

## Algal subsidies enhance invertebrate prey for threatened shorebirds: A novel conservation tool on ocean beaches?



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### ABSTRACT

Birds breeding on ocean beaches are threatened globally, often requiring significant investments in species conservation and habitat management. Conservation actions typically encompass spatial and temporal threat reductions and protection of eggs and broods. Still, populations decline or recover only slowly, calling for fresh approaches in beach-bird conservation.

Because energetic demands are critically high during the nesting and chick rearing phases, and chick survival is particularly low, supplementing prey to breeding birds and their offspring is theoretically attractive as a means to complement more traditional conservation measures.

Prey for plovers and similar species on ocean beaches consists of invertebrates (e.g. small crustaceans, insects) many of which feed on stranded masses of plant material (e.g. kelp and seagrass) and use this 'wrack' as habitat. We added wrack to the upper beach where plovers nest and their chicks forage to test whether algal subsidies promote the abundance and diversity of their invertebrate prey.

Adding wrack to the upper beach significantly increased the abundance and diversity of invertebrate prey items. At wrack subsidies greater than 50% of surface cover invertebrate assemblages became highly distinct compared with those that received smaller additions of wrack. Substantial (2–4 fold) increases in the abundance amphipods and isopods that are principal prey items for plovers drove these shifts.

This proof-of-concept study demonstrates the feasibility of food provisioning for birds on ocean shores. Whilst novel, it is practicable, inexpensive and does not introduce further restrictions or man-made structures. Thus, it can meaningfully add to the broader arsenal of conservation tools for threatened species that are wholly reliant on sandy beaches as breeding and foraging habitats.

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### 1. Introduction

*Even as poor birds, deceived with painted grapes,*

*Do surfeit by the eye and pine the maw,*

*Even so she languisheth in her mishaps,*

*As those poor birds that helpless berries saw.*

Venus and Adonis, William Shakespeare

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Ocean beaches are irreplaceable habitats for several species of birds that breed and feed exclusively on wave-exposed sandy shores. Many beach-obligate birds are in decline and threatened globally, requiring active conservation management (Clemens et al., 2016). The standard repertoire of conservation actions undertaken for beach-obligate species includes any combination of four principal types of measures: a) reducing risks and threats to individuals

at small scales using physical barriers to human intrusion (e.g. temporary fencing) and restrictions on types of shore use (e.g. dog-free and vehicle-free zones or periods); b) conserving and restoring habitats at larger scales (e.g. spatial conservation planning); c) reducing ambient threats that operate at larger scales (e.g. reducing populations of invasive predators) and d) improving survival and reproductive output during breeding (e.g. nest shelters; Maslo and Lockwood, 2009; Weston et al., 2014; Schlacher et al., 2015a). Many populations fail, however, to recover, or continue to decline, illustrating that fresh and complementary approaches are needed for effective shorebird conservation.

Ocean beaches are archetypical examples of subsidized ecosystems: very low primary production on the non-vegetated parts of the beach renders imports of organic material from the sea critical to sustaining animal consumers, including the prey species of beach-obligate birds (Schlacher et al., 2015b). On many beaches these imports from the sea take the form of detached marine plant material (seagrass, algae) that becomes stranded by waves and tides as 'wrack' on the beach. Onshore transport of wrack can be substantial (e.g. ~ 1000 kg m<sup>-1</sup> year<sup>-1</sup>; Dugan et al., 2011), and large accumulations create bio-geochemical hotspots of carbon processing (Coupland et al., 2007).

In the context of conserving threatened beach-obligate species, a key function of wrack is to support populations of invertebrates (e.g. smaller crustaceans, beetles and other insects) that are important prey items for birds (Colombini and Chelazzi, 2003). A sizeable body of evidence illustrates positive 'wrack effects' in the form of enhanced density and diversity of invertebrates on ocean beaches, either by reporting striking differences in the abundance of potential prey items between wrack patches and bare sand (Olabarria et al., 2007; Coupland and McDonald, 2008; Rodil et al., 2008, 2015b; MacMillan and Quijon, 2012; Rodil et al., 2015b; Ruiz-Delgado et al., 2015; Heerhartz et al., 2016) or by positive correlations between the biomass of wrack and invertebrates (Stenton-Dozey and Griffiths, 1983; Dugan et al., 2003). In addition, isotopic tracing of wrack carbon and nitrogen to the tissues of invertebrate consumers indicates trophic transfer of wrack material to prey species consumed by birds (Crawley et al., 2006; Ince et al., 2007; Mellbrand et al., 2011; Bessa et al., 2014; Fox et al., 2014; Morrow et al., 2014).

The near ubiquity of positive effects that wrack appears to have on invertebrates and the threatened beach-obligate birds that depend on them opens up the interesting possibility of actively enhancing prey resources by supplementing wrack to beaches. This would be particularly beneficial during the nesting and chick-rearing phases when energetic demands and mortality rates are especially high (Colwell et al., 2007). In fact, low chick survival is a key factor in the demographics of bird populations, particularly on sandy beaches where chicks forage independently along the strandline for small invertebrates, which are often associated with accumulations of stranded plant material and other marine debris (Cuttriss et al., 2015). On many beaches, anthropogenic disturbance can severely disrupt such foraging, potentially aggravating energetic bottlenecks for chicks (Maguire et al., 2011).

Here we test the feasibility of wrack augmentation as a conservation tool for the threatened Eastern Hooded Plover (*Thinornis rubricollis rubricollis*) breeding on wave-exposed beaches of southern Australia. We measured the response of assemblages of invertebrate prey in plots to which we added wrack and monitored these plots for potential plover predators.

## 2. Material and methods

### 2.1. The model species

Eastern Hooded Plovers are a threatened, beach-nesting bird

species endemic to southern Australian sandy beach and dune habitats. They typically nest close to the strandline near the base of the dune or in the foredunes, establishing territories usually extending for up to 1 km. The precocial chicks forage for invertebrates mostly on the beach, especially at the strandline and near wrack, where they mostly consume smaller crustaceans (e.g. amphipods, isopods), and various insects (Weston and Elgar, 2005a). Hooded Plovers also use aged wrack higher on the beach for crypsis of their eggs and young (their primary anti-predator defense) and occasionally use wrack as a nesting material; they may also consume some wrack, but such consumption may be incidental (Maguire et al., 2012).

### 2.2. Study site and experimental design

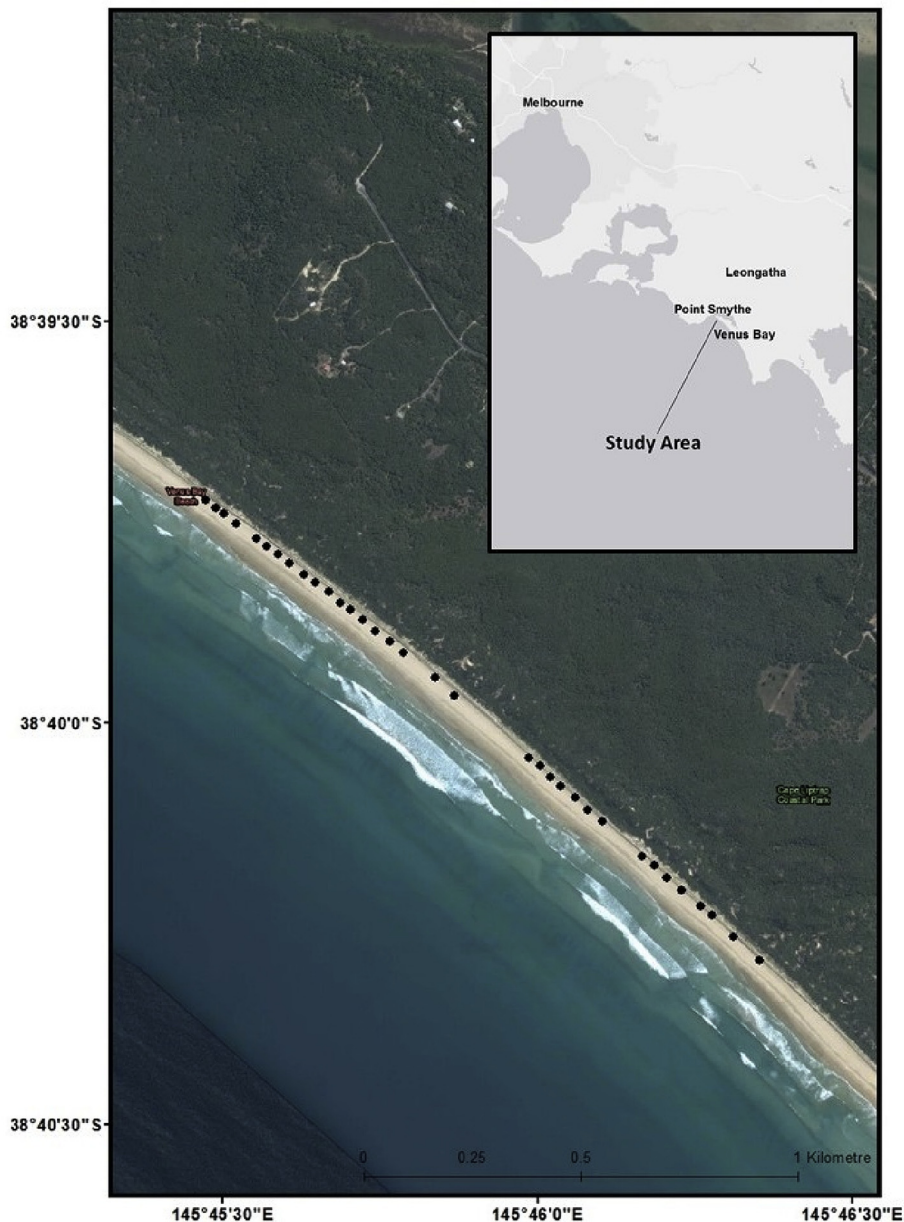
We conducted experiments at Venus Bay Ocean Beach (−38°39'43"S, 145°45'28"E), in the Cape Liptrap Coastal Park (Victoria, Australia; Fig. 1). The beach is a known breeding habitat for Hooded Plovers, and it contains abundant beach-cast material of marine algae. The area where the experiment was done was only lightly used by humans (<1 person per day). Waves average 1.8 m high, mean sediment grain size is 189 μm (±0.89 se; range: 183–211 μm), and the beach slopes at 11.30° (2.31 se; range: 5.00–25.50°).

We established experimental plots (1 m × 1 m) on a 1.7-km long, south-west-facing stretch (Fig. 1). The design included eleven treatment levels of wrack supplementation (in increments of 10%, see below and Fig. 2), with four replicates per treatment level, resulting in 44 plots being initially established in the supralittoral zone between the drift line and the base of the dunes. Plots were dispersed alongshore (min. separation 22 m) in a manner to avoid active breeding territories of plovers and beach access paths used by humans.

We supplemented wrack by transferring macroalgae from the lower beach to treatment plots, creating an experimental sequence of wrack cover in increments of approximately 10% (Fig. 2). Wrack cover was estimated visually, subdividing the plot into segments to improve accuracy. Three researchers made the estimates per plot in the field. Such visual estimates of cover are an accepted and widely used technique in terrestrial settings (e.g. Jennings et al., 1999). Freshly-added wrack piles were approximately 25 cm high, typically compressing to half this height within 24 h. Existing wrack cover prior to supplementation was always less than 5% surface cover for all plots. Since our experiment aimed to mimic the steps in any future conservation practice aimed at enhancing wrack cover on beaches where plovers rear chicks, we deliberately employed visual estimates and wrack transfers that would be done by rangers and volunteers without imposing unnecessary technical demands. The dominant drift macrophyte species in the study area is *Macrocystis angustifolia* Bory, which was also the dominant material in our experiments. Two other species, *Phyllospora comosa* (Labillardière) C. Agardh and *Sargassum* sp., which occurred on the beach in low amounts, were used sparingly in supplementation to mimic natural environmental variation. The experiment was run from 16 to 30 Nov. 2015.

### 2.3. Indexing fauna and environmental conditions

We sampled surface-active invertebrates using pitfall traps (diameter: 75 mm; depth: 110 mm; three-quarters filled with seawater mixed with a small volume of dishwashing detergent, and buried so that the opening was flush with the surface of the sand). One trap was placed in the centre of each plot and, following Olabarria et al. (2007), an additional trap was placed one metre to the left or right (randomized) to correct for potential spatial



**Fig. 1.** The study area at Venus Bay (Victoria, Australia) and location of plots on the ocean shore where experimental wrack supplementation was trialed. Plots are unequally dispersed alongshore to avoid breeding territories of hooded plovers and beach access points.

variation in invertebrates not closely attributed to experimental manipulation of wrack (Fig. 3). All pitfall sampling occurred three days after wrack supplementation to a plot, a time interval that has been shown elsewhere to coincide with peak colonization by invertebrates to stranded wrack (Inglis, 1989; Olabarria et al., 2007; Rodil et al., 2008). Traps were deployed in the late afternoon near sunset and retrieved the following day (mean deployment period:  $20.04 \pm 0.48$  (se) hours). Trapping period is included as a co-variate in all statistical analyses.

To monitor whether vertebrate predators were attracted to plots, we deployed a motion-sensing Scoutguard camera (Scoutguard DTC530V; normal sensitivity; 3 image capture with no delay between triggers) at the base of the foredune directed at each experimental plot (Fig. 3). A predator was deemed as an animal that has been reported to eat eggs or chicks (e.g. raven, magpie, fox) photographed within approximately three metres of an

experimental plot.

We obtained air temperature data (30-min recording interval) from the Bureau of Meteorology's closest weather station at Pound Creek ( $-38^{\circ}37'47''\text{S}$ ,  $145^{\circ}48'39''\text{E}$ ). Wave height was visually estimated during field work. Grain size was determined by sieving dried ( $80^{\circ}\text{C}$ , 30 min) surface sand samples (ca. 250 ml, top 2–3 cm) taken from each plot. Beach slope was determined trigonometrically using a spirit level and measuring tape.

#### 2.4. Numerical analyses

Two complementary modelling approaches were used to test the response of invertebrates to wrack supplementation: i) distance-based linear models (DISTLMs; McArdle and Anderson, 2001) for multivariate data of assemblage structure, and ii) generalised additive models (GAMs; Hastie and Tibshirani, 1990; Guisan et al., 2002)

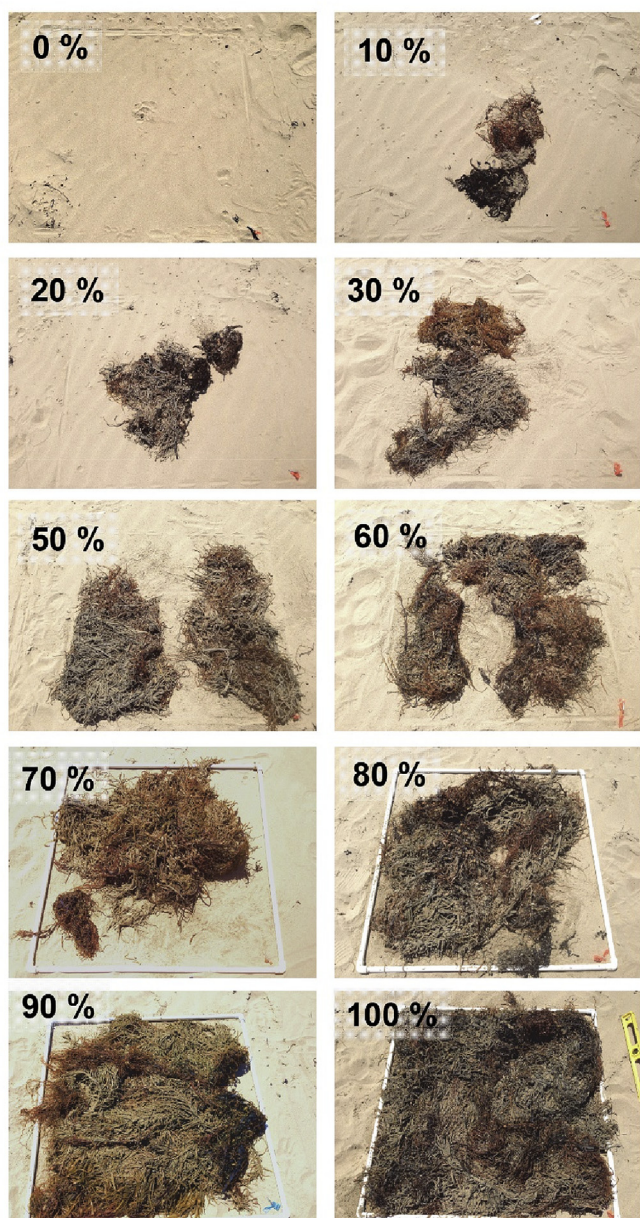


Fig. 2. Examples of experimental treatment levels consisting of increasing surface cover of macrophyte wrack added to 1 × 1 m plots (n = 44) on the upper beach.

for composite measures of total abundance and species richness.

In the multivariate domain, we analysed, with DISTLM, the relationship between experimental wrack addition, environmental variables (i.e. pre-existing wrack cover, sediment compactness) and co-variables (i.e. temperature, deployment time) and a similarity matrix based on Bray-Curtis resemblance of species catches (no. individuals per trap). We ran generalised additive models (GAMs) to identify which variables most closely correlate with total catches (i.e. number of individuals per trap) and richness (i.e. number of species per trap). We used GAMs to include possible non-linear relationships, and to avoid model overfitting we restricted the number of predictors to six variables for which either specific expectation (predictive hypothesis) about their influence on invertebrates was made (cover of wrack augmented), or that were considered to have influenced invertebrate catches in addition to wrack (e.g. sediment compactness, pre-existing wrack cover,

temperature, time traps operated in the field). We further reduced overfitting by limiting the number of model knots (individual polynomial functions that combine to form the GAM smooth) to four or fewer (Burnham and Anderson, 2002; Zuur et al., 2009). Models were compared based on the corrected Akaike information criterion (AICc), and ‘best-fit models’ were considered to be the model with the lowest AICc value plus other models with  $\Delta AICc$  scores within 2 of the top model (Burnham and Anderson, 2002). Relative importance of variables was calculated by summing weighted AICc values from each model containing the variable in either the DISTLMs or GAMs.

The probability of a potential egg or chick predator being detected at experimental plots was modelled using logistic regression with the level of wrack supplementation as the predictor and deployment time of cameras as a co-variate (to account for possible difference in detection due to shorter or longer camera operation).

### 3. Results

A total of 8679 individuals, comprising 68 species of invertebrate, was collected. Catch per unit effort ranged between 40 and 235 individuals (mean:  $106 \pm 6.68$  (se)). Peracarid crustaceans dominated the catches numerically (71% of catch), with the talitrid amphipod *Bellorchestia* sp.1 accounting for 55% of the total catch (4764 ind.) and the isopod *Actaecia thomsoni* for 16% (1430 ind.). Insects comprised 27% of all individuals, with coleopterans being most abundant (1894 ind.), followed by dipterans (435 ind.), ants (39 ind.) and wasps (3 ind.). Spiders (89 ind.) and centipedes (24 ind.) made up less than 1% of the catch. Most (91%) of the collected species were insects (62 spp.) with less speciose groups being spiders (3 spp.), crustaceans (2 spp.), and centipedes (1 spp.). Beetles (30 spp.) made up the bulk of the insect diversity, followed by dipterans (24 spp.), ants (4 spp.), wasps (3 spp.) and hemipterans (1 spp.).

Adding algal wrack to the upper beach significantly increased invertebrate abundance and diversity (Fig. 4, Table 1). Wrack subsidy was the most influential predictor of invertebrate abundance, with catch rates increasing monotonically with the amount of seaweed cover added to experimental plots (Fig. 4). Fewer individuals were caught in plots with coarser sediment, and pre-existing wrack cover slightly elevated catches (Fig. 4). Neither temperature, sand compactness, nor deployment time had a large influence on catches (Fig. 4). As was the case for abundance, the amount of wrack subsidized was also the only examined predictor that was consistently associated with higher levels of species richness across the gradient of wrack subsidy tested (Fig. 4, Table 1). Temperature significantly influenced species richness, but in a non-linear fashion, with more species being caught during either colder or warmer nights; no other examined environmental variable was significantly correlated with species richness (Fig. 4).

Wrack subsidy was most strongly associated with significant shifts in assemblage structure: assemblages at subsidy levels greater than 50% of surface cover were highly distinct compared with those that received smaller additions of wrack (Fig. 5, Table 2). Most of this shift in assemblage structure was driven by substantial (2–4 fold) increases in the abundance of two species of amphipods and isopods; that accounted for 55% of the total dissimilarity between lower (0–50%) and higher (60–100%) wrack subsidies (Table 2). Two species of beetles (*Phycosecis litoralis*, *Scymena* cf. *amphibia*) made moderate (7–8%) contributions in distinguishing between samples from low and high wrack cover and tended to be caught in greater numbers in plots with less seaweed (Table 2). All other taxa were generally less important in distinguishing between low and high wrack treatments and their abundance values were

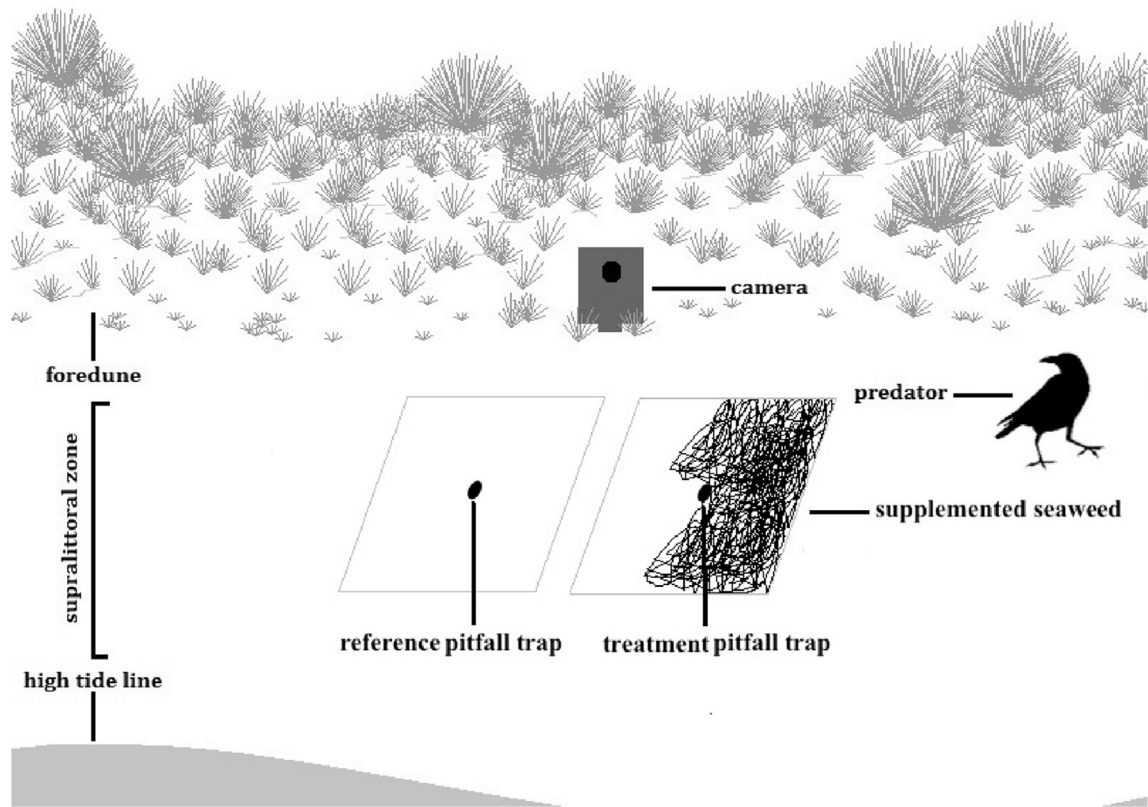


Fig. 3. Sketch illustrating the experimental set-up.

not consistently greater or lower in either treatment (Table 2).

Out of a total 44 cameras monitoring experimental plots, 32 detected at least one visit by a putative egg or chick predator (Table 3). There was, however, no significant effect of wrack supplementation on the likelihood of predator presence (binomial GLM,  $\beta = 0.016 \pm 0.012$  (se),  $p = 0.207$ ).

#### 4. Discussion

##### 4.1. Wrack and beach birds

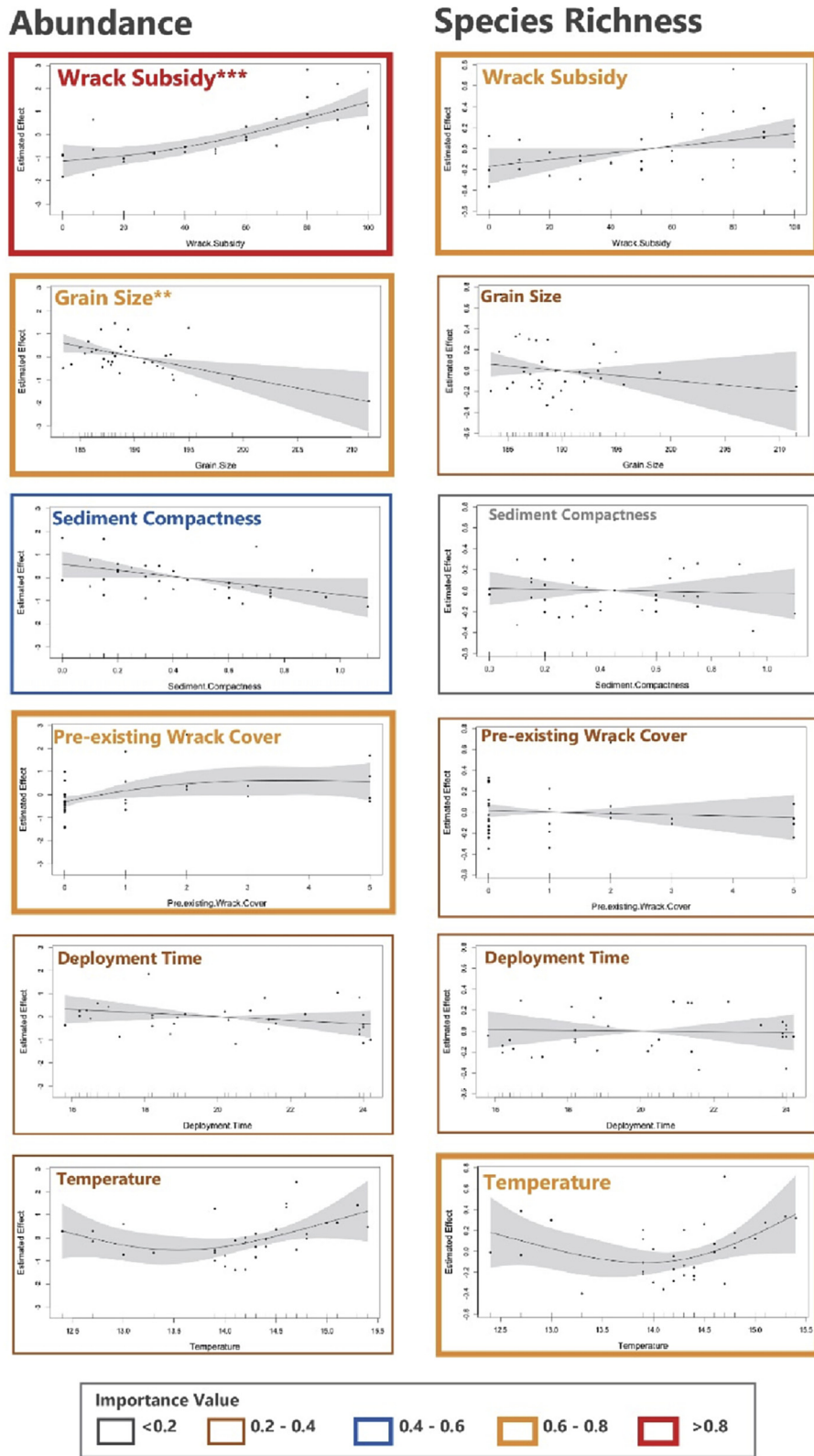
Augmenting wrack to enhance prey availability for birds of conservation concern hinges on demonstrating a positive effect of wrack on birds on ocean beaches. Wrack will benefit birds mostly indirectly via a trophic pathway, increasing local populations of prey species that occur in greater abundance in and under wrack piles. Indeed, our results demonstrate that wrack augmentation resulted in significantly greater numbers of invertebrates on the upper beach near supplemented wrack.

The published evidence for more invertebrates in wrack is comprehensive (Colombini and Chelazzi, 2003; Ince et al., 2007), and the use of wrack by foraging beach birds is similarly convincing (Dugan et al., 2003). For example, on southern Californian beaches, the abundance of two plover species (Black-bellied Plover *Pluvialis squatarola* and Western Snowy Plover *Charadrius alexandrinus nivosus*) was higher on beaches covered with more wrack, which supported more wrack-associated invertebrates. Significantly, both these species forage on surface prey that is typical of wrack patches (e.g. talitrid amphipods, flies) (Dugan et al., 2003). In northern California, greater numbers of plover prey items (e.g. amphipods, flies) occurred on beaches covered with more brown algae, and this

spatial pattern of wrack and invertebrates were reflected by plover distributions, with birds selecting sites that contained significantly more brown algae (Brinck and Colwell, 2011).

Plover species breeding on sandy beaches feed extensively on upper beach invertebrates that are typically found in wrack. Plovers have a catholic diet, preying on a broad range of taxa that encompasses amphipods, isopods, molluscs, polychaete worms, and a variety of insects (e.g. beetles, dipterans, ants; Shaffer and Laporte, 1994; Majka and Shaffer, 2008; Brinck and Colwell, 2011). Apart from plovers, a number of other shorebird species (e.g. turnstones) feed directly on macrophyte patches, either picking invertebrates from the surface of algal fronds or probing, overturning or foot shaking/trembling amongst the plant material (Marchant and Higgins, 1993; Dugan et al., 2003). Plovers have been observed to feed at night sometimes on and often near wrack patches (Dugan, 1981; Staine and Burger, 1994). This is significant in the context of the food subsidies proposed here as many of the wrack-associated invertebrate species are most active at night when they undertake often extensive surface movements to and from wrack (Lastra et al., 2010). In addition to plovers and other 'typical' beach species, insectivorous passerines (e.g. flycatchers, swallows, sparrows, fairy-wrens, starlings) forage regularly along the strandline of beaches where wrack accumulates (Dugan et al., 2003; Meager et al., 2012).

The contribution of carbon from drifting algae and stranded wrack to consumers in coastal food webs is well documented (Ince et al., 2007). Wrack-centred trophic pathways include those where plant material is directly available to animal consumers in the surf-zone or on the beach, as well as for consumers in abutting, functionally linked, coastal dunes (Spiller et al., 2010; Mellbrand et al., 2011). Unexpectedly, trophic links between wrack and birds on

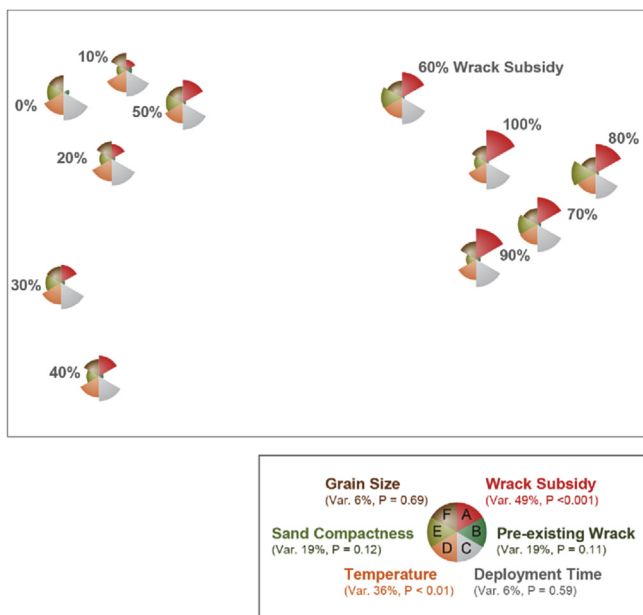


**Fig. 4.** Generalised additive models (GAMs) relating abundance (left panels) and species richness (right panels) of beach invertebrates trapped in experimental plots receiving different amount of wrack subsidy (top row). Additional variables tested included the mean grain size of the substrate, the compactness of the sand, the amount of wrack at the start of the experiment, the time traps were active collecting animals, and the air temperature during trap deployment. Frames of individual panels are colour-coded to reflect importance values of individual predictors in the overall GAMs model (cf. Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**  
Contributions of variables in GAMS and DISTLM models relating three metrics of invertebrate assemblages (1- total catch, 2 - species richness, and 3 - assemblage structure) to experimental wrack additions (subsidy), habitat attributes (pre-existing wrack cover, sediment compactness, grain size, temperature), and the duration for which pitfall traps were deployed. Relative variable contributions are assessed with a multi-model inference approach based on cumulative AICc weights ( $w+(j)$ ) in DISTLM or 'importance values' (IV) in GAMS. Predictors are ordered based on the mean rank of model weights across the three ecological response variables.

Variable	GAMS		DISTLM		
	1 - Catch (Abundance)		2 - Species Richness		3 - Assemblage Structure
	IV	(P)	IV	(P)	$w+(j)$
Wrack Subsidy (%)	1.00	(0.001)	0.68	(0.060)	0.98 #
Temperature (°C)	0.23	(0.180)	0.71	(0.140)	0.68 #
Deployment Time (hrs)	0.39	(0.270)	0.28	(0.870)	0.49
Grain Size (µm)	0.71	(0.005)	0.28	(0.300)	0.32
Pre-existing Wrack Cover (%)	0.64	(0.070)	0.23	(0.630)	0.45 #
Sand Compactness (cm)	0.54	(0.050)	0.19	(0.800)	0.39

# included in best overall model based on lowest AICc value.



**Fig. 5.** Ordination (non-metric multidimensional scaling) of treatment plots based on similarity (Bray-Curtis) in the species composition and abundance of invertebrate assemblages. The size of colour-coded segments is proportional to the mean value of a variable at a treatment level. Information in brackets in legend refers to statistics of marginal tests in distance-based linear models (DISTLM, cf. Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ocean beaches have not been formally tested or traced in experiments; this is an unexpected gap in our understanding of the ecology for species of significant conservation concern. By contrast, direct trophic transfers of beach-cast animal carrion to scavenging birds have been comprehensively documented recently (Huijbers et al., 2013, 2015; Brown et al., 2015; Huijbers et al., 2015; Schlacher et al., 2015a; Huijbers et al., 2016).

#### 4.2. Mechanism(s) of wrack effects

The sizeable body of data on the positive effects that drifting and stranded plant material has on invertebrates usually invokes three complementary mechanisms to explain the observed patterns: a) wrack provides food ('trophic'), b) wrack lowers predation risk ('refuge'); and c) wrack reduces temperature and water stress ('climate'). This 'food and shelter hypothesis' is relevant for planning

food augmentation trials for beach-foraging birds as the purposeful provisioning with prey needs to understand the processes driving planned increases in prey populations.

Stranded plant material is an important part of the diet of invertebrates on sandy beaches, represented mainly by several genera of amphipods and isopods (Lastra et al., 2015). Wrack carbon can be traced isotopically to be assimilated into the tissues of invertebrates occurring on the non-vegetated part of beaches and the abutting dunes (Ince et al., 2007). Also, feeding rates by wrack-associated invertebrates can be substantial (e.g. Lastra et al., 2008 estimate that talitrid amphipods can consume up to 92–100% of stranded wrack between consecutive spring tides). Consumers of wrack have also evolved behaviours that maximize encounters with freshly stranded wrack to rapidly exploit wrack washed up on the beach (Lastra et al., 2010). Thus, the trophic route underpinning observed wrack effects is well supported and hence the palatability and dietary attractiveness of added wrack is critically important.

Wrack piles retain moisture in the sand matrix, buffer against temperature extremes, and block light, thereby reducing thermal, desiccation and UV stress for beach invertebrates (Colombini and Chelazzi, 2003; Ruiz-Delgado et al., 2015). Whilst this is an attractive hypothesis, it needs to be tested using field data obtained from inside and under wrack patches matched with data on physiological tolerance of preferred prey species using these patches. This could have a bearing on the height and type of wrack experimentally added to create an optimal humidity and temperature environment for the infauna.

That wrack provides a refuge from predators is conceptually appealing. In the surf-zone of beaches, detached and drifting macrophytes are hypothesized to protect smaller fish from predation by larger fish and cormorants by physically impeding the feeding actions of predators (Crawley et al., 2006). Wrack stranded on the beach has also been postulated to reduce predation pressure on smaller invertebrates (Colombini et al., 2000), but remarkably, this hypothesis remains untested. By contrast, it is plausible that predation risks are higher near wrack patches provided that predators have evolved, or learned, foraging strategies to exploit resources supplied by marine debris. This is clearly the case for beach-cast carrion that is consumed by a diversity of birds and mammals scavenging along the strandline of beaches (Schlacher et al., 2013a, 2013b). Importantly, the *raison d'être* for augmenting wrack near the breeding territories of plovers is to increase the abundance of the birds' prey species that feed on wrack and use it as habitat. It follows that wrack patches may increase predation risk for beach invertebrates. This hypothesis is supported by frequent observations of plovers foraging for wrack-invertebrates around the edges of wrack piles (M. Weston pers. obs.).

**Table 2**

Summary of SIMPER (Similarity Percentage) analysis contrasting experimental treatment groups with 'low' and 'high' wrack subsidies (cf. Fig. 5). Bold numbers denote higher mean abundance in pairwise comparisons.

Taxon	'Low' Wrack Subsidy (0–50% Cover)	'High' Wrack Subsidy (0–50% Cover)	Av.Diss	Diss/SD	Contrib. %	Cum. %
	Mean Abundance (ind. trap <sup>-1</sup> )	Mean Abundance (ind. trap <sup>-1</sup> )				
Crustacea (Talitridae), <i>Bellorchestia</i> sp.1	35.15	<b>78.92</b>	19.83	3.27	42.33	42.33
Crustacea (Actaeciidae), <i>Actaecia thomsoni</i>	4.28	<b>16.42</b>	6.01	1.23	12.84	55.17
Coleoptera (Tenebrionidae), <i>Scymena</i> cf. <i>amphibia</i>	<b>9.62</b>	1.26	3.89	1.66	8.31	63.48
Coleoptera (Phycosecidae), <i>Phycosecis litoralis</i>	<b>13.52</b>	11.61	3.17	1.37	6.77	70.24
Coleoptera (Staphylinidae), <i>Sartallus signatus</i>	0.25	<b>5.14</b>	2.14	0.67	4.57	74.81
Coleoptera (Staphylinidae), <i>Cafius</i> sp.1	<b>3.3</b>	0.18	1.43	2.69	3.06	77.87
Coleoptera (Phycosecidae), <i>Phycosecis litoralis</i> (larvae)	0.33	<b>3.38</b>	1.39	1.04	2.97	80.84
Coleoptera (Staphylinidae), <i>Bledius</i> sp.1	<b>2.13</b>	1.68	1.02	1.47	2.17	83.01
Coleoptera - Larvae OTU-L2	2.07	<b>3.24</b>	0.95	1.14	2.03	85.04
Diptera (Dolichopodidae)	<b>2.47</b>	1.76	0.84	1.3	1.8	86.84
Diptera (Canacidae) OTU-D2	0.4	<b>1.51</b>	0.55	0.97	1.18	88.02
Aranea (Lycosidae), OUT-A1	<b>1.53</b>	0.93	0.5	1.28	1.07	89.09
Dipteran - OTU-D5	1.07	<b>1.17</b>	0.43	1.45	0.92	90.02

**Table 3**

Occurrence of potential egg and chick predators recorded at experimental plots. (entries are the number of plots in which a predator was captured with wildlife cameras; the number of plots per treatment was four).

Wrack supplementation	Magpie No. Plots (n)	Raven No. Plots (n)	Silver gull No. Plots (n)	Red Fox No. Plots (n)
0%	2	1	0	0
10%	2	0	0	0
20%	2	0	0	0
30%	2	1	0	0
40%	2	0	0	1
50%	2	1	1	0
60%	1	1	0	1
70%	4	2	0	1
80%	3	1	0	0
90%	3	1	0	0
100%	2	1	1	0

#### 4.3. Sharpening the wrack augmentation tool

Our experiment is fundamentally a proof of concept study, examining whether enhancing prey for breeding plovers and their chicks is feasible as a future management tool on wave-exposed sandy beaches. It was purposefully relatively undemanding, in a technical, sense to simulate how volunteers and other field personnel would likely carry out these activities in practice. Notwithstanding the positive overall outcome of locally enhancing invertebrates, protocols will need many further refinements before larger field trials are undertaken. This may be complex as multiple factors can influence the size of any prey enhancement and feeding of plovers on these prey, including the geometry of patches (e.g. size, edge-to-area ratio, height), material properties (e.g. species, age), and spatial configuration (e.g. number of patches, elevation, distance from nest).

Previous experimental work on wrack has included only very small patches over a limited size range (0.09–0.5m<sup>2</sup>; Olabarria et al., 2007; Rodil et al., 2008; MacMillan and Quijon, 2012). Small patches may decompose faster, support fewer species, and may be more prone to removal by waves (Olabarria et al., 2007), whilst larger patches may be more labour-intensive to establish. At this stage, however, the optimal patch size remains to be determined. Because plovers tend to forage around the edges of wrack piles, patches with more jagged edges could provide better feeding opportunities for plovers, especially when wrack piles exchange mobile invertebrates with the bare sand areas surrounding them. As is the case for patch size, the optimal shape and edge-to-area ratio needs to be experimentally determined, measuring both invertebrates accessible to plovers and plover microhabitat

preferences. In the absence of experimental data, a sensible approach is to mimic the size and shape spectrum of wrack patches naturally occurring on the beach.

Wrack can be taxonomically diverse (Baring et al., 2014) and species of drifting and stranded macrophytes can differ considerably in physical and chemical attributes which may change as wrack ages on a beach (Rodil et al., 2008, 2015b). More buoyant species of algae stranded on the beach can be re-suspended more frequently (Orr et al., 2005), and hence less buoyant species may be preferred for augmentation. Algae and seagrass are the principal components of wrack, theoretically creating a choice in augmentation trials. Wrack associated invertebrates may either prefer algae (Adin and Riera, 2003; Lastra et al., 2008; MacMillan and Quijon, 2012) or seagrass (Mellbrand et al., 2011). Thus, while choices exist, we recommend that a sensible approach is to use algae and seagrass in the same ratio as they occur naturally in wrack patches unless food preferences are clearly demonstrated. Because the most plausible mechanism by which wrack enhances prey populations used by birds is as food to herbivores, factors influencing feeding and food quality are important. A broad range of physical and chemical properties (e.g. toughness, water content, bio-chemical composition, phenols) control palatability and rates of consumption of wrack by invertebrates (Duarte et al., 2010; MacMillan and Quijon, 2012; Lastra et al., 2015; Rodil et al., 2015a, 2015b). Nevertheless, it is theoretically feasible to improve the performance of wrack augmentation by identifying wrack attributes that yield the highest rates of invertebrate consumption and production.

Because the longevity of wrack patches will typically be shorter than the typical period from egg laying to chick fledging, decisions will have to be made about whether patches should be replaced,



and when they should be deployed. Ideally, this should be informed by the breeding ecology of the target shorebird and changes in the 'performance' of patches as they age. Deployment strategies could: 1) target temporal energetic bottlenecks of breeding plovers and 2) recognize that disturbance resulting from deployment could be damaging (Maguire et al., 2012). Adult condition of biparental incubators such as the Hooded Plover is maintained during the egg phase but reduces rather dramatically during brood-rearing, when the chicks require substantial prey resources to fuel their rapid growth (c. 30–35 days to fledging), and adults are often simultaneously engaged in the energetically demanding process of moulting their primary feathers (Weston and Elgar, 2005b; Rogers et al., 2014). Disturbance by people is problematic for many breeding plovers (e.g. Weston and Elgar, 2005a), and pre-laying and laying periods would sensibly be avoided for supplementary wrack deployment (Maguire et al., 2012). Given that the first week post-hatching is the period of greatest chick mortality (Dowling and Weston, 1999), a pre-hatching deployment of wrack would seem the basic approach, with possible replacement supplementation later in the brood-rearing phase.

Colonization of experimentally created wrack piles is generally fast, but abundance can vary over the course of weeks. For example, in NW Spain, fauna rapidly colonized experimental wrack patches (e.g. 83–86% of species present by day 3) and showed complex patterns of abundance changes among taxa over the course of three weeks. However, several of the most abundant species (mainly flies and beetles) peaked around 3–7 days after the placement of wrack piles and declined thereafter (Olabarria et al., 2007; Rodil et al., 2008). Similarly, in Western Australia, peak densities of weevils and spiders occurred on day 4 of the colonization experiments (Mellbrand et al., 2011); a pattern of rapid colonization (peak densities at day 3) was also reported for litter bag experiments in New Zealand (Inglis, 1989). Thus, knowing the time course of 'attractiveness' of wrack piles to invertebrates has important implications in terms of the frequency at which wrack material is renewed in attempts of bird-food subsidy management. Furthermore, decomposition and desiccation will vary with weather conditions (slower desiccation rates but possibly faster bacterial decomposition during rainy weather and vice versa during dry conditions). Lastra et al., (2008) show that amphipods feed more on either fresh (~0–3 days) or decomposed (~2 weeks) material, but time courses of consumption rates are complex, being dependent on age of individuals, water content of algae and the humidity under which they decay, and the species composition of algae in the wrack.

While 'snapshot' studies show wrack accumulation varies between Hooded Plover territories, the temporal variation within territories remains undocumented (Cuttriss et al., 2015). Thus, a critical information gap is to identify those territories that would benefit from wrack subsidies. The input and persistence of wrack on individual beaches depends on numerous oceanographic, geomorphological and ecological features, including the presence and extent of nearby macrophyte beds that can supply uprooted plants as wrack, wave regimes and exposure, tides, beach dimensions (length, slope) and substrate coarseness, and landscape features such as backing bluffs (Orr et al., 2005; Barreiro et al., 2011; MacMillan and Quijon, 2012; Baring et al., 2014; Lastra et al., 2015). Most fundamentally, wrack washed up on narrower and steeper beaches may be more frequently removed by more turbulent swash (i.e. short retention) whilst on wider and flatter beaches floating macrophytes may become stranded high up on the shore where they dry quickly (i.e. less protection from desiccation) (Tewfik et al., 2016). Theoretically, intermediate beaches may offer more favourable conditions for wrack placement, but this needs to be tested for local candidate beaches, ideally during pilot studies that are

conducted well before breeding starts. Such beaches may also be relatively wrack and food-rich and not benefit from supplementation as much as other beaches.

Material deposited higher on the shore (i.e. above the drift line) will tend to remain longer, but may support fewer invertebrates compared with wrack lower on the beach (i.e. at or below the current drift line), which has higher numbers of invertebrates underneath patches (Jaramillo et al., 2006). This may not be a universal feature, however, as neither Rodil et al. (2008) nor Ruiz-Delgado et al. (2015) found consistent differences in either the abundance or diversity of invertebrates in wrack patches with respect to being below, at or above the driftline. This suggests that wrack augmentation is certainly practicable in the supratidal zone. Thus, placement of wrack patches across the swash-dune gradient will likely be a compromise between greater retention (higher on shore) and possibly greater habitat suitability (lower on shore) for invertebrates. Foraging birds will be able to access supratidal patches irrespective of tidal phase, whereas more seaward patches are inaccessible during high tides.

The spatial configuration of patches needs to be optimized (in part using assumptions from optimal foraging theory) based on empirical data on five key inputs: 1) temporal feeding opportunities (e.g. tidal restrictions on access); 2) enhancement effects on prey (e.g. temperature and humidity condition at different shore elevations); 3) natural foraging zones and preferences (e.g. plovers utilizing different parts of the swash to dune gradient); 4) spatial variation in risk (e.g. swept by large swashes, exposure to predators in intertidal); and 5) management goals (e.g. encouraging broods away from access points or to remain within already protected areas). All of these can be empirically measured in the field or quantified from behavioural models and hence models predicting the 'best' spatial configuration are feasible; these could present a practicable step forward in developing prey enhancement further as a tool in beach-bird conservation.

#### 4.4. Positive and negative side effects?

Besides providing food and adding physical structure to beaches, wrack plays an important role in habitat-forming processes and nutrient cycling. Macrophyte wrack is instrumental in initiating the formation of hummocks and embryo dunes by wind-driven sand, often starting the sequences of dune formation and beach accretion (Dugan et al., 2005). Wrack piles that become a catalyst for beach formation on the upper shore are particularly important after significant erosion events that eliminate part of the nesting areas for beach-obligate bird species. Embryo dunes, especially those with pioneer strandline plants, are also used for nesting and by adults and chicks to shelter during inimical weather and high tides. Microbial breakdown of the organic fraction of wrack re-mineralises nutrients that can in turn promote primary production by surf-zone phytoplankton, ultimately underpinning trophic pathways leading to invertebrate prey species on the beach-face (Soares et al., 1997; Barreiro et al., 2013).

Trophic pathways that link wrack-associated invertebrates with higher-order predators are not limited to plovers and other birds feeding on ocean beaches. A number of other vertebrates have been reported to assimilate wrack-derived carbon, mostly by foraging on invertebrates supported by stranded macrophytes at the land-ocean boundary; these include songbirds (Meager et al., 2012; Heerhartz, 2013), fishes (Romanuk and Levings, 2010), lizards (Barrett et al., 2005; Spiller et al., 2010), rodents (Stapp and Polis, 2003), foxes (Ricci et al., 1998), and bears (Fox et al., 2014). This means that active wrack augmentation has the potential to benefit multiple consumers at the beach-dune ecotone beyond shorebirds. The downside of any wrack subsidy effects to multiple vertebrate

species is that these may attract predators with flexible feeding strategies that extend to preying on beach-nesting birds, their eggs and offspring (e.g. foxes, corvids, gulls). Whilst our camera-trap data show that experimental wrack patches did not result in a greater probability of predator occurrence in this particular system, we cannot exclude the possibility of 'predator attraction'. Therefore, an essential and critical step before any wrack supplementation is carried out in a conservation context is to comprehensively assess the risk of predator attraction over the full range of proposed wrack treatments and across prevailing predator regimes. Obviously, this needs to be done on beaches where no birds nest and include recordings that span the full period from egg laying to chick fledging. An optimized supplementation program should be tested within an adaptive management framework to determine whether supplementation enhances chick survival and condition, and confirm that the benefits outweigh any potential problems in relation to plover population demographics.

## 5. Conclusions

Supplementing wrack to the upper beach measurably increased the abundance and diversity of prey items regularly consumed by Hooded Plovers and the practice does not appear to attract potential predators. The method is feasible, technically undemanding, cheap and relatively un-intrusive and minimally invasive. As a management tool, it will benefit from prioritization (i.e. where and when it will likely confer benefits to plovers) and fine-tuning with respect to patch properties (e.g. size, species composition, shape), spatial configuration of patches (elevation, distance from nests), and replacement frequency. Therefore, wrack supplementation appears practicable as a complementary action to improve breeding success in threatened birds that require active management.

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## References

- Adin, R., Riera, P., 2003. Preferential food source utilization among stranded macroalgae by *Talitrus saltator* (Amphipod, Talitridae): a stable isotopes study in the northern coast of Brittany (France). *Estuar. Coast. Shelf Sci.* 56, 91–98.
- Baring, R.J., Fairweather, P.G., Lester, R.E., 2014. Storm versus calm: variation in fauna associated with drifting macrophytes in sandy beach surf zones. *J. Exp. Mar. Biol. Ecol.* 461, 397–406.
- Barreiro, F., Gómez, M., Lastra, M., López, J., De la Huz, R., 2011. Annual cycle of wrack supply to sandy beaches: effect of the physical environment. *Mar. Ecol. Prog. Ser.* 433, 65–74.
- Barreiro, F., Gómez, M., López, J., Lastra, M., de la Huz, R., 2013. Coupling between macroalgal inputs and nutrients outcrop in exposed sandy beaches. *Hydrobiologia* 700, 73–84.
- Barrett, K., Anderson, W.B., Wait, D.A., Grismer, L.L., Polis, G.A., Rose, M.D., 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations. *Oikos* 109, 145–153.
- Bessa, F., Baeta, A., Marques, J.C., 2014. Niche segregation amongst sympatric species at exposed sandy shores with contrasting wrack availabilities illustrated by stable isotopic analysis. *Ecol. Indic.* 36, 694–702.
- Brindock, K.M., Colwell, M.A., 2011. Habitat selection by western snowy plovers during the nonbreeding season. *J. Wildl. Manag.* 75, 786–793.
- Brown, M.B., Schlacher, T.A., Schoeman, D.S., Weston, M.A., Huijbers, C.M., Olds, A.D., Connolly, R.M., 2015. Invasive carnivores alter ecological function and enhance complementarity in scavenger assemblages on ocean beaches. *Ecology* 96, 2715–2725.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multi-model Inference*. Springer, New York.
- Clemens, R.S., Rogers, D.I., Hansen, B.D., Gosbell, K., Minton, C.D.T., Straw, P., Bamford, M., Woehler, E.J., Milton, D.A., Weston, M.A., Venables, B., Weller, D., Hassell, C., Rutherford, B., Onton, K., Herrod, A., Studds, C.E., Choi, C.Y., Dhanjal-Adams, K.L., Murray, N.J., Skilleter, G.A., Fuller, R.A., 2016. Continental-scale decreases in shorebird populations in Australia. *Emu* 116, 119–135.
- Colombini, I., Aloia, A., Fallaci, M., Pezzoli, G., Chelazzi, L., 2000. Temporal and spatial use of stranded wrack by the macrofauna of a tropical sandy beach. *Mar. Biol.* 136, 531–541.
- Colombini, I., Chelazzi, L., 2003. Influence of marine allochthonous input on sandy beach communities. *Oceanography and Marine Biology. An Annu. Rev.* 41, 115–159.
- Colwell, M.A., Hurley, S.J., Hall, J.N., Dinsmore, S.J., 2007. Age-related survival and behavior of Snowy Plover chicks. *Condor* 109, 638–647.
- Coupland, G.T., Duarte, C.M., Walker, D.I., 2007. High metabolic rates in beach cast communities. *Ecosystems* 10, 1341–1350.
- Coupland, G.T., McDonald, J.L., 2008. Extraordinarily high earthworm abundance in deposits of marine macrodetritus along two semi-arid beaches. *Mar. Ecol. Prog. Ser.* 361, 181–189.
- Crawley, K.R., Hyndes, G.A., Ayzvazian, S.G., 2006. Influence of different volumes and types of detached macrophytes on fish community structure in surf zones of sandy beaches. *Mar. Ecol. Prog. Ser.* 307, 233–246.
- Cuttriss, A., Maguire, G.S., Ehmke, G., Weston, M.A., 2015. Breeding habitat selection in an obligate beach bird: a test of the food resource hypothesis. *Mar. Freshw. Res.* 66, 841–846.
- Dowling, B., Weston, M.A., 1999. Managing a breeding population of the Hooded Plover *Thinornis rubricollis* in a high-use recreational environment. *Bird Conserv. Int.* 9, 255–270.
- Duarte, C., Navarro, J.M., Acuña, K., Gómez, I., 2010. Feeding preferences of the sandhopper *Orchestoidea tuberculata*: the importance of algal traits. *Hydrobiologia* 651, 291–303.
- Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine, Coast. Shelf Sci.* 58, 25–40.
- Dugan, J.E., Hubbard, D.M., and Page, H. M., 2005. Ecological effects of grooming on exposed sandy beaches in Southern California. Pages 824–826 in California and the World Ocean - Proceedings of the Conference.
- Dugan, J.E., Hubbard, D.M., Page, H.M., Schimel, J.P., 2011. Marine macrophyte wrack inputs and dissolved nutrients in beach sands. *Estuaries Coasts* 34, 839–850.
- Dugan, P., 1981. The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. In: Jone, N.V., Wolff, W.J. (Eds.), *Feeding and Survival Strategies of Estuarine Organisms*. Springer, NY, pp. 251–260.
- Fox, C.H., El-Sabaawi, R., Paquet, P.C., Reimchen, T.E., 2014. Pacific herring *Clupea pallasii* and wrack macrophytes subsidize semi-terrestrial detritivores. *Mar. Ecol. Prog. Ser.* 495, 49–64.
- Guisan, A., Edwards Jr., T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Model.* 157, 89–100.
- Hastie, T.J., Tibshirani, R.J., 1990. *Generalized Additive Models*. CRC Press.
- Heerhartz, S.M., 2013. *Shoreline Armoring Disrupts Marine-terrestrial Connectivity across the Nearshore Ecotone*. Doctoral dissertation. University of Washington, Seattle.
- Heerhartz, S.M., Toft, J.D., Cordell, J.R., Dethier, M.N., Ogston, A.S., 2016. Shoreline armoring in an estuary constrains wrack-associated invertebrate communities. *Estuaries Coasts* 39, 171–188.
- Huijbers, C.M., Schlacher, T.A., McVeigh, R.R., Schoeman, D.S., Olds, A.D., Brown, M.B., Ekanayake, K.B., Weston, M.A., Connolly, R.M., Ferrari, M., 2016. Functional replacement across species pools of vertebrate scavengers separated at a continental scale maintains an ecosystem function. *Funct. Ecol.* 30, 998–1005.
- Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Olds, A.D., Weston, M.A., Connolly, R.M., 2015. Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. *Divers. Distributions* 21, 55–63.
- Huijbers, C.M., Schlacher, T.A., Schoeman, D.S., Weston, M.A., Connolly, R.M., 2013. Urbanisation alters processing of marine carrion on sandy beaches. *Landsc. Urban Plan.* 119, 1–8.
- Ince, R., Hyndes, G.A., Lavery, P.S., Vanderklift, M.A., 2007. Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. *Estuarine, Coast. Shelf Sci.* 74, 77–86.
- Inglis, G., 1989. The colonisation and degradation of stranded *Macrocystis pyrifera* (L.) C. Ag. by the macrofauna of a New Zealand sandy beach. *J. Exp. Mar. Biol. Ecol.* 125, 203–217.
- Jaramillo, E., De La Huz, R., Duarte, C., Contreras, H., 2006. Algal wrack deposits and macroinfaunal arthropods on sandy beaches of the Chilean coast. *Rev. Chil. Hist. Nat.* 79, 337–351.
- Jennings, S.B., Brown, N.D., Sheil, D., 1999. Assessing forest canopies and understory illumination: canopy closure, canopy cover and other measures. *Forestry* 72, 59–74.
- Lastra, M., López, J., Neves, G., 2015. Algal decay, temperature and body size influencing trophic behaviour of wrack consumers in sandy beaches. *Mar. Biol.* 162, 221–233.
- Lastra, M., Page, H.M., Dugan, J.E., Hubbard, D.M., Rodil, I.F., 2008. Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. *Mar. Biol.* 154, 163–174.
- Lastra, M., Schlacher, T.A., Olabarria, C., 2010. Niche segregation in sandy beach animals: an analysis with surface-active peracarid crustaceans on the Atlantic coast of Spain. *Mar. Biol.* 157, 613–625.
- MacMillan, M.R., Quijon, P.A., 2012. Wrack patches and their influence on upper-

- shore macrofaunal abundance in an Atlantic Canada sandy beach system. *J. Sea Res.* 72, 28–37.
- Maguire, G., Cullen, M., Mead, R., 2012. Managing the Hooded Plover in Victoria: a Site by Site Assessment of Threats and Prioritisation of Management Investment on Parks Victoria Managed Land. Report to Parks Victoria, 315 pp.
- Maguire, G.S., Duivenvoorden, A.K., Weston, M.A., Adams, R., 2011. Provision of artificial shelter on beaches is associated with improved shorebird fledging success. *Bird. Conserv. Int.* 21, 172–185.
- Majka, C.G., Shaffer, F., 2008. Beetles (Coleoptera) in the diet of Piping Plovers in the Iles de la Madeleine, Québec, Canada. *Wader Study Group Bull.* 115, 77–83.
- Marchant, S., Higgins, P.J., 1993. Handbook of Australian. In: New Zealand and Antarctic Birds, vol. 2. Oxford University Press, Melbourne.
- Maslo, B., Lockwood, J.L., 2009. Evidence-based decisions on the use of predator enclosures in shorebird conservation. *Biol. Conserv.* 142, 3213–3218.
- McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82, 290–297.
- Meager, J.J., Schlacher, T.A., Nielsen, T., 2012. Humans alter habitat selection of birds on ocean-exposed sandy beaches. *Divers. Distributions* 18, 294–306.
- Mellbrand, K., Lavery, P.S., Hyndes, G., Hambäck, P.A., 2011. Linking land and sea: different pathways for marine subsidies. *Ecosystems* 14, 732–744.
- Morrow, K., Bell, S.S., Tewfik, A., 2014. Variation in ghost crab trophic links on sandy beaches. *Mar. Ecol. Prog. Ser.* 502, 197–206.
- Olabarria, C., Lastra, M., Garrido, J., 2007. Succession of macrofauna on macroalgal wrack of an exposed sandy beach: effects of patch size and site. *Mar. Environ. Res.* 63, 19–40.
- Orr, M., Zimmer, M., Jelinski, D.E., Mews, M., 2005. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. *Ecology* 86, 1496–1507.
- Ricci, S., Colombini, I., Fallaci, M., Scocciati, C., Chelazzi, L., 1998. Arthropods as bioindicators of the red fox foraging activity in a Mediterranean beach-dune system. *J. Arid Environ.* 38, 335–348.
- Rodil, I.F., Lucena-Moya, P., Olabarria, C., Arenas, F., 2015a. Alteration of macroalgal subsidies by climate-associated stressors affects behavior of wrack-reliant beach consumers. *Ecosystems* 18, 428–440.
- Rodil, I.F., Olabarria, C., Lastra, M., Arenas, F., 2015b. Combined effects of wrack identity and solar radiation on associated beach macrofaunal assemblages. *Mar. Ecol. Prog. Ser.* 531, 167–178.
- Rodil, I.F., Olabarria, C., Lastra, M., López, J., 2008. Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. *J. Exp. Mar. Biol. Ecol.* 358, 1–13.
- Rogers, K.G., Rogers, D.I., Weston, M.A., 2014. Prolonged and flexible primary moult overlaps extensively with breeding in beach-nesting Hooded Plovers *Thinornis rubricollis*. *Ibis* 156, 840–849.
- Romanuk, T.N., Levings, C.D., 2010. Reciprocal subsidies and food web pathways leading to chum salmon fry in a temperate marine-terrestrial ecotone. *PLoS One* 5.
- Ruiz-Delgado, M.C., Reyes-Martínez, M.J., Sánchez-Moyano, J.E., López-Pérez, J., García-García, F.J., 2015. Distribution patterns of supralittoral arthropods: wrack deposits as a source of food and refuge on exposed sandy beaches (SW Spain). *Hydrobiologia* 742, 205–219.
- Schlacher, T.A., Strydom, S., Connolly, R.M., 2013a. Multiple scavengers respond rapidly to pulsed carrion resources at the land–ocean interface. *Acta Oecol.* 48, 7–12.
- Schlacher, T.A., Strydom, S., Connolly, R.M., Schoeman, D., 2013b. Donor-control of scavenging food webs at the land-ocean interface. *PLoS One* 8, e68221.
- Schlacher, T.A., Weston, M.A., Lynn, D., Schoeman, D.S., Huijbers, C.M., Olds, A.D., Masters, S., Connolly, R.M., 2015a. Conservation gone to the dogs: when canids rule the beach in small coastal reserves. *Biodivers. Conservation* 24, 493–509.
- Schlacher, T.A., Weston, M.A., Schoeman, D.S., Olds, A.D., Huijbers, C.M., Connolly, R.M., 2015b. Golden opportunities: a horizon scan to expand sandy beach ecology. *Estuar. Coast. Shelf Sci.* 157, 1–6.
- Shaffer, F., Laporte, P., 1994. Diet of Piping Plovers on the Magdalen Islands. *The Wilson Bulletin, Quebec*, pp. 531–536.
- Soares, A.G., Schlacher, T.A., McLachlan, A., 1997. Carbon and nitrogen exchange between sandy beach clams (*Donax serra*) and kelp beds in the Benguela Coastal Upwelling Region. *Mar. Biol.* 127, 657–664.
- Spiller, D.A., Piovia-Scott, J., Wright, A.N., Yang, L.H., Takimoto, G., Schoener, T.W., Iwata, T., 2010. Marine subsidies have multiple effects on coastal food webs. *Ecology* 91, 1424–1434.
- Staine, K.J., Burger, J., 1994. Nocturnal foraging behavior of breeding Piping Plovers (*Charadrius melodus*) in New Jersey. *Auk* 579–587.
- Stapp, P., Polis, G.A., 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia* 134, 496–504.
- Stenton-Dozey, J. M. E., and Griffiths, C. L., 1983. The fauna associated with kelp stranded on a sandy beach. Pages 557–568 in M. A. and T. Erasmus, editors. *Sandy beaches as ecosystems*. Dr. W. Junk, The Hague.
- Tewfik, A., Bell, S.S., McCann, K.S., Morrow, K., 2016. Predator diet and trophic position modified with altered habitat morphology. *PLoS One* 11.
- Weston, M.A., Elgar, M.A., 2005a. Disturbance to brood-rearing Hooded Plover *Thinornis rubricollis*: responses and consequences. *Bird. Conserv. Int.* 15, 193–209.
- Weston, M.A., Elgar, M.A., 2005b. Parental care in hooded plovers (*Thinornis rubricollis*). *Emu* 105, 283–292.
- Weston, M.A., Schlacher, T.A., Lynn, D., 2014. Pro-environmental beach driving is uncommon and ineffective in reducing disturbance to beach-dwelling birds. *Environ. Manag.* 53, 999–1004.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.