Reproductive phenology of the introduced kelp Undaria pinnatifida (Phaeophyceae, Laminariales) in Tasmania, Australia

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For pest management of introduced marine species to succeed, a thorough understanding of reproductive patterns is essential. Undaria pinnatifida is an invasive macroalga that has been introduced into at least 10 countries. Reproductive phenological studies in Tasmania, Australia, were undertaken to provide much-needed quantitative information to support pest management. Zoospore release of U. pinnatifida, an annual kelp, was limited to the larger size classes of sporophytes (> 55 cm length) for most of the growing season, 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. The maximum zoospore release of U. pinnatifida was 62 × 10⁶ zoospores cm⁻² sporophyll tissue h⁻¹, corresponding to a maximum release of 4.3 × 10⁶ zoospores sporophyte⁻¹ h⁻¹. Spore release rates of other kelp species are similar or higher, the latter especially in larger-sized species. Tagged U. pinnatifida individuals in the present study released zoospores for about three months before becoming senescent and disintegrating. 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. The zoospore release of an assemblage of introduced U. pinnatifida at the study site was estimated as 2 × 10⁶ zoospores m⁻² h⁻¹ in the month of January (summer). The two largest size classes released the majority of zoospores. 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.

INTRODUCTION

Invasive species have been identified as a major threat to native marine biodiversity and the value of marine resources because of their capacity to alter ecosystem composition and processes, change community structure and carry parasites and pathogens (e.g. Lubchenco et al. 1991; Carlton 2000; Mack et al. 2000; Elliott 2003). Several invasive macroalgae, such as Caulerpa taxifolia (Vahl) C. Agardh, Codium fragile (Suringar) Hariot ssp. tomentosoides (van Goor) P.C. Silva, Sargassum muticum (Yendo) Fensholt and Undaria pinnatifida (Harvey) Suringar in the thousands of marine species estimated to have been introduced by human activity on a global scale (e.g. Ribera & Boudouresque 1995; Cranfield et al. 1998; Coles et al. 1999; Hewitt et al. 1999; Trowbridge 1999; Ruiz et al. 2000; Boudouresque & Verlaque 2002; CIEM 2002; Hewitt 2002; Leppäkoski et al. 2002; Occhipinti-Ambrogi & Savini 2003; Hewitt et al. 2004), yet few mechanisms are available to manage or control the impacts of nonindigenous macroalgae.

More and more marine researchers are turning towards terrestrial paradigms established for pest management, such as: physical removal or control, modelling of dispersal and spread and assessments of the risk of infecting local vectors, possibly leading to further translocation of the species. Based on these paradigms, a thorough understanding of the life history of an introduced species, particularly the reproductive pattern, is necessary for pest management to prove effective.

Undaria pinnatifida is native to the cold and warm temperate Northwest Pacific phytogeographic bioprovinces [i.e. Zhejiang islands in China, Japan, Korea and Russia; van den Hoek (1984); Tseng (1981)], where sporophytes of this species are extensively cultivated in open ocean aquaculture facilities as a high-value species for human consumption (FAO 2003). However, U. pinnatifida aquaculture in China was established with material introduced from Korea in the 1930s (Tseng 1981). Undaria pinnatifida was first discovered outside its native range on the French Mediterranean coast, believed to have been introduced with oysters from Japan (Pérez et al. 1981; Floc’h et al. 1991; Grizel & Heral 1991). Mediterranean sporophytes were translocated as seedstock for aquaculture of U. pinnatifida on the French Atlantic coast in 1983 (Pérez et al. 1984; Boudouresque et al. 1985; Floc’h et al. 1991). Unintentional anthropogenic spread since the 1970s resulted in the establishment of introduced populations of U. pinnatifida in Argentina (Piriz & Casas 1994; Casas & Piriz 1996), Tasmania and mainland Australia (Sanderson & Barrett 1989; Campbell & Burridge 1998), Belgium (Wallentinus 1999), UK (Fletcher & Manfredi 1995), Italy (Curiel et al. 1998; Cecere et al. 2000), the Netherlands (Wallentinus 1999), New Zealand (Hay & Luckens 1987), Spain (Salinas et al. 1996; Pérez-Cirera et al. 1997) and, most recently, California, USA (Silva et al. 2002) and the Pacific coast of Mexico (Aguilar Rosas & Aguilar Rosas 2004).

In Australia, U. pinnatifida was first recorded in 1988 on
the east coast of Tasmania (Sanderson & Barrett 1989; Sanderson 1990). Within the following 15 years the introduced kelp spread 150 km north and 80 km south of the initial invasion site (Seacare 2003). A second introduction of *U. pinnatifida* in Australia was identified in 1996 in Port Phillip Bay, Victoria, on the Australian mainland (Campbell & Burridge 1998). This introduction was either sourced from native Pacific populations or from New Zealand, but not from Tasmania, because sporophyte morphology in the Port Phillip Bay population is different from that of Tasmanian populations (Campbell & Burridge 1998).

Potential vectors for trans–ocean basin or intercontinental transport (i.e. between noncontiguous biotic provinces) of *U. pinnatifida* are ballast water and hull-fouling, whereas domestic translocations of species (i.e. along coasts within or between contiguous bioregions) are likely to be additionally facilitated by fishing, recreational boating and aquaculture activities (Hay 1990; Lewis 1999). The pattern of spread of *U. pinnatifida* along the Tasmanian east coast supports this because the majority of new introduction sites are in sheltered bays, separated by at least 35 km and associated with boat ramps or mooring sites (Seacare 2003). Currents along the east coast of Tasmania flow generally in a southerly direction generally (CSIRO 1997) and may transport *U. pinnatifida* zoospores, detached gametophytes or drifting mature sporophytes over short distances. *Undaria pinnatifida* drift sporophytes were observed in Tasmania (see below). The importance of kelp dispersal by drift sporophytes is still unclear and has not been extensively studied (see Dayton et al. 1984; Reed et al. 1988).

In its native range *U. pinnatifida* has a distinct annual life cycle (e.g. Akiyama & Kurogi 1982). Recruitment of sporophytes occurs in autumn with main growth occurring during winter and spring, maturation and release of zoospores in spring, followed by senescence in summer. However, at a number of introduced locations (e.g. UK, northern France and New Zealand), sporophytes are present throughout the year with reduced abundance during summer and autumn (Hay & Villouta 1993; Stuart 1997; Brown 1999; Castric-Fey et al. 1999; Fletcher & Farrell 1999). The microscopic gametophytes develop over summer to autumn. This life cycle is matched in Australia under southern hemisphere conditions (Hewitt et al. 2005).

In Japan, zoospore release in *U. pinnatifida* has been observed from March to July (Akiyama & Kurogi 1982), corresponding to the northern hemisphere summer. In some introduced New Zealand populations, mature sporophytes capable of zoospore release are observed throughout the year (Hay & Villouta 1993; Brown 1999); however, significant zoospore release only occurred during summer months (Brown 1999).

This paper presents data on the reproductive phenology of the *U. pinnatifida* sporophyte generation in an introduced population in Tasmania, Australia, including the timing and scale of zoospore release. This information is essential for successful proactive and reactive pest management of this species.

**MATERIAL AND METHODS**

Field sampling was carried out in the Tinderbox Marine Reserve (43°3.60’S, 147°19.95’E), located approximately 30 km south of Hobart, Tasmania, Australia. A more detailed description of the field site is provided in Hewitt et al. (2005).

**The 1998–1999 field surveys**

To establish the feasibility of manual removal of *U. pinnatifida*, an experimental removal was carried out in the Tinderbox Marine Reserve. The design included eight permanent belt transects perpendicular to the shore (four treatment and four control), each measuring 50 × 4 m. The experimental area was, hence, 1600 m². In four transects, *U. pinnatifida* was manually removed by scuba divers monthly from July 1997 to August 1999. In four control (no removal) transects, abundance and sporophyte phenology of *U. pinnatifida* were measured monthly in situ, from July 1998 to August 1999 (further details and results in Hewitt et al. 2005). In the present publication we include further data from this experiment, in particular on the phenology of growth, development and zoospore release of sporophytes.

**The 2000–2001 field collection and tagging of sporophytes**

At least 25 sporophytes with visible sporophylls were collected at the Tinderbox Marine Reserve every month from July 2000 to January 2001. A minimum of five sporophytes of each size class present were collected haphazardly along a snorkelling transect (~ 1 km) on the eastern shore of the reserve during each month.

Twenty sporophytes were marked in the field in July 2000, using numbered tags of underwater paper (Nalge Nunc International, Rochester, NY, USA) attached with 1.5 mm diameter silicone tubing threaded through the holdfast. Sporophytes were selected to represent the *U. pinnatifida* size classes present at the field site at the start of the experiment, i.e. six large sporophytes with apparently mature sporophylls, seven sporophytes with small, developing sporophylls and seven young sporophytes without sporophylls. A further 10 young sporophytes without sporophylls were tagged at each monthly sampling event. Statistical analyses were precluded due to high losses of tagged sporophytes and the difficulty of relocating tagged sporophytes in the field among a dense canopy of *U. pinnatifida* later in the season. Due to these losses, maturation and spore-release periods are only described for 10 sporophytes that were each monitored for at least three continuous months.

**Sporophyte phenology**

Morphological variables were recorded in situ during the 1998–1999 surveys resulting in measurements from 5304 sporophytes. In the 2000–2001 season, variables were recorded in situ from tagged sporophytes and in the laboratory from collected sporophytes (n = 211). The variables measured were total sporophyte length, stipe width (measured immediately below the phyllloid and above the last ‘frill’ of the sporophyll) and presence and dimensions (length and circumference) of reproductive structures (sporophylls). Surface area and dry weight of sporophylls were quantified in 111 of the collected sporophytes. Sporophylls were dissected into flat-lying pieces that were scanned on a flatbed scanner with a standard metric. Surface areas of the sporophyll images were analysed with
REFERENCES

The freeware software package Scion Image Beta 4.0.2 (Scion Corporation, Frederick, MD, USA). The dry weight of sporophylls was determined after drying for 72 h in a fan-forced oven at 60°C.

As reported in Hewitt et al. (2005), stipe width was used as a surrogate measure for total sporophyte length because the latter was frequently unreliable due to distal losses of the phylloid. A strong correlation between the total length of intact sporophytes and stipe width was established ($R^2 = 0.84$, $n = 3634$, total length = 55.2 x stipe width). Daily growth rates were calculated on a per month basis using stipe widths of sporophytes from the removal transects. It was assumed that all plants were removed on a monthly basis and that the measurements represented newly generated sporophytes.

Further information recorded during the 1998–1999 surveys included whether sporophytes in the transects were attached to natural substratum or drifting. The latter category included sporophytes without any substratum, and often without holdfast, as well as sporophytes attached to mobile substrata (such as small rocks or wood).

For analysis of size distributions, five stipe-width size classes were defined: I, ≤ 5 mm; II, 6–10 mm; III, 11–20 mm; IV, 21–30 mm; and V, > 30 mm (roughly equating to total sporophyte lengths of I, ≤ 28 cm; II, 28–55 cm; III, 55–110 cm; IV, 110–165 cm; and V, > 165 cm).

Spore release

Using a cork borer, discs of 8 mm diameter sporophyll tissue were taken from U. pinnatifida sporophytes that had apparent sporophylls at least 8 mm in width. If the sporophyll was large enough, one disc was sampled from each of the top, middle and basal sections of the sporophyll. Discs were always cut from the centre of each ‘frill’. Discs of sporophyll tissue were transferred into 1.5 ml Eppendorf tubes, which were closed and kept overnight in the dark at 4°C. The addition of 1 ml of autoclaved, room temperature (~ 25°C) seawater initiated zoospore release. Subsequently, zoospores were counted after 1 h in a haemocytometer with a counting grid of 25 fields, each measuring 100 x 100 μm. For each sample, zoospore numbers were counted in 10 randomly selected fields.

The estimated number of instantly released zoospores per sporophyte was calculated as the number of zoospores released per area of sporophyll tissue (zoospores cm$^{-2}$ h$^{-1}$) and the size of the sporophyll area per sporophyte. This analysis included only sporophytes where zoospore release was observed.

To estimate instant zoospore release of an U. pinnatifida assemblage (summed over size classes), the larger scale abundance and size distribution data from 1998–1999 were combined with percent maturity and zoospore release data from 2000–2001 for each size class, as follows:

\[
\text{Zoospore release in size class } y = (\text{abundance in size class } y) \times (\text{% maturity in size class } y) \times (\text{average spore release per sporophyte in size class } y).
\]

Statistical analyses

Statistical analyses were performed using the software package Statistica 5.1 (StatSoft, Tulsa, OK, USA). Zoospore release rates in different size classes were analysed with one-factor analysis of variance (ANOVA) separately for each sampling month due to different sample numbers in each sampling month. Data were transformed [log(x + 1)] to meet the assumption of homoscedasticity. The Tukey Honestly Significant Different (HSD) test for unequal sample sizes (Spjotvoll & Stoline test) was used for the post hoc comparisons of means. Relationships between phenological variables and spore release rates were analysed using linear regression.

RESULTS

Abundance, size distribution

For most of the 1998–1999 growth season the average number of attached U. pinnatifida sporophytes per transect (200 m$^2$) was between 70 and 110, with an additional 10–25 drift sporophytes (Fig. 1). At the end of the season in autumn (March 1998), the average numbers per transect were 25 attached and two drift sporophytes. At the peak of recruitment in the following season (August 1999) the average number of attached sporophytes was 516 per transect, and 92 drift sporophytes (Fig. 1). The proportion of drift sporophytes ranged from 13% to 26% of attached sporophyte abundance over the entire sampling period.

The size distribution of attached sporophytes indicated a progression of cohorts through the growing season (Fig. 2). Early in the growth season (July, August, October), high numbers of small sporophytes skewed the size class abundance distribution (Fig. 2a), whereas towards the end of the growth season in late summer (January, February), abundance within sporophyte size classes followed a bell-shaped distribution (Fig. 2a). A similar pattern was apparent in the size distribution of the abundance of drift sporophytes throughout the season (Fig. 2b).

Growth rates (mm width 30 d$^{-1}$) of newly generated sporophytes varied over the growth season with a period of slower growth from May to October and a period of fast growth from November to March (Fig. 3). Maximum growth rates in February were 20 mm stipe width 30 d$^{-1}$ (corresponding to growth rates in total length of 110 cm 30 d$^{-1}$).

Sporophyll presence

Sporophytes in the smallest size class (I) generally had no sporophylls in the early season (July to October). The development of sporophylls in this size class became more prevalent towards the end of the season with 23% sporophyll incidence (63% in drift sporophytes) in January and 100% in February (Fig. 2a, b). However, the overall abundance of size class I sporophytes with sporophylls was very low in the late season, with a maximum of five such sporophytes in the 800 m$^2$ experimental area.

Very few sporophytes in size class II had sporophylls in the early season, but 74–100% of sporophytes in this size class had sporophylls from December to February (100% of drift sporophytes).

Larger sporophytes, in the size classes III and IV, had a high proportion of sporophytes with sporophylls throughout the growing season, except for the recruitment period in July, ranging from 55% to 100% for attached sporophytes and from 50% to 100% in drift sporophytes (Fig. 2a, b). From Decem-
Fig. 1. Average abundance of *U. pinnatifida* sporophytes in 200 m² transects in growth season 1998–1999 and the early season 1999–2000. White bars, attached sporophytes; black bars, drift sporophytes. Error bars represent ±sx (n = 4).

Fig. 2. Average abundance of sporophytes in size classes IV and V to February all sporophytes in the size classes IV and V had a sporophyll.

**Zoospore release**

Measurements of zoospore release were made because the mere presence of a sporophyll does not indicate whether that sporophyll is mature (defined here as actively releasing zoospores).

*Undaria pinnatifida* sporophylls mature first at the base, near the holdfast, and later in the middle and top sections. A meristematic region at the junction of sporophyll and stipe forms new sporophyll tissue throughout the period of maturity. In young sporophylls, only samples from the basal sections of the sporophyll released spores, whereas older sporophylls released most zoospores from the middle section while the basal sections were exhausted and the top sections were still developing.

In November 2000 a large number of sporophytes were collected to establish relationships between sporophyte phenology and rates of spore release. The number of zoospores released per unit sporophyll area increased with increasing sporophyte and sporophyll sizes, indicated by significant linear regressions of sporophyte phenology variables and zoospore release rates (Table 1). Sporophyll dry weight and area were good predictors of zoospore release (R² = 0.58 and 0.54, respectively; Table 1); however, measuring these variables is time consuming and impossible *in situ*. Stipe width was an equally good predictor for zoospore release rates (R² = 0.54, Table 1), as well as being a variable that is easy to measure both *in situ* and after collection.

Spore release rates were analysed in more detail for each of the five size classes. No sporophytes in size class I with sporophylls were sampled in 2000–2001 because abundance of such sporophytes was generally very low (see above). Mature sporophytes in size class II were not found until December, and in January 100% of sporophytes sampled in this size class were mature (Fig. 4). For most of the growth season 2000–2001, zoospore release was limited to the larger size classes III–V, with the percentage of mature sporophytes increasing towards the end of the growth season (Fig. 4).

A similar pattern was seen in zoospore release rates per unit area of sporophyll tissue. In July and August 2000 the number of zoospores released per area of sporophyll tissue was below 30 × 10³ zoospores cm⁻² h⁻¹ for size classes III–V (Fig. 5). From October to December zoospore release was significantly higher in size classes IV and V than in size class III, with averages ranging from 30 × 10³ zoospores cm⁻² h⁻¹ to 60 × 10³ zoospores cm⁻² h⁻¹ (Fig. 5; 1-factor ANOVA for each month; July: F[3,22] = 6.167, August: F[3,31] = 7.956, September: F[3,30] = 13.150, October: F[3,29] = 19.078, November: F[3,48] = 20.061, December: F[3,20] = 35.566; in all months: P < 0.01). Sporophytes in size class II released, on average 1 × 10³ zoospores cm⁻². In January, size classes II–V released similar numbers of zoospores, between 26 × 10³ zoospores cm⁻² h⁻¹ and 46 × 10³ zoospores cm⁻² h⁻¹ (1-factor ANOVA, F[3,24] = 0.405, P = 0.75).

Using the minimum values of the phenological variables obtained for mature sporophytes during the growth season 2000–2001, the smallest mature sporophyte would have a hypothetical stipe width of 6 mm (i.e. size class II), equivalent to about 33.1 cm in total length, with a sporophyll circumference of 7.6 cm and a sporophyll dry weight of 0.2 g.

**Zoospore release of individual sporophytes and of an *U. pinnatifida* assemblage**

The maximum zoospore number released per individual sporophyte was 4.3 × 10⁸ zoospores, the minimum 1 × 10⁵ zoospores sporophyte⁻¹ h⁻¹, the median 1.3 × 10⁷ zoospores sporophyte⁻¹ h⁻¹ and the mean 5.2 × 10⁶ zoospores sporophyte⁻¹ h⁻¹ (standard error sx = 1 × 10⁷ zoospores, n = 82). Split into size classes, the number of zoospores released per sporophyte increased with increasing size of the sporophyte (Fig. 6). Spos-
Fig. 2. Average abundance of *U. pinnatifida* sporophytes in four size classes (based on stipe width: I, \( \leq 0.5 \) cm; II, 0.6–1.0 cm; III, 1.1–2.0 cm; IV, 2.1–3.0 cm; and V, > 3.0 cm) in different sampling months. (a) Attached sporophytes; (b) drift sporophytes. White bars, vegetative sporophytes; grey bars, sporophytes with sporophyll. Error bars represent \( s_x (n = 4) \).

The estimated average abundance of *U. pinnatifida* sporophytes in size class I generally had no sporophyll and were hence not included in further analysis.

The estimated instant zoospore release (i.e. per hour) of an *U. pinnatifida* assemblage showed that most of the zoospore output was from the two largest size classes (IV and V) during the later months of the *U. pinnatifida* growth season of spring to late summer, i.e. November to January (Fig. 7), whereas the smaller size classes contributed much less.

**Tagged sporophytes**

Four mature sporophytes, tagged in July 2000, released zoospores for about three months to October, and by December had senesced and disintegrated. Three immature sporophytes tagged in July formed a mature sporophyll after 40 days, in September, and ceased zoospore release in December, i.e. after about three months. One immature sporophyte tagged in September formed a mature sporophyll after 30 days, in October, and ceased zoospore release in January, after about three months. Two immature sporophytes tagged in December formed only small sporophylls by January, which did not release zoospores.

During a survey on 23 February 2001, almost all sporophytes at the Tinderbox sampling site were senescent, i.e. the phylloid had eroded and only holdfasts, stipes and disintegrating sporophylls were present. Two sporophytes of about 25 cm length without sporophylls were found. Five sporophylls that appeared relatively intact were collected; however, these did not release zoospores.

**DISCUSSION**

The prediction or hind-casting of species characteristics that make a successful invader has been a focus of research in biological invasions (e.g. Lodge 1993; Carlton 1996; Pyšek 1997; Kolar & Lodge 2001; Hayes & Sliwa 2003), although such research rarely captures a generalized concept of what characteristics actually make an invader succeed (Lodge 1993; Pyšek 1997). High fecundity (an r-strategy life trait) is considered to be an important characteristic of successful invasive macroalgal species (Ribera & Boudouresque 1995; Chapman 1999), although the concept that successful invasive species are limited to r-strategists has largely been rejected based on empirical evidence (Lawton & Brown 1986; Lodge 1993).

Zoospore production (fecundity) and sporophyte recruitment in laminarian kelps are very high, yet establishment and survival of recruits to reach visible size is exceedingly low [a chance of less than one in half a million; Chapman (1984, 1986)]. In the present study the maximum spore release of *U. pinnatifida* was \( 62 \times 10^3 \) zoospores cm\(^{-2}\) sporophyll tissue h\(^{-1}\). Spore release rates of other kelp species are similar or higher, the latter especially in the larger-sized species (Table 2).

Parke (1948) estimated a maximum zoospore release in *Laminaria saccharina* of \( 64 \times 10^6 \) zoospores cm\(^{-2}\) of sorus from sporangia counts in sorus sections. Kain (1975) estimated similar zoospore numbers in the longer-lived *L. hyperborea* (Gunnerus) Foslie, \( 23 \times 10^6 \) zoospores cm\(^{-2}\) sorus. These values are theoretical maxima for spore release over the whole sporing season. Direct measurements of zoospore release,
such as in the present study, generally cover only short sampling periods, and figures are likely to be much lower because sporangia mature over a period of time. It is impossible to estimate zoospore release rates over the course of a season with these ‘instant’ zoospore release data. Parke (1948) observed successive development of sporangia in the same area of reproductive tissue in *L. saccharina*; however, there is no published evidence for this in other kelp species. Individual sporophytes of *L. hyperborea* release zoospores for 36–56 days (Kain 1975). In comparison, tagged *U. pinnatifida* individuals in the present study released zoospores for about three months, from a sporophyll maturing from the base to the top.

Zoospore release of whole sporophylls was estimated in this study as between $0.1 \times 10^8$ zoospores h$^{-1}$ and $1.4 \times 10^8$ zoospores h$^{-1}$. Zoospore release from whole *U. pinnatifida* sporophylls in an introduced New Zealand population was higher, ranging from $1 \times 10^8$ zoospores to $7 \times 10^8$ zoospores [release time unknown; Brown (1999)]. However, very high values were only measured in two months, August and September, whereas for the remainder of the study zoospore release per sporophyll was below $2 \times 10^8$ zoospores (Brown 1999).

We did not assess whether zoospores were fully functional, i.e. what proportion were able to germinate. Germination rates of zoospores released from introduced *U. pinnatifida* in Port Phillip Bay, Australia, were 93% at temperatures from 10°C to 25°C (Bité 2001).

Several laminarian kelp species have been accidentally or intentionally introduced, including *Alaria esculenta* (Linnaeus) Greville, *L. japonica* J.E. Areschoug, *L. ochotensis* Miyabe, *Macrocystis pyrifera* (Linnaeus) C. Agardh and *U. pinnatifida* (Wallentinus 1999, 2002). At present however, only two species are known to have successfully established out-

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**Fig. 3.** Average monthly growth rate (mm stipe width) of newly produced sporophytes in removal transects from 1998 to 1999. Error bars represent $s_x$. Number of replicate sporophytes indicated above bars. ns, not sampled.

**Table 1.** Linear regression of *U. pinnatifida* sporophyte morphological variables and zoospores release rates. Samples from 27 November 2000 ($n = 41$). $R^2 =$ regression coefficient. Slopes of the regression were significantly different from 0 ($P$ values $< 0.001$). In equations $y$ represents the number of zoospores released (cm$^{-2}$ h$^{-1}$) and $x$ the respective independent variable.

| Independent variable       | $R^2$ | Equation          |
|----------------------------|-------|-------------------|
| Sporophyll DW (g)          | 0.58  | $y = 3465x + 6810$|
| Stipe width (mm)           | 0.54  | $y = 3687x - 36,688$|
| Sporophyll area (cm$^2$)   | 0.54  | $y = 128x + 990$  |
| Sporophyll circumference (cm) | 0.54 | $y = 3048x - 22,869$|
| Sporophyll length (cm)     | 0.44  | $y = 3958x - 11,255$|
| Total sporophyte length (cm)| 0.39 | $y = 768x - 40,876$|

**Fig. 4.** Proportion of mature (i.e. releasing zoospores) *U. pinnatifida* sporophytes in four size classes (based on stipe width; see Fig. 2) in growth season 2000–2001. Data are the average proportions of at least five sporophytes in each size class.
Fig. 5. Zoospores released per unit area of *U. pinnatifida* sporophyll tissue in four size classes (based on stipe width; see Fig. 2). Error bars represent s_x (n > 5).

Fig. 6. Estimated instant zoospore release of individual *U. pinnatifida* sporophytes in four size classes (based on stipe width; see Fig. 2). Error bars represent s_x (size class II: n = 7; size class III: n = 37; size class IV: n = 27; size class V: n = 12).

side of their native region: *L. japonica* and *U. pinnatifida*. *Laminaria japonica* was accidentally introduced to northern China in 1927 by shipping (Tseng 1981). Both *L. japonica* and *U. pinnatifida* were introduced to the Thau Lagoon, French Mediterranean coast, supposedly with imported Japanese oyster (*Crassostrea gigas* Thunberg) seedstock in the period from 1971 to 1975 (Grizel & Heral 1991). In contrast to *U. pinnatifida*, *L. japonica* appears to be less invasive and has not spread to regions beyond initial incursion sites. Resurveys of the introduction site in the Thau Lagoon in the late 1990s did not detect *L. japonica* (Verlaque 2001); however, no winter surveys were carried out.

Boudouresque & Verlaque (2002) do not consider *U. pinnatifida* to be invasive or a pest species in the Mediterranean Sea. A pest species is generally defined as a species introduction with a negative economic effect (after Williamson & Fitter 1996), whereas an invasive species is an introduced species that spreads from the point of introduction and becomes abundant (after Kolar & Lodge 2001). *Undaria pinnatifida* must be considered an invasive species in other regions, indicated by the continuously expanding introduced range of this species, especially along the European Atlantic coast (Wallentinus 1999), the west coast of USA (Silva et al. 2002) and in several regions of the southern hemisphere (Casas & Piriz 1996; Sinner et al. 2000; Seacare 2003).

High production of laminarian zoospores would facilitate transport by various vectors including uptake in ballast water, the settlement of zoospores or gametophytes on ships’ hulls and aquaculture stock (e.g. oysters) and equipment. This may result from either high zoospore-release rates per se or by high-density source populations at the uptake site. Our results show that zoospore-release rates in *U. pinnatifida* are similar to *L. japonica* and in the midrange of the scale reported for other laminarian species. Hence, it is more likely that dense source populations cause high zoospore availability of *U. pinnatifida*. Maximum zoospore concentration within a dense *L. hyperborea* kelp forest was c. 3000 zoospores l^-1_ seawater during the January peak of zoospore release (Fredriksen et al. 1995). High-density source populations of *U. pinnatifida* and *L. japonica* occur along the Asian North Pacific coasts. Introduced *L. japonica* is now widely cultivated in China, North Korea and Japan, with China producing more than 90% of the annual world production of more than 4 million tonnes (FAO...
2003). The annual world production of farmed *Undaria pinnatifida* is about 300,000 tonnes, mainly produced in South Korea (FAO 2003). Thus in these areas of intensive aquaculture, zoospore availability, and hence the probability of uptake by vectors, is expected to be high for both species. The reasons for the dissimilar introduced distributions of the two kelp species are likely to be dependent on later stages of the invasion process, i.e. journey survival and establishment potential. In New Zealand, *U. pinnatifida* is found in high densities on commercial wharf structures, immediately adjacent to areas of ballast water uptake and release and in close proximity to ships’ hulls (Hay & Luckens 1987; Hay 1990).

*Undaria pinnatifida* sporophytes become mature (i.e. actively releasing zoospores) at a relatively small size. Sporophytes of more than 40 cm in total length and with sporophylls greater than 1.3 g dry weight release zoospores in introduced *U. pinnatifida* in Port Phillip Bay, Australia (Campbell & Burridge 1998). In Tinderbox, Tasmania (present study), we found smaller plants releasing zoospores (size class II, equivalent to total lengths of 28–55 cm), especially towards the end of the season. The smallest mature sporophyll measured only 7 cm in diameter with a dry weight of only 0.3 g. However, these very small mature sporophytes were only present in very small numbers, and the number of zoospores released by them was very low. During the two peaks of growth rate identified (Fig. 3), early (May–June) and late (November–March) in the growth season, the majority of newly generated plants are likely to attain maturity within 30 days.

Using this information, pest control efforts involving the manual removal of *U. pinnatifida* could be rationalized to con-

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**Table 2. Zoospore release rates of laminarian kelps.**

| Species                          | Zoospores released \( \times 10^3 \) cm\(^{-2}\) h\(^{-1}\) | Reference                          |
|---------------------------------|-----------------------------------------------------------|-----------------------------------|
| *Ecklonia maxima* (Osbeck) Papenfuss\(^1\) | 2.0                                                       | Joska & Bolton (1987)             |
| *Laminaria japonica* J.E. Areschoug\(^2\) | 4.7                                                       | Fukuhara *et al.* (2002)          |
| *Ecklonia cava* Kjellman\(^3\) | 3–30                                                     | Suto (1948)                        |
| *Eisenia bicyclis* (Kjellman) Setchell\(^1\) | 3–30                                                     | Suto (1948)                        |
| *Undaria pinnatifida*\(^2\) | 30–62                                                    | this article                      |
| *Undaria pinnatifida*\(^1\) | 30–300                                                   | Suto (1948)                        |
| *Macrocystis pyrifera* (Linnaeus) C. Agardh\(^3\) | 60–300                                                   | Anderson & North (1967)           |
| *Laminaria saccharina* (Linnaeus) Lamouroux\(^2, 3\) | 100–800                                                  | Lee & Brinkhuis (1986)            |
| *Nereocystis luetkeana* (Mertens) Postels & Ruprecht | 13,800                                                   | Amsler & Neushul (1989)           |

\(^1\) Data recalculated from compilation of zoospore release rates per minute obtained by a variety of methods in Amsler & Neushul (1989).

\(^2\) Zoospore release rates measured using sorus discs.

\(^3\) Zoospore release time unknown.
centrate on the removal of the three largest size classes of sporophytes (> 55 cm total length) because they produce the greatest proportion of zoospores in an introduced assemblage. Manual control, involving removal of all visible sporophytes, requires a significant effort to reduce numbers of *U. pinnatifida* sporophytes, i.e. 5 diver days each month for an area of 800 m² (Hewitt et al. 2005). Removal of only the largest sporophytes could lead to significant cost savings due to reduced collection effort. It should be noted however, that the effort should not be equally spaced at monthly (30 days) intervals throughout the growing season but should be reduced to shorter periods (1–2 weeks) between October and February.

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