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# Heading northward to Scandinavia: *Undaria pinnatifida* in the northern Wadden Sea

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**Abstract:** The kelp *Undaria pinnatifida*, native to East Asian shores, was unintentionally introduced with Pacific oysters into the Mediterranean in 1971. Intentional introduction from there to the French Atlantic coast 12 years later led to a gradual spread to the British Isles and the North Sea. Here, we report on the northernmost established population in continental Europe, and suggest a further spread into Scandinavian waters to be almost inevitable. In 2016, several thalli were found washed ashore at the eastern side of the island of Sylt in the northern Wadden Sea (German Bight, Eastern North Sea). Most specimens bore fertile sporophylls and thallus lengths of >1 m were common. In June 2017, 91 sporophytes were found attached to a mixed bed of Pacific oysters and native blue mussels, located just below low tide level in a moderately sheltered position. Mean thallus length was 0.2 m and the longest 0.7 m. Most had distinctive sporophylls and released spores in the laboratory. From sporophylls collected in the previous year, we successfully reared a new generation, demonstrating the kelp's potential for further spread by natural means or human vectors.

**Keywords:** introduced non-native species; neobiota; Pacific oysters; range expansion; *Undaria pinnatifida*.

## Introduction

The brown macroalga *Undaria pinnatifida* is native to South Korea, parts of Japan and China's Zhoushan archipelago (Hay and Villouta 1993, Morelissen et al. 2013). It originally inhabits the lower intertidal and subtidal zones of rocky shores (Hay and Villouta 1993, Morelissen et al. 2013), but can also be found growing on virtually any natural and artificial hard substratum (Floc'h et al. 1991, Wotton et al. 2004). This kelp species has been a well-known food source in Asia and has recently gained increasing attention as an introduced species in many coastal areas worldwide (Hay and Luckens 1987, Nisizawa et al. 1987, Yamanaka and Akiyama 1993, Lowe et al. 2000). The first accidental introduction of *U. pinnatifida* to Europe occurred in 1971 in the Thau lagoon (French Mediterranean). Its introduction is thought to be associated with movement of Pacific oysters [*Magallana* (*Crassostrea*) *gigas*] brought from Japan for farming (Floc'h et al. 1991). In 1983, specimens were brought for cultivation experiments from the Mediterranean to Brittany (France), the first free living specimens were later detected in 1987 (Figure 1A; Minchin and Nunn 2014). These were most likely facilitated by anthropogenic vectors, and *U. pinnatifida* continued to spread along European coasts, first observed in southern England in 1994 and on the shores of Belgium and the Netherlands in 1999. Until now, the most northern occurrence of *U. pinnatifida* was in Belfast Lough (Northern Ireland) in 2015 and on the Dutch island of Terschelling in continental Europe in 2009 (Figure 1B, Gittenberger et al. 2015, Minchin et al. 2017).

In addition to dispersal by aquaculture activities and shipping, overland transport of *Undaria pinnatifida* with fishing gear has been reported (Bollen et al. 2017). Its highly plastic physiology and morphology allow *U. pinnatifida* to adapt well to many new environments, which may explain its success as a worldwide invader (Dean and Hurd 2007). Previous studies suggested that natural dispersal mechanisms, namely spore production and release, as well as severed floating thalli or sporophylls, result in only a limited range expansion of around 100 m per generation (Forrest et al. 2000). Still, the number of offspring potentially produced by individual sporophytes is high. Millions of zoospores are released from each sporophyll and, therefore, populations may grow very rapidly (Shan et al. 2016). The impact of *U. pinnatifida* on native communities may differ depending on the coastal system

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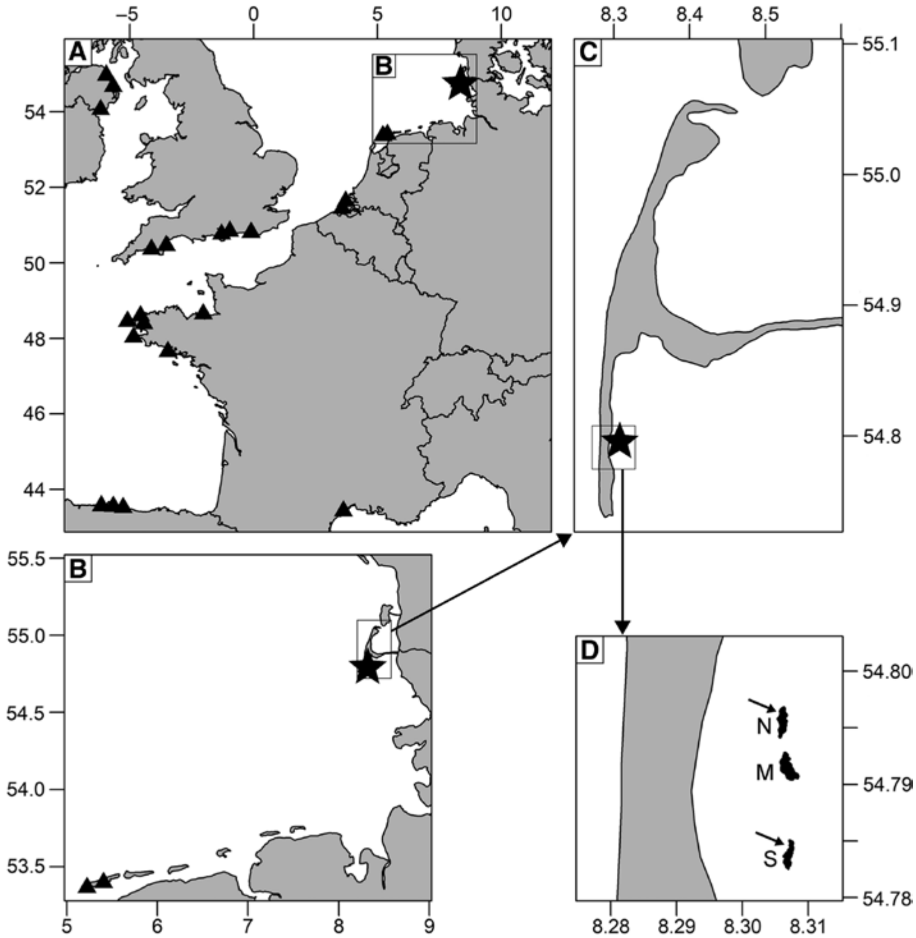


**Figure 1:** Distribution of *Undaria pinnatifida* populations previously reported (triangles) and the newly established one on Sylt (stars). (A) Examples of populations in Europe (Minchin and Nunn 2014, Gittenberger et al. 2015). (B) Easternmost documented European population in 2014 (Gittenberger et al. 2015) and 2017. (C) Island of Sylt with box marking the major *U. pinnatifida* wash-up zone and location of the attached *U. pinnatifida* on the sampled oyster reef (54°47′44.4″N 8°18′24.7″E). (D) Oyster reefs (north, middle, south) off the eastern shore of Sylt with arrows marking the growth sites. Numbers on axes are longitude and latitude in degrees N and E.

investigated. Native species richness may be reduced but, in some circumstances, the alga could have a positive effect where it provides an extra substratum for native species to grow (e.g. Casas et al. 2004; Irigoyen et al. 2011).

Here we report the first detection of *Undaria pinnatifida* in the northern Wadden Sea (southeastern North Sea) and provide a baseline for further research on the population development of this non-native kelp and its potential effects on native communities in the Wadden Sea ecosystem.

## Materials and methods

Individuals of *Undaria pinnatifida* (Harvey) Suringar were first found washed ashore on intertidal sandflats on the eastern side of the island of Sylt in the northern Wadden Sea in August 2016 during a routine non-native species monitoring survey (for detailed information on the monitoring program see Buschbaum et al. 2012). On several occasions between August 2016 and June 2017, a total of more than 100 sporophytes were found washed ashore (hereafter "floating sporophytes") between Rantum and Hörnum in southern Sylt (Figure 1C).

No specimens of *Undaria pinnatifida* were observed during dredge sampling of mussel reefs in the area east of the wash-up zone in March 2017. In June 2017, three oyster reefs, located in the shallow subtidal near the wash-up zone were investigated during low tide (Figure 1D). Contours and profiles of the reefs were recorded using a GPS-based application (MapMyWalk© 2017, Under Armour® Inc., Baltimore, MD, USA) and all *U. pinnatifida* sporophytes found attached to the oyster reefs were collected.

The substratum as well as major components of the associated flora and fauna were identified. *Undaria pinnatifida* sporophytes were transported to the laboratory (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Wadden Sea Station Sylt, Germany), where all individuals were photographed, the presence of sporophylls was recorded and thallus lengths and midrib widths were measured. For damaged thalli, the full length without damage was estimated based on the midrib width and length. Previous studies (Castric-Fey et al. 1999) and our own experience showed that the midrib width can serve as a proxy for full sporophyte size (Schiller et al. unpublished). However, as morphology and size ratios of *U. pinnatifida* vary with growth site and conditions (Castric-Fey et al. 1999, Skriptsova et al. 2004), the midrib width in this study only serves as an independent measurement for sporophyte size distribution.

Floating sporophytes were measured in the field or digitally from photos using Image J (Schneider et al. 2012).

To test for zoospore release *in vitro*, 27 of the attached mature sporophytes were haphazardly selected and a method adapted from Shan and Pang (2009) was used. Sporophylls were cut from the plants, cleaned of epiphytes and dried in closed petri dishes for approximately 24 h at 12°C without light. Pieces of each sporophyll were immersed in petri dishes filled with fresh seawater at room temperature and natural light. They were observed under the microscope after 24 and 48 h.

For germination experiments, a washed up specimen collected in October 2016 was used to release viable spores in the laboratory (Marine Botany, BreMarE, University of Bremen, Germany). Pieces of the sporophyll were cleaned thoroughly as described in Redmond et al. (2014) and desiccated in petri dishes for 24 h at 12°C, before being immersed in Provasoli enriched sterilized natural seawater (PES). After 24–48 h at 20–30 μmol photons $m^{-2}$ $s^{-1}$, 12:12 h L:D and 18°C, spores germinated into gametophytes. In several subsequent experiments, sporophytes were successfully obtained from this culture by adapting the method of Shan et al. (2013). Gametophyte filaments were broken up into fragments and irradiance reduced to 5 μmol photons $m^{-2}$ $s^{-1}$ for 24 h, then increased to 50 μmol photons $m^{-2}$ $s^{-1}$ with medium changes every 3 days.

Statistical analysis was performed in R using a generalized linear model with Gaussian dispersion parameters and $p < 0.05$ (R Core Team 2015).

## Results and discussion

Sea surface temperature in late June ranged between 16 and 17°C (own measurements). However, intense irradiance and air temperatures can increase the temperature range significantly. In total, we found 91 attached specimens of *Undaria pinnatifida* (Figure 2), which were detected only on the western fringe of the northern oyster reefs, except for a single strongly damaged individual on the southern reef.

The community on the reefs was dominated by the filamentous brown alga *Ectocarpus* sp., stretching as a dense floating layer across the tide pools, with *U. pinnatifida* and other species (Table 1) growing underneath and between the *Ectocarpus* filaments. Thalli of *U. pinnatifida* grew in clusters of one to seven individuals as epibionts (attached to living surfaces) of other species (basibionts), with 34 clusters in total, spread over a system of connected tide pools no deeper than 30 cm during low tide.

**Figure 2:** *Undaria pinnatifida* sporophytes collected at Sylt, Germany.
(Left) Specimens washed up in the intertidal between Rantum and Hörnum during low tide. (Middle) Large fertile sporophyte found floating in tide pools of the sampled oyster reef. (Right) Individuals collected growing on oysters in the tide pools.

**Table 1:** *Undaria pinnatifida* associated flora and fauna identified at the northern oyster reef (54°47′44.4″N 8°18′24.7″E), Sylt, Germany.

| **Plantae** | | **Animalia** | |
|---|---|---|---|
| Chlorophyta | *Ulva* sp. (narrow) | Mollusca | *Magallana gigas* |
| | *Ulva* sp. (wide) | | *Mytilus edulis* |
| Rhodophyta | *Gracilaria vermiculophylla* | | *Littorina littorea* |
| | *Chondrus crispus* | | *Crepidula fornicata* |
| | *Dasya baillouviana* | Crustacea | *Carcinus maenas* |
| | *Ceramium rubrum* | | *Semibalanus balanoides* |
| Ochrophyta | *Ectocarpus* sp. | Polychaeta | *Lanice conchilega* |
| | *Sargassum muticum* | | *Arenicola marina* |
| | *Fucus vesiculosus* | Bryozoa | *Electra pilosa* |
| | *Chorda filum* | Echinodermata | *Asterias rubens* |
| | *Dictyota dichotoma* | Cnidaria | *Metridium senile* |

The majority of the thalli (91%) were attached to Pacific oysters *Magallana [Crassostrea] gigas*, while 7.7% were growing on *Mytilus edulis* and a single thallus grew on a sponge.

Nearly all of the sporophytes were damaged at the tip of the blade, likely due to wave exposure and the onset of senescence due to high temperature or age.

The mean actual length ± standard deviation (SD) of the 91 attached sporophytes was 21.5 ± 8.5 cm, while the mean full length ± SD was estimated to be 30.6 ± 10.7 cm (Figure 3). The longest thallus was estimated to be about 70 cm before damage.

Additionally, 41 floating *Undaria pinnatifida* sporophytes were photographed in January 2017 (Figure 2) of which 13 could be reliably measured from the photos and 36 and 16 were measured in late March and June 2017, respectively. Of these, the mean actual length was 68.5 ± 32.2 cm and the mean estimated length 104.7 ± 32.3 cm (Figure 3) with the longest sporophyte estimated to be 149 cm before damage. The significantly longer thalli and wider midribs compared to those found in attached thalli suggest another source habitat. Within the oyster reefs current speed is reduced with stagnant water in low tide pools. Peteiro and Freire (2011) found that *U. pinnatifida* growing at a site moderately exposed to water currents had significantly larger sporophytes, compared to a sheltered site. The average total length reported for a moderately exposed site in Northwest Spain was 122 cm, compared to 86 cm at a sheltered site (Peteiro and Freire 2011). This suggests that our floating sporophytes originate from tidal channels with swift currents rather than from another oyster reef with low tide pools.

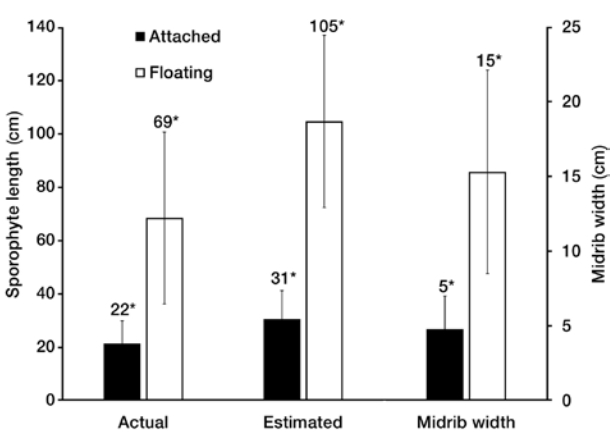


**Figure 3:** *Undaria pinnatifida*: actual and estimated length (left) and midrib width (right) of 91 attached (black) and 73 floating (white) sporophytes.
Values above bars are means; bars indicate standard deviations. Significant differences ($p \leq 0.05$) between the attached and floating specimens of each parameter are indicated by asterisks.

Floating sporophytes were collected over a period of more than 6 months, and they always had sporophylls, suggesting that different states of the population and several generations were documented. This agrees with the observation that *Undaria pinnatifida* sporophytes occurred year round with several recruitment pulses where maximum sea surface temperatures are ≤19.4°C (James et al. 2015 and references therein).

We identified 69 (76%) of the attached individuals that had formed sporophylls. Out of 27 tested for spore release, 85% had released spores after 4 h. After 24 h, 89% had released spores of which 82% had formed germination tubes. However, it has been noted by Forrest et al. (2000) that germination into gametophytes could occur up to 14 days after the release of spores. The high spore release and germination rates, together with the successful growth of sporophytes from this material, provide strong evidence that reproduction and potential range expansion are possible in the *Undaria pinnatifida* population from Sylt.

From field observations, it was concluded that *Undaria pinnatifida* arrived at the oyster reefs by natural dispersal through floating mature thalli. The fact that attached individuals were found only on the landward side of the reef and in tide pools, suggests that floating individuals were trapped in these pools during low tide. Spores released there are likely to remain in these pools, allowing them to settle in the observed patches. Pang and Shan (2008) argued that water velocity was the most important factor for spore attachment. *Undaria pinnatifida* spores were able to attach best under low water velocities, but attached permanently to the substratum if allowed to settle for an hour before exposure to higher velocities (Pang and Shan 2008). The tide pools sampled near Sylt provide the necessary time for settlement during low tide.

*Undaria pinnatifida* was not found in any harbour on Sylt, nor on the neighbouring island of Föhr or in any other oyster reef around Sylt that was surveyed. Additionally, thalli were only washed up in a rather narrow beach area on Sylt. Therefore, it is likely that only one main population exists in subtidal waters and that this is the source of the large floating sporophytes. Further surveys in a wider area will be conducted to locate this population.

Compared to other invasions in Europe and worldwide, the presence exclusively on natural substratum is rather unusual, as *Undaria pinnatifida* has shown a preference for artificial substrates (Minchin and Nunn 2014). In cases where it was found in natural habitats, it was usually after a population had been observed first on man-made structures (i.e. James and Shears 2016). Prior to the findings on Sylt, several other German marinas closer to the known Dutch populations (Emden, Bensersiel, Wilhelmshaven, Cuxhaven, Brunsbüttel, Büsum, Langeoog, Borkum, Helgoland) had been screened but *U. pinnatifida* was found in none of them (Schiller/Lackschewitz, own observations). During assessments of non-native species in the Dutch Wadden Sea by Gittenberger et al. (2015), no populations were found east of Terschelling, even though areas of hard substrate were sampled all the way to the German border.

Forrest et al. (2000) illustrated that the natural spread of *Undaria pinnatifida* is generally restricted to approximately 100 m per year even when considering floating sporophylls. The direct distance between Terschelling and Sylt is 240 km and along the coast it is 300 km (Figure 1B), so that it is unlikely that this present record of range expansion is due to natural dispersal. Coastal shipping has been shown to play a significant role in the dispersal of *U. pinnatifida* (Hay 1990), and during summer many recreational boats visit Sylt. Extensive mussel cultures on ropes and the sea floor are located in the proximity of the reported *U. pinnatifida* localities. These relied on seed mussel translocations from other North Sea regions in the past and farming vessels still frequently transfer between Sylt and other farms.

## Conclusion

Our study documents the successful establishment of a *Undaria pinnatifida* population much further north on the European continental coast than previously known. Laboratory experiments proved that the majority of the sporophytes had reached maturity and released spores that were capable of germinating and forming a new generation of sporophytes *in vitro*. Thus, we conclude that a self-sustaining population now exists in the Northern Wadden Sea and may disperse northwards from there. By continuous monitoring, ecophysiological characterization, interaction studies, genetic analyses and species distribution modelling, we will aim to understand and predict its further spread.

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