighet, kotula, spridningsmekanism, Östersjön

Table of Contents

List of tables

List of figures

Introduction

To be defined as invasive, an alien plant species has to fulfill certain criteria. First, it must be introduced into a new ecosystem by man, either intentionally or unintentionally. No species that has spontaneously immigrated on its own can therefore be referred to as invasive. Secondly, it must be able to establish, reproduce and spread in the new environment on its own, otherwise it could never be much of a threat. Which brings us to the last criterion which is, it must cause some kind of problem for man and/or his agricultural economy or, as we will be focusing on here, causing harm to the native ecosystem by altering its community and/or processes and therefore threaten the biological diversity (Strand et al., 2018). It should be noted that only a small fraction of all introduced alien species becomes invasive (Daehler, 2003).

The biological diversity can be threatened by an invasive plant species in numerous ways (Figure 1). These can be categorized into two main ways, based on their negative impacts on i) native species; or ii) native habitats or ecosystem (Sandvik et al., 2017).

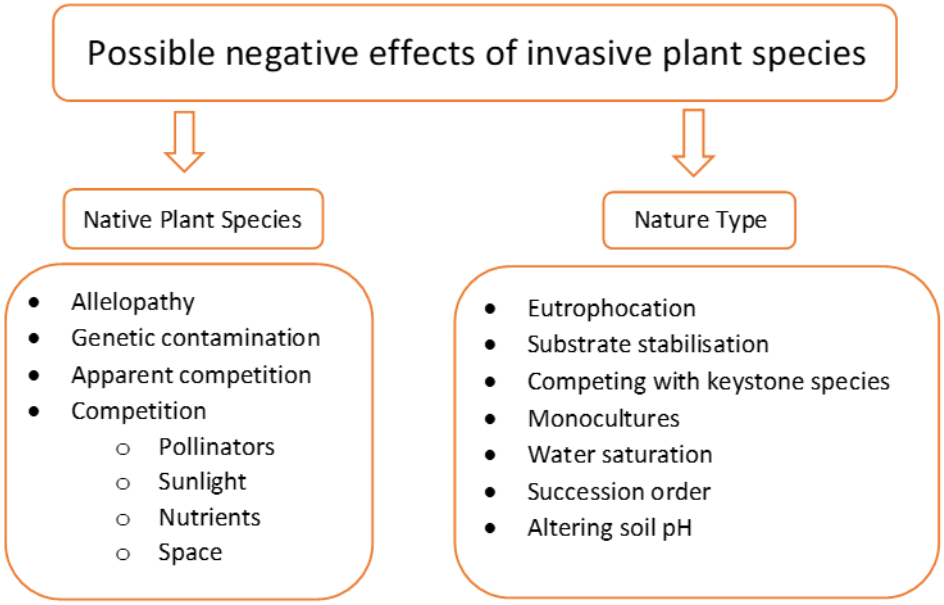

Figure 1. *Possible negative effects of an invasive plant species. Note that these possible effects can differ depending on geography and ecosystems and this figure is created out of a northern European perspective.*

The recent expansion of *Cotula coronopifolia* on the island of Öland in Sweden has raised questions about its potential invasiveness. Öland is today the province of Sweden where the spread of cotula has been the fastest and that now houses the largest population (Artportalen, 2018). When this study started there was almost no knowledge about the behavior of this species in Sweden. Most of the information was basic species knowledge and reported findings including the finders guesses about the pathway of introduction.

The species

Cotula coronopifolia is an annual species within the family Asteraceae. It has many common names like: kotula, water cotula, common brassbuttons, buttonweed and bachelor's-button, all depending on your location in the world (GBIF Backbone Taxonomy, 2017). Further on in this thesis it will be referred to as cotula. Cotula originates from South Africa and Namibia (EPPO, 2019) but occurs in many parts of the world as a pioneer plant in nutrient rich soils of wetlands and sea shores, in both fresh and brackish waters (Weber, 2017). Most countries refer to cotula as an annual species, however, in e.g. the USA, California (Brusati & DiTomaso, 2005), and in Chile (Belov, 2009) it is referred to as perennial. In its native range it occurs as both annual and perennial (Powel et al., 2014). Its stems and leaves are fleshy and glabrous, the leaves are more or less lanceolate, oblong and toothed and the base of the leaves forms a fused sheath around the stems (Watson, 2012; Powell et al., 2014) (Figure 2). The yellow tubular florets, disk flowers, form a dense flower head, a discoid, which gives the resemblance of a button. The flower heads are 6–15 mm in diameter. According to van der Toorn (1980) every plant produces around 20,000-50,000 achenes, which is the type of fruit of the members of Asteraceae, hereafter referred to as seeds. It is a single seeded fruit with a dry pericarp (Encyclopaedia Britannica, 2016). The seeds do not need a cold pre-treatment for germination and neither does the germination follow any other seasonal changes (Noe & Zedler, 2000). The seeds germinate easily in a wide range of different soils (Lopes, 2014) and are viable for one to two years (Weber, 2017). Seeds are mainly dispersed by water, but cotula is also able to spread vegetatively because of its good rooting ability of stem fragments (Lopes, 2014).

Figure 2. Cotula coronopifolia. *Photo: Lina Tomasson*

Cotula was likely brought from southern Africa to Europe by man during the 18th century. The pathways of introduction and spread is to this day unknown. There are theories that cotula achenes came to Europe with ship ballast water (Kindström & Carlsson, 2016). There are also theories about the further spread within Europe with waterfowls as a vector, this has been observed possible by van der Toorn (1980) but suggested to rarely occur. Ecological Flora of the British Isles (Fitter & Peat, 1994) states it was introduced by man for horticultural purposes in Great Britain. On at least two occasions, in Great Britain (Clement, 1993) and Belgium (Verloove, 2011), the achenes have been mentioned as a contaminant in wool transports. This is interesting because a study done by Noe and Zedler (2000) shows that dry storage of the achenes for seven months decreased the germination rate by 59%. This creates further questions about cotula's demography, floating ability and seed viability in water addressed in question number one in the next paragraph.

This study

Out of the examples in Figure 1 some can be excluded when investigating the possible invasiveness of cotula in Sweden. For example, genetic contamination or introgression is not likely to occur because hybridization mainly occur between closely related taxa (Tyler et al., 2015) and such relatives are absent or not considered native in the Swedish flora (Dyntaxa, 2018). Competition for nutrients is neither likely because the plants of interest are growing on the seashores of the Baltic Sea, which has gone through human-related eutrophication during many decades (HELCOM, 2018). But, cotula populations are present in areas listed within EU's Habitats Directive (Annex I of Council Directive 92/43/EEC, 1992) which are protected under Natura 2000 (European Environment Agency, 2019) in Sweden. These areas are protected to ensure biodiversity through conservation of natural habitats and their species. EU has not yet given any directions about how alien species within these areas should be handled given that they do not harm the habitats structure or function. (Council Directive 92/43/EEC, 1992). Examples of red-listed vascular plants (Red List category according to IUCN) reported from the same area and habitat as cotula is: *Halimione pedunculata* (EN), *Blysmus rufus* (NT), *Bupleurum tenuissimum* (NT) and *Cerastium subtetrandrum* (NT). If one would look at potential habitats and other red-listed plants that could be potentially threatened by cotula one could mention: *Halimione portulacoides* (CR), *Carex maritima* (EN), *Parapholis strigosa* (EN), *Limonium vulgare* (VU), *Cochlearia officinalis* subsp. *anglica* (NT), *Lotus tenuis* (NT) and potentially even *Carex glareosa* (NT). These species are all weak competitors that are threatened by overgrowth and have a more or less overlapping niche with cotula (Artportalen, 2019; ArtDatabanken, 2019). Cotula is able to form large and dense monocultures on the island of Öland (Andersson & Gunnarsson, 2017), and species that may form large monocultures are a more severe threat to native species and nature types than species occuring more sparsely (Tyler et al., 2015). Therefore, the most likely negative impact from cotula is through spatial competition with native species which might affect the protected biodiversity at these sites.

Therefore, the aim of this study was to investigate the following:

1. How and when did cotula first arrive in Sweden and what are the dispersal mechanisms and vectors? I hypothesize that its floating ability is important for its dispersal and that the previous belief of birds acting as vectors is an exaggeration.
2. Do the populations expand and in what habitats are they present? I expect them to expand within a clear niche.
3. Are there any indications of spatial competition between cotula and native plant species in those areas where cotula is present? I hypothesize that if Cotula is present in a habitat, it is so at spatial expense of native species.

The answers to these questions are crucial for the objective of this study: Is *Cotula coronopifolia* to be considered an invasive plant in Sweden?

Material and methods

Literature review

To answer the question of how and when Cotula came to Sweden, how it is spreading, as well as its potential invasiveness, different sources of information was used. For example, papers and journals through Google Scholar, Sweden's Virtual Herbarium, Artportalen and older botanical journals.

Field study and study sites

This two-year project started with a pre-study in August 2018 to get an overview of the species lifecycle and habitat preferences. This was done on the east coast of Öland where most of the reports on Artportalen are from (Figure 3). Field observation notes can be found in Appendix 1. During the field observations, suitable areas for further field studies were selected. Two areas were distinctive in the way of housing dense populations over relatively large areas, Hästhagen in Bredsätra and Skäret in Södviken (Figure 4). Both have a medium to high human impact in the form of grazing cattle. The natural dynamics are essential factors of these habitats, seasonal flooding and long evaporation periods during summer affects the soil salinity and creates zonation. Other disturbances, such as grazing, wave action, periodical anaerobic root zones, wrack deposits and ice scouring highly affects the vegetation in the lower parts of the habitat (Wanner et al., 2007). Therefore, the lower area of the marsh is inhabited by annual, early successional plants and opportunists. The second year, 2019, also Själsgrund, another part of Södviken, was included in the study (Figure 4).

Figure 3. *Reports from Öland on Artportalen, SLU.*

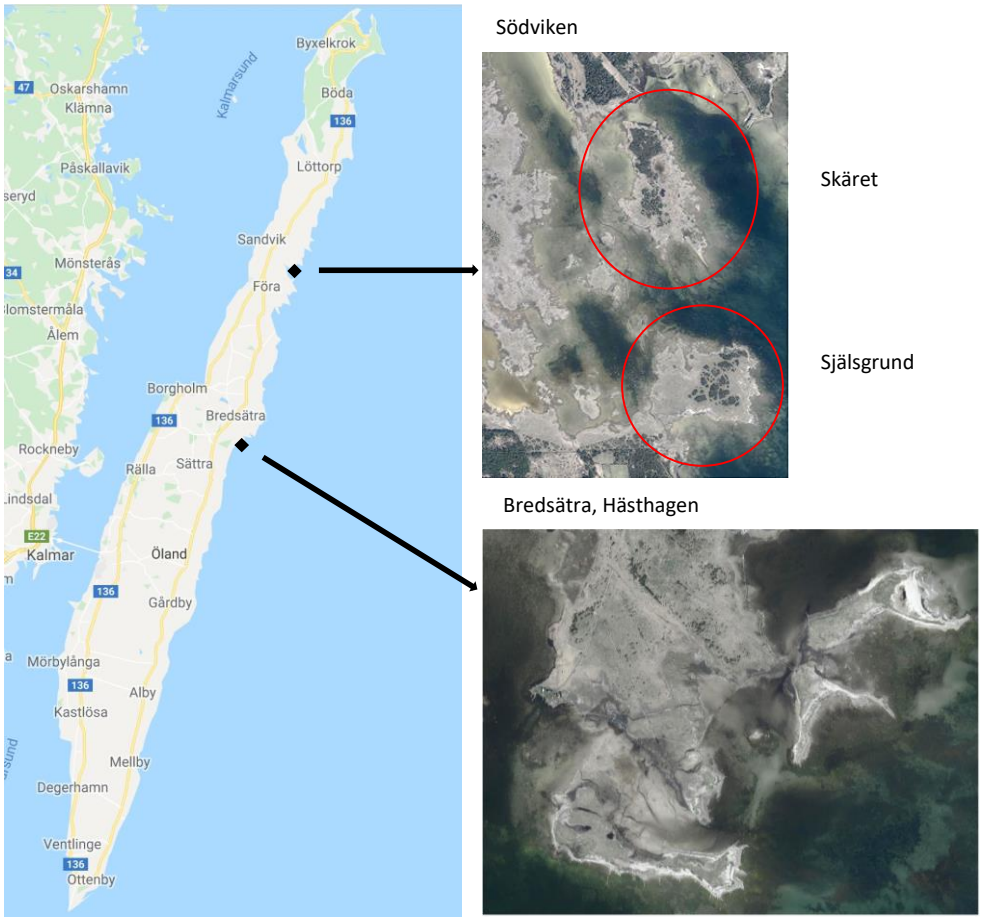

Figure 4. *Overview of study sites on Öland, Sweden. (Google maps, 2018 & GSD-Ortofoto, 2015 ©Lantmäteriet)*

Both Hästhagen and Södviken are included in the Convention on Wetlands, also known as the Ramsar Convention (The Ramsar Sites Information Service (RSIS), 2019). Södviken is protected within EU's Habitats Directive/Natura 2000, and the habitats have been listed (European Environment Agency, 2019). Of the listed habitats in Södviken, cotula is present in: "Mudflats and sandflats not covered by seawater at low tide" (1140), "Coastal lagoons" (1150), "*Salicornia* and other annuals colonizing mud and sand" (1310) and "Boreal Baltic coastal meadows" (1630). The conservation status of the first habitat is assessed as "Unfavorable-Inadequate" and the other three as "Unfavorable-Bad" according to the latest update of the Habitats Directive - Article 17, period 2013 – 2018 (Article 17 web tool, 2019).

Floating ability

Since I observed during early field visits that it was not uncommon to find whole plants and plant parts of cotula washed ashore or floating along the shoreline, this raised a question about its floating ability and was therefore experimentally tested.

Whole plants floating ability was tested by placing five adult plants in buckets filled with seawater which was collected at the same time and from the same place as the plants at Hästhagen. Each plant were placed in its own bucket with enough water so they did not touch the bottom of the bucket when being afloat, even if

the root end of the plant would start to sink. This experiment was executed outdoors and was initiated on October 2nd, 2018 and lasted for 99 days until January 9th, 2019. (Mean temperatures: October 9.5 °C, November 5.7 °C, December 2.9 °C (SMHI, 2018)).

Another bucket was installed with twelve flower heads. These were removed from plants by gentle pulling without applying pressure or twisting. All to make it as close to a natural wave force-induced disassembly as possible. This floating experiment was executed in room temperature and were initiated on October 2nd, 2018 and lasted for 22 days.

Seed floating ability was tested by placing fifty ripe seeds in seawater, collected at the same time and place as the seeds, in glasses. All in all, five glasses and ten seeds in each. They were kept at room temperature (ca. +20°C) and sunken seeds were recorded frequently at first and less frequently the longer the time went by. When the seeds had started to germinate, the seedlings were transferred to a container with substrate from Södviken in hope of further growth. The seeds floating ability experiment was initiated in September 1st, 2019 and lasted for 10 days.

Estimating distribution and expansion

I recorded the population area during the two years, 2018 and 2019, to estimate whether the population expands or not and if it does, expansion speed can be estimated. In total, five maps were created over two seasons and from them the area of occupation was extracted and compared.

The smartphone application NextGIS was used with its track-record function that records coordinates every two seconds. In this way the population was encircled by walking along its edges. The margin of error was around 2m. After recording the occupied area, a map was created in QGIS. Distribution mapping of Hästhagen and Södviken was done on October 5th and 9th, respectively (Figures 9 & 10). In 2019, at the end of September and further in October, the distribution mapping of the same two sites was repeated. In addition to this, the Själsgrund population was also mapped. In total three maps were created in 2019 in QGIS (Figures 11, 12 & 13). In addition, yearly data over cotula's "Area of Occurrence" (AOO), was accessed through request from Swedish Species Information Centre (ArtDatabanken, 2019). AOO is the sum of the reported occupied grid cells which is based on a grid across Sweden using a standardized grid cell area of 4 km^2 (IUCN, 2012). Multiple reports from the same grid cell in the same year does not affect the outcome. The data was processed to visualize the potential expansion in Sweden (Figure 7). AOO is normally calculated for taxon that is under investigation for red-listing in accordance to IUCN Red List Categories and Criteria (2012) but was also used during the work of risk assessments of alien species in Sweden and Norway (Sandvik et al., 2017).

Demography

Another way to estimate a species potential expansion speed and dispersal potential is to investigate its demography (Sandvik et al., 2017) and to be able to quantify seed output, 10 flower heads were studied by measuring diameter and by counting flowers per head. During the inventory, the number of flower heads per

plant was counted on 40 individuals that were somewhat isolated to increase the probability that they were actually one individual. Also heads per unit area was counted to be able to estimate seed production per square meter. During seed floating ability experiments, the germination rate was estimated and used in this demographical study.

Plot survey of percent cover

To investigate if there are any signs of spatial interspecific competition, a survey of percent cover was conducted. A square frame of 0.25m^2 (0.5 x 0.5 m) that was divided into four smaller plots, each of area 0.0625 m^2, were used to study the percent cover of the vegetation occurring together with cotula. Statistical analyses of the percent cover were performed using the small plots (0.0625 m^2) because the microhabitats vary widely on a small scale. The percent cover of all individual herbs, graminoids, bare soil and species number was recorded in 290 plots. Graminoids were grouped together because the flowering season for the majority of them was over when the inventory started, making species identification difficult. The placement of the quadrat was not standardized but instead placed selectively according to the presence of cotula and its potential habitat. All 290 plots were placed within the area of occupation in Figure 9 – 12. The inventory was done during September and early October in 2019. The data from the 290 plots was analyzed with respect to correlations between the cover of the different variables using both parametric and non-parametric tests. The results were very similar so only the results from the non-parametric tests are presented further.

Results

Literature review (distribution and spread)

The literature about cotula is very limited and most of the literature refers to one study done in 1980 by van der Toorns in the Netherlands.

Cotula has been reported from many countries in the world (Figure 5). These reports should of course be interpreted with a bit of care because it appears that some reports come from botanical gardens and freshwater ponds in cities. For example, in Finland there are no reports from natural habitats but several from one pond in Helsinki (Finnish Biodiversity Information Facility, 2019). There is a large number of online shopping sites, especially in the United Kingdom, where one can buy seeds and plants to decorate one's garden pond. What reading the reports does tell us is that cotula has a wide tolerance to different environments as long as they are at least seasonally wet. Almost all the reports come from different kinds of wetlands and most of them from saline wetlands. Because of this, it is fairly interesting that the Red List of South African Plants refers to cotula as a freshwater plant (Powell et al., 2013). South Africa and Namibia are those countries that the majority of researched sources would call the native range. One of cotulas habitats distinguishes itself, roadsides in New Zealand where the roads are salted in winter. This anthropogenic salt input favors cotula's growth over the native, less salt-tolerant, species (Hulme, 2014).

Figure 5. *World distribution map. Red symbolizes countries where Cotula coronopifolia has been recorded. Created with mapchart.net based on data from GBIF (2019), CABI (2019), EPPO (2019) and USDA (2019).*

In Sweden there is a report based on an herbarium specimen from Medelpad (North location in figure 6a) in 1887 which came in with the comment “ballast” which means that the person reporting knew, or suspected, the origin. The species was reported from the same site also in 1890, three years later. Then there were more reports with comments pointing towards ballast as the vector (Sweden's Virtual Herbarium, 2018). This indicates that ballast is one of the ways this species has been spread around the world.

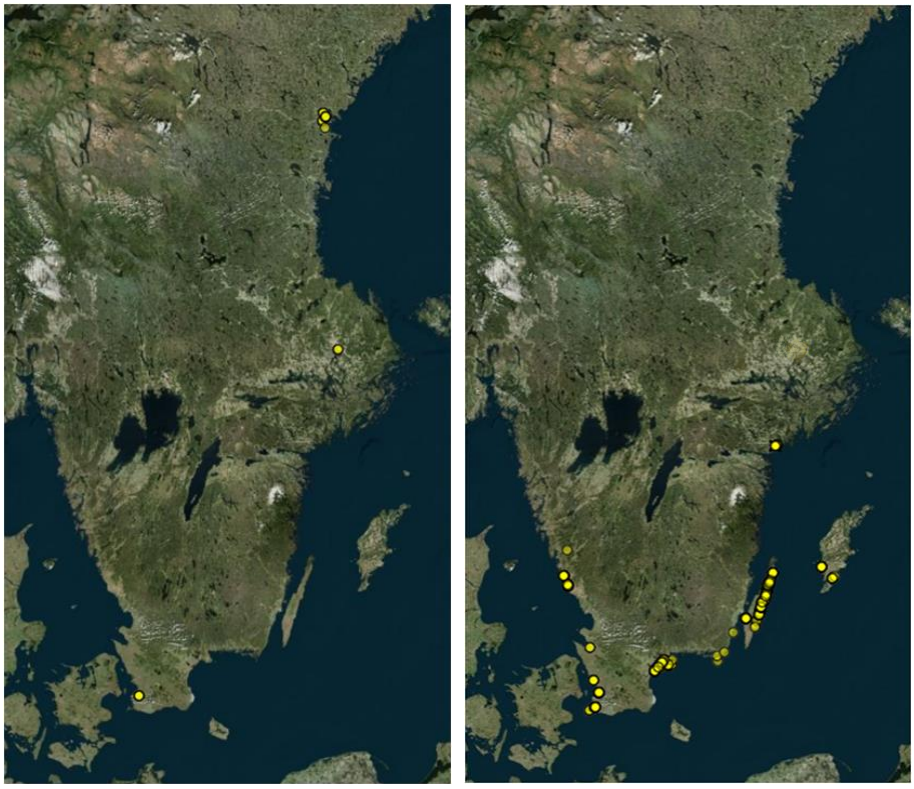

Figure 6a & 6b. *Maps over reported findings on Artportalen. a) before year 2002. b) After year 2002. (Artportalen, SLU. 2019)*

After that, it took 112 years (in 2002) until cotula occurred in a natural habitat in Sweden again (natural habitat in the regard of an area not directly connected to or affected by horticultural activities). In 2002, there is an observation in Sölvesborg, Blekinge, in the south-east of Sweden, with the comment “seashore meadow or beach bed” and an estimation of 2000-3000 plants in that area. From that year on the reports keep coming in from around the area of Sölvesborg (Figure 6b). A majority of the reports are from natural habitats without big harbors or other human related activities close by. In 2010, the first observations from Öland was done, also here the majority of the reports comes from natural habitats. (Sweden's Virtual Herbarium & Artportalen, 2018). The increase of reports between 2002 and 2019 is shown in Figure 7 which shows Area of Occupancy (AOO), i.e. the sum of the area of occupied 2 x2 km^2 grid cells in Sweden. From reading the reports, I assume that the most likely scenario for the introduction into Sweden is a secondary introduction or tertiary spread which means that it is likely dispersed from neighboring countries, into which it has been intentionally or unintentionally introduced by man. If this secondary or tertiary spread is driven by birds or water is difficult to tell, but when studying each report, the majority seems to be water dispersed based on locations, but in a few cases, birds seems more likely than water solely by the location of the reported individuals. They are clearly located in habitats too far from the sea.

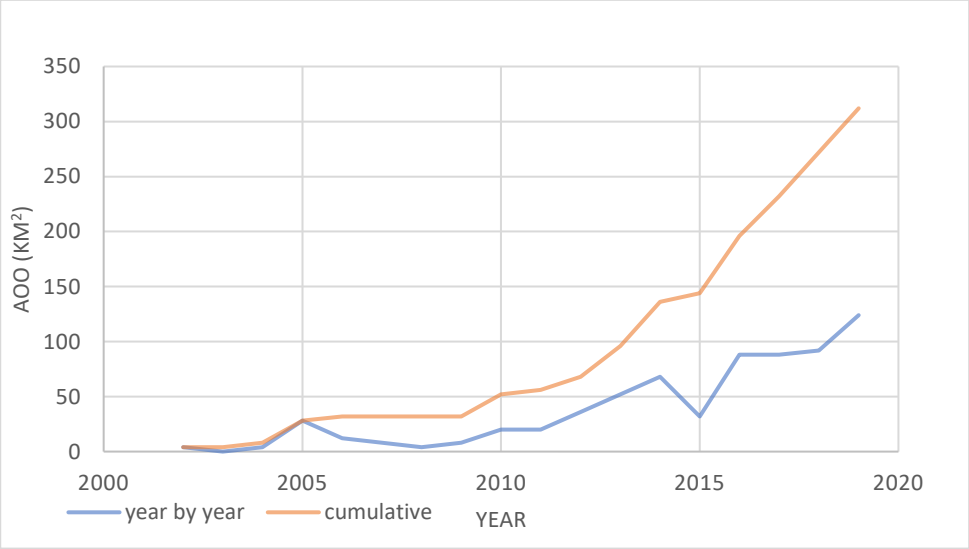

Figure 7. *AOO (Area of Occupancy) based on reports from Artportalen year by year from 2002 to 2019 as well as the cumulative result. Data accessed through request from ArtDatabanken (Swedish Species Information Centre).*

Field study

Field observation notes can be found in Appendix 1. The study sites, Hästhagen and Skäret, have a couple of characteristics in common: like most of the eastern coast of Öland the bedrock is flat with a slight inclination towards the sea, while these places have the ability to accumulate and keep a low relocation of clay, silt and detritus. They have both relatively large areas of shallow and nutrient rich waters, which have enabled cotula to occupy a larger continuous area. Hästhagen has a big

area of shallow water that is shielded from wave action by a barrier island and Skäret itself is an island that acts as a barrier. The cotula population on Skäret is located on the south west part of the island, towards the lagoon of Södviken. It is clear that cotula is an early successional and opportunistic plant when walking among the occupied habitats. Newly disturbed soil, trampled ground of cattle hoofs or the wash fringe of the sea, houses the most prosperous specimens of cotula. In many places visited, the distribution was scattered and/or following the shoreline like a thin belt. This seem to be the common distribution pattern during the early stages of the colonization. The specimens further ashore, in denser vegetation, such as meadows with shortly grazed but dense grasses, are often small with few flower heads. Despite intensive monitoring, no grazing damages could be observed on any cotula plants, neither in 2018 nor in 2019. I even tried feeding cotula to a calf, but it was not accepted. The biggest problem for a potential eradication management action would be the difficult terrain. Cotula often grows in saturated deep mud which cannot carry human weight and even less the weight of machines. I often found flower heads, plant parts and whole plants with intact root system, washed ashore by waves, especially after windy weather. In 2018, it was very unusual to find cotula in the salt pans on the beach but not in 2019. The salt pans dry out during the summer months and thus host only drought resistant and salt tolerant plants. In 2019, cotula was also found on sand and stone shores that also dry out during low water levels during summer. Therefore, my field study showed cotula to be more drought resistant than the existing literature indicated. Also, the flowering season for this part of the world is rather July to December than July to September, as stated in Ecological Flora of the British Isles (Fitter & Peat, 1994). Field observation notes can be found in Appendix 1.

Based on field studies and literature studies, zoochory, (animal dispersal) is unlikely the main method of dispersal because, (i) the achenes lack all evolutionary morphology for this. Neither adhesive mucus, nor spines, nor barbs. (ii) The localities of the biggest populations on the east coast of Sweden all show a pattern; south east placed coast lines all in the direct contact with the main waterbody of the Baltic Sea. If waterfowl would had been the dispersal vector along the coast, the populations should just as likely have been found further inland, in the wetlands, bays and lagoons as well as where they occur today. This was not the case. Also, I observed that the chance of finding cotula in the lagoon of Södviken decreased with the distance to the sea.

Floating ability

Plant floating ability experiment started on October 2nd, 2018. After 55 days, on November 25, there was ice in the buckets with cotula. From there on, the ice melted and froze again as the temperature variated around zero degrees celsius until November 28 (3 days). After that a week of mild weather followed. The plants survived and still showed a healthy green color without any discolorations, weaknesses or bruising due to the temperature or ice pressure. This proves cotula does survive frost and freezing.

From the 17th of December the bucket water froze again and after four days of continuous ice, a few leaves showed signs of frost damage. Two days after that,

December 23, some leaves were dead and some more were damaged. On December 28, the ice had melted and only a few leaves were still alive, two plants were close to sinking. On December 31, all the individuals had started to sink but did not touch the bottom of the bucket. Air temperature was around 0°C. Nine days later, all individuals become afloat again, now at an air temperature of +4°C. Not much of the plants where alive at this point and they were also heavily covered by algae. Since the plants were not considered healthy enough to recover then, the experiment was terminated. The experiment lasted for 99 days (3.5 months) and all plants kept floating the whole time.

Flower head floating ability experiment started October 2nd, 2018. After 19 days, October 21st, eight out of twelve flower heads had sunk. The day after that, one more. After 22 days, all twelve heads had sunk. This gives a mean floating time of 20 days (SD 0.86).

Seed floating ability and germination rate. The experiment lasted for ten day. Two of the 50 seeds sank immediately and five never sank. On the tenth day, 18 seeds had germinated and some of the germinated seeds sank while others became afloat again. That was the reason to cancel the experiment. Because five seeds never sank before the experiment was terminated, the results will look a little bit different if you include them or not. Mean floating time, if including the five seeds that still floated until germination (Table 1 & Figure 8), was 40 hours (Median 9, SD 50). If those five were excluded the mean floating time was 29 hours (Median 8, SD 38).

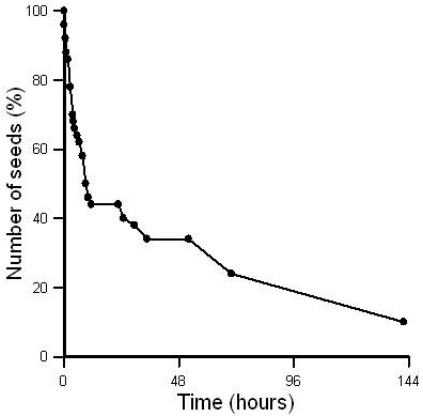

Figure 8. *Floating time of 50 seeds in percentage over hours.*

Table 1. *Seed floating time.*

N=50	Floating time (hours)
Minimum	0
Maximum	142
Median	9
Arithmetic Mean	40
Standard Deviation	50

Two days after germinating, 30 seedlings were transferred to a container with substrate from Södviken but not a single seedling survived. Approximately 80% of the seeds germinated.

Distribution and expansion

Green fields in figure 9-13 symbolize populations dense enough to record and green dots are a dense but small group of individuals or a couple of sparsely dispersed individuals. When comparing figure 9 and 10 one can see how the niche is expanding from the more protected mudflats to the sandy and rocky shorelines and even up to the salt pans on the barrier island. The protected mudflat that houses the big population in 2018 is not as dense in 2019, this is due to relocation of the substrate before the season in 2019, which made a part of the mudflat deeper than the year before. The bay in the middle of the picture did house a few individuals in 2018 but so few it was not recorded. We can also see an indication that areas shielded from wave action is preferred.

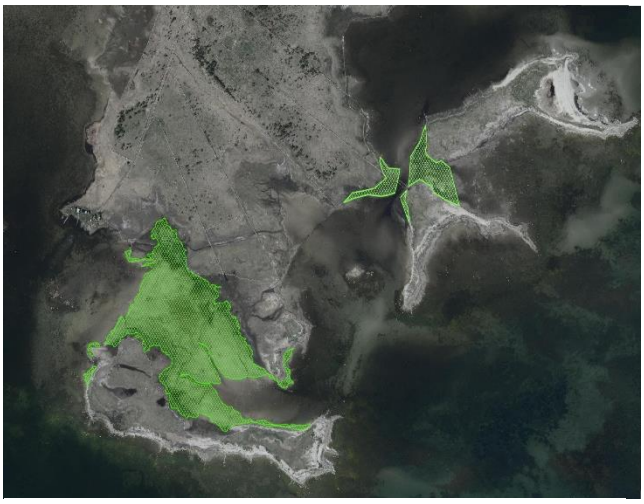

Figure 9. *Distribution Hästhagen 2018. Made with GSD-ortofoto (2015). ortofotoRgb025. ©Lantmäteriet*

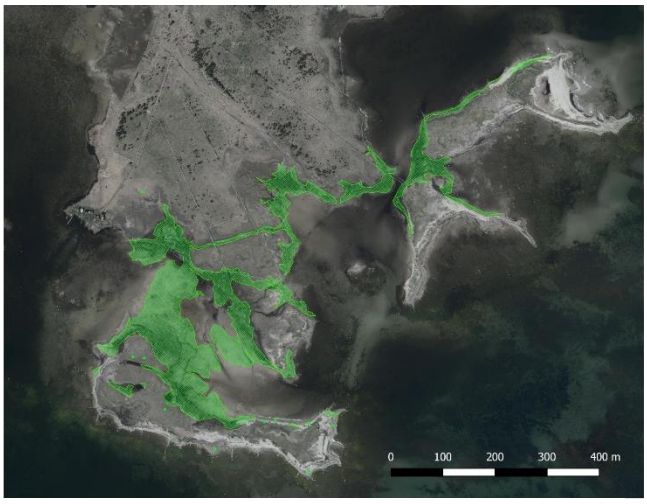

Figure 10. *Distribution Hästhagen 2019. Made with GSD-ortofoto (2015). ortofotoRgb025. ©Lantmäteriet*

In figure 11 and 12 one can see that cotula has spread around the island of Skäret up to the north-east side where, in 2018, not a single individual was found. Even though it has spread it has barely founded any new populations. It occurs as sparsely dispersed small stands and single individuals. One can see that it has spread further ashore, here as well, even though it is not as obvious as in previous figures. One can see that it has spread to the outlet of the big saltpan north-east on the island but not yet reached the saltpan.

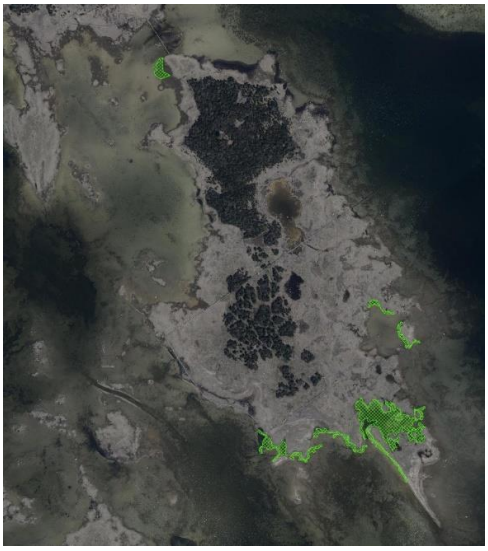

Figure 11. *Distribution Skäret 2018. Made with GSD-ortofoto (2015). ortofotoRgb025. ©Lantmäteriet*

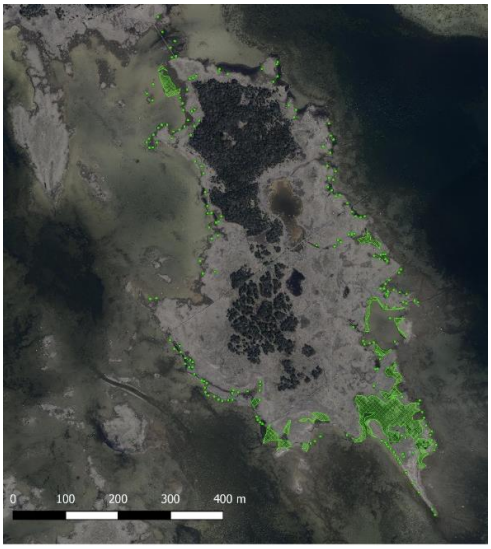

Figure 12. *Distribution Skäret 2019. Made with GSD-ortofoto (2015). ortofotoRgb025. ©Lantmäteriet*

A new population not present in 2018, Själsgrund was found in 2019 (Figure 13). In 2018 there was only a few specimens present on this peninsula which is located right across the inlet of the lagoon relative to Skäret. Depending on whether the new population is included or not, the area increase differs. If Själsgrund is included the total increase is 310% (350208 m^2), if not, the total increase is 127% (143367 m^2). In terms of expansion speed the results are either 591.78 m in the first case or 378.64 m in the second. Cotula individuals were found further into the lagoon, west of Skäret and Själsgrund, but only in small, sparsely distributed stands or single individuals.

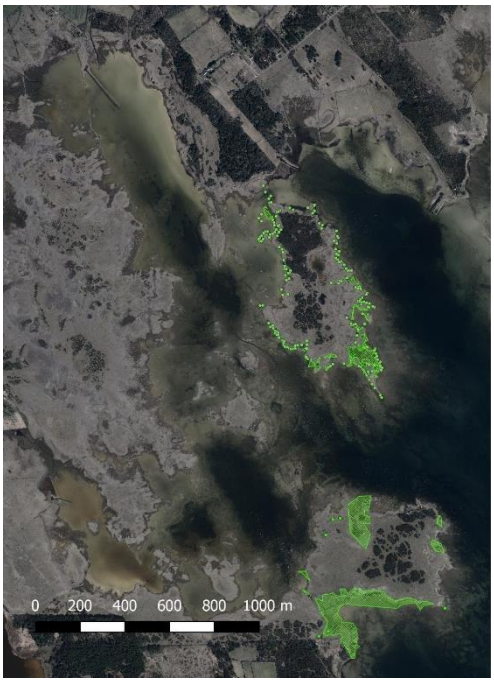

Figure 13. *Distribution Södviken including Skäret and Själsgrund in 2019. Made with GSD-Ortofoto. (2015). ortofotoRgb025. ©Lantmäteriet*

Demography

Ten flower heads were measured and flowers per flower head was counted, there was no significant variation in flower per diameter, hence the low number of examined heads. This resulting in a mean of 243 flowers per flower head (SD 18). This in relation to counted flower heads per plant, (mean 44 and SD 37) gives a mean seed output of 10 762 per plant. The estimated germination rate (0.8) from the seed floating ability experiment gives a potential seedling production per plant of 8 610 (Table 2). To extrapolate this to seedlings per unit area, the total number of flower heads in an area (0.045 m^2) of cotula monoculture was counted, resulting in 9 911 heads per square meter. This leads to 2.4 million seeds per m^2 and correspondingly to 1,9 million seedlings per m^2.

Table 2. *Demographic numbers with means and standard deviations*

	Mean	SD
Flower head/plant:	44	37
Flower/flower head:	243	18
Seeds/plant:	10 762	
Germination rate:	0.8	
Seedlings/plant:	8 610	

Plot survey of percent cover

A total of 16 herb species was recorded in the 290 plots (Appendix 2). The herbs that occured most frequently together with cotula was *Lysimachia maritima*, *Plantago maritima*, *Salicornia europaea* and *Spergularia marina*. Except for *L. maritima*, there is a significant negative correlation between the cover of cotula and the cover of the other species, including graminoids (Table 3). Number of species also correlates negatively with cover of cotula (Figure 14). But at the same time there is no significant correlation with bare soil.

Table 3. *Cover correlations, p-value and their significance.*

Coverage of	Cotula	p	
Cotula coronopifolia	1		
Bare soil	-0,143	0,522	ns
Lysimachia maritima	-0,054	1,000	ns
Graminoids	-0,266	<0,001	***
Herbs	-0,466	<0,001	***
Number of species	-0,332	<0,001	***
Plantago maritima	-0,258	<0,001	***
Salicornia europaea	-0,266	<0,001	***
Spergularia marina	-0,253	<0,001	***

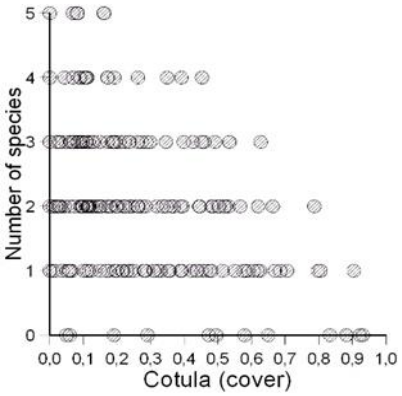

Figure 14. *Correlations between cotula cover and the number of species.*

After that the plots that had cotula present were divided into groups based on percent cover of cotula (Table 4). Any group that had more than 30% cover of cotula showed a greater difference in coverage of most of the other species. This was not true in the case of *L. maritima*, in which no significant difference could be found. This data was tested in a parametric ANOVA test as well, but it gave a very similar result and was therefore not included in the table. Once again it was clear that the number of species decreased with increased cotula cover at the same time as bare soil only was slightly affected. At a closer view, there was a negative correlation between number of species and bare soil, but no covariance was found.

Table 4. *Grouped cotula cover compared to others cover. Tested with "Conover- Inman Test for All Pairwise Comparisons" (Green marks indicates the largest difference in row four) and "Kruskal-Wallis Test" and given their p-values.*

	Cover of Cotula	N	Cover (%)	SD	Kruskal-Wallis Test Statistic	p
Bare soil	0 - 10%	127	27.2	24.8	4.95	0.084
	10 - 30%	87	21	23.2		
	> 30 %	76	20.6	15.9		
Graminoids	0 - 10%	127	26.5	23.2	23.43	<0.001
	10 - 30%	87	27.6	23.7		
	> 30 %	76	11.5	11.2		
S. marina	0 - 10%	127	9.5	13.1	20.77	<0.001
	10 - 30%	87	7.5	10.6		
	> 30 %	76	3.9	7		
L. maritima	0 - 10%	127	8.5	15.8	0.249	0.883
	10 - 30%	87	7	11		
	> 30 %	76	6.6	9.8		
S. europaea	0 - 10%	127	19	26.8	18.51	<0.001
	10 - 30%	87	14.3	22.4		
	> 30 %	76	3.8	8.2		
P. maritima	0 - 10%	127	4.1	10.9	20.7	<0.001
	10 - 30%	87	0.9	2.9		
	> 30 %	76	0.2	0.8		
Herbs	0 - 10%	127	43.7	27	56.79	<0.001
	10 - 30%	87	33	24.5		
	> 30 %	76	16.6	15.7		
Number of species	0 - 10%	127	2.4	1	29.13	<0.001
	10 - 30%	87	2.2	1.1		
	> 30 %	76	1.6	1		

Discussion

One could argue that as soon as an alien species is naturalized in a new habitat it must have an impact on the ecosystem. Whether it is by space occupation, allelopathy or reduction of resources that otherwise should have been available, it still affects the ecosystem. It is though hard to prove the possible effects if the interactions are not studied over a long time period or in a controlled environment, like in a green house. These two options were not available during this study. So rather than proving anything, this study gives an indication about the possible interspecific competition.

The distribution of the populations and individuals in Hästhagen and Skäret (Figures 9-12) indicates that cotula prefers microhabitats shielded from wave action. This can be the reason for the many findings of whole plants with intact root systems washed ashore but also due to these habitats ability to accumulate sediments. The fact that cotula specimens were found higher up on land in 2019 compared to 2018 (Figures 9–12) could be due to further spread of the existing population or, because the water levels were higher during one big seed dispersal event. It should also be mentioned that the summer of 2018 was extraordinarily dry and the fall included a quite big storm. These two factors could have affected the distribution observed in 2019. It was observed that individuals of cotula in denser vegetation were smaller and had fewer flower heads compared to those growing in newly disturbed soil. This can be interpreted such it shows a negative response to both interspecific and intraspecific competition and confirms that it is, indeed, an early successional species.

Whole plant floating ability tests were executed outdoor but without the impact of waves. The fact that they started to sink a couple of centimeters and later float back up to the surface could be due to the weather, the temperature rose to +4^{o}C from previously lower degrees, the temperature at which water has the highest density. Another possibility for the changing buoyancy can be due to decaying processes in which carbon dioxide and methane is produced. Some time after that, at the end, the plants were heavily covered with algae, which may have increased their floating ability while at this time not much of the plants were still alive. The fact that they did survive frost and ice does not correlate well with previous literature, for example, Portugal's assessment that stated that cotula does not tolerate frost at all (Lopes, 2014). This might be due to local adaptations even though that seems speculative considering founder-effects and its supposed small genetic variation, which is generally the case for invaders (Daehler, 2003). Both seed and flower head floating ability were tested at room temperature, which may have had an impact on the result. But in comparison to van der Toorns (1980) seed floating ability test, where most seeds sank within 10 minutes, the temperature should not have that big of an impact. In this experiment less than 1% of the seeds sank within 10 minutes. This discrepancy in sinking time in this experiment compared to van der Toorns is not clear because van der Toorns does not described how his experiment was performed. Wave simulations may have been conducted and/or he may have done the experiment in the field.

The demographic study is built on a number of assumptions because of sparse data in some of the steps. The approximated 0.8 germination rate does correspond well to Noe & Zedler's (2000) research, but the step where flower heads per plant was counted, only 40 individuals were studied and the quite large standard deviation tells us that that number is too low. Also, considering that the individuals counted were standing isolated from conspecifics to increase the probability that they were actually one individual, it can be so that they had a higher number of heads per plant because they lacked the effect of density. The number of heads per plant is later one of the foundations for the rest of the calculations in this demographic study and is the weakest link. Flower heads per unit area in a monocultural stand was also counted and this number should be more accurate considering that it does include the effect of density. It is further that number that is used to estimate seed production per square meter.

When comparing figure 7 and figure 15, which is a conceptual model of the phases of invasion of any organism new to its environment, it appears that the cotula population in Sweden is still in the expansion phase of the invasion. Based on this, the observed habitat niche and expansion speed from my studies, I assume that further spread in Sweden is very likely.

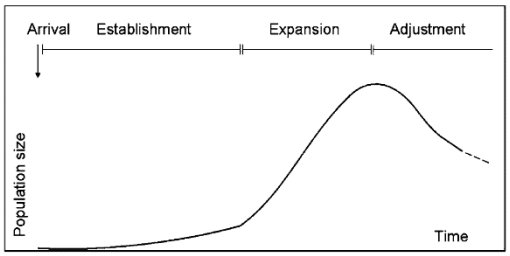

Figure 15. *Phases of invasion. (Reise et al., 2006. ©Springer-Verlag and AWI)*

The placement of the plots during inventory could not be randomized, this because the mapped area of the population is highly irregular in the sense of microhabitats. Therefore, the whole areas mapped in figures 9-12 is not potential habitat, but at the same time, the differences in the microhabitats are so small (< $2m^2$) it would not show on the maps. The < $2m^2$ limit is due to the margin of error of the recording app. It would, of course, have been desirable to have an even more accurate mapping device available. Yet, the results of the expansion speed (380 m or 590 m) correlates well with the California Invasive Plant Council's assessment where 350-450 meter a year is stated (Brusati & DiTomaso, 2005). This also agrees with what van der Toorns (1980) states in his study, which uses the exact same numbers.

The significant negative correlation between the cover of cotula and that of the other species, indicates that the native species and cotula affects each other but it cannot be proven which species is disrupting which. It should also be mentioned that if two species frequently competitively exclude each other in an area, the species may co-occur less frequently. This can only be tested ex situ or over a long period of time. The negative correlations between the cover of cotula and the native species may also be caused by factors that co-vary with the presence of cotula. These factors could have been excluded in a controlled ex-situ experiment.

The literature review, field study and experiments all indicate that dispersal by water should be considered the main dispersal mechanism. Dispersal by waterfowl cannot be excluded and is possible under rare circumstances. An experiment showed that seeds are viable after passing through intestines of geese, but yet unlikely because, as van der Toorns himself expresses, seeds are "incidentally eaten

by birds" (van der Toorns, 1980). I would like to confirm this as well since I was unable to find any grazing damages despite intense search. It should also be noted that plants in coastal habitats generally are adapted to aquatic dispersal. Together with the positive floating ability results, dispersal by water together with wind and waves must be seen as a possible way of long-distance dispersal. Therefore, it is likely that cotula came to Sweden across the Baltic sea from Germany or Denmark, regarding the location of the first observations from a more natural habitat in 2002.

A number of publications (Carson et al., 2005; Weber, 2017), where cotula is seen as an invasive species, state that hand pulling is the only possible way of management. But neither of these publications refers to any studies on this or explain why. Therefore, this has to be studied and I would propose different types of eradication experiments in stable populations to be able to evaluate their effectiveness. One study from the Pacific coast in the USA (Lambrinos, 2007), showed increased growth and expansion of cotula when doing eradication experiments on a, for them invasive grass species (*Spartina alterniflora*). This shows that eradication experiments on cotula have to be done with care to not open up more newly disturbed soil and hence enable further spread. The most difficult part of a potential big scale eradication experiment would be the unstable terrain with big areas of soft sediments. Because of this it should be further investigated if other types of livestock, not only bovine, would show any interest in grazing cotula. I would suggest ovine or caprine cattle (sheep or goat).

I observed that Södviken's lagoon still has large areas of apparently suitable habitat that was not populated by cotula. The colonization of these last unoccupied parts is probably only a question of time. And considering that Södviken is protected by Natura 2000, partly for its habitats, I would suggest that this place is worth protecting from further spread. It should also be taken as a warning for the entire southern part of Sweden that roadside verges of salted roads in New Zealand have been populated by cotula. The salt input favors cotula in comparison to the native, less salt-tolerant, species. Mowed meadow species and many other threatened species are relying on these roadside verges (ArtDatabanken, SLU. 2018). Future climate change will most likely have a positive effect on cotula in Sweden. The lack of cold winters and big fluctuations in precipitation (Lindegård, 2019) might be beneficial considering the prolonged flowering season and because of how well it endures stochasticity.

Conclusion

The literature review, field study and experiments all indicate that dispersal by water should be considered the main dispersal mechanism. The demographic study showed that 2.4 million seed per occupied square meter can be produced and seeds remain afloat for 40 hours in average. Also, a whole, uprooted plant with seeds can stay afloat for months until it dies. The existing population of cotula in Sweden was introduced in 2002 and is most likely due to secondary spread by water across the Baltic Sea, based on its good floating ability and the unlikeliness of zoochory.

The populations that were mapped in 2018 and 2019, expanded by, at least, 380 m and showed a broader habitat niche than indicated by the literature. The species may populate seasonally dry soils and not only salt marshes and sea shores. This study indicates that there is competition between cotula and the native species, but this study cannot differentiate the potential effects of cotula or other biotic or abiotic factors. This spatial competition must be experimentally quantified to be able to prove whether or not it is cotula that has a negative effect.

I also found that cotula does survive frost and freezing during a shorter period and future climate change will most likely have a positive effect on cotula in Sweden. The lack of cold winters and big fluctuations in precipitation (Lindegård, 2019) should be beneficial considering the prolonged flowering season and because of how well it endures stochasticity. Therefore, further spread of cotula in Sweden is to be considered most likely. Also, a large part of the Baltic coast is suitable for colonization by cotula. Hence, there is a need for an action plan to prevent further establishment and a readiness for rapid eradication once the species reaches new areas. Eradication experiments needs to be done to form an efficient action plan.

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Figure 5 was created with mapchart.net [2019-01-13]

Appendix 1

Field observations

- 28/8 – 2018 Södviken and Skäret

Individuals seems to be washed free out of the soil by wave action. Washed up adult individuals on the shore. Root system still intact. Pools, salt pans on higher ground are not invaded. No traces of any herbivory or grazing damage. Flower discoids seems to dry up and fall of after seed dispersal.

- 30/8 – 2018 Sillgrundet

There is a clear connection between newly disturbed ground and occurrence of Cotula. It does not seem to be adapted to or able to endure periodically dried out soil.

- 3/9 – 2018 Hästhagen

It is obvious that under the right circumstances cotula is able to form monocultures. Waterlogged muddy clay. It seems that cotula and Salicornia are the ones that are able to grow in these wet circumstances.

- 4/9 – 2018 South of Södviken

Very few plants on the inside of the bay. Only a few on the outside of Själsgrund. This could free the geese from accusation of being the vector, also the pools and salt pans on higher ground lack individuals. It could of course be the higher salt concentrations in the salt pans that are the cause of the lack of individuals there. The habitat here has less mud and clay and less salicornia as well.

- 2/10 – 2018 Hästhagen

After the storm Knud. Very high water levels. 34 cm according to SMHI. This is the first time I notice that discoids, in all development states, has come off and been washed ashore without the rest of the plant. This could maybe be a result of the storm. Besides that, I observe whole plants enmeshed in floating mats made of other plant material and alge, e.g Fucus vesiculosus, and other species. This wrack deposit has been washed up several meters up on land. Individuals were collected for floating experiments.

- 28/12 – 2018 Skäret

A few plants are still alive. Approximately around 10% of the population. There are big areas covered by a thick wrack deposit of seaweeds.

- 1/7 – 2019 Skäret

Cotulas found are small and not dominant at all. Has begun to disperse seeds. Observed dispersal with the strong winds, only short distance though, approximately 20-30 cm maximum. Small individuals found on the north side of Skäret, where no individuals were found last year. A couple of big plants in trampled ground far north. A dozen found in the south part of the canal that runs from south to north on the east side of Skäret. These are also new for this year.

- 19/7 -2019 Skäret

Seed collecting. Bigger spread and areas of individuals on the south side this year compared to last year. Big areas of wrack deposit where Cotula grows only if it keeps moist.

- 24/7 -2019 Hästhagen

Individuals are found on much higher ground/further up on land compared to last year. Quite many plants up in the small pools and salt pans where they were not growing last year.

- 20/8 -2019 Hästhagen

Individuals are found growing on both stone gravel beach and on sand beach. This speaks against what I previously thought, that it has a low resistance to drought. These places where it was found today definitely dries out during dry summer months.

- 27/8 -2019 West part of the lagoon of Södviken

3 plants found but there is definitely a lot of suitable habitat. Again this speaks against geese as the common vector.

Appendix 2

List of recorded species in the plot survey

- *Armeria maritima*
- *Artemisia maritima* subsp. *humifusa*
- *Atriplex prostrata*
- *Cotula coronopifolia*
- *Lysimachia maritima*
- *Halimione pedunculata*
- *Plantago maritima*
- *Polygonum aviculare*
- *Argentina anserina*
- *Salicornia europaea*
- *Spergularia marina*
- *Suaeda maritima*
- *Taraxacum* sp.
- *Tripolium pannonicum*
- *Tripleurospermum maritimum*