Assemblage and understory carbon production of native and invasive canopy-forming macroalgae

Leigh W. Tait a,b,⁎, Paul M. South a, Stacie A. Lilley a, Mads S. Thomsen a, David R. Schiel a

⁎ Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

a National Institute of Water and Atmospheric Research Ltd, PO Box 8602, Riccarton, Christchurch 8440, New Zealand

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A B S T R A C T

Carbon flow is essential to the function of all ecosystems, yet there is little mechanistic understanding of how non-indigenous macroalgal alter rates of carbon fixation in marine ecosystems. The spread of fast-growing non-indigenous species, such as the annual kelp Undaria pinnatifida (Harvey) Suringer, can potentially change trophic links through variable photosynthetic parameters relative to indigenous species. Here we use in situ photospirometry to compare rates of net primary productivity (NPP) of assemblages dominated by U. pinnatifida and two native canopy-forming species, Cystophora torulosa and Durvillea antarctica. The three assemblages had different light-use dynamics across a full light range, with the indigenous macroalgae showing no sign of saturated NPP at high irradiance, but with U. pinnatifida showing saturated NPP beyond 1000 μmol m−2 s−1. Using incident irradiance collected over a full year, we show small differences in modeled average daily NPP during spring between U. pinnatifida assemblages (8 g C m−2 day−1) and those dominated by C. torulosa (7 g C m−2 day−1), whereas D. antarctica assemblages were the most productive (10 g C m−2 day−1). The proportion of NPP provided by the sub-canopy component of assemblages varied between the canopy-forming species, where D. antarctica had a low sub-canopy contribution compared to stands dominated by U. pinnatifida or C. torulosa. High biomass turnover associated with the annual life history of U. pinnatifida has the potential to increase carbon export to surrounding ecosystems compared to perennial fucoid species. Therefore, U. pinnatifida may have a positive effect on carbon flow, fixing similar quantities of carbon in a 6-month period as the native C. torulosa in a year. It appears that U. pinnatifida has the potential to contribute a great deal of carbon and alter the biomass export regime as it spreads across shallow coastal habitats.

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1. Introduction

Non-indigenous species (NIS) have been shown to cause measurable changes to ecosystem properties worldwide (Grosholz, 2005; Levine et al., 2003; Olden et al., 2004; Parker et al., 1989; Strayer et al., 2006), including alteration of carbon production dynamics in algal assemblages (Casu et al., 2009; Krumhansl and Scheibling, 2012a; Pedersen et al., 2005; Salvaterra et al., 2013). Impacts of non-indigenous macroalgae include an increase in net primary productivity (NPP) (Vaz-Pinto et al., 2013), or declining NPP (Salvaterra et al., 2013; Tait and Schiel, 2011a), alteration of nutrient cycling within sediments (Rossi et al., 2010) and changes in species diversity or composition (Britton-Simmons, 2004; Engelen et al., 2013; Wernberg et al., 2004). The NIS expected to have the greatest impacts are those that directly or indirectly modify recipient habitats, potentially causing cascading effects on resident biota (Crooks, 2002; Thomsen et al., 2010). Despite the habitat and ecosystem modifying potential of invasive macroalgae, there have been few in situ evaluations of alterations to biogeochemical cycles caused by them (although see Pedersen et al., 2005; Salvaterra et al., 2013).

Canopy-forming seaweeds provide essential services to benthic sub-canopy assemblages (Erikkson et al., 2006; Schiel, 2006) and the surrounding ecosystem (Hill et al., 2006; Leclerc et al., 2013; Yorke et al., 2013). Changes to the composition of algal canopies can alter detrital subsidies and nutritional quality that may affect the coupling of benthic macroalgal beds to recipient habitats (Krumhansl and Scheibling, 2012a). Although there is little evidence of U. pinnatifida displacing native canopy-forming algae (Thompson and Schiel, 2012; Valentine and Johnson, 2005), high
rates of primary productivity have the potential to subsidise carbon production in the near-shore environment. Elevated primary productivity following invasions by fast-growing macroalgae have been shown for U. pinnatifida (Sfriso and Facca, 2013), Sargassum muticum (Pedersen et al., 2005), Gracilaria vermiculophylla (Nejrup and Pedersen, 2010; Thomsen and McGlathery, 2007) and Codium fragile (Thomsen and McGlathery, 2007). The high standing biomass of native perennial canopy-forming algae (dominated by fucoxids) in the intertidal and upper sub-tidal zones of much of southern New Zealand (up to 80 kg per m² for Durvillaea antarctica; Schiel, 2006) represents a markedly different strategy to the annual life-cycle of U. pinnatifida (Saito, 1972). The high turnover of U. pinnatifida relative to native canopy-forming fucoid algae has the potential to increase the export of carbon from rocky reefs to surrounding habitats, as has been observed for another non-indigenous alga, Codium fragile (Krumhansl and Scheibling, 2012a).

U. pinnatifida has successfully invaded temperate coastal zones worldwide (Hay and Villouta, 1993; Russell et al., 2008; Thompson and Schiel, 2012; Valentine and Johnson, 2003) and is able to use nutrients efficiently to achieve high growth rates (Dean and Hud, 2007; Russell et al., 2008; Schiel and Foster, 2006). This high growth rate could result in ‘positive impacts’ on many local species because U. pinnatifida forms a canopy that potentially provides biogenic habitat for sub-canopy macroalgae (Lilley and Schiel, 2006; Schiel, 2006; Wernberg et al., 2003) and invertebrates (Lilley and Schiel, 2006; Wikström and Kaursky, 2007). Furthermore, experimental evidence suggests U. pinnatifida has little impact on native algal species and largely fills disturbed patches where canopy species have been removed (Valentine and Johnson, 2003) or recruiting into turf-assemblages dominated by coralline algae (Thompson and Schiel, 2012). However, the impacts of an additional fast-growing canopy-forming alga on production dynamics has rarely been studied in the context of native algal assemblages and could represent a substantial addition to total carbon fixation.

We compared the relative contribution of U. pinnatifida and two dominant native fucoid canopy-forming alga (C. torulosa and D. antarctica) to the net primary production (NPP) of low-intertidal assemblages on a per area basis. Using parameters generated from photosynthesis-irradiance (P–E) curves, we modeled annual primary production using in situ irradiance to determine the relative contribution of the annual U. pinnatifida and the native perennial fucoids C. torulosa and D. antarctica. Furthermore, the impacts of invasive canopy-forming macroalgae on the contribution of sub-canopy macroalgae to total NPP have not been considered, despite the importance of canopy shading on sub-canopy NPP dynamics (Harrer et al., 2013; Tait and Schiel, 2011b). We examined the relative impacts of the three canopy-forming species on sub-canopy NPP. Variable shading dynamics associated with thallus thickness and morphology of the three canopy-forming species has the potential to affect the carbon balance of sub-canopy assemblages with implications for whole assemblage NPP. We test the hypothesis that U. pinnatifida has the potential to add significantly to near-shore NPP and that U. pinnatifida will have minimal impacts on sub-canopy contribution relative to the native fucoid canopies.

2. Methods

To test the contribution of the invasive, U. pinnatifida and the native canopy-forming D. antarctica and C. torulosa to carbon fixation we quantified NPP across a full light gradient. We used in situ photospirometry to determine rates of NPP and respiration by measuring changes in dissolved oxygen, which were converted to changes in carbon uptake using a P:Q (photosynthetic quotient) ratio of 1:1 (Kirk, 1994) and standardized to carbon uptake m⁻² of reef surface (g C m⁻² h⁻¹). P–E curves for assemblages dominated by canopies of U. pinnatifida, D. antarctica, and C. torulosa and including sub-canopy macroalgae were used to determine total NPP per m⁻² of reef surface. Modeled rates of carbon fixation were based on the incident light intensity measured for one year in the low intertidal of the Moeraki peninsula (South Island, New Zealand).

2.1. Study site

The primary production of in situ assemblages and the incident irradiance were collected from ‘The Point’ Moeraki peninsula, southeastern New Zealand (45° 11′S, 170° 98′E). Assemblages dominated by the three co-occurring (at the same tidal height) canopy-forming macroalgae D. antarctica, C. torulosa, and U. pinnatifida were incubated in benthic chambers. Due to size constraints of the incubation chambers, all thalli were limited to 0.30 m tall. We quantified photosynthetic performance of the three canopy-forming species and associated sub-canopy assemblages at ambient densities in situ. Macroalgal assemblage composition (percent cover) was measured using a small (25 × 25 cm) grid quadrat and biomass (wet and dry) was measured following incubations by clearing all algal material within incubation plots.

2.2. Photosynthetic performance

Macroalgal assemblages were incubated in 30 cm high 20 cm diameter circular clear Perspex chambers (with a 10 mm thick clear base plate and lid, see Fig. 1). Water was mixed using a submerged magnetic water pump (turbulent vortex mixing) and exchanged after 20 min to avoid oxygen saturation and nutrient depletion. Large mobile invertebrates were removed before incubations. NPP was determined by measuring changes in oxygen concentration across a full range of natural light intensities (0–2000 μmol m⁻² s⁻¹), and P–E curves were generated. Change in dissolved oxygen was measured using a Hach® LDO (HQ40d) meter and light intensity was measured with HOBO (Onset©) data loggers and cross-calibrated with a LiCor (LI-192 quantum sensor) photosynthetically active radiation (PAR) sensor.

In situ NPP was measured for each canopy former and their associated understory using chambers with an open attachment base to fit around the reef substratum (see Tait and Schiel, 2010 for detailed attachment and incubation protocol). Three replicate assemblages were incubated for each canopy former across the

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Fig. 1. In situ photospirometry chamber fitted around a macroalgal assemblage, dominated by Undaria pinnatifida at ‘The Point’ Moeraki, New Zealand.
full natural light gradient. Assemblage respiration rates were measured by covering chambers to omit light. Incubations were performed over 2 weeks during the lowest monthly tides between 17–21 September, 13–18 October, and 22–25 November 2010. Chambers were fixed to the plots early each day (07:00–09:00) and incubations were performed as the incoming tide surrounded the chambers (08:00–13:00).

Oxygen change was converted to carbon fixation using a photosynthetic quotient of 1:1 (Axelsson, 1988; Kirk, 1994). The P–E curves were fitted to the data using the exponential function:

$$ P_n = R + (P_m - R)(1-e^{-\alpha E}) $$

[1]

where \( R \) is the respiration rate, \( P_m \) is the maximum NPP, and \( \alpha \) is the light-use efficiency (initial slope). Compensating irradiance (\( E_c \)) was also estimated for each replicate assemblage using light-use efficiency (\( \alpha \)) and respiration (\( R \)) to calculate the x-intercept (i.e., the point of no net oxygen change where photosynthesis and respiration are equal). The curve was fitted using GraphPad Prism software using \( R, P_m, \) and \( \alpha \) for in situ assemblages.

2.3. Sub-canopy contribution to assemblage NPP

To understand the relative effects of the three canopy-forming species on sub-canopy contribution to total assemblage NPP, a separate experiment was done manipulating canopy and sub-canopy presence in situ. Six individual plots, to which chambers were attached, were assigned to sub-canopy removal (\( n = 3 \)) or control treatments with the sub-canopy intact (\( n = 3 \)). Selected plots were at the same shore-height as canopy-forming macroalgae and were dominated by the coralline algae *Corallina officinalis*, as seen in the sub-canopy of all three canopy-forming species (Table 1). While shading by the canopies reduces photon-flux to the sub-canopy and therefore affects NPP, the canopies can also have variable physical effects on the sub-canopy. In particular, *D. antarctica* had large effects on the recruitment of sub-canopy species and reduced the height of calcareous turf through ‘whip-lash’ effects (Taylor and Schiel, 2005). Therefore, we tested the relative effects of shading by the three canopy species (*U. pinnatifida*, *C. torulosa*, and *D. antarctica*) on photosynthetic performance, but without the physical forces shaping differences in sub-canopy composition or morphology.

Raw Plugs with eyelets attached were fitted into the center of the plots for attaching canopy-forming macroalgae at the holdfast using zip ties. Each plot was incubated with all canopy-forming species in a randomized order, and without any canopy-forming species (i.e., no algae in incubation chambers or sub-canopy only). Incubations were performed over a 5-day period, 15–19 October 2013 at ‘The point’, Moeraki. All incubations were performed at light intensities between 500 and 800 \( \mu \text{mol m}^{-2} \text{s}^{-1} \).

To estimate the contribution of the sub-canopy to total assemblage productivity, NPP was measured in plots with the sub-canopy, for each canopy-forming species, and compared to the NPP of the canopy former alone (i.e., each canopy-forming macroalgae in plots with the sub-canopy removed). The difference between the two was calculated as the proportional contribution of the sub-canopy to assemblage NPP, thereby taking into account differences in maximum NPP of each canopy-forming species.

2.4. Primary productivity model

To estimate primary productivity on an ecologically relevant scale, we used *in situ* irradiance collected at the Moeraki Peninsula between 2010 and 2011, to model NPP of the three canopy-forming macroalgae and the associated sub-canopy assemblage. Irradiance was logged every 5 min from April 2010 till April 2011 with HOBO (Onset Corporation) data loggers. Loggers were deployed in the low intertidal in stainless steel mesh cages, with the light sensor unobstructed and facing vertically. To convert light intensity measured as lumen/ft\(^2\) by HOBO data loggers to PAR irradiance, we cross-calibrated three HOBO loggers with a LiCor (LI-192 quantum sensor) PAR sensor in seawater. The light sensors were cleaned monthly for fouling during the spring–summer months (September till February) and bi-monthly during autumn–winter (March till August). An exponential function was fitted to the raw HOBO data to convert lumen/ft\(^2\) to PAR (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)), similar to Long et al. (2012), shown by the following equation:

$$ \text{PAR} = (A_1 - Y_0)(1 - \exp(T_c \text{HOBO})) $$

[2]

where \( A_1, Y_0, \) and \( T_c \) are constants (2337, –7.837 and 8.0 \( \times \) \( 10^{-5} \), respectively), and HOBO is the light intensity measured by the HOBO loggers in lumen/ft\(^2\). Once the data were converted to PAR, rates of primary productivity at each recorded light intensity were estimated using Eq. (1) for each replicate assemblage (\( n = 3 \) for each canopy-forming species). Although the HOBO loggers are unable to provide an integrated light intensity measure, but instead log events, values of light intensity compared well with the LiCor sensor following manual calibration (Long et al., 2012).

Carbon fixation was modeled by extrapolating NPP from *in situ* irradiance on a daily basis and summed for a whole year for all three canopy-forming species and their associated assemblages. However, due to the annual life-cycle of *U. pinnatifida*, NPP was modeled only for the 6 months (July till December) when it occurs at high densities and biomass (Schiel and Thompson, 2012). Although temperature (Tait and Schiel, 2013) and desiccation (Matt and Chapman, 1995) are important modifiers of macroalgal primary productivity, these assemblages were present in the low intertidal and were emersed for approximately 4–8 h per month during the winter–spring growing season of *U. pinnatifida*. However, since we did not measure emersed primary productivity, the model assumed constant submergence, which in some fucoid assemblages may approximate realistic values of NPP (Gollety et al., 2008). Seasonal
2.5. Statistical analysis

Differences in photosynthetic parameters ($\alpha$, $P_m$, $R$, $E_e$) and annual NPP were analyzed using ANOVA, with species (U. pinnatifida, C. torulosa, and D. antarctica) as fixed factors. Sub-canopy contribution under the three canopy-forming species was analyzed by one-way ANOVA and Tukey's post hoc tests.

To evaluate the sensitivity of the total daily fixed carbon model to the photosynthetic parameters, we examined the slope of the daily NPP response to the range of parameter values (Appendix 1). The parameter values were the upper and lower 95% confidence intervals and the mean values for light-use efficiency ($\alpha$), maximum NPP ($P_m$), and respiration ($R$). To calculate the variation in NPP, two of the three parameters were varied while keeping the target parameter fixed at both lower 95% confidence, upper 95% confidence, and the mean. To compensate for the increased probability of type I error, significance tests were considered robust if $p < 0.01$ instead of $p < 0.05$.

The sensitivity of NPP to the three photosynthetic parameters on NPP was tested by analyzing the slopes of the NPP response to the calcuated range of the parameters. Slopes of the linear regressions were analyzed for each of the three species using ANOVA and the mean. To compensate for the increased probability of type I error, significance tests were considered robust if $p < 0.01$ instead of $p < 0.05$.

3. Results

Assemblages dominated by U. pinnatifida, C. torulosa, and D. antarctica contained a variety of sub-canopy species, dominated by the turf forming coralline alga, C. officinalis, ephemeral species such as Lophothamnion hirund, and fucoid algae such as Xiphophora gladiata and Cystophora retroflexa (Table 1). While species composition differed between assemblages dominated by different canopy species, the total biomass of the sub-canopy within incubation plots was not significantly different between assemblages dominated by U. pinnatifida, D. antarctica, and C. torulosa ($F_{2,12} = 2.6$, $p = 0.12$).

3.1. Photosynthetic performance

$P-E$ curves fitted for each macroalgal assemblage had subtle differences in shape (Fig. 2). In particular, assemblages dominated by C. torulosa and D. antarctica showed no signs of saturation, whereas U. pinnatifida showed saturated NPP at high light intensities (>1000 µmol m$^{-2}$ s$^{-1}$).

Photosynthetic efficiency ($\alpha$, Fig. 3A) varied between assemblages of D. antarctica, C. torulosa, and U. pinnatifida ($F_{2,12} = 11.3$, $p = 0.0017$), with U. pinnatifida showing the highest light-use efficiency. Maximum NPP ($P_m$, Fig. 3B) was higher in D. antarctica assemblages than those dominated by C. torulosa and U. pinnatifida ($F_{2,12} = 4.6$, $p = 0.032$).

Respiration rates ($R$, Fig. 3C) were highest in U. pinnatifida and lowest in C. torulosa ($F_{2,12} = 14.8$, $p = 0.0006$). Compensating irradiance ($E_c$, Fig. 3D) also varied between species ($F_{2,12} = 4.1$, $p = 0.044$), with C. torulosa showing the highest compensating irradiance and D. antarctica showing the lowest compensating irradiance. Combined, these results showed that all photosynthetic parameters varied between species, with U. pinnatifida showing higher respiration rates and higher photosynthetic efficiency than the native canopy-forming macroalgal species.

3.2. Sub-canopy contribution to assemblage NPP

The sub-canopy contribution to total assemblage NPP was more than twice as high in assemblages dominated by C. torulosa and U. pinnatifida than in D. antarctica dominated assemblages (Fig. 4). The sub-canopy beneath a D. antarctica assemblage contributed only 7.5% ($\pm 2.0$ SE) of total fixed carbon, but beneath an overlying canopy of C. torulosa and U. pinnatifida, the sub-canopy contributed 23.3 ($\pm 2.2$ SE) and 16.1% ($\pm 1.9$ SE), respectively, of the total carbon fixed ($F_{2,8} = 16.0$, $p = 0.004$), Tukey’s post hoc test showed differences among U. pinnatifida and D. antarctica ($q = 4.6$, $p = 0.04$) and among C. torulosa and D. antarctica ($q = 8.0$, $p = 0.01$).

3.3. Modeled daily and annual primary productivity

NPP extrapolated from incident irradiance showed varying daily NPP of the three canopy-forming species (Fig. 5). Days of extensive cloud cover, coupled with high tides during peak irradiance (i.e., midday zenith), often resulted in net carbon loss because light intensity was on average lower than assemblage compensating irradiance ($E_c$), particularly for U. pinnatifida during late winter (Fig. 5A). Although C. torulosa had the lowest $P_m$, it had less variation in daily fixed carbon across the 6-month period, whereas D. antarctica had the highest overall carbon fixation rates and the highest day to day variability. Sub-canopy contribution to total NPP showed that while D. antarctica assemblages had the highest total NPP, the contribution of the sub-canopy was small (0.3 $\pm$ 0.1 g C m$^{-2}$ annum$^{-1}$) and similar to that of U. pinnatifida (0.2 $\pm$ 0.07 g C m$^{-2}$ annum$^{-1}$). However, sub-canopy contribution of U. pinnatifida assemblages per annum would be expected to increase dramatically given the loss of U. pinnatifida canopies for up to 6 months.

During maximum U. pinnatifida biomass (i.e., winter–spring), daily carbon fixation of U. pinnatifida averaged 8 g C m$^{-2}$ day$^{-1}$, which equated to 1.5 kg m$^{-2}$ annum$^{-1}$ (Fig. 5D). Daily carbon fixation of C. torulosa averaged 6.5 g C m$^{-2}$ day$^{-1}$ and 2.5 kg m$^{-2}$ annum$^{-1}$ (Fig. 5E). D. antarctica had the highest daily rates of carbon fixation, with an average of 10 g C m$^{-2}$ day$^{-1}$ and 4 kg m$^{-2}$ annum$^{-1}$ (Fig. 5F). Average daily NPP varied between species ($F_{2,12} = 4.1$, $p = 0.045$) as did annual NPP ($F_{2,12} = 3.9$, $p = 0.05$).
4. Discussion

Overall, our results predict lower annual rates of carbon fixation by the invasive Undaria pinnatifida relative to two native fucoid dominated assemblages in southern New Zealand. However, despite the limited growing season, U. pinnatifida assemblages were almost as productive as assemblages dominated by the perennial C. torulosa. Studies that have tested for impacts of U. pinnatifida on plant community composition show mixed results (Casas et al., 2004; Curiel et al., 1998; Forrest and Taylor, 2002; Valentine and Johnson, 2005), but our research indicates that U. pinnatifida has the potential to alter ecosystem processes compared to non-invaded baseline conditions. Furthermore, the lack of displacement of native canopy-forming algae (Forrest and Taylor, 2002; Thompson and Schiel, 2012; Valentine and Johnson, 2005) suggests that invasion of rocky intertidal systems by U. pinnatifida may result in a net gain in carbon production and export.

U. pinnatifida has invaded temperate coastal habitats worldwide (Russell et al., 2008; Thompson and Schiel, 2012; Valentine and Johnson, 2003), and its success is often attributed to high growth rates and an annual life history capable of keying into disturbances (Schiel and Thompson, 2012; Valentine and Johnson, 2003). While U. pinnatifida averaged higher daily rates of carbon fixation than C. torulosa during peak abundance, its annual life history resulted in reduced annual NPP compared to the two native perennial fucoids. Although C. torulosa and D. antarctica are susceptible to partial mortality through physical disturbance (Schiel, 2006), herbivory (Taylor and Schiel, 2010), and large-scale loss due to major storm events (Schiel, 2011), turnover rates of annual species such as U. pinnatifida are inherently higher (Pedersen et al., 2005). Furthermore, constant erosion of tissue at the distal margins of U. pinnatifida (Stuart et al., 1999) like other kelps (de Bettignies et al., 2013; Krumhansl and Scheibling, 2012b) may represent an important addition to suspended particulate organic carbon (POC) and nitrogen (PON), although Yorke et al. (2013) estimated that only <0.2% of the POC at Mohawke Reef (California, USA) was from the giant kelp Macrocystis pyrifera. However, POC and PON from macroalgae have been shown to be an important dietary component of filter feeding invertebrates (Hill et al., 2006), and alterations in the dynamics of carbon cycling could have beneficial or deleterious impacts depending on the scale considered and the organisms directly and indirectly impacted.

The transfer of resources across habitats plays a vital role in shaping ecological patterns and processes (Heck et al., 2008), and adjacent ecosystems can be reliant upon the export of kelp detritus (Dugan et al., 2003; Duggins et al., 1989; Vanderklift and Wernberg, 2008). Variation in the bioavailability and breakdown of detritus from laminarian and fucoid algae (Hulatt et al., 2009) may have important implications for secondary production and the suites of species either benefiting or harmed by alterations to resource quality and quantity. While autotrophic invaders are expected to have strong negative effects on the same trophic levels, higher trophic levels are likely to be less negatively affected (Thomsen et al., 2014), but the consequences of such changes although beneficial for some species can reverberate in unknown ways through ecosystems.
Our results demonstrate the utility of using photosynthetic parameters to identify potential changes to biogeochemical cycles caused by invasive canopy-forming macroalgae relative to native competitors. While *Undaria pinnatifida* had higher light-use efficiency (\(\alpha\)) than *C. torulosa* and *D. antarctica*, differences in respiration rate and maximum NPP among these species resulted in similar modeled NPP. Also, of the three canopy-forming species, *D. antarctica* had the greatest effect on sub-canopy contribution, whereas *U. pinnatifida* and *C. torulosa* both supported high sub-canopy contribution (with >15% of the total assemblage NPP compared to <10% for *D. antarctica*). This is likely caused by different levels of canopy shading, with the thick, broad thalli of *D. antarctica* absorbing a larger proportion of light. Variations in the shape of \(P-E\) curves between species, particularly at high irradiance (Tait and Schiel, 2011b), are likely to be associated with sub-canopy light fields, including self-shading of the canopy species (Sand-Jensen et al., 2007; Stewart and Carpenter, 2003). Examining photosynthetic properties of the invaded assemblages provides an estimation of the impacts of NIS on ecosystem function that measurements of biodiversity (or related metrics) are often unable to uncover (Didham et al., 2005). We encourage the use of biogeochemical measures of NIS contribution to ecosystem properties in order to uncover their impacts on marine systems that may not be directly apparent from other metrics of impact.

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Appendix 1. Contribution of photosynthetic parameters to the production model

All three photosynthetic parameters had an influence on total daily rates of carbon fixation, but respiration and light-use efficiency had the most dramatic impact on the slope of the average daily NPP response (Fig. 6). Light-use efficiency of *in situ* assemblages had a large influence on modeled rates of carbon fixation. Maximum NPP (\(P_m\)) affected daily rates of carbon fixation for *in situ* assemblies of all three species (*D. antarctica*; \(F_{1,13} = 4.3, p = 0.06, r^2 = 0.25\); *U. pinnatifida*, \(F_{1,13} = 5.0, p = 0.04, r^2 = 0.28\); Cystophora torulosa, \(F_{1,13} = 5.0, p = 0.04, r^2 = 0.28\)). Respiration rates had a little effect on modeled carbon fixation of *D. antarctica* (in situ \(F_{1,7} = 2.9, p = 0.11, r^2 = 0.18\)) but greatly affected modeled carbon fixation of *U. pinnatifida* and *C. torulosa* (in situ \(F_{1,7} = 12.5, p = 0.004, r^2 = 0.49\); *C. torulosa*, \(F_{1,7} = 10.0, p = 0.008, r^2 = 0.43\)). Taken together, these results showed that respiration rate (\(R\)) and light-use efficiency (\(\alpha\)) are major determinants of net carbon fixation, but differences between laboratory and *in situ* results have the potential to dramatically affect estimations of carbon fixation.

(See Appendix 1.)
Appendix 1. Sensitivity of daily rates of carbon fixation to variation in the three photosynthetic parameters used to generate modeled NPP. Variation in light-use efficiency ($\alpha$), maximum NPP ($P_{\text{MAX}}$), and respiration rate ($R$) were generated using 95% confidence intervals (minimum and maximum) for Undaria pinnatifida (panels A, D, and G), Cystophora torulosa (panels B, E, and H), and Durvillaea antarctica (panels C, F, and I).

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