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The Japanese brown alga *Undaria pinnatifida* on the coast of France and its possible establishment in European waters

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The first observations of the seaweed *Undaria pinnatifida* (Harv.) Sur. in France were made in 1971 in the Étang de Thau in the Mediterranean, after the alga had been accidentally introduced with oysters from Japan. Since the species is of commercial interest, the prospect of cultivating it on the French Atlantic coast was explored. The risk of its dispersal from the farm site was considered minimal by the French authorities. Field experiments with farming on ropes have been conducted by IFREMER at three sites since 1983, two of which were soon abandoned. On the island of Ouessant, Brittany, the experiments with rope cultivation in the field have continued with plantules raised in a local hatchery. Based on the literature, an evaluation of the possible establishment of the species on the European Atlantic coast was made by the ICES Working Group on Introductions and Transfers of Marine Organisms. It was suggested that a control programme including a study of the main grazers should be carried out by French algologists. Since 1987, after a visit to the Asian seaweed communities including *Undaria* (in Korea, Japan, and China), a survey of fertile plants and naturally settled sporophytes has been undertaken by the first two authors at Ouessant. In 1987, *Undaria* sporophytes were found in the bay of Lampaul on the west coast of Brittany, growing vigorously on immersed supporting structures of a mussel farm, both old and newly built. A few plants were also recorded from rocks down to a depth of 5 m, occasionally down to 18 m. The occurrence of mature sporophytes and the colonization in the autumn of 1987 on structures built that summer indicated that the species had reproduced on the French Atlantic coast. However, the significance of natural reproduction for the native seaweed communities in the area will depend also on competition with other species and on the grazing pressure. An experimental control programme was begun in May 1988 to check the competition between the newly introduced *Undaria* and the native seaweed communities on the rocky shore of Ouessant. Thus the ecological importance of the species in these waters will have to be evaluated after the final results of the control programme are available.

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1. World distribution and environmental conditions for growth and reproduction

Introduction

The major hazards associated with transfers and introductions of non-indigenous species are those of spreading diseases and parasites, but the risks of introducing a species which is a strong competitor with native species must also be considered.

The potential geographical distribution area of seaweeds depends on their physiological tolerance limits, i.e. being regulated by their basic demands for growth and reproduction. Within a geographical area, where the water has the physical/chemical properties corresponding to these requirements, the establishment of a species further depends on the chance of diaspores reaching a site, on the competition with other species, and on predation. The assessment of whether or not a marine alga could become an established species in a particular locality thus has to be based on both the environmental conditions and its ecological performance.

Consideration of the *Undaria* "case" by the ICES Working Group

After the start of *Undaria pinnatifida* farming in France (see Part 2) the risks of introducing the species into the Atlantic were taken up by the ICES Working Group on Introductions and Transfers of Marine Organisms at the meetings in Halifax, Canada, in 1984 (ICES CM 1984/F: 35) and Gothenburg, Sweden, in 1985 (ICES CM 1985/F: 60). The meetings resulted in ICES resolutions to continue the monitoring and to carry out a risk assessment (ICES C. Res: 1984/2: 33, ICES C. Res. 1985/2: 36b and 1985/2: 35, respectively). The risk assessment (I. W.) was presented at the ICES Working Group meeting in Gdynia, Poland, in 1986 (ICES CM 1986/F: 51 App. V), and it was recommended that a pilot study should be encouraged; this started in 1987 (J.Y.F., see further, Part 2). The ICES Working Group visited the farming site at Ouessant, Brittany, in June 1987 and a detailed report was given in the documentation from the Working Group meeting in Brest, France in 1987 (ICES CM 1987/F: 35). The results accomplished in the field work (J.Y.F. and R.P.) until summer 1988 are presented in Part 2. They were also presented at the ICES Working Group meeting in Dublin, Ireland in 1989 (ICES CM 1989/F: 16), and provided a foundation for the ICES recommendations relative to future cultivation of the species on the Atlantic coasts of Europe (ICES C. Res. 1989/4: 4). Such applications had until then not been approved (ICES CM 1988/F: 20).

Life history and distribution

Undaria pinnatifida (Laminariales, Phaeophyceae), as other members of the order, has a heteromorphic life cycle with a large sporophyte, usually annual, and microscopic female and male gametophytes (Fig. 1). In spring–summer the basal parts of the sporophytes develop undulated wing-like sporophylles with zoosporangial sori along the midrib. In most areas the sporophyte with its pinnate lamina reaches a length of 1 to 2 or even 3 m (e.g. Kurogi and Akiyama, 1957; Perez *et al.*, 1981, 1984; Akiyama and Kurogi, 1982; Koh, 1983; Zhang *et al.*, 1984; Hay and Luckens, 1987; Stapleton, 1988; Sanderson, 1990, pers. comm., see also Part 2), but usually less than 1 m in the USSR (Zinova, 1954; Perestenko, 1980) and at some of the localities in the Mediterranean Sea (Boudouresque *et al.*, 1985, but see also Part 2). 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).

Undaria pinnatifida is a native species of the Japan Sea and the Japanese coast of the NW Pacific, where it grows on most suitable coasts of Japan, excluding the N and E coasts of Hokkaido (e.g. Saito, 1975; Akiyama and Kurogi, 1982) and the coasts of Korea (Kang, 1966). For centuries it has also been utilized as a food resource on the outer Chinese islands of Zheijang, although most of the *Undaria* populations in China today originate from introductions from Korea during the 1930s (Tseng, 1981). It is now a common Chinese species in the areas around Qing-dao, Shidao, Yantai, and Dahlian, while limited numbers are found on the outer islands (Zhang *et al.*, 1984). There are also reports of the species being found in the USSR near Vladivostok (Bay of Peter the Great: Funahashi, 1966, 1974; Perestenko, 1980) and in the Okhotsk Sea (Bay of Kylky, Islands of Rejneke: Zinova, 1954).

The species was introduced accidentally to the French Mediterranean coast (see Part 2) and recently also to the east coast of Tasmania, Australia (Sanderson, 1988, 1990), to Wellington Harbour, New Zealand (Hay, 1987; Hay and Luckens, 1987; Stapleton, 1988), and to Timaru, on the east coast of the South Island, New Zealand (Hay, pers. comm.). The introductions to the

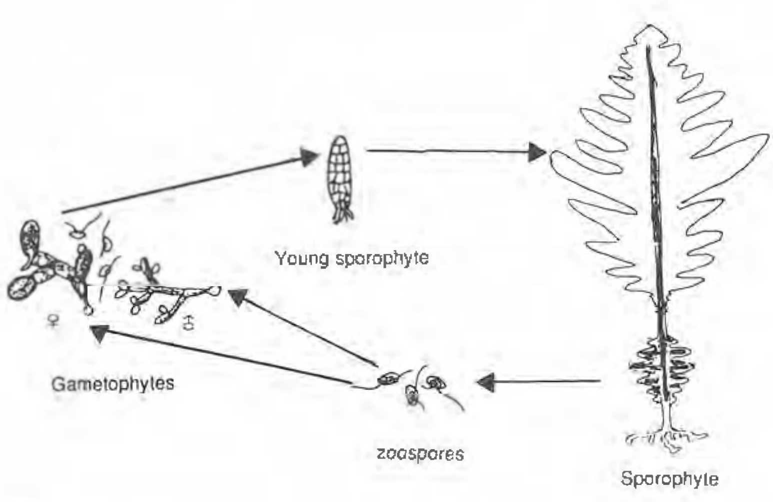


Figure 1. The life cycle of Undaria pinnatifida.

southern hemisphere are believed to originate from ballast water from Japanese ships and this might be a further indication of the species having a potential for dispersal to new areas. So far there are no reports of *Undaria pinnatifida* from European countries other than France.

Habitat

According to the literature, *Undaria pinnatifida* grows on both natural and artificial hard substrates, with a preference for sparsely covered surfaces. The high affinity for artificial substrates could facilitate dispersal in areas with soft substrate, where structures used in aquaculture and marinas, for example, are common. Its depth range in the non-European areas is from the lower intertidal to about 10 m, and sometimes 15 m depth (e.g. Kanda, 1936; Saito, 1975; Akiyama and Kurogi, 1982; Kim *et al.*, 1983; Sohn, 1983; Hay and Luckens, 1987, Hay, pers. comm.; Sanderson, 1990, pers. comm.); the maximum depth depending on ambient light conditions. Saito (1975) stated that zoospore attachment is inhibited in currents above 14 cm s^{-1} and would be adversely affected at speeds above 8 cm s^{-1}, which might be found in areas with strong tidal currents.

Factors influencing growth and reproduction

Temperature

Before *Undaria* farming was started in Brittany, it was hypothesized (see Part 2) that the species would not be able to reproduce *in situ* because the temperature would be too low for the female gametophytes to reach maturity. Thus one of the main tasks for evaluating the risks of its future dispersal was to find experimental data on the effects of different temperatures, as well as to compare temperature regimes for areas where the species reproduces naturally in Asia with temperature regimes in European Atlantic waters. The same approach was also used in the discussions at the first two meetings of the ICES Working Group, when the subject of cultivation of *Undaria* was raised.

Data on temperature optima and/or tolerance limits for sporophytic growth are given in Table 1, together with seasons when the sporophytes appear and disappear in different areas. The suitability of temperatures for enhancement of sporophytic growth was the main prerequisite for starting the farming in Brittany (see, further, Part 2), which is in agreement with the published data. However, release of zoospores, i.e. maturation of the sporophyte, is one of the requirements to enable a species to complete its life history, and the rather wide limits given by different scientists (Table 2) support the hypothesis that the species on the Atlantic coast can indeed produce zoospores, germinating into gametophytes (see also Part 2). Taniguchi *et al.* (1981) also noted that zoospore release started earlier in the inner part of a bay than in the outer.

The development of eggs and spermatozoids was also considered crucial for completion of the life cycle in the Atlantic. The temperature ranges given (Table 3) vary considerably, but are in many cases well within the temperature regimes found at the farming site in Brittany. According to many Japanese and Chinese studies (for references see Table 3), sporophytes can be formed at rather low temperatures, but need longer to grow to

Table 1. Temperature ranges and seasons for growth of sporophytes of *Undaria pinnatifida*.

Optimum	Range	Appear	Disappear	Area	Reference
	4–25°C	Oct–Nov	Jul–Aug	NE Honshu, Japan	Akiyama and Kurogi, 1982
		Dec–Feb	End summer	SE Hokkaido, Japan	Kanda, 1936
			Aug–Sep(–Oct)	N Japan	Kurogi and Akiyama, 1957
		Dec	Jun	E coast, Korea	Koh, 1983
5–10°C		Feb–Apr		Zheijang, China	Zhang *et al.*, 1984
	ca. 10–17°C	Aug	Late summer	Tasmania, Australia	Sanderson, 1990, pers. comm.
	ca. 13–18°C	May–Dec	Late summer (Feb)	New Zealand	Hay, pers. comm.
		Nov–Mar	Jun–Jul	Mediterr., France	Pérez *et al.*, 1981, 1984
			Aug	Mediterr., France	This paper
		All year		Brittany, France	This paper
10–20°C (young thalli)					Akiyama, 1965
15–17°C (young thalli)					Saito, 1975
<12–13°C (old thalli)					Saito, 1975
10–15°C			Sep >20°C		Arasaki and Arasaki, 1983
	0–20°C				Tseng, ICES CM 1985/F: 60
>10°C					Fang, ICES CM 1985/F: 60
15–20°C					Yan, ICES CM 1985/F: 60

Table 2. Temperatures and seasons for zoospore maturity and release in *Undaria pinnatifida*.

Optimum	Range	Month/Season	Area	Reference
	ca. 7–23°C	Mar–Jul	NE Honshu, Japan	Akiyama and Kurogi, 1982
		Jun–Jul	SE Hokkaido, Japan	Kanda, 1936
		Mar–Apr to Aug	NE Honshu, Japan	Kurogi and Akiyama, 1957
		Aug–Jan	Tasmania, Australia	Sanderson, 1990, pers. comm
	ca. 12–18°C	Sep–Feb	New Zealand	Hay, pers. comm.
		May–Jun	Mediterr., France	Pérez *et al.*, 1981, 1984
		May–>Oct	Brittany, France	This paper
17–22°C	14–23°C			Saito, 1975
	17–20°C			Arasaki and Arasaki, 1983
	5–15°C			Tseng, ICES CM, 1985/F: 60
	6–18°C			Fang, ICES CM, 1985/F: 60
	14–22°C			Yan, ICES CM, 1985/F: 60

the same size as those grown at higher temperatures (see, e.g., Kurogi and Akiyama, 1957; Akiyama, 1965: Table 4). Furthermore, in the areas with established *Undaria* in the southern hemisphere the temperatures in the austral summer only reach about 17°C (Greig *et al.*, 1988; Hay, pers. comm.; Sanderson, pers. comm.).

By comparing summer and winter isotherms for the native area of *Undaria pinnatifida* in Asia with those of the European Atlantic coast (Fig. 2) and with the ranges for development of the two stages discussed above, it would appear that a large part of the European Atlantic coast (at least up to about Scotland and Norway) is a potential area for establishment of *Undaria pinnatifida*. However, in the more boreal areas the seasonal appearance and development of the sporophyte would probably be delayed, as is also reported for more northern Japanese waters (e.g. Kanda, 1936; Kurogi and Akiyama, 1957). There might also be an almost continuous period when temperatures are suitable for both maturity of zoosporangia and gametophyte development, which can facilitate natural "seeding". By comparing water temperatures Sanderson (1990) also predicted a further spread of *Undaria* to the coast of southern Australia.

Salinity and nutrients

Most of the experiments reported in the literature have been performed in normal sea water, but salinities above 15‰ Cl (>27‰ S) were quoted by Saito (1975) as necessary for growth of sporophytes and gametophyte development. That range would be found on most European coasts, except for estuaries, the Kattegat, and the Baltic Sea. For attachment of zoospores Saito (1975) gave a lower threshold of >10‰ Cl (>18‰ S). At Wellington, New Zealand, salinities are generally around 33‰ S, but can temporarily fall to about 22–23‰ S (Hay, pers. comm.).

There are few available data on nutrient requirements. Kurogi and Akiyama (1957) reported that gametophyte maturity was inhibited in cultures poor in nutrients, while they grew well in the ones to which N and P had been added.

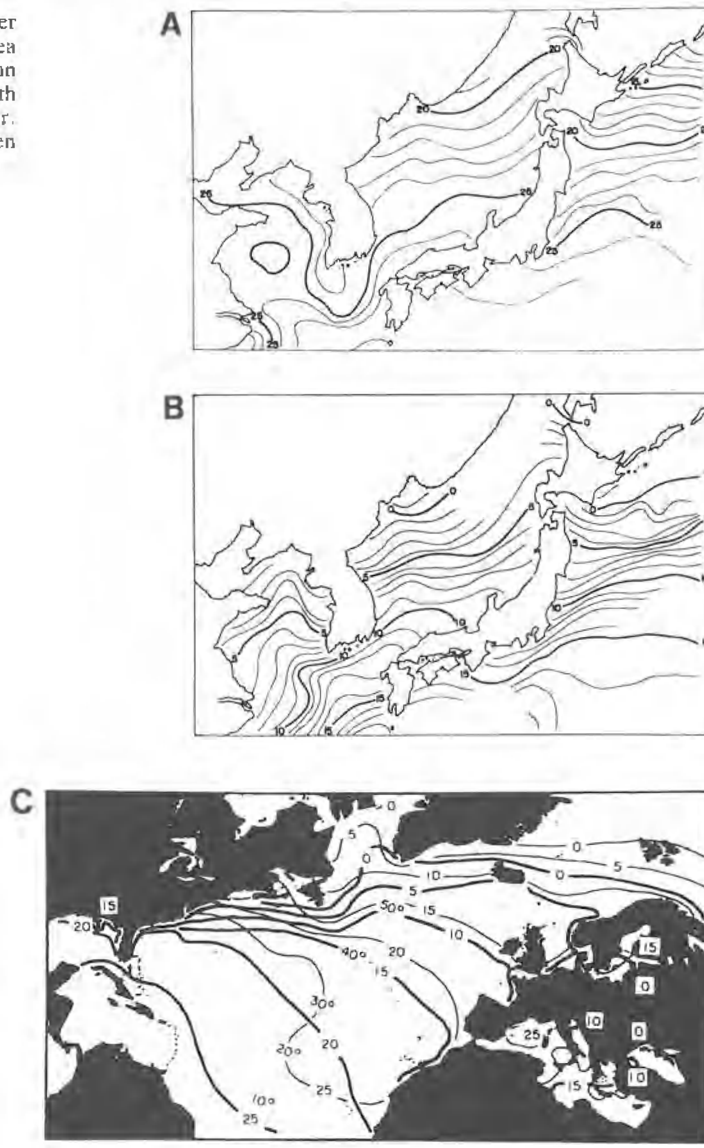
Light

Growth and photosynthesis of the sporophytes are possible over quite a wide range of light intensities (Table 4). Growth and maturation of the gametophytes (Table 4) have rather low light requirements, which allows *Undaria pinnatifida* to develop beneath canopy species,

Table 3. Temperature ranges for growth of gametophytes and release of gametes in *Undaria pinnatifida*.

Growth	Maturity	Fertilization	Reference
15–20°C (optimal)	15–20°C (optimal)	15–20°C (optimal)	Akiyama, 1965
5–28°C (possible)	5–28°C (possible)	5–28°C (possible)	Akiyama, 1965
−1–28°C (survival)			Akiyama, 1965
>15°C	>15°C		Kanda, 1936
15–20°C (optimal)	15–20°C (optimal)		Fang *et al.*, 1982
17–24°C (optimal)	<20–22°C	<20°C	Saito, 1975
15–24°C (possible)			Saito, 1975
−1–30°C (survival)			Saito, 1975
	17–20°C		Arasaki and Arasaki, 1983
0–25°C	5–15°C		Tseng, ICES CM, 1985/F: 60
0–26°C		8–15°C	Fang, ICES CM, 1985/F: 60
23–28°C (optimal)	17–20°C	20–23°C	Yan, ICES CM, 1985/F: 60

Figure 2. Surface water isotherms of summer (August) and winter (February). (A) The Japan Sea and the E coast of Japan, summer; (B) the Japan Sea and the E coast of Japan, winter; (C) the North Atlantic, thick lines winter and thin lines summer. (A–B) From Funahashi 1974, (C) from van den Hoek 1982.



providing space is available among the perennial organisms. Light intensity would therefore matter more in determining vertical rather than regional distribution. However, very turbid coastal waters restrict distribution in some areas (e.g. Zhang *et al.*, 1984). The dormance capacity of the gametophytes (Arasaki and Arasaki, 1983), especially under low light conditions, might also facilitate long-distance dispersal, in ballast water, for example, which is how the species is supposed to have been introduced into the southern hemisphere.

The sporophytes develop mainly during short days (e.g. Saito, 1975), but can also grow during long days (Akiyama, 1965). Most of the data on sporophyte appearance in nature (Table 1) correspond to the seasons of short days, but that is of course dependent on the integrated light and temperature regimes. For the development of the gametophytes, long days (Akiyama, 1965), short days (Akiyama, 1965; Saito, 1975) and a L:D period of 10:14 (Fang *et al.*, 1982) have been considered optimal. Since latitudes are similar for the different parts of the world under consideration (ca. 30–45°N or S), any possible influence of short- or long-day conditions would only be of interest when discussing a possible dispersal to the northernmost part of the European Atlantic coast, where the temperature probably would be more crucial than the length of the day.

Competitive ability

Undaria pinnatifida is often found in small numbers among large seaweeds or sessile macrofauna (e.g. Kurogi and Akiyama, 1957; Sakai, 1977; Sanderson, 1990;

Table 4. Light in experiments with growth/production of the sporophytes and growth/maturity of the gametophytes of *Undaria pinnatifida* (I_k is the light saturation point for photosynthesis).

Sporophyte	Gametophyte	Photosynthesis	Reference
570–4000 lux (young)	570–4000 lux		Akiyama, 1965
	1000 lux (optimal)		Akiyama and Kurogi, 1982
	1500 lux (optimal)		Fang *et al.*, 1982
	<400 lux		Pérez *et al.*, 1981
	2000–6000 (optimal)		Saito, 1975
	<150 lux (no maturation)		Saito, 1975
500–3000 lux			Saito, 1962
		I_k ca. 100–450 μE $m^{-2}s^{-1}$ (= 500–22 500 lux)	Matsuyama, 1983
		I_k 18 000 lux	Wu *et al.*, 1981

Hay, pers. comm.), which implies a low competitive ability. This might indicate a smaller risk of excluding native perennial canopy species than in the case of some other introduced species; however, *Undaria* might possibly compete with other annuals which also have periodic recruitment. Its often dense coverage on secondary substrates (see also Part 2), might indicate a tendency of an opportunistic colonization strategy, although it lacks many other characteristics of true opportunists such as many generations per year, a high reproductive output and high metabolic rates.

High grazing rates on *Undaria*, mainly by sea urchins, have been reported (e.g. Noro and Masakai, 1983; Boudouresque, pers. comm.; Part 2), although in the southern hemisphere, these are considerably lower than its growth rate (Sanderson, 1990; Hay, pers. comm.). However, insufficient is known to predict to what extent grazing would influence the establishment of *Undaria pinnatifida* along the European Atlantic coasts.

2. *Undaria pinnatifida* on the French coasts

Undaria pinnatifida in the Mediterranean Sea

The Étang de Thau

Undaria pinnatifida was first found in the Étang de Thau in 1971. The Étang de Thau (18 × 4 km) is situated in the south of France (Fig. 3), close to the city of Sète. It communicates with the Mediterranean Sea by channels and supports very active oyster aquaculture. It is probably one of the European marine sites where the largest number of alien organisms can be found (Boudouresque *et al.*, 1985). The biology of the alga in Thau was reported by Pérez *et al.* (1981, 1984) to be similar to that in Korea and Japan: the sporophytes are visible in autumn, the growth is maximal in March, the sporophylles are mature from May to July, and the sporophytes disappear in July from the natural sites.

A visit to the Étang de Thau in April 1988 (J.Y.F.) confirmed that *Undaria pinnatifida* was still there, attached to the permanent structures of the oyster farms. Since the vertical ropes supporting the oysters are frequently cleaned, *Undaria pinnatifida* has no chance to colonize them. As a consequence the alga is not a real nuisance for the fishermen, who are actually more concerned about another introduced brown alga *Sargassum muticum* (Yendo) Fensholt.

Undaria *dispersal out of the Étang de Thau*

Tidal fluctuations are very small in the Étang de Thau, as they are in the Mediterranean Sea generally. The currents, which are essentially produced by the wind, are weak, and the channel between the Étang de Thau and the open sea is narrow. This is probably why it was not until 1981, i.e. ten years after its discovery in the Étang de Thau, that *Undaria pinnatifida* was reported on the open coast, on the pier of the harbour of Sète (Pérez *et al.*, 1981). It seems that from that year the alga spread faster along the Mediterranean coast. In fact, the species had already been found in 1981 at Port La Nouvelle, 70 km SW of Sète (Boudouresque *et al.*, 1985), but it was not until 1984 that these authors studied a well-developed population of *Undaria pinnatifida* at this site. The present known southern limit of the species is the harbour of Port Vendres, 60 km S of Port La Nouvelle and 10 km from the Spanish border (Fig. 3) (Knoeppfler-Peguy and Floc'h, pers. obs. 1988). It is not known how far the alga has spread E of Sète, but to the west its dispersal seems to follow the well-known currents in the Golfe du Lion. Therefore, it would not be surprising if the species were to reach the Spanish coasts, if it has not already done so.

The general biology of *Undaria pinnatifida* is similar along the parts of the Mediterranean coasts where it has been found so far. However, the size and duration of the sporophytes seem to vary according to the local environmental conditions. For instance, the comparatively smaller size of the alga in Port La Nouvelle (maximum 30 cm, Boudouresque *et al.*, 1985) compared to 100 cm in Port Vendres (Knoeppfler-Peguy and Floc'h, pers. obs. 1988) is probably due to a higher turbidity of the water there, a fact to be compared to

Figure 3. Map showing the sites where *Undaria pinnatifida* was either introduced to or found on the coast of France: (1) Étang de Thau, (2) Port La Nouvelle, (3) Port Vendres, (4) Island of Ouessant, (5) La Rance, (6) Island of Groix.

Table 5. Calendar of the transfers of *Undaria pinnatifida* into the experimental culture field in open sea at Ouessant (J. Y. Moign, Coopérative aquacole, pers. comm.).

Year	Month	Length of transferred ropes with plantlets (km)	Yield of *Undaria* (fresh weight (t))
1983	Oct	0.15	1 (Feb 1984)
1984	Feb	0.2	2 (Jun 1984)
	Nov	1	0
1985	Feb	2	0
	Sep	3	0
1986	Mar	1	0
	Nov	2	0
1987	Sep	2	0
1988	Feb	1	0
	Apr	1	Good (not harvested)

the environmental conditions in the Yellow Sea, where the alga only grows to a small size (Wu, Chang and Xia, pers. comm.).

Undaria pinnatifida in the Atlantic Ocean

Sequence of the intentional transfer of Undaria *to the Atlantic*

In 1983 the French IFREMER decided to transfer *Undaria pinnatifida* from the Mediterranean Sea to the Atlantic Ocean (Pérez *et al.*, 1984). The method followed that used in Korea: the mature sporophylles were cut from the sporophytes found in the Étang de Thau and transferred to Nantes. Subsequently the spores were made to germinate on ropes in a hatchery; they produced gametophytes and then new sporophytes. When the newly formed sporophytes were strong enough, the ropes that supported them were transported to the sea at three different sites in Brittany (Fig. 3): one at the island of Groix in the south, another at the island of Ouessant in the west, the third in the estuary of La Rance in the north.

These experiments were based on two propositions: (1) *Undaria pinnatifida* would grow better in colder water; and (2) the species would not be able to reproduce *in situ* and, as a consequence, the cultures would be fully controllable. The sites of the Rance and Groix were soon abandoned and the island of Ouessant became the only approved French experimental site until 1989 (Table 5).

The aim of the study reported here, restricted to Ouessant at the request of IFREMER, was to check whether the introduced alga had escaped from its experimental site since the first introduction in 1983. Our study started in 1987.

Ecological survey of the introduced *Undaria* at Ouessant

The site of survey

The island of Ouessant is situated 20 km off the western coast of Brittany. The experimental *Undaria* culture field is located in the bay of Lampaul, SW of the island (Fig. 4). Ouessant is famous for its exposure to strong storms and currents. The difference between high and low watermarks can reach 8 m in this area. However, the bay of Lampaul is the most sheltered site around the island. From our own observations the currents seem to be weak inside the bay and the water there is renewed largely by the tidal movements. The substrate of the bay is mainly rocky with some sand patches. The rocks are abundantly covered with seaweeds, the bulk of which are members of Fucales and Laminariales.

The *Undaria* experimental culture field is 200 × 100 m large. A mussel farm situated 50 m W of this field consists of nine horizontal long lines (100 or 125 m long), each supporting 200 to 300 vertical suspensions (5 to 8 m long).

Methods

The first step was to examine the structures of the mussel farm. Since the horizontal lines were found abundantly covered with vigorous *Undaria* sporophytes, it was decided to study the horizontal and vertical distributions of the alga on these structures in detail. These preliminary results would be used to organize the search for *Undaria pinnatifida* on the rocky substrate of the bay.

Since *Undaria pinnatifida* on the mussel suspensions were not found deeper than 5 m from the surface, the subsequent search for the alga on the rocky bottom was first limited from 1.5 m above the lowest tide mark, i.e.

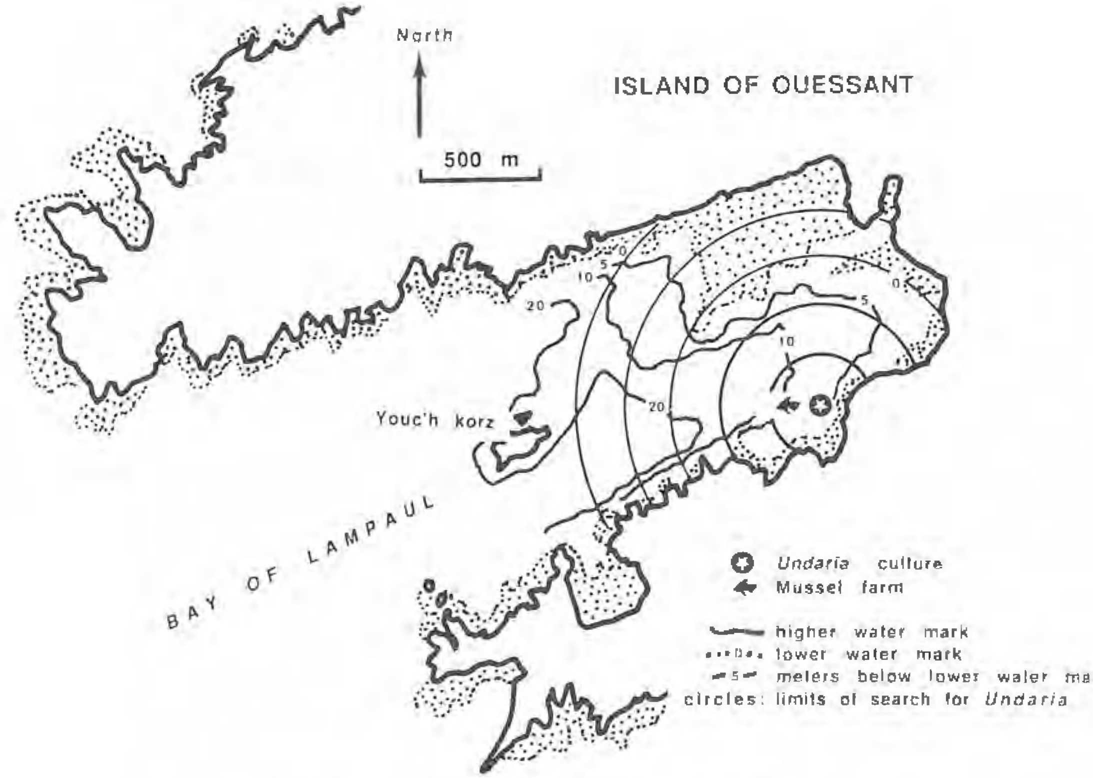


Figure 4. Study site in the SW part of the Island of Ouessant.

the upper limit of *Himanthalia elongata* (L.) S. F. Gray, to 5 m below the lowest tide mark. Using SCUBA diving, sampling quadrats of 80 m^2 were examined for sporophytes of *Undaria pinnatifida*. A total of 75 quadrats, located on concentric circles around the experimental algal culturing field as a centre, were examined in 1987 and 1988. The whole area studied was the eastern part of the bay, situated E of the rock called Youc'h korz (Fig. 4).

Results

Undaria pinnatifida *on the mussel structures*

In the spring of 1987 the distribution of *Undaria pinnatifida* on the horizontal long lines of the mussel farm differed in accordance with their location in the bay. The northern external structures were the most heavily covered by the alga, some of them carrying 6 to 8 sporophytes per metre in March and May of that year.

The vertical distribution of *Undaria pinnatifida* was studied on three suspensions of each horizontal line, one at each end and one in the middle of the lines. The results (Fig. 5) showed that the sporophytes were attached in tufts along the suspensions, each tuft being formed from a few up to 27 sporophytes. The bulk of the *Undaria* population was found within the first 2 m below the surface. Only one sporophyte was found at a depth of 5 m.

The overall distribution of *Undaria* on the mussel structures, horizontal plus vertical, showed that 50% of the algal population was located within the first 0.5 m below the surface (Fig. 6). The *Undaria* sporophytes were found attached to the structures, ropes, or nets, or to the mussels themselves. Other algae were found together with them, mainly the brown algae *Saccorhiza polyschides* (Lightf.) Batt., *Laminaria digitata* (Huds.) Lamour, and the red alga *Asparagopsis armata* Harvey.

The length of the sporophytes was measured in March and May 1987 (Fig. 7A and B). The results showed that the maximum size was found in May (Fig. 7B), most of the sporophytes being between 50 and 120 cm long; some were nearly 2 m long.

Undaria pinnatifida *on the rocky bottom of the bay of Lampaul*

The search for *Undaria pinnatifida* among the native algae of Ouessant was very difficult for several reasons. First, the local marine flora is very rich (Floc'h, 1970; Dizerbo and Floc'h, 1971); the species are numerous, the densities are high and the sizes of the algae are large. Thus *Himanthalia elongata*, situated in the upper part of the studied zone, is 4–5 m long, *Laminaria*

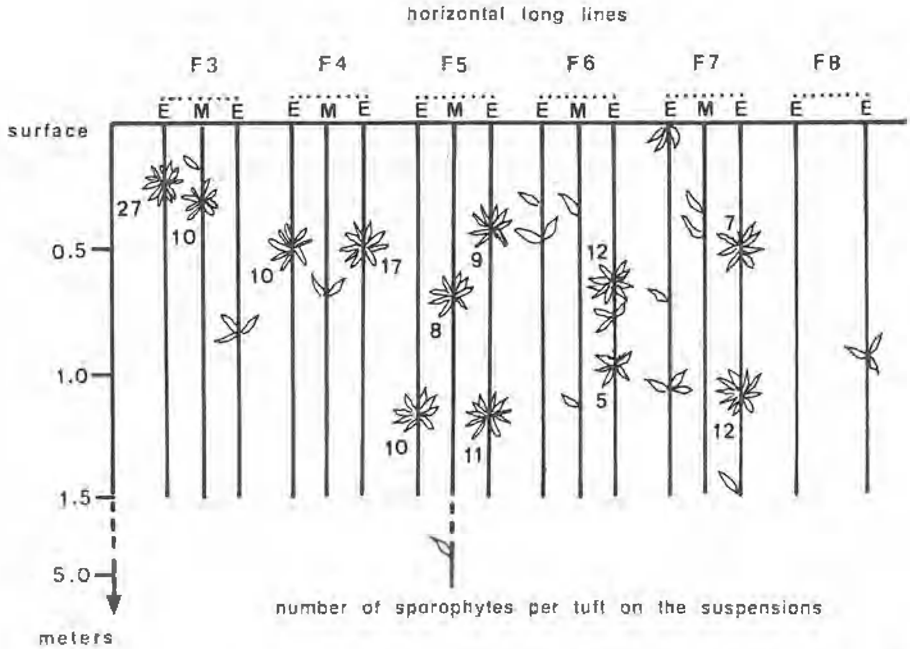


Figure 5. Vertical distribution of *Undaria* sporophytes on the suspensions in the mussel farm at Ouessant. Three suspensions were selected per long line: one at each end (E) and one in the middle (M).

digitata, *Laminaria ochroleuca* Bach. Pyl. and *Laminaria hyperborea* (Gunn.) Foslie, further down, form forests 2–4 m high. Moreover, *Alaria esculenta* (L.) Grev. is common in this area and its sporophytes, when young and immature, are similar to those of *Undaria pinnatifida*, particularly when the latter is young in March (Fig. 7A). Furthermore, not all the quadrats could be visited the same day nor even in the same month, and we did not know anything about the succession of the escaped sporophytes of *Undaria* from the experimental culture field (if any). Therefore, it would have been necessary to examine periodically the quadrats throughout the year to determine whether *Undaria* was there or not – a task beyond the resources of this

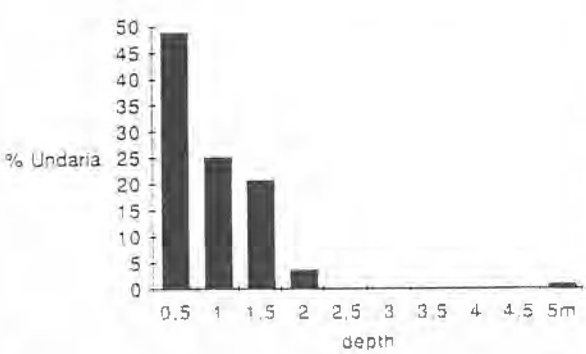


Figure 6. Vertical distribution of *Undaria* sporophytes in the whole mussel farm at Ouessant in 1987.

study. Consequently, the present study was definitely a qualitative one, and no quantitative evaluation of the geographical distribution of *Undaria* in the bay is possible from the following results.

In June 1987, 7 sporophytes, 20 to 80 cm long, were found on the rocky bottom, 5 m beneath the experimental culture field, and 10 sporophytes were found on the rocks 9 m beneath one of the mussel farm structures.

In August about 40 sporophytes were found on rocks at depths between 5 and 18 m. The sizes of the algae were again between 20 and 80 cm long.

From our earlier observations (March and May) these results were unexpected, since no *Undaria* had been found deeper than 5 m on the mussel structures. Moreover, all the sporophytes found on the rocks were very late maturing compared to the plants we saw on the mussel farm at the same period. Therefore it was decided to examine all the *Undaria pinnatifida* already found instead of surveying the whole bay.

The wild Undaria pinnatifida *in October at Ouessant*

The *Undaria* populations we found in October 1987 on the mussel structures were mixed populations of plants of different sizes: some of them were reduced to their bases (with mature sporophylles), some were large (with their stipe, sporophylles, and full blade), others were young and apparently growing. At the same time the sporophytes we had seen before on the rocky bottom were reduced to their bases (with sporophylles, only the margins of which were mature).

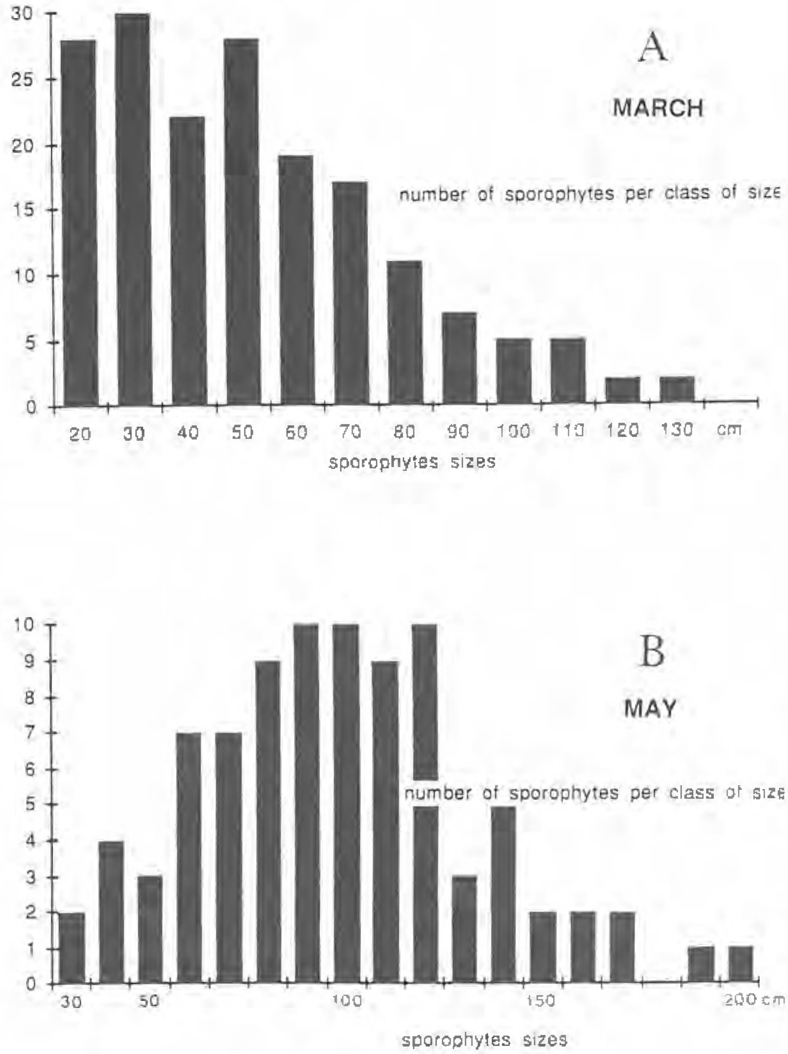


Figure 7. Distribution of *Undaria* sporophytes per size class in the mussel farm at Ouessant in 1987. (A) March. (B) May.

A significant finding was that one mussel suspension, newly built in June 1987, was found to be carrying 18 sporophytes measuring from 30 cm to 100 cm long. These sporophytes must have come from a complete reproduction of the sporophytes we had found in the spring of the same year, since no new culture ropes had been introduced before September (Table 5), and this introduction could not have produced such well-developed plants if they had escaped.

Discussion

The dense populations of *Undaria pinnatifida* found on the mussel farm structures in the spring of 1987 clearly showed that the introduced alien species had escaped from the culture experimental site at Ouessant.

This escape could have two possible origins:

1. Since ropes with plantlets were immersed in the experimental field in November 1986 (Table 5) and the culture was soon after destroyed by a storm, it is possible that the plantlets, or the fertilized eggs, had been detached from the ropes (frames) and reattached to the mussel structures nearby. However, this seems to be rare in Nature and could only happen in quiet waters (Wu, pers. comm.). Therefore, it would be surprising if such a great number of plantlets succeeded in fixing themselves to the mussel structures as the water movements were strong at Ouessant. Indeed the observed densities of 6 to 8 sporophytes per metre on those structures are not far below the best which fishermen can obtain in the cultivation farms (Akiyama and Kurogi, 1982; Pérez *et al.*, 1984).
2. A more plausible hypothesis is that the sporophytes, which had been cultivated and had become mature at the Ouesssant site in 1983 and 1984 (Table 5), had released their spores *in situ* and that the whole

reproductive cycle is completed in the bay each year through the gametophytes. In our opinion this would be a better explanation for the numerous sporophytes of wild *Undaria pinnatifida* found in the bay of Lampaul in 1987 and 1988, a minimum estimate of which on the rocky bottom in 1987 was 20 000.

This conclusion is corroborated by the fact that in October 1987 we observed *Undaria pinnatifida* sporophytes of different sizes and maturity stages on a recently built mussel structure, and by the numerous large wild sporophytes we found again on the mussel structures in the bay in early May 1988, at which time the cultivated algae did not exceed 15 cm (Table 5).

Conclusion

The above results clearly show that *Undaria pinnatifida* does reproduce *in situ* in the Atlantic Ocean at Ouessant, a conclusion that is contrary to the hypothesis previously advanced by the algal culture promoters. Moveover, from the present results, it appears that *Undaria pinnatifida* does not have exactly the same vegetative cycle at Ouessant as in the Mediterranean Sea; thus although the species is annual, the sporophytes can be found all the year long at Ouessant, comparable to for example the biology of *Saccorhiza polyschides*, which is another annual member of the Laminariales that can be found all the year round in this region.

Several questions therefore arise, the first being whether it is possible to foresee the geographical limits of dispersal in the Atlantic coastal regions.

Clearly *Undaria pinnatifida* grows well in Atlantic waters. With extreme temperature limits in Asian waters from 0°C (NW Hokkaïdo) to 27°C (SW Kyushu) (Fig. 2), virtually all Atlantic coastal regions from Norway in the north to Mauritania in the south are potentially available so far as temperature is concerned. Other environmental conditions must also, of course, be favourable and it is known that in Asian Seas (the Pacific Ocean, the Japan Sea, the Yellow Sea) the distribution of *Undaria pinnatifida* is also regulated by factors such as currents, turbidity, and grazing.

Another question is whether *Undaria pinnatifida* will grow differently when introduced, as happened in the colonization of European waters by *Sargassum muticum*. So far, the evidence is that *Undaria pinnatifida* grows to about the same size (1–2 m) both in Japan and Ouessant.

Interactions and competition with local organisms are also important. Grazing pressure on *Undaria pinnatifida* is undoubtedly high, and in the Mediterranean it seems now to be the favourite diet of sea urchins (Boudouresque, pers. comm.). At Ouessant we have seen grazed sporophytes in summer, and here it seems that the fishes are the main grazers on the mussel structures. However, grazing of gametophytes is likely to have a strong influence on controlling *Undaria*, but there is as yet no evidence from which such interactions can be quantified.

Undaria pinnatifida grows well and in high densities at Ouessant on cleaned substrates hanging from the surface structures (the suspensions in the mussel farm). An experiment on competition between *Undaria pinnatifida* and local algae was performed at Ouessant during 1988–1989. These results will be published elsewhere. Anyhow, *Undaria pinnatifida* does not seem to be very competitive, especially if compared to *Saccorhiza polyschides*.

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References

Akiyama, K. 1965. Studies of ecology and culture of *Undaria pinnatifida* (Harv.) Sur. II. Environmental factors affecting the growth and maturation of gametophyte. Bull. Tohoku Reg. Fish. Res. Lab., 25: 143–170. (In Japanese with English summary and legends.)

Akiyama, K., and Kurogi, Z. M. 1982. Cultivation of *Undaria pinnatifida* (Harvey) Suringer. The decrease in crops from natural plants following crop increase from cultivation. Bull. Tohoku Reg. Fish. Res. Lab., 44: 91–100.

Anon. 1984. Report of the Working Group on Introductions and Transfers of Marine Organisms. ICES CM 1984/F: 35, 115 pp.

Anon. 1985. Report of the Working Group on Introductions and Transfers of Marine Organisms. ICES CM 1985/F: 60, 35 pp. + 8 appendices.

Anon. 1986. Report of the Working Group on Introductions and Transfers of Marine Organisms. ICES CM 1986/F: 51, 69 pp.

Anon. 1987. Report of the Working Group on Introductions and Transfers of Marine Organisms. ICES CM 1987/F: 35, 39 pp.

Anon. 1988. Report of the Working Group on Introductions and Transfers of Marine Organisms. ICES CM 1988/F: 20, 43 pp.

Anon. 1989. Report of the Working Group on Introductions and Transfers of Marine Organisms. ICES CM 1989/F: 16, 56 pp.

Arasaki, S., and Arasaki, T. 1983. Vegetables from the sea. Japan Publ. Inc., Tokyo, 196 pp.

Boudouresque, C. F., Gerbal, M., and Knoepffler-Peguy, M. 1985. L'algue japonnaise *Undaria pinnatifida* (Phaeophyceae, Laminariales) en Méditerranée. Phycologia, 24: 364–366.

Dizerbo, A. H., and Floc'h, J. Y. 1971. Excursion en Bretagne (Brest, 17–22 août 1970). Bull. Soc. Phycol. de France, 16: 82–88.

Fang, T. C., Dai, J., and Chen, D. 1982. Parthenogenesis and the genetic properties of parthenosporophytes of *Undaria pinnatifida*. Acta Oceanol. Sinica, 1: 107–111.

Floc'h, J. Y. 1970. Cartographie de la végétation marine dans l'archipel de Molène Finistère. Rev. Trav. Inst. Pêches Marit., 34: 89–120.

Funahashi, S. 1966. Marine algae from Vladivostok and its vicinity. Bull. Jap. Soc. Phycol., 14: 127–145. (In Japanese with English summary.)

Funahashi, S. 1974. Distribution of marine algae in the Japan Sea, with reference to the phytogeographical positions of Vladivostok and Noto Peninsula districts. J. Fac. Sci. Hokkaido Univ. Ser. V (Botany), 10: 1–31.

Gerbal, M., Ben Maiz, M., and Boudouresque, C. F. 1985. Les peuplements à *Sargassum muticum* de l'Étang de Thau: Données préliminaires sur la flore algale. 110e Congr. nat. Soc. savantes, Montpellier 1985, Sci fasc II: 241–254.

Greig, M. J., Ridgway, N. M., and Shakespeare, B. S. 1988. Sea surface temperature variations at coastal sites around New Zealand. N.Z. J. Mar. Freshwater Res., 22: 391–400.

Hay, C. H. 1987. An alien alga in Wellington harbour. New Zealand Environment, 57: 12–14.

Hay, C. H., and Luckens, P. A. 1987. The Asian kelp *Undaria pinnatifida* (Phaeophyta: Laminariales) found in a New Zealand harbour. N.Z. J. Bot., 25: 329–332.

Hoek, C. van den. 1982. The distribution of benthic marine algae in relation to the temperature regulation of their life histories. Biol. J. Linnean Soc., 18: 81–144.

Kanda, T. 1936. On the gametophytes of some Japanese species of Laminariales. Sci. Pap. Inst. Alg. Res., Hokkaido Imp. Univ., 1: 221–260.

Kang, J. W. 1966. On the geographical distribution of marine algae in Korea. Bull. Pusan Fish. Coll., 7: 1–136.

Kim, H. S., Lee, I. K., Koh, C. H., Kim, I. H., Suh, Y. B., and Sung, Z. N. 1983. Studies on the marine benthic communities in intertidal and subtidal zones. I. Analysis of benthic community structures at Aninjin eastern coast of Korea. Proc. Coll. Nat. Sci. (Seoul), 8: 71–108. (In Korean with English summary.)

Koh, C. H. 1983. Community structure and productivity of phytobenthos in Juckdo eastern coast of Korea. 2. Seasonal changes of algal vegetation in relation to annual growth of large brown algae. Korean J. Bot., 26: 181–190. (In Korean with English summary.)

Kurogi, M., and Akiyama, K. 1957. Studies of ecology and culture of *Undaria pinnatifida* (Sur.) Hariot. Bull. Tohoku Reg. Fish. Res. Lab., 10: 95–117. (In Japanese with English summary and legends.)

Matsuyama, K. 1983. Photosynthesis of *Undaria pinnatifida* Suringar f. *distans* Miyabe et Okamura (Phaeophyceae) from Oshoro Bay. I. Seasonal changes of photosynthetic and respiratory rates. Sci. Rep. Hokkaido Fish. Exp. Stn., 25: 187–193. (In Japanese with English summary and legends.)

Noro, T., and Masakai, T. 1983. Sublittoral distribution and reproductive periodicity of crustose coralline algae (Rhodophyta, Cryptonemiales) in southern Hokkaido, Japan. Bull. Fac. Fish. Hokkaido Univ., 34: 1–10.

Perestenko, L. P. 1980. Wodorosli Zaliva Petra Weilikogo. Izd. Akad. Nauk SSSR, Leningrad. 232 pp.

Pérez, R., Kaas, R., and Barbaroux, O. 1984. Culture expérimentale de l'algue *Undaria pinnatifida* sur les Côtes de France. Sci. Pêche, 343: 3–15.

Pérez, R., Lee, J. Y., and Juge, C. 1981. Observations sur la biologie de l'algue japonaise *Undaria pinnatifida* (Harvey) Suringer introduite accidentellement dans l'Étang de Thau. Sci. Pêche, 315: 1–12.

Saito, Y. 1962. Fundamental studies on the propagation of *Undaria pinnatifida* (Harv.) Sur. Contr. Fish. Lab. Fac. Agr. Univ. Tokyo, 3: 1–101. (In Japanese with English summary.)

Saito, Y. 1975. *Undaria*. *In* Advance of Phycology in Japan, pp. 304–320. Ed. by J. Tohida and H. Hirose. Junk., The Hague. 355 pp.

Sakai, Y. 1977. Vegetation structure and standing crop of the marine algae in the *Laminaria*-bed of Otaru City, Hokkaido, Japan. Jap. J. Ecol., 27: 45–51.

Sanderson, J. C. 1988. Japanese invasion of Tasmania's east coast. Third Intern. Phycol. Congr., Monash Univ., Melbourne, Australia, August 14–20, 1988, p. 38 (Abstract).

Sanderson, J. C. 1990. A preliminary survey of the distribution of the introduced macroalga, *Undaria pinnatifida* (Harvey) Suringer on the east coast of Tasmania, Australia. Botanica mar. 33: 153–157.

Sohn, C. H. 1983. A study on the algal communities of Odongdo southern coast of Korea. Bull. Korean Fish. Soc., 16: 368–378. (In Korean with English summary.)

Stapleton, J. C. 1988. Occurrence of *Undaria pinnatifida* (Harvey) Suringar in New Zealand. Jap. J. Phycol., 36: 178–179.

Taniguchi, K., Kito, H., and Akiyama, K. 1981. Morphological variation of *Undaria pinnatifida*. 1. Differences of growth and morphological characteristics of two types at Matsushima Bay, Japan. Bull. Tohoku Reg. Fish. Res. Lab., 42: 1–10. (In Japanese with English summary.)

Tseng, C. K. 1981. Commercial cultivation. *In* The biology of seaweeds, pp. 680–725. Ed. by C. S. Lobban and M. J. Wynne. Blackwell, Oxford. 786 pp.

Wu, C., Wen, Z., Peng, Z., and Zhang, J. 1981. Preliminary study on the productivity of some eco-nomic marine algae. Phycologia, 20: 118 (Abstr.).

Yabo, H. 1964. Early development of several species of Laminariales in Hokkaido. Mem. Fac. Fish., Hokkaido Univ., 12: 1–72.

Zhang, D. M., Miao, G. R., and Pei, L. O. 1984. Studies on *Undaria pinnatifida*. Hydrobiologia, 116/117: 263–265.

Zinova, E. S. 1954. Wodorosli Ochoskogo Mora. Trudy Bot. Inst. Akad. Nauk SSR, Ser 2, 9: 259-310.