

Multiple scavengers respond rapidly to pulsed carrion resources at the land-ocean interface

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Abstract

Sandy beaches are the globe's longest interface region between the oceans and the continents, forming highly permeable boundaries across which material flows readily. Stranded marine carrion supplies a high-quality food source to scavengers, but the role of animal carcasses is generally under-reported in sandy-beach food webs. We examined the response of scavengers to pulsed subsidies in the form of experimental additions of fish carcasses to the dune-beach interface in eastern Australia. Ghost crabs (*Ocypode* spp.) are the dominant invertebrate scavengers in these habitats and they responded strongly and consistently to changed resource availability: densities increased significantly within days of carrion augmentations. Carcasses added experimentally also formed local nuclei for a diversity of vertebrate scavengers that aggregated at food falls; these included large lizards, several species of birds (including raptors), and foxes. Consumption of fish carrion by the vertebrate scavengers was rapid and often complete. There is also evidence for higher-order interactions, where responses of invertebrate scavengers became depressed in plots where vertebrate scavenger activity was intense. Our findings emphasize that carrion can be a pivotal component of beach food webs.

Keywords: carrion; scavengers; ghost crabs; food webs; allochthonous inputs

1. Introduction

Sandy beaches of open coasts form one of the globe's largest interface regions between the sea and the land (Bascom 1980). Their long and highly permeable border with the oceans is crossed by marine matter that drifts ashore with waves, currents and tides, often forming distinct accumulations – strandlines - near the dunes (Barreiro et al. 2011). These strandlines form important structural and functional component of beach ecosystems, including the provision of habitat, food and nutrients (Dugan et al. 2003; Dugan et al. 2011; MacMillan and Quijon 2012).

From an ecosystem perspective, marine organic matter deposited on beaches constitutes a critical dietary input for beach consumers (Colombini and Chelazzi 2003). The importance of such trophic subsidies is predicted to be particularly high for food webs of open-coast beaches for three principal reasons: i) beaches lack attached larger plants and in situ primary production on the unvegetated part of the beach is very low (McLachlan and Brown 2006); ii) marine matter is transported onshore by physical forces (e.g. wind, waves, currents) with little mechanical impedance (Wright and Short 1984), and iii) imported material often accumulates at the base of the foredunes, enhancing its availability as a food resource (Orr et al. 2005; Spiller et al. 2010).

Death of animals is ubiquitous and supplies ecosystems with surprisingly large numbers of animal carcasses generated by non-predation events such as disease and malnutrition (DeVault et al. 2003; Beasley et al. 2012). This rich dietary resource is exploited by a diverse, and abundant assemblage

of scavengers (Houston 1979; Ruxton and Houston 2004). Feeding on carcasses is also more widespread than traditionally acknowledged, and channels substantial amounts of energy through many food webs (Wilson and Wolkovich 2011).

Animal carcasses are part of the spectrum of organic matter stranded on beaches and, as in other ecosystems, are predicted to constitute high-quality food sources exploited by scavengers (Wilson and Wolkovich 2011). Carrion and scavenging are well represented in the literature on sandy shores, spanning a wide taxonomic ambit from gastropods to hyenas (Brown 1982; Skinner et al. 1995). Scavenging on beaches has, however, rarely been contextualised in a broader ecological framework (sensu Beasley et al. 2012).

Fluxes of carrion and other matter between abutting ecosystems constitute important functional linkages in many landscapes (Polis et al. 1997; Schlacher and Connolly 2009). These exchanges also couple production and consumption processes across ecological boundaries, shaping the dynamics and architecture of consumer populations and recipient food webs (Spiller et al. 2010). On sandy shorelines, organic matter of marine provenance is translocated across two ecotones: first, from neritic waters and the surf-zone to the littoral and, secondly, from the littoral to coastal dunes (McLachlan 1991). Movement of material onto the beach is overwhelming by physical vectors, whereas biological vectors are usually more important in translocating marine production to terrestrial consumers and thus systems (Barrett et al. 2005; Mellbrand et al. 2011). These fluxes are largely asymmetrical, with the upland movement of marine matter being the dominant spatial trajectory (Sanchez-Pinero and Polis 2000).

The dependence of sandy-beach food webs on imports of organic matter from the sea (Heymans and McLachlan 1996), and the increasingly recognized importance of carrion and scavenging in many food webs and across ecotones (Wilson and Wolkovich 2011) have led to a conceptual understanding of food webs of open-coast beaches as containing species that have evolved to exploit high-quality carrion efficiently. We tested this prediction experimentally by manipulating the availability of a significant carrion source, fish carcasses, and measuring the response of the key scavenger, ghost crabs (*Ocypode* spp.).

2. Methods

The site for the experiment was an ocean-exposed sandy shore on North Stradbroke Island, in eastern Australia (Fig. 1). The physical habitat characteristics of the beach are typical of much of the subtropical/warm-temperate coast; i.e. intermediate morphodynamic type, waves 1 - 2 m, 5 – 80 m wide beach face, medium sands (Schlacher and Thompson 2007; 2008; Schlacher and Lucrezi 2010).

Carrion supply was experimentally manipulated and the numerical response of beach scavengers measured in 17 experimental plots dispersed over a 3.2 km long stretch of beach (Fig. 1); distance between plots was randomised within a range of 150 to 250 m. Treatments were randomly allocated to plots, with the constraint that not more than two of the same treatment type could abut (Fig. 1). Plots measured 3 m (across-shore) x 10 m (along-shore) following Schlacher and Lucrezi (2010), with the upper edge of plots aligned with the base of the dunes.

Key habitat metrics were highly similar between treatment and control plots: there was no significant difference in mean slope values between treatments ($P = 0.39$, Control: $3.8 \pm 0.8^\circ$; Treatment: $2.9 \pm 0.7^\circ$), in mean grain size ($P = 0.92$; Control: $280 \pm 5 \mu\text{m}$; Treatment: $279 \pm 5 \mu\text{m}$), or in other sediment statistics (sorting: $P = 0.42$, skewness: $P = 0.19$, kurtosis: $P = 0.35$). We therefore consider it highly improbable that outcomes of the experiment were confounded by systematic habitat differences between treatments.

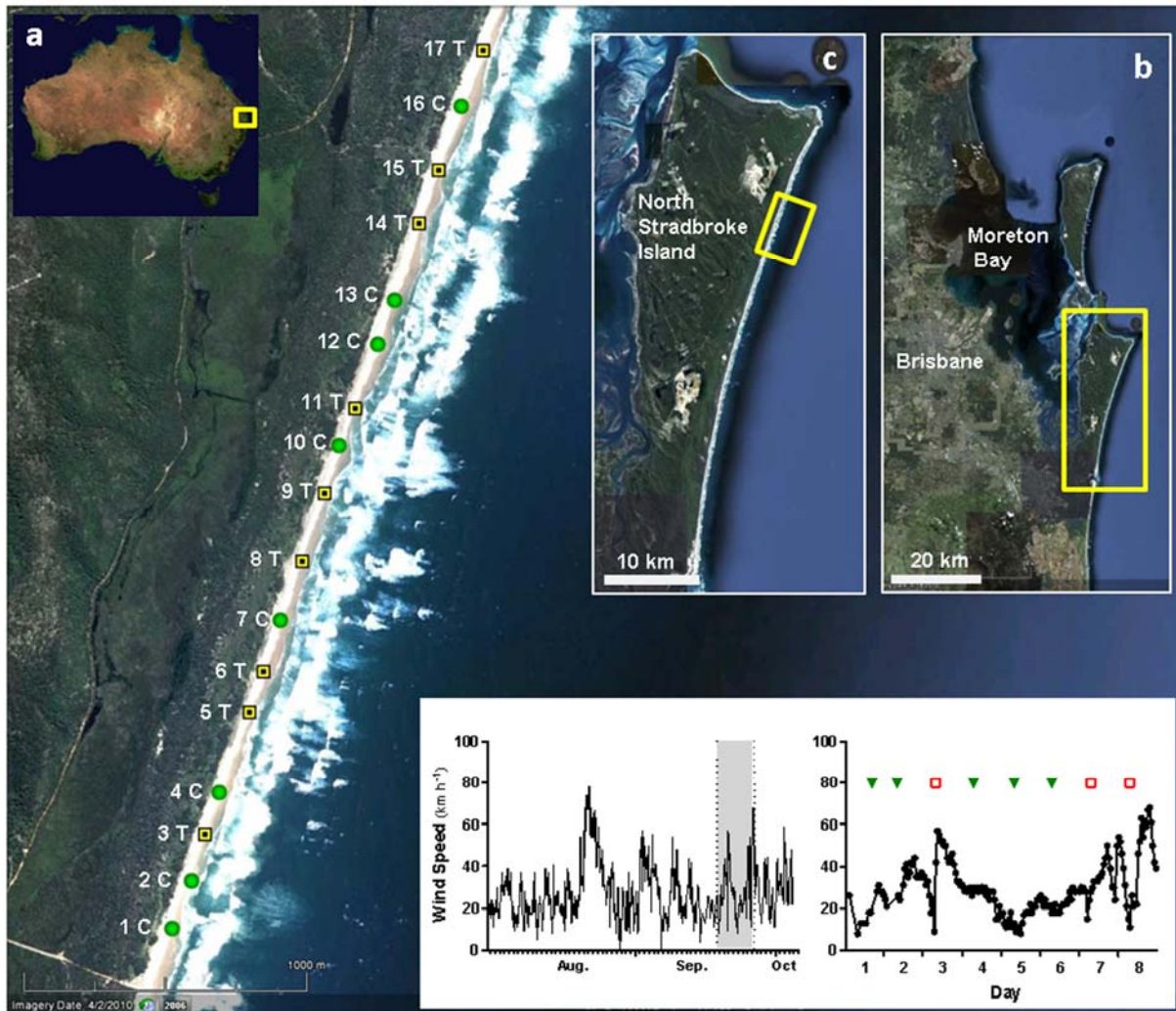


Fig.1 Location of the experiment in eastern Australia (a) on the ocean-exposed beach of North Stradbroke Island (c,b). Main panel shows spatial arrangement of treatment (squares) and control plots (circles). Size of plots not to scale, being 3 m x 10 m. Insert shows wind speeds recorded in the preceding weeks (left panel) and during the experiment. Green arrows: successful burrow counts of ghost crabs; red squares: data discarded on days with strong winds that obliterated burrows.

Carrion was added to the treatment plots in the form of flathead mullet, *Mugil cephalus*. The fish were caught locally in the surf zone by a commercial fisher. They measured 36 cm (TL, \bar{x} = 36.4 cm, se = 0.33, n = 30) and weighed about 500 g (wet weight, \bar{x} = 499 g, se = 9.4, n = 30) and three fish were added to each of the 3 x 10 m treatment plots per day. To achieve greater dispersion of carrion across the plots, each fish was cut into three approximately equal-sized pieces which were scattered haphazardly across the plot, and carrion addition was thus about 1,500 g per day in the form of nine fish pieces. The experiment was conducted over 7 days in the austral summer, from 19 to 26 Sep. 2011. On Day 1, before any manipulation of carrion, sediment samples (three cores per plot) were taken from each plot and the angle of the beach face measured following standard beach survey methods (see Schlacher et al. 2008). Thereafter, carrion was added to the treatment plots (Fig. 1), approximately two hours before sunset, every day for a week. Every morning, within two hours of sunrise, we measured the following variables in each plot: i) number and opening diameter of ghost

crab burrows (see below), ii) number of carrion pieces remaining, and iii) presence of vertebrate scavengers (foxes, birds) or their tracks.

The primary ecological response to carrion augmentation that we measured was the density of ghost crabs. Crab density was quantified via counts of burrow openings on the beach surface, which has become the standard method for abundance estimates in this group of organisms (Schlacher et al. 2011; Noriega et al. 2012). Two species of ghost crabs, *Ocypode ceratophthalma* and *Ocypode cordimana* occur on the beach, but their burrow openings cannot be distinguished with confidence. We therefore report all burrow counts at the genus level (see Schlacher et al. 2007). Strong winds (i.e. > 40 km h⁻¹) on days 2, 7 and 8 obliterated burrow openings and hence these dates were excluded from the numerical analysis.

3. Results

3.1. Invertebrate scavengers

Ghost crab scavengers responded rapidly and strongly to enhanced carrion supply on the beach (Fig. 2; GLM: Day x Treatment $F_{(4,75)} = 7.80$, $P < 0.001$). On day 4, after 3 experimental augmentations of fish carcasses, densities of ghost crabs had increased, on average by 45% and were significantly higher in carrion-treatments than control plots (Fig. 2; $P = 0.034$). Densities of the scavengers continued to increase thereafter, being 75% higher on day 5 ($\Delta_{\text{control/treatment}} = 1.75 \pm 0.19$), and more than double on day 6 of the experiment ($\Delta_{\text{control/treatment}} = 2.13 \pm 0.27$). Conversely, in control plots without experimental food augmentations, crab densities changed comparatively little or declined over the course of the experiment (Fig. 2).

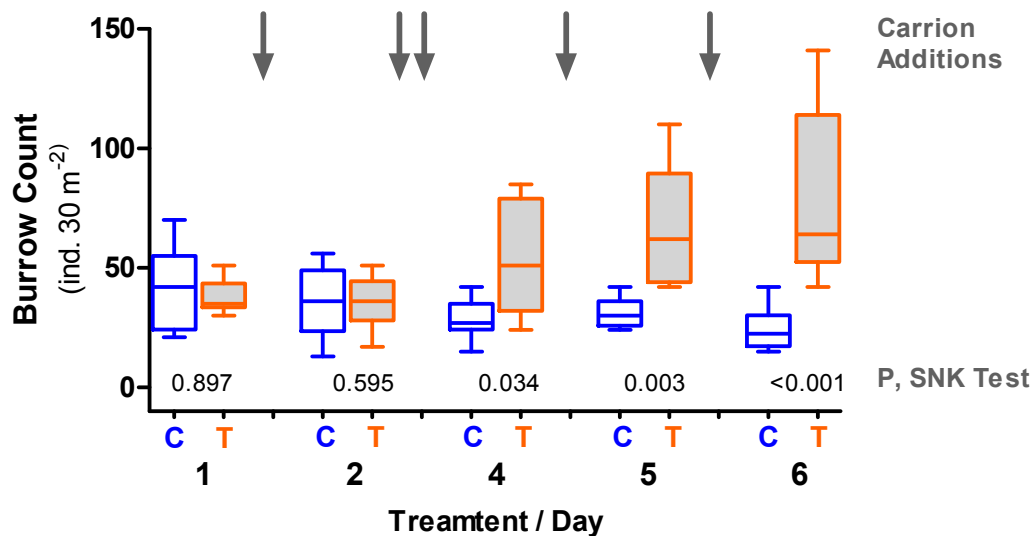


Fig. 2. Effect of pulsed carrion additions on the density of ghost crabs in plots at the base of dunes. The experiment ran for 6 days with carrion (mullet, *Mugil cephalus*) added to plots on 5 days. C = control plots (open bars), T = treatment plots (shaded bars). P values refer to pairwise comparisons (using SNK test) following a significant Time x Treatment interaction term in ANOVA.

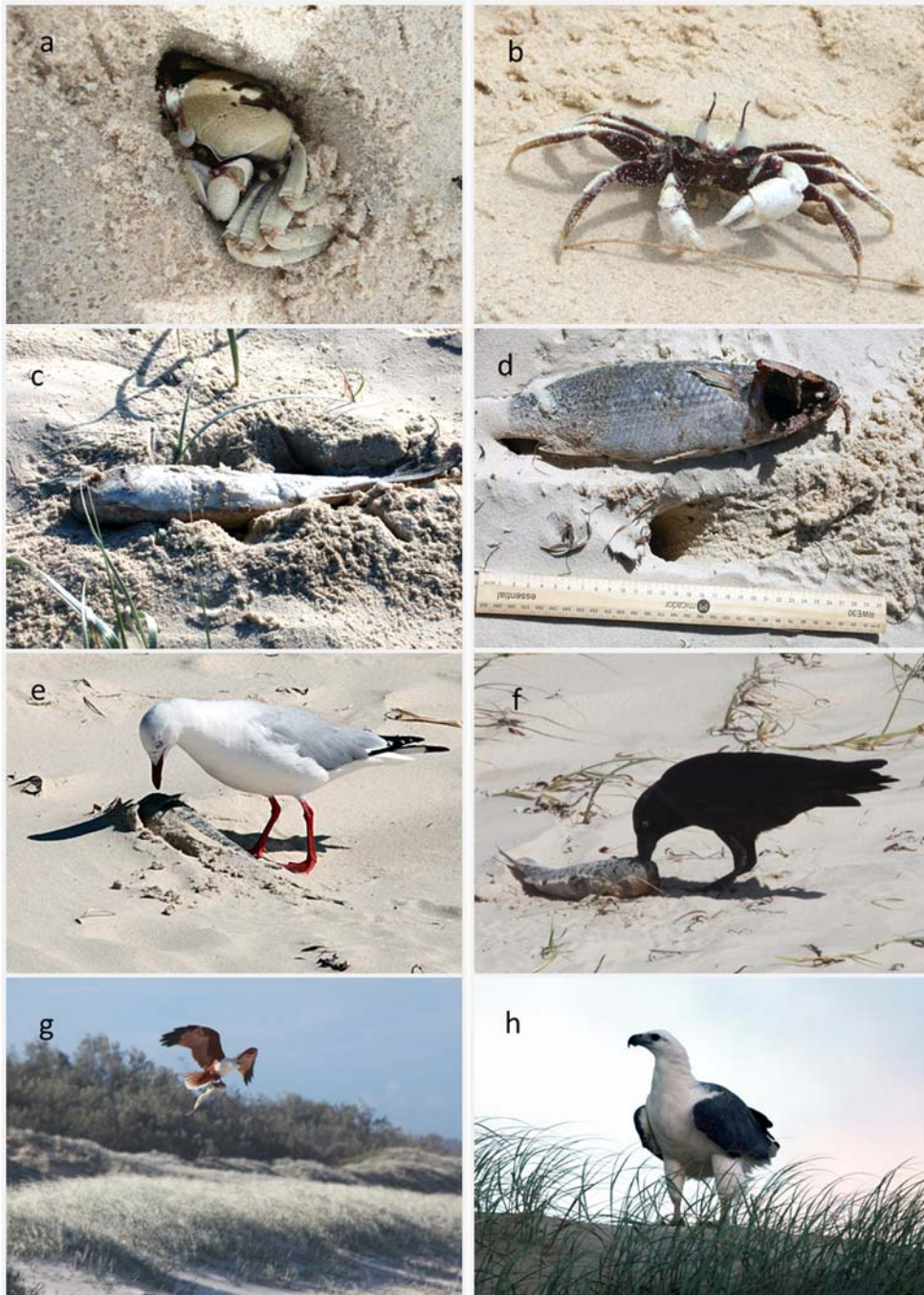


Fig. 3 Ghost crabs and avian scavengers at the beach-dune interface region observed during the study. a) ghost crab (*Ocypode ceratophthalma*) emerging from a burrow and b) active on the beach surface; c) intense burrowing activity of crabs around and under a freshly deposited fish carcass; d) burrow opening of a ghost crab next to a fish carcass showing freshly excavated sediment; e) Silver gull (*Chroicocephalus novaehollandiae*) and f) Torresian crow (*Corvus orro*) feeding on fish carrion; g) Brahminy kite (*Haliastur indus*) lifting a fish carcass from an experimental plot; h) white-bellied sea eagle (*Haliaeetus leucogaster*) perched on the primary dune above an experimental plot to which fish carcasses had been added. All photos T. A. Schlacher.

3.2. Vertebrate scavengers

In addition to ghost crabs, a number of vertebrate scavengers consumed fish carrion in the experimental plots (Table 2, Fig. 3). We directly observed, or recorded prints of, several species of raptors (whistling kite, *Haliastur sphenurus*; Brahminy kite, *Haliastur indus*; white-bellied sea eagle; *Haliaeetus leucogaster*), pied oystercatchers (*Haematopus longirostris*) and silver gulls (*Chroicocephalus novaehollandiae*). Tracks and prints of red foxes (*Vulpes vulpes*) were common, occurring in most plots on most days (Table 1). These vertebrate scavengers had a major impact on carrion during the experiment, as evidenced by: i) of the 324 pieces of fish added to experimental plots over the course of the experiment, all were consumed; ii) in a single night, on average 80% of carrion items were removed (s.e. = 20%), and iii) in two-thirds of plots where carrion was added at dusk, all carcasses had been consumed by the following dawn. These high carrion consumption rates are most probably the result of scavenging by vertebrates for the following reasons: i) we directly observed avian scavengers feeding on carrion in treatment plots, occasionally lifting entire fish off the beach (Fig. 3), ii) fish were too large for ghost crabs to consume them entirely in a single night, and iii) tracks of red foxes converged on carrion pieces and there were clear signs that they had handled the fish carcasses.

Table 1 Occurrence of vertebrate scavengers in the experimental plots, based on either direct observations or tracks/prints left in the sand. Tabulated values are the number of plots (max n = 9) with a positive record.

Vertebrate Scavenger	Day 2	Day 4	Day 5	Day 6	Experiment	
Red fox	6	5	6	6	8	(89%)
Pied oystercatchers	1	2	6	6	8	(89%)
Silver gulls	1	2	4	4	6	(67%)
Raptors (Brahminy kite, whistling kite, white-bellied sea eagle) & crows	2	0	5	4	9	(100%)

3.3. Cascading effects

Vertebrate scavengers modified the numerical response of ghost crab scavengers to enhanced carrion availability (Fig. 4). In experimental plots where raptors, foxes or oystercatchers had been recorded, the abundance of ghost crabs still increased, but by about 20 % less than in plots without these vertebrate scavengers. Higher removal rates of carrion by vertebrate scavengers significantly depressed the aggregative responses of ghost crabs to fish carcasses (Fig. 4).

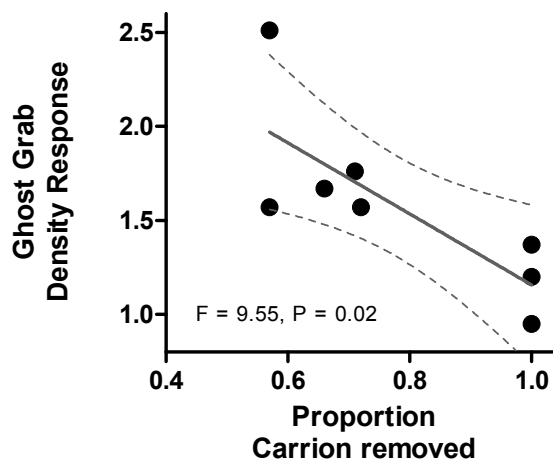


Fig. 4 Numerical response of invertebrate scavengers (ghost crabs) as a function of the proportion of carrion pieces removed by vertebrate scavengers.

Table 2 Examples of published records of carrion and scavengers on beaches.

Scavenger	Carrion type	Location	Reference
Invertebrates			
<i>Whelks (Bullia rhodostoma, B. digitalis)</i>	Cnidarians	Eastern Cape, South Africa	(Brown 1961; 1971; Brown 1982)
<i>Nassarius festivus</i>	Fish carrion	Hong Kong	(Morton and Yuen 2000)
Isopods, Polychaetes, Beetles	Various drift carrion	California, USA	(Dugan et al. 2003)
Ghost crabs (<i>Ocyropsis</i> spp.)	Fish and invertebrates	Eastern Australia, global	This study; (Cott 1929; Wolcott 1978)
Reptiles			
Cottonmouth Snake (<i>Agkistrodon piscivorus conanti</i>)	Various dead fish	Gulf Coast Islands, USA	(Lillywhite and McCleary 2008; Lillywhite et al. 2008)
Birds			
White-Bellied Sea Eagle (<i>Haliaeetus leucogaster</i>)	Various mammals, other birds, fish, crabs	Coastal areas, Australia	(Smith 1985)
Whistling Kite (<i>Haliastur sphenurus</i>)	Various terrestrial and marine animals (rodents, reptiles, fish)	Coastal areas, Australia	(Gosper 1983)
Brahminy Kite (<i>Haliastur indus</i>)	Fish, crabs & other marine carrion	Coastal areas, Australia	(Smith 1992; Lutter et al. 2006)
Mammals			
Coyote (<i>Canis latrans</i>)	Seals, birds, sea turtles, fish, marine arthropods	California, USA	(Rose and Polis 1998)
Tasmanian Devil (<i>Sarcophilus harrisi</i>)	N/A	Tasmania, Australia	(Moore 2002)
Brown Hyena (<i>Parahyaena brunnea</i>)	Seals	Skeleton Coast, Namibia	(Skinner et al. 1995; Kuhn et al. 2008)
Black-backed Jackal (<i>Canus mesomelas</i>)	Seals, birds, fish	Skeleton Coast, Namibia	(Avery et al. 1987)
Dingo (<i>Canis lupus dingo</i>)	Dugong and whale carcasses	Fraser Island, Australia	(Moore 2002)
Lion (<i>Panthera leo</i>)	Seals	Skeleton Coast, Namibia	(Bridgeford 1984)

4. Discussion

Our experimental augmentation of carrion supply demonstrated bottom-up control of consumers, using scavengers as a model on an ocean-exposed sandy beach. Scavengers are a commonly reported component of beach fauna, encompassing a wide diversity of taxa and broad spectrum of carrion types (Table 2). Yet important functional ecological aspects of scavenging remain to be quantified in beach systems, across four broad thematic areas: i) population and community-wide effects of altered carrion resources, ii) the spatial structure of carrion-based food webs on sedimentary shorelines, iii) properties of resource pulses and their influence on scavenger dynamics, and iv) interactions between scavengers.

Our experiment showed a clear aggregative response of scavengers to carrion, significantly changing local densities of consumers to create spatial concentrations of intense feeding along the shore. Although the duration of the experiment did not allow us to measure numerical responses in the populations, these are not implausible for the scavengers examined. Enhanced food resources have been shown to have population-wide consequences for consumers on shorelines, positively affecting reproductive output and population sizes in both invertebrate and vertebrate scavengers benefiting from imports of marine matter (Spiller 1992; Rose and Polis 1998; Roth 2003). Because true numerical responses depend mainly on the generation time of the consumers, these would be predicted to occur within months for ghost crabs, but may take years for raptors (Machant and Higgins 1993). Notwithstanding the time scales required, enhancing local populations of scavenging raptors on shorelines with carrion augmentations offers an opportunity to investigate a potentially novel conservation tool for these threatened species (along the lines of augmented feeding of hen harriers, a vulnerable raptor in the United Kingdom, Thompson et al. 2009).

Aggregative responses of scavengers were distinct in the experimental plots. A central goal of ecology is to derive generalizations about processes that are applicable to broader temporal and spatial scales. In this sense, 'scaling-up' from small-scale field experiments to larger areas will be important (*sensu* Denny and Benedetti-Cecchi 2012). Carrion addition experiments, like the one conducted here, are highly amenable to examine such scale-dependence of ecological processes. At regional scales, the links between scavenger dynamics and their food supply can be determined by manipulating carrion availability among beaches separated sufficiently to avoid mixing of populations (*i.e.* islands or geographically distant beaches). This approach would also lend itself to a still wider scale encompassing latitudinal gradients and different biogeographic provinces, to take account of the putative effect of different taxonomic compositions of scavengers.

Carrion removal in our experiment was rapid and efficient, with most fish carcasses having been completely consumed within a day. This high rate of carrion detection and consumption on beaches rivals, or exceeds, that of other habitats (reviewed by DeVault et al. 2003). It demonstrates that scavengers on beaches are highly adapted to exploit resource bounties in the form of pulsed carrion inputs. More generally, pulsed resources have a major influence on consumer dynamics and food webs across many ecosystems (Yang, L.H. 2010). Factors that modify ecological responses to pulsed resources include the quality, quantity, duration and predictability of the inputs (Yang, L.H. 2008). Although it seems logical to posit that carrion constitutes an unpredictable resource pulse on sandy shores, patterns of marine carrion inputs to beach food webs are essentially unknown. Standing stocks of carrion in the size range of fish carcasses are usually low on beaches. This does not necessarily reflect low inputs of carcasses, but, alternatively, could result from rapid location and consumption of carcasses by efficient scavengers as shown here (see also Rassweiler and Rassweiler 2011).

Ghost crabs aggregated in significantly lower numbers in experimental plots where more intense scavenging activity by birds and foxes had removed more carrion (Fig. 4). This negative relationship between one consumer's response as a function of another consumer's use of a common resource strongly suggests asymmetrical biological interactions between invertebrate and vertebrate scavengers. There are several, interrelated mechanisms that are plausible to explain the observed relationship between smaller aggregative responses of ghost crabs in situations when vertebrate scavengers had removed more of the available carrion: 1.) competition for carrion, resulting in lower food availability to ghost crabs due to removal of carcasses by the competitively dominant vertebrate scavengers, 2.) lower foraging activity of ghost crabs when vertebrate scavengers are more abundant or active, due to higher predation risk for crabs – a trait-mediated effect (*sensu* Werner and Peacor 2003), and/or 3.) predation by birds and foxes of ghost crabs that had aggregated around fish carcasses. Carrion falls and scavengers can profoundly influence predator-prey dynamics and competition (Abrams et al. 1998; Cortés-Avizanda et al. 2009; Berger 2010). Because ghost crabs are

prey for birds on beaches (Schlacher pers. obs.) and vertebrates remove large amounts of carrion, each of the three mechanisms – competition, trait-mediated effects, predation – can operate in this food web. Future experiments that distinguish between multiple biological interactions and determine their interaction strengths in these food webs will be important to determine the structure and dynamics of scavenging food webs at the beach-dune interface.

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