The Sea Aster mining bee *Colletes halophilus* Verhoeff, 1944 (Hymenoptera: Colletidae) widely distributed at the Baltic Sea coast of Denmark and Germany

Die Strandaster-Seidenbiene *Colletes halophilus* Verhoeff, 1944 (Hymenoptera: Colletidae) ist weit verbreitet an der Ostseeküste von Dänemark und Deutschland

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Zusammenfassung

Die Strandaster-Seidenbiene *Colletes halophilus* Verhoeff, 1944 ist ein Endemit der Atlantik- und Nordseeküste Westeuropas und aufgrund ihrer spezifischen Habitatansprüche an Küstenbiotope mit Vorkommen der Strandaster (*Tripolium pannonicum*) als bevorzugter Futterpflanze gebunden. Aufgrund der späten Flugzeit und ihrer Habitatspezifität kann die Art leicht übersehen werden. Durch Funde der Art auf der Insel Fünen (DK) 2019, Rügen (MV) 2020 und Sehlendorf (SH) 2021 wurde deutlich, dass die Art deutlich weiter verbreitet ist und auch im Bereich der kontinentaleren Ostseeküste vorkommt. Durch gezielte Nachsuche im Jahr 2022 konnte die Art in den meisten potentiell geeignet erscheinenden Küstenhabitaten in Schleswig-Holstein und einigen Gebieten in Mecklenburg-Vorpommern festgestellt werden. Der aktuelle Kenntnisstand zur Verbreitung von *C. halophilus* an der Ostseeküste wird vorgestellt und Hypothesen einer möglichen rezenten Ausbreitung der Art werden diskutiert.

Keywords:

first record, solitary bee, distribution, Baltic Sea coast, *Tripolium pannonicum*

Abstract

The Sea Aster mining bee *Colletes halophilus* Verhoeff, 1944 is known as an endemic of the western European coasts of the Atlantic and the North Sea. The species has specific habitat requirements and is restricted to coastal habitats with populations of the Sea Aster (*Tripolium pannonicum*), its preferred host plant. Due to the late summer activity of adults and habitat specialisation, this solitary bee species is easily overlooked. In 2019, *C. halophilus* was first found at the Baltic Sea coast of the island of Fyn (Denmark), 2020 on the island of Rügen (Mecklenburg-Vorpommern, Germany) and in 2021 in Sehlendorf (Schleswig-Holstein, Germany), demonstrating that the species is far more widespread and also occurring along the more continental Western Baltic Sea coast and Kattegat. Targeted sampling in 2022 revealed that *C. halophilus* is now present in most of the potentially suitable coastal habitats in Schleswig-Holstein and at least in some parts of Mecklenburg-Vorpommern. We here present data on the currently known distribution of *C. halophilus* along the Baltic Sea coast of Denmark and Germany and discuss hypotheses of a potential recent range extension.

1. Introduction

The Sea Aster mining bee Colletes halophilus Verhoeff, 1944 belongs to the C. succinctus species-group that, in northwestern Europe, also comprises its close relatives C. hederae Schmidt & Westrich, 1993 and C. succinctus Linnaeus, 1758. Species of this complex are often difficult to identify based on morphology alone but they clearly show differences in habitat preferences, adult phenology and flower specialisation (Kuhlmann et al. 2007, Zenz et al. 2021). Colletes halophilus is associated with coastal dunes and salt marshes and bees are on the wing from the end of July to the beginning of October. The species is specialised on collecting pollen (oligolectic) of Asteraceae flowers (Müller & Kuhlmann 2008) with the Sea Aster (Tripolium pannonicum) as the dominant host plant that is most common in late summer in its natural habitat (Sommeijer et al. 2009, 2012). Colletes halophilus is a solitary and soil nesting bee that prefers horizontal to vertical sandy substrate (Hardy 2013). Larval stages overwinter and development is resumed in April (Sommeijer et al. 2012). Known parasitoids are the cuckoo bees Epeolus variegatus Linnaeus, 1758 (Guichard 1974) and additionally in the southwest of the Netherlands the rare E. tarsalis Morawitz, 1874 (Peeters et al. 1999).

The natural history of the closely related *C. succinctus* and *C. hederae* was summarized by Kuhlmann et al. (2007) and Zenz et al. (2021): *Colletes succinctus* is the most widely distributed of the three species, ranging from western and southern Europe to Kazakhs-

tan in the east. The species is polylectic with a strong preference for Ericaceae (*Calluna, Erica*) and lowland heaths. Its flight period is the earliest of the three species and comprises mid-July to late September, sometimes October. *Colletes hederae* is famous for its ongoing massive range expansion. It is currently spreading from the north Mediterranean to western and Central Europe and with a strong preference for ivy (*Hedera*). The species is inhabiting a wide range of open habitats, including urban sites, and is the latest active of the three species, flying from September to November.

Colletes halophilus is endemic to the west of Europe and due to its specific habitat requirements, the apparently often small and fragmented populations are limited and almost linearly distributed along the coast on sites of special scientific interest and conservation concern. In the European Red List of bees, it is classified as "Near Threatened" (NT) (Nieto et al. 2014) while in Germany it is listed as "extremely rare" (R) (Westrich et al. 2012). In the Red List of Danish bees C. halophilus is mentioned as "data deficient" (DD) (Madsen 2019) because of the limited information available. The known range of C. halophilus stretches along the Atlantic coast of southern France through Belgium, the Netherlands and southern Britain to northwestern Germany (Kuhlmann et al. 2007, Genoud & Dittlo 2007, Gilles 2009). The northernmost published record is from the island of Fanø in Sønderho, southwestern Denmark (Madsen et al. 2015). In Germany

Tab. 1: Records of Colletes halophilus at the Baltic Sea coast and Kattegat of Denmark and Germany

Locality (County) Coordinates Leg. Coll. Date Notes, estimated population size
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Danmark

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1ç	Kattegat: Flyvesandet (Fyn)	N55.6197° E10.2949°	K.R. Poulsen	K.R. Poulsen	24.08.2019	
5♀, 7♂	Kattegat: Flyvesandet (Fyn)	N55.6197° E10.2949°	K.R. Poulsen, N. Lykke	K.R. Poulsen, H.B. Madsen, Natural Histo- ry Museum of Denmark	13.08.2022- 31.08.2022	
19	Kattegat: Lindøhoved (Fyn)	N55.5906° E10.2021°	N. Lykke	Natural Histo- ry Museum of Denmark	02.09.2022	
5₽, 2♂	Marstal (Aeroe)	N54.8463° E10.5329°	L. Pössler, F. Brunßen	L. Pössler, F. Brunßen	26.08.2022	

Germany Schleswig-Holstein

4♀, 1♂	Holnis, Höftsee (Schleswig-Flensburg)	N54.8753° E9.5931°	M. Kuhlmann	M. Kuhlmann	31.08.2022	>30♀ (Kuhlmann)
3ç	Holnis, Kleines Noor (Schleswig-Flensburg)	N54.8697° E9.5862°	M. Kuhlmann	M. Kuhlmann	31.08.2022	>10ç (Kuhlmann)
2♀, 2♂	Geltinger Birk (Schleswig-Flensburg)	N54.7890° E9.9038°	H. Herrmann	H. Herrmann	23.08.2022	>20ç (Herrmann)
1♀, 2♂	Geltinger Birk (Schleswig-Flensburg)	N54.7747° E9.9020°	H. Herrmann	H. Herrmann	23.08.2022	>10ç (Herrmann)
3♀, 1♂	Geltinger Birk, 0.5 km N NABU-Station (Schleswig-Flensburg)	N54.7880° E9.9041°	M. Kuhlmann	M. Kuhlmann	26.08.2022	>30ç (Kuhlmann)
1ç	Geltinger Birk, 0.3 km N Mühle Charlotte (Schleswig-Flensburg)	N54.7744° E9.9022°			26.08.2022	Observation; >5♀ (Kuhlmann)
17♀, 3♂	Oehe-Schleimünde (Schleswig-Flensburg)	N54.6926° E10.0238°	Exk. AG Stech- immen (Adam, Bendixen, Drews, Gräper, Koppitz, Povel), M. Kuhlmann	A. Drews / M. Kuhlmann	20.08.2022- 26.08.2022	>50¢ (Drews)
9♀, 7♂	NSG Bottsand, Wendtorf (Plön)	N54.4278° E10.2954°	A. Drews, M. Kuhlmann	A. Drews / M. Kuhlmann	21.08.2022- 24.08.2022	>30♀ (Drews, Kuhlmann)
8⊊, 9♂	Sehlendorfer Binnensee (Ostholstein)	N54.3101° E10.6805°	A. Drews	A. Drews, K. Adam / M. Kuhlmann	01.09.2021- 03.09.2021	>50º (Drews)
6♀, 23♂	Sehlendorfer Binnensee (Ostholstein)	N54.3101° E10.6805°	A. Drews, M. Kuhlmann	A. Drews / M. Kuhlmann	11.08.2022- 28.08.2022	>509; J on <i>Daucus carota</i> (Drews, Kuhlmann)
3♀, 5♂	Eichholz (Ostholstein)	N54.3820° E10.9400°	A. Drews	A. Drews / M. Kuhlmann	25.08.2022	>300♀ (Drews), small nesting site (>5♀)
3ç	Heiligenhafen, Graswarder (Ostholstein)	N54.3790° E10.9893°	L. Lübker	M. Kuhlmann	04.09.2022	photos; >10♀ (Lübker)
3♀, 3♂	Westermarkelsdorf, Salzensee, Fehmarn (Ostholstein)	N54.5264° E11.0532°	J. Gräper, M. Torök	M. Kuhlmann	29.08.2022	
1ç	Großenbrode (Ostholstein)	N54.3911° E11.1128°	A. Drews	A. Drews / M. Kuhlmann	06.09.2022	>3♀ (Drews)

1ç	Kloster, Hiddensee (Vorpommern-Rügen)	N54.578° E13.112°	K. Kunkel	JC. Kornmilch	14.09.2021	
1ç	Kloster, Hiddensee (Vorpommern-Rügen)	N54.578° E13.112°	K. Kunkel	JC. Kornmilch	06.09.2022- 09-09-2022	
1ç	Vitte, Seglerhafen, Hiddensee (Vorpommern-Rügen)	N54.573° E13.116°	K. Kunkel	JC. Kornmilch	10.09.2022	
1ç	Vitte, Hiddensee (Vorpommern-Rügen)	N54.561° E13.113°	K. Kunkel	JC. Kornmilch	11.09.2022	
1ç	Vitte/Fährinsel, Hiddensee (Vorpommern-Rügen)	N54.545° E13.113°	K. Kunkel	JC. Kornmilch	05.09.2022	
2♀	Klein Zicker. Zur See 6, Rügen (Vorpommern-Rügen)	N54.283° E13.695°	K. Kunkel	JC. Kornmilch	25.08.2022- 28.08.2022	
2♀	Thiessow, Rügen (Vorpommern-Rügen)	N54.279° E13.705°	K. Kunkel	JC. Kornmilch	22.08.2022- 24.08.2022	>109
1ç	Glewitz, Hafen, Rügen (Vorpommern-Rügen)	N54.2414° E13.3157°	WP. Polzin	JC. Kornmilch	04.10.2020	
2♀	Greifswald, Strandbad Eldena (Vorpommern-Greifswald)	N54.093° E13.455°	JC. Kornmilch	JC. Kornmilch	13.09.2022	

Mecklenburg-Vorpommern

for a long time *C. halophilus* was only known from Lower Saxony (Kuhlmann et al. 2007) but was recently also recorded in salt marshes of the North Sea in the Federal State of Schleswig-Holstein (SH) (Klammer et al. 2021). An alleged record of *C. halophilus* from the island of Rügen at the Baltic Sea, that was published without further details by Westrich (2019: 436), turned out to be erroneous (F. Wagner pers. comm. 15 Oct. 2021, following correspondence with P. Westrich). So, to date *C. halophilus* at the northern edge of its range has only been known from coastal habitats of the North Sea (Klammer et al. 2021).

Thus, it came as a surprise that in September 2021 two of us (AD, KA) discovered C. halophilus at the Baltic Sea coast near the Sehlendorfer Binnensee south of Hohwacht in SH. This site is more than 100 km away from the nearest known population at the coast of the North Sea in the west of SH. This raised the question whether this population is isolated or if C. halophilus is more widespread than previously known. A systematic survey and targeted search for C. halophilus at suitable sites along the entire Baltic Sea coast of SH was conducted to find out if the population near Hohwacht is isolated or if C. halophilus is more widespread than previously known. The survey was complemented by searches further east in parts of Mecklenburg-Vorpommern (MV). When colleagues in Denmark (HBM, CR) were informed about C. halophilus existing in the east of SH it turned out that the species has been know from the Danish Baltic Sea coast for some years already. Thus, combining observations and data from both countries opened up the chance for a more comprehensive understanding of the occurrence of *C. halophilus* along the southwest of the Baltic Sea. This might help to get further insights if the present distribution is the result of recent colonisation events or if *C. halophilus* has been simply overlooked due to highly localised and small populations of this late-flying solitary bee species. The goal of this study is to document the current knowledge about the distribution of *C. halophilus* along the Baltic Sea coast of Denmark and Germany and to discuss the possible reasons and implications of this substantial range expansion.

2. Methods

Following the first record of *C. halophilus* at the Baltic Sea coast of SH in 2021 an appeal was started to search for further populations of this species in August and September 2022 involving conservation agencies and amateur naturalists like the "Arbeitsgemeinschaft Stechimmen SH" (Aculeata Recording Society of Schleswig-Holstein). As a guideline, an information leaflet was produced and distributed (Drews & Koppitz 2022, unpublished) that summarized the known distribution and habitat requirements of the bee and

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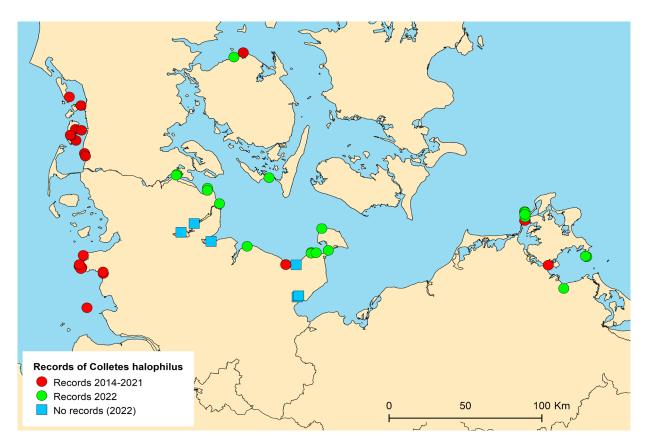


Fig. 1: Records of the Sea Aster mining bee Colletes halophilus Verhoeff, 1944 along the Baltic Sea coast of Denmark and Germany.

occurence records of *T. pannonicum*, its preferred host plant. In addition, colleagues from Denmark and MV were contacted and asked for records for *C. halophilus*. If possible, reference specimens were collected by sweep net or photographs of bees taken as proof of their occurrence. All records of *C. halophilus*, both specimens and photographs, were validated by one or more experienced bee expert(s) and specimens are deposited in various collections (see Table 1). To get an idea of the size of local populations recorders were asked to estimate the number of females at each site, if possible (SH only).

3. Results

Along the Baltic Sea coast of Denmark and Germany, *C. halophilus* so far has been recorded from a total of 20 different sites (3 in Denmark, 17 in Germany: 9 in SH, 8 in MV) with Flyvesandet in Denmark (north coast of the island of Fyn) as the northernmost location and the island of Rügen in Germany as the easternmost location. Linear distance between these extreme sites

is about 250 km but far longer along the Baltic Sea coast (> 500 km depending on how the distance is measured). The known populations of *C. halophilus* at the Baltic Sea are apparently geographically separated from records along the coast of the North Sea in the west. Baltic populations of *C. halophilus* on the peninsula of Holnis in the Flensburg Fjord (SH) are closest to Emmerlev, South Jutland (DK) at a distance of 60 km and Lindøhoved, Fyn (DK) is 106 km away from Møllen, Mandø (DK). All currently known records of *C. halophilus* from the Western Baltic Sea coast and southern Kattegat coast in Denmark and Germany are summarized in Table 1 and mapped in Figure 1.

The targeted search along large parts of the Baltic Sea coast of SH proved that *C. halophilus* seems to occur in almost all suitable habitats, even in relatively small sites (e.g. Holnis – Kleines Noor, Großenbrode). We discovered *C. halophilus* populations in nine localities in SH, most of them apparently consisting of few individuals only. An exception is Eichholz (Figure 2) where several hundred bees were observed and where the only nesting site was found (Figure 3). Overall, populations

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Fig. 2: The largest population of Colletes halophilus found in SH so far is in Eichholz (Photo: Arne Drews).

can be extremely localised and restricted to a few 100 m² even when sites appear to be suitable for a larger scale colonisation, at least to the human eye. Colonised sites were characterised by a rich floral display of *T. pannonicum* in very close vicinity to sunny dry open to sparsely vegetated sandy soil (e.g. costal dunes, dyke) for nesting. The Sea Aster often is the only abundantly available Asteraceae and they are frequently visited by males and females. When males are active before *T. pannonicum* is in bloom they were observed patrolling along and visiting flowers of *Daucus carota* for nectar.

Interestingly, at five sites that superficially appeared to be suitable, *C. halophilus* could not be found. These are Reesholm (N 54,5191° E 9,6302°), Aschau (N 54,4609° E 9,9324°), Weissenhaus (N 54,3074° E 10,7853°), Ulsnis (N 54,5715° E 9,7643°) and Neustädter Binnenwasser (N 54,1100° E 10,7866°) (Fig. 1).

4. Discussion

The present study showed that *C. halophilus* is widespread and well established even in relatively small habitats at the Baltic Sea coast of Denmark and Germany. The bee can be locally abundant but usually populations seem to be small. At the five sites where the species was missing, either populations of the Sea Aster were presumably too small (first three sites) or suitable nesting sites were missing (last site). However, when bee populations are very small, individuals can be easily overlooked. This happened, for example, at the site Bottsand in 2021. When A. Drews visited the locality, he did not see *C. halophilus* while in 2022 he, K. Adam and M. Kuhlmann independently found several individuals there. Thus, it cannot be said with certainty that *C. halophilus* is really missing from those four sites.

Details of the distribution of *C. halophilus* at the northern edge of its range remain unclear. Further targeted search, particularly in north and southeastern Denmark (e.g. the islands Langeland, Lolland, Falster and Møn), neighbouring southern Sweden and western Poland is required for a better understanding of the species' biogeography. A detailed survey within the present range of the species would be desirable for a (re)assessment of the conservation status of this western European costal endemic bee (Westrich et al. 2012, Nieto et al. 2014, Madsen 2019).

To date, the origin and history of the Baltic population of *C. halophilus* remains uncertain. There are no records from the coasts of central or northern Denmark, hence, it is unknown if there is a continuous



Fig. 3: Nesting site of Colletes halophilus in Eichholz (Photo: Arne Drews).

distribution and contact between populations at the North Sea and the Baltic Sea coasts. The northernmost known population on the Danish west coast (North Sea) is on the island of Fanø (Madsen et al. 2015) and in the east (Baltic Sea) on the island of Fyn. However, the occurence of C. halophilus on the west coast of SH and Denmark is assumed to be of relatively recent origin and the result of northern range extensions driven by global warming (Klammer et al. 2021). But as C. halophilus is easily overlooked due to its late seasonal flight activity and the special habitat requirements, it is also possible that the species has a long established and more or less continuous occurrence because coastal sites are often neglected in wider bee surveys. Thus, to get some clarity about this it would be necessary to continously investigate suitable sites along the west coast of Jutland, as the most likely immigration routes and contact zone.

Based on the available distribution data, two potential scenarios can be hypothesized for the existence of *C. halophilus* at the Baltic Sea, that differ in the assumed origin of the colonisation: First, a recent fast and area-wide long-distance range expansion from the North Sea towards the east coast of Denmark and SH with a subsequent eastward spread along the Baltic Sea coast up to at least the island of Rügen. Second, *C. halophilus* has been present at the Baltic Sea for a long time already and, as mentioned above, was simply overlooked due to its late seasonal flight activity and underrecording of coastal habitats. More favourable weather conditions in recent years caused by climate warming (DWD 2017) might have facilitated population growth of small relict populations above detection level and, perhaps, lately even colonisation of new sites. Range expansions of insects driven by climate warming are well documented (e.g. Parmesan et al. 1999, Hickling et al. 2005, Grewe et al. 2013). It has also been assumed for the smaller scale northward range extension of *C. halophilus* at the North Sea in SH and Denmark (Klammer et al. 2021) and seems the most likely driver for both scenarios.

Although it is impossible to falsify any of these hypotheses based on the data currently available, the first scenario appears to be the less likely for several reasons. Generally, most bees are poor dispersers and have problems to reach distant habitats, thus, reports on long-range and rapid geographic expansion and (re) colonization are scarce (Murray et al. 2009, Dellicour et al. 2014). There is no evidence known to us that *C. halophilus* is able to cross a minimum of 60 – 100 km of completely unsuitable habitats of mainland DK and SH from the North Sea east through a climatic gradi-

ent to the coast of the Baltic Sea. In addition, potential source populations of *C. halophilus* at the west coast are small and presumably of recent origin (Klammer et al. 2021), making a present-day large-scale colonisation of multiple sites along an extensive (several hundred km) stretch of the Baltic Sea extremely unlikely. However, there are also notable and well documented examples of indigenous bee species that are rapidly expanding their ranges over large areas, namely the Ivy Bee *C. hederae* (e.g. Frommer 2010, Dellicour et al. 2014, Bogusch et al. 2021), a close relative of *C. halophilus*, and the Great Banded Furrow-Bee *Halictus scabiosae* (Rossi, 1790) (Frommer & Flügel 2005, Hopfenmüller 2014).

The spectacular range expansion of C. hederae apparently started in the late 1990s and its spatial and population genetic dynamics have been studied in great detail (summarized by Frommer 2010, Dellicour et al. 2014, Bogusch et al. 2021 and references therein): The general directions of spread of C. hederae are to NW Europe (including the UK in 2001) and in S Europe to the east while the colonisation of eastern Central Europe is slow. Like for C. halophilus (Klammer et al. 2021), it is suggested that rising temperatures in summer and autumn caused by climate change have been the driver of the range expansion but the mechanism and link to life history traits are unclear. Colonisation seems to start by establishing isolated local populations in the forefront of the previous distribution range as a result of long-range dispersal, followed by subsequent spread into hitherto unoccupied neighbouring habitats to "fill distribution gaps". As in C. hederae, also H. scabiosae started its range expansion in the 1990s, but a couple of years earlier. The spread followed a similar dynamic and spatial pattern as in C. hederae (Frommer & Flügel 2005, Hopfenmüller 2014). For both species, the average rate of range extension was estimated to be about 10 km / year (Frommer 2010, Hopfenmüller 2014). However, caution is needed when relating these examples to C. halophilus, because C. hederae and H. scabiosae have less specific habitat requirements and are widespread in the landscape, while C. halophilus occupies exclusively costal habitats and, thus, might have a spatially more restricted mode of range expansion.

In the second scenario, that seems to be more likely, *C. halophilus* could have persisted for a long time at the Baltic Sea coast in small relict populations, that went unnoticed due to limited survey activities in its

specific habitats (applies at least to Germany). In recent years, facilitated by warm and dry summers as a result of climate warming (DWD 2017), the species might have built up larger populations, colonised even small and isolated sites and, thus, has reached detection level. This scenario better agrees with the available data because populations of C. halophilus at the North Sea are small and apparently of relatively recent origin. Hence, they are unsuitable and improbable as source populations for a large-scale colonisation of the Baltic Sea coast through > 60 km of intensely used, hostile inland habitats. However, ultimately only additional data, both on spatial distribution patterns and population genetic structure (Dellicour et al. 2014), can help to elucidate the origin, dynamics and underlying processes of the occurrence of C. halophilus at the Baltic Sea coast. This would also help to inform conservation measures.

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