

Transient effects of an invasive kelp on the community structure and primary productivity of an intertidal assemblage

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Abstract. Invasive species can have significant impacts on the diversity and productivity of recipient ecological communities. The kelp *Undaria pinnatifida* (Harvey) Suringar is one of the world's most successful invasive species but, although its purported impacts are strong, there is little empirical evidence that it displaces native species. Furthermore, as this species naturalises in local communities, its potential effects on community dynamics have not been well tested. Here, we test the ecological impacts of *Undaria* in intertidal communities in southern New Zealand using a combination of surveys, a 2.5-year press-removal experiment and *in situ* measures of net primary production to gauge its impact on community structure and productivity. *Undaria* had transient effects on the composition of communities, affecting two seasonally abundant species in 1 year, but these impacts did not persist into the following year. Overall, there were only small effects of *Undaria* removal on diversity and abundance of native algae and invertebrates at two sites. However, the presence of *Undaria* more than doubled net primary production of recipient communities during its annual peak abundance when it increased biomass by 606 g DW m⁻². We conclude that the invasion of *Undaria* represents an additional and substantial carbon subsidy to coastal ecosystems with potentially positive effects on nearshore productivity.

Additional keywords: intertidal biodiversity, net primary production, NPP, *Undaria pinnatifida*.

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Introduction

Numerous ecological communities around the world contain non-indigenous species that have become naturalised (Richardson *et al.* 2000). To become naturalised in an exotic location, a non-indigenous species must transition through a series of stages, beginning with transport from its place of origin, release and introduction to its new recipient habitat, followed by establishment of local self-sustaining populations and secondary dispersal to adjacent regions (Blackburn *et al.* 2011). As naturalisation progresses, non-indigenous species can affect the structure and functioning of resident communities (Hulme *et al.* 2013) and impacts may change over time (Strayer *et al.* 2006) depending on the attributes of the invader and of the invaded system as well as on the abiotic environment (Thomsen *et al.* 2011). Testing how non-indigenous species interact and function in their new environment is therefore essential to understanding the long-term consequences of species invasions and,

more generally, the ecology and function of the recipient community following invasion.

The underlying mechanisms that determine the success of non-indigenous species are becoming increasingly understood because transport vectors (Floerl and Inglis 2005), dispersal (McQuaid and Phillips 2000) and establishment (Shinen and Morgan 2009) have been studied in detail in the early invasion phases. By contrast, less is known about how non-indigenous species affect native communities and ecosystem functions, such as provision of biogenic habitat and primary productivity (Crooks 2002). Invasion impacts are known to be variable in magnitude and direction, and to be strongly context-dependent (Thomsen *et al.* 2011; Vilà *et al.* 2011; Hulme *et al.* 2013; Tamburello *et al.* 2013). However, invasion impact studies, particularly those using manipulative experiments, are typically short in duration (Strayer *et al.* 2006), documenting community impacts that might be acute rather than chronic, or *vice versa*

(Simberloff and Gibbons 2004; Strayer *et al.* 2006). Furthermore, impacts of invasions can be difficult to disentangle from other co-occurring natural, anthropogenic or synergistic stressors, leading to uncertainties over whether an invasive species was the cause or effect of ecosystem change (Didham *et al.* 2005; MacDougall and Turkington 2005; Bulleri *et al.* 2010).

Whereas impacts of non-indigenous species on resident communities have been increasingly addressed in experimental studies (Thomsen *et al.* 2014a), invasion impacts on functional aspects of communities have often been overlooked (Crooks 2002; Buschbaum *et al.* 2006). Non-indigenous species can alter ecosystem functioning through changes to species composition, productivity and biomass and, in turn, food availability, habitat provision and the quantity and quality of exported detrital material (Pedersen *et al.* 2005; Krumhansl and Scheibling 2011). In marine systems, in particular, ecosystem engineers, such as canopy-forming macroalgae, regulate biogeochemical cycles through processes associated with uptake, transport and release of carbon, nutrients and oxygen (Crooks 2002; Wallentinus and Nyberg 2007). To better understand the range and complexity of impacts from non-indigenous species, impacts on resident community structure and ecosystem function (e.g. community productivity and respiration) should be considered in concert.

The laminarian alga *Undaria pinnatifida* (Harvey) Suringar is considered one of the world's most invasive species (Lowe *et al.* 2000), has increased its range over much of the temperate zone over the last 30 years (Hay and Luckens 1987; Fletcher and Manfredi 1995; Casas and Piriz 1996; Campbell and Burridge 1998; Curiel *et al.* 1998; Castric-Fey *et al.* 1999; Aguilar-Rosas *et al.* 2004), and has been present in New Zealand since 1987 (Hay and Luckens 1987). *Undaria* is an annual species with a peak in abundance over spring and early summer; a few studies have documented overlapping generations (Hay and Villouta 1993) or multiple cohorts (Schiel and Thompson 2012). Experimental work testing effects of disturbances in stands of canopy-forming algae suggests that *Undaria* is a 'fugitive' species that colonises patches where native canopy-formers have been disturbed or removed (Valentine and Johnson 2003, 2004; Thompson and Schiel 2012). Furthermore, the timing of disturbance relative to favourable recruitment conditions (e.g. cold water temperatures) is important for recruitment success, and the abundance of *Undaria* has been shown to decline with increasing dominance of native canopy-formers (Valentine and Johnson 2003; Thompson and Schiel 2012).

Undaria can attain high abundance in the absence of native canopy-formers or where patches in algal stands are created. In subtidal habitats, for example, three studies have removed *Undaria* canopies experimentally. Casas *et al.* (2004), in Argentina, and Valentine and Johnson (2005), in Tasmania, respectively found negative and neutral effects on resident plant communities. Also in Argentina, Irigoyen *et al.* (2011) found positive effects of *Undaria* on macroinvertebrate richness and diversity. Invasion impacts inferred from mensurative studies appear to be similarly ambiguous, with studies concluding that both negative (Battershill *et al.* 1998) and neutral (Forrest and Taylor 2002) effects occur on resident algal communities. In intertidal areas of southern New Zealand, Schiel and Thompson (2012) showed experimentally that *Undaria* invaded even small

gaps in the native fucoid canopies but was unable to hold this space as native fucoids recruited and grew. The presence of *Undaria* was therefore facilitated by disturbances in native canopies, but the invasive kelp was a poor competitor. Given the work done to date, we expect that *Undaria*'s high growth rates (Schiel and Thompson 2012), rapid nutrient uptake (Dean and Hurd 2007) and high abundance in spring, could lead to substantial subsidies to coastal production through increases in *in situ* (Sfriso and Facca 2013) and exported biomass. However, we are not aware of any study that has quantified *in situ* whole plant estimates of net primary production in areas invaded by *Undaria*.

Here, we tested the impact of *Undaria* on resident community structure and productivity (measured as biomass and net primary production) 8 years after its initial invasion of open coast reefs. We use a long-term press-removal experiment to test the null hypotheses that *Undaria* has no effect on rocky shore intertidal biodiversity or on the abundance of native canopy-forming species. From survey data, we describe patterns of occurrence and biomass. These data are then used to estimate standing stocks and sequestered tissue carbon and nitrogen. Finally, we assess the extent to which *Undaria* contributes to net primary production and discuss the implications of its community effects on coastal production.

Materials and methods

Study sites

This study was done at two sites situated ~1 km apart on the Moeraki Peninsula (45°25'S, 170°51'E) in south-eastern New Zealand. The sites are categorised as semiexposed with swells generally less than 1 m but occasionally up to several metres high (cf. Schiel 2011). Both sites have extensive limestone and conglomerate rock platforms that are dominated in the low intertidal zone by stands of the fucoid 'bull kelp' *Durvillaea antarctica* (Chamisso) Hariot and, in the late-winter to early summer, also by the invasive kelp *Undaria pinnatifida*. See Lilley and Schiel (2006) and Schiel (2006) for fuller descriptions of sites in this area.

Undaria was first reported at Moeraki in 1995, but it did not reach the open coast outside the harbour until 2006, a process that was observed during extensive studies in the area, from the early 1990s onwards (Taylor and Schiel 2005; Schiel 2006, 2011). At least seven species of canopy-forming fucoid algae are found in the intertidal zone of these sites, including *Hormosira banksii* (Turner) Decaisne and several species of *Cystophora*. Prior to invasion by *Undaria*, patches of reef not dominated by fucoids had a virtually complete primary cover of the turfing alga *Corallina officinalis* Linnaeus, which, along with other coralline algae and their algal epiphytes, also dominate the primary benthic cover beneath macroalgal canopies. *Undaria* has since recruited heavily into patches dominated by geniculate coralline algae and in gaps in the native canopy-formers in the low intertidal and shallow subtidal zones (Russell *et al.* 2008; D. R. Schiel, unpubl. data).

Characteristics of invaded habitat

As a precursor to assessing the community effects of *Undaria*, we surveyed the total area covered by *Undaria* and native canopy-forming algae at the two sites by mapping the perimeters

of all contiguous stands of large algae using a Trimble RTK GPS (Trimble Navigation Ltd, Sunnyvale, CA, USA) at Site 1 (September 2012 and October 2013) and Site 2 (September 2012; bad weather made it impossible to repeat in October 2013). These months are when *Undaria* has its greatest cover on reefs (Thompson and Schiel 2012). Survey areas were 3250 m² in Site 1 and 4250 m² in Site 2. To estimate cover and biomass of *Undaria* within individual stands we quantified percentage cover and density from 30 or more haphazardly placed 1-m² quadrats (within the invaded stands). From 100 randomly selected plants, we measured total length (cm), life stage (<10-cm recruits, >10-cm juveniles without a sporophyll, >10-cm adults with sporophyll) and biomass (wet and dry weights, for which algae were dried at 50°C for 72 h). Tissue carbon and nitrogen were quantified in a random subset of plants ($n = 38$) with a Europa Scientific 20/20 isotope analyser (Sercon, Crewe, UK; analyses were done by Waikato Stable Isotope Unit, University of Waikato, New Zealand). Survey and morphometric data were combined to estimate biomass and tissue carbon and nitrogen (m⁻²) in the study sites.

Press-removal experiment

To test the responses of the native community to removal of *Undaria*, 10 haphazardly positioned 1-m² plots were established within dense stands of *Undaria* in September 2011 at Site 1 and October 2011 at Site 2. The plots were randomly assigned to unmanipulated controls (hereafter '+*Undaria*', $n = 5$) and press removals (hereafter '-*Undaria*', $n = 5$). Each plot was 1–5 m from its nearest neighbour. Juvenile and adult *Undaria* plants were removed from the -*Undaria* plots by cutting across the haptera with a knife, whereas recruits were hand-picked. Removals were repeated 16 (Site 1) and 13 (Site 2) times over 2.5 years. During this period, community structure was sampled 10 times at Site 1 and 9 times at Site 2 (monitoring at Site 2 was limited by severe sea conditions). During sampling, percentage cover of all macroalgae and sessile invertebrates (>~5 mm) were estimated for each plot using a 1-m² gridded quadrat. Taxa were identified to the lowest possible resolution, usually to the species level, except for some sponges, hydroids and filamentous algal recruits that were identified to more coarse taxonomic groups. We also counted all mobile invertebrates >~5 mm (excluding cryptic epifauna such as amphipods and microgastropods) and individual plants of all laminarian and fucooid algae.

Net primary production

In situ incubations were used to determine the contribution of *Undaria* to net primary production (NPP) of plots with and without *Undaria* that were interspersed among our press-removal treatments. Incubations showed instantaneous saturated production of plots with and without *Undaria* (i.e. not annual productivity). Photorespirometry chambers were fixed to the reef, and filled with ambient seawater during incubations (see details of methods in Tait and Schiel 2010). Each chamber covered a surface area of 314 cm² and encapsulated the community of coralline turf algae and their epiphytes. +*Undaria* chambers included one adult plant (>30 cm with a sporophyll). Incubations were done in spring (September 2012 and October 2013) under moderate sunlight (500–1000 μmol m⁻² s⁻¹). Irradiance was measured with a Li-Cor light quantum sensor

(LI-192; Li-Cor, Lincoln, NE, USA). Incubations (+ and -*Undaria*, $n = 3$ per treatment) were done on 2 days (between 0900 and 1300 hours). Incubations were for less than 40 min to avoid supersaturation of oxygen or nutrient depletion (Tait and Schiel 2010). All incubations were completed as the rising tide surrounded the chambers during periods of similar light environment. Water samples were extracted from the chambers using a syringe, and oxygen concentration was measured using a Hach LDO meter (HQ40d; Hach Pacific – New Zealand, Auckland, New Zealand). NPP was estimated as the increase in oxygen concentration after 20 and 40 min of incubation (Tait and Schiel 2010). Changes in dissolved oxygen over time were converted to changes in carbon uptake using a P : Q (photosynthetic quotient) ratio of 1 : 1 (Kirk 1994) and standardised to carbon uptake per square metre of reef surface (g C m⁻² h⁻¹) or biomass (g DW⁻¹ h⁻¹) of algal tissue.

Statistical analyses

The press-removal experiment was analysed with repeated-measures analysis of variance to test the effects of site ($n = 2$) and treatment (presence or absence of *Undaria*; $n = 2$) on fixed plots through time ($n = 9$). Experimental monitoring at Site 1 in October 2013 was removed to balance the design across sites. Where data did not conform to the assumptions of homogeneity (Cochran's $P > 0.05$) they were $\log(x + 1)$ (for count data) or arcsine-square-root (for percentage cover data) transformed before analysis. If this did not achieve homogeneity, the P -value was reduced to 0.01. Where data did not conform to the assumption of sphericity (Mauchly test, $P < 0.05$), Wilks' Lambda multivariate test for repeated-measures was used to alter the error degrees of freedom, thereby reducing the chance of a Type I error. Permutation analysis of variance (PERMANOVA) was used to test the treatment effects in the press-removal experiment across the entire community assemblage, with treatment (+ and -*Undaria*, fixed), sites (Sites 1 and 2, random) and time (10 at Site 1, 9 at Site 2, random), using Bray–Curtis measure of similarity on square-root-transformed data. The relative contribution of the species responsible for significant effects was assessed using the SIMPER function in PRIMER 6 (PRIMER-E, Ivybridge, UK). Data were visualised using principal components analysis done on centroids for each site × treatment × time combination. The homogeneity of multivariate dispersion or the variability in community composition in time across treatments and sites was measured using the PERMDISP function (in PERMANOVA+, PRIMER-E). For periods when the impacts of treatments on communities were greatest, data were reanalysed with a less conservative two-way ANOVA with site (Sites 1 and 2, random) and treatment (+ and -*Undaria*, fixed).

Finally, NPP data were standardised for carbon production by reef area (m²) and biomass of algal tissue (g DW). Differences between incubations with and without *Undaria* were analysed with Student's t -tests (pooling data for the 2 years).

Results

Invaded habitat characteristics

The total area covered by macroalgae was 373 m² in 2012 and 299 m² in 2013 at Site 1, and 794 m² at Site 2. At Site 1, *Undaria*

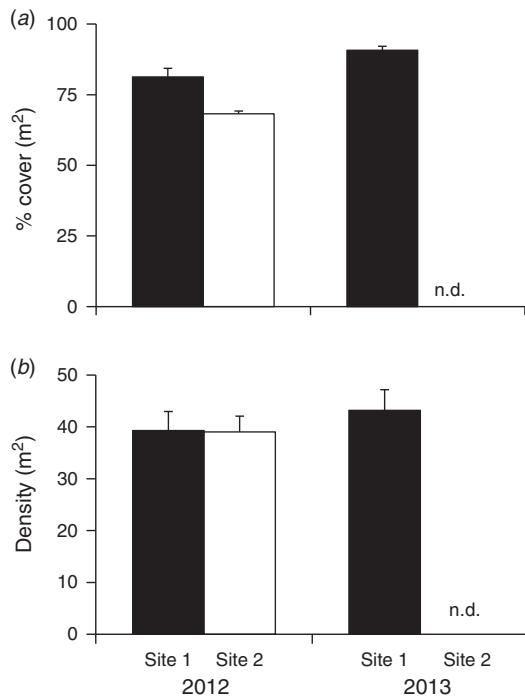


Fig. 1. Mean (+s.e.) *Undaria pinnatifida* percentage cover (a) and density per square metre (b) in stands of *Undaria* in the low intertidal zone at two sites on the Moeraki Peninsula in 2012 and 2013.

comprised 42% (2012) and 45% (2013) of the total macroalgal cover. Within *Undaria* patches at Site 1, its mean cover (Fig. 1a) was $81.3\% \pm 3.02$ (s.e.) (2012) and $90.7\% \pm 1.4$ (2013) and mean density (Fig. 1b) was 39.3 ± 3.71 (2012) plants m^{-2} and 43.2 ± 3.96 (2013). At Site 2, *Undaria* comprised 47% of the total macroalgal cover, with an average cover (Fig. 1a) of $68.2\% \pm 3.59$ and a density (Fig. 1b) of 39.1 ± 3.04 plants m^{-2} in *Undaria* patches. Within the mapped *Undaria* stands, the biomass of *Undaria* was estimated to be 606 (Site 1, 2012), 492 (Site 1, 2013) and 725 (Site 2, 2012) g DW m^{-2} . Percentage carbon of *Undaria* tissue was $28.6\% \pm 0.19$ and percentage nitrogen was $2.1\% \pm 0.03$. Within the mapped *Undaria* stands of Site 1 (2013), for example, these tissue nutrient values (per algal frond) correspond to 140.5 g C DW and 2.66 g N DW per square metre of reef.

Press-removal experiment

The cover of *Undaria* in the removal plots was greatly reduced compared with +*Undaria* plots at the two sites ($F_{8,5} = 125.0$, $P < 0.001$) (Table 1, Fig. 2a), thereby verifying that our press-removal treatment worked. *Undaria* peaked in abundance during September–December (austral spring to early summer), senesced in late summer, and had lowest abundance (<5%) during autumn (Fig. 2a). It should be noted that the cover of *Undaria* in March 2014 at Site 1 was due to a pulse of early recruitment (Fig. 2a, b). In total, 2643 *Undaria* plants were removed from Site 1 plots and 651 from Site 2 (Fig. 2b).

Considering the entire dataset, there were few effects of *Undaria* removal on the main groups of species tested, with no significant treatment or treatment \times site interactions (Table 1). By contrast, most variables showed significant time and site

effects, and there were a few significant three-way interactions of time, site and treatment. The *Undaria* removal had no significant effect on the cover of fucoid algae at either site. However, the common red alga *Lophothamnion hirtum* (J.D. Hooker & Harvey) Womersley had a seasonal peak in cover in the –*Undaria* plots at Site 1 during spring–summer 2013 (Fig. 2d) driving a significant site \times treatment interaction ($F_{1,14} = 6.75$, $P = 0.02$) when *Undaria* had its peak cover. The ephemeral brown alga *Leathesia difformis* Areschoug also had short peaks in cover in –*Undaria* plots at both sites (Fig. 2e), with significant site and time effects (Table 1) and a significant treatment effect at Site 1 in late summer ($F_{1,14} = 5.7$, $P = 0.03$, March data only) 2013. The cover of all native algae combined (excluding coralline taxa that occupied $\sim 100\%$ of basal substrata in all plots) showed a significant site \times time interaction (Fig. 2f, Table 1). Again, during peak *Undaria* abundance in December 2013, the total cover of native algae peaked in –*Undaria* plots, driving a significant site \times treatment interaction ($F_{1,14} = 5.18$, $P = 0.04$).

All measures of algal and invertebrate species richness and diversity showed site and time effects (Fig. 3, Table 1). During winter (July) 2013, there was a significant site \times treatment effect on algal richness ($F_{1,16} = 26.5$, $P = 0.02$), but the greatest effect was seen in the Shannon diversity index for algae in early summer (December) 2013 (treatment \times site $F_{1,14} = 11.0$, $P = 0.005$), with relatively low algal diversity in +*Undaria* treatments of Site 1. Invertebrate species richness and diversity were generally greater at Site 1. During the early summer period, the Shannon diversity index for invertebrates showed a significant treatment \times site effect ($F_{1,14} = 6.13$, $P = 0.03$), with particularly low diversity in the +*Undaria* treatments of Site 2.

On only two of the 10 monitoring times were there differences in the community composition between treatments, and these were only at Site 1 (treatment \times site, pseudo- $F_{8,54} = 4.9$, $P < 0.01$) (Fig. 4). Overall, the trajectories of the assemblages were remarkably similar between treatments, with most of the variation in community composition occurring through time. There was, however, significantly greater variation in the –*Undaria* plots compared with the +*Undaria* plots through time at Site 2, but not at Site 1 (PERMDISP: $F_{3,176} = 9.4$, $P < 0.001$; pairwise tests between treatments in Site 2: $t = 4.3$, $P < 0.001$) (Fig. 4). On those two occasions where there were treatment differences at Site 1, the SIMPER analysis suggested that these were driven primarily by increases in cover of *L. hirtum*, *L. difformis* and the perennial fucoid *Cystophora torulosa* (R. Brown ex Turner) J. Agardh, and a decrease in the abundance of the turbinid gastropod *Lunella smaragdus* Gmelin in –*Undaria* plots.

Net primary production

As expected, there was a significant increase in NPP when *Undaria* was present compared with when it was absent from assemblages (Fig. 5). At both sites, NPP was ~ 2.5 times greater when *Undaria* was present whether standardised by area ($g\ C\ m^{-2}$) ($t = 4.1$, d.f. = 10, $P < 0.01$) or biomass ($mg\ C\ g\ DW^{-1}\ h^{-1}$) ($t = 5.9$, d.f. = 10, $P < 0.001$). By combining survey, morphometric and NPP data we estimate that NPP of *Undaria* at Site 1 was $\sim 220\ g\ C\ h^{-1}$ in September 2012 and $\sim 150\ g\ C\ h^{-1}$ in October 2013.

Table 1. Results from repeated-measures ANOVA testing the effects of site ($n = 2$) and treatment ($n = 2$) in fixed plots through time ($n = 9$) on percentage cover of *Undaria pinnatifida*, Fucales, *Lophothamnion hirtum*, *Leathesia difformis* and total native algae, species richness of algae and invertebrates and Shannon diversity index (H') for algae and invertebrates

Where Cochran's test for homogeneity was not fulfilled, α was reduced to 0.01. Significant results are shown in bold

Source	d.f.	m.s.	<i>F</i>	<i>P</i>	m.s.	<i>F</i>	<i>P</i>	m.s.	<i>F</i>	<i>P</i>
		% <i>Undaria</i>			% Fucales			% <i>Lophothamnion</i>		
Treatment	1	23 492.42	125.03	<0.001	264.41	0.59	0.46	293.46	3.95	0.07
Site	1	1587.83	8.45	0.013	500.86	1.12	0.31	1689.44	22.76	<0.001
Site × Treatment	1	1613.14	8.59	0.010	333.86	0.75	0.40	142.54	1.92	0.19
Error	12	187.89			447.16			74.22		
Time	8	7494.76	140.7^A	<0.001	115.71	2.7 ^A	0.13	1282.74	17.4^A	<0.001
Time × Site	8	1417.31	61.5^A	<0.001	141.00	4.1 ^A	0.07	584.78	3.9 ^A	0.08
Time × Treatment	8	1813.84	126.0^A	<0.001	22.08	0.9 ^A	0.57	146.40	2.9 ^A	0.13
Time × Site × Treatment	8	991.30	30.6^A	<0.001	79.57	5.2^A	0.04	98.08	0.8 ^A	0.64
Error	96	68.18			22.49			37.38		
		% <i>Leathesia</i>			% total native algae			Algal richness		
Treatment	1	109.33	3.18	0.10	5598.3	3.39	0.90	4.18	0.19	0.66
Site	1	860.74	25.06	<0.001	23 139.8	14.00	0.002	252.83	11.57	<0.001
Site × Treatment	1	0.12	<0.01	0.95	95.6	0.06	0.81	91.68	4.19	0.06
Error	12	34.34			1653.2			21.85		
Time	8	301.03	23.6^A	<0.001	3652.2	131.5^A	<0.001	189.63	47.77	<0.001
Time × Site	8	98.36	6.7 ^A	0.03	3327.5	9.5^A	<0.001	108.22	27.26	<0.001
Time × Treatment	8	132.96	6.3 ^A	0.03	466.2	8.3 ^A	0.010	2.75	0.69	0.70
Time × Site × Treatment	8	25.92	5.0 ^A	0.05	467.2	5.1 ^A	0.04	7.09	1.79	0.09
Error	96	16.91			158.3			3.97		
		Algal Shannon index			Invertebrate richness			Invertebrate Shannon index		
Treatment	1	0.29	1.14	0.31	3.50	0.20	0.67	0.05	0.13	0.72
Site	1	6.05	23.74	<0.001	232.72	13.01	0.003	2.85	7.56	0.02
Site × Treatment	1	0.17	0.68	0.43	10.84	0.61	0.45	0.29	0.77	0.40
Error	12	0.25			17.88			0.38		
Time	8	0.90	36.13	<0.001	36.43	11.55	<0.001	1.08	8.43	<0.001
Time × Site	8	0.70	27.89	<0.001	9.32	2.96	0.005	0.46	3.57	<0.001
Time × Treatment	8	0.03	1.03	0.42	2.44	0.77	0.63	0.17	1.36	0.22
Time × Site × Treatment	8	0.08	3.34	0.002	5.58	1.77	0.09	0.19	1.46	0.18
Error	96	0.02			3.15			0.13		

^ATests where the assumption of sphericity was not met and Wilks Lambda adjustment to the degrees of freedom (error d.f. adjusted to 5) made the test more conservative.

Discussion

It is clear that after being present for nearly two decades, *Undaria pinnatifida* is an abundant member of shallow coast benthic assemblages on Moeraki Peninsula. *Undaria* was highly abundant at our sites and along much of the coastline during its annual macroscopic phase and formed dense, closed canopies that persisted for ~5 months of each year. It has been suggested that this invasive kelp displaces native species with detrimental effects on community and ecosystem function (McLaughlan *et al.* 2014). However, we found little evidence to support this. Instead, we found that *Undaria* had few effects on diversity metrics and that it only temporarily affected the abundances of a few native seaweed species on rocky intertidal shores. In all cases, there was significant variability in effects through time, and occasionally significant site-to-site variability. Furthermore, *Undaria* had a significant positive effect on primary productivity when it was at peak abundance within the sites it occupied. These results suggest that the effects of *Undaria* are

additive rather than substitutive, as it did not displace native species but did provide biogenic habitat, biomass and significant inputs of carbon to the reef system. These often overlooked features of non-native species may well represent a net gain to communities and ecosystems. Given that it has generally proved to be impossible to eradicate *Undaria* (Forrest and Hopkins 2013), this may represent a less alarming set of consequences of invasion than is usually envisioned.

Given the life cycle and growth pattern of *Undaria*, there is more carbon, nitrogen and other nutrients sequestered on invaded shores for almost half of the year. Such biomass and nutrients can be redistributed locally through distal erosion (Dean and Hurd 2007; Schiel and Thompson 2012), and exported across the ecosystem as wrack to subsidise nutrients or habitat in other areas of the marine environment (Wernberg *et al.* 2006; Rodil *et al.* 2008; Britton-Simmons *et al.* 2009), as has been found for at least one other non-indigenous alga (Krumhansl and Scheibling 2012).

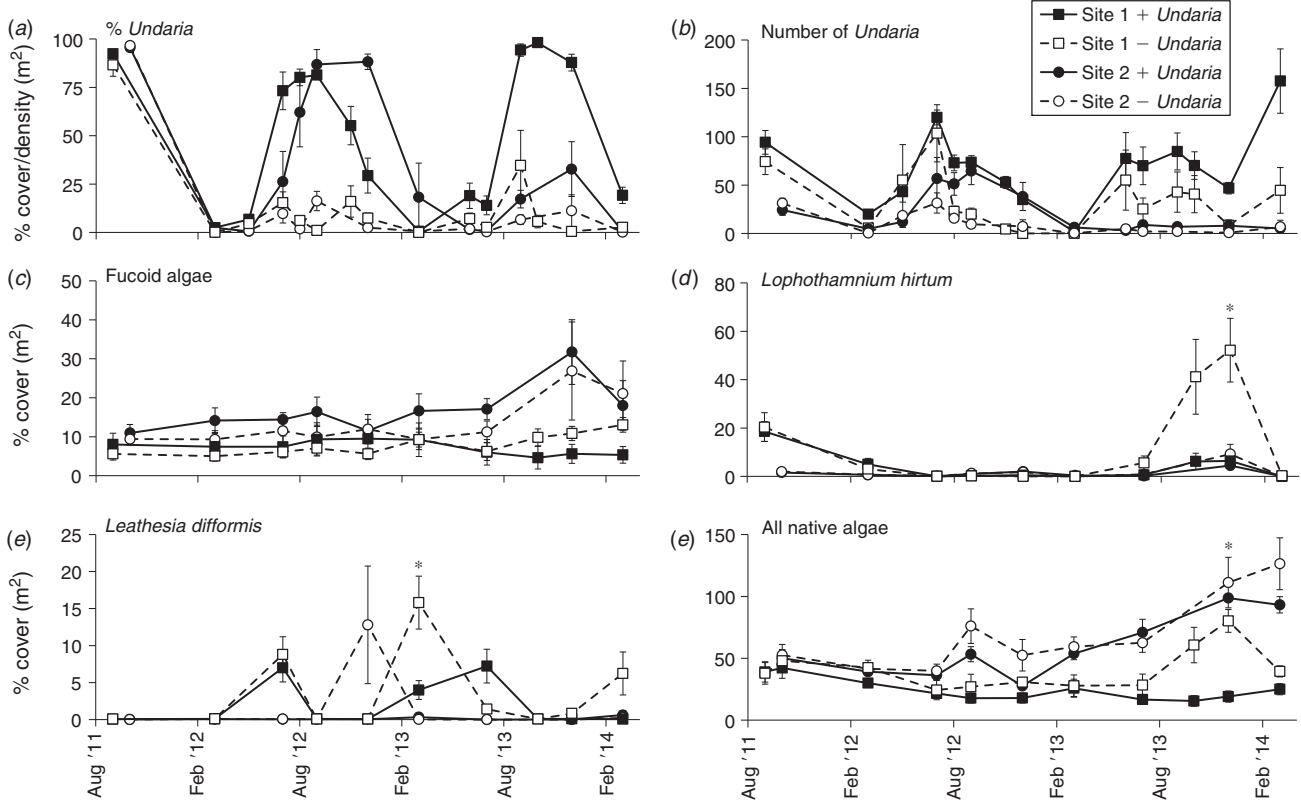


Fig. 2. Mean (\pm s.e.) percentage cover (a) and density per square metre (b) of *Undaria pinnatifida* and mean (\pm s.e.) percentage cover of fucoid algae (c), *Lophothamnium hirtum* (d), *Leathesia difformis* (e) and all native algae (f) in +*Undaria* and -*Undaria* plots at two sites on the Moeraki Peninsula. Note the different y-axis scaling. Asterisks indicate where *post hoc* analyses were done on sites and treatments at a particular date.

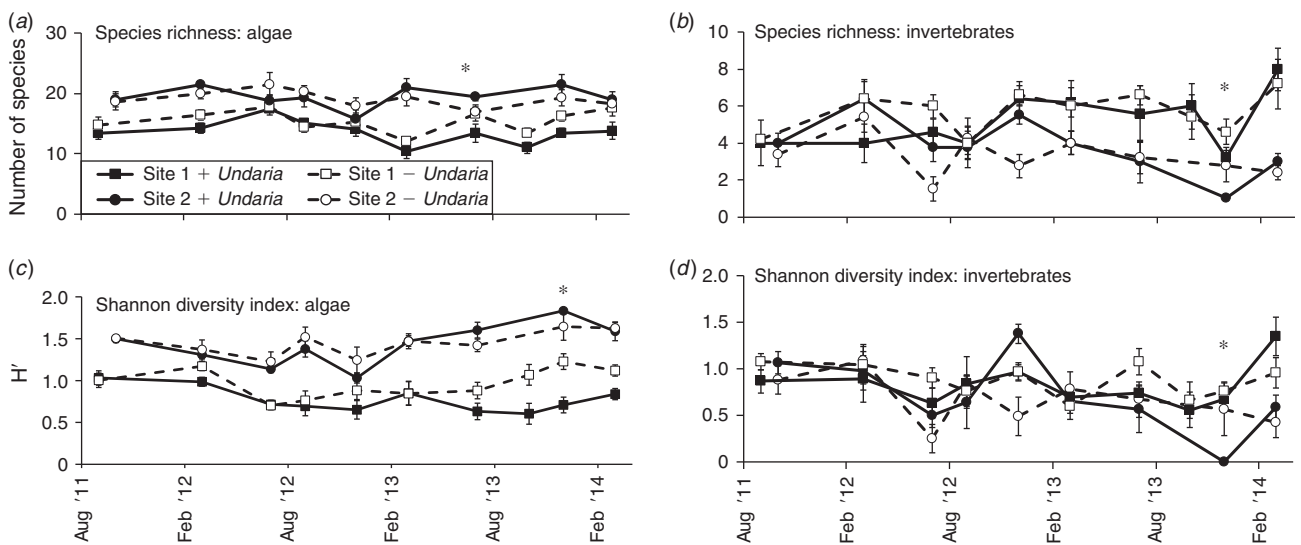


Fig. 3. Mean (\pm s.e.) algal species richness (a), invertebrate species richness (b), algal Shannon diversity index (c) and invertebrate Shannon diversity index (d) in +*Undaria* and -*Undaria* plots at two sites on the Moeraki Peninsula. Note the different y-axis scaling. Asterisks indicate where *post hoc* analyses were done on sites and treatments at a particular date.

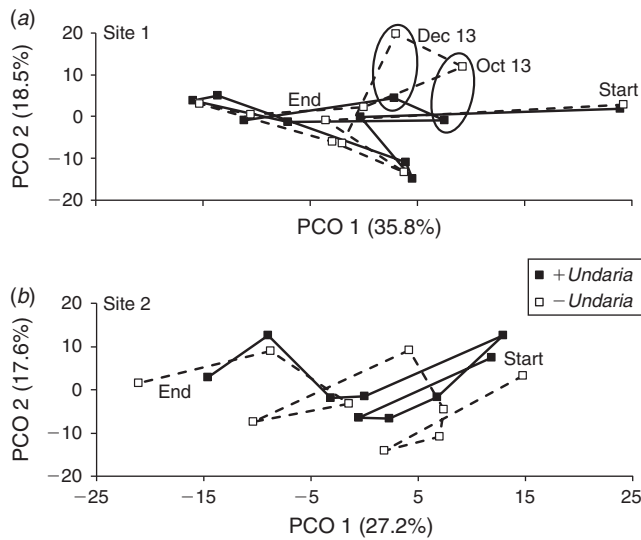


Fig. 4. Principal components plot of the mean community assemblage in +*Undaria* and -*Undaria* treatments at Site 1 (a) and Site 2 (b). Sites are plotted separately for clarity in two dimensions. The start and end points of the experiments are marked along with the two dates (October and December 2013) at Site 1 where there were significant pairwise tests for the significant site × treatment interaction.

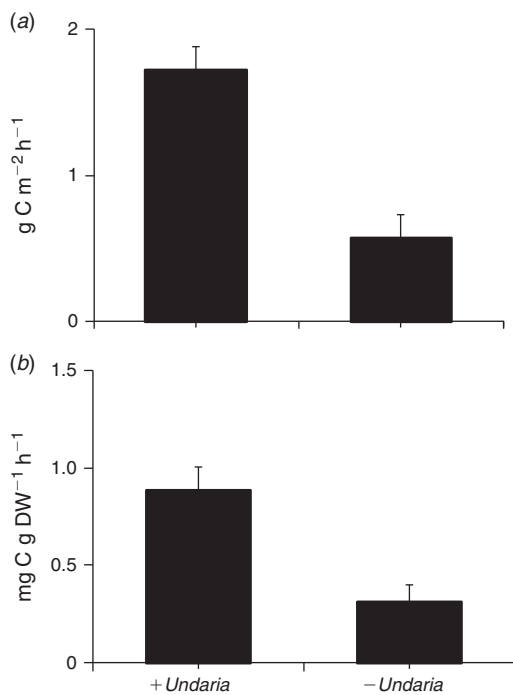


Fig. 5. Mean (+s.e.) net primary production (NPP) of +*Undaria* and -*Undaria* treatments standardised by grams carbon fixed per square metre per hour (a) and milligrams of carbon fixed per gram (dry weight) of macroalgal biomass per hour (b).

The removal of *Undaria* in our study resulted in an ephemeral increase of 46% in the cover of one species, *Lophothamnion hirtum*, a much stronger effect than described by Valentine and Johnson (2005) in Tasmanian subtidal systems, where (brown)

turf algae increased by only 3%. However, consistent with the findings of Valentine and Johnson (2005), our study highlights that the effects of *Undaria* at least in semiexposed rocky intertidal systems, appear to be few and transient in time. By contrast, Casas *et al.* (2004) found that after 8 months, seaweed diversity increased by 175% in subtidal plots following the removal of *Undaria* but, in this case, plots were sampled only once, so it is impossible to know whether these effects were persistent.

We identified short-term, site-specific effects on a few native species because we used press-treatments and repeated long-term sampling on species-specific taxa. There are probably no wider consequences of these effects but this is difficult to determine or predict because very little data exist about the ecological importance of *Lophothamnion* and *Leathesia difformis*. We showed here that both species have temporally highly variable distributions. For example, *Lophothamnion* had low abundance in both treatments during all of 2012, whereas *Leathesia* was an opportunistic ephemeral alga that was particularly abundant in spring and summer, as documented in other studies (Lilley and Schiel 2006).

It appears that the effects of *Undaria* we recorded are minor compared with those of some other successful invasive macroalgae (Thomsen *et al.* 2009) and native canopy-forming macroalgae (Lilley and Schiel 2006; Schiel 2006; Schiel and Lilley 2007). However, in the intertidal zone, the limited effects of *Undaria* shown in this study appear to be similar to those reported for *Sargassum muticum* in Spain (Sánchez and Fernández 2005; Olabarria *et al.* 2009). For example, Olabarria *et al.* (2009) found that removal of *Sargassum* affected the abundance of only one ephemeral species. It should be noted that peak abundance of *Sargassum* in Olabarria *et al.* (2009) and Sánchez and Fernández (2005) was much lower (~40%) than that of *Undaria* on Moeraki Peninsula. In the subtidal zone, however, Britton-Simmons (2004) showed much stronger effects of experimental removals of *Sargassum* that resulted in increased cover and diversity of native canopy-forming species, and increased abundance of a sea urchin, *Strongylocentrotus droebachiensis*. Potentially, differences in effects of invasive macroalgae such as *Undaria* and *Sargassum* between subtidal and intertidal zones reflect patterns of subcanopy light limitation (Sánchez and Fernández 2005) that may not be as important in the intertidal zone, where canopy-forming algae also provide facilitating services such as reductions in temperature stress (Lilley and Schiel 2006). Furthermore, *Undaria* may have had few effects because its seasonal macroscopic life-history is not synchronised with those of many native species, which tend to bloom in spring and summer when *Undaria* is senescing (Lilley and Schiel 2006). Also, many of New Zealand’s canopy-forming fucoids have their reproductive peaks in late summer (Schiel 1988), thereby reducing direct competition with *Undaria* (e.g. Thompson and Schiel 2012).

Increases in productivity following invasions by fast-growing macroalgae have been shown for many species, including *Undaria* in other regions (Sfriso and Facca 2013), *S. muticum* (Pedersen *et al.* 2005), *Gracilaria vermiculophylla*, (Thomsen and McGlathery 2007; Nejrup and Pedersen 2010) and *Codium fragile* (Thomsen and McGlathery 2007). Canopy-forming algae can decrease biomass in understorey species by reducing

light (Reed and Foster 1984) and uptake of nutrients (Eriksson *et al.* 2006). For example, Miller *et al.* (2011) showed that understory algal communities of *Macrocystis pyrifera* sufficiently increased in terms of biomass and net primary production to compensate for the loss of the canopy. This does not appear to be the case in intertidal communities dominated by *Undaria* as its absence, even when understory algae are abundant (i.e. December 2013), dramatically reduced net productivity (biomass, NPP) and no perennial algae recruited in its place. Corallines are some of the least productive algae and their epiphytes, although productive per gram of biomass, have little effect on NPP per area due to low overall biomass (Tait and Schiel 2011). It should be noted that we assessed NPP when *Undaria* was highly abundant during its annual life history to estimate maximum potential production, but at greater temporal scales (i.e. annually) longer-lived more stable species (e.g. corallines) might be relatively more important than shown in this study.

The documented changes in biomass, net primary production and stored tissue nutrients could have cascading impacts on ecosystem functioning at larger spatial scales. The impacts of invasive algae on algal–herbivore and epifauna–predator interactions remain untested. For example, odacid and labrid fish are important consumers of intertidal algae and epifauna respectively (Denny and Schiel 2001; Taylor and Schiel 2010). Increases in food availability could modify population structure (e.g. Irigoyen *et al.* 2011) and indirectly alter the direction and magnitude of trophic interactions and species distributions (Taylor and Schiel 2010; Thomsen *et al.* 2014b).

Many studies on impacts from invasive seaweeds are conducted in disturbed or stressed locations, often modified by anthropogenic activities, or characterised by low local biodiversity (e.g. Stæhr *et al.* 2000; Casas *et al.* 2004; Valentine and Johnson 2005; Bulleri *et al.* 2010). For example, Valentine and Johnson's (2005) study was done on sea urchin barrens and Casas *et al.* (2004) report low algal diversity and no large canopy-forming algae in the study area. *Undaria* is highly successful at colonising such disturbed areas or areas without macroalgal canopies (Valentine and Johnson 2003; Valentine and Johnson 2004; Farrell and Fletcher 2006; Thompson and Schiel 2012). In southern New Zealand, Thompson and Schiel (2012) showed that disturbances to canopies of the fucoid *Carpophyllum maschalocarpum* resulted in a strong recruitment of *Undaria*. However, high recruitment and expansion of *C. maschalocarpum* reduced the abundance of *Undaria* after 1 year. It is interesting, therefore, that *Undaria* has persisted in the general area for so long; perhaps the nature of disturbances along this exposed coastline maintains patches unoccupied by long-lived perennial canopies that are available for *Undaria* colonisation.

This study augments the 'too few studies' that document the effects of invaders on community attributes (Thomsen *et al.* 2014b). We conclude that *Undaria* had only minor effects on intertidal diversity, regardless of the trophic level studied and that this is likely due to (1) its annual life-history and the ability to occupy patches of reef on which other canopy-forming algae have not occupied and (2) that canopy effects in intertidal systems can simultaneously inhibit (through shading and whip-lash) and facilitate (reduce temperature and desiccation stress)

other sessile species. However, *Undaria* makes a significant seasonal contribution to NPP and has many potentially positive effects on resident communities. These findings have broad relevance for invasion impact studies of other ephemeral invasive algae. Given its high abundance in shallow coastal areas along the South Island, its contribution to carbon production, detrital fall, and provision of three-dimensional biogenic habitat, *Undaria* is now a significant player in the ecology of these rocky reefs and adjacent habitats.

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