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Cast adrift: Physiology and dispersal of benthic *Sargassum spinuligerum* in surface rafts

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Abstract

Connectivity of populations through the transfer of individuals is one of the key processes for maintaining ecosystem stability and resilience of coastal ecosystems. During reproduction, dislodged seaweeds of the genus *Sargassum* form large pelagic surface rafts that can persist for several weeks, and potentially act as a dispersal vector. In surface rafts, seaweeds are rapidly exposed to increased light, elevated temperatures, and altered hydrodynamic conditions. Acclimation to surface conditions is necessary for survival during the rafting phase, but there is limited knowledge of seaweed physiology in rafts. To understand the mechanisms for acclimation, we created rafts of floating *Sargassum spinuligerum* for 2 weeks and compared these experimental fronds to those attached to the seafloor. We measured nutrients, photosynthetic and nonphotosynthetic pigments, and phlorotannins to investigate their role in the persistence of mature *Sargassum* at the ocean surface as indicated by photosynthetic rates and reproductive status. We also studied potential surface movement of the rafted seaweed over 3-weeks of particle tracking using an existing oceanographic model. Photosynthesis and reproductive status were similar between benthic and rafted seaweeds, indicating no change to overall metabolic processes during rafting. While phlorotannin concentrations and photosynthetic pigments were unchanged, photoprotective xanthophyll pigments were more abundant in rafted individuals, suggesting acclimation to surface light conditions. Our results suggest that, in the short term, *S. spinuligerum* employ chemical strategies to acclimate and maintain physiological processes in the rafting environment and potentially fix more carbon, allowing these rafts to act as dispersal vectors among populations over tens of kilometers apart.

The dispersal capacity of an individual or species directly affects gene flow and connectivity among populations (Roughgarden et al. 1998; Fraser et al. 2009; Hinojosa et al. 2010; Fraser et al. 2011). A species with higher dispersal potential will be more likely to maintain high levels of connectivity among populations, to colonize new habitats and, potentially, to maintain greater ecosystem stability throughout its range (Kinlan and Gaines 2003; Castorani et al. 2015). In the marine environment, dispersal can occur though either active or passive movement in ocean currents and can significantly impact regional and local demographics. Dispersal of sessile organisms, like seaweeds, typically happens through the passive transportation of small propagules with little or no motility (Kendrick and Walker 1995; Dudgeon et al. 2001), generally over short distances (but see Gaylord et al. 2002). Large fronds of seaweeds with reproductive structures may also be dislodged during storms or seasonally senesce, float to the surface and form rafts that are then transported by oceanic currents in which they occur (Edgar 1987; Hobday 2000*a*).

Seaweeds are one of the more important groups of surface floating organisms in marine environment (Hobday 2000*a*; Vandendriessche et al. 2007) and account for a large portion of the biomass of marine rafting globally (Thiel and Gutow 2005; Fraser et al. 2011). When dislodged, positively buoyant seaweeds can float at the surface for weeks or months (Harrold and Lisin 1989; Holmquist 1994; Graiff et al. 2013; Tala et al. 2013). Surface rafts are thought to be an important dispersal vector for seaweeds (Dudgeon et al. 2001; Engelen

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Additional Supporting Information may be found in the online version of this article.

et al. 2001), and provide dispersal habitat for associated flora and fauna as the rafts may travel long distances (Hobday 2000*b*; Thiel and Gutow 2005; Wichmann et al. 2012).

Once dislodged, the positively buoyant seaweeds form surface rafts that are confronted with higher light conditions as well as wind and swell. Benthic seaweeds exposed to high-surface light, with little or no acclimation period, are at high risk for photo-damage and may experience decreased photosynthesis through loss of photosynthetic pigments (Cabello-Pasini et al. 2000) as well as DNA damage and reduced reproduction (Apprill and Lesser 2003; Karsten et al. 2009). Rafting seaweeds also experience increased herbivory by associated fauna and growth of epiphytes (Rothäusler et al. 2009; Graiff et al. 2016). This causes degradation and sinking of rafted individuals, thereby decreasing the dispersal potential. However, some seaweeds, like the giant kelp *Macrocystis pyrifera,* can quickly acclimate to surface UV radiation (Rothäusler et al. 2011*a*). Some seaweeds are known to increase production of phlorotannins to protect from UV radiation (Swanson and Druehl 2002). Another photoprotective mechanism is to increase de-epoxidation of violaxanthin, a nonphotosynthetic pigment, to intermediate xanthophyll pigments (antheraxanthin and zeaxanthin) that dissipate excess heat (Demmig-Adams and Adams 1996). This de-epoxidation process also helps reduce intercellular oxidative stress by absorbing light energy instead of radicalizing O_2 (reviewed in Adams et al. 1994; Demmig-Adams and Adams 1996). This process has been studied in land plants (Adams et al. 1994; Demmig-Adams et al. 1995) and seagrasses (Ralph et al. 2002) but is less understood in seaweeds (but see Schofield et al. 1998; Gévaert et al. 2003). Seaweeds that quickly acclimate and persist in surface rafts would subsequently have greater longevity and dispersal potential than seaweeds that do not acclimate. Despite our understanding of the dispersal potential of rafts for associated biota (Hobday 2000*b*; Thiel 2003; Fraser et al. 2011), we know much less about the cellular processes that improve acclimation potential and health of seaweeds that form rafts.

Seaweeds of the family Sargassaceae are positively buoyant and found globally throughout temperate and tropical ecosystems (McCourt 1985; Womersley 1987). *Sargassum* species are perennial organisms that cycle through vegetative growth and senescence periods annually (e.g., Wernberg et al. 2000). After internal fertilization, *Sargassum* spp. release negatively buoyant propagules that typically disperse no further than a few meters (Hurka 1971; Kendrick and Walker 1995). Although *Sargassum* propagules do not disperse very far, mature individuals often fragment and form surface rafts that can be transported considerable distances, sometimes over hundreds (Norton 1992) or thousands (van den Hoek 1987) of kilometers. Rafting that results from dislodgement or fragmentation is therefore a potential way to disperse reproductive thalli (Schiel and Foster 2006; Yatsuya 2008). Determining the physiology of *Sargassum* in surface rafts, how far those rafts could potentially travel on local ocean currents and how important they might be for dispersal is crucial to understanding the population connectivity and resilience of regional and global *Sargassum* populations (Mattio et al. 2013).

Here, we use a common seaweed that forms extensive subtidal benthic canopies along temperate and tropical rocky coastlines (*Sargassum spinuligerum* Sonder) to investigate the potential mechanisms employed by reproductive seaweeds to acclimate to rafts and the implications this acclimation may have for dispersal of healthy individuals. We had three primary aims. First, we investigated the effect rafting has on the physiology and nutrient content of *S. spinuligerum* by measuring photosynthetic yield, reproductive status, and carbon and nitrogen content. We also measured isotopic ratios as an indicator of overall seaweed health, as isotopic fractionation may change in response to abiotic conditions and overall photosynthetic activity (Wefer and Killingley 1986; Farquhar et al. 1989). Second, we investigated potential mechanisms of acclimation to the surface environment by quantifying biochemical changes (photosynthetic and nonphotosynthetic pigments, phlorotannin compounds) in tissues of *S. spinuligerum* during the rapid transition from benthic attachment to surface rafting. Finally, we determined the impacts of currents on dispersal capacity of mature *S. spinuligerum* individuals in surface rafts using a combined oceanographic and particle movement model.

Methods

Study location

We carried out two 14-d rafting experiments at three sites around Rottnest Island Western Australia (Fig. 1) during the austral spring from 18th September 2016 to 18th October 2016. The three study sites were nearshore lagoons that were semi-protected by a shallow reef crest and had similar depth but different levels of wind and wave exposure. Subtidal *S. spinuligerum* was our model seaweed (Guiry and Guiry 2018) as it is commonly found throughout Australia (Womersley 1987; Kendrick 1991), Africa (Mattio and Payri 2010), and Southeast Asia (Silva et al. 1996) and was abundant at each study site at 1–4 m depth.

Environmental conditions

We measured temperature and light in the surface and benthic environments every 5 min during the experiments. We measured surface temperature (°C) with a HOBO Tidbit logger shaded in a white enclosure to reduce the effect of incident irradiance, while benthic temperatures were recorded with a HOBO Pendant temperature logger. Surface and benthic irradiances (lux) were measured with HOBO Pendant light loggers. Each rafting logger was attached to a buoy line 10 cm below the surface. Benthic loggers were attached vertically to a star picket 0.5 m above the substratum at each study site. We calculated daily means for temperature and light over the duration of the experiments (Fig. 2). Light averages were calculated

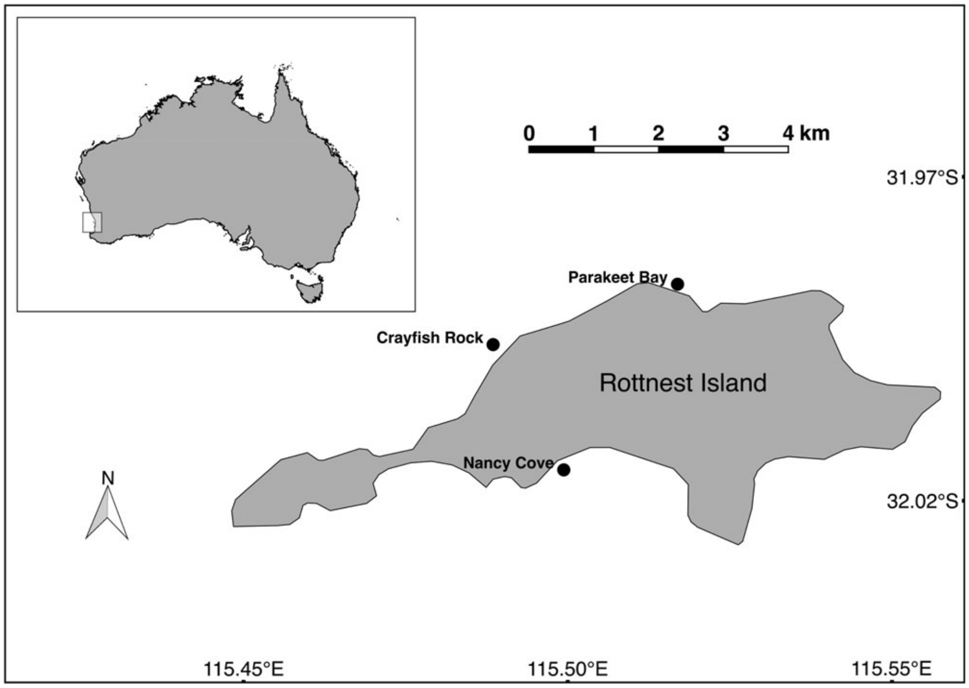

Fig. 1. Map of Rottnest Island, with inset of Australia, showing the three study sites (indicated by black dots) where *S. spinuligerum* was tethered to surface rafts during October 2016.

from measurements between sunrise and sunset while we used 24-h measurements to calculate temperature averages. Light intensities from the surface at Nancy Cove indicated shading artifacts for the duration of the experiments and were excluded from the results.

We calculated the wave exposure of the three study sites as the Baardseth's index (Ruuskanen et al. 1999; Wernberg and Vanderklift 2010), which is a numerical value (0–40) that represents the exposure experienced at a location (0 = no exposure, 40 = complete exposure). For each site, we drew a circle with 15 km diameter and the experimental setup at its center on a 1 : 75,000 nautical chart (WA001: Ocean Reef to Cape Peron, Maritime Cartographical Services, Perth). Each circle was divided into 40 equal pieces resulting in 9° wedges with a 7.5 km fetch. Each wedge was examined for the presence or absence of land and the number of wedges without any land added up to calculate an exposure index ranging from 0 for a completely protected site to 40 for a completely exposed site. Our Baardseth Index calculations for the three study sites indicated that Crayfish Rock was the most exposed (BI = 20), Parakeet Bay (BI = 16) intermediate, and Nancy Cove the most protected (BI = 6) site.

Experimental design

We installed one surface raft at each of the three study sites 25–50 m from shore. Experimental rafts consisted of a surface buoy tethered to a star picket that was driven into an area of sandy substratum near the *Sargassum* bed. The surface buoy was attached to the star picket with metal shackles and a 20 m line. Experimental seaweeds were attached to a floating line (10 m long) that was affixed to the surface buoy to create the experimental raft (Supporting Information Fig. S1). Identical rafts were created as described at each of the three study sites. At each site, 15 *S. spinuligerum* individuals (20–50 cm length, 50–140 g wet weight, including holdfasts) were collected from depths between 2 m and 3 m while scuba diving. Seaweeds were brought back to shore, cleaned of epiphytes, and randomly assigned to a time treatment ($n = 5$ per treatment): initial (0 weeks), 1 week, and 2 weeks of rafting. Individuals assigned to the 1- or 2-week treatments were blotted dry and weighed to the nearest 1.0 g before being attached to the floating line with cable ties and flagging tape at intervals of 25 cm and deployed immediately. Seaweeds were affixed loosely to the surface line as to prevent damage to the stipe from the cable tie attachment. The raft was anchored in the middle of each lagoon in 3–4 m of water so that the rafting seaweed floated at the sea surface and could swing freely with the current.

We collected tissue samples for baseline physiological and chemical measurements from naturally attached benthic seaweeds for the initial treatment (0 weeks) immediately after collection. Sampling was carried out after 7 d and 14 d of deployment when five seaweed fronds were collected from the raft and five natural seaweeds from the seafloor at each site. Tissue samples from the meristem region were collected for further pigment and phlorotannin analyses. Tissues were cleaned of epiphytes, wrapped in foil, and immediately placed in a dry shipper. Samples were taken from the dry shipper

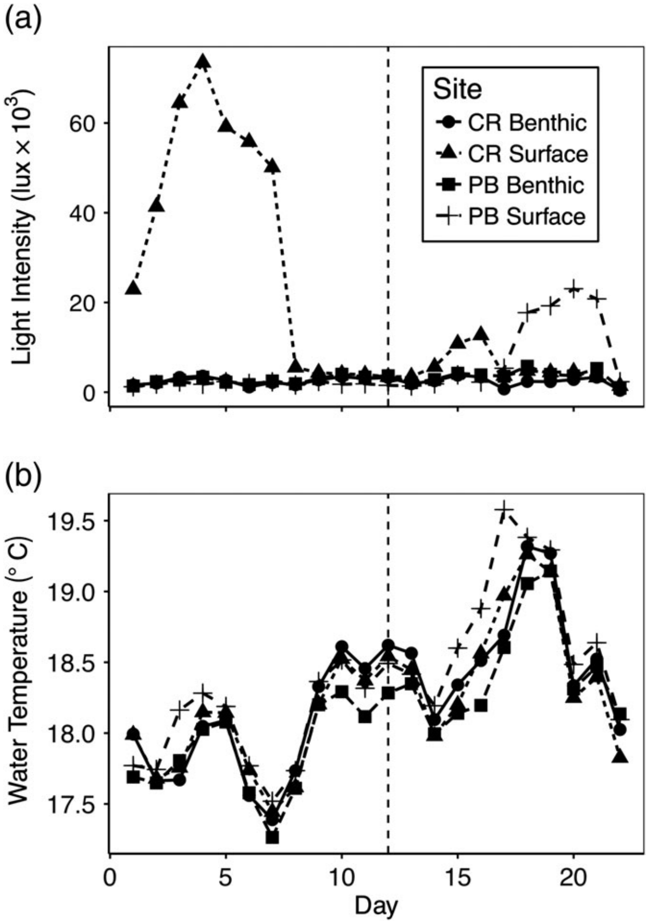

Fig. 2. (**a**) Light intensity (lux) and (**b**) temperature (°C) measurements taken during the two rafting experiments at Crayfish Rock (CR) and Parakeet Bay (PB) on Rottnest Island. Values shown are mean daily averages. Light intensity averages were calculated from values between the time of sunrise and sunset while temperature averages are from 24-h measurements. The vertical line marks the end of the first experiment block and the beginning of the second.

within 2 d of collection and stored at −80°C for pigment analysis or into a freeze-drier for phlorotannin and stable isotope analysis. After 2 weeks, we replicated the experiment at each site with fresh macroalgal fronds collected from the benthos and deployed once again as described above. We replicated the experiment with a blocked design to account for the logistical constraints of only being able to sample a single raft line per bay at a given time point.

Sampling and response variables

Growth and reproductive status

Sargassum grows from multiple apical meristem regions, so change in wet weight is the most efficient way to calculate growth in the field. Therefore, we measured growth of floating *S. spinuligerum* by taking the wet weight (to the nearest gram) of each seaweed before deployment (initial weight [IW]) and then again on removal from the raft (final weight [FW]). Weight change during the rafting period was calculated as ([FW − IW]/IW) (Rothäusler et al. 2011*a*; Cruces et al. 2016). We assessed the reproductive status of each *S. spinuligerum* individual when it was removed from the floating surface line (Supporting Information Fig. S1) by visually inspecting and recording the presence (yes) or absence (no) of receptacles.

Chlorophyll fluorescence

To determine the overall photosystem efficiency, we measured the maximum quantum yield (MQY) of each *S. spinuligerum* individual with a diving-PAM (Walz, Germany) immediately after collection from the raft or benthos. Three randomly selected meristematic regions from each individual were dark-adapted for 15 min. We then measured MQY and averaged the three measurements to give one value per individual. Quantum Yield measurements at each site were always made at the same time of day for week 0, 1, and 2, however, because of the logistical constraints of the experiment, the times were different among the three sites. The MQY of experimental individuals was therefore calculated as a proportion of the MQY values of benthic control seaweeds (Rothäusler et al. 2018). This calculation allowed us to compare across treatments and among sites by removing potential variability in MQY that may exist throughout the daily photocycle period.

Phlorotannin concentration

We measured phlorotannin concentrations of three subsamples per freeze-dried seaweed frond using the Folin–Ciocalteu method, optimized for the microplate reader (van Hees et al. 2017). Ten milligrams of lyophilized meristem tissue were extracted overnight in 1.0 mL of 80% acetone in darkness. Each extract was then diluted 1 : 20 with the addition of Type II Reagent Grade Water. Diluted extracts were then combined with 40 μL of Folin–Ciocalteu reagent and shaken for 5 min. After that, extracts were made alkaline by the addition of 100 μL of sodium carbonate and shaken for an additional 30 s and then incubated for 30 min at 50°C. Fluorescence was then read using a FluoStar Synergy MX Plate Reader at 765 nm. Three replicate samples of each extract were measured and the mean was calculated as the average per extract. Phloroglucinol (Sigma-Aldrich 108-73-6) was used as standards ($n = 3$ per standard) and were run on each plate of extracts. We calculated phlorotannin concentrations as percent dry mass.

Pigments

Photosynthetic (chlorophyll a) and nonphotosynthetic (α- and β-carotene, antheraxanthin, fucoxanthin, violaxanthin, zeaxanthin) pigments were extracted from frozen tissue samples (three compounded meristem samples each) using the high performance liquid chromatography (HPLC) method in Tamm et al. (2015). Tissue samples ($n = 1$ sample per individual) were stored at −80°C and all extractions were made within 4 months of collection. We ground frozen tissue (0.4 g per sample) in cold acetone using a chilled mortar and pestle and then diluted each sample with 5–7 mL of cold acetone. Each sample was wrapped in aluminum foil, sonicated for 5 min, and left to extract overnight at −3°C. The following day, extracts were centrifuged at 16,000 rpm for 5 min. We pipetted 0.9 mL of supernatant into HPLC vials that were stored at −3°C until analysis on the HPLC.

We separated photosynthetic and nonphotosynthetic pigments in accordance with Tamm et al. (2015) with minor modifications. We achieved separation at temperature of 25 ± 1°C in 50 min on a Spherisorb ODS2 (Waters, Milford, Massachusetts, U.S.A.) column (250 mm × 4.6 mm internal diameter with 5 μm particle), using a Waters® HPLC system (600E pump, 717+ auto injector with carousel temperature set at 10°C and 996 photodiode-array detector). The mobile phase consisted of two premixed eluents, A = 80 : 20 methanol : 0.5 M ammonium acetate pH 7.2 and B = 80 : 20 methanol : acetone. Increasing the flow rate from 33.0 mL min^{-1} to 45.0 mL min^{-1} reduced the run time of the analysis. Typical injection volume for samples and standards was 10 μL. The photodiode array acquired data from 350 nm to 750 nm at a resolution of 1.2 nm to enable positive identification of pigments by comparing the retention time and peak spectral information, of standards with those of the samples using Empower® chromatography software (Waters). Detection and quantification of the pigments was achieved at 450 nm with peak area used to calculate all linear calibrations.

We used standards from DHI Waters and Environment Pty Ltd (Hørsholm, Denmark) for all xanthophyll pigments. Fucoxanthin, Chl *a*, and β-carotene were pure chemicals purchased from Sigma-Aldrich (New South Wales, Australia). We used HPLC grade solvents (methanol and acetone) purchased from Sigma-Aldrich that were degassed and filtered to 0.2 μm before use, and utilized helium sparge to degas online. We calculated tissue pigment concentration with the following equation:

$$\frac{\left([\text{Extract pigment}]\left(\mu\text{g mL}^{-1}\right)\right)\times(\text{Acetone volume (mL)})}{\text{Tissue Wet Weight (g)}} = [\text{Pigment}]\left(\mu\text{g g}^{-1}\right)$$

We calculated the proportion of xanthophyll pigments (antheraxanthin, violaxanthin, and zeaxanthin) as the de-epoxidation ratio in benthic and rafted *S. spinuligerum* as:

$$\frac{([\text{Antheraxanthin}]+[\text{Zeaxanthin}])}{([\text{Violaxanthin}]+[\text{Antheraxanthin}]+[\text{Zeaxanthin}])} = \text{de-epoxidation ratio (DR)}$$

Isotope and nutrient content

Between 1.1 mg and 1.2 mg of freeze-dried *S. spinuligerum* (*n* = 1 sample per individual), tissue was packed into tin caps and analyzed for δ^{13}C, δ^{15}N, carbon and nitrogen content using a continuous flow system consisting of a Delta V Plus mass spectrometer connected with a Thermo Flush. Multipoints normalization was then used to reduce the raw values to the international scale (Skrzypek 2013) Normalization was done on the basis of international standards provided by IAEA: δ^{13}C-NBS22, USGS24, NBS19, LSVEC; and for δ^{15}N-N1, N2, USGS32 and laboratory standards. The external error of the tissue analysis (as one standard deviation) is: $\delta^{13}\text{C} = 0.10‰$, $\delta^{15}\text{N} = 0.10‰$, C/N = 0.1.

Statistics

To evaluate changes in physiology and chemistry between benthic and rafted *S. spinuligerum*, we used mixed-effects models that included time (0 week, 1 week, or 2 week) and depth (surface or benthic) as fixed factors and site and experiment as random factors. Including site and experiment as random factors ensured the proper degrees of freedom for factors at the site and experiment level and avoided pseudo-replication. Residual plots of the initial full models indicated heteroscedasticity, so we modeled the variance structure of each model using the "weights" option within the "lme" function (Pinhiero et al. 2018). We chose the optimal variance structure by selecting the model with the lowest Akaike information criterion (AIC) value and comparing standardized residual plots (Zuur et al. 2009).

After we identified the best variance structure, we simplified the model by step-wise reducing the number of factors (Smith et al. 2017). We did this by dropping model terms sequentially until we achieved the lowest AIC using the maximum log-likelihood fit to enable comparison among models (Zuur et al. 2009). Nonsignificant factors were sometimes retained in final models because dropping them increased the AIC (Supporting Information Table S1). We evaluated the final model fixed factors with *p* values based on marginal *t*-tests from the "summary" function and the residual values of the random factors (Supporting Information Table S1). Final model outputs provided comparisons between all levels and interactions of fixed factors, (Table 1). We calculated the change in reproductive status between benthic and rafted seaweeds using a chi-squared test on binary (presence absence) observations of reproductive structures. All statistical analyses were run in R (R Core Team 2017).

Dispersal modeling

The movement of floating particles on the sea surface was simulated with a three-dimensional numerical model MIKE3, coupled to a particle-tracking module (DHI 2010). The model consisted of over 50,000 triangular grid elements of varying areas according to depth to keep the barotropic Courant number low (< 0.8 with ~ 20 s time-steps), and 10 sigma layers on the vertical axis. This allowed releasing of the particles in the shallows and tracking of the surface movement while considering greater synoptic phenomena such as the Offshore

Table 1. Results of final mixed-effects models explaining pigment and phlorotannin content of experimentally rafted *S. spinuligerum* over 14-d rafting experiments. Values shown are from final models following validation and reduction of full-models that included time (0 week, 1 week, and 2 week) and depth (benthic, surface) as fixed factors and experiment and site as random factors. The fixed factor values for time are compared to initial (week 0) values and those for depth are compared to benthic values.

Factor	Value	SE	df	*t* value	*p* value
Chl *a*					
(intercept)	504.35	52.13	97	9.67	< 0.001
Time (week 1)	−69.64	48.56	97	−1.47	0.15
Time (week 2)	13.07	48.56	97	0.27	0.79
Depth (surface)	0	48.56	97	0	1
Time (week 1) : depth (surface)	68.62	68.67	97	1.00	0.32
Time (week 2) : depth (surface)	−1.02.53	68.67	97	−1.49	0.14
α- and β-carotene					
(intercept)	18.87	1.73	97	10.89	< 0.001
Time (week 1)	−2.26	1.95	97	−1.15	0.25
Time (week 2)	−0.13	1.96	97	−0.07	0.95
Depth	0	1.96	97	0	1
Time (week 1) : depth (surface)	1.83	2.77	97	0.66	0.51
Time (week 2) : depth (surface)	−1.82	2.77	97	−0.66	0.51
Antheraxanthin					
(intercept)	4.98	0.61	97	8.18	< 0.001
Time (week 1)	−0.22	0.66	97	−0.34	0.73
Time (week 2)	−0.03	0.66	97	−0.05	0.96
Depth (surface)	0	0.66	97	0	1
Time (week 1) : depth (surface)	1.20	0.93	97	1.30	0.20
Time (week 2) : depth (surface)	2.45	0.94	97	2.6	0.01
Fucoxanthin					
(intercept)	226.51	25.19	97	8.99	< 0.001
Time (week 1)	−40.28	22.36	97	−1.80	0.07
Time (week 2)	−2.17	24.89	97	−0.087	0.93
Depth (surface)	0.00	24.46	97	0.00	1.0
Time (week 1) : depth (surface)	24.76	31.62	97	0.78	0.44
Time (week 2) : depth (surface)	−57.75	35.20	97	−1.64	0.10
Violaxanthin					
(intercept)	27.16	2.63	97	10.32	< 0.001
Time (week 1)	−0.93	2.74	97	−0.34	0.73
Time (week 2)	1.96	2.74	97	0.71	0.48
Depth (surface)	0	2.74	97	0	1
Time (week 1) : depth (surface)	8.78	3.88	97	2.26	0.03
Time (week 2) : depth (surface)	−0.08	3.88	97	−0.02	0.98
Zeaxanthin					
(intercept)	2.22	0.36	97	6.12	< 0.001
Time (week 1)	0.19	0.36	97	0.53	0.60
Time (week 2)	0.20	0.36	97	0.55	0.58
Depth (surface)	0.0	0.35	97	0.0	1.0
Time (week 1) : depth (surface)	1.23	0.58	97	2.14	0.03
Time (week 2) : depth (surface)	2.33	0.83	97	2.82	< 0.01
De-epoxidation ratio					
(intercept)	0.21	0.009	101	22.86	< 0.001
Depth (surface)	0.03	0.014	101	2.34	0.02
Phlorotannins					

(Continues)

Table 1. Continued

Factor	Value	SE	df	*t* value	*p* value
(intercept)	5.53	0.5	173	11.1	< 0.001
Depth (surface)	0.12	0.16	173	0.79	0.43

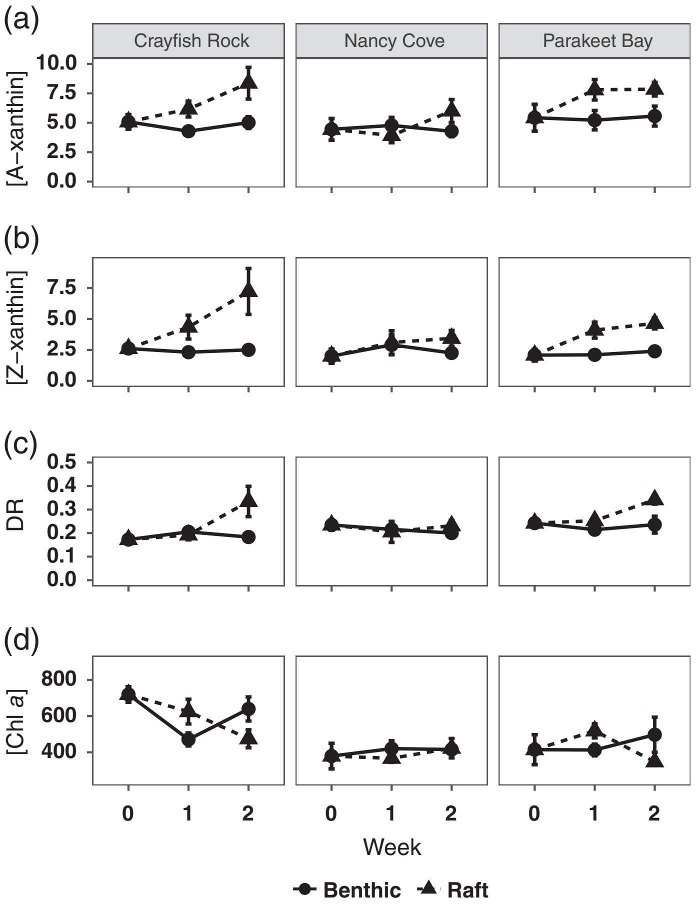

Fig. 3. Antheraxanthin concentration (**a**), zeaxanthin concentration (**b**) the de-epoxidation ratio (DR) (**c**), and Chl *a* concentration (**d**) of benthic (black line) and rafted (dotted line) *S. spinuligerum*. Weekly values for each site were averaged over two 14-d experiments. All pigment concentrations are in μg g^{-1} (wet weight) and data shown are means ± SE.

Leeuwin Current. The diurnal tidal cycles and winds were inputs considered as 2-h intervals for sea level, and 1-min readings for winds recorded at Rottnest Island. The model was previously calibrated for the area with measured data from November 2010 to December 2010 (*see* Ruiz-Montoya and Lowe 2014; Ruiz-Montoya et al. 2015).

The hydrodynamic simulation ran for 2 months, while the release of the particles began after the second week and consisted of 25 particles released per site every hour for the following 3 weeks. The trajectory of each path taken by the particle was recorded every hour and colored maps of overall probability of dispersal were created for each site allowing us to visualize distance traveled and paths taken for transport over different bays. By adapting the existing coupled particle tracking and hydrodynamic models from a previous seagrass study, we were limited to a relatively small number of drifting particles (12,500), a single snapshot of movement (7 d after release), a time window of 2 weeks in November/December that represents the maximum time of release of *Sargassum* thalli at Rottnest (Kendrick and Walker 1994) and small particle size. As such the model output should be used as heuristic and indicative of *Sargassum* drift only.

Results

Environmental conditions

During the experimental period, daily surface light intensities (lux) were at times higher than benthic intensities while temperatures were similar. Rafted seaweeds experienced average daily light intensities that ranged from 2400 lx (like benthic intensities) to almost 38,000 lx (Fig. 2a) and were temporally variable while benthic intensities were consistently between 1500 lx and 3000 lx. Surface irradiances were notably higher than benthic levels at Crayfish Rock during the first half of the experiment while those at Parakeet Bay were higher in the second half. Shading artifacts similar to those observed at Nancy Cove may have created the low surface light readings at Parakeet Bay and Crayfish Rock, but not for the entire experimental period, so we did not exclude them from analysis. While observed differences in surface and benthic irradiances were not consistent, these values suggest the light environment of the surface is at times more intense and variable that of the benthos. Daily temperature averages ranged from 17.4°C to 19.3°C during the experiments and were similar between benthic and raft environments (Fig. 2b), indicating a well-mixed water column.

Physiology and pigments

We observed significant differences in chemical characteristics of benthic and rafted fronds over time in *S. spinuligerum* for some of the measured metrics. Nonphotosynthetic pigment concentrations increased over time in rafted *S. spinuligerum* compared to benthic individuals (Supporting Information Table S2). Antheraxanthin concentrations of rafted *S. spinuligerum* were significantly higher than in benthic seaweeds after 2 weeks ($t = 2.6$, $p = 0.01$, df = 97) (Fig. 3a; Table 1) with concentrations 66% higher at Crayfish Rock and 40% higher at Nancy Cove and Parakeet Bay (Supporting Information Table S2). While zeaxanthin concentrations in benthic *S. spinuligerum* were similar throughout the experiment, concentrations

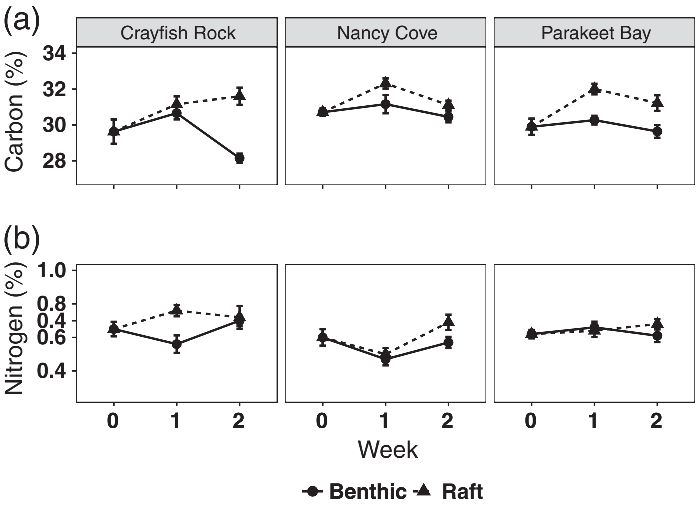

Fig. 4. Carbon (**a**) and nitrogen (**b**) concentrations (% dry weight) of benthic (black line) and rafted (dotted) *S. spinuligerum* over 2 weeks. Individual panels show results from each site averaged over two 14-d experiments. Nutrient concentrations are in % dry weight, represented by means ± SE.

in rafted seaweeds increased by 25% and 49% (Fig. 3b) after 1 week and 2 week, respectively ($t = 2.14$, $p = 0.03$, df = 97; $t = 2.82$, $p < 0.01$, df = 97) (Table 1). This difference was most noticeable at Crayfish Rock, where zeaxanthin concentrations in rafted individuals was 49% higher than in benthic ones (Supporting Information Table S2). Violaxanthin concentrations were also higher in rafted seaweeds after 1 week ($t = 2.26$, $p = 0.03$, df = 97) (Table 1) but returned to be similar at 2 weeks. The de-epoxidation ratio of rafted seaweeds was also over 10% higher than the ratio of benthic seaweeds throughout the experiment ($t = 2.34$, $p = 0.02$, df = 101) (Fig. 3c; Table 1). Fucoxanthin and carotenoid pigment concentrations did not change during 2 weeks in the raft (Supporting Information Table S2). Additionally, the concentrations of photosynthetic Chl *a* (Fig. 3d; Table 1), and phlorotannins (Supporting Information Table S2, Table 1) in *S. spinuligerum* were unchanged in rafted and benthic seaweeds.

While carbon content of rafted *S. spinuligerum* increased over 2 weeks compared to benthic individuals, rafting did not affect stable isotope ratios. Carbon concentration of rafted *S. spinuligerum* was, on average, 1.2% higher than in benthic

Table 2. Results of final mixed-effects models explaining isotope and nutrient content of experimentally rafted and benthic *S. spinuligerum* over 14-d rafting experiments. Values shown are from final models following validation and reduction of full-models that included time (0 week, 1 week, and 2 week) and depth (benthic, surface) as fixed factors and experiment and site as random factors. The fixed factor values for time are compared to initial (week 0) values and those for depth are compared to benthic values.

Factor	Value	SE	df	*t* value	*p* value
δ^{15}N					
(intercept)	3.44	0.083	172	41.20	< 0.001
Time (week 1)	−0.17	0.043	172	−3.85	0.002
Time (week 2)	−0.07	0.035	172	−2.25	0.03
δ^{13}C					
(intercept)	−16.96	0.54	169	−31.3	< 0.001
Time (week 1)	−0.28	0.38	169	−0.74	0.46
Time (week 2)	0.93	0.35	169	2.65	< 0.01
Depth (surface)	0.000	0.38	169	0.00	1.0
Time (week 1) : depth (surface)	0.65	0.53	169	1.23	0.22
Time (week 2) : depth (surface)	0.50	0.49	169	1.02	0.31
Carbon %					
(intercept)	30.08	0.58	169	52.03	< 0.001
Time (week 1)	0.62	0.26	169	2.42	0.02
Time (week 2)	−0.66	0.31	169	−2.12	0.04
Depth (surface)	0	0.23	169	0	1
Time (week 1) : depth (surface)	1.12	0.36	169	3.11	0.002
Time (week 2) : depth (surface)	1.90	0.44	169	4.26	< 0.001
Nitrogen %					
(intercept)	0.61	0.026	173	23.07	< 0.001
Depth (surface)	0.043	0.019	173	2.21	0.03
C : N					
(intercept)	30.13	0.48	172	62.41	< 0.001
Depth (surface	0.85	0.19	172	4.4	< 0.001

Table 3. Results of statistical models explaining reproductive status (presence or absence of receptacles) and MQY of experimentally rafted and benthic *S. spinuligerum* over 14-d rafting experiments. Reproductive status values are the results of a chi-squared test comparing the presence or absence of reproductive structures between benthic and rafted individuals. Quantum yield values shown are from final mixed-effects models following validation and reduction of full mixed-models that included time and depth as fixed factors. The fixed factor value for depth is compared to the benthic value.

(a) Reproductive status	χ^2		**df**		***p* value**
	1.26		1		0.26
(b) MQY	Value	SE	df	*t* value	*p* value
(intercept)	0.57	0.043	173	13.12	< 0.001
Depth (surface)	−0.01	0.01	173	−1.02	0.31

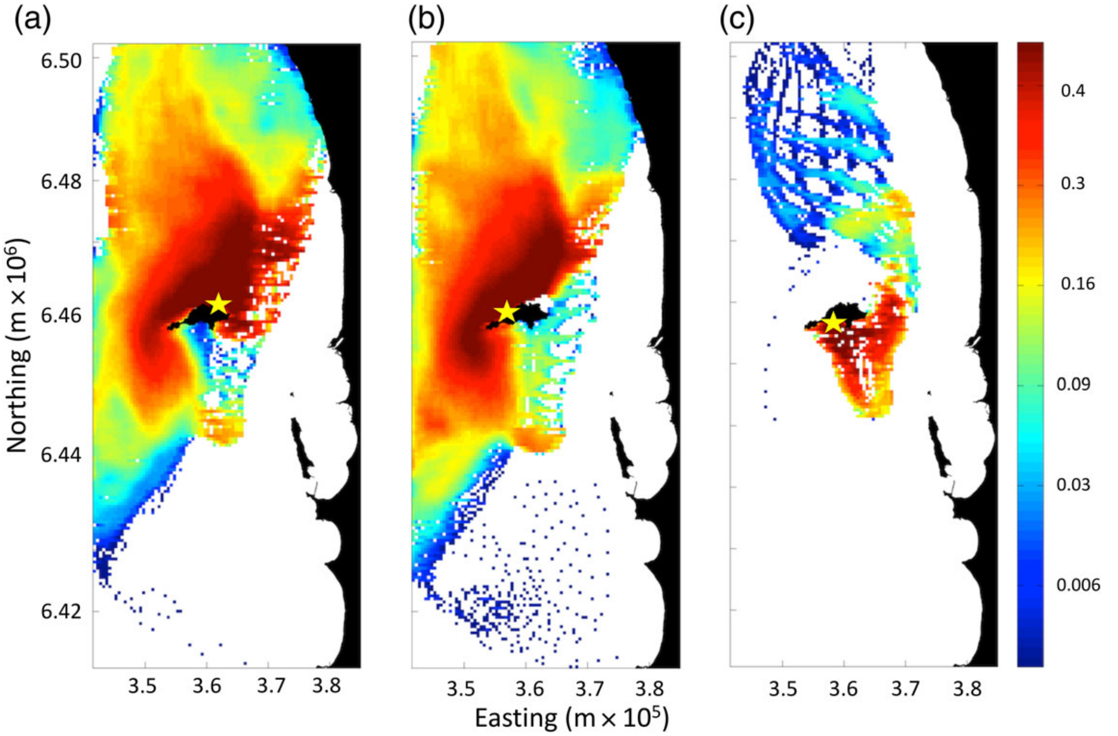

Fig. 5. Probability maps of the movement of model particles (2 cm diameter) with a 5-d lifespan in 7 d during a continuous 3-week release, released from (**a**) Parakeet Bay, (**b**) Crayfish Rock, and (**c**) Nancy Cove at Rottnest Island over a continuous 2-week period. Warmer colors indicate higher probability of dispersal from source locations, indicated with a yellow star.

controls after 1 week and 1.8% higher after 2 weeks ($t = 3.11$, $p = 0.002$, df = 169; $t = 4.26$, $p < 0.001$, df = 169, respectively) (Fig. 4a; Table 2) The largest differences in carbon content were 3.1% higher concentrations in rafted seaweeds at Crayfish Rock after 2 weeks while concentrations were 0.6% higher at Nancy Cove (Supporting Information Table S2). Although nitrogen content of rafted *S. spinuligerum* was statistically different from benthic individuals ($t = 2.21$, $p = 0.03$, df = 173) (Fig. 4b; Table 2), it was only 0.03–0.1% higher in rafted individuals (Supporting Information Table S2). Although $\delta^{13}C$ and $\delta^{15}N$ concentrations increased over 2 weeks ($t = 2.65$, $p < 0.01$, df = 169; $t = -2.25$, $p = 0.03$, df = 172, respectively), we observed no effect of rafting on isotope concentrations (Table 2).

There were no changes to chlorophyll fluorescence and reproductive status of *S. spinuligerum* in surface rafts. MQY and reproductive status were similar between benthic and rafted *S. spinuligerum* after 1 week and 2 week (Supporting Information Table S2, Table 3). The reproductive status was also similar between benthic and rafted individuals throughout our experiments. During tidal exchanges and in response to wave action and currents, the floating surface line would swing around and sometimes get tangled around itself or the surface buoy. This caused the loss of large pieces of the rafted seaweeds, which therefore saw considerable reductions (2–30 g week^{-1}) in total biomass during the experiments (Supporting Information Table S2).

Dispersal

Hydrodynamic models and field observations indicate a general northward flow of inshore waters during the summer. Dispersal of floating *S. spinuligerum* from the two more exposed study sites (Crayfish Rock and Parakeet Bay) was highest (0.4 probability) to the north, east, and west, showing high dispersal probabilities for these open embayments (Fig. 5a,b). This probability of dispersal was slightly reduced at Nancy Cove (~ 0.3); physical barriers to the overall transport such as land to the north diminished the probability of transport and restricted overall dispersal distance (Fig. 5c). Dispersal distances of particles commonly reached up to around 50 km during the 5-d tracking periods and extended beyond the model domain. Thus, extrapolation outside of our model domain would easily allow particles to travel hundreds of kilometers during a 2-week simulation.

Discussion

While the longevity of kelp-based seaweed rafts and dispersal of associated biota has been studied in regions such as the eastern Pacific (Hobday 2000*b*; Tala et al. 2013), we know less about the mechanisms by which seaweeds rapidly acclimate to surface conditions or the role of rafting in *Sargassum* spp. dispersal and connectivity (but see Yatsuya 2008, Mattio et al. 2013). In our raft experiments, *S. spinuligerum* in surface rafts remained afloat, appeared healthy throughout our experiments, and exhibited chemical changes that suggest protective strategies to acclimate to the surface environment. We identified potential chemical mechanisms by which *S. spinuligerum* acclimates to the conditions at the sea surface. Individuals in surface rafts had increased xanthophyll pigment concentrations as well as carbon content compared to benthic individuals. All other physiological and chemical characteristics were unchanged, indicating environmental conditions were within the seaweed's physiological tolerances in surface rafts at least over the short term. Although surface light conditions were, at times, 3–4 orders of magnitude more intense than on the bottom, rafted and benthic *S. spinuligerum* were photosynthetically and reproductively identical. Our dispersal models showed that these healthy individuals disperse tens of kilometers (~ 50 km) during a 5-d period and could have traveled hundreds of kilometers in 2 weeks, potentially creating connected populations throughout the range of *S. spinuligerum* in Western Australia.

Seaweed acclimation to surface stressors

Floating seaweeds are exposed to high UV radiation compared to benthic individuals because of rapid attenuation of UV radiation in the water column. Acclimation to these increased light conditions is necessary for rafted seaweeds to persist. *Sargassum spinuligerum* in our experimental rafts had elevated primary and intermediate xanthophyll pigment pools as well as higher de-epoxidation ratios than benthic seaweeds but we saw no difference in α- and β-carotene concentrations. Similarly, *Sargassum natans*, a pelagic species in the Sargasso Sea, had higher proportions of nonphotosynthetic to photosynthetic carotenoids during daylight hours (Schofield et al. 1998). Zeaxanthin concentration also increased during low tide in *Laminaria saccharina* (Gévaert et al. 2003) and under high light in *S. natans* (Schofield et al. 1998). Larger pools of intermediate xanthophyll pigments have been observed in sun-acclimated land plants (Thayer and Björkman 1990) as well as seagrasses (Ralph et al. 2002) compared to shade-acclimated individuals. The increases in intermediate xanthophyll pigments we observed potentially prevented photoinhibition in *S. spinuligerum*, allowing photosynthetic pigments like α- and β-carotene to remain consistent. This is dissimilar to some rafting seaweeds, like *Durvillaea antarctica*, that showed daily photodegradation under high-light conditions in surface rafts (Tala et al. 2017). Rafted *M. pyrifera* also had decreased pigments (Rothäusler et al. 2011*a*,*b*) as a photoprotective mechanism. Interestingly, other proposed light-mediating compounds in *S. spinuligerum*, such as phlorotannins (Pavia et al. 1997; Creis et al. 2015), did not change in the rafts. Although phlorotannins are thought to be a photoprotective mechanism (Abdala-Díaz et al. 2006), they are not known to dissipate heat like intermediate xanthophyll pigments. Therefore, the physiological benefits of elevated xanthophyll pigments may eliminate the need for UV protection from higher phlorotannin concentrations.

In addition to increased radiation, rafted seaweeds are exposed to other physical stressors such as wind and swell, and these conditions vary throughout a seaweeds geographic distribution. Indeed, chemical concentrations of seaweeds are known to change over scales of meters to hundreds of kilometers (Van Alstyne et al. 2007; van Hees et al. 2017). Rafting persistence also varies geographically. For example, the persistence of floating kelps was higher at mid-latitude sites (Rothäusler et al. 2011*b*). Here, while xanthophyll concentrations generally increased throughout our experiments, the increase was not consistent among the three sites. Antheraxanthin and zeaxanthin concentrations in floating seaweeds were similar to concentrations in benthic individuals at Nancy Cove but higher at Crayfish Rock and Parakeet Bay. Nancy Cove was the most protected (lowest BI) and had the lowest surface light intensities of our three sites. Therefore, the cumulative stress levels experienced by individuals at Nancy Cove may be lower than those at Crayfish Rock and Parakeet Bay and may not have passed some unmeasured stress threshold that resulted in increase of the xanthophyll cycle we observed at Crayfish Rock and Parakeet Bay. This type of synergy of stressors was seen when rafted *M. pyrifera* acclimated to a combination of stressors but not individual ones (Rothäusler et al. 2011*c*). Therefore, rafted individuals experiencing more favorable conditions like those found in Nancy Cove would rely less on mechanisms to acclimate to surface conditions compared to the other study sites. Additional environmental factors relating to exposure, such as wave turbulence and wind, may create differences among sites, as chemical differences among sites were loosely related to exposure but not light intensity.

Seaweeds in our experimental rafts showed higher carbon than benthic individuals. Although we did not measure enzymatic activity, this elevated nutrient content of rafted seaweeds we observed might result from elevated production of storage carbohydrates. Seaweeds produce a multitude of intracellular storage carbohydrates (reviewed in Hurd et al. 2014). Light-dependent production of these compounds is primarily driven by carbonic anhydrase (CA) that converts oceanic HCO_3^- and this activity varies depending on environmental conditions. The red alga *Rissoella verruculosa* had elevated CA activity in presence of UV light (Flores-Moya et al. 1998) and *M. pyrifera* showed elevated CA activity after 5 d of rafting (Rothäusler et al. 2011*c*). Rafted *S. spinuligerum* may have flourished at the surface because they were actively storing carbon instead of using internal carbon to persist at the surface, as we would expect to find in unhealthy individuals.

Floating seaweed impacts on dispersal and connectivity

Dispersal of fertilized seaweed propagules generally occurs over short distances (Kendrick and Walker 1995; Kinlan and Gaines 2003) but reproductive individuals may be transported farther distances in surface rafts, thereby increasing the dispersal of viable progeny (van den Hoek 1987; McKenzie and Bellgrove 2008). However, rafted seaweeds must remain healthy and reproductively viable in surface conditions if they are to effectively use rafts as dispersal mechanisms. The reproductive longevity of *M. pyrifera* in surface rafts allows viable propagule dispersal over distances up to 1000 km (Hernández-Carmona et al. 2006). Similarly, rafted fucoid seaweeds from New Zealand actively released viable propagules for up to 60 d (Hawes 2008) and mature *Sargassum patens* formed receptacles while floating (Yatsuya 2008). We saw no change in the occurrence of reproductive receptacles or to MQY of rafted *S. spinuligerum*, suggesting individuals quickly acclimated to the surface environment and that surviving at the surface does not have overall fitness costs relative to being attached to the benthos. Had there been any significant changes to overall metabolic processes, we would have also expected to see a change to the isotopic fractionation in floating individuals. Isotopic fractionation can change in response to photosynthetic relationships to light and other environmental conditions (Cooper and DeNiro 1989; Vanderklift and Bearham 2014; Drobnitch et al. 2018). However, isotopic ratios were similar between benthic and rafted seaweeds, providing further evidence that overall photosynthetic ability was not impacted by rafting. Additionally, *S. spinuligerum* acclimated to the surface environment despite experiencing tissue losses throughout the experiment. Tissue loss through entanglement and abrasion can be a significant source of stress for seaweeds, as stress potentially results in trade-offs in energy distribution to vital processes throughout the seaweed (Graham 2002). However, this did not appear elicit a stress response in rafted *S. spinuligerum*. Because of this, rafting of *S. spinuligerum* is likely a viable means for dispersing mature reproductive individuals among geographically isolated populations.

Our dispersal models indicated that seaweeds from any of the three study sites would potentially disperse to sites all around Rottnest Island after 2 weeks in a raft. Oceanic currents are known to connect seemingly distant macroalgal populations globally (Hinojosa et al. 2010; Wichmann et al. 2012; Li et al. 2017) and the same is likely true for *S. spinuligerum*. *Sargassum* has previously been estimated to travel in rafts from hundreds (Mattio et al. 2013) to thousands of kilometers (Yatsuya 2008) among populations. Since rafted *S. spinuligerum* individuals appeared healthy after 2 weeks, we do not know the physiological limitations of this particular species in surface conditions but other mature *Sargassum* spp. remained afloat for up to 8 weeks (Yatsuya 2008). *Sargassum spinuligerum* would likely disperse farther than predicted by our 2-week experiment and dispersal modeling.

Long-distance dispersal via rafting requires individuals remain viable and that they persist in the surface environment. Many species of seaweed remain positively buoyant for long periods of time (van den Hoek 1987; Macaya et al. 2005; Hawes et al. 2017) but not all remain vectors for dispersal because of degradation and sinking (Yatsuya 2008; Rothäusler et al. 2011*c*; Graiff et al. 2016). Rafting is possibly a long-distance dispersal mechanism of reproductive *S. spinuligerum* because of cellular mechanisms that allow individuals to acclimate to the surface environment. Climate change is likely to alter the efficacy of dispersal rafts of seaweeds due to ocean warming and altered currents (Macreadie et al. 2011). Increased storm activity is currently pushing mangrove dispersal ranges northward (Ilka Feller pers. comm.) and tsunami debris is introducing eastern Pacific flora and fauna to North America (Carlton et al. 2017; Miller et al. 2017). Altered temperature regimes and oceanographic currents may push tropical seaweed species distribution limits poleward, resulting in tropicalization (Vergés et al. 2014) if the efficacy of rafting dispersal is maintained (Smale and Wernberg 2013; Wernberg et al. 2013).

Determining the persistence of macroalgal rafts is critical to understanding their efficacy as positive dispersal vectors. *Sargassum spinuligerum* in rafts are likely dispersal vectors over large geographic distances because they can activate protective chemical mechanisms and remain reproductive while rafting. Although we do not know the full extent of their dispersal potential, *S. spinuligerum* appears to be one of the few seaweeds to actively acclimate to the surface conditions (but see Rothäusler et al. 2011*a*). *Sargassum natans* and *S. fluitans* in the West Atlantic Ocean (Sargasso Sea) are examples of *Sargassum* spp. that are fully adapted to rafting conditions, as their vegetative lifecycle is entirely pelagic. Recent changes in environmental conditions (currents, nutrients, etc.) are suspected to be responsible for increased rafting biomass in recent years (Smetacek and Zingone 2013). As rafting occurs more frequently and over longer distances from large storms (Carlton et al. 2017; Miller et al. 2017), our understanding of rafting ecosystems will be critical in determining the impacts of rafting events. These impacts may reach farther than we currently know, as these rafts transport not only flora and invertebrate fauna, but vertebrates as well (Carr and Meylan 1980). Understanding how the acclimation processes and dispersal capacity of *Sargassum* and other seaweeds are affected by a changing climate will help us understand the connectivity among seaweed populations and their ability to expand frontiers as environmental conditions allow.

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Conflict of Interest

None declared.

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