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

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ABSTRACT

Carbon flow is essential to the function of all ecosystems, yet there is little mechanistic understanding of how non-indigenous macroalgae 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* photorespirometry to compare rates of net primary productivity (NPP) of assemblages dominated by *U. pinnatifida* and two native canopy-forming species, *Cystophora torulosa* and *Durvillaea 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.

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., 1999; 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 (Eriksson 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

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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 fucoids) in the intertidal and upper sub-tidal zones of much of southern New Zealand (up to 80 kg per m^2 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 Hurd, 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 Kautsky, 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* photorespirometry 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) gridded 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(R) 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

Fig. 1. *In situ* photorespirometry chamber fitted around a macroalgal assemblage, dominated by *Undaria pinnatifida* at 'The Point' Moeraki, New Zealand.