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Photosynthetic response of monospecific macroalgal stands to density

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ABSTRACT: Photosynthesis by benthic marine macroalgae makes an important contribution to the productivity of coastal seas. Quantification of photosynthesis and productivity of macroalgal assemblages is therefore important in understanding ecosystem functioning in coastal seas and providing realistic values for coastal productivity in global models. Estimates of macroalgal productivity are often based on the photosynthetic characteristics of thallus pieces or whole thalli, and not on those of communities. Such methods may overestimate rates of productivity as they do not account for neighborhood shading effects that may reduce photosynthetic rates in macroalgal stands that typically have high densities. In order to determine whether productivity estimates based on individuals differ from those based on communities, a controlled laboratory experiment was conducted with 3 dominant sub-canopy macroalgal species (*Cystophora scalaris*, *Xiphophora gladiata* and *Undaria pinnatifida*) from southern New Zealand. Photosynthetic parameters (initial slope of the photosynthesis vs. irradiance [*P*–*E*] curve α, saturation irradiance E_k, maximum rate of photosynthesis P_{max} and dark-respiration R_d) were obtained via *P*–*E* experiments using a custom-built respirometry chamber for a range of densities that corresponded to the minimum, average and maximum densities of these species in the field. A 5 to 7-fold decrease in P_{max} was observed when the density of the algal stand was above 1 ind. m^{-2}. R_d and α were also lower in communities than for individuals. Results illustrate that estimates based on single specimens substantially overestimate productivity and we recommend that the densities used in experiments reflect those observed in the field.

KEY WORDS: Density · Photosynthesis · Primary production · Respiration · Seaweed · New Zealand · *Cystophora scalaris* · *Undaria pinnatifida* · *Xiphophora gladiata*

INTRODUCTION

Marine macroalgae supply the majority of coastal primary production in temperate reefs and provide habitat and food for near-shore benthic communities (e.g. Mann 1973, Duggins et al. 1989, Charpy-Roubaud & Sournia 1990, Hurd et al. 2004). Coastal seas supply 90% of all fish caught (Pauly & Christensen 1995), signifying the importance of macroalgal productivity in coastal marine food webs. Knowledge of macroalgal based production rates are consequently fundamental in understanding coastal ecosystem functioning.

Rates of net photosynthesis are often used as an estimate of primary production of plants and algae (Falkowski & Raven 2007). Photosynthetic rates of macroalgae are typically obtained by enclosing thallus sections or, less frequently, whole thalli in chambers and recording the change in O_2 concentration at a range of irradiances, and in the dark to determine dark-respiration (R_d). Such experiments have been conducted under controlled laboratory conditions (Bidwell & McLachlan 1985, Binzer & Sand-Jensen 2002, Binzer & Middelboe 2005, Middelboe et al. 2006, Miller & Dunton 2007) or less often in the field (Longstaff et al. 2002, Copertino et al. 2009). A photosynthesis–irradiance (*P*–*E*) curve is then generated by fitting a model (e.g. Henley 1993) to the data, and resultant curves are used to determine α, the initial slope of the curve (an indicator of light harvesting efficiency at sub-saturating irradiances); P_{max}, the maximum rate of photosynthesis; E_k, the irradiance at which

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Table 1. Symbols and abbreviations used in the present study. WW: wet weight

Symbol	Definition	Unit
α	Initial slope of the *P–E* curve	
β	Photoinhibition	
E_k	Saturation irradiance	µmol photons m^{-2} s^{-1}
PAR	Photosynthetically active radiation	µmol photons m^{-2} s^{-1}
PFD	Photon flux density	µmol photons m^{-2} s^{-1}
P–E curve	Photosynthesis vs. irradiance curve	
P_{max}	Maximum rate of photosynthesis	µmol O_2 g^{-1} WW s^{-1}
R_d	Dark respiration	µmol O_2 g^{-1} WW s^{-1}

P_{max} is reached; R_d; and β, the level of photoinhibition at high irradiances (Falkowski & Raven 2007) (Table 1).

The photosynthetic parameters derived from *P–E* curves can be used to predict rates of primary production at different irradiances (Falkowski & Raven 2007). The most accurate approach is to use whole seaweeds, so that they remain connected to their storage reserves, which, for large seaweeds such as species from the Orders Fucales and Laminariales, may be located in the holdfast and stipe, i.e. for entire individuals the carbon and nitrogen sinks are still accessible (Gevaert et al. 2008). Consequently, for structurally complex seaweeds, photosynthetic responses obtained from thallus pieces versus intact individuals can be quite different (Binzer & Middelboe 2005, Middelboe et al. 2006, Sand-Jensen et al. 2007). Similarly, for nutrient uptake by members of the Fucales, the rates of thallus sections can be up to 10 times higher than those of whole algae (Harrison & Druehl 1982, Hurd & Dring 1990). Further, larger macroalgae are frequently cut to fit into the measuring system used to estimate O_2 exchange and therefore may exhibit oxygen-sensitive wound respiration unless aged for over 12 h (Bidwell & McLachlan 1985, Miller & Dunton 2007). Additionally, Binzer & Middelboe (2005) showed that when a macroalgal community was used, the photosynthetic parameters differed from those of individuals, and the variability surrounding P_{max} was also greater for individual thalli than groups of the same species. Importantly, studies where thallus pieces or single individuals are used do not account for neighborhood shading effects which occur in natural macroalgal assemblages and may reduce photosynthetic rates and hence productivity of these communities (Sand-Jensen et al. 2007, Copertino et al. 2009). Thus, community productivity rates that are extrapolated from rates of net photosynthesis of thallus pieces, or individuals, may be overestimates.

Our goal was to examine the effect of density on rates of net photosynthesis, in particular to test our hypothesis that the P_{max} measured using individuals will be greater than that using communities. To achieve this, we first obtained density measurements from published literature (Russell et al. 2008, Hepburn et al. 2011) and/or from underwater surveys of the density of 3 dominant sub-canopy macroalgal species along the coastline of North Otago, South Island, New Zealand: *Cystophora scalaris* J. Agardh and *Xiphophora gladiata* (Labillardière) Montagne ex Kjellman which are native members of the Order Fucales, and the introduced Laminarian kelp *Undaria pinnatifida* (Harvey) Suringar. For each species, we then measured *P–E* curves for (1) an individual, (2) an assemblage at a density similar to the average density recorded in the field, and (3) an assemblage approximating the maximum field density. Experiments were conducted in a custom-built respirometry chamber. Our results illustrate the need for caution when extrapolating values derived from individuals to obtain community productivity estimates.

MATERIALS AND METHODS

Field densities of macroalgae. Seven replicate shallow (<6 m) subtidal areas were sampled along 22 km of a semi-exposed coast, South Island, New Zealand (Fig. 1) from February 3 to August 6, 2009. At each site, 5 depth strata were surveyed by snorkeling or SCUBA: 0 m (low tide mark), 0.1 m, 0.5 m, 1–3 and 3–6 m depth. Depths were corrected to the mean low water mark to

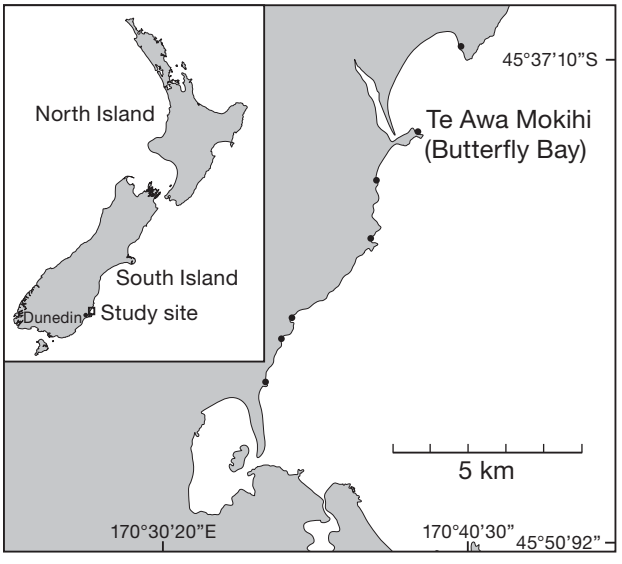

Fig. 1. Macroalgal survey and collection sites along a 22 km stretch of semi-exposed coast, South Island, New Zealand

ensure accurate positioning of sampling quadrats within the desired strata. At each site and within each stratum, a 30 m lead-weighted transect line was placed parallel to the shore and ten 1 m^2 quadrats were placed randomly along the transect line. The number of *Undaria pinnatifida*, *Cystophora scalaris* and *Xiphophora gladiata* was recorded within each quadrat.

Collection and experimental design. ***Undaria pinnatifida:*** *U. pinnatifida* sporophytes that were between 0.1 and 0.2 m long were collected from a single tide pool at low tide at Mapoutahi (45° 46′ 6.36″ S, 170° 37′ 3.23″ E) on October 21 (70 sporophytes) and October 27 (110 sporophytes), 2008. Epiphytes were removed and sporophytes were placed in seawater in a 10 l container for transport to the Portobello Marine Laboratory, University of Otago, 1 h away. At the laboratory, sporophytes were stored in an outdoor tank (0.95 × 0.65 × 0.15 m) with flowing seawater (13 ± 0.5°C), with a maximal photosynthetically active radiation (PAR) of ~900 µmol photons m^{-2} s^{-1}. The maximum time between collection and use in an experiment was 5 d. Individual sporophytes were randomly allocated to experimental treatments.

P–E experiments were conducted in a custom-built respirometry chamber that had a 30 l 'test section' in which seaweeds were incubated, and seaweeds were attached to a 0.2 × 0.2 m Perspex® plate (Fig. 2). In order to mimic the thallus length per unit area of substratum in natural *Undaria pinnatifida* communities without cutting the seaweeds, we constructed artificial communities using juveniles whose length was $\frac{1}{25}$ of the average length of mature fronds found in the field. For example, scaling down 1 m^2 of substratum that has a 2.5 m tall individual on it by $\frac{1}{25}$ results in a 0.1 m tall individual on a 0.04 m^2 plate. Five experimental treatments were used (1, 5, 9, 13, and 25 ind. per 0.04 m^2 plate) which were equivalent to field densities of 1 to 25 ind. m^{-2}; for simplicity, within the text we refer to seaweed densities as ind. m^{-2}. The treatments applied are typical densities of *U. pinnatifida* in southern New Zealand (Dean & Hurd 2007, Russell et al. 2008).

Twelve hours prior to each experiment an appropriate number of individuals between 0.1 and 0.2 m long were randomly sampled from the pool of collected sporophytes and attached to the Perspex® plate (which had multiple holes drilled through it, spaced 40 mm apart) using a cable tie through each holdfast. Individuals were attached to the plate at an even distance from one another to prevent 'clumping' of the individuals at the higher densities to ensure that each replicate plate was equivalent. Plates with individuals attached were then placed back into the flow-through holding tank for at least 12 h.

On each experimental day (8 d in total), a randomly selected plate was placed into the test section of the respirometry chamber (Fig. 2). There were 3 replicates for each density treatment. Two 4 h experiments were conducted on each day, and treatments were randomly assigned to an 'experimental time slot' to remove any potential afternoon or morning affects on metabolic rates. Experiments started at approximately 09:00 h and were finished before 18:00 h. The concentration of O_2 in the seawater used in experiments was lowered to ~50% by bubbling compressed nitrogen (10 min) into a 20 l Nalgene™ carboy full of filtered (1 µm) sea-

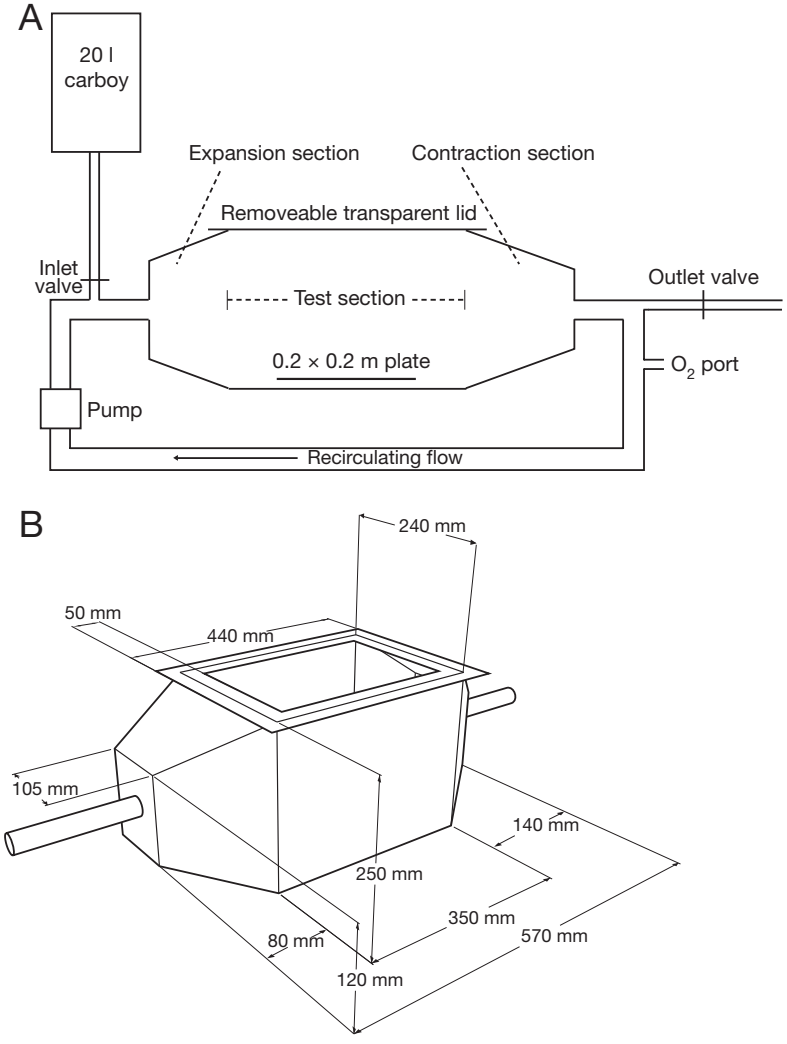

Fig. 2. (A) Schematic of the 30 l respirometry chamber showing the position of the Little Giant® 1-AA-MD pump, inlet and outlet valves, port for O_2 probe, 20 l Nalgene™ carboy filled with O_2-reduced seawater, and expansion, test and contraction sections. The 0.2 × 0.2 m plate was positioned centrally in the test section. (B) Scaled schematic of the 30 l respirometry chamber showing dimensions in mm

water. The experimental plate with seaweeds attached was placed in the chamber, and seawater added through the inlet valve until the chamber was completely filled (Fig. 2A). The chamber was then sealed and an in-line pump (Little Giant® 1-AA-MD) switched on, which delivered a flow rate of ~10 l min^{-1} through the chamber.

The respirometry chamber was designed so that the seawater within the chamber could be partially replaced with reduced-O_2 seawater halfway through each experiment while it remained sealed. This process, termed flushing, involved the replacement of 10 l of experimental seawater during each experiment, and maintained the O_2 concentration in the chamber between 5 and 10% of the starting value (Richards 2010). Flushing was achieved by opening the inlet and outlet valves simultaneously, allowing the gravity fed reduced-O_2 seawater from the carboy to enter the chamber as seawater drained from the outlet pipe (Fig. 2A). Flushing the system in this manner prevented external O_2 from entering the chamber, and prevented O_2 concentrations from increasing to levels that might cause photorespiration.

Cystophora scalaris and Xiphophora gladiata: Individuals that were 0.02 to 0.1 m long were collected from Te Awa Mokihi (Butterfly Bay), Karitane (Fig. 1) (45° 38′ 16.92″ S, 170° 40′ 7.63″ E) on March 14, 22 and 29, 2010, and treated as for *Undaria pinnatifida* except the experimental pre-treatment temperature was 14 ± 0.5°C. In total 275 ind. of each species were used in experiments. The experimental procedure used was similar to that for *U. pinnatifida* except that there were 3 density treatments (1, 13, and 41 ind. per plate) instead of 5 (Fig. 3), the maximum-density treatment was 41 ind. instead of 25 ind. per plate, and replication was also increased from 3 to 5. The reason for these differences was that observed field densities for these species were greater than those observed for *U. pinnatifida* (see 'Results: Field densities of macroalgae' and Fig. 4). The number of irradiances used was reduced from 10 to 6, which reduced the maximum length of incubations from 4 to 3 h, allowing 3 experiments per day instead of 2.

Measurement of photosynthetic and respiration rates, and *P–E* curves. Experiments were conducted in the 30 l respirometry chamber placed inside a climate-controlled room set to 12°C (*Undaria pinnatifida*) and 13°C (*Cystophora scalaris* and *Xiphophora gladiata*). Changes in O_2 concentration inside the respirometry chamber due to photosynthesis and respiration were detected using a Foxy-OR 125-73 mm fiber optic oxygen sensing optode (Ocean Optics) attached to the outlet section of the return pipe, and connected to a computer that registered the signal once per second. During experiments the oxygen concentration was continuously followed on a computer via Ocean Optics software. Illumination was provided overhead by a SON-T AGRO 400 W high-pressure sodium lamp, and 4 Philips Aqua Relle (TLD 36 W/89) fluorescent bulbs, delivering a maximum PAR of 977 µmol photons m^{-2} s^{-1} (*U. pinnatifida* experiments) and 1113 µmol photons m^{-2} s^{-1} (*C. scalaris* and *X. gladiata* experiments) at the surface of the chamber. PAR was reduced using E-colour neutral density filters (Rosco) between the light source and the surface of the chamber to obtain PAR levels (average PAR inside the chamber) of 0, 13, 19, 48, 70, 136, 184, 266, 519 and 749 µmol photons m^{-2} s^{-1} for the *U. pinnatifida* experiments and 0, 8, 21, 80, 304, 595 and 858 µmol photons m^{-2} s^{-1} for the *C. scalaris* and *X. gladiata* experiments. Experiments always started with the dark treatment and levels of PAR were increased until the maximum PAR treatment.

To ensure that light entered only at the top of the chamber, black polythene plastic was attached to the sides and base. This enabled the accurate measure-

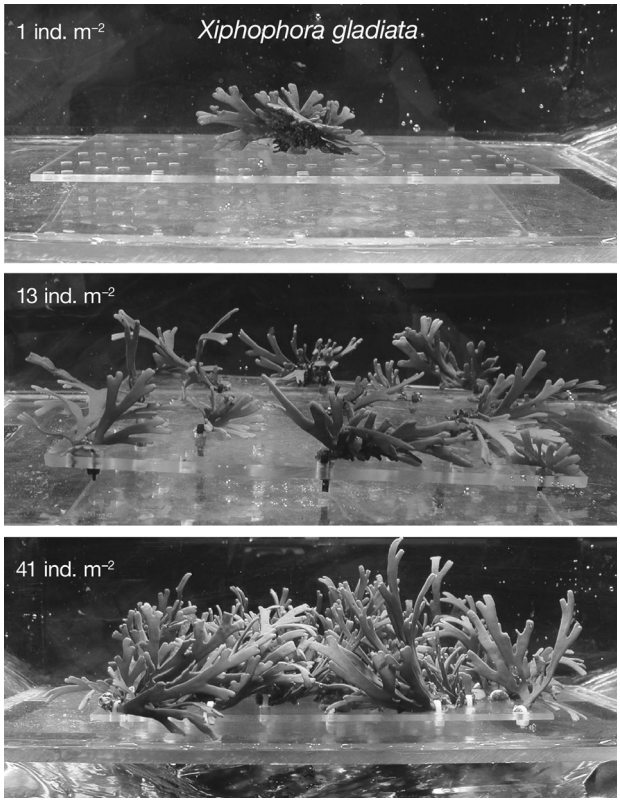

Fig. 3. *Xiphophora gladiata*. Density experiments showing how seaweeds were orientated within the 30 l re-circulating respirometry chamber. Density treatments were 1, 13 and 41 juvenile or small individuals per 0.04 m^2 plate, which represent the scaled equivalent of 1, 13, and 41 mature individuals per m^2 (see 'Materials and methods: Collection and experimental design. *Cystophora scalaris and Xiphophora gladiata*')

ment of PAR entering the chamber. Prior to the initial *P–E* trial, PAR was measured using a LI-193 SA quantum sensor (LI-COR) at 5 positions at the chamber surface (before the application of the filters), and then averaged. PAR within the chamber (lid on, filled with seawater but no seaweeds) was measured at 3 depths (top, middle, bottom). The attenuation coefficient (K_d) was then determined and used to obtain the average irradiance inside the chamber. In addition, for the *Cystophora scalaris* and *Xiphophora gladiata* experiments PAR was measured underneath the chamber at 2 positions to give the percentage reduction in PAR through the algal canopy for each replicate of the density treatments.

The oxygen optode was calibrated each morning by taking readings in air-saturated (100%) and oxygen-free (0%) seawater, at the experimental temperature, by bubbling air for the 100% standard or compressed nitrogen for the 0% standard into separate 1 l glass flasks. Calibration points were measured once the O_2 signal leveled out and remained constant (after approximately 10 min).

Rates of photosynthesis and dark respiration were calculated from the linear slopes of curves for oxygen concentration versus time after constant rates (≥10 min) had been attained. At the end of the experiment the wet weight (g) of all individuals was determined and rates of photosynthesis and respiration expressed per unit wet biomass in the chamber (µmol O_2 g^{-1} wet wt s^{-1}).

For each replicate, a *P–E* curve was fitted and photosynthetic parameters determined following Webb et al. (1974):

$$P = P_{max}(1 - e^{-\alpha E/P_{max}}) + R_d \quad (1)$$

where α = initial slope of the light-limited region of the curve; E is the incident irradiance, and R_d is the dark respiration rate. When photoinhibition (β) occurred, the equation of Walsby (1997) was used:

$$P = P_{max}[(1 - e^{-\alpha E/P_{max}}) + \beta E] + R_d \quad (2)$$

Statistical analyses. Two-way analyses of variance (ANOVA) were used to determine whether there were statistical differences in the amount of PAR attenuated by *Cystophora scalaris* and *Xiphophora gladiata* canopies at densities of 1, 13 and 41 ind. m^{-2}. For each species (*Undaria pinnatifida*, *C. scalaris* and *X. gladiata*), differences in the photosynthetic parameters (P_{max}, α, R_d and E_k) between density treatments were tested using 1-way ANOVA, with post hoc tests to verify significant differences among groups (Tukey's HSD, $p < 0.05$). All data met the ANOVA requirements of normality and homogeneity of variances. Tests were performed according to Zar (1996), using the software package SigmaStat 2.03 (SPSS).

RESULTS

Field densities of macroalgae

The density of *Undaria pinnatifida* and *Cystophora scalaris* ranged from 0 to 31 sporophytes m^{-2}, and the average densities were greatest at 0.5 m depth with 13.1 ± 2.58 ind. m^{-2} and 15.6 ± 1.41 ind. m^{-2}, respectively (Fig. 4). For *Xiphophora gladiata*, density ranged from 0 to 70 ind. m^{-2}, and the greatest average density (30.7 ± 8.27 ind. m^{-2}) occurred at 0.1 m depth (Fig. 4).

Attenuation of PAR by *Cystophora scalaris* and *Xiphophora gladiata*

Significantly more PAR was attenuated by the *X. gladiata* canopy at densities of 1 and 41 ind. m^{-2} compared to *C. scalaris* at the same densities (Tukey's HSD, $p < 0.01$; Fig. 5). For *X. gladiata*, as density of the macroalgal stand increased, PAR attenuation increased (Tukey's HSD, $p < 0.001$) and values of percent surface PAR remaining under the canopy ranged from 18 % (41 ind. m^{-2}) to 39% (1 ind. m^{-2}) (Fig. 5). For *C. scalaris* at 1 ind. m^{-2}, incident PAR was reduced by 50% and this value was significantly lower than those for the 13 and 41 ind. m^{-2} treatments, which attenuated more light (Tukey's HSD, $p < 0.001$) and were similar to each other (25 and 24% respectively, Tukey's HSD, $p = 0.883$; Fig. 5).

P–E curves and photosynthetic parameters

The shape of the *P–E* curves, and hence the photosynthetic parameters, differed between species and with density (Figs. 6 & 7, Table 2). In most cases, P_{max}

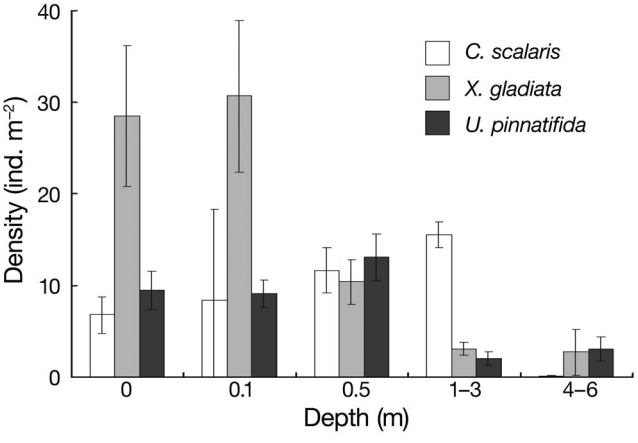

Fig. 4. Average (±SE, n = 7) field densities of *Cystophora scalaris*, *Xiphophora gladiata* and *Undaria pinnatifida* at 5 depth strata (0, 0.1, 0.5, 1–3 and 4–6 m)

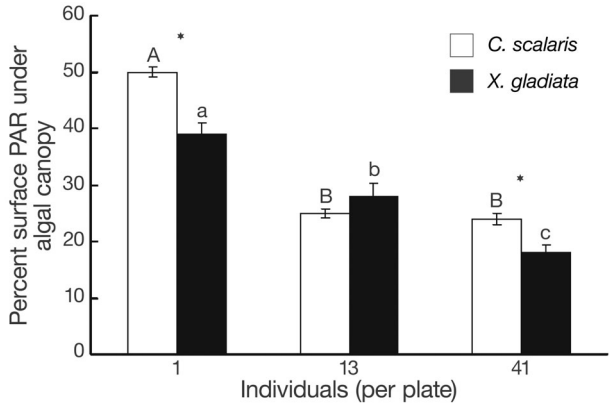

Fig. 5. Average (±SE, n = 5) percentage of incident photosynthetically active radiation (PAR) beneath a canopy of *Cystophora scalaris* (white) and *Xiphophora gladiata* (black) for the 3 density treatments (1, 13 and 41 ind. per 0.04 m^2 plate). *Significant differences between species within density treatments. Within each species, common letters denote densities that are not significantly different from one another (Tukey's HSD, $p < 0.05$)

was reached within the irradiance range tested i.e. ≤800 µmol photons m^{-2} s^{-1}. The exception was *Xiphophora gladiata* at a density of 13 ind. m^{-2}, where P_{max} was not reached (Fig. 7B) and Eq. (1) did not model the data at low or high photon flux densities (PFDs); therefore photosynthetic parameters were not obtained for this treatment (Table 2). For *X. gladiata* at 1 ind. m^{-2}, there was evidence of photoinhibition at the highest irradiance used (Table 2, Fig. 7B) and Eq. (2) gave a significantly better fit to average photosynthetic rates than Eq. (1) (*F*-test on residual sums of squares, $F_{1,3} = 126.87$, $p = 0.0015$).

For *Undaria pinnatifida*, average values of P_{max} and R_d for the 1 ind. m^{-2} treatment were ~4 times greater than for all other density treatments (Tukey's HSD, $p < 0.001$ and $p < 0.018$, respectively; Table 2). A similar trend was observed for α, however this was non-significant ($F_{4,14} = 3.28$, $p = 0.058$). There were no differences in E_k between density treatments ($F_{4,14} = 2.08$, $p = 0.159$; Table 2).

For *Cystophora scalaris*, P_{max} was ~7 times greater in the 1 ind. m^{-2} treatment compared to the other densities (Tukey's HSD, $p < 0.0014$) and α was 25 times greater in the 1 ind. m^{-2} treatment (Tukey's HSD, $p < 0.038$ respectively). For R_d, the 41 ind. m^{-2} treatment was significantly lower than the 1 ind. m^{-2} treatment (Tukey's HSD, $p = 0.024$), however there was no difference compared to the 13 ind. m^{-2} density (Tukey's HSD, $p = 0.072$), nor was there a difference between the 1 and 13 ind. m^{-2} treatments (Tukey's HSD, $p = 0.093$; Table 2). E_k for the 41 ind. m^{-2} treatment was 19 times greater compared to 1 ind. m^{-2}, and 4.5 times greater compared to 13 ind. m^{-2} (Tukey's HSD, $p < 0.001$; Table 2).

P_{max} for *Xiphophora gladiata* was 6.5 times greater in the 1 ind. m^{-2} treatment compared to that of 41 ind. m^{-2} (Tukey's HSD, $p < 0.001$). R_d was 470 times greater in the 1 ind. m^{-2} treatment when compared to the 41 ind. m^{-2} treatment (Tukey's HSD, $p < 0.001$) whereas α was 280 times greater than the 41 ind. m^{-2} treatment (Tukey's HSD, $p < 0.001$). E_k for the 41 ind. m^{-2} treatment was ~25 times higher than for the 1 ind. m^{-2} treatment (Tukey's HSD, $p < 0.001$; Table 2).

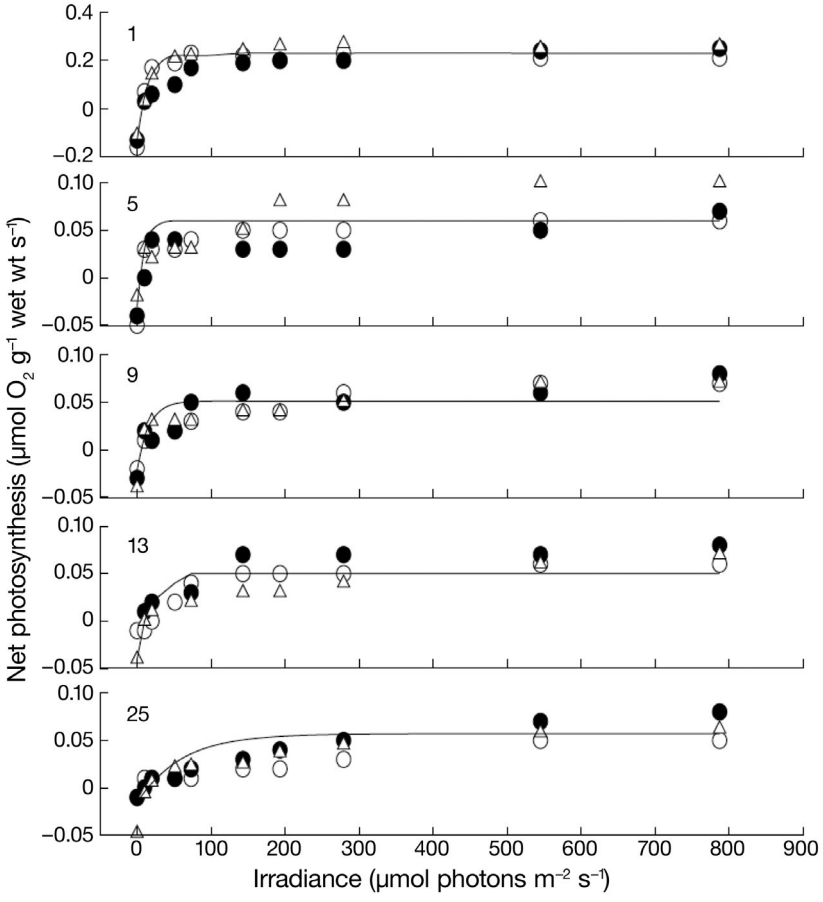

Fig. 6. Photosynthesis vs. irradiance plots for *Undaria pinnatifida* for 5 density treatments: 1, 5, 9, 13 and 25 ind. per 0.04 m^2. Different symbols represent replicates of each treatment. Note that the *y*-axis of the top graph differs from the others

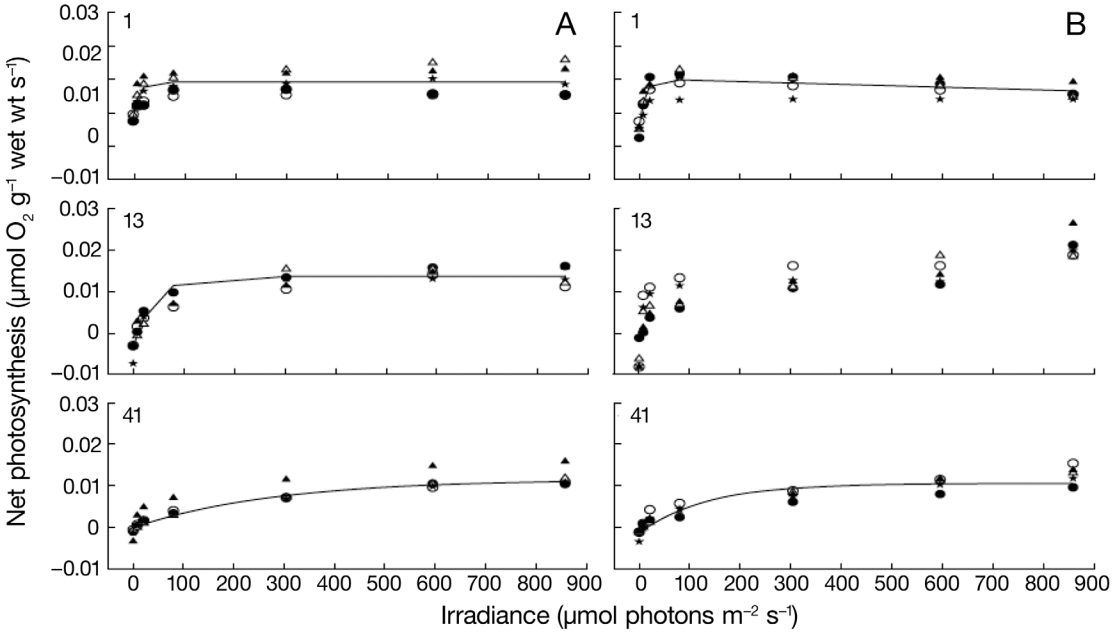

Fig. 7. Photosynthesis vs. irradiance plots for (A) *Cystophora scalaris* and (B) *Xiphophora gladiata* for 3 density treatments: 1, 13 and 41 ind. per 0.04 m^2. Different symbols represent replicates of each treatment

Table 2. *P–E* parameters (±SE) (see Table 1 for definitions and units) for *Undaria pinnatifida*, *Cystophora scalaris* and *Xiphophora gladiata* at different densities (ind. per 0.04 m^2). Treatment groups with common letters are not significantly different from one another (Tukey's HSD, $p < 0.05$). No data (ND) are presented for *X. gladiata* at 13 ind. per 0.04 m^2, because P_{max} was not reached (see 'Results: *P–E* curves and photosynthetic parameters')

Density	P_{max}	α	R_d	E_k
U. pinnatifida **(n = 3)**				
1	0.226 ± 0.012^A	0.025 ± 0.008^A	-0.126 ± 0.020^A	20 ± 6^A
5	0.062 ± 0.020^B	0.009 ± 0.005^A	-0.032 ± 0.017^B	56 ± 49^A
9	0.057 ± 0.009^B	0.004 ± 0.003^A	-0.020 ± 0.012^B	72 ± 45^A
13	0.050 ± 0.007^B	0.005 ± 0.002^A	-0.040 ± 0.012^B	27 ± 11^A
25	0.057 ± 0.012^B	0.001 ± 0.001^A	-0.016 ± 0.013^B	191 ± 83^A
C. scalaris **(n = 5)**				
1	0.092 ± 0.016^A	0.010 ± 0.004^A	-0.014 ± 0.005^A	15 ± 3^A
13	0.014 ± 0.001^B	0.0004 ± 0.0002^B	-0.004 ± 0.002^{AB}	59 ± 16^A
41	$0.012 \pm <0.001^B$	$0.00004 \pm <0.00001^B$	$-0.0001 \pm <0.001^B$	283 ± 21^B
X. gladiata **(n = 5)**				
1	0.085 ± 0.012^A	0.014 ± 0.0025^A	-0.047 ± 0.008^A	12 ± 1^A
13	ND	ND	ND	ND
41	0.013 ± 0.001^B	0.00005 ± 0.00001^B	$-0.0001 \pm <0.001^B$	309 ± 49^B

DISCUSSION

P–E experiments using monospecific stands revealed that once seaweed density was above 1 ind. m^{-2}, rates of P_{max} decreased up to 7-fold for *Undaria pinnatifida*, *Cystophora scalaris* and *Xiphophora gladiata*. Furthermore, R_d and α decreased with increasing density, whereas E_k increased. *U. pinnatifida*, *C. scalaris* and *X. gladiata* grow either in monospecific stands or as part of a mixed community, therefore photosynthetic rates based on individuals will have little application to field conditions. Neighborhood shading effects are probably a key mechanism for the observed reductions in P_{max} due to the decrease in PAR underneath the algal canopy for the higher density treatments when compared to an individual; the observed increases in E_k values as density increased lend support to this idea.

Our results support those of Copertino et al. (2009) for turf algal communities in which P_{max}, α and R_d were inversely related to biomass, but are opposite to those of Binzer & Sand-Jensen (2002) who found that for *Fucus serratus*, P_{max} and α increased with increasing density. The difference between the results can be explained by the different ways in which photosynthetic rates are standardised: Binzer & Sand-Jensen (2002) standardise to unit ground area whereas we and Copertino et al. (2009) have used biomass. When our results for P_{max} are standardised to unit ground area (i.e. per m^{-2}) rather than biomass we find the same pattern as Binzer & Sand-Jensen (2002) of increasing P_{max} with increas-

ing density and this simply reflects the greater amount of material per unit area.

Respiration was reduced in all density treatments exceeding 1 ind. m^{-2} for all species examined, similar to Copertino et al. (2009) who compared high (>0.5 g ash free dry wt [AFDW] $plate^{-1}$) and low (<0.5 g AFDW $plate^{-1}$) turf biomass. Other studies have observed the opposite effect, with increasing R_d as community density increased, but as for P_{max}, the different pattern is due to different methods of standardisation (Binzer & Sand-Jensen 2002, Sand-Jensen et al. 2007). The reason for reduced R_d as algal density increases is unclear but may be a result of flow-attenuation within canopies (Hurd 2000). Seaweed canopies can substantially reduce mainstream flows (Gaylord et al. 2007, L. T. Kregting et al. unpubl.), and this can result in diffusion boundary layer (DBL) formation, which can reduce the flux of O_2 and dissolved inorganic carbon (DIC) to and from blade surfaces. In our experiment, a reduced supply due to thicker boundary layers might result in a lower R_d for canopies compared to individuals. If so, DBL formation within canopies could also be a contributing factor for the lower rates of P_{max} with increased density, due to reduced DIC flux. However, our flow rates of 10 l min^{-1} were sufficiently fast to cause the seaweeds to move back and forth during experiments, and our suggestion of increased DBL thicknesses for canopies requires experimental testing.

For most of our experiments P_{max} was achieved and Eq. (1) produced curves that reflected the photosynthetic responses to increasing light; but this was not the case for *Xiphophora gladiata* at 13 ind. m^{-2} for which rates of photosynthesis increased linearly between 21 and 800 µmol photons m^{-2} s^{-1} and Eq. (1) did not model the data at either low or high PFDs. A similar response was recorded for a mixed-canopy of *Cystophora tortulosa* and *Hormosira banksii*, in which case P_{max} was not achieved at PFDs of 2000 µmol photons m^{-2} s^{-1} (Tait & Schiel 2011); those authors were also unable to apply 'traditional' P vs. E models to their data. The explanation for these trends is that when growing in canopies, seaweeds self-shade: while the uppermost blades in a canopy may reach P_{max}, or even exhibit photoinhibition, the lower blades will receive much less light and exhibit un-saturated rates of photosynthesis (Middelboe & Binzer 2004). It is not clear why the trend observed at 13 ind. m^{-2} for *Xiphophora* was not seen at 41 ind. m^{-2}, but it is possible that if we had used higher PFDs we may have observed a pattern similar to Tait & Schiel (2011) and to that for the 13 ind. m^{-2} treatment in this study.

Recent studies have revealed that multi-species communities may be able to maintain higher biomass per unit ground area than single-species communities through the different species supplementing each other temporally and spatially (Middelboe & Binzer 2004, Sand-Jensen et al. 2007). Therefore, to accurately determine the photosynthetic performance of macroalgal communities, studies need to be conducted not only on realistic densities obtained from field observations, but with natural mixed species assemblages, and realistic wave and flow conditions which tend to disrupt self- and neighbourhood shading effects. The present study highlights the problem of determining productivity rates from a single individual in enclosed chamber experiments (which is common), and then extrapolating those values into productivity estimates on a coast-wide scale. For example, if the present study had used P_{max} values obtained from 1 individual and applied it to a coastal population, our results suggest that this would overestimate production by 4 to 7 times. This clearly demonstrates that single-specimen estimates of productivity based on O_2 evolution could be substantially overestimated, and we recommend that productivity estimates be made using densities that reflect those observed in the field.

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