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Human threats to sandy beaches: A meta-analysis of ghost crabs illustrates global anthropogenic impacts.

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ABSTRACT

Beach and coastal dune systems are increasingly subjected to a broad range of anthropogenic pressures that on many shorelines require significant conservation and mitigation interventions. But these interventions require reliable data on the severity and frequency of adverse ecological impacts. Such evidence is often obtained by measuring the response of 'indicator species'.

Ghost crabs are the largest invertebrates inhabiting tropical and subtropical sandy shores and are frequently used to assess human impacts on ocean beaches. Here we present the first global meta-analysis of these impacts, and analyse the design properties and metrics of studies using ghost-crabs in their assessment. This was complemented by a gap analysis to identify thematic areas of anthropogenic pressures on sandy beach ecosystems that are under-represented in the published literature.

Our meta-analysis demonstrates a broad geographic reach, encompassing studies on shores of the Pacific, Indian, and Atlantic Oceans, as well as the South China Sea. It also reveals what are, arguably, two major limitations: i) the near-universal use of proxies (i.e. burrow counts to estimate abundance) at the cost of directly measuring biological traits and bio-markers in the organism itself; and ii) descriptive or correlative study designs that rarely extend beyond a simple 'compare and contrast approach', and hence fail to identify the mechanistic cause(s) of observed contrasts.

Evidence for a historically narrow range of assessed pressures (i.e., chiefly urbanisation, vehicles, beach nourishment, and recreation) is juxtaposed with rich opportunities for the broader integration of ghost crabs as a model taxon in studies of disturbance and impact assessments on ocean beaches. Tangible advances will most likely occur where ghost crabs provide foci for experiments that test specific hypotheses associated with effects of chemical, light and acoustic pollution, as well as the consequences of climate change (e.g. species range shifts).

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1. Introduction

"I'll try you on the shore"

William Shakespeare: Antony and Cleopatra (1606)

Accelerating environmental impacts on ocean beaches and coastal dunes call for effective environmental planning and biological conservation. These interventions should meet two cardinal criteria: 1.) environmental values and conservation goals must be clearly identified for broad and inclusive segments of the population (Harris et al., 2014; Vivian and Schlacher, 2015); and 2.) management decisions must be based on impact assessments that produce defensible and biologically relevant information (Harris et al., 2015).

A sizeable part of this information comes from documenting the response of organisms (at various levels of ecological organisation ranging from individuals to ecosystems) to human activities or anthropogenic habitat change (Defeo et al., 2009; Schlacher et al., 2007a). On ocean shores, a broad range of animals (e.g. benthic invertebrates, birds, marine turtles) has been used to detect biological effects attributed to an equally diverse spectrum of anthropogenic pressures, ranging from vehicle impacts to urbanisation (e.g. Huijbers et al., 2015b; Marshall et al., 2014; Reyes-Martínez et al., 2015; Walker and Schlacher, 2011).

Ghost crabs (Genera *Ocypode* and *Hoplocypode*) are perhaps the most widely-studied invertebrate indicator species on ocean-beaches (e.g. Barros, 2001). Ghost crabs are attractive as ecological indicators for a number of reasons: i) they are widespread in the subtropics and tropics; ii) they occur on both the non-vegetated beaches and in the dunes backing beaches; iii) they are relatively large, often locally abundant, arguably charismatic, and require no specialised tools to sample; iv) their taxonomy is well known and identification not overly difficult; and v) they construct semi-permanent burrows with clearly visible openings at the beach surface (Lucrezi and Schlacher, 2014; Schoeman et al., 2015). It is the fossorial habits of ghost crabs, in particular, that has led to their widespread adoption as ecological indicators, chiefly because estimates of abundance and body size can be made from counts and measurements of burrow sizes without the need to physically collect the organisms (Barros, 2001).

Given the extensive use of ghost crabs as ecological indicators on ocean beaches, a formal review and meta-analysis of this practice is warranted. To this end, here we synthesise the literature and address five broad questions:

1) What are the *types of human pressures* acting on beach-dune systems that have been assessed with ghost crabs?
2.) What is the magnitude of reported ecological *effect sizes* for different stressors?
3.) Which *metrics* (response variables) have been used?
4.) What are the *gaps* in terms of human pressures currently not adequately assessed using ghost crabs?
5.) What *opportunities* exist to advance the use of ghost crabs as ecological indicators on ocean beaches?

2. Methods

Studies that examined the response of ghost crabs to anthropogenic activities (sensu lato) were obtained by first searching the Web of Science, Scopus, and Google Scholar using "ghost crabs" OR "*Ocypode* OR *Hoplocypode* " as key words. From this pool we identified studies reporting on human impact assessments by reading the original documents. Sources from literature searches were supplemented by examining the cited reference lists of publications in hand; this yielded several additional reports from government agencies (e.g. U.S. Fish & Wildlife Service, Natal Parks Board). No filter was applied with respect to the types of impacts. Nevertheless, all studies were required to meet two minimum criteria for inclusion in the meta-analysis: peer-review or an equivalent quality control was likely to have been completed, and quantitative data on changes/differences of at least one response variable could be extracted from a publication (e.g. contrasts in burrow counts between beach sections with and without vehicle traffic). In all cases, we classified the intensity of human use or habitat modification by following the original descriptions provided by the authors of each study, usually representing a 'high impact/use treatment' condition that was compared with a 'low use/reference/control' condition. In most cases it was not possible to quantify or rank the intensity or level of pressure from the original descriptions; hence, all analyses here are performed using a binary classification of 'impact' vs. 'reference', irrespective of differences in impact intensity that may have existed among studies.

We quantified the magnitude of effects on measured ghost crab biological metrics by using the log-response ratio, *ln* R, which is a common statistic of ecological effect sizes in meta-analyses: $ln\ R = \ln(\text{mean}_{\text{impact}}/\text{mean}_{\text{control}})$ (Borenstein et al., 2009). 'Impact' refers to sites or beaches that were categorised by authors as being evidently more influenced by a particular human stressor of interest and hence usually represent values from 'impact' groups or 'treatments'. Conversely, 'control' values usually represent localities where the stressor of interest was judged (by the original study authors) to be substantially less influential or absent and hence represent 'reference conditions' in the context of individual studies. Half of the studies in our database did not report sufficient details on samples sizes, variances, statistical tests used, or P-values; in other papers these statistics could not be reliably extracted or inferred from graphs or tables. These omissions precluded the calculation of standardised effect-size statistics such as Cohen's d and Hedges' g (Harrison, 2011) for the majority of studies. For these reasons, we limit our analysis to unweighted one-sample t-tests of the hypothesis that the mean log-response ratio is 0 (*i.e.*, that there is, on average, no effect; i.e. raw response ratio = 1).

The term 'indicator species' has multiple meanings in ecology and environmental science, with little or no consistency of usage amongst authors. Broadly, five main types of usage can be identified to: 1.) measure the biological responses to anthropogenic stressors, pollutants, human activities, management actions, or restoration efforts (i.e. 'indicator species' are used as biological monitors that are thought to react in predictable ways to changes in the environment) (Carignan and Villard, 2002; Diekmann and Dupré, 1997; Jonsell and Nordlander, 2002; Krmpotić et al., 2015; Siddig et al., 2016); 2.) characterize assemblages or habitats (i.e. 'indicator species' are those that are viewed as 'typical' species, showing consistent fidelity to a set of biological or environmental attributes) (Antonelli et al., 2015; De Cáceres et al., 2010; Dufrêne and Legendre, 1997; Hogle et al., 2015; Hwang et al., 2015; Peterken, 1974; Ricotta et al., 2015; Sarrazin et al., 2015); 3.) reflect more than one process, condition, or biological attribute that may or may not be linked to human interventions (i.e. 'indicator species' serve as multiple proxies, the specific meaning being often dependent on the study context) (Lindenmayer, 1999; Niemi et al., 1997; Regehr and Montevecchi, 1997); 4.) act as surrogates for species that are difficult to detect or sample, or to reflect specific environmental

conditions (i.e. 'indicator species' are functionally closely associated with other species or environmental attributes required by those species) (Pérez-García et al., 2015; Schaefer and Hocking, 2015; Turner and McGraw, 2015; Weaver, 1995); and 5.) serve as surrogates for biodiversity at the assemblage or ecosystem level (i.e. 'indicator species' are surrogates for biological diversity at higher levels of ecological organisation) (Morelli, 2015). Historically, indicator species were often used in the context of biodiversity surrogates or being other proxies, whereas many modern studies predominantly use indicator species to describe habitats or assemblages, or to assess biological effects of environmental change, generally linked to human stressors (Siddig et al., 2016). In this paper the term 'indicator species', as applied to ghost crabs, represents usage to assess anthropogenic threats and environmental change.

3. Results

3.1. Coverage, variables, replication, scale

In terms of geographic provenance, just over half (53%) of studies are from Atlantic beaches, nearly a third from the Pacific (32%), with the remainder coming from the Indian Ocean (13%), and the South China Sea (3%; Table 1, Fig. 1). Papers from Australia (34%) and the USA (32%) make up the bulk of publications examining human impacts on ghost crabs, complemented by significant contributions from Brazil (13%) and South Africa (8%; Table 1). All studies reviewed here were conducted in the tropics (74%) and subtropics (26%), with the average latitude being 26.1° (s = 9.35°; Fig. 1). With respect to usage as an ecological indicator, *Ocypode quadrata* was most often studied (18 studies), followed by *Ocypode cordimanus* (13) and *Ocypode ceratophthalma* (10); other species, including *Hoplocypode occidentalis*, the single species in this genus, are rarely used. Low coverage of species in the literature should, however, not be interpreted as inferring that certain undersampled species perform more poorly as ecological indicators.

The number of response variables measured per study is limited. Most authors measured only one (47%) or two (29%) variables, usually abundance and diameter of burrow openings (Table 1). We also found a surprisingly narrow range of the type of variables measured by authors and a dominance of indirect proxies. Indeed, only four of the 38 studies reviewed by us have measured the response of ghost crabs to human disturbance directly, rather than extrapolating from proxies related to burrow metrics. Schlacher and Lucrezi (2010a) tracked crabs to test whether disturbance by vehicles affected home-range size and habitat use. Body condition of individuals was used to predict the availability and quality of food resources, as this metric indicates altered trophic conditions for ghost crabs, as occurs where food scraps are discarded by campers in coastal dunes abutting beaches (Schlacher et al., 2011a). Wolcott and Wolcott (1984) and Schlacher et al. (2007c) used an experimental approach to measure the rate at which vehicles driven on beaches injure and crush individuals, both whilst crabs were inside burrows at various depths and whilst they were active on the beach surface at night.

All study designs contained some element of spatial replication. On average, five sites were sampled (se = 0.67), ranging up to a maximum of 21 sites (Schlacher et al., 2011a). However, half of the studies sampled fewer than four sites, with ten studies (26%) having sampled two sites only (mostly a classic unreplicated 'compare and contrast' approach), and eight studies (21%) having examined three sites. The mean spatial extent over which sites were dispersed was relatively large at 39 km (se = 11). This statistic is, however, attributable to three studies that had sites extending over 200 km or farther: i) Barros (2001) assessed the effects of seawalls on urban beaches in south-eastern Australia, measuring burrow densities on three beaches dispersed along ca. 310 km of coast; ii) Ocaña et al. (2012) estimated the consequences of coastal

Table 1
Attributes of reviewed publications that measured the response of ghost crabs to human activities or anthropogenic habitat changes on ocean-exposed sandy beaches. (Details for individual publications are provided in Table 1 of the supplementary material).

1 – Geographic distribution

Ocean Basin/Sea (no. studies)				
Atlantic	*Pacific*	*Indian*	*South China Sea*	
20	12	5	1	
Countries (no. studies)				
Australia	*USA*	*Brazil*	*South Africa*	*Others#*
13	12	5	3	5
Latitude (°)				
min	*max*	*mean*	*sd*	
1.30	38.24	26.10	9.35	
Tropics	**Subtropics**			
28	10			

2 – Species

Species	No. studies
O. quadrata	18
O. cordimanus	13
O ceratophthalma	10
O ryderi	4
O. africana	2
O. madagascariensis	2
O. cursor	1

3 – Response metrics

3.1. No. metrics measured per study			
min	max	mean	sd
1	6	1.95	1.27

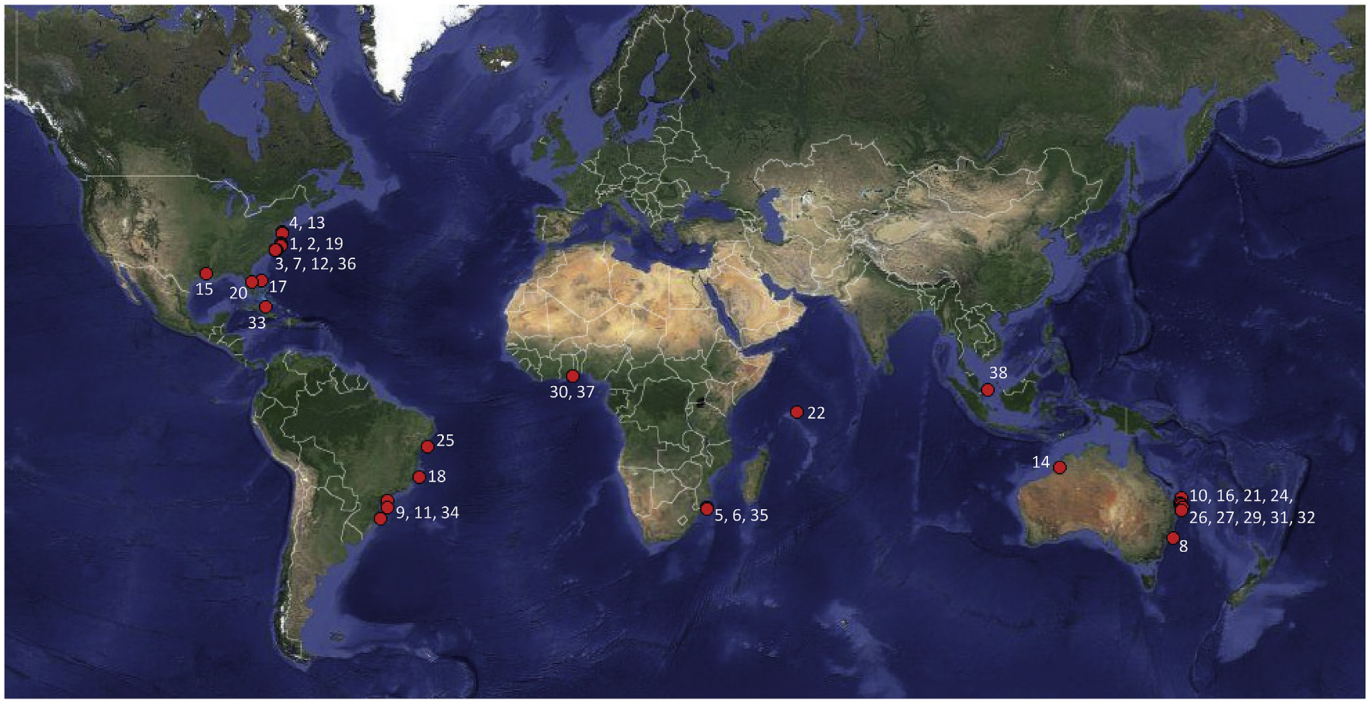
3.2. No. studies using x metrics			
1 Metric	2 Metrics	3 Metrics	>3 Metrics
18	11	6	3

3.3. Types of metrics used			
3.3.1. – Direct (organism)	*No. studies*	*3.3.2. – Indirect (burrows)*	*No. studies*
Mortality	2	Abundance	38
Home range	1	Diameter	19
Body condition	1	Depth	3
Trail length	1	Length	3
Turns in trail	1	Angle	2
		Weight	2
		Orientation	1

4 – Replication and scale

Spatial	min	max	mean	sd
No. sites (n)	2	21	5.16	4.11
Spatial ambit (km)	0.05	310	38.69	66.10
Temporal	min	max	mean	sd
No. times measured (n)	2	27	8.89	6.77
Duration (days)	1	1370	158.47	267.34

Ghana: 2, Cuba: 1, Seychelles: 1, Singapore: 1.



1 - Florschuts & Williamson (1978); 2 - Fisher & Tevesz (1979); 3 - Wolcott & Wolcott (1984); 4 - Christoffers (1986); 5 - McGwynne (1988); 6 –Robertson & Kruger (1995); 7 - Peterson et al. (2000); 8 – Barros (2001); 9 – Blankensteyn (2006); 10 – Moss & McPhee (2006); 11 – Neves & Bemvenuti (2006); 12 – Peterson et al. (2006); 13 – Bisson (2007); 14 - Foster-Smith et al. (2007); 15 – Maccarone & Mathews (2007); 16 – Schlacher et al. (2007); 17 – Barton & Roth (2008); 18 – De Araújo et al. (2008); 19 – Hobbs et al. (2008); 20 – Irlandi & Arnold (2008); 21 – Thompson & Schlacher (2008); 22 – Brook et al. (2009); 23 – Lucrezi et al. (2009a); 24 – Lucrezi et al. (2009b); 25 – Magalhaes et al. (2009); 26 – Lucrezi et al. (2010); 27 – Lucrezi & Schlacher (2010); 28 – Schlacher & Lucrezi (2010a); 29 – Schlacher & Lucrezi (2010b); 30 – Aheto et al. (2011); 31 – Schlacher et al. (2011); 32 – Noriega et al. (2012); 33 – Ocaña et al. (2012); 34 – Guilherme (2013); 35 – Lucrezi et al. (2014); 36 – Peterson et al. (2014); 37 – Jonah et al. (2015); 38 – Lim & Yong (2015)

Fig. 1. Distribution of studies reporting effects of human pressures on ghost crabs on ocean beaches.

development for ghost crabs at eight beaches along 200 km of the NE coast of Cuba; iii) Fisher and Tevesz (1979) worked over a similar spatial range, surveying the response of O. *quadrata* to urbanisation and trampling at 13 sites ranging over 200 km from Cape Henry, Virginia to Cape Hatteras, North Carolina. Notwithstanding a few relatively large-scale designs, half of the studies were completed over less than 15 km. Small-scale (<10 km) studies are not uncommon in the ghost crab literature: 7 papers (18%) sampled sites covering less than 1 km and 15 papers (39%) surveyed sites over less than 10 km.

Ten studies (26%) were 'spot measurements', lacking temporal replication in their design. In studies that made repeated estimates of ghost crab responses, the average number of temporal replicates was 8.89 (se = 1.28), ranging up to 27 temporal replicates (Lucrezi et al., 2010). Studies that were particularly well replicated in time include: Moss and McPhee (2006) assessed vehicle effects on ghost crabs in Eastern Australia (n = 20); Peterson et al. (2014) quantified the consequences of beach nourishment in North Carolina (n = 20); and Irlandi and Arnold (2008) report on nourishment effects in Florida (n = 22). The average duration of temporally replicated impact studies was 180 days (se = 53), and only four studies spanned less than a week. By contrast, the duration of four studies was close to a year or longer: Robertson and Kruger (1995) who gauged the effects of artisanal fisheries on ghost crabs in South Africa (330 days), and Christoffers' (1986) work on the effects of recreational activities at Assateague Island (488 days). The two papers with the longest duration both dealt with nourishment impacts: Irlandi and Arnold (2008) spanning 640 days, and Peterson et al. (2014) lasting 1370 days.

3.2. Effect sizes

The reported responses of ghost crabs to human activities and associated habitat changes on beaches generally show consistently negative impacts of human pressures on the number of burrow openings (a proxy for abundance), but highly variable or non-significant effects on burrow diameter (a proxy for body size; Table 2; Fig. 2).

Response ratios of abundance denote a significant ($t = 6.32$, $df = 36$, $P < 0.001$) mean density decrease ($ln\,R = -1.35 \pm 0.21$se), at impacted locations for all stressors combined (Table 2; Fig. 2); mean response ratios significantly smaller than unity are evident for the effects of vehicles ($ln\,R = -1.42 \pm 0.45$se, $P < 0.01$), nourishment ($ln\,R = -1.27 \pm 0.36$se, $P = 0.038$), and urbanisation ($lnR = -1.52 \pm 0.30$, $P < 0.001$). Fewer individuals associated with more intense human use (e.g. more vehicles or trampling) or greater habitat conversions (e.g. seawalls, development, nourishment) were reported in 35 of the 37 papers that measured abundance (via burrow counts). Of the 26 studies (70%) that undertook some form of statistical test, or adequately described the results of such tests between control and impact conditions, 23 (88%) report significant differences in burrow counts between 'impact' and 'control' sites, 21 studies (81%) reported fewer burrows, whilst only two studies (8%) reported more burrows associated with putative human pressures.

In contrast to the largely significant and negative effects on crab abundance (assessed by proxy using burrow counts), responses of the diameter of burrow openings (a proxy for crab size) are inconsistent, both in terms of the direction and the magnitude of

Table 2
Summary statistics of response ratios *ln* R in ghost crabs, testing the biological effects of human pressures on ocean beaches in terms of changes to the abundance and size of crab burrows. Response ratios, *ln* R, are the log quotient of the mean value at impact sites divided by the mean at reference sites: $ln\ R = mean_{impact}/mean_{control}$ (Borenstein et al., 2009). Values of *ln* R < 0 denote decreases in abundance or size, whilst *ln* R > 0 signifies more or larger burrows at sites classified as 'impacted' by authors. (Tabulated *ln* R values are for stressor assessed by at least three studies; for all full listing of all studies refer to Table S1 and Fig. 2.).

xxx	Abundance (burrow counts)				Size (burrow diameter)			
Stressor	n	mean	(95% CI)	P	n	mean	(95% CI)r	P
All stressors	37	−1.35	(−1.78 to −0.92)	<0.0001	13	−0.15	(−0.35 to 0.05)	0.1327
Vehicles	11	−1.43	(−2.42 to −0.43)	0.0095	5	−0.07	(−0.27 to 0.13)	0.3772
Nourishment	4	−1.27	(−2.41 to −0.13)	0.0378	0	na	na	na
Urbanisation & Recreation	13	−1.52	(−2.16 to −0.87)	0.0003	3	−0.19	(−1.23 to 0.84)	0.5064

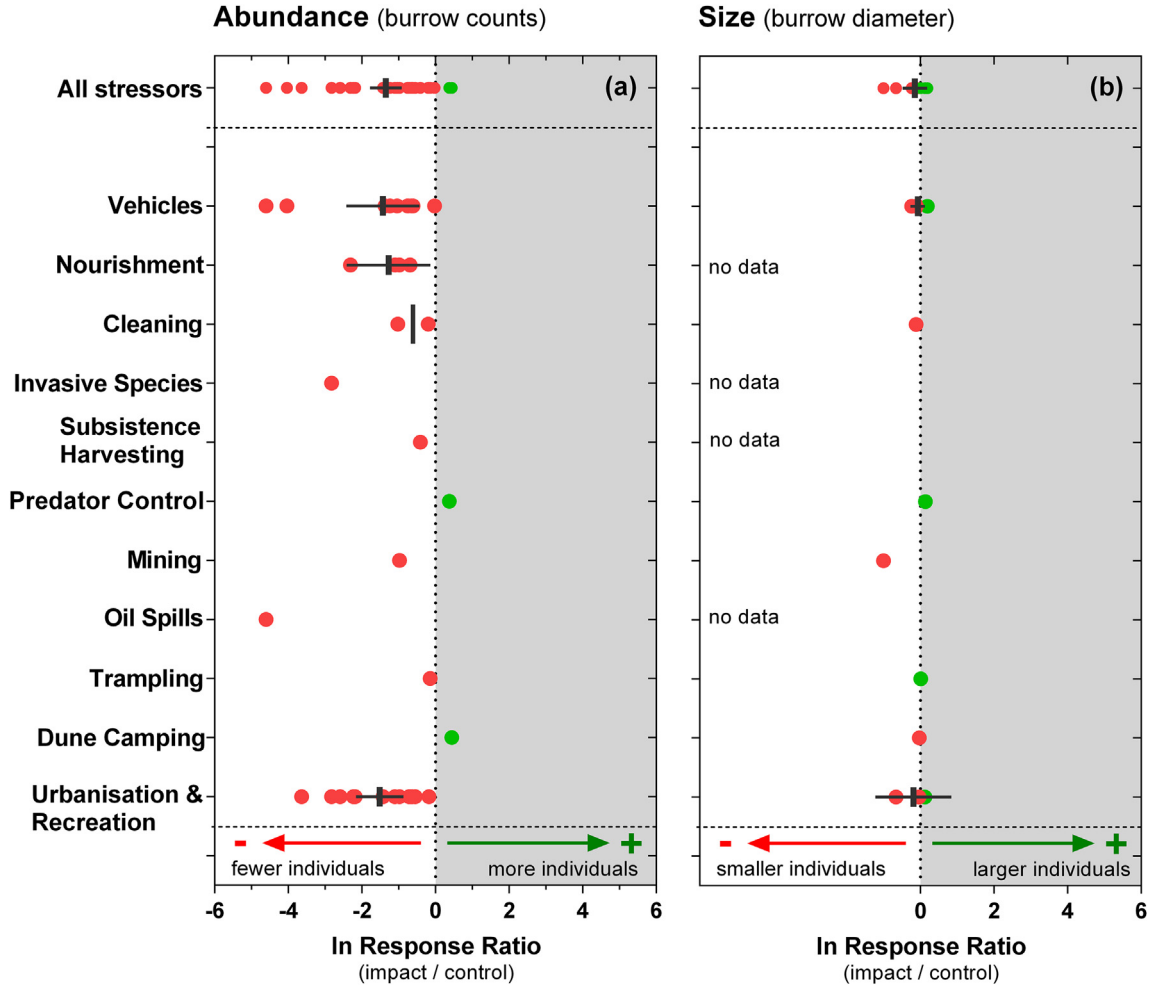


Fig. 2. Effect sizes attributed to different types of human pressures on the abundance (left panel) and size (right panel) of ghost crab burrow openings on ocean beaches. Plotted values are response ratios ln(R), calculated as the log of the quotient of the mean value recorded for impact sites, divided by the mean value at corresponding reference sites in individual studies: $ln\ R = mean_{impact}/mean_{control}$ (Borenstein et al., 2009). Dots represent response ratios from individual studies. Vertical lines are means and horizontal lines are the 95% confidence intervals for data groups with $n \geq 3$.

responses to tested pressures (Table 2, Fig. 2). Although sample size was limited, the mean response ratio ($ln\ R = -0.15 \pm 0.09$) suggests that burrows tended to be slightly smaller at impacted sites. This effect was, however, not consistent among studies. Thirteen out of 38 (34%) studies measured changes in burrow size, which allowed calculation of response ratios. Of these, 12 (92%) tested for differences between mean diameter, with eight reporting significant differences in burrow diameter: two studies document smaller diameter burrows, whilst six document larger ones at impact sites (Table 2, Fig. 2).

Limited (one or two papers depending on the type of pressure) information is available on abundance changes attributable to stressors other than vehicles, nourishment, or urbanisation. Notwithstanding this limitation, lower burrow counts appear to be associated with oil spills ($ln\ R = -4.61$), invasive plants ($ln\ R = -2.81$), subsistence harvesting ($ln\ R = -0.42$), mining ($ln\ R = -0.97$), and trampling ($ln\ R = -0.14$). Conversely, a greater number of burrows have been reported from dune areas frequented by campers ($ln\ R = 0.44$) and following human controls on the crabs' predators (i.e. culling of racoons to protect turtle eggs and hatchlings; $ln\ R = 0.38$) (Barton and Roth, 2008).

The three papers that measured variables other than the

number and diameter of burrow openings report decreases in the extent of daily home range (ln R = −0.80), trail length (ln R = −0.31), burrow depth (ln R = −0.20), burrow volume (ln R = −0.11), and burrow angle (ln R = −0.36). A single paper describes a 50% increase in body condition of crabs collected from camp grounds in dunes relative to reference sites without camping (Schlacher et al., 2011a).

3.3. Addressing pressures: gaps and opportunities

In terms of how ghost crabs can be used to assess ecological effects arising from the main types of human stressors acting on sandy beaches, six clusters emerge based on the degree of missing information ('data deficiency') and the likely reliability of ghost-crabs as indicator species to deliver these data ('suitability') in the future (Table 3, Fig. 3).

1.) Pressures that both lack data regarding their ecological impacts and can be readily addressed using ghost crabs as suitable indicators in future studies: five aspects of pollution (artificial night light, chemical pollutants, marine debris, noise, and sewage) and warming of the atmosphere and oceans associated with climate change.
2.) Pressures that lack data and can be gauged with ghost-crabs, albeit at slightly lower confidence or scope than those in the first cluster: altered current regimes and upwelling under climate change, the effects of invasive algae, and thermal-discharge impacts.
3.) A broad suite of pressures for which some data on their ecological effects do exist (i.e. moderate data deficiency) and for which ghost crabs would be good ecological indicators for future assessments: urbanisation stressors (armouring, urbanisation, grooming), invasive carnivores and dune plants, fisheries and mining impacts, and the consequences of sea-level rise and altered storm regimes.
4.) Three pressures that have both moderate data availability and can be measured with ghost crabs at moderate levels of indicator performance: dune camping, recreational fishing, and trampling.
5.) Ghost crabs are very well suited to assess the biological effects of vehicles and sand nourishment on beaches and this is reflected by an adequate level of available information for these two pressures.
6.) Few or no data currently exist for the biological effects of ocean acidification, altered precipitation, and motorised watercraft in beach systems; however, ghost crabs will rarely be the indicator taxon of first choice in impact assessments targeting these specific stressors (Table 3, Fig. 3).

4. Discussion

4.1. Time for new directions?

A sizeable body of evidence is now available that strengthens arguments for the use of ghost crabs as indicator species to assess the biological and ecological consequences of human activities and habitat changes on sandy beaches (Table 1, Fig. 2). In addition, there is a reasonably broad geographic distribution of published studies (Fig. 1) and coverage of issues (Fig. 2), suggesting that the use of ghost crabs as ecological indicator species is widely applicable and versatile. Much of this reach stems from the ease with which population estimates can be made by counting burrow entrances. However, what is – in a technical sense – a fortuitous trait of ghost crabs, has also led to a prevalence of simple 'compare and contrast designs' that usually fail to measure response variables of the organisms directly, instead relying overwhelmingly on burrow numbers and sizes as proxies (Table 1).

Notwithstanding the broad usage of the technique, there are, in our opinion, five new directions that future environmental studies using ghost crabs should take. 1.) Establishing the mechanistic links that account for observed spatial contrasts ('processes'). 2.) Adopting more diverse designs, especially those that encompass experiments aimed at discerning causality in the relationship between functional responses and the intensity and nature of putative stressors on one hand, and the resulting biological effects on the other ('dose–response studies'). 3.) Separating individual causative agents among suites of putative predictors ('specificity and unconfounding'). 4.) Including modern genetic, bio-chemical and physiological biomarkers and assays that reflect the state of the art in ecotoxicology and behavioural ecology. 5.) Broadening the scope of environmental pressures that are addressed in future impact assessments using ghost-crabs as "canaries in the mine" ('scope and thematic ambit').

Resolving the first four issues above will essentially be a question of aligning ghost-crab studies with modern statistical and ecotoxicological design principles that will yield more robust and reliable attribution and inference. Expanding the thematic ambit to be truly reflective of the diverse nature of anthropogenic stressors acting on sandy beach and dune systems is potentially a very large undertaking, but offers, in our opinion, rich opportunities – we sketch these prospects and their rationale in the following sections.

4.2. Addressing significant anthropogenic beach stressors using ghost crabs as indicators

4.2.1. Climate-change-associated effects: sea-level rise, warming, current and rainfall changes, ocean acidification

Beaches are malleable and dynamic landscapes, responding readily to changes in external physical forcing (Schlacher et al., 2015b). The key physical beach controls that are modified by climate change are accelerated sea-level rise (IPCC, 2013), altered wave and large-scale weather regimes (Barnard et al., 2015; Hemer et al., 2013; Johnson et al., 2015), possibly augmented by storminess (Emanuel, 2013). These can have dramatic impacts on beach and dune geomorphology, resulting in greater erosion and shoreline retreat, and more widespread and frequent coastal flooding during storms (Johnson et al., 2015; Woodruff et al., 2013).

Changes to the beach and coastal morphology attributable to global change can be accurately measured and, in part, predicted (Levin, 2011; Woodruff et al., 2013). However, the ecological consequences of these habitat alterations are less well understood; in this context, ghost crabs can be useful indicators to gauge these consequences. For example, it is possible that local populations of ghost crabs will become extinct in extreme cases of beach or dune erosion, especially where the upper beach habitat near the strandline is lost and where high and persistent beach scarps are formed that block movement of crabs between the non-vegetated beach and the dunes. Local extirpations of invertebrates inhabiting the upper beach and lower dunes have already been reported for Californian beaches under high urbanisation pressure (Hubbard et al., 2014). Ghost crabs may respond in a similar fashion on subtropical and tropical beaches that have undergone recent extreme or repeated erosion events: such effects may be exacerbated by delayed recovery on beaches with seawalls or similar structures on the landward margin (Lucrezi et al., 2010).

Rising temperatures associated with climate change are predicted to cause a broad range of biological and ecological responses in marine organisms, including altered physiology, phenology, demography, behaviour, and shifts in distributions and species ranges (Burrows et al., 2014; García Molinos, 2015; Poloczanska

Table 3
Gap analysis of the application of ghost crabs as indicator species to quantify the ecological consequences of human pressures on ocean beaches and coastal dunes.

Main pressures[a]	Habitat & environmental changes/Effects (predicted)[a]	Expected Response(s) of ghost crabs	Suitability of ghost crabs as Indicator species [b]	Data deficiency (Lack of published evidence for ghost Crabs)[c]
Climate change				
Sea-level rise, storms	Erosion, shoreline retreat, elimination of upper beach and frontal dune habitats.	Population decrease(s), local extirpations, delayed recovery from erosion events, limited recruitment in beaches with (seasonal) scarps.	●●● (good)	ΔΔ (moderate)
Warming	Temperature (increase).	Altered physiology, phenology, demography, geographic range, behaviour.	●●● (good)	ΔΔΔ (high)
Currents, upwelling	Altered organism dispersal, primary productivity, marine carrion availability, wrack deposition.	Changes to recruitment and geographic distribution, altered nutritional status, condition and physiological performance.	●● (acceptable)	ΔΔΔ (high)
Altered precipitation	Changes to dune vegetation, height of water table, thermal environment of sand wedge, aquifer outcrops on beach.	Possibly, altered distribution and population size, but direction and magnitude difficult to predict.	● (poor)	ΔΔΔ (high)
Acidification	Diverse biological effects on marine organisms (e.g. decreased survival, calcification, growth, development, abundance in response to acidification and altered life histories).	Multiple detrimental developmental and survivorship effects during larval (fully marine) phase possible, possibly lowering recruitment to beaches.	● (poor)	ΔΔΔ (high)
Recreation				
Vehicles	Substantially lower habitat quality, direct kills of individuals, behavioural changes.	Lower abundance, altered habitat use, population structure, and behaviour.	●●● (good)	Δ (low)
Trampling	Lower habitat quality, direct kills of individuals, behavioural changes.	Lower abundance, altered habitat use & behaviour.	●● (acceptable)	ΔΔ (moderate)
Camping (dunes)	Increased food resources, altered habitat quality, behavioural changes.	Changed abundance, altered habitat use & behaviour	●● (acceptable)	ΔΔ (moderate)
Motorised watercrafts (jet skis, boats)	Noise and chemical pollution, wildlife strikes.	Altered behaviour and time budgets, toxicity, kills, etc.	● (poor)	ΔΔΔ (high)
Recreational fishing & bait collecting	Population impacts on target species, by-catch, fauna impacts and habitat changes associated with vehicle-based access by fishers.	Individuals crushed by vehicles, food subsidies from fisheries discards.	●● (acceptable)	ΔΔ (moderate)
Pollution				
Sewage and Storm-water	Changes to interstitial chemistry, inputs of toxicants, nutrient enrichment.	Uptake of sewage-derived nutrients and pollutants via direct exposure and food-web transfers.	●●● (good)	ΔΔΔ (high)
Debris	Ingestion (microplastics) or entanglement (larger litter), changes to structural attributes of beach habitat.	Physiological and other health impairment from ingestion of microplastics, altered distribution and higher abundance in areas of abundant larger litter items deposited on shore.	●●● (good)	ΔΔΔ (high)
Thermal discharges	Increased habitat temperature and thermal variability.	Altered recruitment dynamics, possible health effects from anti bio-fouling treatment.	●● (acceptable)	ΔΔΔ (high)
Chemicals	Toxicity from contaminants (e.g. crude oil spills).	Multiple and varied consequences of toxicity, from sub-lethal physiological and behavioural effects to impairment of reproduction and population persistence.	●●● (good)	ΔΔΔ (high)
Noise	Acoustic environment (altered intensity and frequency spectrum).	Behavioural changes, altered behavioural time budgets and predation risks, endocrine disruptions.	●●● (good)	ΔΔΔ (high)
Artificial Night Light	Light environment (altered intensity and frequency spectrum).	Behavioural changes, altered behavioural time budgets and predation risks, endocrine disruptions.	●●● (good)	ΔΔΔ (high)
Urbanisation				
Buildings, infrastructure, roads	Conversion or loss of natural habitat, especially the upper shore and dunes.	Smaller population sizes, shifts in distributions and possibly species interactions.	●●● (good)	ΔΔ (moderate)
Grooming (raking, cleaning)	Habitat losses (upper beach), impedes dune formation, lowers beach stability, fewer food resources.	Smaller population sizes, shifts in distributions and possibly species interactions.	●●● (good)	ΔΔ (moderate)
Nourishment	Mortality of fauna (crushing, burial), reduced habitat suitability.	Smaller population sizes, shifts in distributions and possibly species interactions.	●●● (good)	● (poor)
Armouring (seawalls, groins, revetments, breakwaters)	Loss of habitat, increased rates of beach erosion and habitat instability.	Smaller population sizes, shifts in distributions and possibly species interactions.	●●● (good)	ΔΔ (moderate)
Invasive species				
Exotic predators and feral animals	Predation, possible competition for carrion.	Smaller population sizes, altered population structure	●●● (good)	ΔΔ (moderate)

Table 3 (*continued*)

Main pressures[a]	Habitat & environmental changes/Effects (predicted)[a]	Expected Response(s) of ghost crabs	Suitability of ghost crabs as Indicator species [b]	Data deficiency (Lack of published evidence for ghost Crabs)[c]
Invasive dune plants	Altered habitat quality and stability.	Altered population sizes and/or structure	●●● (good)	ΔΔ (moderate)
Exotic algae and seagrass species	Modified wrack composition and properties.	Unknown, but possibly negative if exotic wrack material lowers habitat use of strandline by ghost crabs.	●● (acceptable)	ΔΔΔ (high)
Fishing and mining				
Fisheries	Overfishing of target species.	Smaller population sizes, altered population structure	●●● (good)	ΔΔ (moderate)
Mining	Contamination and/or loss of habitat, direct mortality, habitat modification through exacerbated erosion.	Smaller population sizes, altered population structure, toxic effects	●●● (good)	ΔΔ (moderate)

[a] Pressures and their environmental effects are adapted from Defeo et al. (2009) and Schlacher et al. (2007a; 2014a; 2008a; 2014b; 2006).

[b] **Suitability as ecological indicator**: ● – POOR (Responses to specific environmental change(s) or human activities **IMPROBABLE** because mechanistic links are biologically implausible or unknown); ●● – ACCEPTABLE (Responses to specific environmental change(s) or human activities PLAUSIBLE, but mechanistic links are incompletely known in many cases); ●●● – GOOD (Responses to specific environmental change(s) or human activities are **PROBABLE IN MOST CASES**, consistent with expectations derived from known biological effects or mechanistic links).

[c] **Data Deficiency (Lack of Published Evidence for Ghost Crabs)**: ΔΔΔ – High (No published information on response(s) to specific pressures); ΔΔ – Moderate (Few (<3) papers documenting response(s) to specific pressures); Δ – Low (Three or more papers documenting response(s) to specific pressures).

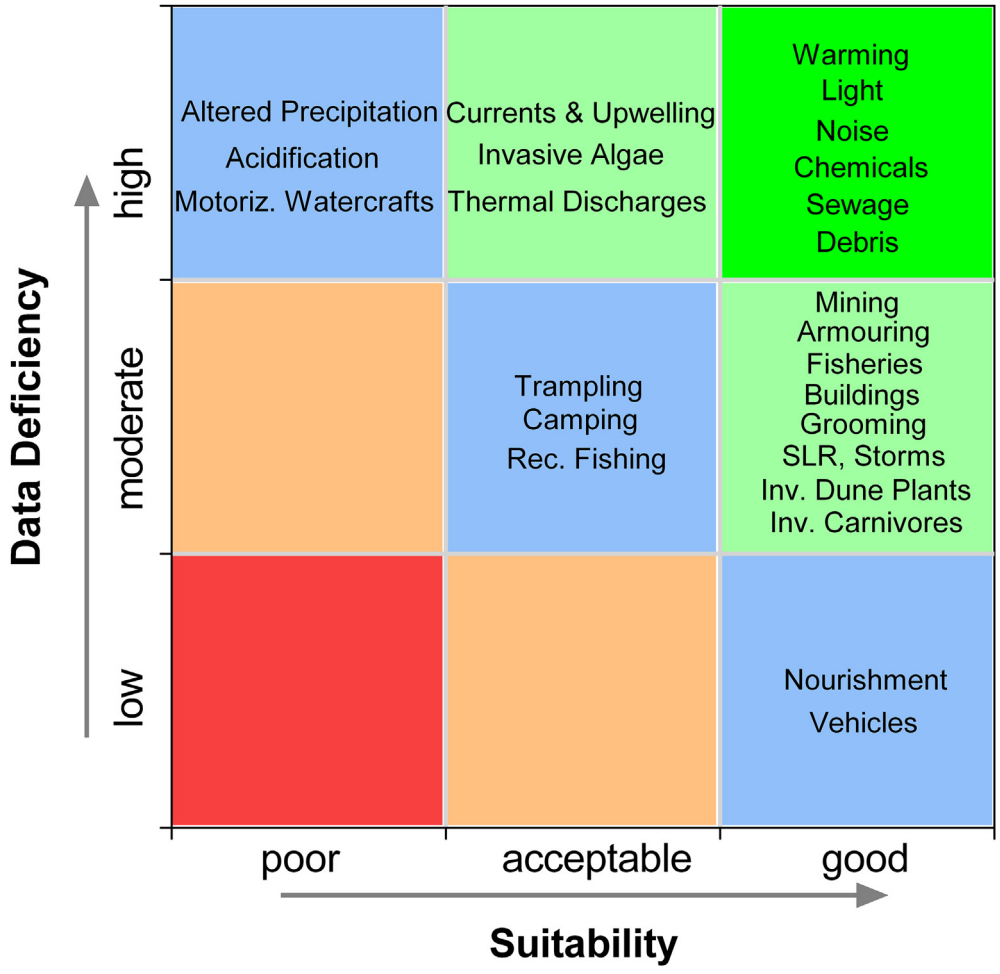


Fig. 3. Classification of ecological impact assessment for specific human pressures with respect to the amount of information that is currently available about their effects on ghost crabs (y axis) and how sensitive and reliable ghost crabs are likely to be as indicator species in impacts studies targeting a particular pressure (x axis). Pressures in the top right are both information-poor (i.e. high data deficiency) and may be best quantified using ghost crabs (i.e. good suitability).

et al., 2013; Sunday et al., 2015). We predict that several of the temperature effects recorded in other marine species at the land–ocean interface will be detectable in ghost crabs, and these can be tested experimentally. In fact, ghost crabs are good model organisms for such tests because they are abundant, widespread, usually not of significant or legal conservation concern, and relatively large bodied. These traits particularly favour their use in physiological studies (laboratory and field-based) and in investigations examining geographic range shifts of beach species (Schoeman et al., 2015). Interestingly, temperature will likely also affect larvae by increasing metabolic and therefore development rates – earlier metamorphsis is likely to result, potentially reducing time in the plankton, and therefore dispersal (Gerber et al., 2014; O'Connor et al., 2009).

Altered oceanographic current regimes and greater variability or intensity in oceanographic forcing, such as upwelling (Black et al., 2014; Sydeman et al., 2014), may affect the dispersal and survivorship of larvae, and are predicted to modify the geographic patterns and magnitude of ghost-crab recruitment onto beaches. It is certainly feasible to measure recruitment dynamics in relation to changes in oceanographic forcing, and this can be combined with genetic work to examine changes in connectivity amongst populations and beaches (e.g. Austin et al., 2015). Effects associated with altered primary productivity, upwelling intensity, or the availability of marine carrion deposited on the shore may be more varied, but some expectations are plausible. Ocean currents, and their nearshore compensatory counter-currents, are more important in terms of dispersal of recruits, whereas storms are more likely to generate wrack and carrion. One interesting exception here is the eastern boundary current upwelling systems, with evidence suggesting upwelling might intensify, and perhaps shift poleward (Sydeman et al., 2014; Wang et al., 2015). Ghost crabs currently do not occur in sizeable numbers on beaches bordering some of the strongest and most persistent eastern boundary upwelling areas, except in the Humboldt (Lucrezi and Schlacher, 2014). Thus, shifts in ghost crab distributions may be a sensitive indicator to gauge the broader ecological impacts of altered upwelling for sedimentary shore ecosystems.

Notwithstanding uncertainties and large geographic variation in response, higher rainfall is possible in response to climate change (Thorpe and Andrews, 2014). Plausible consequences for beach and dune systems are altered dune vegetation (e.g. increased cover, shifts in species composition) and changes in aquifers underlying dunes and beaches (e.g. increased height of water table, wider low-salinity zones in the intertidal, increased discharge of groundwater to surf-zones) (Feagin et al., 2005; Werner et al., 2013). Both are expected to affect ghosts crabs, and several predictive hypotheses can be tested in the future: i) moderate increases in vegetation cover may enhance habitat stability of dunes, leading to increased population abundance of crabs; ii) very dense vegetation, especially species with extensive root networks, will impede burrowing and lead to lower crab abundance; iii) because crabs avoid constructing burrows that reach the water table, higher ground-water levels might limit crab populations (this effect is hypothesized to be strongest at the poleward edge of the range where deep burrows are thought to provide a thermal refuge during winter; Schoeman et al., 2015).

Ocean acidification has profound and varied impacts at multiple levels of biological and ecological organisation; it affects organismal physiology, health, growth, survivorship, and abundance, and these effects can propagate to changes at the assemblage and system scale (Byrne and Przeslawski, 2013; Gaylord et al., 2015; Kroeker et al., 2013; Nagelkerken and Connell, 2015). Acidification is predicted to affect ghost crabs during their larval phase, which could depress recruitment to beaches if growth and/or survivorship are impaired. Recruitment could be monitored, but it is unlikely that this would be considered an efficient variable to measure to assess the effects of ocean acidification in beach ecosystems.

4.2.2. Recreation effects: vehicles, trampling, camping, motorised watercraft, recreational fishing & bait collecting

The environmental impacts of vehicles on beach-dune ecosystems are mostly well documented. A solid body of evidence clearly demonstrates widespread, and often massive, environmental harm caused by vehicles driven on beaches and in dunes, including adverse impacts on ghost crabs (Groom et al., 2007; Moss and McPhee, 2006; Schlacher et al., 2013c; Walker and Schlacher, 2011). Vehicle effects are also among the few stressors for which the *mechanisms* of impacts (i.e. crushing, collisions with wildlife) have been identified or quantified (Schlacher and Lucrezi, 2010b; Schlacher et al., 2007c; Schlacher et al., 2008b). What is generally not known, but of great importance to management and conservation, are the *thresholds* of use (e.g. traffic volumes, allowed vehicle types, distribution across shores) above which negative biological effects rise steeply or become irreversible (Schlacher et al., 2008b). In this context, more and better-designed impact studies that determine the 'dose–response curves' for ghost crabs and other beach species (including charismatic flagship species such as turtles and birds provided that ethical and permitting issues can be overcome for these vertebrates) for a variety of stressors are a critical information gap to inform ecologically responsible management actions.

Trampling is a near-ubiquitous disturbance agent in sandy shore systems, having multiple effects on biota. These effects have been documented for species and assemblages in both the dunes (Brunbjerg et al., 2014) and the non-vegetated beach seawards of the dunes (Reyes-Martínez et al., 2015; Schlacher and Thompson, 2012). Surprisingly, given how common trampling is on many shores worldwide, only a single paper has examined the short-term changes to ghost-crab burrow density and size distribution following intense trampling by people on an urban beach (Lucrezi et al., 2009a). Effects were small and crabs do not appear to be strongly affected by intense trampling over a period of three days (Lucrezi et al., 2009a). Effects may well be stronger if trampling is particularly extreme at small scales (~100 m^2; e.g. beach volleyball games) or sustained over much of the year (Turra et al., 2005). Several papers have ostensibly measured the effects of 'trampling', but tests are invariably confounded with other stressors superimposed at the same site, most often shore armouring and urbanisation of the supratidal and the dunes. Thus, carefully designed studies are needed that separate the impacts caused by trampling from other human pressures.

Camping in coastal dunes close to beaches is a popular leisure activity. Whilst the environmental impacts of 'beach-camping' are likely to be diverse, significant clearing of vegetation and vehicle-associated impacts (e.g. tracks, erosion) are the most prominent and frequent adverse effects. Food discarded by campers can provide additional resources for ghost crabs and other scavengers (Schlacher et al., 2011a); whether this is a benign, positive, or negative practice is debatable and will largely depend on the population of scavengers that is 'subsidised' (i.e. larger numbers of crows, foxes, or racoons attracted to campground are predicted to increase predation pressure on ground-nesting shorebirds and possibly also on ghost crabs). Populations of ghost crabs in dunes are negatively impacted by vehicle tracks (Schlacher et al., 2011a), whilst benefiting – in terms of better body condition – from food subsidies (Schlacher et al., 2011a). This illustrates that applications of ghost crabs in environmental assessments can fruitfully extend beyond simple burrow counts. For example, they may encompass tissue stable isotope measurements to test for the uptake of fecal

matter deposited by beach campers or the tissue analysis of hydrocarbons typical of off-road vehicle emissions (Schlacher pers. obs.).

The use of personal motorised watercraft (e.g. jet skis, water scooters, inflatable boats) in the surf-zone is a popular leisure activity globally. However, there are numerous, often severe, environmental consequences arising from this practice, poignantly summarised by Josephson (2007): "*These machines cannot be operated without loss of life or habitat*". Broad types of environmental impacts encompass direct strikes on wildlife, bioacoustic impacts on fauna, chemical pollution (fuel spillages, exhaust emissions, antifouling paints), and alterations to wave climates and turbidity (Erbe, 2013; Whitfield and Becker, 2014). Ghost crabs generally enter the surf-zone only when gravid females release eggs in the swash. Thus, impacts of watercraft on ghost crabs are expected to be much smaller than for truly marine species (e.g. mammals, fish, and seabirds). However, chemical pollution arising from motorised watercraft may be evident, as may be habitat changes from enhanced wave-driven beach erosion, crushing of crabs during launching and retrieval of boats and jet skis, and bioacoustic impacts.

Beaches, especially their surf-zones, are important sites for coastal fisheries (Gutiérrez et al., 2011; McLachlan et al., 1996). Many beach fisheries are small-scale (artisanal, subsistence), particularly in less-developed countries, but recreational angling is widespread irrespective of socio-economic conditions (Sowman, 2006). Where ghost crabs are harvested as part of subsistence fisheries, they are susceptible to population impacts that can be measured using standard fishery-assessment techniques (Kyle et al., 1997). On beaches without direct harvests of ghost crabs, ecological impacts caused by fishing may still be detectable. Because a large fraction (on some beaches the vast majority) of beach vehicle traffic is attributable to recreational fishers, impacts on ghost crabs often arise indirectly from shore-based angling via vehicles. Discards of bait, by-catch, and fish frames are readily consumed by birds on beaches (Rees et al., 2014). Consequently, it is possible that carrion subsidies provided by fisherman enhance food intake in ghost crabs in similar ways. Arguably, this may be a positive effect. Conversely, discarded fishing line may kill individuals that become entangled in it. Hypotheses concerning impacts of carrion subsidy or fishing-line mortality have not been tested for ghost crabs to date.

4.2.3. *Pollution: sewage and storm-water, debris, thermal discharges, chemicals, noise, artificial night light*

Contamination of beaches with sewage and storm-water is a worldwide problem. The issue is regularly managed for human health risks (Brownell et al., 2007; Sabino et al., 2014), but very rarely in the context of its biological impacts (Mearns et al., 2014; Schlacher et al., 2006). Disregarding the broader environmental consequences of sewage inputs to dunes and beaches ignores, however, the facts that transfers of sewage-derived matter to beach invertebrates has been demonstrated on ocean shores (Schlacher and Connolly, 2009), and that wastewater can have numerous detrimental impacts on the health of organisms (Ings et al., 2012; Schlacher et al., 2007b). Ghost crabs are likely to be exposed to human waste material via direct contact with solid waste and via water-borne material contained in the aquifer and, to a small degree, the swash. Because pathogens (viruses, bacteria, fungi) and xenobiotics are not restricted to the water, but are also found in beach sands (Sabino et al., 2014), the intense contact of crabs with the sediment during burrow construction and maintenance and feeding, increases the likelihood of exposure, uptake, and detrimental effects. A broad arsenal of biomarkers (e.g. genetic, hormonal, immunological, cytological, enzymatic, histological) is available to assess such health effects (e.g. Gillis et al., 2014), but surprisingly, biomarkers in ghost crabs have not been used for ecological assessments; this line of enquiry thus offers multiple opportunities to better assess the status of dune and beach systems in biologically more meaningful ways using a suite of different biomarkers.

Man-made debris, mostly plastics, is now one of the most common, widespread and persistent pollutants in marine waters and beaches worldwide (Moore, 2008). The last decade has seen an exponential rise in the number of scientific papers examining the biological impacts of marine debris, reflecting a growing recognition of severe environmental harm arising mostly from plastics (Gall and Thompson, 2015). Detrimental effects of larger marine debris on marine wildlife are often dramatic (e.g. whales entangled in fishing nets, turtles succumbing from ingested plastic bags, seabirds ingesting large volumes of floating plastics) (Vegter et al., 2014). Evidence is also rapidly accumulating that smaller debris, microplastics (<5 mm), has equally deleterious effects in a broad range of marine organisms, ranging from toxicant magnification to incorporation of microspheres into consumers' tissues (Ivar Do Sul and Costa, 2014; Law and Thompson, 2014). Beaches are deposition sites for floating marine debris, accumulating both larger litter items and high concentrations of microplastics up to 2 m deep into the sediments (Fisner et al., 2013; Turra et al., 2014). Alarmingly, beach deposits can contain the toxic break-down products of styrofoam in large quantities (Kwon et al., 2015).

Accurately measuring and predicting the environmental risks that marine debris poses for wildlife is a research priority for beaches and beyond (Brennecke et al., 2015; Vegter et al., 2014). Because beaches are prime sites for accumulation of debris, they are ideal model sites to test the ecological effects of debris. These effects are likely to differ between larger litter items and microplastics (Law and Thompson, 2014). Hypothetically, large debris may add habitat complexity and heterogeneity to beach environments and increase sediment stability at small, patchy scales; these habitat modifications may propagate to greater abundance and/or longevity of crab burrows and other invertebrates. Conversely, ingestion and tissue transfer of microplastics and associated toxicants by ghost crabs is possible (Brennecke et al., 2015), with potential knock-on effects on the health and fitness of organisms that may propagate to impacts (untested) at the assemblage and system level (Brennecke et al., 2015; Browne et al., 2015).

The few available studies on the ecological effects of marine debris are often correlational or lack empirical data on mechanisms, making the interpretation of reported conclusions somewhat problematic (Browne et al., 2015). We propose that ghost crabs are suitable organisms to undertake such experiments on biological debris effects, given that their distribution overlaps with the stranding zone of most marine debris and that they can be relatively easily manipulated and enumerated in experiments (e.g. Schlacher et al., 2007c).

In addition to the global effects of climate change, localised human modifications to the thermal environment in coastal areas arise mainly from discharges of cooling water required in power plants, typically at temperatures 8–12.5 °C above the intake water (Wither et al., 2012). Altered temperature affects the behaviour, phenology, distribution, reproduction and movement of many marine organisms subjected to thermal effluents (Mazik et al., 2013; Wither et al., 2012). On beaches, patterns of surf-clam abundance on a shore subjected to thermal discharge were broadly suggestive that a localised density effect may be possible (Hussain et al., 2010), but attribution was highly uncertain, and impacts on high-energy coasts are likely to be limited to 100s of metres (Cardoso-Mohedano et al., 2015). Because ghost crabs rarely enter the swash post settlement they are not routinely exposed for

significant periods to thermal discharges where these occur in the surf-zone of beaches. Hence ghost crabs are unlikely to show strong and persistent temperature responses to this particular stressor. It is possible, however, that thermal plumes may modify larval behaviour, dispersal, and recruitment to beaches. Also, traces of biocides (added to cooling water to prevent bio-fouling) may have broader effects on the condition of exposed individuals close to discharge points (Mazik et al., 2013).

Chemical contaminants, toxicants, and xenobiotics are a major class of anthropogenic stressor in marine ecosystems. The biological effects, and their ecological ramifications, of chemical contaminants are as diverse as their sources, and new threats are continually being identified (Mearns et al., 2014). The issue of chemical pollution in dune-beach systems is treated very cursorily (Defeo et al., 2009; Nel et al., 2014); however, there is no reason to suspect that species and dune-beach ecosystems are less susceptible to inputs of toxic chemicals than other marine ecosystems. The one exception to the dearth of data on chemical pollution effects in beach systems is crude oil spills. Probably due to the high public profile of spill events, short-term ecological changes in beach systems following shipping accidents and well failures have been reported for several incidents globally (de la Huz et al., 2005; Engel and Gupta, 2014; Schlacher et al., 2011b; Stevens et al., 2012), although questions about recovery remain mostly unanswered (Peterson et al., 2003). The biological impacts of many chemicals are truly global, but they are often most evident near cities in developed countries. Ghost crabs occur regularly in dunes and beaches in and near coastal cities, making them appropriate sentinel species to monitor ecological effects in these settings. Also, ghost crabs are the apex invertebrate predators on sandy shores, creating opportunities to measure chemical contaminant transfers through food webs. How oil spills affect ghost crabs has also not been quantified, representing an obvious opportunity to include them in future spill assessments. Furthermore, ghost crabs may directly consume toxic flakes of antifouling paint where small boats are scrapped and re-painted directly on the beach.

Humans emit a range of chemical and physical stimuli that disturb animals and interfere with the perceptual processing of important signals and cues, creating sensory pollution in many ecosystems (Halfwerk and Slabbekoorn, 2015). Man-made noises have become near ubiquitous (Radford et al., 2014), creating an acoustic environment that presents novel challenges to many animal species (Morley et al., 2014; Shannon et al., 2015). Whilst the biological effects arising in this altered acoustic landscape are manifold, they most often encompass shifts in physiology (e.g. impaired hearing, elevated stress hormone levels), changes to key behaviours (e.g. foraging, mating, vigilance, movement), interference with the ability to detect important natural sounds (e.g. vocalisations of conspecifics, acoustic signals of prey or predators), and direct fitness consequences (e.g. survival, reproduction) (Morley et al., 2014; Shannon et al., 2015). Vertebrates (especially birds, mammals and fish) are by the far most-studied group in terms of noise pollution, but impacts are equally detectable – and arguably of comparable biological significance – in invertebrates (Morley et al., 2014).

Hearing and sound production in brachyuran crabs provides essential environmental information (Hughes et al., 2014) and facilitates channels for communication, which can be in the form of elaborate audio–visual displays in ghost crabs (Clayton, 2008). Crabs are also sensitive to noise pollution, detectable as physiological stress (Wale et al., 2013b), altered development (Pine et al., 2012), shifts in foraging behaviour (Wale et al., 2013a), or impaired predator avoidance (Chan et al., 2010). Contemporary beach and dune habitats present strongly altered acoustic landscapes for ghost crabs and other species, so the potential exists for biological and ecological impacts arising from man-made noise in sandy shore systems.

Two aspects of ghost crab biology appear particularly intriguing to us in the context of assessing noise pollution on beaches: behavioural shifts in responses to predation risks as a result of altered acoustic landscapes and distorted acoustic settlement cues. Man-made noise can reduce an animal's fitness by impairing its ability to respond normally to a potential predator; such altered risk assessment to predation has been experimentally demonstrated for hermit crabs exposed to boat noise (Chan et al., 2010). Significantly, hermit crabs share several traits with ghost crabs, most notably being conspicuous, semi-terrestrial animals displaying a distinct predator avoidance behaviour that relies on hiding (hermit crabs retreat into their shells whilst ghost crabs flee into their burrows). This offers the intriguing possibility of assessing noise pollution in beach animals using 'behavioural acoustic bioassays' in ghost crabs. Because brachyuran shore crabs use habitat-specific acoustic cues for settlement, acoustic sensory pollution may impact on recruitment intensity and patterns, as suggested for estuarine crabs based on limited lab experiments (Pine et al., 2012). It is possible, but untested, that noise from personal watercraft may interfere with settlement cues important for late-stage larvae of ghost crabs in the surf-zone off beaches. Anthropogenic noise may also mask the acoustic signals produced by prey that predators use during foraging (Halfwerk and Slabbekoorn, 2015). Ghost crabs are omnivorous predators and scavengers of catholic tastes (Lucrezi and Schlacher, 2014), and it is thus possible, but untested, that prey detection and foraging efficiency in ghost crabs in altered acoustic landscapes changes – this offers intriguing possibilities for acoustic bio-assays.

Global light regimes have changed profoundly in intensity, spectral signatures, spatial patterns, and periodicity (Kyba et al., 2015). Such changes to the light environment experienced by organisms are amplified in the coastal fringe where a growing part of the human population is concentrated in expanding coastal cities (Davies et al., 2014). How organisms respond to these new illumination domains created by artificial night light, and the ecological ramifications of their responses, are equally profound; they include changes to gene expression, physiology, behaviour, distributions, and the composition of communities (Davies et al., 2015; Gaston et al., 2013, 2014).

The adverse effects of artificial night light on beach biota are well publicised for marine turtles: fewer nests generally occur on more brightly lit sections of sandy coasts where hatchlings become disorientated by shore-based lights (Kamrowski et al., 2014; Mazor et al., 2013; Verutes et al., 2014). With the exception of a single study on beach mice, impacts of artificial night light on other beach species, including ghost crabs remain untested, but are certainly plausible. For example, navigation in mobile beach invertebrates (e.g. amphipods, isopods) can be complex and relies on multiple cues that can include moonlight. It follows that artificial night light has the potential to disrupt orientation and movement in sandy-shore animals (Scapini, 2014); it is not known whether ghost crabs also use light cues to orient (e.g. homing behaviour), but effects of light pollution on movement and orientation cannot be precluded and hence could be measured using behavioural assays.

Moonlight is important in determining activity in many animal species, mainly related to changes in predation risk and reproductive cycles (Kronfeld-Schor et al., 2013). Many beaches are artificially illuminated at night (in addition to the more diffuse but widespread skyglow) potentially interfering with natural cycles of lunar signals that are particularly important in nocturnally-foraging species. In beach mice, nocturnal movement is modulated by moon phases, presumably in response to higher predation risk during full-moon nights (Wilkinson et al., 2013). Consequently,

beach mice exposed to artificial light feed significantly less and exploit fewer food patches (Bird et al., 2004). Ghost crabs have a functionally similar foraging behaviour (i.e. regular nocturnal excursion from burrows). Their foraging behaviour and activity rhythms may therefore be equally sensitive to artificial light at night and could possibly have fitness implications (e.g. body condition, fertility etc.). Artificial light may also extend the foraging window of visually-orientated predators into the nocturnal activity period of ghost crabs, and facilitate prey detection by both native consumers (e.g. shorebirds) and feral or invasive carnivores (e.g. foxes, cats). Thus, changes to foraging behaviour and predation risk in ghost crabs that are associated with artificial night light could be used to gauge the biological implications of light pollution in sandy shore species.

4.2.4. 'Urbanisation': buildings, grooming, armouring, nourishment

At least half of the global human population lives in cities, and these urban populations will grow exponentially in the coming decades, fuelling an escalating expansion of cities globally, many of which border the ocean (Seto et al., 2012; Strauss et al., 2015). Coastal cities are hotspots of current and future urbanisation, including in Australia, where most (>80%) of the population is concentrated in urban centres, which are mostly located near beaches (Hallegatte et al., 2013). Pervasive ecological changes in cities commonly include biotic homogenisation, biodiversity declines, altered population dynamics of species, and shifts in the species composition of assemblages (Aronson et al., 2014; Sol et al., 2014).

Because beaches represent highly attractive and valuable nodes for coastal development, coastal urbanisation is frequently intense along sandy coastlines (Mills et al., in press; Nordstrom et al., 2000). The ecological ramifications of this 'beach urbanisation' span a broad ambit of reported impacts, ranging from impediments to turtle nesting to local extirpations of invertebrates and functional losses of key vertebrate groups (Hubbard et al., 2014; Huijbers et al., 2015b, 2013; Schlacher et al., 2015a). 'Urbanisation effects' have also been reported for ghost crabs in several urban beach studies (e.g. Barros, 2001). Except for a few isolated cases (e.g. habitat loss caused by urban seawall construction; Dugan et al., 2008), the underlying causes and mechanisms that produce the observed biological responses to urbanisation remain, however, largely unresolved. Failures to isolate, and mechanistically explain, the causative stressors in urban beach studies arise either from employing inadequate study designs, or simply reflect the multiple nature of man-made pressures in these environments where noise pollution, artificial night light, shore-defences, trampling, grooming, and nourishment often coincide in space and time (Acuña and Jaramillo, 2015). From a conservation perspective it is, however, critical to resolve which of the putative factors causes the most environmental harm, as this will guide prioritisation of management interventions. It is also unknown how, and to which degree, these urban pressures interact to produce the observed ecological effects on urban beaches (but see Lucrezi et al., 2010).

Many urban beaches are regularly cleaned ('groomed' or 'raked') to remove beach-cast algae and seagrass ('wrack') and litter, mainly for aesthetic and public-health reasons. Wrack constitutes, however, an important habitat and food resource in beach ecosystems (Colombini and Chelazzi, 2003). Consequently, beach cleaning operations have multiple ecological flow-on effects: loss of upper beach habitat and strandline vegetation (Dugan and Hubbard, 2010); reduced abundance and diversity of invertebrates reliant on wrack (Gilburn, 2012; Llewellyn and Shackley, 1996); and diminished abundance, density, and fitness of beach-nesting birds and beach-spawning fishes (Dugan et al., 2003; Martin et al., 2006; Pietrelli and Biondi, 2012).

Beach cleaning targets mainly the upper shore, which is the main habitat of ghost crabs. Expectations are therefore that cleaning will adversely impact ghost crabs, but this has not been explicitly tested. From a management perspective, it will be important to develop best practices for beach cleaning operations (assuming a continued public mandate to clean beaches) that reduce ecological impacts; in this context, 'dose–response' type studies using ghost crabs, combined with experiments that compare techniques and procedures (e.g. manual removal, different equipment, depth of raking, etc.) in terms of their ecological impacts will be useful. Since abundance estimates for ghost crabs via counts of burrows are less costly than sampling other beach invertebrate, they provide an advantage by allowing more treatment types and replication levels.

Shoreline recession is a major risk to public and private assets located on eroding sedimentary coastlines (Johnson et al., 2015). Conventional approaches to combat beach erosion are to replace the lost sand volumes ('dredge-and-fill', 'nourishment') or to stabilise shore position with fixed, hard structures ('seawalls', 'shore armouring'). With respect to adverse environmental impacts, nourishment has traditionally been viewed as a less harmful option than armouring, but adverse ecological outcomes of beach filling are not uncommon. These include significant reductions in the abundance of infaunal organisms, resulting from a combination of limited recruitment, unsuitable new sediment, and direct mortality from crushing and burial (Manning et al., 2014; Peterson et al., 2006). Impacts of nourishment on invertebrates propagate upwards to shorebirds and fishes through loss of prey organisms and deteriorating feeding conditions on nourished beaches (Manning et al., 2013; Peterson et al., 2006). These effects can be long-lasting, with recovery from nourishment impacts taking several years or longer (Peterson et al., 2014; Schlacher et al., 2012).

Nourishment impacts are well documented for ghost crabs in a few locations, where significant declines in population density have been detected following sand placement, and reduced recruitment has been recorded at nourished sites (Peterson and Bishop, 2005; Peterson et al., 2000). There remains, however, considerable scope to use ghost crabs in targeted experiments that establish threshold levels of nourishment procedures that are less damaging than current practices (e.g. acceptable depth of burial, frequency of application, spatial extent of single sand placement, etc.).

Engineered structures aimed at stabilising shorelines are widely constructed to protect human assets on soft, sedimentary shorelines, particularly in response to beach erosion (Nordstrom, 2014). Whilst the practice of 'shore armouring' with seawalls and similar structures has occurred for millennia, its ecological impacts have been recognised only in the last two decades (Dugan et al., 2011). In brief, shore armouring significantly diminishes habitat extent and quality, resulting in severe reductions and local extirpations of animal and plant species inhabiting the interface between the dunes and the beach on armoured beaches (Dugan et al., 2008; Hubbard et al., 2014); these impacts propagate to shorebirds and are publicly well recognised for turtles where seawalls create significant barriers to nesting (Witherington et al., 2011).

Although the adverse effects of shore armouring have been relatively well documented for ghost crabs (e.g. Barros, 2001; Lucrezi et al., 2010), there remains a great potential for studies that identify the biological returns from creative alternatives to traditional shore defence (e.g. structures that are smaller, or below ground, or constructed from materials that improves habitat values, etc.; Nordstrom, 2014) and biological returns from restoration of habitats by removing armouring structures (Toft et al., 2014). Biota *can* respond relatively quickly to habitat restoration on beaches (Toft et al., 2014), but wider uptake of environmentally less destructive practices will require broad political and public

acceptance (Nordstrom, 2014). Demonstrating positive biological responses of key biota is important to achieve better acceptance, and species of public appeal are central in this process (Huijbers et al., 2015b). Arguably, amongst the beach invertebrates, ghost crabs (as a taxonomic group) are a prime candidate to be used in this context, particularly as the basic patterns of their response to traditional shore armouring is already known (e.g. Barros, 2001; Lucrezi et al., 2010).

4.2.5. Invasive species: non-native carnivores, dune plants and seaweeds

Invasive, predominantly non-native, species have the potential to significantly alter the architecture and function of ecosystems (Ehrenfeld, 2010). Traditional views concerning the effects of invasive species have emphasised major adverse impacts (Courchamp et al., 2003; Norton, 2009), but a more nuanced view is emerging (Davis et al., 2011; Pysek et al., 2012; Strayer, 2012). Whilst invasive species effects are highly topical in the broader ecological literature (Moran and Alexander, 2014; Yelenik and D'Antonio, 2013), beach ecology is somewhat lagging in this respect.

Information on the effects of non-native species in coastal dune and beach systems is largely restricted to: i) trophic impacts of exotic mammalian carnivores (Brown et al., 2015; Huijbers et al., 2015a, 2015b, 2013; Maslo and Lockwood, 2009; Schlacher et al., 2013a, 2013b); ii) how exotic vegetation modifies dune geomorphology and habitat quality for dune-associated species (Johnson and De León, 2015; Nordstrom et al., 2011; Zarnetske et al., 2012); and iii) the implications of fire ants for nesting success in marine turtles (Allen et al., 2001). Much less is known about the effects of invasive species on the non-vegetated part of the beach and in the surf-zone. However, non-native species of macroalgae that are invading the nearshore zone off beaches alter wrack composition and quality, resulting in changes to animal use of wrack and possible flow-on effects on feeding and fitness of wrack-associated consumers (Lastra et al., 2008; Rodil et al., 2015, 2008).

Effects of invasive species on ghost crabs have been documented in only a single study reporting lower density of *O. cordimanus* in areas dominated by exotic vegetation (Brook et al., 2009). Other effects are, however, plausible, involving any of the mechanisms above (e.g. top-down control by exotic and feral carnivores, infestation with fire ants) and hence can be fruitfully measured.

4.2.6. Fishing and mining

A pivotal ecosystem service provided by sandy beaches on many shorelines globally is the provision of harvestable species for human consumption. These 'beach fisheries' target both vertebrates (i.e. bony fishes, sharks, rays) and invertebrates, mostly benthic bivalves (McLachlan et al., 1996). The economic nature of beach fisheries ranges from the occasional collection of individuals for subsistence to true commercial operations (Castilla and Defeo, 2001), and are subject to the same problems (e.g. overharvesting, social conflicts, socio-economic cohesion) as are often evident in open-water finfish operations (Gutiérrez et al., 2011). Species in both the intertidal and the surf-zone are harvested (Turra et al., 2015), and such harvests are not limited to 'less developed' economies but occur globally (Gray et al., 2014; Gutiérrez et al., 2011).

There exist very few data on ghost crab harvesting with respect to species targeted, geographic distribution, frequency and population impacts. The single ghost crab fishery for which published data are available (e.g. eastern KwaZulu-Natal, South Africa) appears to have, historically, had few adverse population-level effects under low intensities of subsistence collecting (Beckley et al., 1996; Kyle et al., 1997; Robertson and Kruger, 1995). However, these are historical estimates and human population growth, coupled with changing economic conditions, may have increased harvesting pressures considerably. It is also very plausible that ghost crabs are harvested for subsistence purposes in many other small-scale artisanal fisheries (A. Turra pers. comm.); whether these artisanal harvests constitute significant ecological impacts is unknown.

Sand and gravel (aggregates) are among the globe's most valuable mineral resources, being mined world-wide and account for the largest volume of solid material extracted (Peduzzi, 2014). Most of the mined aggregates are used for construction and land reclamation, complemented by applications in road embankments, asphalt pavements, and manufacturing (glass, electronics; (Peduzzi, 2014). Two developments in aggregate extractions have particularly dramatic repercussions for sandy beaches: i) the volumes of mined marine sand exceed the volumes of sand delivered by rivers to the ocean; and ii) as inland sources of aggregates are becoming exhausted, mining has increasingly shifted to shorelines (Peduzzi, 2014).

Not surprisingly, removing often large volumes of sand from beaches can lead to significant changes in landforms and sediment properties, and can accelerate erosion (Jonah et al., 2015) to the point where mining on sandy-shores has been labelled as effectively constituting "active destruction" of beaches (Pilkey and Cooper, 2014). Further geo-morphological impacts arise from the disposal of tailings or slurries on the beach or into the nearshore zone (Castilla, 1983). Habitat alterations caused by mining operations on beaches and in dunes translate into significant ecological harm, generally manifested as reductions in abundance, biomass, and diversity of beach-associated species, local extirpations, and major shifts in the species composition of assemblages exposed to mining (Pulfrich and Branch, 2014; Simmons, 2005). Ghost crabs can respond in a similar pattern to habitat changes arising from sand extraction, but the generalisations about biological impacts are impossible to make from a single study (Jonah et al., 2015). Thus, ecological cause-and-effect studies of beach and dune mining using ghost crabs as ecological indicator species in more locations, and using more response variables, have future potential.

5. Conclusions

Notwithstanding the sizeable number of studies that have examined 'urbanisation effects' on ghost crabs, generalisations that can be developed into credible conservation actions in this domain remain largely very unsatisfactory, chiefly because knowledge about mechanistic links are poorly known. Whilst this situation is not unique to beach science, bedevilling urban ecology more widely (McDonnell and Hahs, 2013), we contend that it presents an opportunity rather than a malaise: future urban beach studies can build on the considerable knowledge about ghost crab biology and use the design principles established for ecological experiments to employ logically consistent and powerful designs that will yield stronger inference and attribution about urban effects; such experiments will also need to draw upon more refined predictor and response variables that better match the hypotheses tested (Browne et al., 2015; McDonnell and Hahs, 2013).

Whereas ghost crabs have proven to serve well to monitor conditions of sandy beaches throughout the tropical and subtropical latitudes, standard assessment metrics currently involve inferring abundances from numbers of burrows and sizes from burrow diameters. The failure to observe and make direct measurements on the crabs themselves, including modern biomarkers, inhibits strong inference about the mechanistic process or processes that cause differences in burrow counts or in burrow diameters. It also limits our ability to identify critical biological harm where it may occur.

Nevertheless, sampling of individual ghost crabs and using them in experiments that test explicit hypotheses is feasible and could expand the range of process-oriented inferences about specific drivers of observed burrow abundance differences. While some manipulative experiments could be piggybacked on field studies of real-world coastal impacts, especially if these studies can be initiated in advance of the putative impact, much could also be learned by fundamental experimental work in the laboratory. Thus, further progress is contingent on a better mechanistic understanding of what drives observed responses in ghost crabs, from the individual to the population levels, and more rigorous attribution to specific anthropogenic stressors.

In any respect, ghost crabs lend themselves almost ideally to such studies, therefore representing a powerful model organism for detection of ecological impacts in warm-temperate to tropical coastal systems. The scope of anthropogenic impacts on ocean beach ecosystems promises more and growing needs for impact evaluations. Ghost crabs can continue to provide a strong indicator of impact from studies of counting and/or sizing burrows. However, these widespread dune dominants may be used to provide even more specific indicators of process and causation as they are further used in future experiments.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2015.11.025.

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