

# The ecological role of invading *Undaria pinnatifida*: an experimental test of the driver–passenger models

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**Abstract** There have been dramatic increases in the frequency of invasions and distributions of invaders worldwide, yet the ecological roles of invasive macroalgae are poorly understood. Here, hypotheses about (1) the mechanisms and (2) the impact of invasion in stands of native canopy-forming algae were tested. First, native canopies were removed to possibly facilitate an invasion by *Undaria pinnatifida*. Then, invading *U. pinnatifida* was removed from half of the disturbed plots to test for its impact on early succession and recovery of the recipient assemblage. Recruitment success of the invader, per cent cover of sessile species, counts of mobile macroinvertebrates and recruitment of canopy-forming species were contrasted among disturbed and non-disturbed plots characterized by either native canopies or established *U. pinnatifida* stands. The removal of native canopies resulted in strong recruitment of *U. pinnatifida*, whereas only low abundance was found in plots dominated by native canopy-formers. There

were few effects of invading *U. pinnatifida* on native sub-canopy species or the recruitment of furoid algae. The only significant invasion effect within the disturbed plots was a negative effect on the alga, *Colpomenia sinuosa* that was also facilitated by disturbance. Together these results suggest that *U. pinnatifida* was a “passenger”, not “driver”, of ecological change. This study supports the notion that invasion success can be decoupled from invasion impact, particularly for invaders that only dominate in limited temporal windows. *U. pinnatifida* is a highly successful cosmopolitan invader, but its direct impacts on local intertidal communities appear limited and specific to species that have similar traits.

## Introduction

Non-native macroalgae have invaded habitats around the world often with dramatic impacts on local species, assemblage structure and biogeochemical cycling (Gribben et al. 2013; Maggi et al. 2015; Thomsen et al. 2016a; Williams and Smith 2007). A key consideration about the impact of any successful invasive species is whether it is the “driver” (cause) or a “passenger” (effect) of ecological change (sensu MacDougall and Turkington 2005). Ecological drivers modify recipient assemblages through competitive interactions, while passengers require change (i.e., biotic or abiotic disturbance) to free resources that then facilitate their recruitment and growth (MacDougall and Turkington 2005). Bauer (2012) augmented these models, suggesting that some invasive species are “back-seat drivers” that have to first benefit from degradation to natural systems (i.e., are passengers) before they can modify assemblage dynamics (i.e., become drivers) (Bulleri et al. 2010). Determining how invasive marine macroalgae fit these models requires

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experiments that separate the processes driving their distributions from their effects on the recipient assemblages.

Many invasive macroalgae are poor colonizers of areas dominated by large structurally intact native canopy-forming species, but are able to colonize and monopolize space quickly following disturbance to native stands (Bulleri et al. 2010; Levin et al. 2002; Scheibling and Gagnon 2006; Thompson and Schiel 2012; Valentine and Johnson 2004). It is possible that many effects of invaders only eventuate following disturbance *and* colonization *and* space monopolization by the invader. Testing whether an invasive species impacts the recovery and successional trajectories of native assemblages following disturbance, requires a simulated initial disturbance followed by removals of colonizing invaders (to be contrasted with similarly disturbed plots where the colonizing invader is left intact). Importantly, this method also addresses many of the limitations associated with standard manipulative removal experiments, because habitats and environmental conditions are more similar among experimental plots.

We are only aware of two studies (Bulleri et al. 2010; Mulas and Bertocci 2016) that have tested the driver–passenger models with similar methods for marine macroalgal invaders, in both cases documenting that highly invasive macroalgae (*Caulerpa racemosa* and *Grateloupia turuturu*, respectively) were not the primary “drivers” of ecological change (MacDougall and Turkington 2005), but, in the case of *C. racemosa* on Mediterranean coasts, could subsequently prevent the recovery of native assemblages (Bulleri et al. 2010). In this instance, *C. racemosa* was neither a primary driver nor a passive passenger of change.

In southern New Zealand, the laminarian kelp *Undaria pinnatifida* (Harvey) Suringar has become prolific and often forms dense canopies during its annual macroscopic phase in the austral spring and early summer (Heiser et al. 2014; Hewitt et al. 2005; Russell et al. 2008; South et al. 2016). Most manipulative studies that have tested for the impacts of *U. pinnatifida* have removed the invader from areas with large established populations of *U. pinnatifida* that may have already been permanently altered by this invader (Casas et al. 2004; Irigoyen et al. 2011a; South et al. 2016). We are not aware of any study that has experimentally tested for the impact of *U. pinnatifida* during the initial invasion process when a novel invader might determine the magnitude and direction of change in the recipient assemblage. *U. pinnatifida* rarely occurs within dense stands of furoid algae that have been shown to resist invasion unless the canopy is disturbed (Thompson and Schiel 2012; Valentine and Johnson 2003). Therefore, it appears that intact stands of furoids resist colonization by *U. pinnatifida* (and therefore represent typical un-impacted native assemblages). Following the experimental work of Valentine and Johnson (2003, 2004) and Thompson and Schiel

(2012), it was hypothesized that the loss of native canopies would facilitate the invasion by *U. pinnatifida* from adjacent populations and that this invasion would subsequently modify the post-disturbance successional sequence. The invasion process in stands of native canopy-forming macroalgae was examined to determine the assemblage-level impact of *U. pinnatifida*. More specifically, we first tested whether *U. pinnatifida* was a passenger of disturbance to stands of native canopy-forming algae by contrasting its recruitment in plots that had high cover of native canopy-forming species with plots where the canopy-formers had been removed. Subsequently, colonizing *U. pinnatifida* was removed from half of the canopy-removed plots to test whether its invasion affected the recovery dynamics of the recipient assemblage (including algae, mobile invertebrates and sessile invertebrates) during early successional stages.

## Materials and methods

### Study area

This study was done on the eastern shoreline of Pile Bay, in Lyttelton Harbour, New Zealand (latitude  $-43.618262^\circ$ , longitude  $172.763659^\circ$ ). The shore is generally steep creating a narrow intertidal zone that is dominated in the low-water spring—low-water neap zone by the native furoid algae *Cystophora torulosa* (R. Brown ex Turner) J. Agardh, *Cystophora scalaris* J. Agardh and, in winter—early summer, the invasive laminarian kelp *U. pinnatifida*. These *Cystophora* species are relatively large (>30 cm) perennial canopy-forming species that can control local patterns of biodiversity in the lower zones of semi-protected rocky shores in New Zealand (Schiel 2006). Understorey and low-lying communities are dominated by encrusting coralline algae with patches of the geniculate coralline *Corallina officinalis* Linnaeus. *U. pinnatifida* has been in Pile Bay since at least 2008 (Barrie Forrest pers. comm.). This study was done within dense stands of *Cystophora* spp. that occupied two small bays (~30 metres long) that were separated by ~50 m.

### Distribution of native canopy-forming macroalgae and *Undaria pinnatifida*

To describe their patterns of distribution and co-occurrence, the percentage cover of *U. pinnatifida* and all dominant native canopy-forming species was estimated in 100 haphazardly located  $50 \times 50$  cm quadrats in the low-water neap—low-water spring zone along 150 m of coastline. This survey was repeated on the 1st of December 2014 and the 20th of February 2015, which roughly correspond to the maximum and minimum cover and frond size of *U.*

*pinnatifida*, respectively. *Cystophora* species form mixed canopies at this site and were pooled in this survey. However, a more detailed survey (18.25 × 25 cm quadrats) demonstrated that the mixed *Cystophora* spp. canopies at Pile Bay were dominated by *C. torulosa* and to a lesser extent *C. scalaris* (i.e., 88.4 ± 6.4 SE, 22 ± 6.6 SE, and 0.9 ± 0.6 SE of the total per cent cover of *Cystophora* for *C. torulosa*, *C. scalaris* and *Cystophora retroflexa* (Labilardière) J. Agardh, respectively).

### Experimental tests of the driver–passenger models

We hypothesized that *U. pinnatifida* is a passenger of change that is facilitated by the loss of native canopy-forming algae. To test this hypothesis, all individuals of native furoid canopy-forming algae (including their recruits) were removed in May 2014 (when macroscopic *U. pinnatifida* is almost absent from the shoreline) from 6 50 × 50 cm plots (hereafter C−) at 2 sites (hereafter Sites 1, 2). Three undisturbed control plots (hereafter C+) were also established in each site. The canopy of native algae within the two sites was dominated by *C. torulosa* (5610 ± 1161 SE g WW m<sup>2</sup>) and *C. scalaris* (1038 ± 284 SE g WW m<sup>2</sup>) with much less of other native canopy-formers (the two most important being *Carpophyllum maschalocarpum* (Turner) Greville with 77 ± 66 SE g WW m<sup>2</sup> and *Hormosira banksii* (Turner) Decaisne with 137 ± 56 SE g WW m<sup>2</sup>—wet weight data were derived from 12 replicate 25 × 25 cm samples). All plots were surveyed prior to experimental manipulations and no *U. pinnatifida* was present in any of the plots at the start of the study.

To test whether colonizing *U. pinnatifida* could drive assemblage change and impact the recovery of native assemblages following the disturbance, half of the native canopy removal plots were assigned to an *U. pinnatifida* removal treatment (hereafter C − U− *n* = 3 per site). More specifically, we removed all *U. pinnatifida* fronds larger than >0.5 cm (recruits barely visible to the naked eye) within the plots but also removed all larger fronds (>5 cm) in a 25 cm buffer zone around each removal plot. The occurrence of *U. pinnatifida* was not manipulated in the other plots from which native canopy algae were removed (hereafter C − U+ *n* = 3 per site). The *U. pinnatifida* removals were press removals and plots were retreated on the 15/6/14, 10/8/14 and 7/10/14.

In December 2014 (~6 months after initial manipulations of the native canopy) *U. pinnatifida* thalli were macroscopic and reproductive, allowing a further treatment (*n* = 3 per site) to be added in stands of high *U. pinnatifida* cover (85 % ± 8.91 SE, hereafter U+) that had developed outside of the native canopy stands during our experiment. Together, the four treatments (C+, U+, C − U−, C − U+) thereby include key ecological contrasts. First, comparing C+ to C − U+ tested whether *U. pinnatifida* could

invade intact native canopies (i.e., was a driver), or requires a disturbance (i.e., was a passenger). Second, comparing C − U+ versus C − U− tested whether colonization by *U. pinnatifida* can affect the recovery of native assemblages following the loss of the native canopy. Thirdly, comparing C+ to U+ represented a typical mensurative control–impact study that is commonly used to describe differences between invaded and uninvaded assemblages.

The percentage cover of algae and sessile invertebrates was estimated by eye, using a gridded quadrat. Mobile macroinvertebrates (>5 mm) and new recruits (>5 mm) of native canopy-forming algae (February 2015 only) were counted. These taxa were identified to the highest possible resolution, usually to species, but occasionally to genus or family. All field data were recorded by one observer with >10 years of experience in identifying and quantifying these local intertidal assemblages.

Finally, effects on small epifauna were tested by deploying identical artificial units of habitat (hereafter AUHS, Underwood and Chapman (2006)) into each plot in October 2014. The AUHS used were Tuffly™ (Clorox Company) branded plastic scouring pads (80 × 80 × 60 mm, 8.75 g in weight). These AUHS are structurally complex and were deployed to mimic understory seaweeds (i.e., below the dominant canopy-forming furoids) that provide refuge for small invertebrates from desiccation and large predators (see Menge 1992). AUHS were collected in December 2014, bagged individually in the field and stored frozen at −20 °C upon return to the laboratory. Animals were washed onto a 500 µm sieve and preserved in 70 % ethanol. These taxa were identified to coarser taxonomic groups (usually order or family).

### Statistical analyses

Mean (±SE) percentage cover of dominant canopy-forming algae in quadrats (*n* = 100) was derived for each sampling occasion (December 2014, February 2015). The cover of native canopy-forming algae was correlated (Spearman's rank correlation coefficient) to *U. pinnatifida* cover in December 2014 and February 2015 to describe patterns of co-occurrence.

The cover, density and holdfast cover of *U. pinnatifida* were analysed with analysis of variance (ANOVA) with treatment (4 levels; C+, U+, C − U−, C − U+, fixed) crossed with site (sites 1, 2, random). The effects of the four treatments and two sites on multivariate assemblages of algae and mobile and sessile invertebrates were analysed with principle coordinate analysis (PCO) and tested with permutational analysis of variance (PERMANOVA) using 9999 permutations done on Bray-Curtis similarity matrices of square-root (algae) or un-transformed (sessile and mobile invertebrates) data. Invertebrate data were sparse; therefore,

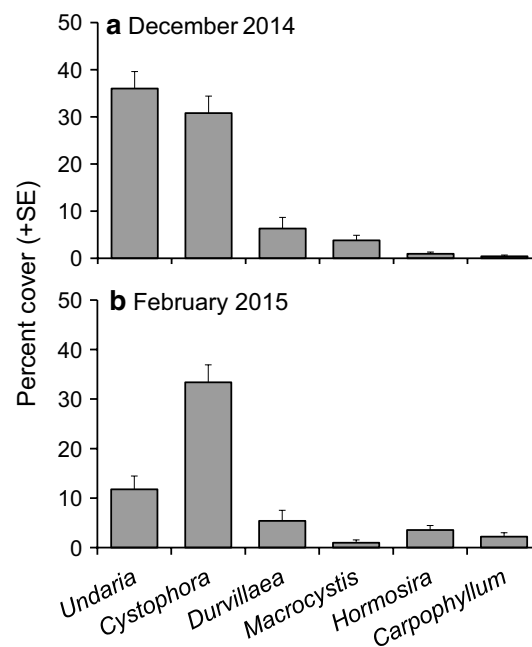
a dummy variable (value 1) was added to each of the invertebrate matrices in order to stabilize data dispersion (Clarke et al. 2006). Each sample event (December 2014 and February 2015) was analysed separately. Pairwise PERMANOVA was used as a post hoc test to determine between-treatment differences. The relative importance of taxa contributing to between-treatment differences was assessed using similarity of percentages (SIMPER). Permutational tests of homogeneity of multivariate dispersions (PERMDISP) were used to assess within-treatment variability. The effects of treatment and site on taxa richness, the Shannon diversity index and Pielou's evenness index of algae (scarcity of animal species precluded calculation of diversity indices for invertebrates) were tested with ANOVA. Cover values for the manipulated taxa were excluded from these analyses to test specifically for effects of the canopy-formers on the understory assemblages (Thomsen et al. 2016b).

The effects of the four treatments and two sites on a range of response variables were tested with ANOVA. The response variables included the percentage cover of conspicuous sessile organisms such as *Colpomenia sinuosa* (Mertens ex Roth) Derbès and Solier, encrusting coralline algae (the dominant occupier of primary space) and total algae; and counts of dominant mobile invertebrates, including *Lunella smaragdus* (Gmelin), *Cantharidella tessellata* (A. Adams), *Micrelenchus* spp., and total Trochidae. Finally, recruits of native canopy-forming algae (*Cystophora* spp. and *H. banksii*) were counted in February 2015. Homogeneity of variances was tested with Cochran's C test, and data were log ( $x + 1$ ) (count-data) or arcsine [square-root ( $x$ )] (cover-data) transformed to make variances homogeneous where this was necessary. Where transformation failed to reduce heterogeneity in the model, test statistics were interpreted at the more conservative level of significance of  $p < 0.01$ , instead of  $p < 0.05$  to compensate for the increased probability of Type 1 error. Significant effects were tested with Tukey's post hoc tests. Univariate and multivariate analyses were done in STATISTICA 12 (StatSoft Inc, Tulsa, Oklahoma, USA) and PRIMER 6 and PERMANOVA + (PRIMER-E Ltd., Ivybridge, U.K.), respectively. Similar statistical tests were used on key epifaunal organisms from the AUHs, including univariate (amphipods, herbivorous gastropods, polychaetes, total animal abundance) and multivariate (assemblage of invertebrate taxa) responses.

## Results

### Distribution of native canopy-forming macroalgae and *Undaria pinnatifida*

*Undaria pinnatifida* and *Cystophora* spp. (dominated by *C. torulosa*) were the most abundant taxa surveyed in



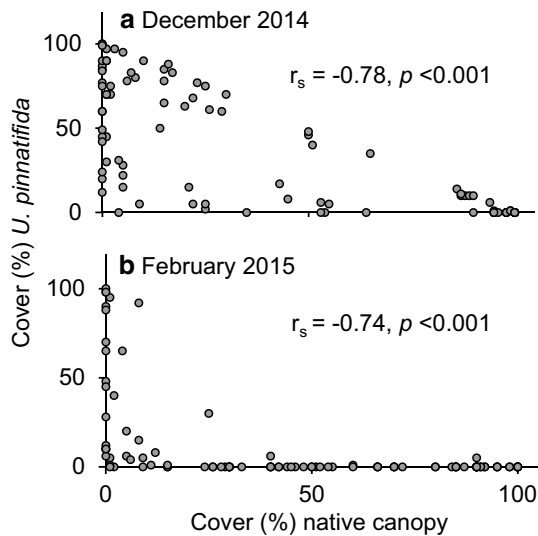
**Fig. 1** Per cent cover (mean + SE) of native canopy-forming taxa and *Undaria pinnatifida* in 100 50 × 50 cm quadrats at Pile Bay in December 2014 and February 2015

December 2014 accounting for 35.6 (±3.6 SE) and 30.8 (±3.6 SE) of the total percentage cover of canopy-forming algae, respectively (Fig. 1a). *Durvillaea antarctica* (Chamisso) Hariot constituted 6.1 % (±2.4 SE) of the cover while no other canopy-forming alga accounted for more than 5 % (Fig. 1a). In February 2015, *Cystophora* spp. (33.4 ± 3.6 SE) were the dominant taxa (Fig. 1b) and the per cent cover of *U. pinnatifida* had reduced to 11.8 (± 2.7 SE). The per cent cover of native canopy-forming algae was negatively correlated with the cover of *U. pinnatifida* in both December 2014 ( $r_s = -0.78$ ,  $p < 0.001$ ; Fig. 2a) and February 2015 ( $r_s = -0.74$ ,  $p < 0.001$ ; Fig. 2b).

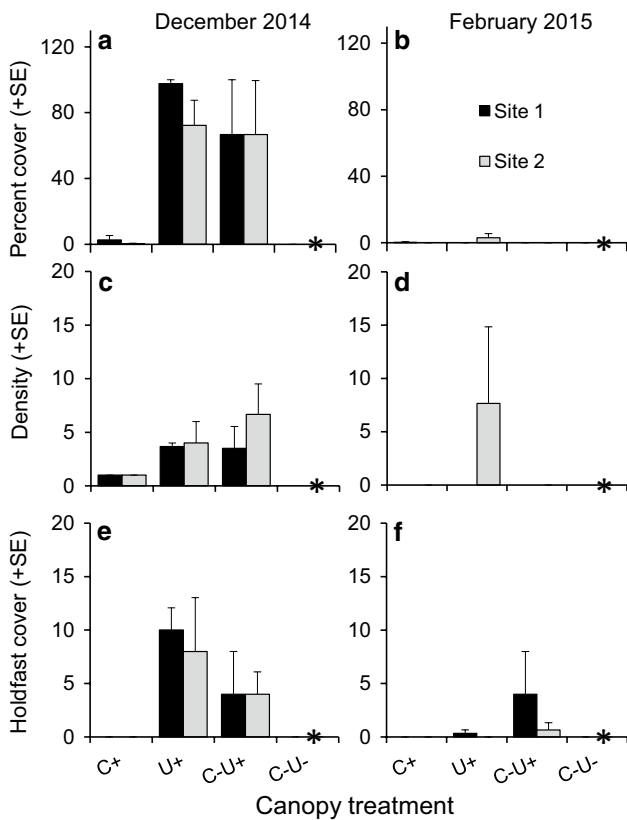
### Experimental tests of the driver–passenger models

#### *Is Undaria pinnatifida* a driver or passenger of ecological change?

*Undaria pinnatifida* recruited into the C – U– and C – U+ plots although with some variability, (e.g., *U. pinnatifida* failed to colonize one of the C– plots at each site, Fig. 3). In December 2014, there was a significant effect of treatment (Table 1) due to high cover of *U. pinnatifida* in C – U+ and U+ compared to the C+ plots (*U. pinnatifida* did recruit into the C+ plots, but in very low abundance, and never grew into large fronds) (Fig. 3a). By February 2015, only two months later, there was virtually no *U. pinnatifida* left in any plots and therefore there were no effects



**Fig. 2** Total cover of all native canopy-forming algae vs. *Undaria pinnatifida* in 100 × 50 cm quadrats in December 2014 (a) and February 2015 (b).  $r_s$  = Spearman’s correlation coefficient



**Fig. 3** Mean (+SE) per cent canopy cover (a, b), density (c, d) and per cent holdfast cover (e, f) of *Undaria pinnatifida* in canopy treatments at two sites in December 2014 and February 2015 (left and right panels, respectively). Asterisks indicate treatments from which *Undaria* has been experimentally removed.  $n = 3$  per treatment × site combination

of treatment on the cover of *U. pinnatifida* (Fig. 3b). There was a significant effect of treatment (Table 1) on the density of *U. pinnatifida* with greater numbers of individuals in the C – U+ plots in December 2014 (Fig. 3c), but not in February 2015 when *U. pinnatifida* individuals were only found in the U+ plots (Fig. 3d). In December 2014, there was a significant effect of treatment (Table 1) due to greater cover of *U. pinnatifida* holdfasts in the C – U+ (Fig. 3e) and U+ plots (Fig. 3e). By February 2015, cover of *U. pinnatifida* holdfasts was 3.5 % ( $\pm 0.8$  SE) in C – U+ plots and less than one per cent in the U+ plots (Fig. 3f). During the course of the experiment 815 *U. pinnatifida* recruits were removed from the six C – U– plots (we did not count individuals removed from the buffer zone).

*Does colonizing Undaria pinnatifida drive assemblage change?*

There was a significant effect of canopy treatment (Fig. 4a; Table 2) on the multivariate structure of the algal assemblage in December 2014. At this sampling date, pairwise t tests suggested no difference in assemblage structure between C+ and C – U+ plots, whereas the C – U+ plots differed from the C – U– plots ( $t = 1.65, p < 0.05$ ). SIMPER analysis indicated that greater abundance of *C. sinuosa* and less encrusting and geniculate coralline algae in the C – U– plots compared to all other treatments made important contributions to these differences. Algal assemblages were significantly different in the C+ compared to U+ plots ( $t = 1.88, < 0.01$ ) due to more of the turfing algae *Halopteris* spp. and less encrusting coralline algae in the U+ plots. In February 2015, there was again a significant effect of canopy treatment on the composition of the algal assemblage (Fig. 4b). The C+ plots were now significantly different from the C – U+ plots ( $t = 2.11, p < 0.01$ ), with more encrusting coralline algae and less *C. sinuosa* in the C+ plots. However, the C – U+ and C – U– plots were no longer significantly different in February 2015 ( $t = 1.1, p > 0.05$ ). All other pairwise contrasts were similar to results from December 2014.

There was a significant effect of canopy treatment on the assemblage composition of mobile invertebrates in December 2014 (Fig. 4c; Table 2). SIMPER analysis indicated that greater abundances of the trochid snail *C. tessellata* and the turbonid snail *L. smaragdus* in the C+, U+, and C – U+ plots (all characterized by high canopy cover) compared to the C – U– plots (without any canopy cover) made larger contributions to the between-sample dissimilarity. Finally, relatively high abundance of sessile invertebrates was found in U+ plots compared to all other treatments, but this was not significant during the study (Table 2).

There were no significant effects of treatment on taxa richness (Fig. 5a, b; Table 3), although there was a significant effect of site in February 2015 due to greater taxa

**Table 1** Results from analyses of variance done to test effects of canopy treatment, site and their interaction on canopy cover, density and holdfast cover of *Undaria pinnatifida* during its periods of maximum (December 2014) and minimum (February 2015) abundance

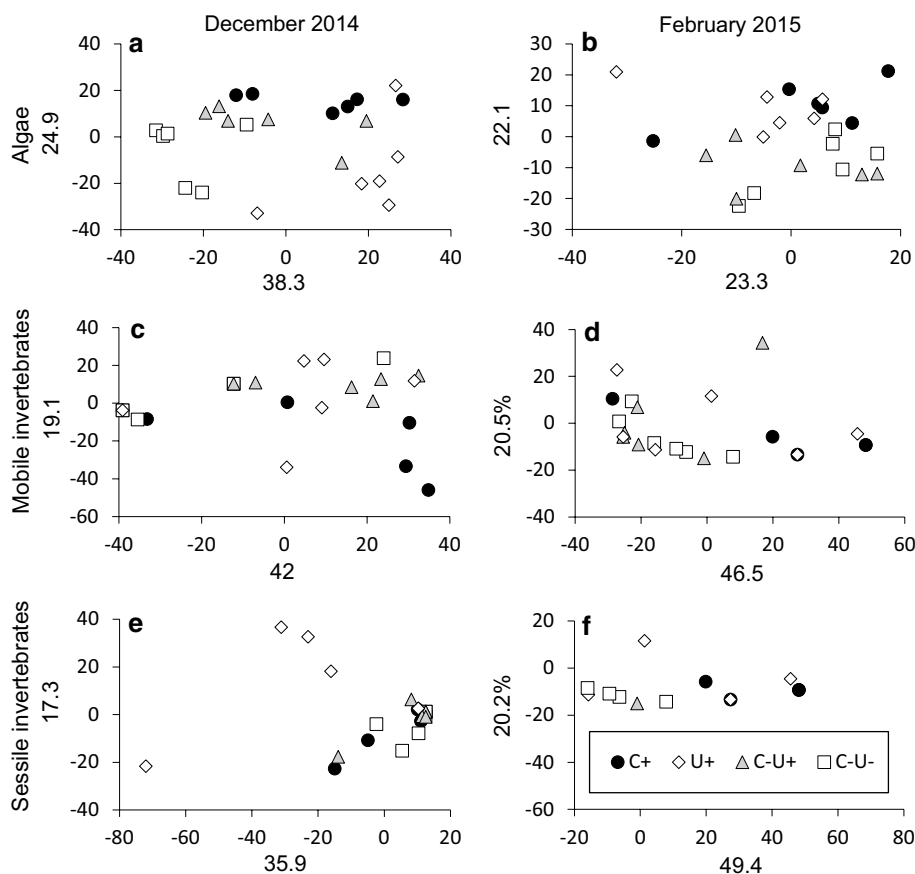
	Source	f/r	d.f.	<i>Undaria</i> cover (%)			<i>Undaria</i> density			<i>Undaria</i> holdfast cover (%)		
				m.s.	F	p	m.s.	F	p	m.s.	F	p
December 2014	Treatment	f	3	<b>2.58</b>	<b>39.64</b>	<b>0.007</b>	<b>0.66</b>	<b>3.00</b>	<b>0.043</b>	<b>0.11</b>	<b>41.63</b>	<b>0.006</b>
	Site	r	1	0.09	1.41	0.320	0.05	3.00	0.435	0.00	0.02	0.900
	Treatment × site	r	3	0.07	0.32	0.814	0.06	16.00	0.411	0.00	0.24	0.865
	Error		16	0.21			0.06			0.01		
February 2015	Treatment	f	3	0.01	0.95	0.517	0.12	1.00	0.500	7.82	1.99	0.293
	Site	r	1	0.00	0.53	0.520	0.12	1.00	0.391	5.04	1.28	0.340
	Treatment × site	r	3	0.01	2.06	0.146	0.12	1.80	0.188	3.93	0.63	0.604
	Error		16	0.00			0.06			6.21		

Cochran's test on arcsine ( $\sqrt{(x+1)}$ ) data in December 2014  $C = 0.84$ ,  $p = 0.01$  for *Undaria* cover (%)

Tukey's test December 2014; *Undaria* cover (%)  $C+ = C - U- < U+ = C - U+$  ( $p < 0.01$ ); *Undaria* density  $C+ = C - U- < U+ = C - U+$  ( $p < 0.05$ ); *Undaria* holdfast cover (%)  $C+ = C - U- < U+ = C - U+$  ( $p < 0.01$ )

Bold values indicate significance at  $p < 0.05$  or  $p < 0.01$  where data were heterogeneous

**Fig. 4** Principle coordinate analyses of algal, mobile invertebrate and sessile invertebrate assemblage structures in C+, U+, C - U+ and C - U- plots in December 2014 (left panel) and February 2015 (right panel). PERMANOVA showed significant effects of canopy treatment in a-c. Axis labels indicate the per cent of total variation explained by that axis. Note different scales on axes



richness at Site 2 (Fig. 5b; Table 3). In December 2014, there was a significant treatment × site effect due to lower values for the Shannon diversity index in C+ at sites 1 and 2 and U+ at Site 1 compared to all other treatments (Fig. 5c; Table 3). There were no significant effects on Pielou's evenness index of either treatment or site (Fig. 5e, f; Table 3).

In December 2014, the cover of *C. sinuosa* was significantly greater in the C - U- plots compared to all other treatments (Fig. 5g; Table 3). There were no significant effects on the cover of *C. sinuosa* in February 2015 (Fig. 5h; Table 3). Data transformation failed to homogenize variances for encrusting coralline algae, and therefore,

**Table 2** Results from permutational analyses of variance done to test for the effects of canopy treatment, site and their interaction on algal, mobile invertebrate and sessile invertebrate assemblages when *Unda-**ria* was at its maximum (December 2014) and minimum (February 2015) abundance

	Source	<i>f</i> / <i>r</i>	<i>d.f.</i>	Algae			Mobile invertebrates			Sessile invertebrates		
				<i>m.s.</i>	<i>F</i>	<i>p</i>	<i>m.s.</i>	<i>F</i>	<i>p</i>	<i>m.s.</i>	<i>F</i>	<i>p</i>
December 2014	Treatment	<i>f</i>	3	<b>3387.40</b>	<b>5.88</b>	<b>0.022</b>	<b>2797.50</b>	<b>2.88</b>	<b>0.033</b>	1998.40	2.63	0.837
	Site	<i>r</i>	1	<b>2568.30</b>	<b>3.66</b>	<b>0.007</b>	1023.20	0.63	0.652	1234.20	1.18	0.300
	Treatment × site	<i>r</i>	3	575.91	0.82	0.642	970.09	0.60	0.859	760.68	0.73	0.836
	Error		16	702.26			1618.00			1046.20		
February 2015	Treatment	<i>f</i>	3	<b>1495.50</b>	<b>3.03</b>	<b>0.023</b>	2617.00	2.29	0.159	999.97	1.32	0.307
	Site	<i>r</i>	1	501.93	0.85	0.536	1992.00	1.50	0.209	1097.40	1.25	0.277
	Treatment × site	<i>r</i>	3	493.95	0.83	0.656	1145.10	0.86	0.583	759.73	0.87	0.571
	Error		16	592.13			1327.30			874.67		

PERMDISP &gt;0.05 for all analyses

Bold values indicate significance at  $p < 0.05$ 

we interpreted the results more cautiously with  $p < 0.01$  although we note that its cover was lower in U+ and C – U– plots compared to other treatments in December 2014 (Fig. 5i; Table 3).

Mobile invertebrates were similar among treatments, except there were significantly more trochid snails in the C+ compared to the C – U– plots in December 2014, but not in February 2015 (Fig. 5kl; Table 3).

In February 2015, there were significant main effects of treatment and site (Fig. 5m; Table 3) on recruitment of *H. banksii*, which were likely driven by fewer *H. banksii* recruits in the C+ and U+ plots compared to the C – U– and C – U+ treatments (Fig. 5m) although there were no significant post hoc pairwise Tukey's tests. There were no effects of treatment or sites on the number of recruits of *Cystophora* spp. (Fig. 5n; Table 3).

There were no effects of canopy treatment or site on the abundance of conspicuous taxa (gammarid amphipods, herbivorous gastropods, polychaetes and total individuals) or composition of epifaunal assemblages in AUHs in December 2014 when *U. pinnatifida* was at its maximum abundance.

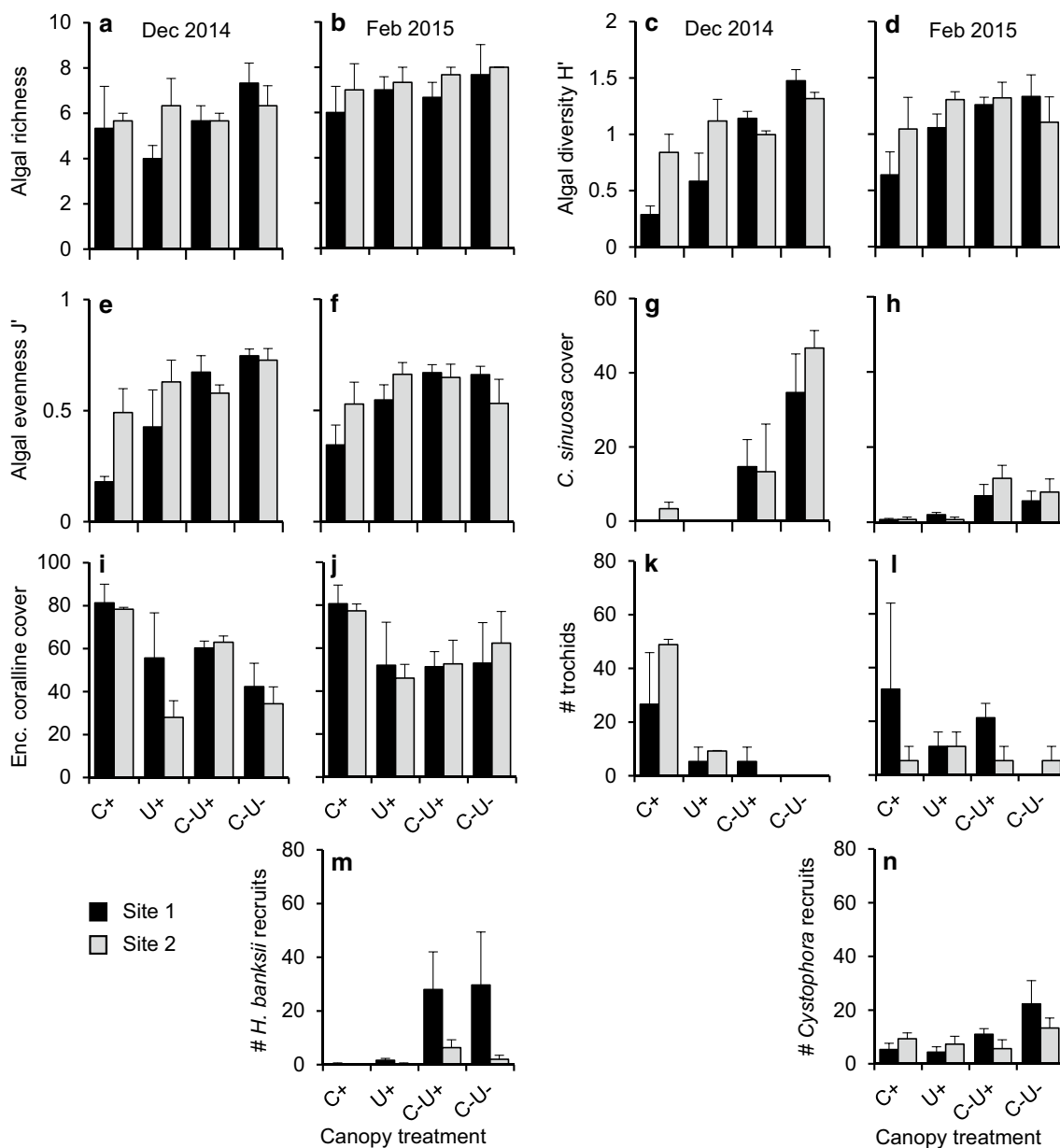
## Discussion

*Undaria pinnatifida* is a highly successful invader that has the potential to continue to expand its distribution (James et al. 2015) and alter coastal communities (Arnold et al. 2015; Carnell and Keough 2014; Casas et al. 2004; South et al. 2016; Thomsen et al. 2009). Here, the driver–passenger models (MacDougall and Turkington 2005) were experimentally tested on a rocky intertidal platform by first initiating a disturbance (native canopy removal) that freed up essential resources (e.g., space and light), which facilitated an invasion by *U. pinnatifida*. Then, that invasion

was controlled by removing the *U. pinnatifida* from half of the invaded plots (Bulleri et al. 2010; Mulas and Bertocci 2016). The results presented here support previous studies that found that *U. pinnatifida* was a passenger of change to stands of native canopy-forming algae; in this instance, canopy loss facilitated *U. pinnatifida* recruitment (Thompson and Schiel 2012; Valentine and Johnson 2003, 2004). The *U. pinnatifida* canopy that developed had only weak and transient impacts suggesting that *U. pinnatifida* is a benign addition for the majority of species in the recipient assemblage, at least at the beginning of its invasion and at the relatively small spatial scale examined in this study.

The ability of native canopies in experimental plots to resist invasion by *U. pinnatifida* (Fig. 3a), coupled with the strong negative correlation between native and *U. pinnatifida* canopy cover (Fig. 2) suggests that *U. pinnatifida* is not competitive to native canopy-formers and might not be a direct driver of change in these stands. The experimental removal of native canopy-formers facilitated the recruitment of *U. pinnatifida* in high abundance, as it has done in other studies in the region (Thompson and Schiel 2012; Valentine and Johnson 2003). An opportunistic “weedy” life history has been implicated in the success of many invasive macroalgae (Bulleri et al. 2010; Scheibling and Gagnon 2006); perhaps, *U. pinnatifida* could be considered the archetype of a weedy species because it has fast growth, large reproductive output and an ability to colonize a wide variety of substrata (see Schiel and Thompson 2012). Indeed, the life-history characteristics of *U. pinnatifida* are more similar to fast growing ephemeral algae (e.g., *Ulva*) than they are to other laminarians allowing it to effectively occupy space following disturbance (Dean and Hurd 2007; Schiel and Thompson 2012).

The *U. pinnatifida* that colonized removal plots (C – U+) had few effects on assemblage structure and displaced only one ephemeral alga. It appears that while



**Fig. 5** Effects of canopy treatment and site on univariate response variables in December 2014 and February 2015 (left and right panels, respectively).  $n = 3$  per treatment  $\times$  site combination

*U. pinnatifida* did drive some ecological change within the native canopy at Pile Bay, this effect was transient and directly associated with its adult biomass. Such subtle effects are rarely reported in the initial stages of macroalgal invasions because when and where an invasion will occur are difficult to predict. Typically the impacts of invaders have been assessed after they have become established when the ecological assemblage might already have been irreversibly altered by the invasive species (e.g., Scheibling and Gagnon 2006; South et al. 2016; Valentine and Johnson 2005). In such a scenario, removal of the invader could result in a different assemblage compared to the ‘true’

pre-invasion assemblage (Bulleri et al. 2010; Sánchez and Fernández 2005). Furthermore, it is possible that the non-native species has only invaded environmentally stressed habitats where native species are already limited. Here, the removal of the native canopy created the best possible conditions to test the effects of *U. pinnatifida* in a habitat that had likely not already altered, or where it was present due to some other un-manipulated factor.

At Pile Bay, algal assemblages were different between native and *U. pinnatifida* canopies (i.e., C+ vs. U+ plots) that recruited outside of the experimental plots (Fig. 4a). A typical mensurative control–impact analysis could conclude



**Table 3** Results from analyses of variance done to test for effects of canopy treatment, site and their interaction when *Undaria* was at its maximum (December 2014) and minimum (February 2015) abundance

	Source	<i>f/r</i>	<i>d.f.</i>	<i>m.s.</i>	<i>F</i>	<i>p</i>	<i>m.s.</i>	<i>F</i>	<i>p</i>	<i>m.s.</i>	<i>F</i>	<i>p</i>
				Algal richness			Algal evenness <i>J'</i>			Algal Shannon index <i>H'</i>		
December 2014	Treatment	<i>f</i>	3	3.15	1.08	0.477	0.17	3.25	0.179	0.74	3.07	0.191
	Site	<i>r</i>	1	1.04	0.36	0.593	0.06	1.12	0.367	0.23	0.95	0.401
	Treatment × Site	<i>r</i>	3	2.93	1.05	0.398	0.05	2.38	0.108	<b>0.24</b>	<b>4.31</b>	<b>0.021</b>
	Error		16	2.79			0.02			0.06		
February 2015	Treatment	<i>f</i>	3	1.78	8.00	0.061	0.05	1.87	0.310	0.24	2.13	0.275
	Site	<i>r</i>	1	<b>2.67</b>	<b>12.00</b>	<b>0.041</b>	0.01	0.28	0.631	0.09	0.80	0.436
	Treatment × Site	<i>r</i>	3	0.22	0.10	0.957	0.03	1.81	0.186	0.11	1.19	0.345
	Error		16	2.17			0.02			0.09		
				<i>C. sinuosa</i> cover			Enc. coralline cover			Trochidae density		
December 2014	Treatment	<i>f</i>	3	<b>0.56</b>	<b>36.91</b>	<b>0.007</b>	0.26	9.61	0.048	<b>1.48</b>	<b>13.13</b>	<b>0.031</b>
	Site	<i>r</i>	1	0.02	1.16	0.360	0.06	2.22	0.233	0.01	0.08	0.792
	Treatment × Site	<i>r</i>	3	0.02	0.43	0.731	0.03	0.78	0.525	0.11	0.25	0.859
	Error		16	0.03			0.04			0.45		
February 2015	Treatment	<i>f</i>	3	0.07	8.33	0.058	0.05	0.85	0.551	0.33	0.74	0.595
	Site	<i>r</i>	1	0.00	0.13	0.739	0.03	0.48	0.539	0.01	0.02	0.894
	Treatment × Site	<i>r</i>	3	0.01	1.11	0.375	0.05	0.67	0.582	0.45	1.27	0.318
	Error		16	0.01			0.08			0.35		
				<i>H. banksii</i> recruits			<i>Cystophora</i> spp. recruits					
February 2015	Treatment	<i>f</i>	3	<b>8.95</b>	<b>12.24</b>	<b>0.034</b>	0.64	0.30	0.824			
	Site	<i>r</i>	1	<b>15.65</b>	<b>21.40</b>	<b>0.019</b>	3.39	1.61	0.294			
	Treatment × Site	<i>r</i>	3	0.73	0.13	0.943	2.11	1.63	0.222			
	Error		16	5.76			1.30					

Cochran's test on arcsine ( $\sqrt{(x+1)}$ ) data in December 2014: *Colpomenia sinuosa*  $C = 0.48$ ,  $p = 0.02$ ; Enc. coralline algae  $C = 0.56$ ,  $p = 0.04$   
 Tukey's tests of significant effects: December 2014; *C. sinuosa* C+, U+, C – U+ > C – U+ (0.001); Trochidae C – U– < C+, U+, C – U+

Shannon diversity index for algae C + S1, C + S2, U + S1 < all other treatments

February 2015 Algal richness and *Hormosira banksii* recruits Tukey's tests were inconclusive

Bold values indicate significance at  $p < 0.05$  or  $p < 0.01$  where data were heterogeneous

that *U. pinnatifida* caused these differences (see Forrest and Taylor 2002). However, this is unlikely given that *U. pinnatifida* did not recruit beneath the native algal canopy in high abundance and only had weak effects on other species compared to where it was experimentally removed. Yet, *U. pinnatifida* was the most abundant and conspicuous component of the intertidal assemblage at Pile Bay in December 2014 (Fig. 1), indicating that areas lacking native canopy cover might provide niche space that is essential to the proliferation and maintenance of *U. pinnatifida* on these reefs (Fig. 2).

Colonization by *U. pinnatifida* decreased the cover of *C. sinuosa*, another alga that also is facilitated by disturbance, in December 2014 (Fig. 5g). However, this effect had diminished by February 2015 when *U. pinnatifida* and *C. sinuosa* were much less abundant on the reef. These results supplement our previous experiment that showed established *U. pinnatifida* stands can have similar negative effects on seasonal, ephemeral native macroalgae (South

et al. 2016). These effects appear weaker than those documented in other studies of invasive *U. pinnatifida*. For example, in subtidal areas of Argentina *U. pinnatifida* has been shown to have negative effects on algal richness and diversity, and positive effects on macrofaunal abundance and diversity (Casas et al. 2004; Irigoyen et al. 2011a, respectively).

The implications of the disruption of *C. sinuosa* by *U. pinnatifida* are difficult to gauge, in part because very little is known about the ecology of *C. sinuosa* (this study, Lilley and Schiel 2006), *Lophothamnion hirtum* (South et al. 2016) and other ephemeral algae that are facilitated by disturbances. The distribution of *U. pinnatifida* was observed to be temporally similar distribution to *C. sinuosa*; perhaps, both species facilitate other species following disturbances by buffering against negative effects of native canopy loss through stress reduction (e.g., by decreasing desiccation and UV stress) (Lilley and Schiel 2006). For example, there were more recruits of the canopy-forming

fucoid, *H. banksii*, in plots where native canopies had been removed, both in the plots where *U. pinnatifida* colonized (C – U+) and the other removal plots (C – U–) where *C. sinuosa* had colonized (Fig. 5g). *Cystophora* spp. have been shown to prevent *H. banksii* recruitment (Schiel 2006). Speculatively, *H. banksii* might have first benefited from reduced competition with *Cystophora* spp. and subsequently benefited from reduced abiotic stress (desiccation in particular) under *U. pinnatifida* or *C. sinuosa* during the summer months. Critically, fucoid canopy-forming algae appearable to recolonise disturbed areas despite high *U. pinnatifida* cover (Thompson and Schiel 2012; Valentine and Johnson 2003, 2004). The weak impact of *U. pinnatifida* on the recruitment of canopy-forming algae contrasts with the impact of other invasive canopy-forming macroalgae that typically prohibit recolonization by native species (Britton-Simmons 2004; Bulleri et al. 2010; De Wreede 1983; Scheibling and Gagnon 2006). For example, *Codium fragile* ssp. *tomentosoides* prevented recruitment of the otherwise dominant kelp *Laminaria digitata* suggesting that *C. fragile* ssp. *tomentosoides* could have long-term impacts on invaded reefs in Canada by suppressing new recruitment and early life stages of native kelps. (Scheibling and Gagnon, 2006).

Many invasive macroalgae can have positive effects on higher trophic levels through the provision of food and habitat for mesograzers (Bulleri et al. 2006; Gribben et al. 2013; Thomsen et al. 2014, 2010; Wernberg et al. 2004). Data on mobile macroinvertebrates supported this notion because invertebrates were more abundant on, and assemblage structure similar between, native and *U. pinnatifida* canopies (i.e., C+, U+ and C – N+) compared to canopy-free plots (C – U–) (Fig. 4b). These findings indicate that any canopy cover was better for mobile invertebrates at the small spatial scales examined in this study. Therefore, *U. pinnatifida* appears to at least partially buffer the effects of native canopy loss for these invertebrates. Indeed, at larger scales than were tested here, *U. pinnatifida* can have a positive effect on invertebrate abundances (Irigoyen et al. 2011a). In this context, it is surprising that canopy removal did not affect the distribution of epifauna captured in AUHs. Perhaps, the taxa quantified at Pile Bay are more influenced by benthic conditions rather than canopy or water column conditions, and the AUHs themselves may provide sufficient refuge to mitigate effects of both canopies and canopy loss.

Few experiments test simultaneously for the mechanisms of invasion and invasion impact, but this approach is essential to understanding the dual roles of invaders. First, manipulating native canopies allowed the ability of *U. pinnatifida* to colonize disturbed habitats to be assessed. Second, manipulating the abundance of the invader then

allowed its ecological effects to be tested within a system (stands of native canopy-forming algae) that had not been previously degraded. However, there are a number of caveats that should be considered here. Firstly, this study was done at a relatively small spatial scale testing for differences among treatments that were applied to three 50 × 50 cm plots in each of two sites (but with added removals of larger fronds in 25 cm buffer zones). These sites were themselves close together (50 m apart) and within one particular area; therefore, we are cautious to generalize these results to other regions where impacts of *U. pinnatifida* on early successional assemblages might vary. Secondly, this study took place at a relatively small temporal scale (10 months) and documented the effects of *U. pinnatifida* over the course of its initial invasion. The possible impacts of *U. pinnatifida* following our canopy removals were limited to the taxa involved in the post-disturbance successional sequence, and while this is unique among experimental studies of *U. pinnatifida*, the longer-term implications of our findings need to be tested with more experiments and surveys.

The Pile Bay data do suggest that *U. pinnatifida* can be a passenger of ecological change (MacDougal and Turkington 2005), because it colonized the plots that had lost their native canopy cover (see also Thompson and Schiel 2012; Valentine and Johnson 2003). In the 10 months following the removal of the native canopy, *U. pinnatifida* had no effect on the recruitment of native canopy-forming algae, indicating that it might not be important in the recovery dynamics of these species. However, invading *U. pinnatifida* did inhibit a single ephemeral alga that was also facilitated by disturbance to the native stands, indicating that it can have effects on species with similar traits or temporal distributions. This study also showed that *U. pinnatifida* was the most abundant species in the lower-shore zone at Pile Bay in some months. Possible ecological implications, which warrant further studies, are that *U. pinnatifida* potentially increases coastal production (South et al. 2016; Tait et al. 2015), export biomass (Irigoyen et al. 2011b; Krumhansl and Scheibling 2012a; Wernberg et al. 2006) and modifies nutrient cycling (Dean and Hurd 2007; Tait et al. 2015)—all effects that can have cascading indirect effects within and across habitats and ecosystems (Krumhansl and Scheibling 2012b; Thomsen et al. 2010).

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## Compliance with ethical standards

**Conflict of interest** The authors declare no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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