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ALIEN SPECIES ALERT: *UNDARIA PINNATIFIDA* (WAKAME OR JAPANESE KELP)

Inger Wallentinus
Department of Marine Ecology, Marine Botany
Göteborg University
PO Box 461
SE-405 30 Göteborg, Sweden
inger.wallentinus@marbot.gu.se

Undaria pinnatifida in Monterey, California, USA.
Photo by Steve Lonhart, Monterey Bay National Marine Sanctuary

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer
H. C. Andersens Boulevard 44–46
DK-1553 Copenhagen V
Denmark
Telephone (+45) 33 38 67 00
Telefax (+45) 33 93 42 15
www.ices.dk
info@ices.dk

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Contents

Key points

Since the early 2000s, the Japanese kelp, *Undaria pinnatifida*, native to the northwest Pacific, occurs on all continents except – so far – Africa and Antarctica, and it has become one of the main target species for biosecurity. In an analysis ranking species traits of 113 introduced seaweeds in Europe, it was the third most invasive seaweed. There are several reasons for its success as an invader, especially its great ability to colonize artificial substrates and disturbed areas rapidly, as well as shells of oysters and mussels, and it can grow very fast, reaching lengths of up to 2–3 metres. Other reasons are its high tolerance for adverse conditions, such as high turbidity and eutrophication, and the nearly invisible gametophytes' ability to survive being out of water for more than a month and act as a "seed bank". The reproductive output is large, and zoospores may be released all year-round, which contributes to its colonization potential. Further, *Undaria* often develops into a fouling problem. This not only affects ships and boats, but also structures used in aquaculture and molluscs growing on the seabed. On the other hand, it has economic value as a source of food ("wakame"), which has been the motivation for intentional introductions to some areas for farming.

In the early 1970s, it made its first appearance on another continent as an unintentional introduction with oysters that were brought from Japan to the French Mediterranean coast. In the early 1980s, it was intentionally introduced from the Mediterranean Sea for farming in Brittany, northwestern France, from where it later dispersed to other northern European countries. In the late 1980s, it was recorded both in New Zealand and Australia, having been brought by shipping from Asia, which also was the vector for its spread to Argentina in the early 1990s. Thus, the main vectors for unintentional introductions have been ships or small boats as well as oyster movements in aquaculture (including illegal ones).

It can be assumed that, hitherto, we have not seen the final global distribution of *U. pinnatifida*. Assuming that surface salinities remain greater than 18 psu, threatened areas are the remaining parts of the warm and cold temperate coasts of Europe, North and South America, Australia, and New Zealand, as well as the same climate zones of Africa. Disturbed areas, if not too exposed, seem to be more vulnerable than densely vegetated substrates. The prospect of controlling further dispersal is poor, owing to the extreme hardiness of the microscopic gametophytes. To reduce risk, fouling algae should be dislodged from affected ships, boats, aquaculture structures, and floating objects when they are out of the water using hot water treatment, and detached plants should be destroyed. Quarantine facilities are needed when live molluscs are transferred from areas where *U. pinnatifida* occurs to non-colonized areas because there is a high probability that they carry germlings or gametophytes. Farming of or experiments with *U. pinnatifida* should not be carried out if the species does not already occur abundantly in the area, nor should flow-through seawater systems be used. Management by manual removal or commercial harvest might have some success, but requires a long-term commitment followed by large-scale monitoring for many years.

1 Introduction

The Japanese kelp, *Undaria pinnatifida* (Harvey) Suringar 1873, is native to the northwestern Pacific. It was first carried to another continent (see Section 4 for details) as an unintentional introduction with oysters that were brought from Japan to the French Mediterranean coast. In the early 1980s, it was intentionally introduced from the Mediterranean Sea for farming in Brittany, northwestern France, from where it was later dispersed to other European countries. In the late 1980s, it was recorded in both New Zealand and Australia, having been brought by shipping from Asia, the same vector that spread it to Argentina in the early 1990s. Since the early 2000s, it occurs on all continents except – so far – Africa and Antarctica (Table 1.1).

Table 1.1. Distribution of *Undaria pinnatifida* in early 2006.

Ocean	Area	Vector	First record	Eradication/management attempted
NW Pacific	Japan (excl. N and E Hokkaido)	*Native*	–	–
	Korea	*Native*	–	–
	SE Russia	*Native*	–	–
	E China	*Native*	–	–
	China, elsewhere	Farming	1930s	– (?)
	Taiwan	Farming	1981	– (?)
N Mediterranean	S France	With oysters	1971	–
	NE and S Italy	With oysters or shipping	1992	Tried experimentally in Venice, failed but recommended
NE Atlantic	NW France	Farming	1983	–
	N Spain	With oysters	1990	– (?)
	S UK	Recreational boats	1994	Tried and failed
	the Netherlands	With oysters or shipping	1999	Cleared in mussel harvest areas
	Belgium	Boats?	1999	–
	Portugal	?	200?[1]	?
SW Pacific and Tasman Sea	New Zealand	Shipping (ballast or hull)	1987	Tried, limited success
	Australia	Shipping (ballast)	1988	Tried in marine reserve + harvest
SW Atlantic	Argentina	Shipping	1992	Not tried; recommended
E Pacific	California	Shipping	2000	Tried in some harbours
	Mexico	?	2003	?

[1] As stated in Section 4.2.1, it has not been confirmed that the species occurs in Portugal. There are reports that it has reached some estuaries, but there is no published evidence. Because it is farmed in Spain very close to the Portuguese border, however, it seems likely it would have dispersed over the border.

The size of this canopy species and its beltforming growth pattern, its high tolerance for adverse conditions, and its great ability to grow on artificial substrates have made it one of the main target species for biosecurity (see also e.g. Hewitt *et al.*, 2005; GISD, 2006). Fletcher and Farrell (1999) listed eight characteristics that have contributed to its success:

- Ability to rapidly colonize new or disturbed substrate (pioneering species);
- Ability to colonize a wide range of artificial structures;
- Ability to colonize a wide range of substrate, including plants and animals;
- High growth rate, resulting in sporophytes with a large canopy;
- Large reproductive output, where spore release may occur year-round;
- Plants may be present all year;

- Wide physiological tolerances for temperature, light, and salinity;
- Wide vertical distribution.

For a summary of ecological interactions found in different areas, see Table 4.7.1.

In a paper ranking specific traits of 113 seaweeds introduced into Europe for the three main categories – dispersal, establishment, and ecological impact – *U. pinnatifida* ranked third overall as the most invasive seaweed (Nyberg and Wallentinus, 2005). When ranking introduced marine animals and algae with the highest human, economic, and environmental impacts for all species already present in Australia, *U. pinnatifida* would rank ninth, if the maximum scores were used (Hayes *et al.*, 2005).

However, *U. pinnatifida* is also the third most harvested and cultivated seaweed, being used for human consumption (e.g. Yamanaka and Akiyama, 1993; Zemke-White and Ohno, 1999; Wu *et al.,* 2004). It is also used as a food item for cultured abalone (e.g. Lee, 2004).

Voisin *et al.* (2005), using two intergenic noncoding mitochondrial loci, studied within-species genetic variation of *U. pinnatifida* and found 25 haplotypes over the whole data set (524 individuals and 24 populations). In the native range, there was a low diversity within and a high differentiation among populations, a pattern not observed in the introduced range of this species. Contrary to classical expectations of founding effects associated with accidental introduction of exotic species, most of the introduced *U. pinnatida* populations showed high genetic diversity. At the regional level, genetic diversity and sequence divergence showed contrasting patterns in the two main areas of introduction (Europe and Australasia), suggesting different processes of introduction in the two regions. Genetic analyses pointed to aquaculture as a major vector of introduction and spread in Europe, but implicated maritime traffic in promoting recurrent migration events from the native range to Australasia. The multiplicity of processes and genetic signatures associated with the successful invasions confirmed that multiple factors, for instance aquaculture practices (e.g. several strains might have been imported), alteration of habitats, and increased traffic, have acted in synergy at the worldwide level, facilitating successful pandemic introductions. That different processes were involved in different areas was confirmed by Daguin *et al.* (2005), who used microsatellite markers for populations from Japan, France, and New Zealand.

2 Identification

Common names (according to GISD, 2006):

Wakame (Japanese); miyeuk (Korean); haijiecai, qundaicai (Chinese); Japanese kelp, Asian kelp, apron-ribbon vegetable (English).

Phylum	Heterokontophyta	OLD SYNONYMS
Class	Phaeophyceae	
Order	Laminariales	
Family	Alariaceae	
Genus	*Undaria*	*Alaria pinnatifida* Harvey 1860
Species	*pinnatifida*	*Ulopteryx pinnatifida* (Harvey) Kjellman 1885

2.1 Characteristics of different stages of *Undaria pinnatifida*

Like other kelps in the order Laminariales, the species has a heteromorphic, diplohaplontic life cycle (Figure 2.1.1), with a large sporophyte and separate microscopic female and male gametophytes. In most areas, the sporophyte reaches a total length (Figure 2.1.2a) of 1 to 2 or even 3 m (Okamura, 1926; Peréz *et al.,* 1984; Hay, 1990; Sanderson, 1990; Floc'h *et al.,* 1991; Hay and Villouta, 1993; Casas and Piriz, 1996; Castric-Fey and L'Hardy-Halos, 1996; Castric-Fey *et al.,* 1999a, 1999b). However, it is usually less than 1 m in the Mediterranean Sea (Boudouresque *et al.,* 1985; Curiel *et al.,* 1998, 2002), on the Spanish coast (Santiago Caamaño *et al.,* 1990), in some populations in New Zealand (Hay and Villouta, 1993; Brown and Lamare, 1994), and in Victoria, Australia (Campell and Burridge, 1998), as well as in waters with high turbidity (e.g. Floc'h *et al.,* 1996; Curiel *et al.,* 2002).

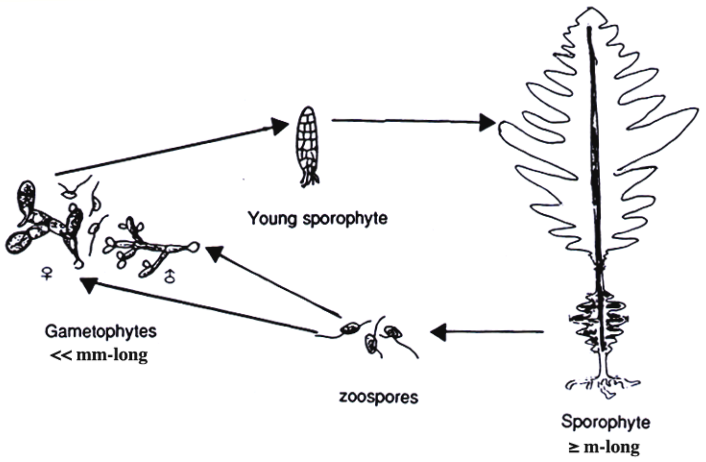

Figure 2.1.1. The life cycle of *Undaria pinnatifida*.

The sporophyte has a yellowish-brown to brown, membranous to leathery lamina, becoming greenish olive when drying. The stipe – forms with short or long stipes can occur together (e.g. Castric-Fey *et al.,* 1999a) – is lighter in colour and attached by root-like hapters, as with most other kelps (Figure 2.1.2b). The length of the stipe, in some introduced areas, is approximately 10%–50% of the total length (Castric-Fey *et al.,* 1999b; Stuart *et al.,* 1999).

(a) (b)

Figure 2.1.2. *Undaria pinnatifida*. (a) Mature alga, almost 2 m long, with sporophylls all along the stipe, Monterey, California. Photo by Steve Lonhart, Monterey Bay National Marine Sanctuary; (b) Details of hapters and sporophylls on the base of the stipes on sporophytes from Venice. Photo by Davide Tagliapietra, ISMAR CNR, Venezia.

The ca. 50–80 cm broad lamina is pinnate, but sometimes, the formation of lobes can be suppressed (Okamura, 1926), with an evident midrib all the way through, which can be up to 1–3 cm wide. Very young plants (<5–10 cm long) lack a midrib (Figure 2.1.3b). As in other kelps, the growing zone is located between the top of the stipe and the lamina, making the top of the lamina the oldest part. The basal part of the mature sporophyte develops two undulated, wing-like, frilly sporophylls (one along each side of the stipe, but they may become interleaved and look like one unit; e.g. Figure 2.1.2b) with zoosporangial sori, producing millions of spores per gramme tissue (Saito, 1975; but cf. also Section 4.4.4).

U. pinnatifida has an annual life cycle. Photosynthesis slows down and growth stops in most areas at high water temperatures (see below), when most of the lamina deteriorates; the stipe and holdfast usually disappear during the end of summer (Saito, 1975; Boudouresque *et al.*, 1985; Brown and Lamare, 1994; Casas and Piriz, 1996; Oh and Koh, 1996; Castric-Fey *et al.*, 1999b), but may also persist (Hay and Villouta, 1993; Thornber *et al.*, 2004). Some introduced populations have two to several generations during a year, i.e. both small and large sporophytes are found together (Hay, 1990; Floc'h *et al.*, 1991; Castric-Fey *et al.*, 1993; Hay and Villouta, 1993; Casas and Piriz, 1996; Castric-Fey *et al.*, 1999b). The species is not known to reproduce vegetatively by fragmentation. However, asexual reproduction through unfertilized eggs, which can develop into parthenogenetic sporophytes, has been recorded in laboratory experiments (Yabo, 1964; Fang *et al.*, 1982). During the early 1990s, a technique using mass cultivation of fragmented gametophytic clones was developed to produce new young sporophytes for cultivation (Liu *et al.*, 2004; Wu *et al.*, 2004).

The microscopic gametophytes (Figure 2.1.1) are very difficult to spot in the field because of their minute size. There are also reports that, sometimes, they may occur endophytically in some filamentous red algae (Kim *et al.*, 2004). The female gametophytes consist of only one to a few cells, bearing the oogonia, and the male gametophytes consist of more, smaller cells, bearing antheridia. The gametophytes may have a dormancy period and, thus, could act as a seed bank (Thornber *et al.*, 2004; Hewitt *et al.*, 2005), especially at low light, and they are capable of surviving adverse conditions as thick-walled resting stages (Saito, 1975). After fertilization, young sporophytes develop, at first attached to the female gametophyte. Liu *et al.*

(2004) showed that disturbance by light, as low as 5–6 µmol photons m^{-2} s^{-1}, caused detachment of eggs from the female gametophytes, and those eggs did not develop into sporophytes. Very young sporophytes (<5–10 cm) lack a midrib (Figure 2.1.3b), but from a size of about 1 cm, they are distinguishable from those of other kelps through their glandular cells (Yendo, 1909, 1911; Okamura, 1926; Castric-Fey *et al.,* 1999a), appearing as small dark dots visible at close inspection (Figure 2.1.4).

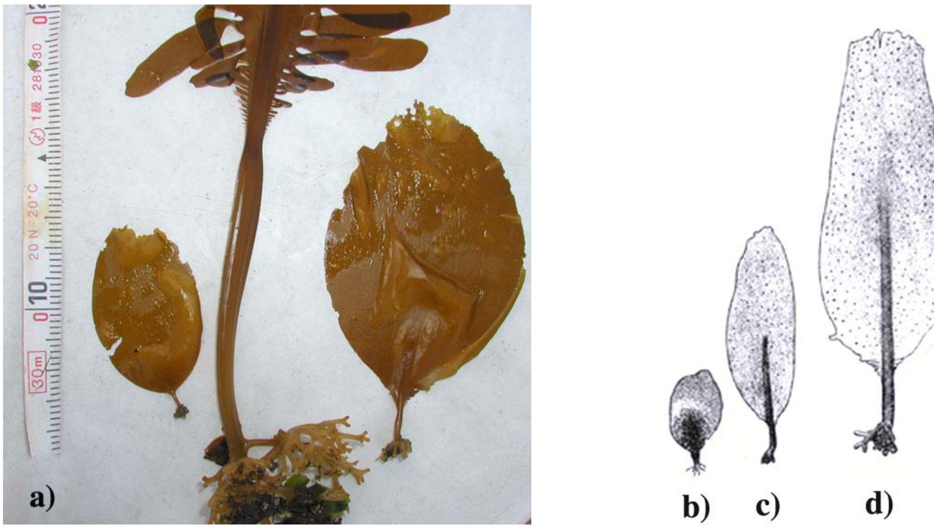

Figure 2.1.3. (a) Sporophytes of different ages, Monterey, California. Photo by Steve Lonhart, Monterey Bay National Marine Sanctuary; (b) Very young sporophyte without a midrib (Okamura, 1926); (c–d) young sporophytes with a midrib (Yendo, 1911).

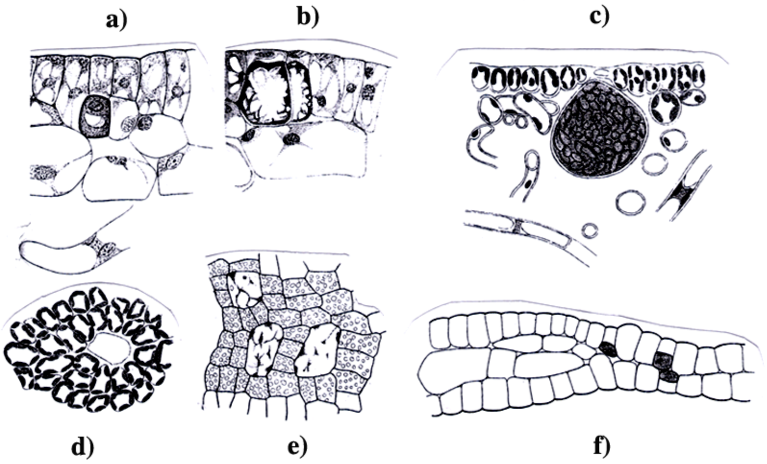

Figure 2.1.4. (a) Young gland cell in transverse section; (b) two older gland cells in transverse section; (c) mature gland cell in transverse section; (d) young gland cell seen from the surface; e) older gland cells seen from the surface; f) three gland cells in a transverse section of a pinnula. (a)–(d) from Yendo (1909); (e) from Okamura (1926); (f) from Yendo (1911). Also see drawings by Castric-Fey *et al.* (1999a).

The species include at least two morphological forms, f. *typica* Yendo and f. *distans* Miyabe and Okamura, the latter with a longer stipe and with sporophylls that often do not reach all the way up to the lamina (Okamura, 1926). Guiry *et al.* (2006) listed two varieties, *U. pinnatifida* var. *vulgaris* Suringar 1872 and *U. pinnatifida* var. *elongata* Suringar 1872, which may correspond to the two forms above. The possible genetic differences in these forms have been discussed (Hay and Villouta, 1993; Castric-Fey *et al.,* 1999a). However, according to Uwai *et* *al.* (2006) genetic analyses do not support the two forms. Furthermore, Stuart *et al.* (1999) studied the effects of seasonal variation in growth rate on the morphology of *U. pinnatifida* to define the form growing in Otago Harbour, New Zealand, by using correspondence analysis. They found that the variation in morphology was largely explained by varying growth rates. So, defining the form of the *U. pinnatifida* growing in Otago Harbour is ambiguous, because morphological characteristics of both f. *typica* and f. *distans* could be found at different times of the year.

2.2 Similar species

There are two other species of the genus *Undaria*: *U. undarioides* (Yendo) Okamura 1915, occurring in Japan, being broader and more ovate with fewer lobes (e.g. Okamura, 1926), and *U. crenata* Y-P. Lee and J. T. Yoon 1998, described from Korea. A third species in these areas, *U. peterseniana* (Kjellman) Okamura 1915, has been moved subsequently to the genus *Undariella* (Guiry *et al.,* 2006). Compared with *U. pinnatifida*, this species has a long, rounded, or oblong-shaped lamina with entire margins (e.g. Okamura, 1926). These species might be misidentified as *Undaria pinnatifida*, but they are not known to have been introduced to other regions.

The grown-out sporophytes of *U. pinnatida* are very characteristic, with an obvious midrib (Figure 2.1.2a) and can hardly be misidentified in European waters. The only other European kelp with a midrib in the lamina is the much narrower and up to 4-m long plant *Alaria esculenta* (L.) Greville 1830, with an entire lamina not split into pinnate lobes, although the lamina might look lobed in an eroded state. The two species are also easy to separate by the form of the sporophylls. The genus *Alaria*, comprising several circumboreal species (see Guiry *et al.,* 2006, with accompanying images) ranging from 0.15 to 15 m, of which *A. marginata* Postels and Ruprecht 1840 is common along the North American west coast. This genus is characterized by several dm-long, thick, leaf-like sporophylls at the base of the stipe protruding from each side, and clearly much different from the undulated “frills” of *U. pinnatida.* However, the margin of the lamina of *A. marginata* may be winged. Undulated, wing-like sporophylls along the stipe are also developed in the genus *Saccorhiza,* especially on *S. polyschides* (Lightfoot) Batters 1902, while they may not occur on *S. dermatodea* (Bachelot de la Pylaie) Areschoug 1875 (for distributions and images, see Guiry *et al.,* 2006). *S. polyschides* often grows next to *U. pinnatifida* in European waters. However, *S. polyschides* lacks a midrib and has a lamina deeply cleft into many linear vertical segments, and young plants do not have gland cells. Furthermore, its characteristic bell-shaped, warted basal area above the disc, with short attaching hapters, is very different from the long, branched, root-like hapters of *Undaria* and other kelps. For information about very young *Undaria* sporophytes without a well-developed midrib, see above about the special gland cells. A midrib, but no separate sporophylls at all, is also seen in some other North American Pacific kelps, such as *Pleurophycus gardneri* Setchell and Saunders ex Tilden 1900, and *Dictyoneuropsis reticulata* (Saunders) G. M. Smith 1942 (for images see Guiry *et al.,* 2006). Some smaller species of the genus *Ecklonia*, which above all is common in the warm temperate areas of the southern hemisphere, but also in the northwestern Pacific (for distribution and images, see Guiry *et al.,* 2006), might be mistaken for *U. pinnatifida*. However, they do not have a midrib, but the often quite narrow primary blade (e.g. *E. radiata* (C. Agardh) J. Agardh 1848) has rows of lateral blades, which can superficially resemble *Undaria*. Furthermore, there are no separate sporophylls at the base of the *Ecklonia* plants, and the reproductive sori are formed primarily, but not exclusively, on the secondary blades.

3 Biology in the native range

Undaria pinnatifida is native along the northwestern Pacific shores: along most of the coasts of Japan, excluding northern and eastern Hokkaido (Okamura, 1926; Saito, 1975; Uwai *et al.,* 2006), Korea (Kang, 1966), some eastern parts of China (Tseng, 1981; Zhang *et al.,* 1984), and in southeast Russia in Peter the Great Bay near Vladivostok (Funahashi, 1966, 1974; Prestenko, 1980) and in the Okhotsk Sea (Zinova, 1954).

3.1 Current status, population demographics, and growth rate

Most of the recent literature from the native areas deals with farmed *U. pinnatifida*, and so more information is needed to elucidate densities, population dynamics, and growth rates of wild plants today (see next paragraph on hybridization between wild and farmed plants).

Uwai *et al.* (2006) studied the intraspecific genetic diversity of the kelp *U. pinnatifida* in plants from 21 localities along the Japanese coast, using DNA sequences of the mitochondrial cytochrome oxidase subunit 3 (cox3) gene and internal transcribed spacer 1 (ITS1) of nuclear ribosomal DNA. They found nine haplotypes (106 plants analysed) that differed from each other by 1–7 base-pairs. Haplotype I was distributed in Hokkaido and on the northern Pacific coast of Honshu, while haplotype III was found along the Sea of Japan coast of Honshu. Other types were found along the central and southern coasts of Honshu. Along the Sea of Japan and on the northern coasts, there was a lower genetic differentiation, which might be the result of the recent establishment (after the middle of the last glacial period) of the flora of the Sea of Japan. The haplotype of cultivated plants was found also in natural populations occurring close to cultivation sites, which suggested that, possibly, cultivated plants had escaped and spread or crossed with wild plants. There were no correlations between morphological characteristics and cox3 haplotypes.

In the South Korean Yeongil Bay, Yoo (2003) reported *U. pinnatifida* to be one of three brown algae dominating the biomass in the subtidal, occurring both in the upper and mid-subtidal zone.

At the northern distribution limit of *U. pinnatifida* in Peter the Great Bay, the Sea of Japan, Russia, the growth, morphology, alginate yield, and composition of *U. pinnatifida* were studied from March to August by Skriptsova *et al.* (2004), who found an average sporophyte growth rate of 2%–5% d^{-1} and that sporulation caused changes in morphology, as well as in alginate yield and composition.

3.2 Natural history (tolerance limits for abiotic factors) in the native region

Substrate and depth

According to Saito (1975), *U. pinnatifida* grows naturally on rocks and reefs at depths of ca. 1–15 m. On the coast of Hokkaido, Japan, Agatsuma *et al.* (1997) studied areas grazed by sea urchins, constituting coralline flats, and found that, after removal of the sea urchins, these areas were recolonized by attaching diatoms, small annual macroalgae such as the green alga *Ulva pertusa* and the red alga *Polysiphonia morrowii* (also introduced into Europe), large annual brown algae such as *Undaria pinnatifida* and *Desmarestia viridis*, and small perennial macroalgae such as the brown alga *Dictyopteris divaricata*, followed by the large perennial brown alga *Sargassum confusum*.

Temperature

Because *U. pinnatifida* is widely distributed along the Japanese coasts, the growth and maturation times differ with changes in temperature (Saito, 1975). The temperature range for optimal growth of young sporophytes was considered by him to be between 15°C and 17°C, whereas old thalli grow better at somewhat lower temperatures. Akiyama and Kurogi (1982) gave a total range of 4°C–25°C for growth of sporophytes from NE Honshu, Japan, where plants generally appear in October/November and disappear in July/August, but may stay until September (/October) in some northern areas (Kurogi and Akiyama, 1957). Later experimental studies, measuring growth rates of young sporophytes (Morita *et al.,* 2003a), showed that the sporophytes have an optimum at 20°C (a relative growth rate of ca. 25% per day), with an upper level of 27°C and a lower limit of less than 5°C (a relative growth rate of ca. 8% per day at 5°C). On the east coast of Korea, the sporophyte growth period is between December and June (Koh, 1983). In northeastern Honshu, Japan, maturation of zoospores occurs in March to July, at a temperature range of 7°C–23°C (Akiyama and Kurogi, 1982), while Saito (1975) stated that zoospore release needs a ten-day average temperature of ≥14°C and that 17°C–22°C is optimal. The microscopic gametophytes can survive a temperature range of −1°C to 30°C (Saito, 1975), and he stated that gametophyte growth is possible between 15°C and 24°C. However, according to Akiyama (1965), it is possible for gametophytes to grow, mature, and release male gametes over a total temperature range of 5°C–28°C, but their optimum is at 15°C–20°C. Morita *et al.* (2003b) showed that growth of gametophytes has an upper critical level of 28°C and that growth is optimal at 20°C (lower limit not determined). According to them, the optimal temperature range for maturation of gametophytes is 10°C–15°C, the major factor explaining the geographical border in Japan between *U. pinnatifida* and the more warm-temperate species *U. undarioides* with an optimum at around 20°C.

Light

The light saturation levels (I_k) of photosynthesis in sporophytes vary with seasonal changes (Matsuyama, 1983; Oh and Koh, 1996), ranging from around 120 to 500 µE m^{-2} s^{-1} (Figure 1 in Matsuyama, 1983) or even around or below 100 µE m^{-2} s^{-1} (Oh and Koh, 1996). The light compensation point (I_c), i.e. the light intensity below which no net photosynthesis occurs, is very low and only amounts to a few µE m^{-2} s^{-1} (Wu *et al.,* 1981; Matsuyama, 1983; Oh and Koh, 1996), and it has very low respiration rates (Oh and Koh, 1996). The gametophytes are able to survive in darkness for at least seven months (Kim and Nam, 1997), and continuous darkness between 17°C and 25°C was recommended by them as the best way of preserving gametophytes. Experiments in Japan showed that gametophytes and very young sporophytes died within hours when exposed to 50%–100% direct sunlight, and also when exposed to 16%–28% and upwards of natural UV (Akyiama, 1965). He also found that, in some populations, gametophytes matured under both long and short nights, while others needed long nights.

Salinity

Most of the experiments reported in the literature have been performed in normal seawater, but a salinity above 15‰ Cl (>27 psu) was quoted by Saito (1975) as necessary for growth of sporophytes, and gametophyte development, although zoospores could attach above 10‰ Cl (>19 psu).

Nutrients

Tests with slow-leaking fertilizers (ammonium) increased both yield and number of harvests in Japanese farms (Ogawa and Fuijita, 1997). In spring, the low supply of inorganic nitrogen in the water was found to decrease the growth rate (Yoshikawa *et al.,* 2001). In experiments with juvenile sporelings, Wu *et al.* (2004) found that inorganic nutrient concentrations around 300 µmol nitrate-N l^{-1} and 20 µmol phosphate-P l^{-1} were sufficient to maintain a high daily growth rate.

3.3 Reproduction

For the relation of temperature to reproductive stages, see above. According to Saito (1975), current velocities above 14 m s^{-1} make the zoospores drift away from the substrate, and any establishment then depends on whether the spores come across a new surface to settle on within one to two days.

3.4 Ecological impact

In many native areas, *U. pinnatifida* is just one of many large canopy species, often growing together with others, and so there is little information available on its impact. In southern Korea, Kim *et al.* (1998) examined shelf, crest, and drop-off areas and found that the maximum species diversity occurred during winter with the large algae, including the red alga *Gracilaria textorii,* the brown algae *Ecklonia cava*, and *Undaria pinnatifida*, becoming particularly abundant in spring. As autumn approached, the cover of large perennial species decreased. The brown algae *Sargassum horneri, S. confusum, Undaria pinnatifida*, and *Myagropsis myagroides* had high cover in the crest habitat, while the subtidal shelf habitat showed an assemblage of bushy or thin-bladed forms such as the green alga *Ulva pertusa*, the brown alga *S. thunbergii*, and the red alga *Corallina officinalis*.

3.5 Grazers and disease agents

Along the southeastern Korean coast, farmed *U. pinnatifida* has been attacked by harpacticoid copepods (*Thalestris* sp.), punching holes in the fronds, as well as by amphipods (*Ceinina japonica*), making tunnels in the midrib (Kang, 1981). He also reported green spots that accelerate plant decay and are caused by many different bacterial strains. A white rot disease, caused by the phycomycet *Olpidipopsis*, can attack cultivated *Undaria* plants in Japan (Akiyama, 1977).

3.6 Utilization and aquaculture

A thorough description of the farming of *U. pinnatifida* in Japan was given by Saito (1975), although the techniques used probably have changed much since then. Akiyama and Kurogi (1982) reported that the harvest of natural plants had decreased, since cultivation (which was described in detail) increased during the 1970s, producing about 5–10 kg ww per metre line. Proceedings from a workshop in Pusan, Korea, in 1991 gave a status report of cultivation and processes at that time (FAO, 2006). Production and erosion of the commercially mass-cultured kelp *U. pinnatifida* f. *distans* were investigated in spring 1998 in Otsuchi Bay, northeastern Japan (Yoshikawa *et al.,* 2001). They measured a steady growth in total kelp length from January to March, with rates of 1.1 to 1.8 cm day^{-1}. In the same bay, maximum growth rates of 3.5 cm day^{-1} were measured in early February by Saitoh *et al.* (1999). Yoshikawa *et al.* (2001) also measured erosion rates of the thalli, which were consistently low in January and February, but increased to 0.5 cm day^{-1} in March, when the erosion rate was comparable with the growth rate in April. Biomass erosion represented 30%–40% of the production in March and over 80% in April. The greater erosion in April was attributed to a low supply of dissolved inorganic nitrogen and ageing of the alga, leading to 81% of the total production being harvested, while 19% was lost through erosion. In terms of nitrogen, 33% of the total production was eroded, while 67% was harvested.

Tseng (1981) reported that most populations utilized today in China were introduced for aquaculture during the 1930s from Japan to Dalian, and in the early 1940s, plants were brought from Korea to Qingdao (Tseng, 2001). *U. pinnatifida* is now the third most important cultivated species in China (Wu and Meng, 1997; Wu *et al.,* 2004), and experiments with tip-cutting of the lamina have shown an increase in production by 9% (Wu and Meng, 1997). Clones of gametophytes are produced to enhance the production of young sporophytes (Wu *et al.,* 2004). During the 1990s Chinese scientists were engaged in developing genetically modified seaweeds, among them *U. pinnatifida* (Qin *et al.,* 2004), by using promotors from other organisms and virus, causing transient expression of the GUS reporter gene. Furthermore, they also used foreign genes to induce zygotic sporophytic formation of gametophytes, and it seems that some of these GMO plants have also been cultivated in the sea.

In 1981, *U. pinnatifida* was intentionally introduced to Taiwan from Japan for farming (Liao and Liu, 1989).

Skriptsova *et al.* (2004) considered the conditions at its northern distribution limit in Peter the Great Bay, the Sea of Japan, Russia, to be favourable for farming of this species, naming June as the optimum month for harvesting. The highest alginate content (51% dw) was obtained from the lamina, with lower values from sporophylls and midribs, and with an increase occurring before sporulation.

In Korea, *U. pinnatifida* thalli have been used traditionally to promote maternal health, which works through the seaweed's scavenging effect of free radicals (Han *et al.,* 2002).

4 Non-native distribution

For details of the European distribution in 2006, see Figure 4.1.1.1.

4.1 The Mediterranean Sea

4.1.1 Date and mode of introduction and source region

The first European record of *Undaria pinnatifida* is from the Thau lagoon on the French Mediterranean coast in 1971, most likely the result of the import of oysters from Japan (Peréz *et al.,* 1981; Boudouresque *et al.,* 1985; Floc'h *et al.,* 1991; Wallentinus, 1999). This vector has also resulted in the establishment of several other unintentionally introduced Japanese algae in that area (e.g. Boudouresque *et al.,* 1985; Verlaque, 1996, 2001; Wallentinus, 1999, 2002). Later, it spread outside the lagoon (Boudouresque *et al.,* 1985), and in 1988, was found close to the Spanish coast at Port Vendres (Floc'h *et al.,* 1991), but so far it has not been reported on the Spanish Mediterranean coast (Wallentinus, 1999; Guiry *et al.,* 2006).

U. pinnatifida has occurred in Venice since 1992 (Curiel *et al.,* 1994, 1998, 2002), and was first recorded along the banks in Choggia, a site where oysters are cultivated. Therefore, this occurrence might be an unintentional introduction with molluscs for farming. However, shipping cannot be excluded as a vector (Floc'h *et al.,* 1996), because *U. pinnatifida* grows in several dock areas (Curiel *et al.,* 1998). In 1998, the species was found in the polluted Mar Piccolo, in the Ionian Sea at Taranto, southern Italy, probably carried there by oysters imported from France (Cecere *et al.,* 2000; Occhipinti Ambrogi, 2002).

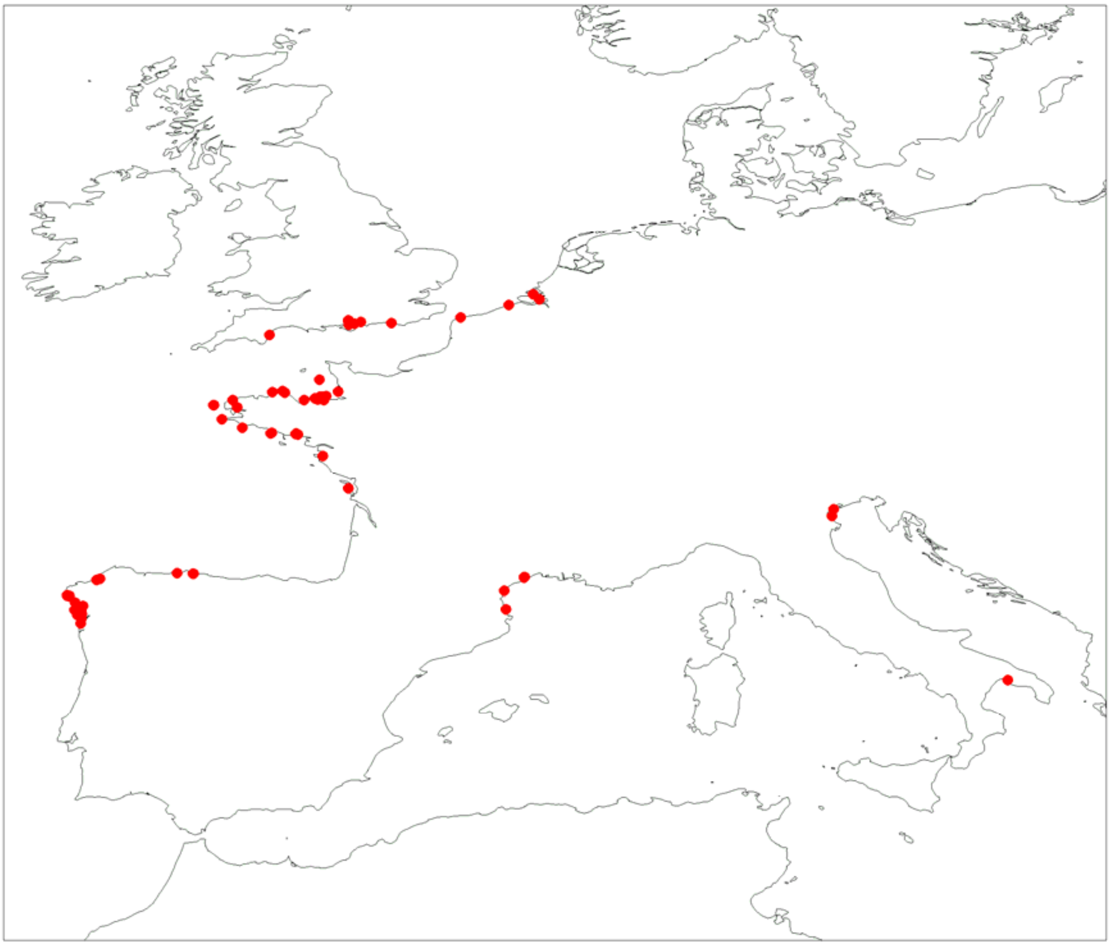

Figure 4.1.1.1. Details of the distribution of *Undaria pinnatifida* in Europe in 2006. Compiled by Frederic Mineur, Queen's University of Belfast (unpublished data).

4.1.2 Current status, population demographics, and growth rate

According to Verlaque (2001), *U. pinnatifida* was still occurring in the Thau lagoon in the late 1990s. However, it does not seem to persist at the localities outside the lagoon (F. Mineur, pers. comm.). In Venice, Curiel *et al.* (2002) believed it to be continuously expanding in the canals in 1999. A density of more than ten plants m^{-2} could be found, most of them 50–80 cm long, but reaching up to 2 m in more current-exposed areas, while at low-current sites they only were 20–30 cm long with 1–3 individuals m^{-2} (Curiel *et al.*, 2002). At Giudecca Island, they found densities of around 100 plants m^{-2}, reaching a peak in biomass of >1 kg dw m^{-2} in May. It was observed to be abundant in the city's canals in spring 2004 (Wallentinus, pers. obs.).

4.1.3 Natural history (tolerance limits for abiotic factors) in the region

Substrate and depth

U. pinnatifida grows both on stones (patchy to dense) and on artificial substrate, including supporting structures used in aquaculture (Peréz *et al.,* 1981; Boudouresque *et al.,* 1985; Floc'h *et al.,* 1991), as well as on embankments of the canals and other objects in Venice (Figure 4.1.3.1), where it is confined to the upper 1.5 m below LWM (Curiel *et al.,* 1998, 2002).

(a) (b)

Figure 4.1.3.1. *Undaria pinnatifida* in Venice canals growing on: (a) a wall and pole; (b) an iron cable. Photo by Davide Tagliapietra, ISMAR CNR, Venezia.

Temperature

So far, no introduced populations seem to have reached the upper temperature limit of 30°C for survival of gametophytes (Akiyama, 1965), and gametophytes from the Mediterranean had an upper survival limit of 29.5°C (Peters and Breeman, 1992). However, high summer temperatures lead to a lower growth rate of the sporophytes. On the French Mediterranean coast, the sporophytes appear in autumn (November) with a maximal growth in March, and sporophytes disappear in July with zoospores released in May–June (Peréz *et al.,* 1981, 1984; Floc'h *et al.,* 1991). In Venice, young sporophytes appear in December and become dominant in February, with a maximum in April–May, and occur until July, when they become senescent (Curiel *et al.,* 1998, 2002). The range of water temperature in the Venice area is between 5°C and 26°C. They also reported that fertility is at the peak in spring, and because only senescent plants occur in July, there seems to be no overlap in generations.

Salinities

Salinities of 27 psu can occur occasionally in the Thau lagoon, but they are usually higher (Verlaque, 1996). In Venice, the species also grows in waters with a salinity that occasionally can be as low as approximately 20 psu, although mainly in waters above 28 psu (Curiel *et al.,* 2002). This seems to be the lowest salinity in which it has become established. Considering its establishment also in the less saline parts of Venice, adaptation to slightly brackish water cannot be ruled out.

Nutrients

In Venice, *U. pinnatifida* is found growing close to discharges of urban waste water and thrives in nutrient-rich polluted water (e.g. Curiel *et al.,* 1998, 2002), as it also does in southern Italy (Cecere *et al.,* 2000). Prosperous growth among farmed mussels and oysters also indicates enhancement by nutrients, which are recirculated by these animals.

4.1.4 Reproduction

The species is reproductive in the areas where it has been recorded (see also Section 4.1.3). On the French Mediterranean coast, the sporophylls are mature from May to July (Peréz *et al.,* 1981, 1984; Floc'h *et al.,* 1991). In Venice, plants do not necessarily become fertile in the inner canals (Curiel *et al.,* 2002).

4.1.5 Ecological impact

On the French Mediterranean coast, *U. pinnatifida* mostly co-occurs with species of the brown algal genera *Sargassum, Cystoseira,* and *Dictyota*, and with the red algal genus *Gracilaria* (Peréz *et al.,* 1981; Boudouresque *et al.,* 1985). In the lagoon of Venice, *U. pinnatifida* has gradually expanded along the banks of the canals, both at Chioggia and Venice, and has become the dominant species (mainly from February to July) in the local algal community (Curiel *et al.,* 2002). The kelp first colonized the main canals and, subsequently, the small inner ones. Several co-occurring species decrease between April and June/July, when *U. pinnatifida* becomes dominant.

4.1.6 Grazers and disease agents

The main grazers in the Thau lagoon seem to be sea urchins (Peréz *et al.,* 1981; Boudouresque *et al.,* 1985). In Venice, grazing pressure on *U. pinnatifida* appears very low (Curiel *et al.,* 2002).

4.1.7 Utilization and aquaculture

There were less successful attempts at cultivation on the French Mediterranean coast, which were not continued. No reports have been published on the utilization of *U. pinnatifida* in Italy.

4.1.8 Management and control

Eradication attempts made in Venice during the fertile period actually enhanced *U. pinnatifida's* development the following year (Curiel *et al.,* 2002). However, when eradication was performed after the reproductive period, recolonization was seen to start two years later. A significant decrease in the area covered by other species has been observed in Venice, and so to limit the spread of *U. pinnatifida*, it was suggested that mechanical eradication should be made on a large spatial scale and before the zoospores are released (Curiel *et al.,* 2002).

4.2 European Atlantic coast

4.2.1 Date and mode of introduction and source region

In France, *Undaria pinnatifida* was transferred from the Mediterranean by IFREMER (Institut français de recherche pour l'exploitation de la mer) scientists for farming in northern France at three sites around Brittany in 1983: at the islands of Groix and Ouessant and in the Rance estuary (Peréz *et al.,* 1984; Floc'h *et al.,* 1991), after less successful trials in the Mediterranean. Later some new sites were used (Peréz *et al.,* 1984; Floc'h *et al.,* 1991; Castric-Fey *et al.,* 1993; Hay and Villouta, 1993; Wallentinus, 1999), also by CEVA (Centre d'Etude et de Valorisation des Algues). In the 1990s, it was also cultivated farther south on the Isle of Oleron (Castric-Fey *et al.,* 1993), which was later given up. In 1987, reproducing individuals (Figure 4.2.1.1a) were found growing on mussel lines outside the seaweed farm on Ouessant (Floc'h *et al.,* 1991, 1996), and later, naturally recruited plants were also found in other districts at St Malo and in the Rance estuary, (Castric-Fey *et al.,* 1993; Hay and Villouta, 1993; Castric-Fey and L'Hardy-Halos, 1996; Castric-Fey *et al.,* 1999a, 1999b), and even in areas where farming had been abandoned. A record in 1998 from the harbour of Calais, northern France (Stegenga, 1999; Leliaert *et al.,* 2000) might also be the result of shipping, as

(a) (b)

Figure 4.2.1.1. (a) Mature sporophyte of *Undaria pinnatifida* with well-developed sporophylls found in a mussel farm on the island of Ouesson, Brittany, northwest France, in late spring 1987. Photo by Inger Wallentinus. (b) Sporophytes on display (centre) in an aquarium tank, La Rochelle, France. Photo by Xavier Minguez.

well as the records in the harbours of Brest and Grandville in northwestern France in the early 1990s (Floc'h *et al.,* 1996).

In northern Spain, *U. pinnatifida* was reported from Ria Ariosa in 1990 (Santiago Caamaño *et al.,* 1990), probably as a result of oyster movements, and later from other parts of northern Spain (for references, see Hewitt *et al.,* 2005). Through farming, it was later spread along the northern Spanish Atlantic coast down to the Portuguese border, and so its arrival in Portugal is immanent (José Rico, pers. comm.). No published references from Portugal are found in the large algal database run by Guiry *et al.* (2006), but there is some information that it has been found in some estuaries on the Portuguese coast (Jesus Cabal, pers. comm.).

In southern UK, *U. pinnatifida* was recorded in 1994, probably spread by vessels from France or the Channel Islands (Fletcher and Manfredi, 1995; Fletcher and Farrell, 1999), spreading later to other sites on the south coast and was also detected on the Channel Islands (Eno *et al.,* 1997).

A thorough review on the occurrence and ecology of the species in the UK and in the North Atlantic was given by Fletcher and Farrell (1999). All records are from isolated marinas, suggesting that it probably arrived in England with small boats that had visited Brittany, France, and then anchored in marinas on the English south coast. Details are also presented on when different areas were colonized. Local dispersal was slow, amounting to ca. 750 m in three years and 2000 m in four years, while the main dispersal was by small boats in coastal traffic. During 1998, *U. pinnatifida* occurred between Brighton and Torquay, a distance of 270 km, which was reached in a shorter period than for the introduced Japanese brown alga *Sargassum muticum.*

In March 1999, for the first time in the Netherlands, 60-cm long sporophytes of *U. pinnatifida* were recorded on shells in an oyster pond near Yerseke, and in May the same year, one plant was found near Strijenham, both sites in the Oosterschelde (ICES, 2000). There was a rapid colonization and, in some places, 5–6 ha were covered in the Oosterschelde, and plants were also washed ashore on the northern side (Stegenga, 1999). So far, the latter are the northernmost sites in Europe. *U. pinnatifida* was also found in smaller densities in the saltwater Lake Grevlingen, probably transported there by oyster pots. In the Oosterschelde, it grows mainly on *Crassostrea gigas,* but also on mussels, and being slippery, *U. pinnatifida* causes problems for fishers when retrieving oysters, and the pots need to be cleaned before harvest (ICES, 2001). Although no vector was stated, oyster and mussel harvesting is common in the Oosterschelde (H. Stegenga, pers. comm.), but shipping probably cannot be ruled out, because ships frequently enter the area.

In 1999, the species was also reported in Zeebrugge, Belgium (Dumoulin and De Blauwe, 1999; Leliaert *et al.,* 2000). *U. pinnatifida* was still present at the marina of Zeebrugge in 2003, but had not spread since 2000 and was grazed by coots (*Fulicra atra*; ICES, 2004). According to F. Kerckhof (pers. comm.), it was still found there in 2006, and coots can no longer keep the populations in check.

4.2.2 Current status, population demographics, and growth rate

In the St Malo area, the populations increased during 1996–1997, after a period of decrease following heavy grazing (Castric-Fey *et al.,* 1999a). The same scientists (Castric-Fey *et al.*, 1999b) found a maximum growth rate of 2.13 cm per day (average 1.56 cm per day) and a maximum plant size of 150 cm, the thallus weighing 1.47 kg ww. They found the maximum longevity of plants to be 7.5 months, and that plants recruited in spring lived on average for ca. five months, while those appearing in winter lived for six months.

On the English south coast, plants grow quite large (>2 m in length, ca. 1 kg ww) and biomasses may reach up to 25 kg ww m^{-2}.

4.2.3 Natural history (tolerance limits for abiotic factors) in the region

Substrate and depth

In western Brittany, France, *U. pinnatifida* has been found both on rocks, growing together with native large canopy species down to 18-m depth, and on lines in mussel farms down to 5-m depth (Floc'h *et al.,* 1991). It can also be found in the intertidal area up to +1.5 m and seems to have a preference for artificial substrate (Floc'h *et al.,* 1996). Farther east on the French coast, in the St Malo and Dinard area, it was also common on periodically overturned cobbles and boulders, and grew mainly in the lower littoral and upper sublittoral zones (Castric-Fey *et al.,* 1999a), but could also be found down to 12-m depth (Castric-Fey *et al.,* 1993).

Four years after its introduction in southern England, it occurs mainly on vertical sides of floating structures, such as pontoons, hulls of small boats, buoys, ropes, and tyres, as well as on the introduced ascidian *Styela clava*, and very seldom on materials having a fixed position in the water. This probably is because of the sediment load and high turbidity in the water there. In the Torquay marina, however, it grows also on fixed objects and has colonized walls, where native kelps such as *Laminaria digitata* and *L. saccharina* occur, and also co-occurs in places with the annual kelp *Saccorhiza polyschides*, scattered fucoids, and the introduced Japanese brown alga *Sargassum muticum* (Fletcher and Farrell, 1999). They stated that it is more common than native species in sheltered and turbid areas, and that in more exposed areas the competition from native canopy species is quite high.

Temperature

Castric-Fey *et al.* (1999b) found that the lowest temperature for sporophyte recruitment in the Dinard area, northern France, was 5°C and the highest 20°C, but they found that the peaks in recruitment occurred during October and May/June, at temperatures of 13°C–17°C, with two generations during a year. Fully grown sporophytes were found all year-round with a mixture of young and old ones. Although most plants deteriorated in late summer, the sporophylls can appear throughout the year. According to Floc'h *et al.* (1991), sporophytes can appear all year-round in Brittany, with release of zoospores from May until late autumn. On the south coast of England, plants grow tall and occur almost all year, with some senescence in late summer (Fletcher and Farrell, 1999).

Salinity

Most reports of introductions are from areas having salinities well above 30 psu (e.g. in St Malo, northern France a mean of 34 psu, with a range of 31–35; Castric-Fey *et al.,* 1999b). Some populations also exist at lower salinities and 27 psu can occur during February at the localities in Spain where *U. pinnatifida* has been recorded (Santiago Caamaño *et al.*, 1990).

Nutrients

As on the Mediterranean coast, *U. pinnatifida* has been found also in northern France growing close to outlets from urban sewage plants (Castric-Fey *et al.,* 1999a, 1999b).

4.2.4 Reproduction

For appearance and maturity, see Section 4.2.3.

4.2.5 Ecological impact

In the study by Floc'h *et al.* (1996), *U. pinnatifida* was found only sporadically on rocky substrates, whether denuded from native algae or not, and seemed to be less competitive than the native, opportunistic kelp *Saccorhiza polyschides*, which dominated on the rocks. However, they found it co-occurring with the native fucoid *Himanthalia elongata*. Since *U. pinnatifida* prefers artificial substrate, the negative effects might be mainly on the economic side as a fouling organism. On the English south coast, Fletcher and Farrell (1999) did not report any ecological impact on native seaweeds, even when occurring together in some areas. On the whole, they considered the final outcome on rocky substrates to be less predictable, and that *U. pinnatifida* will be established mainly in the shallow sublittoral zone, though it has little competitive ability there. However, it probably will be a major fouling alga in harbour areas. They also pointed out that, because *U. pinnatifida* grows even in areas with high sediment load and lower salinities, where less native vegetation occurs, it may even be beneficial to the ecosystem by providing a nursery ground for small fish and shelter for macrofauna. Later studies have shown that *U. pinnatifida* has outcompeted some native species in a marina (Farrell and Fletcher, 2006). In Belgium, Dumoulin and De Blauwe (1999) reported that the thalli of *U. pinnatifida* were often covered by fouling ascidians (especially *Botryllus schlosseri)*, bryozoans, hydroids, and small seaweeds, which may enhance the decay of the lamina.

4.2.6 Grazers and disease agents

The main grazers on the coast of Brittany, France, are fish and crustaceans and the grazing pressure on the sporophytes is quite high (Floc'h *et al.,* 1991; Floc'h, pers. comm.). In Belgium, birds such as coots may be important grazers (ICES, 2004), but some fish also eat it. In southern England, there is hardly any grazing on *U. pinnatifida* (Fletcher and Farrell, 1999).

4.2.7 Utilization and aquaculture

At least one company cultivates *U. pinnatifida* in northern France, in the St Malo area, where it is farmed in the sea on longlines (C-Weed Aquaculture, 2006). Established wild populations of *U. pinnatifida,* the result of unintentional introductions, have been harvested for wakami products in northern Spain. It is also cultivated in northern Spain as far south as close to the Portuguese border (ICES, 1993; José Rico, pers. comm.). It has been seen on display with native seaweeds in the public aquarium at La Rochelle, western France (F. Mineur, pers. comm.; Figure 4.2.1.1b). Such activities might pose an increased risk, if the species is not already firmly established in the area.

4.2.8 Management and control

When *U. pinnatifida* was first recorded on the English south coasts, all plants found were removed, but because the plants were already fertile, eradication failed, and new plants appeared (Fletcher and Farrell, 1999). In the Netherlands, efforts have been made to clear *U. pinnatifida*, because it hinders mussel harvest (Wetsteyn in ICES, 2001).

4.3 New Zealand

4.3.1 Date and mode of introduction and source

U. pinnatifida was reported as introduced by Japanese ships to New Zealand at Wellington in 1987 and Timaru in 1988 (Stapleton, 1988; Hay, 1990), and spread by local coastal traffic to Oamaru in 1988 and Lyttleton in 1989 (Hay, 1990; Hay and Villouta, 1993), and later also to the harbours of Otaga, Porirua, Picton, and Napier (Hay and Villouta, 1993). Further dispersal by coastal traffic was predicted already in 1990 (Hay, 1990), and plants fouling ships' hulls were found to survive a voyage of more than 4000 km and, during that time (about a month), had grown 10–20 cm. He also concluded that drifting mooring buoys and towed navigational buoys can be responsible for dispersal, directly or by infested vessels, as well as the cleaning of ships' hulls at the seaside with pressure hoses, which should be avoided.

Dispersal of zoospores by water movement might be limited, because no plants were found on the opposite side of a New Zealand harbour until ships fouled with *U. pinnatifida* were moved and anchored there (Hay, pers. comm.). Trailed boats may also disperse the species into new waters because of the extreme tolerance and survival of the microscopic gametophytes for days up to a month in small crevices (Hay 1990, pers. comm.), making many new areas susceptible, especially if the boats are left with a constant waterline at the new site for the time it takes sporophytes to mature.

4.3.2 Current status, population demographics, and growth rate

The overall distribution has not changed (ICES, 2004), and it has not been recorded from the Fiordland, the Chatham Islands, or from the Sub-Antarctic islands. Hurd *et al.* (2004) considered *U. pinnatifida* to be the most serious pest of the 22 alien seaweeds in New Zealand, and also gave details of its distribution in New Zealand at that time.

4.3.3 Natural history (tolerance limits for abiotic factors) in the region

In New Zealand, the lowest temperatures for sporophyte recruitment are 7°C–8°C (Hay and Villouta, 1993; Stuart and Brown, 1996), and plants occur throughout the year. In extreme cases at some localities in New Zealand, salinity values can be as low as 22–23 psu, although they are usually higher (Hay pers. comm.). In a New Zealand study (Dean and Hurd, 1996), nutrient kinetics were measured, the values resulting in about the same uptake rates for nitrate as for other kelp species.

4.3.4 Reproduction

Studies in New Zealand (Forrest *et al.*, 2000) have revealed that, although zoospores may be viable for 5–14 days, spore dispersal from *U. pinnatifida* stands has occurred primarily only at the scale of a few metres to hundreds of metres, while spread at the scales of hundreds of metres to kilometres must depend on dispersal of fertile fragments or whole sporophytes.

4.3.5 Ecological impact

Forrest and Taylor (2002) emphasized the difficulties of assessing the impact of this invasive species, because it was difficult to find the correct experimental design to measure it. Overall there seems to be little impact from *U. pinnatifida* in low shore communities, and compared with control areas, effects that could be interpreted as plausible impacts could probably reflect natural causes equally as well. Owing to the uncertainty in extrapolating impact information to other places and times, they suggested that the precautionary principle should be applied and worst-case impacts assumed, until the scientific uncertainty is reduced. However, such an approach, according to them, should only be applied after an evaluation of the feasibility, costs, and benefits of managing a particular pest in relation to other priorities for invasive species.

4.3.6 Grazers and disease agents

In New Zealand, the grazers are mainly abalone, sea slugs, crustaceans, and some fish (Hay and Luckens, 1987; C. Hay, pers. comm.).

4.3.7 Utilization and aquaculture

A pilot farming programme has been undertaken in areas in New Zealand already colonized by *U. pinnatifida* (Anon., 1998). Furthermore, established wild populations of *U. pinnatifida* have been harvested (e.g. Sinner *et al.,* 2000; Forrest and Blakemore, 2003).

4.3.8 Management and control

In New Zealand, where *U. pinnatifida* has spread around the coasts since the late 1980s, the main emphasis has been on trying to stop it from entering the Sub-Antarctic and the Chatham Islands. Thus, when a fishing vessel with *U. pinnatifida* on the hull sank near a remote island in 2000, the Biosecurity Act forced an eradication of the plants from the hull and a monitoring of the area for three years (ICES, 2004; Wotton *et al.,* 2004). Great efforts have also been made to clear *U. pinnatifida* to protect the biodiversity, but often with limited success (e.g. Sinner *et al.,* 2000; Stuart and Chadderton, 2001). Descriptions of the problem with *U. pinnatifida* can also be found on the Internet (e.g. Hilhorst, 2006).

4.4 Australia

4.4.1 Date and mode of introduction and source

U. pinnatifida was first recorded in eastern Tasmania (Rheban-Triabunna) in 1988, presumably brought in ballast tanks of Japanese ships. Later, it spread along the coast (Sanderson, 1990; AQIS, 1994), and further dispersal to other coastal areas was predicted in 1990 (Sanderson, 1990). The dispersal rate was estimated at 10 km year^{-1}, but secondary introductions have also occurred in Tasmania, because some areas are more than 40 km apart (Hewitt *et al.,* 2005). In 1996, it was reported from Port Philips Bay, Victoria, Australia, probably coming with ships from Japan or New Zealand, because the plants had a different form than the Tasmanian population (Campell and Burridge, 1998; Campbell *et al.,* 1999). In 1997, it was reported from a marine reserve south of Hobart, Tasmania (Hewitt *et al.,* 2005).

4.4.2 Current status, population demographics, and growth rate

No change has been seen in its distribution in Australia since the late 1990s (ICES, 2004), and in 2002, *U. pinnatifida* was reported to have spread 150 km north and 80 km south of the initial site (Hewitt *et al.,* 2005, and references therein). According to the Department of Primary Industries, Water and Environment (2005a), it occurs from the D'Entrecasteaux Channel to north of St Helens.

In Tasmania, Valentine and Johnson (2003) found that disturbance of native canopy algae was crucial to the establishment of *U. pinnatifida*, because only a few plants grew where coverage of native algae was dense. Furthermore, the timing of the disturbance is important, because the highest densities of *U. pinnatifida* were found when clearing was done just before the start of sporophyte growth in winter. The response of *U. pinnatifida* to a natural disruption of a native algal canopy was examined after a significant dieback of a common native canopy forming brown alga (*Phyllospora comosa*) on the east coast of Tasmania (Valentine and Johnson, 2004). They found that *U. pinnatifida* sporophytes were established at high densities (ca. 7 stipes m^{-2}) in dieback areas, but remained rare or entirely absent in control areas, where the native canopy was intact, confirming the importance of disturbance events for the successful establishment of high densities of *U. pinnatifida*. When sea urchins were removed, Valentine and Johnson (2005) found an average biomass of ca. 55 g dw m^{-2} (5.2 plants). Hewitt *et al.* (2005) estimated growth rates by correlating the width of the stipe to the total length and found that plants on average grew 1.2 cm day^{-1} (ranging from 0.2 to 4.7 cm day^{-1}) in transects where *U. pinnatifida* had been removed, while they grew 2.4 cm day^{-1} (ranging from 1.2 to 4.1 cm day^{-1}) in control areas (figures not comparable owing to differences in time). The maximum growth over 30 days was measured to 1.41 m (removal transects) and 1.23 m in controls.

4.4.3 Natural history (tolerance limits for abiotic factors) in the region

Substrate and depth

On the eastern Tasmanian coast, *U. pinnatifida* mainly occupies the sheltered to moderately exposed sublittoral, where it is a conspicuous seaweed mainly found in sea urchin grazed areas, covering 100% of the rocks (Valentine and Johnson, 2005). Hewitt *et al.* (2005) reported it growing on both rocks and boulders, as well as in low abundances on sand and on seagrass leaves.

Temperature

In Tasmania, sporophytes appear in August (Australian late winter) and disappear in late summer (December) with a peak in growth in November (Sanderson, 1990; Valentine and Johnson, 2005). For releases of zoospores see Section 4.4.4. In Port Phillip Bay, Victoria, sporophytes grow rapidly from winter (July) through to spring (September) and become senescent in early summer, with no sporophytes left in January (Campbell *et al.,* 1999).

Light

Campbell *et al.* (1999) measured photosynthetic performance, dark respiration, pigment concentration, tissue nutrient concentration, and fresh:dry weight ratios in juvenile and adult sporophytes of *U. pinnatifida* from Port Phillip Bay throughout the growing season. They found that photosynthetic rates (15 to 42 mg O_2 g^{-1} dw h^{-1}) of the various sporophyte stages on a dry weight basis were higher in spring than in summer, coinciding with the rapid growth of juvenile sporophytes in spring. The dw:fw ratios found in adult sporophytes were higher than in young sporophytes. Characters of the production vs. irradiance curve, P_{max} and alpha (the angle of the initial slope of the curve) on a Chl *a* basis, were found to have seasonal trends in juvenile plants and could be explained by higher pigment (Chl *a, c*, fucoxanthin) concentrations in spring than in summer. Differences in pigment content, and their ratios, in the various sporophyte life stages may indicate light adaptation by juvenile plants. Lower saturated light requirements (I_k) and compensation points (I_c) were observed in spring than in summer plants, and lower I_k values of juvenile sporophytes than adult sporophytes were also found during spring. Spring and summer compensation points in this study mostly ranged from 7.63 to 15.49 µmol m^{-2} s^{-1}. Low I_k and I_c, and high P_{max}, alpha, and pigment contents may enhance the capacity of juvenile *U. pinnatifida* to utilize low photon flux rates. No seasonal differences were found between respiration rates on a dry weight basis or between respiration in young and adult sporophytes. Respiration rates, normalized to Chl *a*, were 2–3 times higher in summer for both young and adult stages.

Nutrients

In Port Phillips Bay, Victoria, Campbell (1999) found that *U. pinnatifida* had an intermediate capacity for ammonium uptake, which depended on blade maturity. Furthermore, he considered that the relationships between nutrient uptake and growth would afford mature *U. pinnatifida* a competitive advantage for ammonium uptake in winter, when there was a high N availability. Campbell *et al.* (1999) found that the C:N ratios for both juvenile and adult sporophytes were higher in summer, indicating N limitation in summer, and generally highest in juveniles, pointing to a higher accumulation of reserve carbohydrates. Low N:P ratios in spring and summer for both stages also suggest N limitation. The overall high N availability in Port Phillip Bay, and the low-light adapted physiological characteristics of *U. pinnatifida*, provide it with a competitive advantage over other fast-growing macroalgae.

4.4.4 Reproduction

Reproductive phenological studies (Schaffelke *et al.,* 2005) were undertaken in Tasmania to provide the much-needed quantitative information to support pest management. For most of the growing season, zoospore release was limited to the larger size classes of the annual sporophytes (>55-cm length), with the proportion of mature sporophytes increasing towards the end of the season. Small sporophytes with mature sporophylls were not observed until late in the growing season, i.e. after November (late spring). The maximum zoospore release of *U.*

pinnatifida was 62 × 10^3 zoospores cm^{-2} sporophyll tissue h^{-1}, corresponding to a maximum release of 4.3 × 10^8 zoospores $sporophyte^{-1}$ h^{-1}, being similar to or lower than other kelps. The two largest size classes released the most zoospores. Tagged sporophytes released zoospores for about three months before they became senescent and disintegrated. Hypothetically, the smallest mature sporophyte would have a stipe width of 0.6 cm, corresponding to about 33 cm in total length, with a sporophyll circumference of 7.6 cm and a sporophyll biomass of 0.2 g dw. The zoospore release from a stand of *U. pinnatifida* was estimated to be 2 × 10^9 zoospores m^{-2} h^{-1} in January (summer in the southern hemisphere), the majority coming from the two largest size classes. Thus, management efforts involving the manual removal of *U. pinnatifida* to control this species could be rationalized by concentrating on the removal of only larger sporophytes (>55 cm), potentially resulting in significant cost savings. Hewitt *et al.* (2005) suggested that a seed bank of microscopic stages with a significant longevity seems likely, because sporophytes reappeared early in the season, even when all sporophytes had been removed and only few plants were fertile.

4.4.5 Ecological impact

On eastern Tasmania, Edgar *et al.* (2004) studied for a year the effects of algal canopy clearance on plant, fish, and macroinvertebrate communities for blocks cleared of fucoid, laminarian, and dictyotalean algae compared with control blocks. When they removed canopy-forming plants, there was a smaller change to biotic assemblages than reported in studies elsewhere; with the magnitude of the changes for fish and invertebrate taxa lower than between-site variations, the changes were comparable with monthly variations. *U. pinnatifida* exhibited the only pronounced response to canopy removal among algal taxa, with a fivefold increase in cleared blocks compared with control blocks. Marine reserves were suggested to assist reef communities in resisting invasion by *U. pinnatifida* through an indirect mechanism, involving increased predation pressure on sea urchins and reduced formation of urchin barrens, which are subject to *U. pinnatifida* propagation.

4.4.6 Grazers and disease agents

The main grazers in Tasmania are sea urchins (Sanderson, 1990; Valentine and Johnson, 2005). To answer questions about the mechanisms permitting *U. pinnatifida* to persist on sea urchin (*Heliocidaris erythrogramma*) “barrens”, Valentine and Johnson (2005) made a factorial manipulative experiment over a 30-month period. The dense stands of *U. pinnatifida* on sea urchin barrens suggest that disturbance in the form of grazing by sea urchins prevents recovery of native canopy-forming species. By using treatments comprising all possible combinations of +/− urchins, +/− *U. pinnatifida*, and +/− enhanced native algal spore inoculum, they found that the sea urchin *H. erythrogramma* can have a significant impact on *U. pinnatifida* abundance. The response was most dramatic in the 2001 sporophyte growing season, when sea urchins destructively grazed *U. pinnatifida* sporophytes in experimental plots on the urchin barren. In other years, when there was higher recruitment of *U. pinnatifida* sporophytes, urchins reduced sporophyte abundance, but did not prevent development of a *U. pinnatifida* canopy. Removal of sea urchins resulted in a slow increase in the cover of understorey red algae, but only limited recovery of native canopy-forming species. In experiments, where both sea urchins and *U. pinnatifida* were removed, the cover of canopy-forming species did not exceed 6% during the study period. Thus, in the absence of sea urchin grazing, there was no evidence of inhibition of *U. pinnatifida* by native algae. Although the intensity of sea urchin grazing may directly influence the extent of the *U. pinnatifida* canopy, recovery of native canopy-forming species was apparently influenced by a combination of factors, including sea urchin grazing, depth, and most importantly, the degree of sediment accumulation on the rocky substratum. The manipulations showed that the removal of sea urchin grazing, while ostensibly facilitating replacement of native canopy-forming algae by *U. pinnatifida*, did not result in the recovery of native canopy-forming algae.

4.4.7 Utilization and aquaculture

Unintentionally introduced populations have been commercially utilized in Tasmania (AQIS, 1994). In 2005, there were harvest operations on the east coast of Tasmania (Department of Primary Industries, Water and Environment, 2005a). The department pointed out that there is no need for concern about the sustainability of this fishery, but also that, so far, the harvest has not been enough to slow the spread. There is no farming of *U. pinnatifida* in Tasmania (M. Gregg, pers. comm.).

4.4.8 Management and control

As early as the mid-1990s, the Department of Primary Industries, Water and Environment (2005b) realized that an eradication programme was not feasible for the whole eastern Tasmanian coast, and harvest was started as a control measure. However, it was not sufficient. In the late 1990s, removal experiments were carried out at the Tinderbox Marine Reserve, south of Hobart, Tasmania, to reveal if eradication by divers could significantly reduce the sporophyte abundances of *U. pinnatifida*, which it did when carried out monthly (Hewitt *et al.,* 2005; see more under Section 7). Because of the risk of a seed bank of microscopic stages, it was considered necessary to find a treatment to remove these persistent stages. Several Internet-based information campaigns have been launched, e.g. CSIRO (2000) and Department of Primary Industries, Water and Environment (2005b), the latter also providing advice to boat owners on how to act.

4.5 Argentina

4.5.1 Date and mode of introduction and source

U. pinnatifida is assumed to have arrived with cargo or fishing vessels from Korea or Japan into the Neuvo Gulf, Argentina in 1992 (Casas and Piriz, 1996; Orensanz *et al.,* 2002; Casas *et al.,* 2004), where it was recorded close to the international dock at Puerto Madryn in central Patagonia. During the first two years, it had spread along ca. 2 km of the coast (Casas and Piriz, 1996).

4.5.2 Current status, population demographics, and growth rate

Close to Puorto Madryn, Casas *et al.* (2004) found that *U. pinnatifida* could comprise up to 65% of the total seaweed biomass with an average of 3 kg ww m^{-2}. In 1999, it had spread ca. 20 km north and 18 km south of Puerto Madryn (Orensanz *et al.,* 2002), and was also recorded at Caleta Malaspina, ca. 500 km to the south, where it may pose a serious threat to economically utilized seaweeds. It may also pose a threat to the marine park at Golfo San José, north of Nuevo Gulf (Orensanz *et al.,* 2002), and was predicted to spread further along the coast, owing to the benign water temperatures.

4.5.3 Natural history (tolerance limits for abiotic factors) in the region

In the Nuevo Gulf, sporophytes can be seen in the sublittoral zone at depths between 2 to 15 m, and at an annual temperature range of around 8.7°C–18°C (Casas and Piriz, 1996). *U. pinnatifida* has been found growing on various substrates such as rocks, boulders, wharf pilings, on the hull of a wrecked ship, and on ascidians in conditions that are not too exposed. Also in this area, *U. pinnatifida* seems to be enhanced by sewage discharge causing eutrophication effects (Torres *et al*., 2004).

4.5.4 Reproduction

The recruitment occurs in autumn (April–May), and by summer (December), the plants become senescent (Casas and Piriz, 1996; Casas *et al.,* 2004) and only midribs, sporophylls, and holdfasts remain during the late southern hemisphere summer (January–February). Sporophylls occurred from winter (July–August) to summer, but were seen only on plants larger than 70 cm (Casas and Piriz, 1996). Small, young sporophytes were seen together with large ones.

4.5.5 Ecological impact

In southern Patagonia, Argentina, the dominance of *U. pinnatifida* has also changed the composition of beach-cast seaweeds. Since 1998, it has replaced the green algae *Ulva* spp., which has decreased in the beach-cast, as have native species such as the red alga *Gracilaria gracilis* and the kelp *Macrocystis pyrifera* (Piriz *et al.,* 2003). The results of a 7-month manipulative experiment in Nuevo Gulf removing *Undaria pinnatifida* (as a precautionary measure, no additions were made to non-colonized areas) showed that it significantly reduced the species richness and diversity of native seaweeds in comparison with control areas (Casas *et al.,* 2004). The most common subtidal seaweed in the area, the green alga *Codium vermilara,* however, was little affected by the presence of *U. pinnatifida*, and it has been suggested that *C. vermilara* might not be native there, but introduced. Orensanz *et al.* (2002) considered *U. pinnatifida* to be rapidly modifying the nearshore benthic communities in central Patagonia, because it is the only kelp species present and the native seaweeds are relatively small; the canopies reduce light, while the holdfasts may cover other vegetation. Furthermore, when being dislodged and dragged along the bottom by the tides, other species may also be lost by this disturbance.

4.5.6 Grazers and disease agents

According to Orensanz *et al.* (2002), *U. pinnatifida* could be a potential food item for the native gastropod *Tegula patagonica,* and for the sea urchins *Arbacia dufresnii* and *Pseudechinus magellanicus*.

4.5.7 Utilization and aquaculture

It might be attractive for local industries to use *U. pinnatifida*, but no published reports have been found on any utilization from these areas (Casas and Piriz, 1996; Orensanz *et al.,* 2002).

4.5.8 Management and control

Orensanz *et al.* (2002) emphasized that *U. pinnatifida* may become a threat to economically important seaweeds, such as the red algae *Gracilaria gracilis* and *Gigartina skottsbergii* and the kelp *Macrocystis pyrifera*. However, it seems that no attempt has been made to eradicate *U. pinnatifida* because it has been considered a futile enterprise (Casas and Piriz, 1996; Orensanz *et al.,* 2002).

4.6 California and Mexico

4.6.1 Date and mode of introduction and source region

In the US, *U. pinnatifida* was first recorded in Los Angeles Harbor in 2000 (Silva *et al.,* 2002; Thornber *et al.,* 2004) and was later found at several sites in southern California. In 2001, it had been established at Santa Barbara Harbor, Cabrillo Beach at San Pedro, at Channel Islands Harbor at Oxnard, and at Santa Catalina Island, there growing down to 25-m depth, and it was found as far north as Monterey Bay (Figure 4.6.1.1; ICES, 2002; Silva *et al.,* 2002; Lonhart, 2003). It probably arrived with shipping. In 2003, it had increased its abundance in the Monterey area (Lonhart, 2003; ICES, 2004). Thornber *et al.* (2004) predicted a further spread along the coast, where small boats could be an important vector. Silva *et al.* (2002) considered it possible that *U. pinnatifida* could be established from at least Baja California (see below) to British Columbia, Canada, especially in sheltered to partially sheltered waters.

At Todos Santos Islands, in Baja California, Mexico, *U. pinnatifida* was found growing attached to small rocks on a sandy bottom in the subtidal zone at depths of 12–14 m in September 2003. The population consisted of 15 sporophytes, with an average length of 50 cm and with mature sporophylls (Aguilar-Rosas *et al.,* 2004).

(a) (b)

Figure 4.6.1.1. *Undaria pinnatifida* from Monterey, California. (a) Sporophytes of different ages; (b) plants on a floating dock in the harbour. Photo by Steve Lonhart, Monterey Bay National Marine Sanctuary.

4.6.2 Current status, population demographics, and growth rate

The population ecology of both macro- and microscopic stages of the species has been studied in Santa Barbara Harbor, where two different recruitment pulses were seen in one year, depending on temperature (Thornber *et al.,* 2004). They found great differences in survival to maturity, size, and growth rate, and considered these variations in demography, as well as in grazing pressure, to be important for the future spread of *U. pinnatifida* along the Pacific coast of North America. By using tagged plants and the punch-hole technique, they found growth rates in autumn to vary between 1 to 14 cm week^{-1}, with a maximum of 25 cm week^{-1}, until the plants reached 15 weeks old, when growth became negligible. At Monterey with its colder water currents, recruitment might be continuous with an overlap of generations (Lonhart, 2003).

4.6.3 Natural history (tolerance limits for abiotic factors) in the region

Silva *et al.* (2002) described populations on various artificial substrates from shallow waters in harbours, and down to 25-m depth at Santa Catalina Island where it grew on polychaete tubes on sandy bottoms, but also on tires at 6-m depth. In southern California, *U. pinnatifida* occurs in shallow, wave-protected areas, mainly on floating docks in harbours at a temperature range of 12°C–21°C (Thornber *et al.,* 2004). They found recruits on concrete, on solitary ascidians, on old *Undaria* holdfasts, and on the plastic used for tagging the plants. Both field data and laboratory experiments suggested that warmer water inhibited the development and survival of the gametophytes. Furthermore, they noted that zoospore release occurred at lower temperatures than those Saito (1975) claimed to be necessary (but see also Akiyama and Kurogi, 1982; at 7°C–23°C). At Santa Catalina Island in California, Thornber *et al.* (2004) reported that *U. pinnatifida* grew with several other kelps, including *Macrocystis pyrifera* and *Pelagophycus porra*. At Long Beach, southern California, it grew on steep subtidal banks among a dense stand of the green alga *Ulva* sp. (Silva *et al.,* 2002).

4.6.4 Reproduction

At Santa Barbara, Thornber *et al.* (2004) saw two distinct recruitment periods, a short one in autumn from August until September, with densities of up to 0.8 individuals m^{-2} and plants surviving until February; and a longer one from February to May with densities of up to three individuals m^{-2} and plants surviving until mid-June. Both recruitment periods seemed to be triggered by cold water (<15°C), with a lag period of about eight weeks. In the laboratory, they found that zoospores settled after three days, and after eight days, they had developed into gametophytes, with higher densities at 13°C than at 21°C. The time from recruitment to maturity could be as short as four weeks, with a mean of six weeks, and plants as small as 17 cm were found to be fertile.

4.6.5 Ecological impact

So far, the ecological impact seems to have been small. In many areas, the species is still found mainly in harbours, and, even when growing with other kelps at Santa Catalina Island, those were not yet negatively affected (Thornber *et al.,* 2004). They also suggested that the impact might become stronger in the colder waters farther north, where the *Undaria* populations can persist all year-round, compared with farther south, where there are gaps between the generations.

4.6.6 Grazers and disease agents

In Santa Barbara Harbor, Thornber *et al.* (2004) found that almost all plants recruited during winter/spring were quite heavily grazed by the native common kelp crab, *Pugettia producta*, while only half of the population recruited during autumn was eaten. The high grazing pressure in spring prevented most of the plants from becoming fertile, and the crabs could quite efficiently control the population dynamics in spring. The only other grazers noted were occasional amphipods. In laboratory experiments, *U. pinnatifida* was found to be eaten as much by the crab as the otherwise preferred food, the giant kelp, *Macrocystis pyrifera*, and that the crab preferred the lamina of *U. pinnatifida* to the sporophylls.

4.6.7 Utilization and aquaculture

There are no published reports of any utilization of the introduced populations in these areas. According to Lonhart (2003), it has been suggested that *U. pinnatifida* should be harvested in winter/early spring to feed abalone, especially since the native species are less abundant during that time.

4.6.8 Management and control

There has been some eradication in minor areas such as in the harbour of Santa Barbara (Silva *et al.,* 2002; Thornber *et al.,* 2004) and in the harbour of Monterey (Lonhart, 2003; Hewitt *et al.,* 2005).

4.7 Summarized ecological impact

Table 4.7.1. Summarized ecological interactions of *Undaria pinnatifida*.

OCEAN	AREA	GRAZING PRESSURE	EFFECTS ON NATIVE ECOSYSTEM
NW Pacific	Japan (excl. N and E Hokkaido)	Information not available (diseases in farms)	*Part of native seaweed communities*
	Korea	Farms: amphipods and harpacticoids (+ diseases)	*Part of native seaweed communities*
	SE Russia	Information not available	*Part of native seaweed communities*
	E China	Information not available	*Part of native seaweed communities*
	China, elsewhere	Information not available	?
	Taiwan	Information not available	?
N Mediterranean	S France	Sea urchins	Co-occurring with native seaweeds
	NE and S Italy	Very low	Decrease of native seaweeds (spring–summer)
NE Atlantic	NW France	High by fish and crustaceans	Less competitive than native seaweeds; fouling problem, beach cast
	N Spain	?	?
	S UK	Hardly any	Less competitive than native seaweeds, fouling problem; also positive for fauna
	the Netherlands	?	Fouling on molluscs
	Belgium	Birds (coots), some fish	Several fouling organisms on *Undaria*
	Portugal	?	?
SW Pacific and Tasman Sea	New Zealand	Abalone, sea slugs, crustaceans, some fish	?
	Australia	High by sea urchins	Less competitive than native seaweeds; mainly on grazed and disturbed areas
SW Atlantic	Argentina	Potentially gastropods, sea urchins	Reduced seaweed diversity, changes in composition
E Pacific	California	High by kelp crabs; amphipods	Not yet seen but might be stronger further north
	Mexico	?	?

5 Limited records, not suggestive of established introductions

There have been no published reports of the species from areas where it has not later become established.

6 Prospects of further invasions

In general, brackish water areas may be less at risk if salinities are well below 18 psu. The high affinity for artificial substrate also makes areas with sediments susceptible, although soft substrate is not colonized and plants could also grow there on small stones, shells, polychaete tubes, and on other plants. Disturbed rocky shores are more likely to be at risk than those with dense perennial vegetation, if not too exposed (Hay and Villouta, 1993). Great care should be taken when using temperature limits to predict areas of no concern for future establishment, because the species has been able to settle in areas with temperatures far from the optimal ranges given in literature.

European Atlantic coasts (cf. Hay, 1990; Floc'h *et al.,* 1991)

All the rest of England, Wales, Isle of Man, Scotland with the Orkneys and Hebrides, Ireland, western Scandinavia (excluding the Baltic Sea proper, where salinities are too low), all the rest of the North Sea coast, and all the rest of France, Spain, and Portugal.

Mediterranean coasts (including the Black Sea basin)

Presumably all the rest of the western Mediterranean area (Spain, France, Italy) as well as the eastern Adriatic, northern Aegean, and probably also the northern Jonian Sea, and coasts of western Turkey including the Marmara Sea and the Dardanelles. However, surface salinities in the Black Sea are probably too low, except in the central pelagic zone. The western part of the North African coast. It is less easy to predict whether the eastern part of the Mediterranean is also at risk.

African coasts

Cold and warm temperate areas, which would exclude most of the African east coast.

American coasts

Atlantic and Pacific warm and cold temperate coasts of North and South America (cf. Orensanz *et al.,* 2002; Silva *et al.,* 2002).

Australia and New Zealand

All the rest of the warm and cold temperate coasts of Australia (cf. Sanderson, 1990; AQIS, 1994) and most of New Zealand.

7 Prospects for control and management where introductions occur

Since the microscopic gametophytes are very tolerant and not visible to the naked eye, eradication is extremely difficult. Studies on effects of herbicides and antifouling paint have shown that some antifouling paints are efficient at stopping zoospore germination or causing gametophyte mortality, while some herbicides are not (Burridge and Gorski, 1997). However, patches not painted (e.g. covered by supporting structures during painting) or single corroded plates may develop dense lumps of sporophytes (Hay, 1990). Hulls of ships should only be cleaned out of the water, and detached organisms must be dumped out of reach of the sea (AQIS, 1994). Since sporophytes have been found surviving and growing on the hulls for voyages over 4000 km (Hay, 1990), they should be removed before sporophylls are developed (in some cases sporophylls are small and difficult to see) to avoid seeding other areas. If fertile, detached plants should be kept in containers when removed (see also Hewitt *et al.,* 2005), to avoid release of zoospores, because slightly dried sporophylls, which are reimmersed, release zoospores very quickly (Saito, 1975; Liu *et al.,* 2004).

Gametophytes can survive temperatures around 30°C for up to 10–40 days (Kim and Nam, 1997), and so high temperature treatment is needed for cleaning boat hulls, and care must be taken that the hot water penetrates into crevices and other openings. Gametophytes can survive in small moist crevices in the hulls, anchor wells, etc., allowing them to survive even dry docking, as well as transportation on land for days, up to at least about a month (Hay, 1990, pers. comm.). Because they can tolerate darkness for over seven months (Kim and Nam, 1997), ballast transport is also a plausible vector, especially as the gametophytes may form thick-walled resting stages (Saito, 1975), with a potential for surviving also in the sediment. Thus, high temperatures, well above 30°C, are necessary to be a treatment option for ballast water. Exposure to UV light may also be an efficient treatment for growing gametophytes (cf. Akyiama, 1965), although it is not known if this affects the thick-walled resting stages.

Also pontoons, towed buoys, or drifting objects, such as plastics, ropes, etc., may contribute to the dispersal; those should be removed from the water and cleaned more thoroughly than by just scraping off plants (cf. Hay, 1990) or be disposed of, when carrying *Undaria* plants. In several cases, attempts at manual eradication have not been successful (see Table 1.1 and details in Section 4).

According to Hewitt *et al.* (2005), the ability to make decisions on when and where a response should occur is limited by poor knowledge of the efficacy and costs. They evaluated manual removal of *U. pinnatifida* sporophytes in a new incursion in the Marine Reserve in Tasmania over a 2.5-year study period. Plants from an 800 m^2 area were removed monthly, to minimize the likelihood of maturation of sporophytes and subsequent release of zoospores. While manual removal appeared to have reduced the number of developing sporophytes significantly, the persistence of hot spots through time suggested that either microscopic stages (zoospores, gametophytes, or sporelings) create a seed bank that persists for longer than 2.5 years, or selective gametophyte survival in microhabitats occurs. For manual removal of *U. pinnatifida* to be effective, a long-term commitment to a removal activity needs to be coupled with vector management and education initiatives to reduce the chances of re-inoculation and spreading. Further, it is necessary to monitor (and respond to) on a larger spatial scale for the early detection of other incursion sites and to find a method to remove persistent microscopic stages.

McEnnulty *et al.* (2002) made a thorough literature review on options for getting rid of established introduced macroalgae. They also discussed whether disease agents and endophytic algae could be an option, but believed that too little is known about any host specificity, and many organisms may be harmful also to native seaweeds, especially kelps.

In aquaculture, proper quarantine treatment, allowing only the release of the next generation, should be used to prevent mussels or oysters from acting as vectors. New rules for free trade and movements of shellfish for fattening between disease-free coastal areas within Europe may bring in *U. pinnatifida* from areas where it occurs, and might be a particular threat for the Irish and British coasts, where such movements have frequently occurred. Farming of *Undaria* should not be considered in areas where it does not yet grow (Anon., 1998), nor should lines and supporting structures in aquaculture be moved from sites with *Undaria* to areas where it does not occur (Hay, 1990; AQIS, 1994).

U. pinnatifida should not be on display in public aquaria if a flow-through system is used, and even if the water is treated and recirculated, there might be a risk of fertile parts reaching the sea if material is taken from the aquarium when cleaning the tank or in emergency situations.

Great care should be taken not to perform scientific experiments in the field or in open flow-through systems in areas where the species does not yet occur. Also material brought in for demonstrations should be carefully disposed of on land, especially when plants with sporophylls are used.

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