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A nonnative habitat-former mitigates native habitat loss for endemic reef fishes

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Abstract. Animals that select the best available habitats are most likely to succeed in degraded environments, but ecological change can create evolutionarily unfamiliar habitats that may be under- or over-utilized by native fauna. In temperate coastal waters, eutrophication and grazing have driven a global decline in native seaweeds and facilitated the establishment of nonnative seaweeds that provide novel macrophyte habitat. We tested whether a nonnative kelp canopy (wakame *Undaria pinnatifida*) functions as a viable habitat or ecological trap for several endemic reef fishes on urchin-grazed reefs in southern Australia. We assessed the willingness of fish to utilize native vs. wakame kelp canopy via a laboratory habitat choice experiment and by recording natural recruitment to specially constructed boulder reefs with manipulated kelp canopy. We also compared fish communities on natural reefs using a before-after-control-impact survey of wakame patches, and to assess the quality of wakame habitat for resident fish, compared fitness metrics for fish collected from habitats with native vs. wakame kelp canopy. Endemic fishes did not distinguish between the native or wakame canopy but preferred both to barren reef habitats. On urchin-grazed natural reefs, fish occurred in higher abundance and diversity where seasonal wakame canopy was present. Fitness metrics in fish collected from wakame patches were comparable to those in fish from adjacent native kelp patches. These findings indicate that the nonnative canopy provides a viable habitat for endemic fish and may play a role in sustaining native fauna populations in this degraded ecosystem. More broadly, we recommend that managers consider the role of nonnative habitats within the context of environmental change, as endemic fauna may benefit from nonnative habitat-formers in areas where their native counterparts cannot persist.

Key words: ecological trap; fitness; habitat quality; habitat selection; HIREC; invasion ecology; kelp canopy; urchin barrens; wakame.

INTRODUCTION

Ecosystems are undergoing dramatic anthropogenic shifts worldwide, with impacts on fauna partially dependent on how individuals respond to altered or degraded habitats. Animals that make adaptive decisions in response to novel risks and resources will be best able to persist in impacted landscapes (Sih et al. 2011, Wong and Candolin 2014), but a lack of evolutionary history in altered environments can create a mismatch between cues and fitness outcomes, causing individuals to make maladaptive decisions (evolutionary trap; Robertson et al. 2013). In the case of habitat selection decisions, this may result in individuals underutilizing high quality but unattractive habitats or selecting low quality but attractive habitats (ecological trap; Robertson and Hutto 2006, Patten and Kelly 2010, Hale and Swearer 2016). Such individual-level responses can exacerbate population-level effects of environmental change if animals are either drawn into attractive population sinks from surrounding higher quality habitats or fail to take advantage of unfamiliar habitats in degraded landscapes (Hale et al. 2015). These processes are difficult to resolve using typical habitat assessment approaches but may be detected when measures of habitat preference and fitness outcomes are considered within the ecological trap conceptual framework. This is particularly important where anthropogenic impacts have created novel ecological conditions (Hale et al. 2015, Sievers et al. 2018).

Nonnative habitat-forming species, including plants and algae, can create novel ecosystems by competing for space with native habitat-formers and by changing the availability of food and shelter for animals (Crooks 2002, Gribben and Wright 2006, Pyšek et al. 2012). Where anthropogenic stressors lead to declines in native habitat-forming species, nonnative habitat-formers may take advantage of vacant niches (MacDougall and Turkington 2005). It is often assumed that nonnative species

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will reduce biodiversity in invaded areas, but the body of evidence is equivocal, particularly for animals (Gribben and Wright 2006, Pyšek et al. 2012, Dijkstra et al. 2017). Effects on biodiversity depend on a range of conditions, including the state of the ecosystem prior to invasion, the quality of the novel habitat for native fauna, and on behavioral responses by native fauna to the novel habitat.

Wakame *Undaria pinnatifida* is a habitat-forming kelp native to East Asia that has now established in Europe, the Americas, and Oceania. Despite its high profile as a serial invader (Schaffelke and Hewitt 2007, Davidson et al. 2015), very little is known about its impacts on animal populations in invaded ecosystems (Raffo et al. 2009, 2014, Thomsen et al. 2009, Irigoyen et al. 2011, Howland 2012). In southeastern Australia, seasonal wakame canopy occurs on artificial substrates and degraded reefs where urchin grazing has driven a decline in perennial native kelps such as *Ecklonia radiata* (Kriegisch et al. 2016, Carnell and Keough 2019; Appendix S1: Fig. S1). Wakame is a weak competitor in undisturbed macroalgal communities (Valentine and Johnson 2003, Edgar et al. 2004, de Leij et al. 2017), but quickly takes advantage of bare substrate and is better able to persist on degraded reefs (Campbell and Burridge 1998, Valentine and Johnson 2003, Edgar et al. 2004, South and Thomsen 2016).

Seasonal wakame growth may mitigate declines in fish biodiversity on urchin-grazed reefs if native fish utilize shelter provided by the nonnative kelp and experience good fitness outcomes. We employ the ecological trap conceptual framework to test three questions about the role of the nonnative canopy for endemic reef fishes: (Q1) Are native fish willing to use the nonnative kelp habitat? (Q2) Does seasonal growth of nonnative kelp canopy on urchin-grazed reefs modify fish assemblages? (Q3) Are measures of fitness comparable between native and nonnative kelp habitats? In addressing these questions, we inform management responses to established nonnative species and demonstrate how the ecological trap concept can be employed in assessments of the effects of nonnative habitat-formers on native fauna.

Methods

Study system

The study took place at five locations in Port Phillip Bay (Fig. 1), a 1,930-km^2 marine embayment in southeastern Australia (location descriptions in Appendix S1: Section S1). Reef habitats in the Bay have been degraded by poor water quality and overabundant urchins, leading to large areas of urchin barrens and microalgal turf (Kriegisch et al. 2016, 2019, Carnell and Keough 2019). Native perennial canopy-forming macrophytes such as the kelp *Ecklonia radiata* have been declining for decades (Carnell and Keough 2019), while wakame was introduced in the 1980s and now occurs on reefs throughout the Bay, with high densities in the northern half. Wakame is a winter annual in this region, forming dense stands during winter–spring and completely senescing in summer.

Question 1: Are native fish willing to use the nonnative kelp habitat?

Habitat choice experiment.—To investigate whether native reef fish prefer native over nonnative kelp, we collected 48 common weedfish (Clinidae: *Heteroclinus perspicillatus*) and 23 little weed whiting (Odacidae: *Neoodax balteatus*). These species are among the most common seaweed-associated fishes in the region. Fish were collected from numerous rocky reef patches in northern Port Phillip Bay dominated by *E. radiata* or mixed native macroalgal cover in August–November 2014, housed in recirculating aquaria with artificial shelters, and used within 2 weeks of collection. No fish were taken from wakame patches. We placed individuals in the center of a four-chambered cross-shaped tank (McDermott and Shima 2006; Appendix S1: Fig. S2) and offered a simultaneous choice between one reference (bare rock, simulating an urchin barren) and three macroalgal habitat cues (similarly sized rocks with wakame, *E. radiata*, or *Sargassum linearifolium* attached via a cable tie on the holdfast). We provided equal volumes of each macroalga, measured by water displacement, and randomized their positions within the tank for each replicate fish. At least 10 specimens of each macroalga were used throughout the experiment, with macroalga specimens, rocks, and chambers randomized between replicate fish. We held fish in a transparent plastic cylinder in the center of the tank for 5 min to permit assessment of habitat cues prior to the commencement of the trial. The cylinder was then raised by a string-and-pulley system with the researcher out of sight but able to view the fish through a small hole in a screen. We recorded both the initial choice of the fish, expected to be a primarily vision-based decision, and the location of the fish after 20 min, expected to be a decision based on multiple cues. No fish chose to remain in the center of the tank.

Recruitment to boulder reefs.—To complement the laboratory choice experiment, we tracked recruitment to specially constructed boulder reefs with manipulated kelp canopy. The Half Moon Bay location (Fig. 1) was selected for the large expanse of sandy substrate at a suitable depth (6 m). During September 2014, we constructed 20 replicate reefs (1 m^2) on sandy substrate, arrayed 20 m apart in a 4 × 5 grid pattern, and randomly assigned each reef to one of three treatments (n = 7 with wakame canopy, n = 7 with *E. radiata* canopy, and n = 6 as unstocked controls) using kelp specimens collected from an adjacent reef and attached using rope and cable ties. Clinids and several other local reef fishes willingly recruit to habitats of this size. We

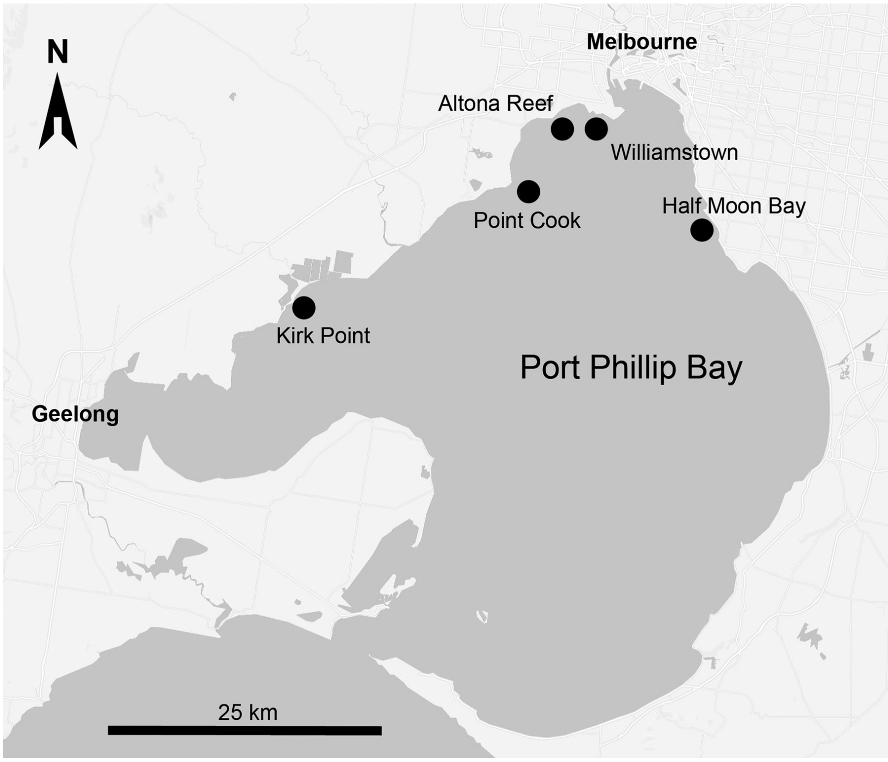

Fig. 1. Map of study locations in Port Phillip Bay, Australia with established wakame kelp populations. Wakame and urchin barrens are present and were surveyed at Kirk Point, Point Cook, Altona Reef, Williamstown, and Half Moon Bay. Williamstown also contains remnant patches of native kelp *Ecklonia radiata* in close proximity to barren and wakame habitats. Underwater visual census and baited remote underwater video surveys of fish populations were done in urchin barren and wakame habitats at all five locations. Diver catch per unit effort surveys and fitness metric comparisons were done in neighboring wakame and *E. radiata* habitats at Williamstown.

stocked kelp in July–August 2015 and recorded natural recruitment of fishes on three occasions throughout spring (September–November 2015). Both kelps were stocked at equal densities (75% coverage) approximating kelp canopy cover on natural reefs at our study locations during peak wakame growing season. Wakame is less robust than *E. radiata* and required regular replenishment as thalli senesced during October–November, and despite these efforts, wakame coverage was lower than *E. radiata* by the end of the recruitment study (42% vs. 73%). As reefs were initially devoid of fish, relative recruitment was quantified in terms of the abundance and diversity of fish present on the reef at each survey date. This metric is likely influenced by both habitat selection and survival.

Question 2: Does seasonal growth of nonnative kelp canopy on urchin-grazed reefs modify fish assemblages?

To test whether habitat preferences in experimental conditions correspond to patterns of fish abundance in the field, we compared fish communities on urchin-grazed reefs with and without seasonal wakame canopy, using underwater visual census (UVC) to target benthic fish species. Five survey locations were selected based on the presence of dense wakame patches on urchin-grazed reefs (Fig. 1).

We primarily focused on a comparison of fish populations in wakame habitat relative to urchin barrens rather than *E. radiata* habitat because (1) the small size and rarity of remaining *E. radiata* habitats in the Bay limited the potential for spatial replication, with Williamstown currently the only location where urchin barrens, wakame patches and dense *E. radiata* beds co-occur on rocky reef, and (2) this invader fills vacant habitat on degraded reefs rather than directly outcompeting native kelps, making the comparison to barren reefs more ecologically relevant in our view. Nonetheless, we did compare fish populations in wakame and *E. radiata* beds using a diver catch per unit effort metric (CPUE) at the Williamstown location, and to complement the UVC and CPUE surveys, a baited remote underwater video (BRUV) survey to investigate habitat-use patterns in larger, more mobile fishes. For comparison, the BRUV survey also included deployments at a relatively pristine reef location (Governor Reef) in southern Port Phillip Bay where dense *E. radiata* was present but urchin barrens and wakame were not. All survey and collection efforts were made by the same researcher (L. Barrett) under calm weather conditions (<15 knots) between 10:00 and 16:00. Efforts were alternated randomly between habitat types to avoid temporal bias.

Underwater visual census.—Replicate circular plots of 12.6 m^2 (2 m radius) were established on reefs with comparable rugosity and depth but differing in the presence or absence of wakame. We surveyed 51 plots (25 wakame and 26 barren) across five locations that offered wakame and barren habitats in close proximity (Fig. 1). We employed a before-after-control-impact (BACI) design by surveying plots with and without seasonal wakame canopy. This was done when the canopy was at its most dense during winter–spring (June–October 2016, "peak season" herein) and then in the following autumn after the canopy had senesced over summer (April–May 2017, "off season" herein). Mature wakame undergo a complete senescence, with no holdfasts remaining by late summer. We haphazardly placed plots on wakame and barren patches at each location, with 10–100 m separating plots. Populations of small benthic and cryptic fishes are strongly influenced by habitat characteristics at this scale (Willis and Anderson 2003). We dropped a weight to mark the middle of the plot and surveyed larger benthic and benthopelagic fish initially by swimming a circular path outside the plot. Small or cryptic species were detected by a diver moving in concentric circular paths from the outer edge to the center of the plot, searching within the reef structure and among algal cover. If fish of the same species were observed multiple times within the plot, they were counted as a single fish unless clearly distinct. Several members of the *Heteroclinus* genus (*H. perspicillatus*, *H. heptaeolus*, *H. adelaidae*, *H. wilsoni*, *H. eckloniae*, *H. macrophthalmus*) are difficult to reliably distinguish in situ, so were treated as a single taxonomic unit for this component of the study. Upon completing the fish census, we visually estimated percent coverage of kelp, all macroalgae and algal turf across the entire plot. Following the initial winter surveys, a short metal stake was driven into the center of the plot to facilitate the off-season repeat survey.

Catch per unit effort.—Collection efforts for *N. balteatus*, *H. perspicillatus*, and *H. heptaeolus* in *E. radiata* and wakame habitat patches at Williamstown (Questions 1 and 3) were timed to allow quantification of CPUE. The Williamstown location contained a mosaic of seasonal wakame growing on urchin-grazed reefs between well-defined remnant patches of *E. radiata* and *Sargassum* spp. Collections were made by hand net on SCUBA. We calculated CPUE on a per species basis, with each collection dive treated as a single statistical replicate where CPUE = (no. fish collected)/(dive duration). Collection dives alternated between habitats over 9 d between 24 October and 28 November 2016.

Baited remote underwater video.—The BRUV survey was conducted during peak season only, during August–September 2016. BRUV deployments were made at the same five locations visited during UVC surveys, with the camera unit dropped onto either wakame patches ($n = 14$) or urchin barrens ($n = 15$). The camera unit consisted of a GoPro Hero3+ camera (Woodman Labs, San Mateo, California, USA) mounted on a weighted plastic crate with a 1 m long bait arm made from 20-mm PVC conduit. Two pilchards (*Sardinops sagax*) were cut in half and placed in a 20 × 20 cm plastic mesh bag attached to the end of the bait arm. Larger baits are often used in BRUV systems, but we wished to minimize the spread of the bait plume as reef patches in the Bay are often very small (10–100 m). Deployments were made at least 50 m apart on comparable reef substrate at depths of 2–4.5 m. Fish observations were made for 20 min from the time when the BRUV unit settled on the sea floor. To assess relative abundance of each species at each deployment while preventing potential double counting of individual fish, we used a conservative metric termed maxN, where maxN is the maximum number of individuals of a given species occurring simultaneously in the video field of view (Willis and Babcock 2000). In the case of sexually dimorphic species or juvenile fishes, we summed the maxN counts for males, females, and juveniles of that species. Where an individual could not be identified to species level, we identified it to the lowest taxonomic rank possible (usually family or genus). We included the southern calamari squid *Sepioteuthis australis* in the analysis as it is functionally similar to carnivorous fishes.

Question 3: Are measures of fitness comparable between native and nonnative kelp habitats?

Fish collected from natural reefs.—We compared body condition metrics in *N. balteatus* (wakame, $n = 22$; *E. radiata*, $n = 23$), *H. perspicillatus* (wakame, $n = 11$; *E. radiata*, $n = 13$) and Ogilby's weedfish *Heteroclinus heptaeolus* (wakame, $n = 9$; *E. radiata*, $n = 9$) collected at Williamstown from wakame and *E. radiata* habitats during October–November 2016. The habitat occupied by each individual was defined by the dominant kelp species within 2 m of the collection site, with percent coverage of macroalgal species estimated visually. Fish were collected using hand nets and killed using clove oil before being placed in sealed plastic bags in an ice slurry. Within 24 h of collection, wet mass and total length were measured and fish dissected to determine sex and mass of the stomach contents, liver, and gonads. Overall body condition was quantified using the relative condition metric recommended by (Le Cren 1951): $K_{\mathrm{rel}} = W/W_{\mathrm{exp}}$, where W is the measured gutted mass and W_{exp} is the gutted mass predicted by the mass-at-length power curve fitted to all available samples (Appendix S1: Fig. S3). Individuals with K_{rel} values > 1 are heavier than average for their length. One *H. perspicillatus* individual from wakame habitat was removed from the K_{rel} analysis (145 mm; 4.7 standard deviations above the mean). Liver and gonad condition were quantified using hepatosomatic and gonadosomatic indices, respectively (HSI or GSI = OW/GW, where OW is wet organ mass and GW is gutted mass). For gravid females, we photographed and counted subsamples of ova (for broadcast spawning *N. balteatus*) or embryos (for live bearing *Heteroclinus* spp.) to assess fecundity.

Fish collected from boulder reefs.—We collected *H. perspicillatus* recruits from the same boulder reefs constructed for our test of Q1 from January to November 2015 for a comparison of body condition and reproductive investment metrics between fish from reefs stocked with wakame (n = 11 fish from seven reefs) or *E. radiata* (n = 20 fish from eight reefs). Individuals were assumed to be resident to the boulder reef that they recruited to, as feeding forays beyond the "home" reef would require a small macrophyte-dependent reef fish to traverse ≥20 m of sand habitat to neighboring boulder reefs, with a much greater distance to the nearest natural reefs. Collection methods were identical to those on natural reefs, with collection efforts alternating between wakame and *E. radiata* stocking treatments. There were not enough *H. perspicillatus* recruits on control (unstocked) reefs for meaningful comparisons of condition on reefs with and without kelp.

Statistical analysis

Laboratory choice data (Q1) were tested for habitat preference using a χ^2 test of proportions implemented in R (R Core Team 2018), with expected (null) proportions equally distributed across the four habitat cues.

Boulder reef recruit abundance and species richness data (Q1) were compared across kelp treatments using Poisson generalized linear mixed effects models implemented in the lme4 package for R (Bates et al. 2015). We included treatment (stocked kelp species: wakame, *E. radiata*, or barren) as a fixed term, KelpCover (percentage coverage of canopy) as a covariate, and as reefs were surveyed repeatedly, a reef identity random intercept term (ReefID) nested within treatment. There was some overdispersion, so we included an observation-level random term to avoid overestimating the predictive ability of model terms (Harrison 2014). We tested for a significant treatment effect by comparing the fit of models with and without the treatment term, while the lsmeans package for R provided Tukey's pairwise post-hoc comparisons of the three treatments (Lenth 2016).

Fish community data from UVC and BRUV surveys (Q2) were fitted with permutational multivariate ANOVA (PERMANOVA) models implemented in PRIMER 6 with the PERMANOVA+ add-on (Anderson et al. 2008). Four PERMANOVA models were fitted: peak-season UVC, off-season UVC, combined UVC, peak-season BRUV. Data were $\log(x + 1)$ transformed to reduce the influence of a few highly abundant species and fitted to a Bray-Curtis similarity resemblance matrix with a dummy variable of 1 to allow definition of dissimilarity between samples with complete absences (Clarke et al. 2006). The peak- and off-season models contained two fixed factors, habitat and location, as well as an interaction term (habitat × location). The location factor contained two levels (north and west), reflecting environmental differences between locations in the north (Point Cook, Altona Bay, Williamstown, Half Moon Bay) and west (Kirk Point) of the Bay. The combined season UVC model also contained a binary factor for season (peak- or off-season), with a corresponding three-way interaction term for habitat × location × season. The models were fitted using Type III sums of squares, with unrestricted permutation of raw data and 9,999 permutations. We also extracted diversity metrics using the diversity function and identified species that were associated most strongly with the observed differences between habitats and locations using the similarity percentage (SIMPER) function. Finally, significant patterns were visualized using canonical analysis of principal coordinates (CAP) plots.

Catch per unit effort data were $\log(x + 1)$-transformed to improve normality and compared across *E. radiata* and wakame habitats using a linear analysis of covariance (lm function in R) with habitat as a fixed factor and sampling date as a continuous variable.

We compared fitness metrics (Q3) in native and nonnative kelp habitats using a series of univariate linear models implemented in R. Response variables were checked for normality and equality of variance and transformed as necessary. We analyzed both weedfish species (*H. perspicillatus* and *H. heptaeolus*) with a single model and included terms for kelp habitat type (habitat), species (species), day of the season (day), and sex (sex). Models for the sequentially hermaphroditic *N. balteatus* included only habitat and day terms. Fitness metrics for *H. perspicillatus* recruits collected from boulder reefs (Q3) were compared across kelp treatments using univariate linear mixed models implemented in lme4, and included treatment, KelpCover, and sex as fixed terms and treatment/ReefID as a random intercept term. In all cases, we tested the significance of the effect of interest by comparing the fit of models with and without the relevant term.

A full list of models is provided in Appendix S1: Table S1. Plots were produced using the ggplot2 package for R (Wickham 2009).

RESULTS

Question 1: Are native fish willing to use the nonnative kelp habitat?

Habitat choice experiment.—Common weedfish *Heteroclinus perspicillatus* were more likely to select macroalgal cover than barren rock, both initially (1.25 × more than expected; $P < 0.0001$; $n = 48$) and after 20 min

(1.22 × more than expected; $P < 0.0001$; $n = 48$; Fig. 2; Appendix S1: Table S2). Of those that chose macroalgae during their initial decision, wakame was preferable to *E. radiata* or *Sargassum* (2.0 × and 2.7 × higher rates, respectively; $P = 0.015$; $n = 44$), but after 20 min, individuals were evenly distributed across the three macroalgal options ($P = 0.9$; $n = 45$; Fig. 2; Appendix S1: Table S2).

Little weed whiting *Neoodax balteatus* also preferred macroalgae to bare rock, both initially (1.16 × more than expected; $P = 0.0004$; $n = 23$) and after 20 min (1.22 × more than expected; $P < 0.0001$; $n = 23$; Fig. 2; Appendix S1: Table S2). However, we observed no clear preference among macroalgal options, either initially ($P = 0.12$; $n = 20$) or after 20 min ($P = 0.4$; $n = 21$; Fig. 2; Appendix S1: Table S2).

Recruitment to boulder reefs.—A 2.5× higher abundance ($P = 0.01$) and 2.4× higher species richness ($P = 0.007$) of reef fish recruited to boulder reefs stocked with kelp relative to those with unstocked controls (Table 1). There was no evidence for differential recruitment between reefs stocked with wakame or *E. radiata* ($P = 0.21$), despite wakame reefs having lower canopy cover on average (42% vs. 73%; Table 1). Per area of canopy, recruitment was 1.4× higher on wakame reefs. The canopy cover covariate positively predicted recruit abundance ($P = 0.05$), indicating that the amount of cover may be more important than the species providing the cover. Canopy cover did not affect species richness ($P = 0.36$).

Question 2: Does seasonal growth of nonnative kelp canopy on urchin-grazed reefs modify fish assemblages?

Underwater visual census.—We recorded 19 fish species across 25 wakame and 26 barren UVC plots during peak-season surveys at five locations (September–October 2016; Appendix S1: Table S3) and found a significant effect of habitat (wakame or barren), location (west or north Port Phillip Bay), and the habitat × location interaction term on fish communities (Appendix S1: Table S4). CAP plots revealed separation of plots with and without wakame (Fig. 3A), driven primarily by a greater abundance of *Heteroclinus* spp. and *Diodon nicthemerus* in wakame plots. SIMPER analysis determined that weedfish *Heteroclinus* spp. (28%), Clarke's threefin *Trinorfolkia clarkei* (23%), and Tasmanian blennies *Parablennius tasmanianus* (10%) contributed most to the observed dissimilarity between habitats (weedfish in wakame plots; threefins and blennies in barren plots). Species richness (2.0×) and total abundance (1.9×) were both higher on wakame plots (Fig. 3C; Appendix S1: Table S5). Barren and wakame plots were placed at comparable depths (mean ± SD: 2.6 ± 0.5 m cf. 2.7 ± 0.4 m, respectively). Barren plots contained 6% ± 2% macroalgal cover, mostly sea lettuce *Ulva* spp. Wakame plots contained 72% ± 3% macroalgal cover, dominated by wakame (58%) with some secondary cover from other ephemeral macroalgae, including *Ulva* spp. and *Gracilaria* spp. Wakame plots did not contain any other brown algal species such as *E. radiata* or *Sargassum* spp. Where *Ulva* or *Gracilaria* were present on wakame plots, clinids *Heteroclinus* spp. and *Cristiceps australis* were generally found in wakame microhabitat (i.e. 12/16 fish found directly underneath a wakame thallus).

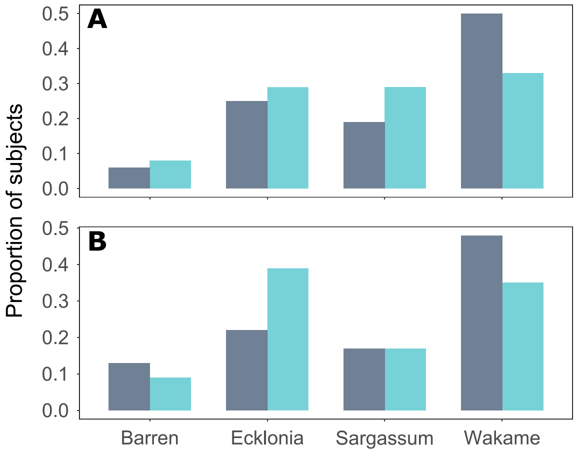

FIG. 2. Habitat choice trial results for (A) common weedfish (*Heteroclinus perspicillatus*), $N = 48$, and (B) little weed whiting (*Neoodax balteatus*), $N = 23$. Preference was recorded initially (dark blue) and after 20 min (light blue).

We resurveyed 18 plots (9 wakame, 9 barren) after the wakame canopy had completely senesced (off season: April–May 2017). Sparse early-stage wakame recruits (<10 cm) were present but provided a negligible amount of macroalgal cover. The effect of the habitat factor on overall fish community structure remained significant but less strongly than when wakame was present (Appendix S1: Table S4, CAP: Fig. 3B). Neither fish species richness nor abundance significantly differed between habitats during off-season surveys (Fig. 3D; Appendix S1: Table S5).

Analyzing peak-season and off-season data together revealed significant overall effects of Habitat, season, and location on fish community structure, as well as a habitat × location interaction (Appendix S1: Table S4). Off-season wakame and barren plots both contained abundant non-canopy-forming ephemeral macroalgae, dominated by *Ulva*, *Gracilaria*, and *Caulerpa*, with greater mean coverage (51% ± 12%) on wakame plots than barren plots (32% ± 12%). We found no evidence that off-season macroalgal cover on resurveyed plots was predicted by peak-season cover of either wakame ($F_{1,\,16} = 0.5$, $P = 0.5$) or all macroalgae ($F_{1,\,16} = 1.5$, $P = 0.24$).

Diver catch per unit effort.—Collection efforts provided 45 *Neoodax balteatus*, 24 *Heteroclinus perspicillatus*, and 18 *Heteroclinus heptaeolus* from 12 dives (total 465 min)

TABLE 1. Summary of fish recruitment (mean ± SE) to mesocosm reefs stocked with wakame (*Undaria pinnatifida*), *Ecklonia radiata*, or left barren.

Treatment	Kelp canopy cover (%)	Abundance (no. fish/reef)			Species richness (no. species/reef)			No. surveys
		Mean	*z*	*P*	Mean	*z*	*P*	
Wakame	42 ± 3	0.9 ± 0.1			0.8 ± 0.1			89
E. radiata	73 ± 2	1.1 ± 0.1			1.1 ± 0.1			89
Barren	5 ± 5	0.4 ± 0.2			0.4 ± 0.2			18
Pairwise comparisons								
Wakame–*E. radiata*			1.7	0.21		1.6	0.24	
Wakame–Barren			2.3	0.05		2.8	**0.02**	
E. radiata–Barren			3.0	**0.008**		3.3	**0.003**	

Notes: Bold face denotes statistical significance at α = 0.05.

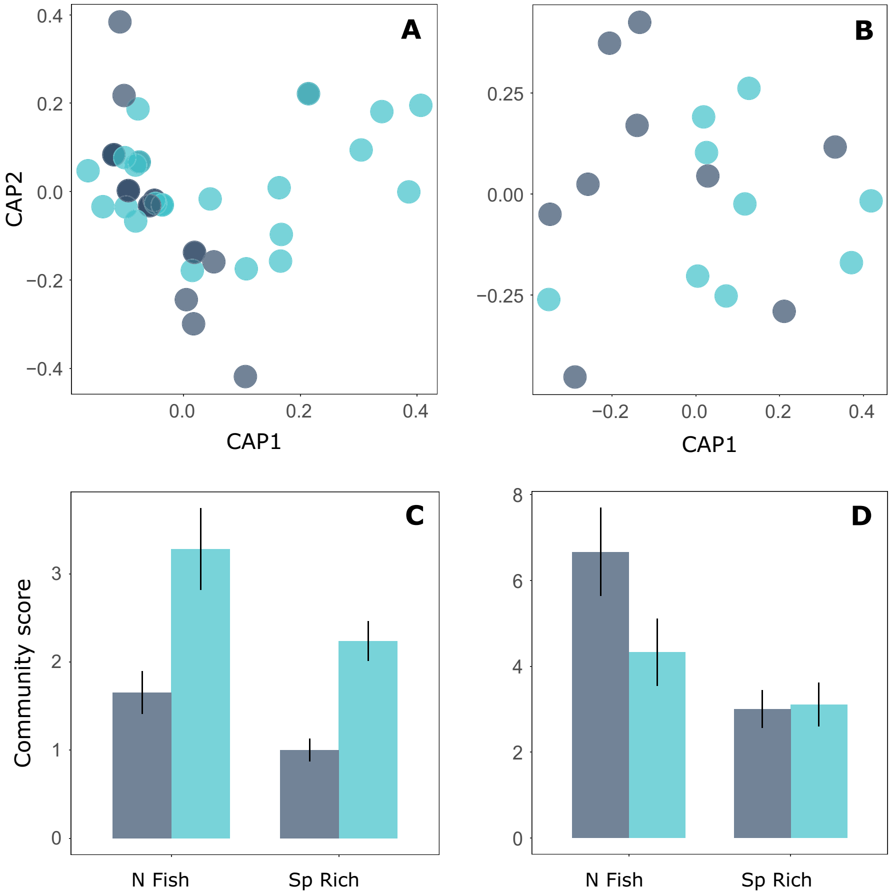

FIG. 3. Representation of reef fish communities in survey plots with and without wakame present (wakame, light markers; barren, dark markers), both during the wakame growing season while canopy cover is present (peak season; A, C) and again after complete senescence of wakame canopy (off season; B, D). Individual panels depict (A) canonical analysis of principal coordinates (CAP) for peak-season surveys; (B) CAP for off-season surveys; (C) total abundance (N Fish) and species richness (Sp Rich) for peak-season surveys; (D) total abundance and species richness for off-season surveys. Bars indicate group mean and standard error.

in wakame and 13 dives in *E. radiata* (total 690 min) habitats over 9 d between 24 October and 28 November 2016. Catch per unit effort (CPUE) of *N. balteatus* was 2.6× higher in *E. radiata* than wakame habitat ($P = 0.04$), but CPUE of *Heteroclinus* spp. did not differ (Table 2). CPUE of *N. balteatus* also increased throughout spring, coinciding with warmer water and greater fish activity (sate covariate: $R^2 = 0.26$, $P = 0.007$; Table 2). There was no evidence that CPUE of *Heteroclinus* spp. increased over time ($P = 0.6$; Table 2). In the course of surveying 26 barren UVC plots during peak season in the northern part of the Bay, we only observed one clinid, an *H. perspicillatus* individual inhabiting a macroalgal microhabitat on an otherwise barren plot, and no *N balteatus* (Appendix S1: Table S3). Accordingly, CPUE in the barrens would likely be close to zero.

Baited remote underwater video.—We recorded 28 fish species across 14 wakame and 15 barren deployments (Appendix S1: Table S3). Fish communities did not differ between wakame and barrens habitats (Appendix S1: Table S6), nor did species richness or combined MaxN (Appendix S1: Table S7). Restricting the analysis to reef-associated fish species did not alter our interpretations.

Question 3: Are measures of fitness comparable between native and nonnative kelp habitats?

Fish collected from natural reefs.—*Neoodax balteatus* individuals collected from *E. radiata* habitat were 1.3× longer ($P = 0.007$) and 2.4× heavier ($P = 0.01$) than those in seasonal wakame habitat (Table 3), and a higher proportion were male (*E. radiata*: 7/23; wakame: 1/22). We found no evidence that body condition or reproductive fitness metrics differed between *E. radiata* and wakame habitats, although the direction of effect for reproductive metrics was generally positive in wakame habitats (Table 3).

We also found little evidence that *H. perspicillatus* or *H. heptaeolus* collected from *E. radiata* or wakame habitats experience differential habitat quality, with no difference in size, body condition or reproductive investment between habitat types (Table 3). However, the proportion of fertilized eggs was 1.4× higher in weedfish living in *E. radiata* habitats ($P = 0.003$; Table 3).

Dietary assessment revealed that almost all clinids had consumed mysid shrimp, in both wakame and *E. radiata* habitats. Some individuals had also consumed amphipods (wakame and *E. radiata*), isopods (wakame only), or decapods (*E. radiata* only). Amphipods were the most frequently identifiable prey items for *N. balteatus* (*E. radiata* only). Animal prey items from *N. balteatus* in wakame habitats were not identifiable, although there was no significant difference in the weight of stomach contents (Table 3).

Fish collected from boulder reefs.—Hepatosomatic index was 2.0× higher in *H. perspicillatus* individuals collected from reefs stocked with wakame canopy vs. *E. radiata* canopy ($P = 0.01$), while other fitness metrics were unaffected by kelp canopy treatment (Table 3).

Discussion

Overall, these results indicate that the presence of the nonnative habitat-former does not create an ecological trap for native fish; rather it may offer valuable habitat for at least some endemic fish species in winter–spring while the canopy is present on urchin-grazed reefs. In testing Q1, we found that fish were equally willing to utilize shelter provided by either kelp and preferred both to barren reefs. For Q2, fish community data indicated that nonnative kelp patches can increase fish abundance and diversity on heavily urchin-grazed reefs where native kelp canopy is lost. Furthermore, body condition and reproductive investment metrics indicate that fish inhabiting these nonnative kelp patches have similar or better body condition to those in adjacent native kelp beds (Q3).

Nonnative habitat-forming species that replace native habitats can negatively affect faunal populations in invaded landscapes if the nonnative habitat is of poor quality, whether the nonnative habitat is avoided (leading to habitat loss; Trammell and Butler 1995, Valentine et al. 2007) or occupied (leading to poor fitness outcomes and an ecological trap; Remeš 2003, Lloyd and Martin 2005, Rodewald et al. 2010). However, where the invader adds physical structure or a novel food source, there can be ameliorative or beneficial effects for some

Table 2. Comparison of reef fish relative abundance (mean ± SE) at Williamstown, estimated by diver catch per unit effort (CPUE), in wakame and *E. radiata* habitats (Habitat effect), and over time (Temporal effect).

	Wakame	*E. radiata*	R^2	No. dives	χ^2	*P*	Cohen's *d*
Habitat effect							
Heteroclinus perspicillatus	0.9 ± 0.3	2.0 ± 0.6		13, 10	1.4	0.12	−0.74
Heteroclinus heptaeolus	0.7 ± 0.2	1.0 ± 0.4		13, 12	0.04	0.91	−0.30
Heteroclinus spp.	1.5 ± 0.4	2.7 ± 0.8		13, 12	0.32	0.73	−0.48
Neoodax balteatus	1.6 ± 0.4	4.1 ± 1.0		9, 10	2.1	**0.04**	−1.08
Temporal effect							
Heteroclinus perspicillatus			−0.02	13, 10	0.74	0.33	
Heteroclinus heptaeolus			0.10	13, 12	0.77	0.19	
Heteroclinus spp.			0.03	13, 12	0.14	0.87	
Neoodax balteatus			0.26	9, 10	3.3	**0.007**	

Notes: Number of collection efforts (No. dives) are given as “wakame, *E. radiata*.” the number of dives differs between species as not all dives targeted all species. Terms are tested by maximum likelihood ratio comparison of fitted and null models (χ^2). Negative Cohen's *d* effect sizes indicate metrics were higher in *E. radiata* habitat.

Bold face denotes statistical significance at $\alpha = 0.05$.

Table 3. Comparison of body condition and reproductive condition metrics (mean ± SE) in reef fishes collected from wakame and *E. radiata* habitats at Williamstown (natural reefs) and Half Moon Bay (constructed boulder reefs).

Metric	Wakame	*E. radiata*	*N*	df	*F*	χ^2	*P*	*d*
Neoodax balteatus, natural reefs								
Length (mm)	73 ± 4	96 ± 6	22, 23	1,42	8.2		**0.007**	−0.97
Gutted mass (g)	3.9 ± 0.9	9.5 ± 1.7	22, 23	1,42	7.2		**0.01**	−0.87
K_{rel}	101 ± 1	99 ± 1	22, 23	1,42	4.0		0.05	+0.50
Hepatosomatic index (×1,000)	30 ± 2	28 ± 2	22, 23	1,42	2.1		0.15	+0.20
Stomach index (×1,000)	25 ± 2	27 ± 2	22, 23	1,42	1.0		0.32	−0.19
Gonadosomatic index (×1,000)	51 ± 8	48 ± 10	22, 23	1,42	0.2		0.67	+0.07
Mature eggs	789 ± 245	516 ± 213	17, 10	1,24	0.5		0.49	+0.30
Eggs	3162 ± 936	2789 ± 850	17, 10	1,24	0.5		0.49	+0.11
Mature eggs per gutted mass (no./g)	198 ± 39	116 ± 29	17, 10	1,21	0.6		0.63	+0.59
Eggs per gutted mass (no./g)	742 ± 128	568 ± 176	17, 10	1,24	0.3		0.34	+0.32
Egg maturity (%)	26 ± 4	24 ± 8	17, 10	1,21	<0.1		0.93	+0.06
Heteroclinus spp., natural reefs								
Length (mm)	74 ± 5	65 ± 2	20, 22	1,36	1.3		0.26	+0.52
Gutted mass (g)	4.1 ± 0.9	2.6 ± 0.3	20, 22	1,36	1.6		0.21	+0.50
K_{rel}	102 ± 3	100 ± 3	20, 22	1,35	0.2		0.63	+0.12
Hepatosomatic index (×1,000)	19 ± 1	21 ± 3	20, 22	1,36	<0.1		0.98	−0.09
Stomach index (×1,000)	24 ± 3	42 ± 17	20, 22	1,36	2.0		0.16	−0.31
Gonadosomatic index (×100)	12 ± 2	11 ± 3	20, 22	1,36	0.6		0.45	+0.10
Embryos	256 ± 35	198 ± 33	13, 12	1,21	0.8		0.39	+0.48
Eggs	516 ± 102	274 ± 66	13, 12	1,21	2.9		0.10	+0.81
Embryos per gutted mass (no./g)	68 ± 9	92 ± 16	13, 12	1,20	2.4		0.14	−0.52
Eggs per gutted mass (no./g)	124 ± 21	126 ± 28	13, 12	1,20	0.3		0.58	−0.02
Egg fertilization (%)	60 ± 6	81 ± 7	13, 12	1,20	11		**0.003**	−0.90
Heteroclinus spp., boulder reefs								
Length (mm)	51 ± 4	62 ± 4	11, 20	1		0.6	0.45	−0.71
Gutted mass (g)	1.3 ± 0.3	2.3 ± 0.4	11, 20	1		0.9	0.35	−0.70
K_{rel}	1.3 ± 0.1	1.3 ± 0.1	11, 20	1		0.3	0.58	+0.01
Hepatosomatic index (×1,000)	43 ± 17	21 ± 3	11, 20	1		5.9	**0.01**	+0.53
Stomach index (×1,000)	16 ± 4	15 ± 3	11, 20	1		<0.1	0.99	+0.08
Gonadosomatic index (×1,000)	12 ± 5	55 ± 19	11, 20	1		0.8	0.37	−2.39

Notes: N is presented as “wakame*, E. radiata*.” Habitat effect is tested by comparing fit of models with and without the habitat term. Negative Cohen’s *d* effect sizes indicate metrics were higher in *E. radiata* habitat. Hepatosomatic and gonadosomatic indices are the wet organ mass divided by the gutted mass.

$K_{rel} = W/W_{exp}$, where W is the measured gutted mass and W_{exp} is the gutted mass predicted by the mass-at-length power curve fitted to all available samples.

Bold face denotes statistical significant habitat effects at $\alpha = 0.05$.

native taxa and increases in local biodiversity (Crooks 2002, Castilla et al. 2004, Byers et al. 2012, Wright et al. 2014, Ramus et al. 2017). The present study highlights the potential benefits of a weakly competitive nonnative habitat-forming species in mitigating the impacts of habitat degradation on native biodiversity.

The functional role of macroalgae for fishes is predicted by the interstitial volume and area that is accessible by prey but not predators (Ware et al. 2019). Tall, branching kelps provide a larger predator-inaccessible space than filamentous macroalgae (Ware et al. 2019), and tend to be preferred as shelter by macroalgae-associated fishes (e.g., O’Brien et al. 2018). Wakame and *E. radiata* are broadly similar in this regard, which may predispose wakame to be a viable functional replacement. In an analogous case, Pessarrodona et al. (2019) reported that the climate-driven replacement of one dominant kelp species with a structurally similar species had relatively minor effects on some key ecosystem processes.

Wakame kelp is highly seasonal and may influence the reproductive success of local reef fishes to the extent that it coincides with reproductive provisioning and larval settlement. Common seaweed-associated reef fishes such as clinids and odacids inhabit wakame patches throughout vitellogenesis and into the spawning period (late winter to late spring: Gunn and Thresher 1991, Neira and Sporcic 2002, this study). Current evidence indicates that wakame supports a similar abundance and diversity of epifauna to native kelps with comparable morphologies (Howland 2012, Suárez-Jiménez et al. 2017). Our data also indicate that adults residing in wakame habitat experience comparable food availability to those in native *E. radiata* habitats, although this may also reflect lower population density and therefore reduced competition in wakame patches (i.e., an ideal free distribution;

Fretwell and Lukas 1969). Regardless, it is unlikely that individuals that choose to reside in wakame habitats during vitellogenesis are falling into a condition-driven ecological trap. We did find evidence that internal fertilization rates were lower in *H. perspicillatus* and *H. heptaeolus* from wakame patches. This may reflect mate-finding difficulty in small habitat patches that contain few if any conspecifics and are separated from adjacent patches by urchin barrens, but wakame patches on these degraded reefs are increasing in size with successive seasons and we expect that this possible Allee effect will ameliorate over time.

The present study focused on juvenile and adult fish, but larval settlement is also important in assessing the role of the nonnative habitat-former. We are not aware of research on the settlement preferences of larval *Heteroclinus* spp. or *Neoodax balteatus*, but clinid larvae are at peak densities in the water column in spring, with settlement occurring during spring–summer (Gunn and Thresher 1991, Neira and Sporcic 2002). This coincides with peak densities of wakame canopy, and it is likely that, if larvae have similar habitat preferences to adults, large numbers may recruit to these habitats shortly before the summer die-off of wakame canopy. Such a loss of cover on otherwise barren reefs warrants investigation as a potential temporal ecological trap for clinid recruits if it increases mortality and outweighs the value of the time spent inhabiting the nonnative kelp. However, the rapid appearance of late-stage juvenile and adult fish on our plots and boulder reefs in summer, together with anecdotal reports of clinids "rafting" in unattached macroalgae, suggests that migration is common. Quantifying movement and mortality of cryptobenthic fishes remains a considerable challenge. Settlement of *N. balteatus* peaks later in summer (Neira and Sporcic 2002), by which time wakame thalli have regressed to sporophyll and holdfasts and may no longer offer attractive habitat for recruits. Such species likely disperse into the nonnative habitat as adults, perhaps through spillover from areas of high population density in remnant native kelp and seagrass habitats. Native kelp coverage in the Bay has declined by 59–98% since the 1980s (Carnell and Keough 2019) with similar declines in seagrass meadows (Ball et al. 2014), but remnant patches are probably still important population sources for macrophyte-associated fishes and their preservation is a key management priority.

Management implications

In contrast to many nonnative ecosystem engineers, wakame is unlikely to be a driver of ecological change (Valentine and Johnson 2003, Edgar et al. 2004, South and Thomsen 2016). Instead, field manipulations indicate that urchin grazing drives native kelp declines in this region regardless of local nutrient or sedimentation levels (Kriegisch et al. 2016, 2019). In the absence of scouring and shading by native kelp thalli, reefs can shift to an alternate stable state dominated by sediment-trapping algal turf that impedes subsequent kelp recruitment (Reeves et al. 2018). Wakame appears better able to persist on heavily grazed reefs and also clears turf, making it a versatile functional replacement for native kelp during its winter–spring growing season (Reeves et al. 2018). It remains unclear whether the presence of wakame helps recovery of native kelp, but it is unlikely to hinder it.

Where a nonnative species has functionally replaced a native species, eradication may not be sufficient to restore the natural ecosystem (Reid et al. 2009), and furthermore, is likely to drive additional biodiversity loss where native fauna depend on the nonnative habitat for food or shelter (Zavaleta et al. 2001). Although wakame probably supports a lower density of fish than native *E. radiata* canopy, the relative abundance and current population trends of wakame and native kelp mean that wakame, in absolute terms, may soon support a larger number of fish on reefs in this embayment than native kelp patches. We suggest that control of established wakame populations should not automatically be a high management priority in this region, potentially freeing resources to target more impactful nonnative species or address the underlying biotic and abiotic stressors that facilitate nonnative species. In the case of southeastern Australia, native kelp recovery will be better served by greater protection of urchin predators, urchin culls and expansion of urchin fisheries in strategic areas (e.g., around remnant native kelp patches), and tighter controls on nutrient inputs to coastal waters.

Analogous cases likely exist in most environments (Schlaepfer et al. 2011), especially those that are heavily impacted by a range of anthropogenic stressors so, more broadly, we recommend that conservation agencies adopt evidence-based strategies that focus on achieving good outcomes for ecosystem function and/or native biodiversity. Nonnative control should not be a goal in itself and should only be undertaken when it aids the aforementioned outcomes, for example, where a nonnative species is highly invasive and likely to exacerbate declines in biodiversity. We are not the first to suggest such an approach to nonnative species management (Zavaleta et al. 2001, Schlaepfer et al. 2011, Ramus et al. 2017), but this study is among the first to demonstrate the ecological trap concept as an assessment framework that can provide evidence needed to guide an outcomes-focused and evidence-based management approach.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1956/full

DATA AVAILABILITY

Data are available at figshare: https://doi.org/10.6084/m9.figshare.7396964.v1