

# Reproductive synchrony in a habitat-forming kelp and its relationship with environmental conditions

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**Abstract** Key biological processes such as the timing and synchrony of reproduction, are sensitive to fluctuations in the environment, as well as alterations in the physiology and behaviour of individuals and the ecology of populations. The main aim of this study was to identify patterns in reproductive timing and relationships with prevailing environmental conditions, for the major habitat-forming alga in temperate Australia, *Ecklonia radiata* (C. Agardh) J. Agardh. We observed strong synchronous patterns of zoospore production across spatial scales from hundreds of metres to tens of kilometres, with populations of *E. radiata* reproducing from mid-summer to the end of autumn. High zoospore densities were positively related to sea temperature and *E. radiata* released zoospores in temperatures well above previously documented thermal tolerance limits for other Laminariales. Reproductive timing was also negatively related to seasonal increase in wave exposure. We conclude that *E. radiata* undergoes synchronous reproduction which can be linked to its annual growth cycle and

natural environmental fluctuations, to promote growth and survival of recruits.

## Introduction

Reproductive synchrony is an important evolutionary adaptation that is widely documented in both marine and terrestrial organisms (Ims 1990). Simultaneous reproduction within a population allows for the release of high densities of gametes or propagules, which can maximise the probability of fertilisation, juvenile survival and the subsequent recruitment into adult assemblages (Isagi et al. 1997; Chen and Hsu 2011). Reproductive synchrony is generally closely linked to the timing of optimal environmental conditions, and in many cases, reproduction is driven and initiated by changes in the environment (Ims 1990). For example, to maximise fertilisation success, coral populations spanning 10° of latitude on the Great Barrier Reef all spawn in the same month each year, presumably induced by rapid changes in sea temperature or increases in solar radiation (Baird et al. 2009). Shifts in important parameters such as temperature may, therefore, interfere with, or disrupt, reproductive cycles. For example, human-induced changes in climate have been shown to alter the phenology of life history processes such as flowering in plant communities, disrupting synchrony and reducing the chances of reproductive success (Yang and Rudolf 2010). Because reproduction is a key biological process that is sensitive to environmental change, understanding temporal patterns in reproduction provides a powerful way to detect future changes in populations (Walther et al. 2002; Yang and Rudolf 2010).

The timing of reproduction in algae can be influenced by prevailing environmental conditions (Lüning 1990; Schiel

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and Foster 2006), specifically, temperature (Thornber et al. 2004), day length (photoperiod), light intensity (Buchholz and Lüning 1999), and hydrodynamic conditions (Serrao et al. 1996). Temperature is considered an important controlling factor for kelp reproduction; for example, *Undaria pinnatifida* in California released zoospores in two distinct pulses which coincided with a 4 °C drop in water temperature (Thornber et al. 2004). Some marine algal communities, such as those on coral reefs in the Caribbean, exhibit simultaneous mass release of gametes when light conditions are optimal (Clifton 1997). For large habitat-forming algae, such as kelp and furoids, gamete release often coincides with changes in water motion, resulting from tidal patterns and wave action (Reed 1987; Amsler and Neushul 1989). In Chile, *Macrocystis pyrifera* collected from wave-exposed locations were fertile all year round, whereas the reproduction of plants situated in protected locations was limited to summer and autumn (Buschmann et al. 2004). The effect of water motion may be species specific, since *Nereocystis luetkeana* in North America released zoospores in the early morning, during maximum tidal movement, while wave action did not appear to play a role (Amsler and Neushul 1989).

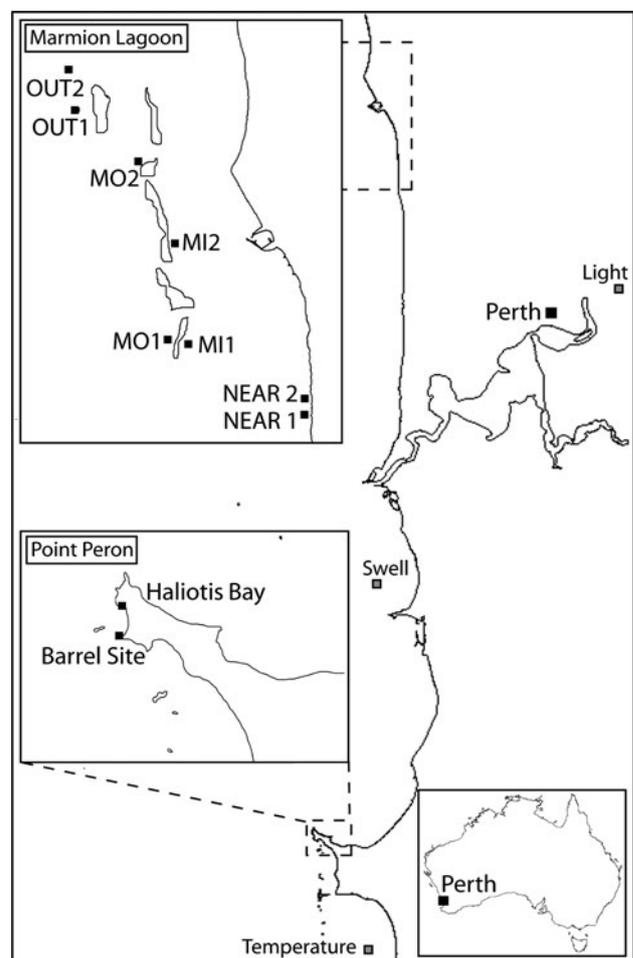
Nutrient concentrations play a major role in controlling growth and energy allocation to reproduction, and so resultant variability in kelp biomass, vegetative growth and sori/sporophyll production can be linked to kelp fertility and fecundity (Reed 1987). Reproduction can also be stimulated and maintained by high nutrient availability (Amsler and Neushul 1990). Since nutrient concentrations stimulate vegetative growth, it is important to understand the link between biomass, and also sori production, and fecundity of kelp. Reed (1987) found that the biomass of *M. pyrifera* in California greatly influenced zoospore production and that a removal of fronds resulted in a marked decline in sporophyll production. Since the relationship between fertility and reproductive tissue is strong, sori area or sporophyll presence is commonly used as a proxy measure for kelp fertility (Reed 1987; Buschmann et al. 2004).

The main habitat-forming macroalga in temperate Australia is the kelp *E. radiata*. These Australian kelp forests support diverse and unique algal, fish and invertebrate communities (Fletcher 1987; Wernberg et al. 2003b; Goodsell et al. 2004; Irving et al. 2004; Tuya et al. 2008) and play an important ecological role in most shallow, temperate marine ecosystems and food webs (Steinberg and Kendrick 1999; Wernberg et al. 2006; Vanderklift et al. 2009). Despite its ecological significance, very little is known about the reproductive ecology of this species, including when it reproduces, the extent to which populations exhibit reproductive synchrony and what environmental conditions might explain patterns of reproduction. In this study, we aimed to identify patterns of reproductive

timing for *E. radiata* across spatial scales from hundreds of metres to tens of kilometres. We also aimed to test the degree to which reproductive timing could be explained by environmental conditions (sea temperature, wave action, day length and irradiation) and intrinsic biological variables (thallus size and sorus area).

## Methods

In order to identify the patterns of reproductive synchrony of *E. radiata*, zoospore release densities were quantified over a range of spatial and temporal scales: locally on a weekly basis, and regionally every second month for a period of 2 years. The localised sampling was carried out at two sites (Barrel Site and Haliotis Bay North) at Point Peron, Western Australia (Fig. 1), between 2 and 4 m



**Fig. 1** Locations for thallus collection and environmental data. *Upper inset* Locations in Marmion Lagoon positioned over the reef-line used for bimonthly sampling. *Lower inset* Barrel Site and Haliotis Bay North at Point Peron, Rockingham, used for weekly collections. Also shown are locations of data loggers for sea temperature, swell height and solar radiation

depth. These two sites were sampled approximately every week between September 2009 and May 2011 (20 months). Regional sampling was carried out at eight subtidal reefs, ranging in depth from 8 to 12 m, within Marmion Lagoon (Fig. 1). These reefs were sampled every second month between November 2009 and April 2011 (18 months). Reefs were sampled in a nested design, with pairs of reefs nested within four reef-lines of increasing distances from shore: near-shore (<200 m offshore), mid-inner (1–3 km), mid-outer (3–5 km), and outer (5–7 km). These reef-lines were selected in this design as they represent a natural gradient in many environmental conditions (e.g. wave exposure, nutrients; Smale et al. 2011), and have been used for similar studies in the past where *E. radiata* productivity has been compared to environmental patterns (Vanderklift et al. 2009). All reefs supported dense beds (4–14 individuals  $m^{-2}$ ) growing on limestone substratum (Wernberg 2009).

During each sampling period, four haphazardly selected thalli were harvested from each reef and returned to the laboratory for processing. Thalli were collected by cutting the stipe just above the holdfast. Thalli were stored in a damp, labelled calico bag, which was wrapped in plastic and kept on ice until processing (<6 h). Upon return to the laboratory, thalli were weighed (fresh weight) and the lateral branches were cut away from the central lamina (*E. radiata* is characterised by one central lamina lined on either side by lateral branches; Mann and Kirkman 1981) for ease of sample abscission and sori identification. The central lamina was towel-dried and then allowed to desiccate at room temperature for 1 h (to induce and promote optimum zoospore release; Mohring et al. unpublished review of sporulation methodologies). During this time, basic size characteristics were measured following Wernberg et al. (2003a). The length of the central lamina was measured from its distal tip to the point where the stipe meets the central lamina and the first diminutive laterals were visible. The width of the central lamina was measured halfway along its length using vernier callipers. *E. radiata* does not produce distinct sporophylls for zoospore release. Instead, the central lamina has areas covered with sori, which under careful examination stand out as slightly raised, discoloured patches. A transparent sheet with a 1-cm grid was laid over the lamina and the tissue type (sori or not) determined under each point. This was converted to a percentage of the central lamina, which was covered with sori.

From each individual thallus (four from each site), ten 27-mm-diameter discs of tissue (total surface area 11,451.1  $mm^2$ ) were punched from the central lamina with a PVC corer, starting at the distal end of the plant. Following the desiccation period, all ten discs of tissue from each individual were placed in a single cup containing

50 mL of seawater and gently stirred over a 20-min period to encourage zoospore release. After 20 min, 10 mL of zoospore solution was added to a vial with 0.1 mL of 70 % ethanol (final concentration 0.07 mL ethanol/9.93 mL SW) and vigorously shaken to ensure adequate mixing. One millilitre of the zoospore/ethanol solution was placed onto a Neubauer counting chamber, and the number of zoospores in two 1-mm (0.1  $\mu L$ ) grids was counted (Reed 1990). This was repeated three times (total of six grids per sample), and the results averaged and converted to number of zoospores released per area of lamina sampled (total area of discs of tissue). Reproductively active thalli were defined as those where zoospore densities (taken from counts of the zoospores released from the total area of 11,451.1  $mm^2$  of lamina tissue) exceeded 15 zoospores  $mm^{-2}$  tissue.

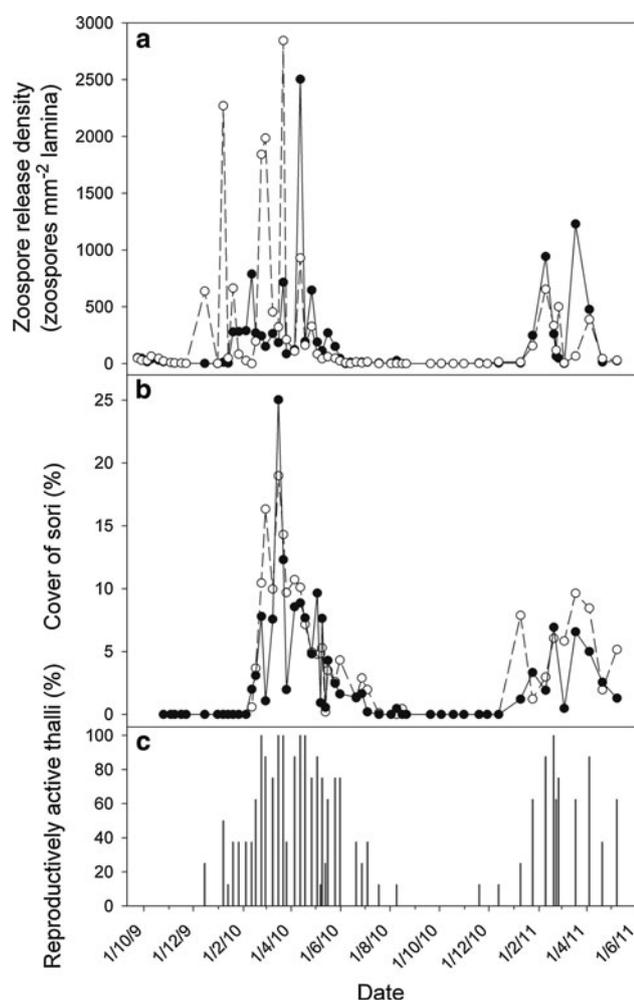
Environmental data were collated over the 20 months of sampling to be regressed against the biological characteristics of *E. radiata* reproduction collected during the weekly sampling. These data included sea temperature ( $^{\circ}C$ ), significant wave height (m), solar radiation ( $MJ m^{-2}$ ) and day length (photoperiod; hours). Sea temperature was obtained from the Western Australian Department of Fisheries and was measured daily using temperature loggers deployed in Warnbro Sound near Rockingham (Fig. 1). Wave height was measured using a digital data recording wave buoy every 30 min at Owen Anchorage (Fig. 1) by Western Australian Department of Transport. Day length data were obtained from Geoscience Australia (<http://www.ga.gov.au>). Solar radiation was measured daily at Perth Airport (Fig. 1) by the Australian Bureau of Meteorology (<http://www.bom.gov.au>). While solar radiation data were collected 30 km from the collection sites, these have previously successfully been used as a proxy for subtidal gross irradiance in the study area (Wernberg and Goldberg 2008). All data were averaged for each week and across sites, and averages were used for analysis.

Zoospore release densities were regressed against the per cent cover of sori and proportion of reproductively active thalli using stepwise multiple regression. Stepwise regression was also used to relate environmental data to zoospore densities because environmental variables tend to co-vary in marine systems and the effects of an individual factor are often difficult to tease apart from overall relationships (Wernberg and Goldberg 2008). Thallus size can be a good predictor of kelp fecundity (Reed 1987), so stepwise regressions were used to relate biomass, lamina length and width, to zoospore release densities. The bimonthly data were analysed using a partially hierarchical analysis of variance (ANOVA), with the factors sample time (random), reef-line (fixed) and reefs (random) nested within reef-line. Student–Newman–Keuls (SNK) tests were carried to compare treatment levels within all significant factors. Prior to analysis, homogeneity of variances were

tested using Cochran's  $C$  test; however, no transformation was required. All analyses were carried out using GMAV and Minitab.

## Results

Distinct temporal patterns in zoospore release densities were recorded for *E. radiata* at both Barrel Site and Haliotis Bay (Fig. 2a). In 2009, the first reproductively active thalli (>15 zoospores  $\text{mm}^{-2}$  lamina tissue) appeared in summer on 15 December. The period of high zoospore release densities lasted for 5 months, with the final sample of reproductively active thalli recorded in autumn on 31 May 2010. The highest zoospore density during the



**Fig. 2** **a** Mean number of zoospores per millimetre of lamina tissue in *Ecklonia radiata* thalli each week for more than one year (September 2009–May 2011). **b** Percentage of the central lamina exhibiting sori every week over 20 months. **c** Proportion of thalli collected ( $n = 8$ ) which had more than 15 zoospores  $\text{mm}^{-2}$  tissue (reproductively active thalli). Two sites were Barrel Site (white hollow circles) and Haliotis Bay North (black solid circles)

2009/10 season was recorded at Barrel Site in March 2010 with 2,845 zoospores  $\text{mm}^{-2}$  tissue, and in April 2010, zoospore densities at Haliotis Bay reached 2,503 zoospores  $\text{mm}^{-2}$  tissue. The reproductive period varied a little between years, with greater zoospore release occurring slightly later and for a shorter period in 2011 compared with 2010. Zoospores and sori appeared at almost the same time in both years (Fig. 2a, b). However, in 2010, zoospores were found 4 weeks before the first sori appeared, and sori were observed 6 weeks after the last zoospores. Similarly, in 2011, only small traces of sori were recorded prior to zoospore release. There was a weak but significant positive relationship between zoospore densities and the cover of sori tissue for both sites (Barrel Site  $p < 0.001$ ,  $r^2 = 0.103$ ; Haliotis Bay  $p < 0.001$ ,  $r^2 = 0.132$ ), and between zoospore densities and the proportion of reproductively active thalli (Barrel Site  $p < 0.001$ ,  $r^2 = 0.130$ ; Haliotis Bay  $p < 0.001$ ,  $r^2 = 0.178$ ).

Thallus size was found to be a significant but weak predictor of *E. radiata* fecundity, although different measures of size were significant at different sites (Table 1). The stepwise regression showed that thallus weight ( $p < 0.001$ ,  $r^2 = 0.040$ ) and length ( $p < 0.001$ ,  $r^2 = 0.033$ ) were significant predictors of zoospore density at Barrel Site and lamina length ( $p < 0.05$ ,  $r^2 = 0.049$ ) at Haliotis Bay. Thallus weight ( $p < 0.05$ ,  $r^2 = 0.039$ ) and length ( $p < 0.05$ ,  $r^2 = 0.066$ ) were also weak predictors of the cover of sori tissue, but there were no relationships between morphological variables and the proportion of reproductively active thalli. Thallus width could not be significantly related to any of the reproductive measures.

Regressing environmental data against zoospore release densities, cover of sori and proportion of reproductively active thalli revealed several significant relationships (Table 1). A significant positive relationship existed between sea temperature and zoospore release density (Barrel site  $p < 0.05$ ,  $r^2 = 0.353$ ; Haliotis Bay  $p < 0.05$ ,  $r^2 = 0.265$ ; Table 1; Fig. 3a, b). Maximum zoospore densities were found at 22.5 and 21.2 °C at Barrel Site and Haliotis Bay, respectively. Sea temperature was also positively related to the per cent cover of sori ( $p < 0.05$ ,  $r^2 = 0.428$ ; Table 1; Fig. 3c) and proportion of reproductively active thalli ( $p < 0.001$ ,  $r^2 = 0.517$ ; Fig. 3d). In contrast, swell height was negatively related to the proportion of reproductively active thalli ( $p < 0.05$ ,  $r^2 = -0.284$ ; Table 1; Fig. 3e) with zoospores reaching maximum density when swell height was 1.98 m. There were no significant relationships between day length or light intensity and zoospore density (Table 1).

The broader spatial sampling showed two distinct periods of zoospore release over the 20 months of sampling (Fig. 4), similar to those recorded in the local study at Barrel Site and Haliotis Bay. While higher zoospore

**Table 1** Results of the regressions of zoospore release densities, the proportion of reproductively active thalli, and per cent cover of sori against thalli weight, length, width and various environmental conditions

	Barrel site		Haliotis Bay		Reproductively active thalli		Cover of sori	
	$r^2$	$p$ Value	$r^2$	$p$ Value	$r^2$	$p$ Value	$r^2$	$p$ Value
Thalli weight	0.040	<0.001	0.013	0.086	0.006	0.556	0.039	0.002
Thalli length	0.033	<0.001	0.049	0.001	0.016	0.326	0.066	0.021
Thalli width	0.060	0.113	0.004	0.340	0.001	0.822	0.009	0.271
Day length	0.184	0.152	-0.013	0.921	-0.184	0.153	-0.140	0.277
Light intensity	0.198	0.122	0.038	0.769	-0.113	0.382	-0.041	0.753
Wave height	-0.139	0.282	-0.165	0.200	-0.284	0.026	-0.218	0.089
Sea temperature	0.353	0.005	0.265	0.038	0.517	<0.001	0.428	0.001

Results presented are  $p$  values and regression coefficients

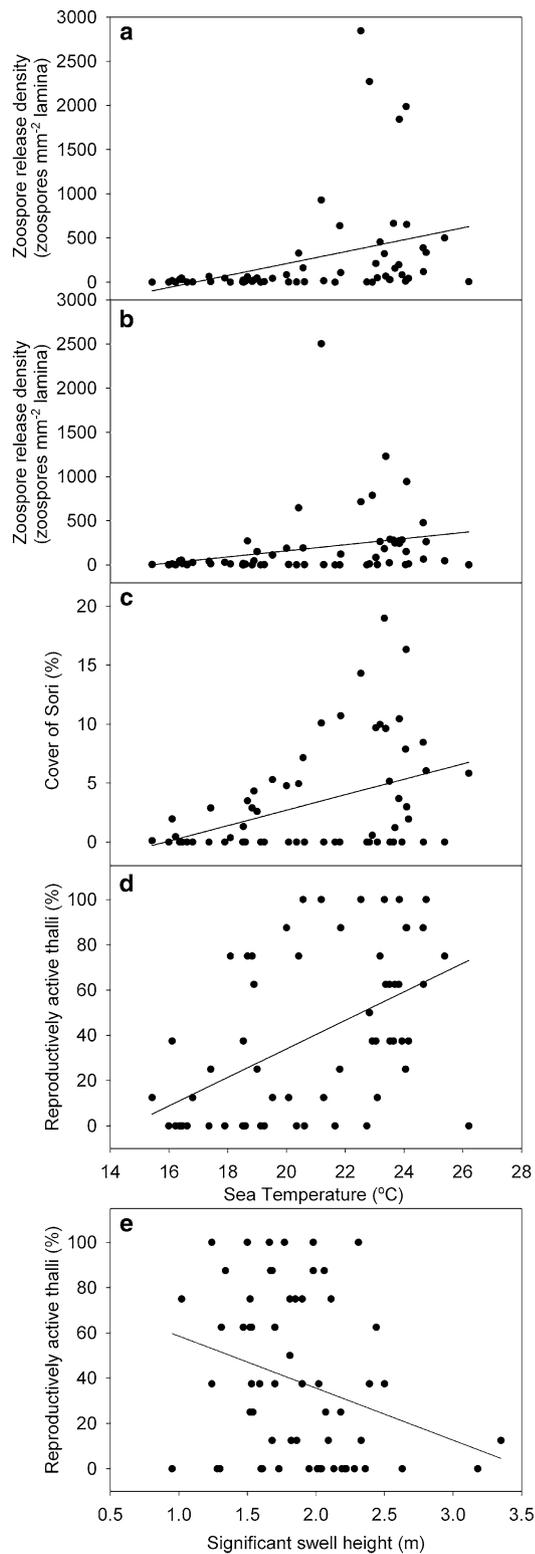
densities were recorded at both Barrel Site and Haliotis Bay compared with all the locations across the shelf in Marmion Lagoon, the timing of reproduction was similar. There was a distinct season of fecundity recorded at all reef locations each year, and similar (Table 2) densities of zoospores were recorded at all the reefs over the entire sample period. There was, however, a significant difference in zoospore release densities among sample periods (Table 2) and a significant interaction between time and reef-line indicating that the timing of the zoospore season varied with distance from shore. Higher zoospore densities were recorded earliest at the near-shore reefs; zoospores were not recorded on thalli at the mid-reef locations until the following sampling period. *E. radiata* on mid-reef locations (Inner and Outer) produced zoospores at the same time during the first season; however, in 2011, the onset of zoospore production was delayed by 2 months for the outer mid-reef locations. In both years, kelps at the outer locations were last to present zoospores.

## Discussion

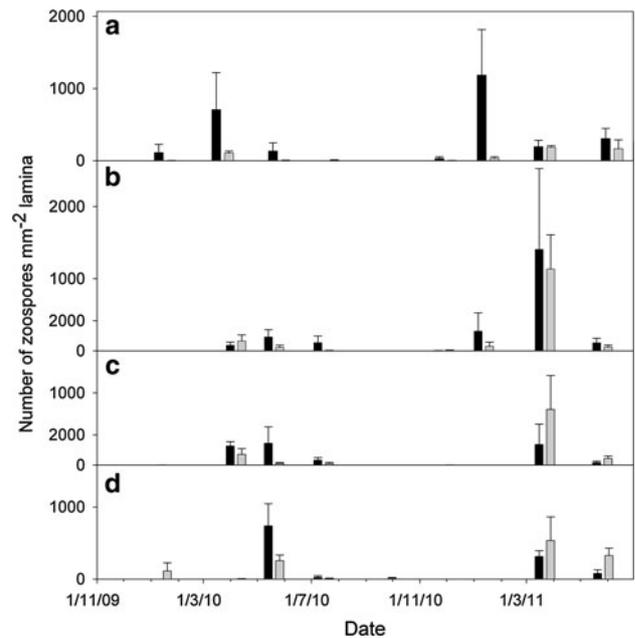
In this study, strong seasonal patterns in the timing of reproduction and zoospore production were observed for the kelp *E. radiata*. Thalli were reproductive from mid-summer through to the end of autumn, and this pattern was consistent across spatial scales from hundreds of metres to tens of kilometres. The similarity in reproductive timing across these spatial scales suggests that *E. radiata* exhibits some level of reproductive synchrony or concurrent zoospore production. High reproductive output was found to be positively related to thallus size and water temperature, and negatively related to wave height, suggesting that seasonal variation in these variables could drive the onset of reproduction in this species.

Of the environmental variables examined, only temperature and swell height were significantly related to

reproduction (zoospore release densities and sorus area). Zoospore densities were highest when water temperatures were between 21 and 23 °C. This finding contrasts with previous studies of thermal tolerances of kelp (Laminariales) which show that most kelp are fertile (Thorner et al. 2004) and release zoospores (Fredersdorf et al. 2009) at much cooler temperatures (between 2 and 20 °C, optimum <15 °C). It is, therefore, clear that *E. radiata* is reproducing and releasing zoospores when water temperatures are similar to, or in excess of, the thermal maxima for gametophyte survival in other kelp (Lee and Brinkuis 1988; Dieck 1993). For example, Bolton and Lüning (1982) tested the thermal tolerances of gametophytes from five species of *Laminaria* and found highest survival of gametophytes between 10 and 15 °C and upper tolerance levels to range from 18 to 23 °C. While we only studied patterns in zoospore release densities, it is interesting to note that recruits from most other genera within Laminariales would be unable to survive if released into the same conditions as *E. radiata* zoospores in Western Australia. This supports previous suggestions that *E. radiata* is one of the most thermo-tolerant kelps (Dieck 1993; Bolton and Anderson 1994). The proportion of reproductively active thalli was negatively related to swell height. Increased wave action resulted in fewer individuals presenting zoospores, whereas when swells were low, more thalli released zoospores. Other studies have found that increased wave action in autumn and winter resulted in zoospores being dislodged from the plant and released (Amsler and Neushul 1989), thus facilitating dispersal (Gaylord et al. 2002). Reed et al. (1988) found that dispersal in Laminariales was limited to a few metres from the adult plant unless assisted by water motion. These authors found that long-distance dispersal of two species of Laminariales zoospores, and successful colonisation of distant habitat patches, was only achieved after a major storm event. It is, therefore, reasonable to suggest that similar mechanisms operate in Western Australian kelp beds, where high-density zoospore release occurred



**Fig. 3** Significant regressions of reproduction against environmental conditions. Sea temperature against **a** zoospore densities at Barrel Site, **b** zoospore densities at Haliotis Bay, **c** cover of sorus tissue, **d** proportion of reproductively active thalli and **e** swell height against proportion of reproductively active thalli



**Fig. 4** Mean number of zoospores per millimetre of lamina every second month from November 2009 to January 2010 (mean  $\pm$  SE). In each plot; **a** nearshore (Near 1–black, Near 2–grey), **b** mid-inner (MI 1–black, MI 2–grey), **c** mid-outer (MO 1–black, MO 2–grey), **d** outer (OUT 1–black, OUT 2–grey)

**Table 2** Analysis of variance testing the effects of sampling time (random), reef-line (fixed) and reefs (random) nested within each reef-line on zoospore release densities from kelps in Marmion Lagoon

Source of variation	df	MS	F	p Value
Sampling time	9	95.65	8.34	<0.01
Reef-line	3	4.22	0.74	0.58
Reef (reef-line)	4	5.67	1.43	0.24
Sampling time x reef-line	27	11.48	2.90	<0.01
Sampling time x reef (reef-line)	36	3.95	1.34	0.10
Residual	240	2.94		

immediately before and during increased wave conditions, which may aid dispersal and remote colonisation.

Fecundity and the timing of reproduction have been linked to thallus biomass in other kelp. Reed (1987) found that during the period of high nutrient concentrations, thalli were able to grow large and apportion energy for gamete production. Once winter storms commenced, thalli were eroded and zoospores were abraded from the laterals, resulting in an overall reduction in plant biomass. This mechanism appears to also apply for *E. radiata* reproduction, since there was a weak relationship between thallus weight, size and zoospore output.

Day length and light levels were expected to play a major role in controlling the timing of reproduction, as these variables have previously been found to drive the physiology of gametophytes in other kelp species (Bolton and Levitt 1985; Wiencke et al. 2000; Nelson 2005). However, no relationship was found between the timing of reproduction and either of these variables. The lack of relationship between day length and light intensity, and the reproduction of *E. radiata* from Perth, could possibly be due to the relatively low latitude (32°S) and the implied low seasonal variation (Kain 1989) relative to other kelp beds which are predominantly found at higher latitudes (Steneck et al. 2002; Bolton 2010).

The positive relationship between zoospore release density and per cent cover of sorus tissue on the thalli suggests that the abundance of this visible tissue can be used as a proxy for the fecundity of *E. radiata* individuals. However, the relationships were weak, and the patterns were discordant at the extremes of the reproductive season where zoospores were observed before sori, at the beginning of the season, and sori were identified at the end of the season, after zoospores were no longer recorded. This suggests sorus tissue only becomes evident post-zoospore release or very late in the zoospore maturation and release process. The laboratory method used in this work was designed for measuring zoospore presence and thalli fecundity, thus defining the season of reproduction. However, this may not represent an accurate measure of zoospore production and release in natural situations and does not allow inferences about whether zoospores are released and replenished constantly throughout the season of reproduction or whether they remain on the thalli through the season and are released in an once-off pulse. Without *in situ* collections of released zoospores (for example, Joska and Bolton 1987), it is unclear how the current results relate to the natural release and recruitment throughout the season.

Synchrony in reproduction allows for the release of high densities of zoospores, which increases subsequent fertilisation success of gametophytes. Reproduction can often be linked to environmental variation; for example, propagules are released under favourable conditions for growth and survival. In the current study, the habitat-forming alga, *E. radiata*, conformed to this model and was reproductively active from the middle of the Austral summer to the end of autumn. This timing relates to a seasonal pattern in growth, increasing temperatures and the onset of winter storms. *E. radiata* kelp beds are found in warmer waters than most other kelp beds, and reproduction occurs outside the thermal optima for other kelps. We hypothesise that this is an adaptation to ensure that new sporophytes are ready to recruit at a time when space is released through canopy loss during winter storms and temperatures are decreasing to become more favourable for growth and productivity.

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