

# Ghost crabs as ecological indicators of human stressors on sandy beaches

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# GHOST CRABS AS ECOLOGICAL INDICATORS

OF

# HUMAN STRESSORS ON SANDY BEACHES

# GHOST CRABS AS ECOLOGICAL INDICATORS OF

#### HUMAN STRESSORS ON SANDY BEACHES

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### KEYWORDS

Sandy beaches

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Human disturbance

**Environmental impacts** 

Stressor

Recreation

Trampling

Armouring

Erosion

Off-road vehicle (ORV)

Climate change

Storm impacts

Recovery

Pulse disturbance

Monitoring

Assessment

Coastal management

Animal movement

Burrows

Behaviour

#### ABSTRACT

Sandy beaches geographically dominate the globe's shorelines. They offer critical ecosystem services, provide habitat for threatened species, and support biodiversity, and recycle nutrients and organic matter. Human pressures on sandy beaches are escalating, chiefly as a result of the high demand for recreation and coastal development. Direct human impacts on sandy shores include dune removal and infrastructure construction, soft (nourishment) and hard (armouring)-engineering solutions, pedestrian trampling, and ORV traffic. Global climate change and its predicted effects (e.g. increasing storm intensity and frequency; sea level rise) place additional stressors on ocean-exposed sandy shores.

Assessing and monitoring the ecological effects of human pressures are critical steps in developing and implementing adequate coastal management strategies that are effective in conserving beach ecosystems. However, monitoring programs are currently impeded by the lack of scientifically robust biological indicators. Consequently, this thesis examined the utility of ghost crab (genus *Ocypode*) to measure biological responses to several types of human disturbance on sandy shores.

Densities of ghost crab burrow openings – which are the best proxies for population density - were quantified across- and along-shore at several beach sites in SE Queensland (Australia), exposed to both high levels of human disturbance (i.e. trampling; shoreline armouring; ORV traffic) and low / no human disturbance. In addition, changes in the number, size and position of burrow counts were used to gauge the additive effects of storms and shoreline

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armouring, and estimate recovery from severe weather events. Shifts in behaviour, measured as home range, following vehicle disturbance were also assessed. Finally, modifications to burrow architecture (i.e. burrow depth, length, shape, size) as a result of recreational ORV traffic were tested by comparing beaches open and closed to vehicles, and by conducting controlled impact experiments.

Ghost crab densities declined significantly (up to 50%) in beach areas affected by heavy trampling and ORV traffic, and their intertidal distribution was shifted further seawards as a result of shoreline armouring. Moreover, small storm events caused significant decreases in *Ocypode* numbers. Post-storm recovery of ghost crab populations was not evident in the short-term, and was significantly prolonged in areas where the natural dunes have been replaced by armouring structures. Finally, ghost crab responded to recreational vehicle traffic on beaches by: 1) tunneling deeper in the sediment; 2) simplifying burrow shape; and 3) compressing their home ranges and changing their movement patterns.

The research clearly demonstrates that spatial contrasts of ghost crab burrow counts are a useful tool to measure the extent of anthropogenic impacts on sandy beaches, when predictable sources of interference are small in field measurements or can be either avoided or accommodated in numerical analyses. Results from the present research also support a model of active behavioural responses / changes to human disturbance which can act as an early warning signal for wider negative ecological impacts (e.g. reduced abundances), emphasizing the need to incorporate sub-lethal effects in the

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assessment and management of ecological changes resulting from human disturbance on sandy shores.

#### **CERTIFICATE OF AUTHORSHIP**

I, Serena Lucrezi certify that I am the sole author of the thesis submitted entitled *Ghost Crabs as Ecological Indicator of Human Stressors on Sandy Beaches* (except as specifically indicated in footnotes, quotations and the reference list) in accordance with the requirements for a thesis issued by the University of the Sunshine Coast Research Degrees Committee.

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#### PUBLICATIONS

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Lucrezi S, Schlacher TA, Robinson W (2009) Human disturbance as a cause of bias in ecological indicators for sandy beaches: Experimental evidence for the effects of human trampling on ghost crabs (*Ocypode* spp.). Ecological Indicators 9: 913-921

Lucrezi S, Schlacher TA (2010) Impacts of off-road vehicles (ORVs) on burrow architecture of ghost crabs (genus *Ocypode*) on sandy beaches. Environmental Management DOI 10.1007/s00267-010-9491-5

Lucrezi S, Schlacher TA, Robinson W (in press) Can storms and shore armouring exert additive effects on sandy beach habitats and biota? Marine and Freshwater Research in press: accepted 27 January 2010

Lucrezi S, Schlacher TA Experimental evidence that vehicle traffic changes burrow architecture and reduces population density of ghost crabs on sandy beaches. Vie et Milieu, Life and the Environment: submitted 13 April 2010

Lucrezi S, Schlacher TA Compression of home ranges in ghost crabs on sandy beaches impacted by vehicle traffic. Marine Biology: submitted 26 March 2010 Schlacher TA, Lucrezi S (2009) Monitoring beach impacts: a case for ghost crabs as ecological indicators? 2<sup>nd</sup> Queensland Coastal Conference, Gold Coast, May 2009

Schlacher TA, Lucrezi S (2009) Canaries on the beach: the utility of ghost crabs (*Ocypode* sp.) as indicators of ecological change on sandy beaches. AMSA 2009 Marine Connectivity, Adelaide, South Australia, 5-9 July 2009

#### INTRODUCTION

Sandy beaches comprise most of the world's shores (Bascom 1980) and are the most intensively used type of coastline globally (Schlacher and others 2006). Rapid growth of coastal populations has occurred over the past few decades, with two major outcomes: first, increasing coastal development (e.g. roads, buildings) (Nordstrom 2000); second, increasing use of beaches for recreational purposes (Davenport and Davenport 2006). The ecological importance of sandy beaches has often been neglected in the past, partly because of a public misconception that sandy shores resemble marine deserts. On the contrary, sandy beaches form the connection between the land and the sea, and provide crucial ecosystem services such as nutrient recycling and water filtration (McLachlan and Brown 2006). Sandy beaches host a variety of organisms from small invertebrates (e.g. isopods, amphipods, molluscs, crustaceans, nematodes) (Schlacher and others 2008a) to endangered vertebrates including birds and turtles (Burger 1991; Rumbold and others 2001).

Recent work suggests that impacts such as escalating recreational use of beaches and coastal armouring constitute an ecologically harmful pressure on sandy shores (Dugan and Hubbard 2006; Schlacher and others 2007b; Schlacher and Thompson 2007), but adequate ecological information on putative impacts is in many cases not available. Thus, the development and implementation of conservation and management measures for sandy beaches is seldom underpinned by robust ecological information. Part of this deficiency stems from the lack of indicator to measure ecological responses to human disturbance; therefore, this research is aimed at providing such data.

An alternative to the collection of data on the distribution, diversity and abundance of entire benthic assemblages is the use of selected species that can serve as a proxy or surrogate for other beach biota. Such indicator species can be used to measure the quality and changes in environmental conditions and aspects of community composition (Aubry and Elliot 2006).

Ghost crabs (genus *Ocypode*) are the top invertebrate predators on sandy beaches (Wolcott 1978). Thus, they represent an important link in the food chain of the sandy beach ecosystem. As anthropogenic impacts on ghost crabs can alter the density and behaviour of these animals, there can be repercussions on other trophic levels (Britton 1979), including birds (some of which are known to feed on ghost crabs) and smaller invertebrates (which the ghost crabs prey upon). This is an important argument to select ghost crabs as indicators of anthropogenic pressures on sandy beaches, since a reduction in their population density can impact the population density of other species inhabiting sandy beaches.

Ghost crabs have been used as indicator of anthropogenic disturbance on sandy beaches (Barros 2001; Schlacher and others 2007b). However, some information is still lacking in regards to the degree of impact that every specific type of human activity (e.g. urban development, recreation, pollution) has on the life of *Ocypode* crabs. For instance, reports on the effects of recreational four-wheel driving on the density and distribution of ghost crabs have been lacking for a while and just recently started to re-appear in peer-reviewed journals (Schlacher and others 2007b; Schlacher and Thompson 2007; Moss and Mcphee 2006). The effects of urban development and recreational trampling on the density and distribution of ghost crabs have not been reported on a regular basis either (Barros 2001; Steiner and Leatherman 1981; Jaramillo and others 1996).

The proposed research aims at widening the knowledge of the responses that ghost crab populations have to human disturbances such as trampling, hard engineering, and four-wheel driving, and to other stressors such as increasing storminess deriving from climate change.

A pre-requisite for the application of a species as indicator of ecological health is detailed information about its biology. This is necessary to interpret the results of any monitoring studies in the appropriate ecological context. Lunar cycles, tidal cycles and other environmental variables have a great influence on some aspects of the life of ghost crabs (Schober and Christy 1993) including reproduction, recruitment and distribution across the beach. For instance, ghost crabs migrate up and down the beach in response to the tides, leading to varying densities across the beach at different times of the day (Quijòn and others 2001). It is therefore important to understand the dynamics of ghost crab behaviour in response to external environmental drivers when carrying out a monitoring study and interpreting its outcomes.

Although proven to be successful, the technique of ghost crab burrow count may be sensitive to produce a bias in situations where the population density is actually not affected, and may be unlikely to distinguish between actual biological impacts (i.e. individuals killed by trampling) and apparent impacts (i.e. negative bias of population sizes caused by collapsed entrances) on urban beaches. This situation arises most likely on urban beaches that are subjected to high volumes of pedestrian traffic, which both collapses the burrow entrances of crabs and crushes crabs inside their burrows. The present research aims at testing whether short-term human trampling makes ghost

crab burrow counts a less robust ecological indicator by introducing measurement bias, or whether it lowers crab abundances by lethally crushing individuals.

Human impacts on sandy shores (e.g. off-road vehicle traffic) can have sublethal effects on ghost crab populations which are manifest before any reductions in population sizes from direct kills, habitat degradation, or both. Detecting sublethal effects of human impacts on ecological indicators becomes important when a precautionary principle is to be applied in environmental management (Gray and Bewers 1996). Sublethal effects may include energy-demanding changes in key ecological aspects of *Ocypode* such as burrowing and movement, which have not yet been investigated properly. Therefore, the detection of preliminary behavioural responses of ghost crabs to human stressors can constitute a solid alternative to estimating population sizes during monitoring surveys. The present research aims at assessing the use of sublethal indicators of human stressors on sandy beaches with ghost crabs as a model system.

#### Aims and objectives

The aims and objectives of this research were to:

- Examine to what degree population estimates of ghost crabs on sandy beaches are influenced by external environmental factors;
- Examine whether measured responses of ghost crabs in relation to human disturbance (armouring, trampling and off-road vehicle traffic) are consistent across space and time;
- Test whether shoreline armouring and intense human trampling cause significant reductions in ghost crab population densities;

- 4.) Test whether short-term human trampling makes ghost crab burrow counts simply a less robust ecological indicator by introducing measurement bias, or whether it significantly lowers crab abundances by lethally crushing individuals;
- Measure changes in beach habitat and ghost crab population density caused by a severe climatic event (storm event);
- Measure whether shore armouring influences the susceptibility of the sandy beach habitat and of ghost crab population densities to storms;
- 7.) Measure whether the sandy beach habitat and ghost crab population densities recover from storms, and whether the presence of a shore armouring structure affects recovery rates of ghost crab populations;
- 8.) Investigate whether ghost crabs change their burrow architecture in response to physical disturbance to their habitat in the form of off-road vehicle (ORV) traffic;
- 9.) Test whether experimentally controlled ORV traffic on sandy beaches leads to significant reductions in the density of ghost crabs and results in changes to the architecture of crab burrows;
- Test whether crucial mechanistic elements in ghost crab biology including movement patterns and home ranges respond predictably to disturbance such as by ORVs.
# LITERATURE REVIEW

#### Ghost Crabs: Genus Ocypode

#### Taxonomy and distribution

The family Ocypodidae comprises semi-terrestrial crabs of the two genera *Ocypode* (ghost crabs) and *Uca* (fiddler crabs) (Ng and others 2008; De Grave and others 2009) (Table 1). There are 28 known species of *Ocypode* (Ng and others 2008) which inhabit tropical, subtropical and warm-temperate sandy beaches (Dahl 1953). Within this latitudinal band, ghost crabs are found on all continents (Table 2). The genus *Uca* (fiddler crabs) which comprises 103 species (Ng and others 2008) is distributed on tropical, subtropical (Spivak and others 1991) and temperate (Montague 1980) regions around the world. While ghost crabs are one of the dominant species of malacostraca crustaceans on exposed sandy shores (Dahl 1953), fiddler crabs are amongst the most abundant animals in tropical mangrove forests (Jones 1984; Davie 1994), although they also occupy the intertidal zone of muddy marshes, estuaries and sandy beaches (Crane 1975).

#### Table 1 Ocypode taxonomy

Domain Eukaryota (Whittaker and Margulis 1978) Kingdom Animalia (Linneaus 1758) Subkingdom Bilateria (Cavalier-Smith 1983) Branch Protostomia (Grobben 1908) Infrakingdom Ecdysozoa (Aguinaldo and others 1997) Superphylum Panarthropoda (Cuvier 1812) Phylum Arthropoda (Latreille 1829) Subphylum Mandibulata (Snodgrass 1938) Superclass Crustacea (Pennant 1777) **Epiclass Eucrustacea** Class Malacostraca (Latreille 1802) Subclass Eumalacostraca (Grobben 1892) Superorder Eucarida (Calman 1904) Order Decapoda (Latreille 1802) Suborder Pleocyemata (Burkenroad 1963) Infraorder Brachyura (Linneaus 1758) Section Eubrachyura (de Saint Laurent 1980) Subsection Thoracotremata (Guinot 1977) Superfamily Ocypodoidea (Rafinesque 1815) Family Ocypodidae (Rafinesque 1815) Subfamily Ocypodinae (Rafinesque 1815) Genus Ocypode (Weber 1795)

# Table 2 Geographic distribution of Ocypode species

Species	Known Geographic Distribution	References
<i>O. africana</i> (de Man 1881)	West Africa	Vannini 1980b
O. brevicornis (Milne Edwards 1834-1837)	Oman	Collection Crustacea SMF Senckenberg http://data.gbif.org/occurrences/207920196
O. ceratophthalma (Pallas 1772)	Africa (Kenya to Mossel Bay); Hawaii; Indo-Pacific region (east coast of Australia; Hong Kong; Singapore; Japan; Sandwich Islands); Pakistan	Cott 1929; Vannini 1980b; Jackson and others 1991; Barros 2001; Chan and others 2006; Yong and Lim 2009
<i>O. convexa</i> (Quoy and Gaimard 1824)	West coast of Western Australia, from North-West Cape to Yallingup and Barrow Island	George and Knott 1965
<i>O. cordimanus</i> (or <i>O. cordimana</i> ) (Latreille 1818)	Australia (Kimberly coast (WA) to northern Australia, down to the northern coast of NSW); Seychelles; Somalia; Singapore; Peninsular Malaysia; Philippines; Cocos-Keeling Islands; Timor; Natunas; Red Sea; Gulf of Aden	Jackson and others 1991; Türkay and others 1996; Huang and others 1998; Moss and McPhee 2006; Brook and others 2009
<i>O. cursor</i> (Linneaus 1758)	West Africa; Israel; Mediterranean	Vannini 1980b; Ewa-Oboho 1993; Strachan and others 1999
<i>O. fabricii</i> (Milne Edwards 1834-1837)	Northern and upper west coasts of Australia	George and Knott 1965
O. gaudichaudii (Milne Edwards and Lucas 1843)	Gulf of Fonseca (El Salvador) to Chile; Galápagos Islands	Schober and Christy 1993; Quijon and others 2001
<i>O. jousseaumei</i> (Nobili 1905)	Obock, Gulf of Aden; Oman	Türkay and others 1996; Clayton 2005
<i>O. kuhlii</i> (de Haan 1833-1849)	Indonesia; Malaysia; New Guinea; Bougainville, Krakatau Islands	Jones 1972; Iwamoto 1986; Jones 1988; Jackson and others 1991
<i>O. longicornuta</i> (Dana 1852) (synonym of <i>O. ceratophthalma</i> ; P Davie pers. comm.)	Tongatabu, Pacific Ocean; Singapore	Dana 1852
<i>O. laevis</i> (Fabricius 1798) (possible synonym of <i>O. pallidula</i> ; P Davie pers. comm.)	Hawaii	Fellows 1975

#### Table 2 Continued

Species	Known Geographic Distribution	References
O. macrocera (Milne Edwards 1852)	East coast of India	Rao 1969
O. madagascariensis (Crosnier 1965)	Natal coast (South Africa); Madagascar	McLachlan 1980; Jackson and others 1991
<i>O. minuta</i> (Fabricius 1798)	Unknown geographic location (P Davie pers. comm.)	
O. mortoni (George 1982)	Hong Kong; Cape Murato (Shikoku Island, Japan)	Sakai 2000
<i>O. nobilii</i> (de Man 1902)	Kalimantan (Borneo); Brunei	Jones 1988
O. occidentalis (Stimpson 1860)	Pacific coast of Costa Rica; California	Stimpson 1860; Hughes 1973
O. pallidula (Hombron and Jacquinot 1842-1854)	Indo-West Pacific regions; Coral Sea; eastern Australia	Jones 1988
<i>O. pauliani</i> (Crosnier 1965)	Madagascar	Crosnier 1965
<i>O. platytarsi</i> s (Milne Edwards 1852)	East Coast of India	Rao 1968
<i>O. pygoides</i> (Ortmann 1894)	Central west coast, lower west coast, north-west coast of Western Australia	Balss 1935
O. quadrata (Fabricius 1787)	Rhode Island (USA) to the south regions of Brazil	McLachlan 1980
<i>O. rotundata</i> (Miers 1882)	Southeastern coast of the Arabian Peninsula (Oman) up to North India (including Arabian Gulf)	Vannini 1980b; Türkay and others 1996
<i>O. ryderi</i> (Kingsley 1880)	East Africa; South Africa	Jackson and others 1991; Yousuf and others 2007
<i>O. saratan</i> (Forskål 1775)	Red Sea; African coast of the Gulf of Aden; northeastern Somalia; Eritrea	Vannini 1980b; Türkay and others 1996
O. sinensis (Dai and others 1985)	Indo-Pacific (India; Peninsular Malaysia; Taiwan; Japan; Philippines); Oman	Türkay and others 1996; Huang and others 1998; Clayton 2005
O. stimpsoni (Ortmann 1897)	Asian regions (Japan; Philippines)	Huang and others 1998

#### Key morphological and sensorial traits

Crabs of the genus *Ocypode* are commonly known as 'ghost crabs', due to their usually pale colouration (Cott 1929; Dakin and Bennett 1987), and their great speed which makes them difficult to spot while in motion (Green 1964; Dakin and Bennett 1987). Ghost crabs have a quadrate carapace, large eyestalks, and long ambulatory legs. The chelipeds of ghost crabs are asymmetrical, with the larger chela being either on the left or the right side of the body at a 1:1 ratio as reported for *O. quadrata* (Haley 1969), *O. cursor* (Strachan and others 1999), *O. ceratophthalma* (Barrass 1963), and *O. saratan* (Linsenmair 1967). Predominant right handedness has been recorded for *O. ryderi* (Vannini 1980a), while prevalent left handedness occurs in *O. gaudichaudii* (Trott 1987).

Ghost crabs have acute sensory receptors for taste and smell (Cowles 1908; Wellins and others 1989). They are able to locate sources of volatile cues (for example food) with their chemosensory hairs located on the dactyls which act as the primary olfactory organs (Wellins and others 1989). Chemoreception of volatile cues from potential food sources is also aided by concealed and reduced antennules (Wellins and others 1989). Detection of volatile odours represents an enhancement of *Ocypode*'s ability to scavenge for food (Wellins and others 1989). Ghost crabs also display a highly efficient visual, auditory and vibration signalling behaviour (Cowles 1908; Horch 1971; Popper and others 2001), which is mainly used in territorial defence (stridulation) as well as courtship (tamping and rapping) (Imafuku and others 2001; Clayton 2005; Clayton 2008). Ghost crabs have stalked eyes which can move laterally, backwards and forwards (Cowles 1908). Despite seldom reacting to the movement of objects directly above them, ghost crabs are able to visually detect large objects (e.g. a person) from a distance of at least 45 m (Cowles 1908).

#### Respiration

Ghost crabs are amphibious or semi-terrestrial (Allen and Curran 1974). The lining of the dorsal region of their branchial chamber is modified and contains numerous small folds, the surface of which is covered with invaginations (Al-Wassia and others 1989). The branchiostegal wall thus functions as a lung for oxygen uptake while carbon dioxide is excreted through the gills into the water (Al-Wassia and others 1989). This bimodal form of respiration is a key adaptation to the semi-terrestrial life of ghost crabs.

#### Osmoregulation

Ghost crabs can extract interstitial water from damp sand by capillary action of tufts of hydrophilic setae situated at the base of the walking legs (Rao 1968; Wolcott 1976). Water is then moved from the branchial chambers and absorbed by the gills (Wolcott 1976), which have epithelial cells adapted for ion transport (Storch and Welsch 1975). In some species (e.g. *O. quadrata*), water can be transported into the haemolymph from the foregut (as well as from the gills), after being driven from the branchial chambers to the buccal cavity for floatation feeding (Powers and Bliss 1983).

Ghost crabs are strong osmoregulators (Greenaway 1988). When water is readily available from the sediment, ghost crabs have a high urine flow (Wolcott 1984), which is likely to cause a great potential for salt depletion (Greenaway 1988). In this case, ghost crabs reprocess the urine in their body by passing it to the branchial chambers (where salts and water are reabsorbed through the gills), and thereby reduce the concentration of the final excretory product from 900 to 100-200 mOsm/kg (Wolcott and Wolcott 1985). *Ocypode* also eliminates excess salt in the food by increasing the uptake of water from the soil and flushing the surplus salt with the urine (Greenaway

1988). This ability to maintain haemolymph osmotic concentrations makes ghost crabs withstand long periods within the burrow while submerged by the incoming tide and exposed to high salinity levels (Santos and Moreira 1999).

*Ocypode* has been reported to have limited tolerance to dilute seawater, dying at salinities below 5 psu within seven days in contrast with crabs of the genus *Uca* which can tolerate the same salinity (Ewa-Oboho 1993). Wolcott (1976) demonstrated how ghost crabs also avoid the uptake of fluids that are likely to cause osmotic stress (e.g. distilled water), opposite to seawater which is continuously collected from damp sand with any surplus being expelled through the branchial chambers (Wolcott 1976) or through the antennary glands (AI-Wassia and Eshky 1991).

Salinity tolerances in ghost crabs range between 12.00 and 40.12 psu (Table 3) in the field. Under laboratory conditions on the other hand, this range can be extended to 0.00-48.00 psu (Santos and Moreira 1999). Individuals of *O. cursor* are known to die within two days when exposed to salinity of 0.50 psu, and within seven days at 5.00 psu (Ewa-Oboho 1993).

#### Temperature regulation and tolerance

Depending on the species and the geographic location, ghost crabs exhibit different body temperature ranges and occur at varying air temperatures in the field (Table 3). Overall, ghost crabs are inactive at ambient temperature as low as 12.4°C (Hughes 1966) and exceeding 45.5°C (George and Knott 1965).

The body temperature of *Ocypode* ranges between 23.0°C and 27.5°C at ambient temperatures (Florey and Hoyle 1976; Weinstein 1995), and during activity at

night (air temperature 19-28°C) it has been reported to be 17-28°C (*O. quadrata*) (Weinstein and Full 1994; Weinstein and others 1994). Body temperature may extend from 10 to 35°C under laboratory conditions (*O. ceratophthalma*) (Florey and Hoyle 1976). Moderate temperature changes (from 24 to 15°C and from 24 to 30°C) reduce *O. quadrata*'s locomotory performance substantially (Weinstein and Full 1994; Weinstein and others 1994; Weinstein 1998). Individuals of *O. ceratophthalma* held in seawater above 37°C undergo irreversible damage to their neuromuscular system, whilst at body temperatures of 9-10°C they show no eye or leg movements, although they quickly resume locomotion when temperatures are raised again (Florey and Hoyle 1976). To withstand temperature extremes, ghost crabs (*O. quadrata*) have developed the ability to loose water through evaporation, which maintains body temperature 6°C below ambient temperature also at night (Weinstein and others 1994). Table 3 Temperature and salinity ranges of Ocypode species from various localities. Values of temperature and salinity range gathered from field observational studies do not

necessarily reflect the full physiological tolerance range of ghost crabs, which would require controlled laboratory experiments

Species	Location	Salinity Range (psu)	Air Temperature Range (°C)	Body Temperature Range (℃)	Burrow Temperature Range (℃)	Notes	Reference
O. ceratophthalma	Hong Kong		Lower: 15.0 (October-April) Upper: 34.0 (May- September)		Surface: 45.0-48.0 15 cm depth: 36.0 25 cm depth: 32.0		Chan and others 2006
O. ceratophthalma	Oahu, Hawaii		Close to water temperature Lower: 26.0 Upper: 28.0 (day only, strong winds)	Field: 26.0-27.5 Laboratory: 10.0 (no movement)-35.0 (no movement) (*)	Surface: up to 46.0° Inside: equal to adjacent water temperature	Water temperature: Field: 26.0-28.0°C Laboratory (crabs in seawater of varying temperature): irreversible neuromuscular damage at 37.0°C and no movement / death at 9.0°C (*)	Florey and Hoyle 1976
O. ceratophthalma	Inhaca Island, Moçambique		Lower: 12.4 (activity resumed at 16.0)				Hughes 1966
O. ceratophthalma, O. cordimanus, O. quadrata, O. macrocera, O. stimpsoni	Ganges Delta Complex, India	Lower: 23.00 Upper:38.00	Lower:22.0 (December) Upper:40.0 (May-June)				De 2000
O. cursor	South Nigeria, Africa	Lower: 10.00 Upper: 35.00 Death at 0.50 after 2 days Death at 5.00 after 7 days Optimal salinity: 29.80- 33.50 <b>(*)</b>					Ewa-Oboho 1993

#### **Table 3 Continued**

Species	Location	Salinity Range (psu)	Air Temperature Range (°C)	Body Temperature Range (℃)	Burrow Temperature Range (℃)	Notes	Reference
O. cursor	Northern Cyprus		Lower: 22.8 (06:00; July) Upper: 35.5 (12:00; July)		Surface: 22.8 (06:00)- 51.3'(12:00) 10 cm depth: 30.2-31.7 20 cm depth: 29.9-31.6 30 cm depth: 29.3-32.1 40 cm depth: 29.2-30.5	Burrow temperature varying by <3.0℃ in 24 h	Strachan and others 1999
O. fabricii	Shark Bay, Western Australia, Australia		Upper: 45.5 (13:00)				George and Knott 1965
O. gaudichaudii	Northern Chile				Temperature difference (surface – bottom): 5.6- 23.0		Quijon and others 2001
O. macrocera	East coast of India		Lower: 15 (70% death, 30% growth inhibition) Upper: 34 (moulting inhibition in dark) <b>(*)</b>				Rao 1966
O. macrocera	East coast of India				Surface: 21.0-30.0 Bottom: 22.0-29.0		Rao 1969
O. platytarsis	Oman				Surface during activity: 33.0-38.0		Clayton 2008
O. quadrata	Rio Grande do Sul, southern Brazil		Lower: 18.7 (winter) Upper: 29.1 (summer)			Water temperature: 23.5 (winter)- 26.7℃ (summer)	Antunes and others 2010
O. quadrata	São Paulo State, Brazil	Average: 35.00	Lower: 28.0 Upper: 33.0				Burggren and others 1993
O. quadrata	Paranaguá Bay Complex, southern Brazil	Lower: 14.00 Upper: 32.00				Estuarine habitat	da Rosa and Borzone 2008
O. quadrata	Texas, USA		Lower: 16.0			Inactive January- March	Haley 1972

#### **Table 3 Continued**

Species	Location	Salinity Range (psu)	Air Temperature Range (°C)	Body Temperature Range (℃)	Burrow Temperature Range (℃)	Notes	Reference
O. quadrata	Rio Grande do Sul, southern Brazil		Lower: 21.0 Upper: 26.0				Neves and Bemvenuti 2006
O. quadrata	Sapelo Island, Georgia		Lower: 30.0 (2 cm above sand) Upper: 34.0 (2 cm above sand)		Surface: 30.0		Robertson and Pfeiffer 1982
O. quadrata	São Paulo State, Brazil	Field: 12.00-32.00 Laboratory: 0.00-48.00 <b>(*)</b>					Santos and Moreira 1999
O. quadrata	Veracruz, Mexico		Lower: 22.0 (November) Upper: 30.0 (October)				Valero-Pacheco and others 2007
O. quadrata	Siriú Beach, southern Brazil		Lower: 23.6 Upper: 29.9			Water temperature: 19.2-23.0°C; crabs stay inside burrows during rainy periods	Vinagre and others 2007
O. quadrata	North Carolina, USA			Lower: 23.0 Upper: 27.0	Air temperature 5 cm below burrow mouth: 22.3 (at 20° ambient temperature)		Weinstein 1995
O. quadrata	North Carolina, USA		Lower: 15.0 Upper: 30.0	Lower: 17.0 Upper: 28.0 (at air temperature: 19.0- 28.0° and humidity: 57-95%)			Weinstein and Full 1994; Weinstein and others 1994
O. saratan	Chabahar Bay, Oman Sea	Lower: ~38.75 Upper: 40.12	Lower: ~20.0 Upper: 31.3				Kazemiyan 2008
O. stimpsoni	Wakayama Prefecture, Japan		Lower: 26.0 Upper: 31.0				Imafuku and others 2001

(\*)Laboratory conditions

#### Speed of locomotion

Ghost crabs are the fastest moving crustaceans, and are able to move at speeds of up to 4 m s<sup>-1</sup> (Cott 1929; Hafemann and Hubbard 1969). These speeds are achieved thanks to anatomical specialization, particularly an increase in the length of the terminal segments of the limbs and hook-like dactyli which allow rapid running (Cott 1929; Hafemann and Hubbard 1969).

Locomotion in *Ocypode* occurs by intermittent and brief sideways movements (Full and Weinstein 1992; Weinstein 1995). Under stress, these movements become faster (from a mean of 8.3 to 82.9 cm s<sup>-1</sup>) and have shorter pauses (from a mean of 23.4 to 7.6 s) (Weinstein 1995).

Speed of running in ghost crabs has been reported to be a function of carapace width up to 20 mm, and to decrease with increasing carapace width thereafter (Burrows and Hoyle 1973). Large individuals of *O. quadrata* (70-90 g) do not exceed 0.5 m s<sup>-1</sup> under laboratory conditions, while crabs of intermediate mass (30-50 g) move at greater speed (up to 1.6 m s<sup>-1</sup>) (Blickhan and Full 1987). The decline in speed in larger *Ocypode* individuals can be explained by two factors: first, the ratio between length of the legs and body weight: while the legs increase linearly in length with increasing carapace width, weight increases exponentially; thus, larger crabs carry a heavier body weight on shorter legs, and movement becomes slower (Burrows and Hoyle 1973); second, differences in physiological endurance, with larger crabs reaching maximum oxygen consumption at lower speeds than smaller crabs (Full 1987).

#### The influence of circadian rhythms, artificial light, and lunar cycles

Light is a key determinant of ghost crab activity. In fact, Ocypode guadrata is capable of shifting its activity rhythm when exposed to an inverted (hence unnatural) light cycle (light between 17:30 and 04:00; dark between 04:00 and 17:30) (Palmer 1971). The eyes of Ocypode are also sensitive to large changes in light intensity (Williams 1965): ghost crabs tend to avoid artificial light (Christoffers 1986), which is known to have detrimental effects on several beach species such as turtles (Nicholas 2001; Salmon 2003) and beach mice (Bird and others 2004). Artificial lighting discourages turtles from coming on beaches to nest (Peters and Verhoeven 1994), disorients turtle hatchlings while trying to reach the water (Peters and Verhoeven 1994; National Marine Fisheries Service and U.S. Fish and Wildlife Service 1993), deters beach mice from feeding and seed harvesting (Bird and others 2004), and attracts migrating birds and insects, ultimately causing their death by collision with structures adjacent to the light (Le Corre and others 2002). Wolcott and Wolcott (1984) observed that ghost crabs 'froze' when spotted by the headlights of approaching vehicles on the beach. The flight of ghost crabs following the approaching of vehicles is retarded and random, often leading them under the wheels of off-road vehicles (ORVs), and increasing their mortality by crushing (Wolcott and Wolcott 1984).

Lunar cycles are known to influence the life cycle of *Ocypode*: the occurrence of Ocypodinae (possibly *O. ceratophthalma*) zoeas in Japanese estuaries has been reported to reach a peak during the last and first quarters of the moon (Saigusa 2001), while the incidence of megalopae was high between the new moon and the first quarter of the moon (Saigusa 2001). The adaptive function of circa-lunar rhythms is unclear (Saigusa 2001), although Brooke (1981) suggested that mutual reproductive synchrony may be advantageous: the number of spiral or 'copulation' burrows excavated by adult

males of *O. ceratophthalma* in the Seychelles in preparation for reproduction reaches its greatest number before the new moon, in synchrony with females of the same species carrying eggs 12-15 days before the following new moon (Brooke 1981).

#### Surface activity

*Ocypode* crabs are usually fossorial during the day (Table 4), remaining within their burrows, although diurnal activity has been reported to prevail in species such as *O. gaudichaudii* found in Costa Rica and Panamá, *O. fabricii* in Western Australia, *O. stimpsoni* in Japan, and *O. quadrata* in Georgia (George and Knott 1965; Robertson and Pfeiffer 1982; Schober and Christy 1993; Trott 1998; Imafuku and others 2001). On tropical beaches without human disturbance, indviduals of all sizes can be regularly seen active on the beach surface in daylight (Jones 1972; Evans and others 1976; Dakin and Bennett 1987; Trott 1998; Valero-Pacheco and others 2007). Juvenile ghost crabs are also surface-active during the day on subtropical beaches with humans present (TA Schlacher pers. obs.). Diurnal activity may also be influenced by food availability and preferred feeding mode. For example, *O. gaudichaudii* from Costa Rica, which is primarily a deposit feeder (algae) and a scavenger (dead fish, crabs and cast up material) is a diurnal species (Trott 1988), whilst *O. quadrata* from North Carolina feeds on 90% live prey and is therefore a nocturnal species (Wolcott 1978).

Ghost crabs usually emerge out of their burrows at dusk (Table 4) (Cott 1929), feeding in the open (Valero-Pacheco and others 2007), and cease activity at dawn (Clayton 2005). Surface activity is mainly for feeding, burrow construction and maintenance (Clayton 2005), wandering (general purposeless movements around the burrow (Vannini and Cannicci 1995)), and mating (Hughes 1973).

Individuals of *O. quadrata* can travel distances as long as 300 m along the shore during feeding (Wolcott 1978), and move up to 500 m inland (Wolcott 1978). *O. convexa* from Western Australia has been reported to forage up to one-third of a mile inland following heavy rain (Douglas and Ride 1962). Rao (1968) observed crabs of *O. cordimanus* up to 180 m away from the sea along beaches of the eastern coast of India. On the other hand, *O. platytarsis* and *O. macrocera* from the same region were strictly intertidal, heavily relying on interstitial sea water for survival (Rao 1968). Ghost crabs show seasonality in the spatial distribution across the shore: in autumn and spring for instance, *O. cursor* from the Israeli coast is located 15-25 m from the sea, while it distributes only 5-10 m from the sea in the summer (Shuchman and Warburg 1978).

Despite the ratio of male to female ghost crabs (e.g. *O. ceratophthalma*, *O. gaudichaudii*, *O. ryderi* and *O. cordimanus*) usually being the same within a population (Vannini 1976; Brooke 1981; Trott 1998), there are reported differences between sexes in the spatial distribution across the shore. On the beaches of Costa Rica for example, large *O. gaudichaudii* sexually mature males tend to occur on the upper intertidal zone in double proportion compared to females, while females are twice as abundant as males in the low intertidal zone (low water line) (Trott 1998).

The difference in across-shore distribution between sexes in ghost crabs has been suggested to depend on the different behaviour of males and females (Trott 1998): adult males of *Ocypode* tend to have a territorial behaviour, spending more time around their burrows (Wright 1968). Ovigerous females on the other hand tend to be closer to the swash as a result of the need to let sea water run through the egg mass (Milne and Milne 1946), and to release the eggs during spawning (Trott 1998).

However, why immature females aggregate in the low intertidal zone together with ovigerous females is unclear (Trott 1998).

# Table 4 Summary of reported emergence times (i.e. activity on beach surface) for species of

# Ocypode

Species	Location	Emergence and Activity (Start-Finish)	Reference
O. ceratophthalma	Inhaca Island, Moçambique	18:00-06:00 (juveniles are also diurnal); rapid emergence at neap tides and when a spring tide occurs before nightfall (sediment is well drained and ready for burrowing)	Barrass 1963
O. ceratophthalma	Cousin, Seychelles	16:00-08:00 (until midday if conditions are cloudy and cool)	Brooke 1981
O. ceratophthalma	East Island, French Frigate Shoals	Twenty minutes before sunset to dawn	Lighter 1974
O. ceratophthalma	Inhaca Island, Moçambique	"Sunset to dawn"	Hughes 1973
O. cursor	Israel	All seasons except winter	Shuchman and Warburg 1978
O. cursor	Northern Cyprus	Adults: 18:00-08:00; Juveniles: 24 h	Strachan and others 1999
O. fabricii	Shark Bay, Western Australia, Australia	09:30-16:30	George and Knott 1965
O. gaudichaudii	Costa Rica	Diurnal; active at low tide and burrowed during high tide	Trott 1998
O. gaudichaudii	Culebra Island, Pacific coast of Panamá	Diurnal, burrow maintenance completed 2 h before low tide	Schober and Christy 1993
O. jousseaumei	Oman	Full emergence by low tide (according to observations made during afternoon ebb spring tides on four consecutive days after a new moon)	Clayton 2005
O. kuhlii	Watamu, Kenya	Mainly nocturnal (some activity during the day)	Evans and others 1976
O. macrocera	East coast of India	Late evening-early morning	Rao 1969
O. platytarsis	Oman	Nocturnal	Clayton 2008
O. quadrata	Loggerhead Key, Florida, USA	17:00-11:00	Cowles 1908
O. quadrata	Assateague Island, Maryland-Virginia, USA	Dusk-08:00 (diurnal activity also observed)	Christoffers 1986
O. quadrata	Bogue Banks, North Carolina, USA	Nocturnal; extreme seasonality, with peak activity in August-September across entire beach range	Leber 1982
O. quadrata	Bermuda	Nocturnal; occasional activity during the day	Palmer 1971
O. quadrata	Sapelo Island, Georgia	Observed diurnally, due to the secluded nature of the beach (10:00-13:00), although may also be active at later times	Robertson and Pfeiffer 1982
O. quadrata	Veracruz, Mexico	15:45-10:45	Valero-Pacheco and others 2007
O. quadrata	New Jersey, USA	Evening (entire population has emerged by 10pm)-dawn	Williams 1965
O. quadrata	North Carolina, USA	Dusk-dawn; Late May-October	Wolcott 1978
O. stimpsoni	Wakayama Prefecture, Japan	09:30-17:30; mainly at low tide	Imafuku and others 2001

#### Life history

Some species of ghost crabs (e.g. *O. quadrata*) breed throughout the year while others show seasonality in their reproduction (Brooke 1981). For example, optimal conditions for gonad development in *O. quadrata* females are met during the warmer and rainy season, while low temperatures may delay egg development and larval release (Hughes 1973). Species such as *O. ceratophthalma* on the other hand breed all year round (Haley 1973; Brooke 1981).

Not all adult individuals within a population may mate during the reproductive season: Brooke (1981) observed that out of 7,955 mature (carapace width > 30 mm) *O. ceratophthalma* females captured in the Seychelles during 1978 and 1979, only 2.98% of the females were carrying externally visible eggs, leading to the suggestion that no more than 10% of the females bred every month. At Ubatuba, southeastern Brazil, only 6.2% of 241 females of *O. quadrata* captured in 1998 were ovigerous (Negreiros-Fransozo and others 2002). Despite low numbers of ovigerous *Ocypode* females being encountered in more than one occasion (Brooke 1981; Alberto and Fontoura 1999; Negreiros-Fransozo and others 2002), it has been suggested that females stay in the burrows for egg protection and leave the burrows exclusively for larval release (Negreiros-Fransozo and others 2002). Thus the number of captured ovigerous females may not truly represent the real proportion of egg-carrying females in a population (Negreiros-Fransozo and others 2002).

Ghost crabs have been reported to show lunar rhythmicity in reproduction: for instance, being the construction and defence of copulation burrows energy-costly to adult males, females and males reach mutual synchrony of reproductive activities with

the lunar cycle, so that time and metabolic energy are saved and directed towards other activities (Negreiros-Fransozo and others 2002).

Four species of ghost crab (*O. ceratophthalma*, *O. saratan*, *O. gaudichaudii*, and *O. jousseaumei*; see Table 8) are known to build specific burrows for mating, named 'copulation burrows' (Hughes 1973), while other species (e.g. *O. quadrata*) mate on the beach surface. 'Copulation burrows' have a characteristic spiral shape and often end in a chamber where mating is thought to take place (Brooke 1981).

After mating, females usually stay in the burrows while gravid (Trott 1998). However, egg-bearing females have been observed to wander into the water, open the brood cavity, rock their body upside down, and force water through between the eggs with discrete violence (Milne and Milne 1946). Gravid *Ocypode* females are easily recognizable as their abdomen hangs lower, held away from the ventral cephalothorax by the dark-coloured mass of eggs attached to the swimmerets (Milne and Milne 1946). Female ghost crabs often release the mature eggs into the swash in synchrony with the lunar cycle (Table 5): *O. ceratophthalma* females release their eggs all year round during the full moon (Brooke 1981), as well as ovigerous *O. quadrata* which also spawn during the new moon (Wellins and others 1989).

Under laboratory conditions, the period between ovulation and hatching takes 43 days in *Ocypode laevis* (Haley 1972), while the period between hatching and the first crab stage spans 60 days in *O. quadrata* (Haley 1972). Megalopae of *Ocypode* recruit back to the beach transported onto the intertidal zone by the swash (Crane 1940), and do so on different months of the year depending on the species (Table 5). The recruitment period in some common species (including *O. ceratophthalma*, *O. madagascariensis*, and *O. ryderi*) occurs exclusively on the warmer months (spring,

summer and early autumn). Species such as *O. quadrata* on the other hand show all year round recruitment, with peaks in the summer (Table 5).

Megalopae of ghost crabs have developed a series of adaptations to a semiterrestrial way of life: they have tufts of setae at the base of the walking legs associated with respiration (Smith 1873); they have a thick cuticle, a rounded form, and appendages that fold efficiently (Crane 1940). Megalopae of *O. quadrata* have a carapace ranging between 4.01 (McDermott 2009) and 6.5 mm (Smith 1873) in width and between 5.18 (McDermott 2009) and 7.40 mm (Diaz and Costlow 1972) in length.

Puberty in *Ocypode* is reached at different carapace sizes depending on the species and the gender: for instance, males of *O. quadrata* reach puberty at a carapace width of 24 mm (Haley 1969), and grow at more rapid rates than females (Wolcott 1988), which reach sexual maturity at a size of 26 mm (Haley 1969). Rao (1968) calculated that *O. cordimanus* undergoes 7 moultings to reach a carapace width of 25 mm which is equivalent to the time of puberty.

Information on the life span of ghost crabs is scant. The only record from the literature is by Haley (1972), who reported the life span of *O. quadrata* to be 3 years (Haley 1972).

Species	Geographic Locality	Mating Season	Spam of Eggs' Maturation	Time of Larval Release	Duration of Larval Stage	Main Recruitment Period	Life Spam	Notes	Reference
O. ceratophthalma	Cousin, Seychelles	All year round / one week before new moon	2-3 weeks	All year (full moon); peak in July-September					Brooke 1981
O. ceratophthalma	Hawaii	All year (peak of vitellogenesis April-August)						Male puberty: carapace width=27 mm; male reproductive maturity: carapace width >33 mm; female reproductive maturity: carapace width=33 mm	Haley 1973
O. ceratophthalma, O. madagascariensis, O. ryderi	Eastern Cape, South Africa					Late summer			McLachlan 1980
O. cursor	Northern Cyprus					August			Strachan and others 1999
O. gaudichaudii	Panamá			March					Crane 1940
O. occidentalis	Pacific coast of Costa Rica	August							Hughes 1973
O. platytarsis	Oman	May							Clayton 2008
O. quadrata	Ubatuba, southeastern Brazil	October-May				All year	Up to 3 years		Alberto and Fontoura 1999
O. quadrata	Rio Grande do Sul, southern Brazil	All year; peak in the summer							Antunes and others 2010

# **Table 5** Life history characteristics for different Ocypode species from various localities

Table	5 C	ont	inu	ed
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Species	Geographic Locality	Mating Season	Spam of Eggs' Maturation	Time of Larval Release	Duration of Larval Stage	Main Recruitment Period	Life Spam	Notes	Reference
O. quadrata	Assateague Island, Maryland-Virginia, USA	June- September				June-November		Reproduction close to the new moon or full moon; close to the water's edge; maturity reached 13 months following recruitment	Christoffers 1986
O. quadrata	Loggerhead Key, Florida, USA	Spring; early summer				possibly March			Cowles 1908
O. quadrata	North Carolina, USA	Summer (Leber 1982)		New moon and full moon, after dark within 40 min of high tide (Wellins and others 1989)	34 days (under laboratory conditions: 25°at 35 psu)				Diaz and Costlow 1972
O. quadrata	Mustang Island, Texas, USA	All year (peak in summer)	45 days at 23 ℃ ( <i>O. laevis</i> )			July to October	3 years	Gonad maturation: 24 mm carapace width in males and 26 mm females; 10- 12 months between first crab stage and puberty	Haley 1969; Haley 1972
O. quadrata	Ubatuba, southeastern Brazil	October-May		Feb-May, Oct- Nov		All year; peak in Jan-March		Gonad maturation: 20.0 mm carapace width in males and 23.0 mm in females; carapace width of ovigerous females: 34.5-39.0 mm	Negreiros-Fransozo and others 2002
O. quadrata	Long Island; Fire Island Beach, USA					August-September			Smith 1873
O. quadrata	Siriú Beach, southern Brazil	Spring		Late summer (February and March)					Vinagre and others 2007
O. quadrata	Carolinas			April-July (Coues 1871)					Williams 1965

Т	Table 5 Continued								
Species	Geographic Locality	Mating Season	Spam of Eggs' Maturation	Time of Larval Release	Duration of Larval Stage	Main Recruitment Period	Life Spam	Notes	Reference
O. saratan	Chabahar Bay, Oman Sea	All year		Spring (March- June); autumn (August- November)					Kazemiyan 2008
O. stimpsoni	Wakayama Prefecture, Japan	July							Imafuku and others 2001

#### **Trophic biology**

Ghost crabs essentially occupy an intermediate trophic level in the food webs of sandy beaches, being both consumer and prey. Ghost crabs are frequently the top invertebrate predator on beaches, and 90% of their diet consists of live prey items, mostly shallow-burrowing macroinvertebrates such as isopods, clams and annelids (Wolcott 1978). Moreover, ghost crabs prey on turtle hatchlings and eggs (Barton and Roth 2008), bird eggs (Wolcott and Wolcott 1999), mole crabs (*Emerita talpoida*) (Fales 1976; Wolcott 1978) and other ghost crabs (Cowles 1908; Hughes 1966).

However, the diet of ghost crabs can be more diverse involving scavenging (Cott 1929; Jones 1972; Evans and others 1976), feeding on stranded seaweed, decaying roots, leaves, siphonophores, stalked barnacles, driftwood, meat, fish, and bread (Jones 1972; Evans and others 1976; Strachan and others 1999). Some species of *Ocypode* also deposit-feed (Crane 1941; Robertson and Pfeiffer 1982; Trott 1988), and consume detritus such as seeds (Iwamoto 1986).

Ghost crabs feed at different locations across the shore, depending on the feeding mode and the type of food (Table 6). Active predators including *O*. *ceratophthalma* and *O. quadrata* feed on prey items such as pipis and mole crabs on the lower beach (high tide mark or the water line) (Hughes 1966; Wolcott 1978). However, *O. ceratophthalma* has been observed overcoming individuals of *Lupa* and *Calappa* spp. as far as 500 m from the wave beach on sand flats (Hughes 1966). *O. kuhlii* is more likely to be found on the upper beach, where live insects, fruit and seeds are abundant (Iwamoto 1986). Deposit feeding also occurs primarily on the lower shore (Table 6). Ghost crabs have been reported to prey on turtle and bird eggs and hatchlings (e.g. *O. cursor* and *O. quadrata*) on the upper shore, in the proximity of

nests (Strachan and others 1999; Wolcott and Wolcott 1999). Scavenging may occur at any location across the shore (Table 6).

It has been suggested that ghost crabs occur in higher numbers on beaches used intensively for recreation due to the presence of food scraps left behind by the visitors (Evans and others 1976; Steiner and Leatherman 1981), and crabs actively scavenge for food scraps on camping sites located in dunes (TA Schlacher and LM Thompson pers. obs.).

Despite having impressive eyesight (Daumer and others 1963), ghost crabs obtain most information by means of other senses such as olfaction (Wellins and others 1989). For instance, ghost crabs find foods on the beach by detecting and following volatile odours that signal potential food sources (food cues) through hairs on the dactyls. This enhances the crabs' ability to scavenge when regular prey items are in short supply (Wellins and others 1989). Crabs react to odours from animal, plant, and faecal material (Wellins and others 1989), but carcasses in advanced states of decay are less attractive (Brooke 1981).

Ghost crabs also represent a link in the food web which connects land and sea, being themselves regular prey to other ghost crabs and to many vertebrate species including birds, mammals, and reptiles (Table 7). Predation of *Caretta caretta* eggs by *O. quadrata* in Florida (USA) is diminished thanks to ghost crab predation by raccoons (Barton and Roth 2008). Non-native species including the red fox as well as domesticated animals (dogs) are also known to disturb and feed on *Ocypode*. Ghost crabs are also of economic importance in some localities, being both harvested by man in Kwazulu-Natal, Africa (Jackson and others 1991; Kyle and others 1997), and used as a medicinal resource in Brazil (Costa Neto and Lima 2000).

# Table 6 Overview of reported prey items of Ocypode species

Species	Prey items	Feeding Mode	Feeding Location / Position	Geographic Locality	Notes	Reference
O. ceratophthalma	Macrophthalmus grandiderii (Ocypodidae); live insects; other Ocypode individuals; Uca (Ocypodidae); Donax faba and D. incarnata (clams); Calappa (box crabs); Lupa pelagica; dead birds (petrels); decomposing Tridacna (giant clam); sand pellet feeding; washed up Holothuria hilla (sea cucumber) and Thyone sacellus (Echinodermata)	Active predator; facultative scavenger; deposit feeder	Middle and lower beach / high tide mark; lower shore / wave fringe; intertidal sand flats / up to 500 m away from the wave beach (on sand flats)	Inhaca Island. Moçambique		Hughes 1966
O. ceratophthalma	Eurydicid isopods; annelids; <i>Cymodocea</i> ; filamentous algae; diatom algae	Active predator; deposit feeder	Lower beach	Watamu, Kenya	Sheltered beaches	Jones 1972
O. cursor	Beached fish; cow carcass; dead rats; food discarded by tourists (watermelon skins; bread); turtle eggs; turtle hatchlings; butterflies; flies	Active predator; facultative scavenger	Upper beach	Northern Cyprus	Communal feeding was observed	Strachan and others 1999
O. gaudichaudii	"Microscopic organic matter"	Deposit feeder; predator as young	Lower beach / water line	Costa Rica		Crane 1941
O. gaudichaudii	Filamentous green algae growing on exposed rocks; dead Coenobita compressus (octopus); dead Gecarcinus lateralis (land crab); dead juveniles of O. gaudichaudii and O. occidentalis; dead adult of Uca panamensis (fiddler crab); dead shore birds; dead triggerfish; seed pods; bananas; scarab beetles	Deposit feeder; facultative scavenger	Entire intertidal zone of sand flats	Osa Peninsula, Costa Rica		Trott 1988
O. kuhlii	Fruit and seeds; live arthropods	Detritus feeder (32.4%); active predator (67.6%)	Upper beach / <i>Casuarina</i> forest floors; upper barren slopes	Krakatau Islands		Iwamoto 1986
O. kuhlii	Stranded roots and leaves of <i>Cymodocea ciliata</i> ; dead fish; siphonophores; stalked barnacles; meat and bread (placed on beach from the observer)	Detritus feeder; facultative scavenger	Upper beach	Watamu, Kenya	Exposed sandy beaches (vs. <i>O.</i> <i>ceratophthalma</i> in sheltered locations)	Jones 1972; Evans and others 1976
O. quadrata	Malaclemys terrapin (diamondback terrapin, hatchlings)	Active predator	Upper beach / foredunes; dune lee	New Jersey, USA		Arndt 1991
O. quadrata	Caretta caretta (loggerhead turtle) eggs	Active predator	Upper beach / turtle nesting sites	Florida, USA		Barton and Roth 2008

#### Table 6 Continued

Species	Prey items	Feeding Mode	Feeding Location / Position	Geographic Locality	Notes	Reference
O. quadrata	Atherina laticeps (sardines of the Gulf); Ocypode quadrata (juvenile); stranded fish; coconut, seaweed, bread, turtle meat, coffee grounds, potatoes; ham fat, jelly-fish	Active predator; facultative scavenger	Lower beach / water line	Loggerhead Key, Florida, USA		Cowles 1908
O. quadrata	Orchestia (amphipod beach fleas)	Active predator		New Jersey, USA		Fowler 1911
O. quadrata	Charadrius melodus (piping plover) chicks	Active predator	Lower beach	Assateague Island, Maryland-Virginia, USA		Loegering and others 1995
O. quadrata	Diatom algae	Deposit feeder	Areas of the beach covered with visible patches of benthic diatoms	Sapelo Island, Georgia	Can extract 70% of available algae from substratum	Robertson and Pfeiffer 1982
O. quadrata	Sterna fuscata fuscata (sooty tern chicks)	Active predator	Upper beach / foredunes	Florida Keys, USA		Sprunt 1948
O. quadrata	Food scraps left by beach visitors	Scavenger	Entire beach profile / from foredunes to the swash	Assateague Island, Maryland-Virginia, USA	This behaviour was observed in zones of pedestrian use	Steiner and Leatherman 1981
O. quadrata	Vargula harveyi (ostracode); dead fish	Deposit feeder; facultative scavenger	Lower beach / water's edge	Southern Bahamas	Causes luminescence in the crabs	Felder 1982
O. quadrata	<i>Emerita talpoida</i> (mole crabs); <i>O. quadrata</i> (ghost crabs); cast up material (horse manure; horseshoe crabs; sea gulls; cooked shrimp; peanuts; potato chips; candy wrappers; beach wrack)	Active predator; facultative scavenger; cannibal	Lower beach / along the tide lines; water's edge	North Carolina, USA		Wellins and others 1989
O. quadrata	Beached fish; refuse	Facultative scavenger	Lower beach / along the drift line	New Jersey, USA		Williams 1965
O. quadrata	<i>Emerita talpoida</i> (mole crabs); <i>Donax variabilis</i> (wedge clams); cast up material (dead birds; barnacle-laden timber)	Active predator (90%); facultative scavenger (10%)	Lower beach / swash (predation); middle beach / above the drift line (scavenging)	North Carolina, USA		Wolcott 1978
O. quadrata	<i>Charadrius melodus</i> (piping plover, eggs and chicks)	Active predator	Lower beach; berm; vegetated dunes (nests)	Assateague Island, Maryland-Virginia, USA	Not directly observed; crabs manipulate eggs and taste them using chemoreceptors	Wolcott and Wolcott 1999
O. ryderi	Stranded Physalia (jelly-fish)	Facultative scavenger	Supralittoral zone of open beaches	Eastern Cape, South Africa		McLachlan 1980

# Table 7 Predators of Ocypode species

Species	Predators	Feeding Location / Position	Geographic Locality	Notes	Reference
Ocypode sp.	Canis latrans (coyote); Vulpes vulpes (red fox)	Intertidal zone	Gulf of California, USA	Up to 106 burrows excavated in one night by coyotes	Rose and Polis 1998
O. ceratophthalma, O. madagascariensis; O. ryderi	Indigenous humans (harvesting)	Intertidal zone	Northern Kwazulu- Natal, South Africa		Jackson and others 1991; Kyle and others 1997
O. kuhlii	Varanus sarvator (two banded monitor)	Upper beach / coastal forests	Krakatau Islands		Iwamoto 1986
O. macrocera	Haliastur indus (brahminy kites)		India		Alcock 1902
O. quadrata	Procyon lotor (raccoon)	Intertidal zone	Florida, USA		Barton and Roth 2008
O. quadrata	Humans		Bahia State, Brazil	Crabs are used as a medicinal resource	Costa Neto and Lima 2000
O. ryderi	<i>Myonax pulverulentius</i> (Cape Grey mongoose); <i>Cyncitis pencillata</i> (yellow mongoose)	Supralittoral zone of open beaches	Eastern Cape, South Africa	Crabs are dug out of their burrows	McLachlan 1980

#### Burrowing

Burrows are key structures in the ecology of ghost crabs, providing shelter against predators, weather extremes, conspecifics, and tides (Christoffers 1986). Burrows may also be used for protection either during moulting (Christoffers 1986) or egg development (Haley 1973). Williams (1965) suggested that burrows are used by ghost crabs to hibernate. Burrowing mainly takes place during surface activity at night (Trevallion and others 1970; Strachan and others 1999; Valero-Pacheco and others 2007; Souza and others 2008; Brook and others 2009).

The position of burrows across the beach is most often governed by: the compactness of the sand (Hughes 1966), with crabs preferring loose sediment (Jones 1972; Brook and others 2009); inundation by tides, with most individuals burrowing above the high tide mark (Barrass 1963).

Juvenile ghost crabs are frequently found closer to the swash, while the distribution of adults is centred further up the beach (Fisher and Tevesz 1979; Chakrabarti 1981; Valero-Pacheco and others 2007). This pattern often reflects: high recruitment of juvenile crabs in a population; territoriality of adult crabs; the necessity of water by young crabs which forces them to remain close to the swash in the lower foreshore; avoidance of adults by juveniles to reduce competition and possibly cannibalism (Fisher and Tevesz 1979; Chakrabarti 1981; Ewa-Oboho 1993; Barros 2001; Magalhaes and others 2009). For other ghost crab species (*O. quadrata, O. laevis* and *O. ryderi*), distribution may continue beyond the high tide mark into the dunes (Table 8), extending up to 400 m inland (Jones 1972; Fellows 1975). Individuals of *O. quadrata* from a barrier island have been reported to move over 800 m to the interior of the island and back to the shore in one night (Wolcott 1995).

*Ocypode* burrows have a funnel-shaped opening which leads to a circular- or oval-sectioned tunnel (Duncan 1986; Strachan and others 1999). Burrows decrease in inclination and increase in length from the shoreward limit of burrow occurrence towards land (Bakshi and others 1980). The end of the tunnel is either cigar-shaped (Braithwaite and Talbot 1972) or inflated to form a chamber (Evans and others 1976). Burrows situated above the high tide mark may be occupied by the same crab for up to 9 days, while burrows located below the high-tide mark are less permanent. According to Evans and others (1976), out of 117 ghost crab burrows located in the tidal range, more than 50% was vacated after 24 hours, and 100% was abandoned after seven days. Two burrows examined above the high water mark on the other hand were occupied by the same ghost crab for up to nine days (Evans and others 1976).

Since ghost crabs walk sideways, they burrow with the side of the body bearing the smaller chela facing downwards; conversely, the larger chela is the first to appear as the crab comes out of a hole after digging (Hughes 1973). Pyramidal structures are often found outside male burrows; their function is to either signal other male crabs of the presence of an occupied burrow, or to attract females (Braithwaite and Talbot 1972; Evans and others 1976; Bakshi and others 1980). Feeding pellets are often seen around the entrance of burrows (Vannini 1980b).

Typical burrow shapes of juveniles resemble the letters 'I', 'J', 'U' and 'Y' ((Vannini 1980b); S Lucrezi pers. obs.). Adult shapes include 'J', 'Y', and spiral (S-shaped) burrows or 'copulation burrows' (Vannini 1980b). Overall, out of all the burrow forms, ghost crabs mainly excavate Y-shaped burrows, followed by J-shaped, I-shaped and U-shaped burrows (Table 8). S-shaped burrows are also common in some ghost crab species, although they are excavated exclusively by males during the reproductive

season (Hughes 1973). Rare burrow forms include multi-branched (or M-shaped) burrows and L-shaped burrows. The former are the product of an abandoned burrow being re-excavated by a new occupant, and are often located in the backshore which is not disturbed by regular wave action (Chakrabarti 1981). The latter have been reported to be typical of *O. cursor* only (Strachan and others 1999). Burrow orientation is often seaward (Chakrabarti 1981; Chakrabarti 1993) in the backshore-foreshore transition zone, and random in inter-dune flats and other parts of the shore (Hill and Hunter 1973; Duncan 1986; Chakrabarti 1993).

Fossilized burrows of *Ocypode*-like crabs from the Jurassic and Cretaceous periods (Frey and others 1984) to the Tertiary period (Miocene (Radwanski 1977) and Pleistocene (Stephenson 1965)) have been found at many localities around the world. The burrows of *Ocypode* have palaeoenvironmental significance (Seike and Nara 2007). In semi-consolidated substrates such as beach sediment, the sand particles are bound together by surface tension of interstitial water, thus having enough strength to retain burrow walls through time and preserve both *Ocypode* burrows and the characteristic bioglyphs (sculptural patterns occurring on the burrow walls) formed by ghost crabs (Nara 1998). Thus, fossilized burrows with such sculptural patterns indicate that they were excavated in semi-consolidated substrates (Nara 1998), helping palaeologists understand the position and the characteristics of ancient shorelines (Frey 1970; Duncan 1986; Chakrabarti 1993). Finally, sediment pellets produced during food sifting by the crabs and radiating outside the burrow entrance are preserved in ancient sediments, becoming useful in determining palaeomicroenvironments (Chakrabarti 1972; De 2000).

Species	Geographic	Across-Shore	M -shape	U- shape	J - shape	l - shape	Y - shape	Spiral -	Notes	Reference
·	Locality	Location	·	·	·			shape		
Ocypode (fossil)	Korytnica Basin, Holy Cross Mountains, Poland	Shallow intertidal marine environment		~50%	~50%				Longest fragment: 75.0 cm; diameter 4.0-6.0 cm	Radwanski 1977
O. africana	Congo, Africa						100%			Rathbun 1921
O. africana	Nigeria, Africa				100%					Bruce-Chwatt and Fitz- John 1951
O. ceratophthalma	Seychelles	Middle-lower beach			~30%	~30%	~30%	~10%	Diameter: 1.0-6.0 cm; depth: 10.0-50.0 cm	Braithwaite and Talbot 1972
O. ceratophthalma	Hong Kong	Above high water mark			23%; Diameter: 1.5 cm Inclination: 85° Depth: 16.0 cm	19%; Diameter: 4.6 cm Inclination: 73° Depth: 32.0 cm	39% ; Diameter: 2.7 cm Inclination: 75°Depth: 36.0 cm	19%; Diameter: 3.3 cm Depth: 41.0 cm		Chan and others 2006
O. ceratophthalma	Western Sundarbans, west Bengal, India	Backshore; beach crest		~30%	~40%		~30%		Inclination: 70-80°, sand pyramid outside entrance; grazing marks radially arranged outside entrance	Bakshi and others 1980
O. ceratophthalma	Cousin, Seychelles	Below the high tide mark						Present	S-shaped burrows; sand pyramid 10.0- 15.0 cm high; burrow life spam: 8-20 hours	Brooke 1981
O. ceratophthalma	Gopalpur, east coast of India	From the upper part of the foreshore slope to the base of the coastal dunes	15% (backshore- foreshore transition zone)	15% (upper part of the foreshore slope)	15% (upper part of the foreshore slope)	15% (backshore region)	40% (backshore region; upper part of the foreshore slope)		Depth: up to 100.0 cm; burrows sloping shoreward	Chakrabarti 1981
O. ceratophthalma	Hawaii							Present		Fellows 1966

# **Table 8** Distribution and characteristics of burrows in species of Ocypode, including relative frequency of different burrow shapes

Species	Geographic	Across-Shore	м -	U- shape	J - shape	I - shape	Y - shape	Spiral -	Notes	Reference
	Locality	Location	shape					shape		
O. ceratophthalma; O. cordimanus; O. macrocera; O. stimpsoni	Ganges Delta Complex, India	Intertidal and supratidal flats	~20% (post- tidal; upper intertidal zone)	~20% (post-tidal; middle intertidal zone)	~20% (pre-tidal; lower intertidal zone)	~20% (pre-tidal; lower intertidal zone)	~20% (post-tidal; upper intertidal zone)		Diameter: 3.6-5.1 cm; length:6.0 -87.0 cm; inclination: 70-85° in the upper intertidal zone, up to 90° in the lower intertidal zone; secondary arms in landward direction	De 2005
O. ceratophthalma, O. sinensis	Irino Coast, Japan	Upper foreshore; backshore; dune subenvironments	~10%			~45%	~45%		Diameter: 1.0-4.0 cm diameter; depth: 10.0- 90.0 cm; length: up to 140.0 cm	Seike and Nara 2007
O. cordimanus	Seychelles	Around and above the high water springs; beach crest							Diameter: 1.0-6.0 cm	Braithwaite and Talbot 1972
O. cordimanus	Sar Uanle Beach, Somalia, Africa					100%				Vannini 1980b
O. cursor	Israel	5-25 m from the sea, depending on the season		~20% (closer to the sea)			~70%		Shoe-type burrows observed, possibly 10%	Shuchman and Warburg 1978
O. cursor	Northern Cyprus	3-16 m from water's edge			100%				Some burrows L- shaped	Strachan and others 1999
O. gaudichaudii	Culebra Island, Pacific coast of Panamá			38% in males; 56.7% in females	27.8% in males; 10% in females	16.2% in males; 30% in females		18% in males; 3.3% in females	Diameter: 1.5-5.5 cm	Schober and Christy 1993
O. jousseaumei	Oman	Over-dispersed in the intertidal zone						Present		Clayton 2005
O. laevis	Hawaii	Intertidal zone to grassy areas			~28%	~15%	~57%		Seaward orientation decreases with distance from water	Fellows 1966
O. occidentalis	Central America			~35%	~30%		~35%			Peters 1955

Species	Geographic	Across-Shore	M -	U- shape	J - shape	I - shape	Y - shape	Spiral -	Notes	Reference
O. quadrata	Beaufort, North Carolina, USA	Backshore zone; low foredune ridge	~1%	~50%			~49%	Shape	Diameter: 2.0-7.5 cm	Allen and Curran 1974
O. quadrata	Assateague Island, Maryland- Virginia, USA	From the lower shore to beyond the dunes		~30%	~30%		~40%			Christoffers 1986
O. quadrata	Padre Island and Mustang Island, Texas, USA	From the lower foreshore to the vegetated foredune ridge		~25% (lower backshore; diameter: 1.0-2.0 cm; length: 20.0- 30.0 cm)	~25% (lower backshore; diameter: 1.0- 2.0 cm; length: 20.0-30.0 cm)	~25% (foreshore; diameter: 1.0- 1.5 cm; length: 10.0-15.0 cm); (dunes; diameter: 2.0- 2.5 cm)	~25% (mid and upper backshore; diameter: 1.5- 2.0 cm; length: 30.0- 70.0 cm); (interdune flats; diameter: 1.5 cm; length: 20.0- 30.0 cm)			Hill and Hunter 1973
O. rotundata	Bandarabass, Iran				100%				Depth: up to 200.0 cm	Pretzmann 1975
O. ryderi	Sar Uanle Beach, Somalia, Africa	Shore and dune area			~10%	~40%	~50%		Depth: up to 50.0 cm; Length: up to 100.0 cm; Openings pointing seawards	Vannini 1980b
O. saratan	Red Sea							100%		Linsenmair 1967
O. stimpsoni	Western Sundarbans, west Bengal, India	Foreshore		~50%		~50%			Inclination: 75-85°, grazing marks radially arranged outside entrance	Bakshi and others 1980
O. stimpsoni	Japan				31%	23%	46%			Utashiro and Horii 1965

#### Agonistic behaviour

A number of ghost crab species show a complex agonistic behaviour, which is considered to be an important spacing mechanism (Evans and others 1976; Vannini 1980a). Agonistic displays are observed when large numbers of ghost crabs are feeding on the shore at night, and can be grouped into two distinct types: lateral merus display, where the chelae are extended laterally and held almost horizontally; chela display, where the chelae are held almost vertically in front of the crab with the tip pointing downwards (Evans and others 1976; Clayton 2008). The former display usually occurs both as a burrow-defence mechanism, following the trespassing of a burrow by a foraging conspecific, and as a way to discourage a conspecific to excavate too close to an existing burrow (Evans and others 1976). The latter display is often observed in encounters over food (Evans and others 1976; Vannini 1980a). Agonistic displays are typically followed by pouncing, where a crab confronts an opponent and brings the chelae down towards it (Evans and others 1976). Most agonistic encounters end with the expulsion of the intruding crab from the burrow or territory (Clayton 2005). Another spacing mechanism used by ghost crabs involves burrow plugging or filling, where the crab fills a neighbouring burrow with sand, forcing the occupant of the neighbouring burrow to evacuate (Jones 1972).

#### **Orientation and homing**

*O. ceratophthalma* is capable of returning to its burrow (homing behaviour) after travelling up to 100-200 m away from it (Balss 1955-1956). Hughes (1966) observed that individuals of the same species constructing burrows closer to land were able to forage up to 30 m away from the burrows and to occupy the burrows for 10 days. On the other hand, Linsenmair (1967) found that only 2 out of 23 adult males of a population of *O. saratan* from Eritrea were able to return back to the burrows after

being experimentally displaced. Homing can be aided by visual cues such as sediment mounds constructed near the burrow (Hughes 1966). Individuals of *O. saratan* have been observed building sand cones in the proximity of their burrows, and wander around them in a regular manner, possibly to incorporate any landmarks into their memory before setting out on long excursions (Linsenmair 1967). *Ocypode* can also use menotactic relocation (orientation of the long body axis is at a fixed angle to the stimulus): under laboratory conditions (within a 50 cm wide circular arena), 3 out of 5 individuals of *O. ceratophthalma* were able to orient menotactically to the pattern of polarized light when returning to their artificial shelter hole after inspecting a piece of bait (Daumer and others 1963). When relocation is not successful (due to the displacement of the visual cues (Field and others 2007), eviction by another individual (Wolcott 1988), and burrow deterioration (Micheli and others 1991)), crabs are forced to excavate a new burrow, thus facing higher risks of predation as well as wasting metabolic energy.

The ability to return to the same food source after a first forage is an important aspect of *Ocypode* behaviour which increases feeding success: Evans and others (1976) found that up to 30 out of 52 *O. kuhlii* individuals on a Kenyan beach made regular trips to food sources (e.g. meat and fish placed on the beach by an observer). These crabs were able to return to the food source by learning its position in relation to the burrow (Evans and others 1976). Moreover, the discovery of food on one forage stimulated a more attentive search for it in the next forages (defined as non-associative behaviour) (Evans and others 1976).
#### Human Impacts on Sandy Beaches

Seventy-five percent of the world's population is predicted to live within 60 km of the coastline by 2020 (UNCED 1992). This will place massive pressures on coastal ecosystems which are already thought to be substantial for sandy beaches (Defeo and others 2009). Escalating anthropogenic threats to sandy shore ecosystems are primarily underpinned by rapid expansions of coastal tourism, coastal population increases, and accompanying coastal infrastructure development (Brown and others 2008).

Ecological impacts on sandy beaches are numerous, including: predicted effects of climate change such as increasing storminess (Jones and others 2007; Poloczanska and others 2007); habitat loss and modifications from coastal development (e.g. infrastructure and roads) and urbanization (Nordstrom and Jackson 1998; Nordstrom 2000; Barros 2001); armouring (Sobocinski 2003; Dugan and Hubbard 2006; Dugan and others 2008); nourishment (Peterson and others 2000; Peterson and others 2006; Jones and others 2008); beach cleaning (Llewellyn and Shackley 1996; Gheskiere and others 2006); introduction of alien and exotic species (Brook and others 2009); trampling (Rickard and others 1994; Moffett and others 1998), off-road vehicle use (Godfrey and Godfrey 1980; van der Merwe and van der Merwe 1991; Moss and McPhee 2006; Schlacher and Thompson 2007; Schlacher and others 2007b; Hobbs and others 2008; Schlacher and Thompson 2008), camping (de Jager 2009), and fishing / harvesting (Defeo and de Alava 1995; McLachlan and others 1996).

In the following literature, some of the key anthropogenic stressors to exposed and sheltered sandy shores are summarized and synthesized, together with the physical and ecological effects deriving from these stressors.

#### Shore armouring

Armouring of soft shorelines is defined as 'The placement of bulkhead, seawalls, and riprap (mounds or walls of stone) in areas previously lacking hard substrate' (Davis and others 2002). The prime function of armouring is to protect the shoreline from retreat and changes in sea-level (Charlier and others 2005). Armouring structures are designed to break up waves (Brown and others 2008), to stabilize and support the shoreline, and to prevent erosion of urbanized coastal areas (Spencer 1999; Meyer-Arendt 2001; Wong 2003; Phillips and Jones 2006). The application of coastal armouring has increased substantially in many developed countries over the past few decades (Wong 2003), and is expected to increase further as a result of escalating human settlement along the coast, pooled with increasing beach erosion and sea-level rise deriving from climate change (Dugan and others 2008).

Armouring has a number of detrimental environmental impacts, both in terms of physical habitat changes and flow-on biological impacts (Dugan and Hubbard 2006; Dugan and others 2008). The first of the most damaging physical effects of shoreline armouring is erosion (Meyer-Arendt 2001; Hartman 2002; Sobocinski 2003; Dugan and Hubbard 2006). A second and equally damaging physical effect of shoreline armouring is the deterioration and elimination of coastal dunes (Ranwell and Boar 1986; Sobocinski 2003; El Banna 2004), which act as the shoreline's sand reservoir and first line of defence deterring the movement of storm waves and tides into the area behind the beach (El Banna 2004). Armouring structures built landward of the beach prevent the natural landward migration of the coastline in response to sea-level rise and depletion of sediment budgets (Brown and others 2008).

Other physical effects of shoreline armouring on sandy shores include increased sediment suspension, reduced onshore sediment transport and increased longshore sediment transport (Miles and others 2001). Beach width can decrease due to reflection of wave energy, passive erosion and erosion seaward of armouring structures (Dugan and Hubbard 2006). Furthermore, armouring causes alterations of the physical properties of the sediment, including coarsening (Sobocinski 2003) and lower moisture levels (Rice 2006). Accretion and erosion may alternate on armoured beaches (Walker and others 2008b), with accretion occurring as newly-available sand is recruited, causing beaches to advance seawards or increase in height (Brown and McLachlan 2002). Finally, armouring structures such as breakwaters can interrupt longshore sediment transport, inducing further expensive practices such as dredging (Pruszak 2004).

One of the main ecological consequences of armouring in exposed shores and sheltered marinas, inlets and bays is the loss of habitat and resources (e.g. wrack deposits) for many invertebrate species such as limpets and barnacles, and for vertebrate species including birds and turtles (Table 9). For instance, the standing crop of wrack has been reported to be substantially lower on armoured exposed shores compared to natural sites (Sobocinski 2003; Dugan and Hubbard 2006), with direct effects on prey availability for shorebirds.

Another ecological effect of armouring, both in exposed and sheltered shores, is the replacement of natural habitat with artificial habitat (Table 9). Armoured sites of both sheltered and exposed sandy shores and rocky shores are known to host a less diverse and abundant array of faunal species compared to natural locations. This is a result of habitat loss and changes in the physical properties of the substratum (Table 9). For instance, only half of the mobile invertebrate species otherwise hosted by other

natural intertidal habitats have been reported to occur on armoured shores of Sydney Harbour, Australia (Chapman 2003); richness and density of species including birds and macroinvertebrates were substantially lower on armoured sandy beaches of California, when compared to natural sites (Dugan and others 2008). Exposed beaches with seawalls have been estimated to have lower turtle nesting success than beaches without seawalls, possibly as a result of the reduction of available nesting habitat in the armoured sites (Mosier and Witherington 2002). The presence of armouring structures (e.g. revetment walls) in sheltered bays has also been accounted to facilitate invasion of exotic species and reduction of native species by inter-specific competition (Glasby and others 2007).

Armouring structures have been reported not to affect certain categories of fauna on exposed shores in few occasions: crustaceans were more abundant on armoured beaches in central Puget Sound (Washington) than in unchanged beaches (Sobocinski 2003). Jaramillo and others (2002) found that armoured sandy beaches of Chile did not undergo any modifications in the physical properties of the sediment, putatively thanks to the high degree of plasticity of sandy beaches (Jaramillo and others 2002). In the case of sheltered locations including harbours, inlets and bays, the presence of structures such as jetties may aid the accumulation of drifting invertebrate eggs which are then preyed upon by shorebirds (Botton 1994).

Reference	Geographic Location	Type of Structure	Type of Habitat	Effect: Physical / Habitat	Effect: Biological and Ecological		
Shore-parallel structures built on the backshore (classical seawalls)							
Barros 2001	Sydney, New South Wales, Australia	Concrete wall	Exposed sandy beach	Dune elimination	Significantly fewer (up to 3x) ghost crab burrows in urban beaches ( <i>p</i> =0.020) compared to reference sites; significantly lower burrow density (almost 10x) below the foredune / wall in urban beaches than in non-urban beaches		
Miles and others 2001	England, UK	Wall of granite rocks, parallel to the shore	Exposed sandy beach	Increased wave reflection; increased suspended sediment concentration (3x) compared to natural sites; reduced onshore sediment transport by incident waves; increased longshore currents; increased longshore sediment transport (1x) compared to natural sites			
Hartman 2002	California, USA	Seawall	Exposed sandy beach	Severe erosion during the winter months			
Jaramillo and others 2002	Chile, South America	Concrete seawall	Exposed sandy beach	No substantial modification of the physical properties of the beach	No detectable changes in density, diversity and body size of macrobenthic species		
Mosier and Witherington 2002	Jupiter Island, Florida, USA	Seawall (vertical; with or without dunes in front)	Exposed sandy beach	Dune elimination	Over 2x less turtle nests in armoured stretches without dunes in front compared to sites with dunes in front		
Sobocinski 2003	Puget Sound, Washington, USA	Seawall	Exposed sandy beach	Sediment coarsening; downshore erosion; elimination of supralittoral zone	Reduced wrack deposits; loss of habitat due to the elimination of supralittoral zone; reduced invertebrate species richness and density (except for crustaceans)		

# Table 9 Summary of reported environmental effects of shoreline armouring on exposed sandy beaches and other coastal environments

Reference	Geographic Location	Type of Structure	Type of Habitat	Effect: Physical / Habitat	Effect: Biological and Ecological		
Shore-parallel structures built on the backshore (classical seawalls)							
Bulleri and Chapman 2004	Italy	Rock walls	Exposed rocky shores		Reduced species richness compared to rocky shores; dominance of encrusting algae (up to 23x more abundant encrusting corallines and up to 64x more <i>Ralfsia</i> than in rocky shores); absence of common species; lowered variability of assemblages within and among patches		
El Banna 2004	Egypt	Rock wall	Exposed sandy beach	Dune destruction; increased deterioration (destruction phase) of dunes by seawater flooding	Vegetation removal		
Turra and others 2005	Saõ Paulo State, southeastern Brazil	Rock walls	Low-energy tide- dominated beach		Reduced ghost crab density (up to 10x) compared to reference; burrow density in upper intertidal zone of undisturbed beaches with vegetated dunes >10x greater than density in upper intertidal zone of armoured beaches ( $p$ <0.001) Significantly smaller (means up o10 mm smaller) burrows in armoured beaches than reference ( $p$ <0.010)		
Dugan and Hubbard 2006	Santa Barbara County, California, USA	Nearly vertical concrete wall	Exposed sandy beach	Beach narrowing through reflection of wave energy, passive erosion and erosion downshore; elimination of the supralittoral zone (upper shore compressed by up to 60%)	Elimination of habitat for shorebirds; reduced wrack deposits (food source); lower bird density (almost 10x) and species richness (2x) compared to unarmoured sites		

Reference	Geographic Location	Type of Structure	Type of Habitat	Effect: Physical / Habitat	Effect: Biological and Ecological		
Shore-parallel structures built on the backshore (classical seawalls)							
Rice 2006	Puget Sound, Washington, USA	Seawall	Exposed sandy beach	Increased substrate and air temperature; reduced relative humidity	Increased exposure of fish (surf smelt) embryos to thermal stress and desiccation from vegetation removal and increased exposure to sunlight; reduced number of surf smelt eggs and embryos (50%) compared to control site		
Yasué and Dearden 2006	Gulf of Thailand	Seawall	Exposed sandy beach	Elimination of dunes; reduced beach width	Elimination of habitat for breeding adult plovers and chicks; increased (by ~50%) likelihood of nest and chick inundation; reduced shade and feeding grounds for adult plovers and chicks; reduced productivity (up to 50%)		
Dugan and others 2008	Santa Barbara County, California, USA	Nearly vertical concrete seawall	Exposed sandy beach	Elimination of the dry upper beach zone; narrowing of middle beach zone (>2x compared to unarmoured beaches)	Reduced density, biomass and size of macrobenthic species; lower bird species richness (2x) and density (>3x) compared to unarmoured sites		
Veloso and others 2008	Spain; Rio de Janeiro, Brazil	Concrete wall	Exposed sandy beach	Removal of sand dunes	Reduced density of talitrid amphipods (over 5x) compared to reference sites; impacts exacerbated by urbanization		
Lucrezi and others 2009b	Eastern Australia	Concrete wall	Exposed sandy beach		Reduced density (up to 50%) of ghost crab burrows compared to reference sites; 25% more burrows on the upper shore of reference site compared to armoured site		
Magalhaes and others 2009	Bahia, northeastern Brazil	Concrete wall	Exposed sandy beach		Up to 5x fewer ghost crab burrows compared to control ( <i>p</i> =0.003); urban beach lacking frontal dunes had the smallest number of burrows		

Reference	Geographic Location	Type of Structure	Type of Habitat	Effect: Physical / Habitat	Effect: Biological and Ecological		
Shore-parallel structures built on the backshore (classical seawalls)							
Lucrezi and others in press	Eastern Australia	Rock wall	Exposed sandy beach	Slower recovery of beach profiles past a severe weather event compared to unarmoured site	Up to 3x greater decline in ghost crab burrows past a severe weather event compared to unarmoured site		
Shore-parallel structures in the surf (breakwaters)							
Botton 1994	Delaware, USA	Jetties	Sheltered bay		Enhanced accumulation of drifting horseshoe crab ( <i>Limulus</i> ) eggs; greater abundance (up to 2x) of migratory shorebirds compared to other natural sites		
Martin and others 2005	Spain; Italy; UK	Structures of rubble parallel to the shore and regularly overtopped by waves (Low Crested Structures or LCS)	Exposed sandy beach	Creation of a 'mosaic' of habitats; altered wave energy regimes (reduced hydrodynamics); accumulation of sediments mainly on the landward side of LCS	Overall increased species diversity (soft bottom and mobile fauna assemblages); patchiness of assemblage structure; changes in trophic structure of assemblages; reduced benthic fauna when silty sediments over-accumulate around LCS; impoverished infauna in micro-tidal shores (UK) where muddy and anoxic sediments accumulate around LCS		
Bertasi and others 2007	Italy	Breakwaters (low crested structures) parallel to the shoreline and connected to land by groynes creating a sheltered condition	Exposed sandy beach	Changes in hydrodynamic patterns (reduction of current flows and increase in residence time of water during storms); 50% reduction in wave energy compared to exposed sites	Greater species richness (almost 2x), but lower abundance (more than 4x) compared to more exposed sites with respect to wave action; changes in community structures		

Reference	Geographic Location	Type of Structure	Type of Habitat	Effect: Physical / Habitat	Effect: Biological and Ecological		
Shore-normal structures (e.g. groynes)							
Meyer-Arendt 2001	Mexico	Rock and timber groynes	Exposed sandy beach	Dune destruction; down-drift erosion alternated with accretion			
Pinn and others 2005	England, UK	Rubble groynes	Exposed sandy beach		Reduced species richness (~40%) compared to rocky shores; species richness increases with ageing of groyne (by 1/3 from one to two year old groynes, and by another ¼ from two to seven year old groynes); with groyne ageing perennial species become more abundant and ephemeral species less abundant		
Fanini and others 2007	Italy	Groynes	Exposed sandy beach	Reduced beach width; possible increase in longshore sediment transport and erosion; increase in grain size with decreasing beach slope	Shifts in sandhopper orientation (adapted to shoreline direction)		
Walker and others 2008b	Gold Coast, Queensland, Australia	Groyne of rock boulders, perpendicular to the shore	Exposed sandy beach	Accretion on one side of groyne and erosion on the other side; coarsening of sediment within 10 m of groyne on either side	Greater macrofauna species richness (35-59%) closer (<10 m distance) to the northern (accreting) side of the groyne compared to southern (eroding) side; no effect past 10 m distance from either side		

Reference	Geographic Location	Type of Structure	Type of Habitat	Effect: Physical / Habitat	Effect: Biological and Ecological		
Revetments and retaining walls in sheltered locations (e.g. estuaries), harbours and marinas							
Davis and others 2002	California, USA	Riprap (granite boulders)	Paired exposed and sheltered sites in San Diego Bay	Altered wave energy regimes (higher wave energy)	Introduction of open-coast species including barnacles <i>Tetraclita</i> and <i>Balanus</i> , limpets <i>Collisella</i> , <i>Littorina</i> snails, and sponge <i>Aplysina</i> (closer to the bay mouth); introduction of non- coastal species such as the slipper snail <i>Crepidula</i> , sponge <i>Leucetta</i> , bryozoans of <i>Watersipora</i> , tunicates <i>Botryllus</i> , and algae of <i>Enteromorpha</i> in most shelteres sites; stretching of vertical range of intertidal species		
Chapman 2003	Sydney, New South Wales, Australia	Seawall of quarried sandstone blocks	Sheltered estuarine harbour	Replacement of natural rocky shores	No detectable effect on algae and sessile species; 50% reduction richness of mobile species compared to rocky shores; lower proportion of rarer taxa compared to control		
Chapman and Bulleri 2003	Sydney, New South Wales, Australia	Vertical sandstone wall	Sheltered estuarine harbour	Replacement of natural rocky shores	Reduced density and cover of dominant benthic species (algae, sessile and mobile invertebrates)		
Bulleri 2005	Sydney, New South Wales, Australia	Seawall	Sheltered estuarine harbour	Replacement of natural rocky shores	Reduced cover of algae and barnacles (up to 100%) compared to rocky shores; increased cover of biofilm compared to rocky shores		
Glasby and others 2007	Sydney, New South Wales, Australia	Sandstone brick seawalls; fibreglass or concrete pontoons; concrete pilings; wooden pilings		Different substrate compared to rocky reefs	Increased number of nonindigenous species (up to 3x) compared to native epibiota; invasion of nonindigenous species via entry points (pontoons and pilings acting as beachheads)		
Moreira and others 2006	Sydney, New South Wales, Australia	Vertical seawalls	Sheltered estuarine harbour		Reduced limpet size (24% more large adults in rocky shores); reduced number (up to 3x less) and mass of limpet eggs on seawall compared to rocky shores; minimal contribution to the reproductive output of limpets in a given area		

#### Beach nourishment

Beach nourishment is an engineering intervention intended to protect infrastructure from wave surges, improve beaches for recreation, and decelerate beach erosion (Finkl and Walker 2002; Nordstrom 2005). Sediment is transported from accreting beaches to eroding beaches via bypassing and backpassing operations (Brown and others 2008). Bypassing is by definition the 'Movement of material past a littoral drift barrier and downdrift to a shore which suffers from erosion due to a littoral drift barrier' (Bruun 1990). Backpassing on the other hand is defined as the 'Transfer of material "back to shore" by a mechanism which moves material from offshore to the beach or to the nearshore bottom' (Bruun 1990). Beach nourishment is used either as an alternative to shore armouring or to complement it (Nordstrom 2005; Speybroeck and others 2006).

Although sometimes referred to as a soft-engineering solution to shore erosion (as opposed to the 'harder' solution of armouring), this term does not necessarily imply that nourishment is without ecological consequences, particularly when the grain size and type of imported sediment (borrow) is not compatible with sediment from the host beach (Finkl and Walker 2002). Direct negative impacts on sandy beach species include injury and mortality through deep burial (Peterson and others 2000; Speybroeck and others 2006; Jones and others 2008). Indirect impacts consist of changes in habitat characteristics (e.g. sediment compactness) which degrade the value of habitat for many species including birds and turtles (Table 10). Peters and others (2006) reported on the reduction by over 90% in habitat use by shorebirds on nourished beaches of North Carolina, in contrast with control sites; over a six-fold reduction in turtle nesting sites and an increase of the same proportion in the number

of false nests occurred on beaches of Florida post nourishment in 1995 (Rumbold and others 2001).

Recovery of macrobenthic (e.g. mole crabs, amphipods and clams) species is known to occur on exposed shores, although it may take from a few months to a year (Rakocinski and others 1996; Peterson and others 2000; Peterson and others 2006; Jones and others 2008). 
 Table 10 Summary of reported environmental effects of nourishment on sandy shores (exposed and sheltered)

Reference	Geographic Locality	Type of Habitat	Effect: Physical	Effects: Biological and Ecological
Rakocinski and others 1996	Florida, USA	Exposed sandy beach	Increased silt and clay; increased depth profiles	Reduced macrobenthic species richness and density (up to 10x) compared to pre-nourishment times; shifts in macrobenthic assemblage structure; development of macrobenthic assemblages characteristic of steep depth profiles; long-term impacts (up to one year after nourishment)
Rumbold and others 2001	Florida, USA	Exposed sandy beach		Reduced turtle nesting (up to 5.4 times fewer nests per kilometre per day) compared to before nourishment; increase in false nests (up to 5.6 more false nests per kilometre per day)
Peterson and others 2000	North Carolina, USA	Exposed sandy beach	Altered sediment size and characteristics (finer; higher levels of shell hash compared to host beach)	Reduction in mole crab (99% <i>Emerita</i> ) and clam (86% <i>Donax</i> ) density post nourishment; no recovery by the summer (sediment was pumped in spring); 37% reduction in mole crabs three months post bulldozing; 5x greater abundance of clams post bulldozing
Pruszak 2004	Poland	Exposed sandy beach and sheltered harbour	Offshore shoreline displacement; enlargement of underwater bar; shoaling of the foreshore in form of an underwater terrace	
Peterson and others 2006	North Carolina, USA	Exposed sandy beach	Altered sediment size (coarser sediment from borrow compared to host beach; increased shell cover); 14-29% reduction in habitat area	Decline in macroinvertebrate density (over 90% for clams and amphipods compared to control); mole crab population recovery by mid-summer (nourishment ended in spring); degrading habitat value for foraging birds; up to 90% reduction in habitat use by shorebirds
Fanini and others 2007	Italy	Exposed sandy beach	Increased sediment penetrability	Reduced density of talitrid amphipods, which increased in number with increasing distance from nourished sites; better orientation of talitrid amphipods compared to natural sites
Jones and others 2008	Sydney, New South Wales, Australia	Exposed sandy beach	No detectable differences in sediment properties compared to pre-nourishment	Complete disappearance of talitrid amphipods from intertidal habitat, possibly by burial; recovery started 9 weeks post nourishment; full recovery after one year

#### Trampling

Trampling on sandy shores is mostly associated with recreational activities, coastal tourism and extreme urbanization along the shorelines, all of which have increased substantially over the past decades (Neves and Bemvenuti 2006). The direct and indirect impacts of trampling range from physical to ecological, and extend from coastal dunes to the lower intertidal zone of sandy beaches and mud flats (Table 11).

Trampling on coastal dunes can have reversible or extreme negative effects when it occurs either in the short-term or long-term (Boorman and Fuller 1977). Amongst the main physical effects of trampling are the increase in soil bulk density and compactness, and the decrease in soil penetration depth (Table 11). Trampling also crushes and destroys dune plants, causing a reduction in dune vegetation cover and species richness, enhancing erosion rates, and increasing the temperature of the soil (Table 11). Boorman and Fuller (1977) reported that 2000 pedestrian passes can completely destroy the vegetation along a 0.4 m wide path on the coastal dunes of England. Trampling on coastal dunes has negative ecological effects on bird species that breed, nest and roost in the vegetation: birds (e.g. black skimmers) are directly disturbed by trampling during the breeding season (Safina and Burger 1983); the disturbance of breeding birds by trampling also decreases the likelihood of clutches hatching and chicks surviving (Yasué and Dearden 2006).

Although no detectable effects have been observed in some instances (Jaramillo and others 1996), trampling can cause alterations in the physical properties of unvegetated intertidal beaches (Table 11), by reducing the sediment grain size and increasing soil compactness (Yong and Lim 2009). Direct ecological effects of trampling on unvegetated sandy beaches include: crushing of invertebrates (e.g.

clams, mysids and amphipods) by over 50% (after 500 passes); reduced density of ghost crabs and bubbler crabs; death of turtle and bird embryos by direct crushing of eggs; disturbance of feeding, resting, breeding and incubating birds which fly or move to less disturbed locations; disturbance of turtle hatchlings trying to reach the surf (Table 11). Indirect ecological effects of trampling range from reduced feeding and activity rates of birds (e.g. plovers, sanderlings and dotterels), to reduced survival of bird hatchlings (over 50%), to increased risk of predation of turtle hatchlings trying to reach the surf (Table 11).

Light trampling often has little effect on the macrobenthic species of the intertidal zone (Jaramillo and others 1996). Beach visitors may also leave food scraps behind (Steiner and Leatherman 1981; Barros 2001), and their consumption by ghost crabs and other fauna may lead to dietary and distributional shifts which can benefit these species (Steiner and Leatherman 1981).

Despite being different from sandy shores and coastal dunes, intertidal rocky shores are also susceptible to impacts from pedestrian trampling (Table 11), proving the importance of monitoring and managing impacts of recreational activities on all coastal habitats. Physical impacts on bare rock habitat have been reported not to be significant (Povey and Keough 1991). However, trampling on rocky shores severely reduces the percent cover of brown algae (e.g. *Hormosira* spp. and *Cytoseira* spp.) by 20% in a single pass, and by 100% at more intense trampling regimes (Table 11). Impacts can persist for up to four years (Keough and Quinn 1998). Polychaetes associated with articulated coralline algae are significantly reduced in response to pedestrian disturbance (Brown and Taylor 1999), although many species of molluscs are only dislodged by trampling, while limpet densities are increased (Table 11).

Table 11 Summary of reported environmental effects of pedestrian trampling and trampling-based activities on coastal dunes, intertidal mud flats and

## unvegetated sandy beaches

Reference	Geographic Location	Physical Effects	Direct Biological and Ecological Effects	Indirect Biological and Ecological Effects
Coastal Dunes				
Liddle and Moore 1974	North Wales, UK	Changes in the soil microclimate from vegetation removal; increase in soil strength and bulk density; more extreme temperature of tracks (dry soil) compared to adjacent vegetation (warmer in the day and cooler in the night)	Removal of tall surface vegetation	
Liddle and Greig-Smith 1975a	North Wales, UK	Sediment compaction (down to 6 cm for short-term trampling); increased bulk density and penetration resistance of soil		
Liddle and Greig-Smith 1975b	North Wales, UK		Reduced plant biomass and species richness; shifts in the composition of dune vegetation	
Boorman and Fuller 1977	England, UK	Almost 14% dune area affected	High vulnerability of grasses vs. low vulnerability of woodland and short grass scrub; reduced vegetation height (80%) and cover (14%) from 80 passes a month; complete destruction of vegetation (0.4 m wide path) from 2000 passes a year	
Hylgaard and Liddle 1981	Denmark	Lowering of the soil surface (28 mm after 2560 passes)	Reduced vegetation cover (50%) after 200 passes	
McDonnell 1981	Massachusetts, USA		Reduced vegetation species richness and cover; shifts in the horizontal pattern of vegetation (expanding width of foredune plant community and reducing width of interdune community)	
Safina and Burger 1983	Long Island, NY, USA			Bird (black skimmers) disturbance during the breeding season (incubation and egg- laying); bird migration to undisturbed sites where nesting occurs with other bird species; increased vulnerability of chicks to predation

Reference	Geographic Location	Physical Effects	Direct Biological and Ecological Effects	Indirect Biological and Ecological Effects
Coastal Dunes				
Carlson and Godfrey 1989	Massachusetts, USA		Reduced vegetation species richness and cover	
Rickard and others 1994	Eastern Cape, South Africa		Reduced vegetation height and cover immediately post impact (250 passes); followed by further decline in the following months	
Andersen 1995	Denmark	Dunes most vulnerable to impact; salt marsh least vulnerable to impact; grassland intermediate vulnerability	Reduced vegetation species richness, diversity and cover (particularly for therophytes and hemicryptophytes)	
Kutiel and others 1999	Israel	Greater soil compactness and moisture in heavily trampled paths compared to paths subject to light trampling	Reduced vegetation cover, height, species richness and diversity; reduced soil organic content; impact on vegetation is more localized (6 m perpendicular to trails) in heavily used trails, and dispersed over a larger area in lightly used trails (path borders less visually defined)	
Kutiel and others 2000	Israel	Reduced penetration depth of soil; no significant effect on moisture and organic matter content of upper soil layer	Reduction in vegetation height, species richness and diversity (from 500 passes)	
Fanini and others 2005	Italy		No significant effect of trampling on sandhoppers (talitrid amphipods), possibly thanks to their ability to move along and across the shore to less trampled beach zones, to then re-colonize the beach after disturbance	
Yasué and Dearden 2006	Gulf of Thailand	Enhanced beach erosion rates		Reduced likelihood of bird (plover) clutches hatching and chicks feeding; reduced productivity of birds

Reference	Geographic Location	Physical Effects	Direct Biological and Ecological Effects	Indirect Biological and Ecological Effects
Intertidal Mud Flats				
Sherman and Coull 1980	South Carolina, USA		70% removal of meiofauna; re-establishment of fauna after one tidal cycle; subsequent adaptation to small scale disturbance	
Verhulst and others 2001	Holland			Disturbance to incubating birds (oystercatchers); reduction of incubation time of birds; reduced foraging activity of birds; decreased nest attendance by birds
Rossi and others 2007	Netherlands	No detectable changes	Reduced density of macrobenthic species (clams and cockles); direct killing of adult clams and cockles by crushing or burial; enhanced recruitment of juvenile clams; small scale reduction in microphytobenthos	
Unvegetated Sandy Beach				
Fisher and Tevesz 1979	Virginia to North Carolina, USA		1.5x less ghost crab burrows in ORV zones than pedestrian sites; significantly altered juvenile:adult ratio in heavily disturbed sites (up to 1 adult:21 juveniles in ORV sites vs. 1 adult: 3 juveniles in trampling sites)	
Burger 1981	Atlantic Coast, USA		Rapid movements (e.g. jogging) caused the most disturbance to birds	68% reduction in bird activity
Hosier and others 1981	North Carolina, USA		Impediment for turtle hatchlings to reach the surf	Increased risk of predation of turtle hatchlings while trying to reach the surf
Steiner and Leatherman 1981	Assateague Island, Maryland-Virginia, USA		Ghost crab burrow density in beaches with light recreation ~2x greater than in undisturbed beaches, ~20x greater than in beaches with light ORV impact, and >60x greater than in beaches with heavy ORV traffic	Increased ghost crab densities possibly due to the benefits of the presence of foods left behind by visitors

Reference	Geographic Location	Physical Effects	Direct Biological and Ecological Effects	Indirect Biological and Ecological Effects
Unvegetated Sandy Beach				
Arianoutsou 1988	Greece, Europe		Direct crushing of turtle ( <i>Caretta caretta</i> ) eggs; destruction of turtle nests; premature hatching of turtles by accidental or deliberate nest digging	Increased predation risk of premature turtle hatchlings; death of turtle hatchlings
Burger and Gochfeld 1991	Florida, USA		Disturbance of foraging birds (sanderlings) which leads them to fly or move to undisturbed areas	Decreased foraging time and increased alertness time in birds; inverse relationship between bird foraging time and number of disturbance events
Roberts and Evans 1993	Florida, USA		Disturbance to birds (sanderlings) which causes them to fly	Domino effect of disturbance (birds fly or move as a response to other birds reacting to disturbance)
Burger 1994	New Jersey, USA		Disturbance to feeding birds (piping plovers)	40% reduction of foraging activity by birds (piping plovers)
Jaramillo and others 1996	Chile, South America	No substantial physical impact	No substantial biological impacts	
Moffett and others 1998	South Africa		Up to 70% direct damage to beach macrofauna (including surf clam and mysids) from up to 500 passes and volleyball simulations	
Weslawski and others 2000	Poland, Europe		Reduced density (87%) of talitrid amphipods	
Lafferty 2001a	California, USA		Disturbance to bird activity (mostly on the lower beach), which leads them to fly or move; up to 70% birds fly when disturbed during short observation periods	Reduced bird activity
Lafferty 2001b	California, USA		Disturbance to birds (snowy plovers) which causes them to move or fly; average disturbance occurred every half hour in weekends	Decreased feeding rates by birds; no acclimation of birds to disturbance
Lord and others 2001	North Island, New Zealand		Disturbance to incubating birds (dotterels); disturbance which leads the birds to move or fly (from 1) Dogs; 2) Running; 3) Walking)	Incubation failure
Moellman and Corbisier 2003	Saõ Paulo State, southeastern Brazil		Reduced maiofauna densities; meiofauna burrows deeper in the sediment (below 5 cm)	

Reference	Geographic Location	Physical Effects	Direct Biological and Ecological Effects	Indirect Biological and Ecological Effects
Unvegetated Sandy Beach				
Ruhlen and others 2003	California, USA			Reduced snowy plover chick survival (up to 72% greater than expected) during holiday and weekend periods
Neuman and others 2004	California, USA		Crushing of bird (snowy plover) eggs	
Gheskiere and others 2005	Italy; Poland		Reduced % total organic matter (food source for meiofauna), accentuated in the upper beach; reduced meiofauna species richness and density	
Turra and others 2005	Saõ Paulo State, southeastern Brazil		Density of ghost crabs up to 10x greater in non- urban than control Significantly smaller (means up o10 mm smaller) ghost crab burrows than control Re-distribution of ghost crabs away from beach zones heavily used by people (upper intertidal zone)	
Yasué 2005	British Columbia, Canada		Disturbance to feeding birds (plovers)	Reduced feeding rates of birds (plovers)
Blankensteyn 2006	Santa Catarina, Brazil		No harmful effects to ghost crab populations in beaches with light recreation (e.g. trampling)	Possibly indirect benefits of the presence of foods left behind by visitors
Neves and Bemvenuti 2006	Rio Grande do Sul, Brazil		Density of ghost crabs in undisturbed beach up to 6x greater than in beach with heavy trampling and light vehicle traffic, and up to 6x greater than in beach with light trampling and heavy ORV traffic	
Veloso and others 2006	Rio de Janeiro, Brazil		Reduced density of mole crabs and insects; complete absence of amphipod <i>Pseudorchestoidea brasiliensis</i> at most urbanized and used beaches	
Maccarone and Mathews 2007	Texas, USA		Burrow density 3x greater in low-impact beach; burrows further from water in low-impact beach (p<0.001)	

Reference	Geographic Location	Physical Effects	Direct Biological and Ecological Effects	Indirect Biological and Ecological Effects
Unvegetated Sandy Beach				
Ugolini and others 2008	Italy	No detectable changes	Negative correlation between talitrid amphipod density and number of swimmers on the beach; direct killing of talitrid amphipods by crushing	
Veloso and others 2008	Spain; Rio de Janeiro, Brazil		Reduced density of talitrid amphipods, aggravated by urbanization	
Intertidal Rocky Shores				
Povey and Keough 1991	Eastern Australia		Dislodgement of molluscs; removal of 20% brown algae ( <i>Hormosira</i> spp.) with a single footstep (maximum loss: 75%); five months post sustained trampling (33 days over 4 months) algal cover was still <50% of pre-treatment levels; 4000 days post impact algal cover only 60% of pre-treatment values	
Brosnan and Crumrine 1994	Oregon, USA		70% reduction in algal cover within one month of trampling; >80% reduction in foliose algae cover five months into trampling impact; 90% reduction in barnacle cover in four months; 50% reduction in mussel in one day; recovery of canopy after a year post impact; no marked recovery of fauna years post trampling	
Keough and Quinn 1998	Eastern Australia		High levels of trampling eliminated brown algae within 2 years; 30% reduction in brown algae up to 4 years post intermediate trampling	Enhanced density of herbivorous molluscs and reduced density of articulated coralline algae
Brown and Taylor 1999	New Zealand		50% reduction in articulated coralline algae	Polychaetes associated with algal turf highly susceptible to low levels of trampling
Benedetti-Cecchi and others 2001	Italy		Complete absence of turf-forming algae ( <i>Cystoseira</i> spp.)	

#### Beach cleaning

Beach cleaning on exposed and sheltered sandy shores is practiced to get rid of litter and dangerous items (e.g. needles and glass) from the sand, as well as to remove deposits of wrack (e.g. seagrass, algae, jellyfish) which detract from the recreational and aesthetic value of sandy beaches (Llewellyn and Shackley 1996; Engelhard and Withers 1997). Ecological impacts caused by grooming usually depend on the type of equipment used in the process. For instance, Kinzelman and others (2004) described how density of *E. coli* in the sediment of beaches of the Great Lakes (Winsconsin) was 80% greater after deep grooming with finisher, compared to sites groomed without finisher. Beach cleaning may range from litter hand-picking to mechanical operations, where sand is sifted and either organic matter or garbage are removed (Davenport and Davenport 2006). Mechanical beach cleaning uses mobile machines (e.g. converted potato pickers) that have a conveyor belt raking mechanism and scrape the sediment to a depth of up to 20 cm (Llewellyn and Shackley 1996).

Beach cleaning is likely to cause both direct and indirect impacts on sandy beach species (Table 12). Wrack and organic matter stranded on the beach represent critical sources of shelter and food not only for small invertebrates (Coupland and others 2007; Brown and others 2008), but also for scavenging vertebrates including birds and mammals (Dugan and others 2003; Davenport and Davenport 2006). Although wrack is continuously deposited on the beach by the incoming tides (Gheskiere and others 2006), its frequent removal by beach cleaning can decrease the diversity and abundance of consumers depending on it for survival (Llewellyn and Shackley 1996; Dugan and others 2000; Dugan and others 2003). For instance, reductions in density of macrofauna species have been reported to exceed 50% on mechanically cleaned beaches of the United States, Europe and South-East Asia

(Table 12). Mechanical beach cleaning is also known to reduce the performance of native coastal dune plants by reducing their seedbank, survival, and reproduction, and by causing alterations in the stability of dunes (Dugan and Hubbard 2010). Plants are weighed down by the unbalanced sand sheet and sand movement produced by the grooming regime (Dugan and Hubbard 2010).

Table 12 Summary of reported environmental effe	s of mechanical beach cleaning on sand	ly shores (exposed and sheltered	d) and coastal dunes
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Reference	Geographic Locality	Type of Habitat	Effect: Physical	Effects: Biological and Ecological
Davidson and others 1991	Great Britain		Reduced dune stability	Damage to and reduction of invertebrate populations (no effect sizes available)
Kirby 1992	UK			Damage to isopods, ground beetles and flies that use driftwood and jetsam as shelter (no effect sizes provided)
Llewellyn and Shackley 1996	UK	Sandy shore in bay	Sediment compression; scouring; erosion	Reduced and density (up to 100%) of strandline-related species (Coleoptera; Diptera; Amphipoda); burial of invertebrates
Engelhard and Withers 1997	Texas, USA	Exposed sandy beach		Benthic organisms (e.g. polychaete) and wrack-associated organisms (e.g. insects and <i>Orchestia</i> spp.) affected by cleaning within three days; recovery within 14 days post cleaning
Dugan and others 2000	California, USA	Exposed sandy beach		Reduced macrophyte wrack cover (up to 99%) compared to sites not subject to grooming; intertidal cover of marine wrack (up to 90%); reduced macrofauna species richness (up to 70%) and density (up to 97%)
Dugan and others 2003	California, USA	Exposed sandy beach	Sediment compression; scouring	Reduced marina macrophyte wrack cover (up to 99%) compared to reference beaches; reduced macrofauna species richness (up to 80%) and density (up to 100%)
Kinzelman and others 2004	Winsconsin, USA	Sandy beach of the Great Lakes		Increased <i>Escherichia coli</i> content in the sediment (up to 80%) using deep grooming compared to grooming without finisher

Reference	Geographic Locality	Type of Habitat	Effect: Physical	Effects: Biological and Ecological
Malm and others 2004	Sweden	Exposed sandy beach	Reduced sediment organic content	Reduced number of bacteria in the sea water (3x) compared to reference beaches; reduced number of large ciliates (over 50%); reduced density of <i>Mysis / Praunus</i> (70%); changes in community structure (dominance of palnktivore shrimps, bacteria and ciliates
Fanini and others 2005	Italy	Exposed sandy beach		Reduced density of talitrid amphipods; 5x greater impact on talitrid populations compared to reference sites
Gheskiere and others 2006	Belgium	Exposed sandy beach		Reduced organic matter (50%); reduced density of meiofauna assemblages (50%); changes in community structure
Martin and others 2006	California, USA	Exposed sandy beach		15-25% loss of grunion eggs (Leuresthes spp.)
Souza and others 2008	Northeastern Brazil	Exposed sandy beach		Removal of organic matter; reduced number of species related to organic matter (e.g. <i>Emerita</i> spp.)
Yong and Lim 2009	Singapore	Exposed sandy beach	Sediment disruption	Wrack removal; reduced density of ghost crab burrows (up to 50%); potential depletion of food sources for ghost crabs; potential reduction in the quality of substratum for ghost crab burrow construction
Dugan and Hubbard 2010	California, USA	Exposed sandy beach and dunes	Increased width of unvegetated dry sand zones (4x) compared to reference sites; increased aeolian sand transport	Reduced macrophyte wrack cover (over 9x); reduced plant abundance (15x); reduced plant richness (over 3x)

#### Vehicle traffic

Off-road vehicles (ORVs) have become common on many sandy beaches and coastal dunes since the late 1960s (Fialka 1975). Due to higher demands for coastal recreation, more leisure time, and economical affluence, 'mechanized recreation' using four-wheel drive (4WD) cars, quad bikes, motorbikes and other 'off-highway' vehicles has increased in many coastal regions (Fialka 1975; Godfrey and Godfrey 1980), becoming an important resource for the economy of many coastal populations around the world (Fialka 1975). The use of off-road vehicle recreation can be controversial as it is associated with a wide range of negative physical and ecological impacts (Silberman and Andereck 2006), and it is often perceived as an environmentally degrading practice (Priskin 2003b). However, Silberman and Andereck (2006) discussed the necessity to compare the costs of off-road vehicle use to the consumer surplus (the economic measure of one's satisfaction beyond all financial costs) deriving from ORV-associated recreation, when critical decisions in the regulations of ORV use have to be made. The economic benefits of ORV recreation can be high (almost 100 US dollars per capita), and therefore have to be included in land management policies (Silberman and Andereck 2006).

There is a growing body of scientific evidence about the negative environmental consequences of vehicle use on beaches and dunes. Detrimental effects range from physical alterations to the habitats to significant changes in species density and assemblage structure (Table 13).

The physical impacts of ORV use on coastal dunes are wide and include: increased bulk density, penetration resistance, and sediment compactness of the soil; severe rutting and incisions of the dune-beach interface; sediment displacement and

enhanced wind and water driven erosion rates; increased shoreline retreat (Table 13). These physical impacts are exacerbated by the considerable destruction and displacement of dune vegetation, particularly in vehicle tracks (up to 100%). The crushing of plant seeds is chiefly detrimental as it eliminates the potential for embryo dune formation (Godfrey and Godfrey 1980). Many species of invertebrates (e.g. ghost crabs), birds (e.g. sanderlings), mammals (e.g. rodents) and reptiles (e.g. lizards) reliant on coastal dune habitats are heavily affected by ORV impacts, which cause reductions in species density, richness and diversity (Table 13).

Recovery of species from the passage of vehicles on the dunes may be very slow and take up to four years or more, depending on the intensity of the impact (Godfrey and Godfrey 1980): Kutiel and others (2000) reported that the damage of 100 motorcycle passes on coastal dunes was still visible after 45 days, with species richness and diversity remaining lower than control sites by 25 and 30% respectively (Kutiel and others 2000). Rickard and others (1994) observed that the effects of intense experimental ORV traffic on the survival of dune vegetation were not evident until three months post-impact, when all the vegetation traversed finally died (Rickard and others 1994). Godfrey and Godfrey (1980) showed that on exposed beaches of North Carolina, 50 vehicle passes stopped seaward dune growth completely, while 70 to 175 passes reduced the dune plant biomass to nearly zero. Thompson and Schlacher (2008) found that vehicle access tracks in camping zones of world heritage listed Fraser Island caused the loss of one-fifth of the dune front.

Off-road vehicle traffic inflicts severe and measurable damage to unvegetated sandy shores (Table 13). Vehicles travelling along the beach leave deep rutting and tracks that can cover up to 90% of the intertidal zone (Schlacher and Thompson 2008), reducing sand compactness (Schlacher and others 2008c) and enhancing downshore

sediment displacement (Schlacher and Thompson 2008). Rutting of the intertidal beach overlaps with the distribution of intertidal fauna and results in the disruption of the habitat matrix of macrofaunal species burrowing to a depth of 30 cm (Schlacher and Thompson 2008). Critical ecological impacts of off-road vehicle use on the beach affect invertebrate species as well as threatened vertebrate species, and include: crushing and reduced density of key invertebrates such as clams (over 50% population reductions), gastropods (over 10% population reductions), mysids (up to 70% population reductions), ghost crabs (up to 100% population reductions) and bubbler crabs (up to 100% population reductions); destruction of bird nests, eggs and hatchlings; reduced density of bird species such as plovers and oystercatchers; crushing of turtle eggs; killing of turtle hatchlings; impairment of turtle hatchlings to reach the surf; increased predation risk of turtle hatchlings (Table 13).

Recovery of fauna from ORV impacts is possible when restrictions are applied for long enough periods of time: the banning of vehicles from beaches of North Carolina (24 hours a day for six months) have proven to result in significant recovery of ghost crab populations (Hobbs and others 2008), while a substantial increase in breeding rates and densities of shorebirds occurred one to two years following banning of off-road vehicles on the sandy shores of South Africa (Williams and others 2004).

Physical and ecological impacts that off-road vehicle use has on coastal dunes and unvegetated sandy shores are summarized in Table 13. Of the studies summarized in the table, 39% report the results of work done in the USA, 34% are from surveys on Australian shores, 15% are from Africa (South Africa in particular), while only 5% are from South America, 5% from Europe (UK), and the remaining 2% from Asia (Israel). Almost twice as many of the following studies were done on intertidal sandy beaches as were on vegetated coastal dunes (Table 13). Moreover, 29% of the

surveys dealt with ORV impacts on vegetation cover and plant species richness and diversity, versus 71% describing impacts on density, species richness and diversity of fauna (Table 13).

## Table 13 Summary of reported environmental effects of vehicle traffic on coastal dunes and beaches

Reference	Geographic Locality	Area of Impact	Effect: Physical	Effects: Biological and Ecological			
Coastal Dunes and Unvegetated Sandy Beach							
Fialka 1975	USA	Coastal dunes; unvegetated sandy beach	Sediment compaction	Local extinction of ghost crabs, sanderlings and turtles			
Liddle and Greig-Smith 1975a	Wales, UK	Coastal dunes	Increased bulk density (up to 30% more than pedestrian trampling); increased penetration resistance (up to 100% more than pedestrian trampling) and sediment compaction (>6 cm depth); water content of soil greater than adjacent undisturbed areas	Increase in water content of soil, which may aid survival of plants in tracks			
Liddle and Greig-Smith 1975b	Wales, UK	Coastal dunes		Changed composition of dune vegetation; reduced vegetation cover (up to 60%) and species richness (up to 60% in dry sand and 70% in wet sand) compared to reference			
Godfrey and Godfrey 1980	North Carolina, USA	Coastal dunes; unvegetated sandy beach	Cessation of seaward dune growth after 50 vehicle passes (rehabilitation in two years)	Reduction in dune vegetation cover (up to 100%) after 70-175 passes; disturbance of microscopic organisms associated with high drift lines (e.g. diatoms and bacteria); 50% reduction in detritus and bacteria in the backshore; complete destruction of seeds of sprouting beach plants which are deposited along the drift lines and supposedly form embryo dunes; crushing of bird nests and killing of chicks that hide in vehicle tracks			
Hosier and Eaton 1980	North Carolina, USA	Coastal dunes, marsh and grassland	Soil compaction in areas affected by traffic; erosion	Reduced dune vegetation cover (over 45%) and grassland cover (over 27%)			
Gilbertson 1981	Adelaide, Australia	Coastal dunes	Increased soil erosion; destabilized dunes; collapsing of dune ridges and enhanced dune mobility; compacting of clay behind dunes; 4x increase in soil shear strength; reduced water penetration; enhanced water driven erosion	Scrub and sand-binding grass damage			

Reference	Geographic Locality	Area of Impact	Effect: Physical	Effects: Biological and Ecological
Luckenbach and Bury 1983	California, USA	Algodones dunes		Elimination of plants and wildlife in heavily used areas; reduced density of herbaceous and perennial plants compared to control sites; reduced plant density and richness (up to 100%); reduction of the density (5.1x) and richness (1.5x) of rodents; reduction of the density (3.5x) and richness (1.8x) of lizards
Anders and Leatherman 1987a	Fire Island, NY, USA	Coastal dunes; unvegetated sandy beach	Sediment displacement by up to 119,300 m <sup>3</sup> per year for entire shoreline length (island: 53 km long); most displacement in the first ten ORV passes; steeper beaches more susceptible to erosion; dunes most susceptible to erosion followed by intertidal foreshore	
Anders and Leatherman 1987b	Fire Island, NY, USA	Coastal dunes	Over 3x greater shoreline retreat by erosion in site affected by ORV traffic vs. control site	Dune front vegetation retreated by ~0.5 m in sites affected by vehicular traffic (1 ORV pass per week for 12 weeks) vs. dune front vegetation of control sites which advanced by ~0.5 m; after a year of impact at same intensity (1 ORV pass per week), dune front vegetation of impact sites had retreated by ~4.0 m vs. vegetation of control sites which had advanced by over 1.0 m; up to 100% reduction in ground cover of beach grass in impact sites vs. 20% increase in beach grass cover in control sites
Carlson and Godfrey 1989	Massachusetts, USA	Coastal dunes		Reduced vegetation species richness (60%) and percent cover (over 80%)
Rickard and others 1994	Eastern Cape, South Africa	Coastal dunes		Initial decline of vegetation (particularly mature shrub) height and cover (almost 50%) after 100 vehicle passes; turning vehicles more damaging than vehicles driving in a straight line

Reference	Geographic Locality	Area of Impact	Effect: Physical	Effects: Biological and Ecological
Watson and others 1996	Algoa Bay, South Africa	Coastal dunes; unvegetated sandy beach		High susceptibility to traffic by birds nesting within 40 m of the high water mark; oystercatchers most susceptible
Kutiel and others 2000	Israel	Coastal dunes	Decrease in depth of soil penetration (still effective 72 days following 100-200 vehicle passes)	Reduced vegetation cover (50%), height (50%), species richness (30%) and diversity (25%) 18 days after 100 and 200 passes; impacts visible up to 45 days following passes
Priskin 2003a	Western Australia, Australia	Coastal dunes; unvegetated sandy beach	Increasing density of vehicle track number (50%) and length (40%) (on dunes) over the years	
Groom and others 2007	California, USA	Algodones dunes		Reduced (4-5x) density of <i>Astragalus</i> magdalenae var. peirsonii compared to control; 33% reduction in survival of plants with canopy diameter <50 cm
Thompson and Schlacher 2008	Fraser Island, Queensland, Australia	Coastal dunes; unvegetated sandy beach	Destruction of 1/5 <sup>th</sup> of the dune front in camping zones; incisions of the dune- beach interface; erosion and shoreline retreat (scalloping)	Destruction of 60% of dune vegetation in ORV tracks; reduced number of zero count samples of ghost crab burrows in first (30%) and second (80%) dune ridge in vehicle tracks compared to abutting dunes; reduced burrow size (>8%) in tracks compared to dunes
Unvegetated Sandy Beach Only				

Leggett 1975	Back Bay National Wildlife Refuge, Virginia, USA	Unvegetated sandy beach	Reduced ghost crab density and size (effect sizes not available)
Fisher and Tevesz 1979	Virginia to North Carolina, USA	Unvegetated sandy beach	1.5x less ghost crab burrows in ORV zones than pedestrian sites; significantly altered juvenile : adult ratio in heavily disturbed sites (up to 1 adult:21 juveniles in ORV sites vs. 1 adult: 3 juveniles in trampling sites)
Hosier and others 1981	North Carolina, USA	Unvegetated sandy beach	Turtle hatchlings impeded to reach the sea by the rutting from ORVs; inverting of hatchlings trying to climb ruts; reaching of the surf at slower rate, with increasing risk of predation and stress

Reference	Geographic Locality	Area of Impact	Effect: Physical	Effects: Biological and Ecological
Steiner and Leatherman 1981	Assateague Island, Maryland-Virginia, USA	Unvegetated sandy beach		Decrease in ghost crab burrow density (>60x) compared to beaches with light recreation (trampling)
Wolcott and Wolcott 1984	North Carolina, USA	Unvegetated sandy beach		Mole crabs and ghost crabs 5 cm or deeper in the sand relatively immune to ORV traffic, but killed by crushing while surface active; 1.4% mole crabs killed by one ORV pass; surf clams immune to one ORV pass; 100-500 vehicle passes resulted in a 14-98% ghost crab population decrease
Bouwer 1986	KwaZulu-Natal, South Africa	Unvegetated sandy beach		Reduced ghost crab density in areas of ORV traffic (effect sizes not available)
Christoffers 1986	Assateague Island, Maryland-Virginia, USA	Unvegetated sandy beach	Alteration of the moisture content of the surface sediment; drying of surface sediment	Lower density of ghost crab burrows (up to 95%) compared to no-traffic zones and burrow diameter (up to 70%)
Arianoutsou 1988	Greece, Europe	Unvegetated sandy beach		Direct disturbance to nesting turtles which return to the water
Buick and Paton 1989	South Australia, Australia	Unvegetated sandy beach		Destruction of bird nests; 81% (artificial) bird (plover) nests run over by ORVs during the incubating period
van der Merwe and van der Merwe 1991	Eastern Cape, South Africa	Unvegetated sandy beach		Killing of invertebrate species including the mysid <i>G. psammodytes</i> (up to 70% after 10 passes in 1 hour), the clam <i>D. serra</i> (<10% after 50 passes in 1 hour) and the gastropod <i>B. rhodostoma</i> (>10% after 5 passes in 1 hour) (10 cm into the sand); compact sand increases survival chances for clams and whelks; soft-bodied mysids at greater risk; isopods on the upper shore highly vulnerable to traffic due to softer sand and cars following same tracks
National Marine Fisheries Service and U.S. Fish and Wildlife Service 1993	US Caribbean Sea, Atlantic Ocean and Gulf of Mexico	Unvegetated sandy beach		Direct crushing of turtle eggs and hatchlings

Reference	Geographic Locality	Area of Impact	Effect: Physical	Effects: Biological and Ecological
Boon and others 1999	South Africa	Unvegetated sandy beach		Direct crushing of surface active ghost crabs (effect sizes not available); ghost crabs disoriented / attracted by headlights
Hastie 2002	New South Wales, Australia	Unvegetated sandy beach		10-40 vehicle passes caused no significant impact on ghost crab densities
Williams and others 2004	Western Cape, South Africa	Unvegetated sandy beach		Reduced densities of plovers (50%) and oystercatchers (60%) that nest on the beach
Blankensteyn 2006	Santa Catarina, Brazil	Unvegetated sandy beach		No ghost crab burrows in beaches with ORV traffic
Moss and McPhee 2006	North Stradbroke Island, Queensland, Australia	Unvegetated sandy beach		Significantly less (>50%) ghost crab burrows on beaches open to vehicles compared to control
Neves and Bemvenuti 2006	Rio Grande do Sul, Brazil	Unvegetated sandy beach		Density of ghost crab in undisturbed beach up to 6x greater than in beach with heavy trampling and light vehicle traffic, and up to 6x greater than in beach with light trampling and heavy ORV traffic; burrows in beach with light trampling and ORV traffic only found in a 25 m strip protected from traffic
Foster-Smith and others 2007	Broome, Western Australia, Australia	Unvegetated sandy beach		Negative correlation between number of tyre tracks and ghost crab burrow numbers ( <i>p</i> <0.001); <u>no ghost crab burrows</u> in zones of high vehicle use compared to zones of no vehicle use; <u>no bubbler crabs</u> in beach zones with 100% tyre track cover
Maccarone and Mathews 2007	Texas, USA	Unvegetated sandy beach		Reduced ghost crab burrow density (3x) in beaches with high ORV compared to beaches with light impact; re-distribution of ghost crabs on beach strips protected from traffic
Schlacher and Thompson 2007	Eastern Australia	Unvegetated sandy beach		Direct exposure (65%) of intertidal burrowing invertebrate species to traffic

Reference	Geographic Locality	Area of Impact	Effect: Physical	Effects: Biological and Ecological
Schlacher and others 2007b	Eastern Australia	Unvegetated sandy beach		Reduced ghost crab burrow density in areas of heaviest ORV impact (particularly below drift line); 100% mortality by crushing after 10 vehicle passes at 5 cm depth; 0.75% mortality of intertidal ghost crab population after one vehicle pass during surface activity
Hobbs and others 2008	North Carolina, USA	Unvegetated sandy beach		Reduction in ghost crab burrow density (up to 100%); ORV use restrictions (24 h) resulted in significant recovery of densities (up to 30%, $p$ <0.050); ORV restriction 10 h per day (20:00-06:00 June-November 2003) resulted in significant recovery at one site ( $p$ =0.015) but not in at another site ( $p$ =0.113) Significantly smaller burrow size in ORV sites ( $p$ <0.001)
Schlacher and Morrison 2008	Eastern Australia	Unvegetated sandy beach	Severe rutting of intertidal zone (85% after 100 vehicle passes);	
Schlacher and others 2008a	Eastern Australia	Unvegetated sandy beach		Reduced macrobenthic species density in middle shore (70%) and upper shore (almost 100%), reduced richness (over 80% in the upper shore and over 60% in the middle shore) of macrobenthic fauna; shifts in community structure
Schlacher and Thompson 2008	Eastern Australia	Unvegetated sandy beach	Severe rutting (up to 90% of the intertidal beach); sediment displacement (~50% from upper shore)	Overlapping of beach fauna distribution with ORV traffic; disruption (<10%) of faunal habitat matrix (30 cm depth) in one day
Schlacher and others 2008c	Eastern Australia	Unvegetated sandy beach	76% and 85% reduction in sand compactness after 5 and 40 passes (applied in <1 h) of a vehicle turning across the beachface	53% mortality of beach clams ( <i>Donax</i> <i>deltoides</i> ) from 40 passes (applied in <1 h) of a vehicle turning across the beachface; up to 6x greater mortality in softer and drier sand (higher intertidal zone) than in more compact and saturated sand (lower intertidal zone)
# Table 13 Continued

Reference	Geographic Locality	Area of Impact	Effect: Physical	Effects: Biological and Ecological
Sheppard and others 2009	Eastern Australia	Unvegetated sandy beach		16% reduction in body mass index of beach clams ( <i>D. deltoides</i> ) subjected to ORV traffic compared to clams not subjected to traffic; 50% less clams burrowed after being run over by vehicles (30 passes) and dislodged compared to clams from undisturbed sites; run over clams took 2x longer to begin burrowing compared to clams from undisturbed sites
Lucrezi and Schlacher 2010	Eastern Australia	Unvegetated sandy beach		Reduced size (20%) of ghost crab burrow openings compared to control sites; simplification of burrow architecture (from 4 to 2 types) by smaller crabs; increased burrow depth (30%), length and volume (10%) post peak traffic periods

#### Climate change: increased storms

Global climate change is predicted to lead to more intense and destructive storms (Sepp and others 2005; IPCC 2007; Trenberth and others 2007). Storms are a major external control of coastline dynamics and morphology, particularly along soft-sediment shorelines (Feagin and others 2005). The increase in storm intensity and duration is a result of rising sea temperatures (Meehl and others 2007) and changes in atmospheric circulation (stronger winds) (IPCC 2007; Jones and others 2007; Poloczanska and others 2007). However, the destructiveness of storms is also exacerbated by sea level rise (Zhang and others 2002; Bindoff and others 2007).

Storm impacts on beaches are manifested in significant erosion events (Table 14), which translate into loss of habitat and threats to coastal infrastructure (Jones and others 2007), accompanied by shoreline retreat (Ashton and others 2007), flooding (Hughes 2003; Fenger and others 2008), increased deposition of wrack (McLachlan 1985; McGwynne and others 1988), and alterations in beach morphology (Tõnisson and others 2008). The impacts of storm events on sandy beaches have also been reported to be exacerbated on armoured and developed beaches (Nordstrom 2000; Castelle and others 2008), which will impede shoreline retreat. Severe climatic conditions such as those encountered during storms and strong wave action cause short- and long-term changes in the sandy beach habitat, with indirect detrimental impacts on the biota via reduction and elimination of vital resources (Shepherd and others 1991; Ogden 1992), and direct impacts such as death by flooding, burying and drowning (Norkko and others 2002).

Storm tides may cause foredune breakdown and the formation of washover fans via the deposition of sand from the beach through and into the dune zone

(Godfrey and Godfrey 1980). Impacts of increasing storminess such as the formation of washover fans are also exacerbated by vehicular traffic, lowering the resiliency of frontal dune systems (Godfrey and Godfrey 1980; Thompson and Schlacher 2008).

Ecological impacts of severe storms and related climatic events on sandy shores are various (Table 14) and include: complete destruction of mangrove forests; burial and death of shallow-burrowing invertebrates in the intertidal zone; migration of invertebrates such as ghost crabs into the dunes; destruction of dune habitat for vertebrate species including birds and beach mice; stranding, disorientation and death of turtles (Table 14).

Table 14 Reported ecological impacts o	f storms and related climatic events	on sandy shores an	d other coastal environments

Reference	Geographic Location	Coastal Habitat Type	Species	Impact Type	Effect	Reported Recovery
Limpus and Reed 1985	Gulf of Carpentaria, Australia	Estuarine mudflats	<i>Chelonia mydas</i> (green turtle)	Cyclone (Kathy)	Turtles stranding on mudflats; 20% death of stranded turtles; disorientation of stranded turtles	Rescue operations following cyclone
Lohrer and others 2004	North Island of New Zealand	Estuarine mudflats	Macrobenthic communities (including bivalves, polychaetes, gastropods, decapods, amphipods)	Terrigenous sediment runoff from human activities and heavy rainfall	Decrease in density and richness ( <i>p</i> <0.001) 3 days after deposition (3 mm); shallow-burrowing organisms more severely affected than deep-burrowing organisms; repeated depositional events more damaging than single event	
Hobbs and others 2008	Cape Hatteras National Seashore, North Carolina, USA	Sandy beaches; coastal dunes	<i>Ocypode quadrata</i> (ghost crab)	Tropical Depression Henri, Hurricane Fabian, and Hurricane Isabel	Significant decrease in burrow sizes during the storm events (means smaller by up to 15 mm; <i>p</i> <0.001)	Compared to pre-storm values (1-5 months before the storm): up to 30% increase in burrow density after storm events in areas where the lower beach was closed to ORVs ( <i>p</i> <0.050); up to 15% increase after storms in areas where lower beach was closed for 10 hours; up to 10% increase after storm in areas open to ORVs; burrow sizes remained smaller than pre-storm values 2 months after the storm events

# **Table 14 Continued**

Reference	Geographic Location	Coastal Habitat Type	Species	Impact Type	Effect	Reported Recovery
Norkko and others 2002	North Island of New Zealand	Estuarine mudflats	Estuarine macrobenthic communities (e.g. bivalve and mud crab)	Extreme rainfall; flooding; clay deposition; storm event (28 days after clay deposition)	50% reduction in density after 3 days; 90% reduction after 10 days	Mud crab <i>Helice crassa</i> only species to emerge from clay deposit; dispersion of clay following storm event; 408 days following study recover still incomplete
Ogden 1992	South Florida, USA	Mangrove forests	<i>Rhizophora mangle</i> (red mangrove)	Hurricane (Andrew)	Severe defoliation; complete destruction of mature (up to 15 m tall) mangrove forests	32 years post hurricane the height of the destroyed forest only recovered to shrub height
Saintilan and Williams 1999	Southeastern Queensland and New South Wales, Australia	Intertidal mangrove; salt marshes	Mangrove species	Increase in average annual precipitation	Diluting salt in saltmarshes and enhancing colonization of mangrove; landward transgression of species into saltmarsh	
Shepherd and others 1991	Pumpkinseed Island, South Carolina, USA	Maritime forests; marshes	Wading birds (e.g. <i>Casmerodius albus</i> (great egrets); <i>Egretta</i> <i>thula</i> (snowy egrets); <i>Plegadis falcinellus</i> (glossy ibises); <i>Egretta</i> <i>tricolor</i> (tricolor egrets)	Hurricane (Hugo); storm surge 2-3 m above normal	60-75% removal of marsh shrub (nesting site); no breeding pairs during storm for all species	44% and 19% fewer breeding pairs 10 months after the storm (great egrets and tricolor herons); 36% increase for snowy egrets

# **Table 14 Continued**

Reference	Geographic Location	Coastal Habitat Type	Species	Impact Type	Effect	Reported Recovery
Swilling and others 1998	Alabama, USA	Sandy beaches	Peromyscus polionotus ammobates (Alabama beach mice)	Hurricane (Opal); storm surge 3-4 m above normal	Destruction of primary dunes (habitat); population decrease (during storm) up to 70%; significant migration to transition habitat (scrub / transition areas <i>p</i> <0.004)	7-10 months after storm density was still 23-30% lower than pre- storm values
Walker and others 2008a	One Tree Reef, Southern Great Barrier Reef, Australia	Intertidal zone of the coral reef	Sessile species (encrusting ascidians, sponges, bryozoans, bivalves, polychaetes, crustaceans, cnidarians)	Different levels of wave action	Fewer number of species (119%) on exposed low-shore than exposed high-shore; 210% increase in species density from low- to high-shores on the exposed shore; in sheltered sites, the magnitude of the difference was smaller (50% increase in species density from low- to high- shore sites)	

# Ghost Crabs as Indicators of Human Stressors on Sandy Beaches

Sandy beaches are increasingly threatened by a plethora of human pressures and negative ecological consequences of development, resource extraction, pollution and intensive recreational use are evident on many shores worldwide (Defeo and others 2009). Arguably, these developments require a re-focusing of shoreline management from the traditional dominance of geo-physical processes to increasingly include ecological dimensions (Schlacher and others 2006). A fundamental step in ecologically-orientated coastal ecosystem management is to undertake scientifically robust assessments of environmental impacts and accurately measure the efficacy of management interventions (Niemi and McDonald 2004). Therefore, ecological indicators are an important ecosystem management tool (Aubry and Elliot 2006).

# Ecological indicators: definition and characteristics

Ecological indicators are commonly defined as 'The measurable characteristics of the structure, composition, or function of ecological systems' (Niemi and McDonald 2004). Indicators are designed to simplify, quantify and communicate (Aubry and Elliot 2006). They can act as proxy for entire ecosystems, their value can be compared to reference values from pristine locations, and their use facilitates the communication of environmental issues to decision makers and managers (Dale and Beyeler 2001; Niemeijer and de Groot 2008).

To be efficient and effective, indicators must meet several criteria: 1) be easy to identify and measure; 2) be sensitive to stresses on the system; 3) have predictable responses to stress; 4) have low variability in response to stress; 5) be insensitive to expected sources of interference; 6) have a documented reaction to natural and

anthropogenic disturbances in the system; 7) provide information at the right spatial and temporal scales; 8) be anticipatory and predict changes that can be prevented through management; 9) have good statistical properties; 10) require easy data collection skills; 11) have low cost; 12) have large number of species with known response to disturbance; 13) be compatible with other indicators developed and used in other regions (Noss 1990; Niemi and McDonald 2004).

## The use of indicator species

Indicator species are commonly used thanks to their greater ease of study compared to genes, communities, and entire ecosystems (Noss 1990; Lambeck 1997).

Invertebrates in particular are highly effective ecological indicators of human impacts in various ecosystems (Sherman and Coull 1980; Llewellyn and Shackley 1996; Schoeman and others 2000; Moellman and Corbisier 2003; Fanini and others 2005; Gheskiere and others 2005; Veloso and others 2006; Schlacher and others 2007b; Jones and others 2008; Schlacher and others 2008a; Ugolini and others 2008), and have been employed in numerous surveys that assessed the ecological status of sandy beaches around the world (Carignan and Villard 2002). Invertebrates respond to disturbances at a finer spatial scale than other organisms (Schoener 1986), and their density responses are often better correlated with environmental drivers rather than biological factors such as competition and predation (Wenner 1988).

On sandy beaches, several crustaceans appear to be suitable candidate species for ecological indicators, as they are relatively abundant, widespread and sometimes easy to count and collect (Wenner 1988; Lercari and Defeo 1999; Schlacher and others 2007b; Schlacher and others 2008a). In fact, differences in the

population densities of a single species between disturbed and undisturbed locations have successfully provided evidence of negative anthropogenic influences on sandy beaches (Barros 2001).

### Ghost crabs as indicators of human stressors on sandy beaches

Ghost crabs (genus *Ocypode*) are common semi-terrestrial crabs (Ng and others 2008; De Grave and others 2009) that burrow from tropical to warm-temperate sandy beaches worldwide (Dahl 1953). *Ocypode* crabs are ecologically important as they represent the top invertebrate predator on sandy beaches (Wolcott 1978), and are also preyed upon by higher order organisms (Alcock 1902; Iwamoto 1986; Jackson and others 1991; Barton and Roth 2008). Therefore, a reduction in the number of ghost crabs caused by human disturbance may indirectly affect other species that rely on these animals as a source of food.

Ghost crabs have been used to measure different types of anthropogenic pressures (Table 15). However, some stressors have been investigated more often than others, and some stressors have not been examined at all. Pooling most of the studies that used *Ocypode* as ecological indicators, human stressors on sandy shores and coastal dunes have been treated in the following decreasing order of importance: ORV traffic (40%); trampling (24%); urbanization (14%); armouring (9%); storms (5%); camping (2%); habitat change (2%); nourishment and bulldozing (2%); oil pollution (2%). The literature has very little or no record of the employment of ghost crabs as indicator of key pressures including mechanical beach cleaning, pollution (oil and litter), nourishment, camping, and habitat modification via replacement of native with alien plant and tree species (Table 15).

As previously mentioned, amongst the major criteria that indicators must meet to be reliable are the following: the need for a large number of species from the same genus to have a known response to disturbance; compatibility with other indicators developed and used in other regions (Noss 1990; Niemi and McDonald 2004). Out of 28 known species of ghost crabs, only 5 have been employed in monitoring of sandy shores (Table 15). Furthermore, most surveys have taken place on sandy beaches of Australia (38%), followed by the USA (28%), South America (17%) and Africa (14%). *Ocypode* has not been used in monitoring of European coastlines, and there is only one record for Asian regions (Table 15).

Part of building a solid indicator species for monitoring should involve the design of experimental surveys that test whether the species meets the relevant criteria. However, most monitoring studies using ghost crabs as indicator of anthropogenic stressors on sandy beaches have been based on simple 'contrast and compare' methods (Table 15). Only four studies (Wolcott and Wolcott 1984; Hastie 2002; Schlacher and others 2007b; Lucrezi and others 2009a) experimentally measured changes in ghost crab densities as a result of trampling and ORV impacts (Table 15).

During monitoring studies that used ghost crabs as predictor of ecological change from human impacts on sandy shores, several types of response variables have been measured (Table 15). The most used variable yet is the density of ghost crab populations via counts of active burrow openings (>90% studies), followed by crab size via measurements of the diameter of burrow openings (50% studies), and crab distribution across the shore (40%). Body condition has been rarely used (2 studies). Novel indicators such as burrow architecture (shape, depth, length and volume), movement and home ranges, and reproduction (e.g. oogenesis, spawning and

recruitment) should be introduced both to fill in the current literature gaps regarding the ecology and life cycle of ghost crabs, and to add robustness to the role of *Ocypode* as effective indicator of anthropogenic stressors on sandy shores and coastal dunes.

Results from monitoring surveys employing *Ocypode* as indicator species of human stressors on sandy beaches and coastal dunes are summarized in Table 15, where effect sizes (means from impact sites divided by means from control sites) from each study are also reported. The greatest effect sizes (<0.01) for ghost crab burrow densities appear to be produced by combined impacts (from urbanization, recreational ORV use and trampling) (Table 15). Off-road vehicle use and heavy urbanization alone have been reported to generate substantial effect sizes (<0.01), with up to 100% reductions in ghost crab population densities compared to undisturbed sites (Table 15). Armouring also gives effect sizes as great as 0.11 (Barros 2001). Heavy trampling (100 pedestrian passes over 15 m<sup>2</sup>) can produce considerable effect sizes (0.13; Lucrezi and others 2009a), although burrow densities easily recover in the short term (days). No substantial effect sizes have been reported from camping as a stressor (de Jager 2009).

Table 15 The use of	<i>Ocypode</i> as indicator	of human stressors or	n sandy beaches	and coastal dunes
	21		,	

Human Pressure	Species	Geographic Locality	Response Variable	Observed Effects / Impacts	Effect Size(s) x̄ <sub>Impact</sub> / x̄ <sub>Reference</sub>	Notes	Reference
Dune Camping	O. cordimanus	North Stradbroke Island, Queensland, Australia	Density, distribution and size of active burrow openings; body condition index	No significant difference in density between camping and no-camping sites; shifts in distribution across the dune field with crabs attracted to camping sites; higher body condition of crabs in camp sites, presumably as result of feeding on food scraps.	Density: no effect Size: 0.97 Body Condition: 1.06		de Jager 2009
Introduction of alien vegetation	O. ceratophthalma; O. cordimanus; O. ryderi	Central Seychelles	Species richness and density of active burrow openings	Lower species richness (50%) and density (up to 100%), possibly a result of less suitable substrate types for burrowing	Richness: 0.50 Density: <0.01		Brook and others 2009
Multiple: vehicle traffic and trampling	O. quadrata	Virginia to North Carolina, USA	Density and size of active burrow openings	1.5x less burrows in ORV zones than pedestrian sites; significantly altered juvenile : adult ratio in heavily disturbed sites (up to 1 adult:21 juveniles in ORV sites vs. 1 adult: 3 juveniles in trampling sites)	Density: 0.58		Fisher and Tevesz 1979
Multiple: vehicle traffic and trampling	O. quadrata	Assateague Island, Maryland-Virginia, USA	Density of active burrow openings	Burrow density in beaches with light recreation ~2x greater than in undisturbed beaches, ~20x greater than in beaches with light ORV impact, and >60x greater than in beaches with heavy ORV traffic; increase in food sources – food scraps left by visitors possibly beneficial	Density: 1.90 (trampling) Density: 0.03 (vehicle traffic)		Steiner and Leatherman 1981
Multiple: urbanization; armouring	O. ceratophthalma; O. cordimanus	Sydney area, New South Wales, Australia	Density of active burrow openings	Significantly fewer (up to 3x) ghost crab burrows in urban beaches ( $p$ =0.020) compared to reference sites; significantly lower burrow density (almost 10x) below the foredune / wall in urban beaches than in non-urban beaches	Density: 0.11		Barros 2001
Multiple: urbanization and recreation	O. quadrata	Saõ Paulo State, southeastern Brazil	Density, distribution and size of active burrow openings	Density up to 10x greater in non-urban than urban beaches; burrow density in upper intertidal zone of undisturbed beaches with vegetated dunes >10x greater than density in upper intertidal zone of urban beaches with infrastructure ( $p$ <0.001) Significantly smaller (means up 10 mm smaller) burrows in urbanized beaches than non-urban beaches ( $p$ <0.010)	Density: ~0.07 Size: ~0.60		Turra and others 2005

Human Pressure	Species	Geographic Locality	Response Variable	Observed Effects / Impacts	Effect Size(s) X <sub>Impact</sub> / X <sub>Reference</sub>	Notes	Reference
Multiple: vehicle traffic, trampling and fishing	O. quadrata	Santa Catarina, Brazil	Density of active burrow openings	No burrows in beaches with ORV traffic and fishing activity	Density: <0.01	No harmful effects in beaches with light recreation (e.g. trampling), possibly due to an increase in food sources – food scraps left by visitors	Blankensteyn 2006
Multiple trampling; vehicle traffic; urbanization	O. quadrata	Rio Grande do Sul, Brazil	Density and distribution of active burrow openings	Density in undisturbed beach up to 6x greater than in beach with heavy trampling and light vehicle traffic, and up to 6x greater than in beach with light trampling and heavy ORV traffic; burrows in beach with light trampling and ORV traffic only found in a 25 m strip protected from traffic	Density: ~0.17		Neves and Bemvenuti 2006
Multiple: boating; and vehicle traffic; trampling; horse riding	O. ceratophthalma	Broome, Western Australia, Australia	Density of active burrow openings	Negative correlation between number of tyre tracks and burrow numbers ( <i>p</i> <0.001); <u>no</u> <u>burrows</u> in zones of high vehicle use compared to zones of no vehicle use	Density: <0.01		Foster-Smith and others 2007
Multiple: urbanization, trampling, and vehicle traffic	O. quadrata	Texas, USA	Density, distribution, size and compass orientation of active burrow openings	Burrow density 3x greater in low-impact beach; burrows further from water in low-impact beach ( <i>p</i> <0.001); no significant differences in size between ORV sites and No-ORV sites	Density: 0.11 Size: no effect	No differences in burrow orientation between beaches	Maccarone and Mathews 2007
Multiple: storms; vehicle traffic	O. quadrata	North Carolina, USA	Density, distribution and size of active burrow openings	Reduction in ghost crab burrow density (up to 100%); ORV use restrictions (24 h) resulted in significant recovery of densities (up to 30%, $p<0.050$ ); ORV restriction 10 h per day (20:00-06:00 June-November 2003) resulted in significant recovery at one site ( $p=0.015$ ) but not in at another site ( $p=0.113$ ) Significantly smaller burrow size in ORV sites ( $p<0.001$ ); significantly smaller burrow size after storm events (means up to 15 mm smaller, $p<0.001$ )	Density: <0.01 (vehicle traffic) Density: ~0.07 (storm) Size: ~0.60 (storm)	Post-storm re- colonization of beach areas that were closed to vehicle traffic during the storm events	Hobbs and others 2008

# Table 15 Continued

Human	Species	Geographic	Response Variable	Observed Effects / Impacts	Effect Size(s)	Notes	Reference
Pressure		Locality			$ar{x}_{Impact}  /  ar{x}_{Reference}$		
Multiple: urbanization, mechanical beach cleaning	O. quadrata	Pernambuco, northeastern Brazil	Density, distribution and size of active burrow openings	Significantly lower density (up to 100%) in urban beaches ( <i>p</i> <0.050); significantly greater density near the dunes in non-urban beaches; No significant differences in burrow size between urban and non-urban	Density: <0.01 Size: no effect	The positive correlation between organic carrion density and ghost crab density ( <i>p</i> <0.05) suggests that wrack removal by cleaning may have contributed to observed population decline	Souza and others 2008
Multiple: urbanization and armouring	O. quadrata	Bahia State, Northeastern Brazil	Density and distribution of active burrow openings	Up to 5x fewer burrows in urbanized beaches than in non-urbanized beaches ( $p$ =0.003); significantly fewer burrows in dunes of urban than in dunes of non-urban beaches; urban beach lacking frontal dunes had the smallest number of burrows	Density: ~0.21		Magalhaes and others 2009
Multiple: armouring and trampling	O. ceratophthalma; O. cordimanus	Mooloolaba, Queensland, Australia	Density, distribution and size of active burrow openings	Reduced density (up to 50%) of ghost crab burrows compared to reference sites; 25% more burrows on the upper shore of reference site compared to armoured site	Density: 0.54		Lucrezi and others 2009b
Multiple: boating and trampling	O. ceratophthalma	Singapore	Density and size of active burrow openings	Lower density in boating sites (>50%) than in no-boating sites; more burrows near the low tide level of boating sites than of other sites	Density: ~0.39	Significantly smaller burrows in high disturbance sites (means smaller by up to 10 mm <i>p</i> <0.001	Yong and Lim 2009
Multiple: armouring; trampling; storms	O. ceratophthalma; O. cordimanus	Noosa, Queensland, Australia	Density, distribution and size of active burrow openings	Up to 3x greater decline in ghost crab burrows past a severe weather event compared to reference site	Density: 0.64 (storm) Density: 0.16 (armouring on upper 9 m of beach)		Lucrezi and others in press
Nourishment / Bulldozing	O. quadrata	North Carolina, USA	Density of active burrow openings	65% reduction in burrow density three months after bulldozing	Density: 0.50	Observed decreases in density possibly caused by burial (direct effect) and by shifts in sediment characteristics (indirect effect)	Peterson and others 2000

# Table 15 Continued

Human Pressure	Species	Geographic Locality	Response Variable	Observed Effects / Impacts	Effect Size(s) X <sub>Impact</sub> / X <sub>Reference</sub>	Notes	Reference
Pollution / oil	O. ceratophthalma, O. madagascariensis, O. ryderi	Natal / Zululand coast, South Africa	Density of active burrow openings; body condition	39-87% external contamination of counted crabs	Density: 0.66	Behavioural abnormalities – no escape response	Jackson and others 1991
Trampling	Ocypode ceratophthalma; O. cordimanus	Mooloolaba, Queensland, Australia	Density and size of active burrow openings	88% reduction in ghost crab burrow densities following 100 pedestrian passes; little effect after further trampling; recovery of burrow densities by the next morning (no significant changes at the time scale of days); more pronounced impact for larger burrows (no burrows larger than 25 mm in diameter after 100 pedestrian passes)	Density: 0.13 Size: >0.10		Lucrezi and others 2009a
Vehicle traffic	O. quadrata	North Carolina, USA	Density of active burrow openings	100-500 vehicle passes resulted in a 14-98% population decrease	Density: 0.98 (after 1 pass)	Day: completely protected at burrows as shallow as 5 cm in the day Night: respond to headlights by freezing / running toward light source → crushed by cars	Wolcott and Wolcott 1984
Vehicle traffic	O. quadrata	Assateague Island, Maryland-Virginia, USA	Density, distribution and size (diameter and depth) of active burrows	Lower density of ghost crab burrows (up to 95%) compared to no-traffic zones and burrow diameter (up to 70%)	Density: up to 0.05 Size: up to 0.29		Christoffers 1986
Vehicle traffic	O. cordimanus	Arrawarra Beach, New South Wales, Australia	Density of individuals	10-40 vehicle passes caused no significant impact on densities	Density: no effect		Hastie 2002
Vehicle traffic	O. cordimanus	North Stradbroke Island, Queensland, Australia	Density and distribution of active burrow openings	Significantly fewer (>50%) burrows in ORV beaches ( <i>p</i> <0.001); no difference in distribution across the shore	Density: 0.35 Distribution: no effect		Moss and McPhee 2006

Human Pressure	Species	Geographic Locality	Response Variable	Observed Effects / Impacts	Effect Size(s) x̄ <sub>Impact</sub> / x̄ <sub>Reference</sub>	Notes	Reference
Vehicle traffic	O. ceratophthalma, O. cordimanus	North Stradbroke Island, Queensland, Auatralia	Density, size and distribution across the intertidal of active burrow openings; mortality of individuals subjected to experimental vehicle traffic	Significantly fewer (almost 50% fewer) burrows in areas of heavy vehicle impact; significantly fewer crabs below drift line in heavy traffic zone; 100% mortality by crushing after 10 vehicle passes at 5 cm depth; 10-30% mortality at 20 cm depth; no mortality at 30 cm depth (50% population at this depth); 0.75% mortality of intertidal population after one vehicle pass during surface activity	Density: 0.52 Density: 0.31 (below drift line) Size: 0.79	Comment on extrapolations based on observed mortality and traffic volumes	Schlacher and others 2007b
Vehicle traffic	O. ceratophthalma, O. cordimanus	Fraser Island, Queensland, Australia	Density of zero count samples (no visible burrows)	Reduced number of zero count samples of ghost crab burrows in first (30%) and second (80%) dune ridge in vehicle tracks compared to abutting dunes; reduced burrow size (>8%) in tracks compared to dunes	Density: 0.90 (first dune ridge) Density: 0.23 (second dune ridge) Size: 0.92		Thompson and Schlacher 2008
Vehicle traffic	O. ceratophthalma; O. cordimanus	Sunshine Coast, Queensland, Australia	Architectural features of ghost crab burrows; size, length, depth and volume of active burrow openings	Reduced size (20%) of ghost crab burrow openings compared to control sites; simplification of burrow architecture (from 4 to 2 types) by smaller crabs; increased burrow depth (30%), length and volume (10%) post peak traffic periods	Size: 0.89 Depth: 1.40 Weight: 1.11		Lucrezi and Schlacher 2010

Due to the unavailability of effect sizes, the following reports on ghost crabs were not included in the table: Boon and others 1999; Bouwer 1986;

Leggett 1975

Table 15 Continued

# **CHAPTER 1**

# Monitoring human impacts on sandy shore ecosystems: a test of ghost crabs (*Ocypode* spp.) as biological indicators on an urban beach

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# Abstract

Sandy beaches comprise one of the most important coastal resources worldwide, providing habitats to threatened vertebrates, supporting underappreciated invertebrate biodiversity, and delivering crucial ecosystem services and economic benefits to mankind. Monitoring of the natural resource condition of sandy beaches and assessments of the ecological impacts of human disturbance are, however, rare on sandy shores. Because a crucial step in developing beach monitoring is to identify and test biological indicators, we evaluated the utility of using population densities of ghost crabs (genus Ocypode) to measure how beach biota respond to human pressures. Densities of crabs - estimated via burrow counts - were quantified at two sites exposed to high and low levels of human disturbance on an urban beach in eastern Australia. Human disturbance consisted of pedestrian trampling and shoreline armouring which led to the loss of dune habitat. Overall, crab numbers were halved in disturbed areas, but contrasts between impact and control sites were not necessarily consistent over time and varied between different levels of the shore: stronger and more consistent effect sizes were recorded on the upper shore than further seawards. In addition to lowering crab densities, human disturbance also caused shifts in intertidal distributions, with a greater proportion of individuals occurring lower on the shore in the impacted beach sections. The number of visible burrow openings also changed in

response to weather conditions (temperature and wind). We demonstrate that spatial contrasts of burrow counts are broadly useful to indicate the existence of a humaninduced disturbance effect on urban beaches; we also highlight a number of critical, hitherto unknown, issues in the application of this monitoring technique; these encompass three broad dimensions: (1) a need for standardised protocols; (2) unresolved causal links between observed patterns and putative pressures; (3) uncertainties of how organisms respond specifically to both natural and human changes of environmental conditions on sandy shores.

Keywords: sandy beaches; ghost crabs, shore monitoring, coastal management, faunal indicators

# 1.1. Introduction

Sandy beaches rank amongst the most intensively used coastal ecosystems by man, and human uses of beaches are rising sharply (Schlacher and others 2006). Traditionally, management of beaches has almost exclusively focused on maintaining and restoring sand budgets, with scant consideration for ecological dimensions (Nordstrom 2000). Human use of beaches is, however, not without ecological consequences and can result in multiple forms of environmental degradation (Brown and McLachlan 2002; Dugan and Hubbard 2006; Schlacher and others 2007a).

Despite the great social, economic and environmental importance of sandy shores worldwide, environmental monitoring and assessment of sandy beach ecosystems is rare. A monitoring technique which uses ghost crabs as biological indicators to measure the effects of human disturbance on beaches has been applied

on urban shores (Barros 2001; Neves and Bemvenuti 2006), and to assess whether off-road vehicles driven on beaches damage the resident biota (Moss and McPhee 2006; Schlacher and others 2007b); studies generally report lower population densities in areas heavily disturbed by human activities.

Ghost crabs of the genus *Ocypode* are semi-terrestrial invertebrates commonly found on subtropical and tropical shores. They are relatively large animals, occupying the position of apex invertebrate predator on sandy beaches (Wolcott 1978). Ghost crabs switch between surface activity at night to a fossorial lifestyle inside their burrows during the day (Barrass 1963). The crabs construct deep and complex burrows which provide shelter against climatic extremes and predators, and serve as refuges during moulting and maternity (Chan and others 2006). The top of these burrows breaches the sand surface as a clearly visible hole, and therefore counting burrow entrances is an efficient tool to measure densities of ghost crabs on beaches (Moss and McPhee 2006).

Management interventions aimed at reducing negative ecological impacts on beach systems will need to increasingly incorporate biological information, requiring the development of beach monitoring programmes (Schlacher and others 2006). A critical pre-requisite for such monitoring programmes is to identify appropriate indicators and to assess the scientific robustness of the technique. To this end, this paper examines to which degree population estimates of ghost crabs are influenced by external environmental factors, and whether measured responses of ghost crabs in relation to human disturbance are consistent across space and time.

# 1.2. Material and methods

#### 1.2.1. Study area

The study was done on Mooloolaba Beach in SE Queensland, Australia (Fig. 1). The beach is situated in a 1.8 km long embayment bounded in the west by a rocky shore and in the east by a groyne (Fig. 1). The beach has a long history of human engineering interventions and has undergone many morphological changes over the last 60 years (Longhurst 1997). A wooden retaining wall was built in 1952 on the northern backshore area of the beach and replaced by a stone wall in 1959; this structure was the forerunner of today's seawall which is 204 m long and 2.3 m high; this part of the beach also receives the highest number of beach visitors. In 1968 the inlet of the Mooloolah Estuary was artificially stabilized with two rock walls, the northern one forming today's south-eastern boundary of the beach. All natural dune areas of the northern beach have been replaced with recreation infrastructure including playgrounds, toilets and large buildings such as the Surf Life Saving Clubhouse. Dunes (3-4 m tall) are still present on the southern beach, although they have undergone substantial human modifications such as fencing and re-vegetation since 1957 (Longhurst 1997).



**Figure 1** Study area, Mooloolaba Beach, in eastern Australia (a). The urban beach has a heavily modified and armoured section that is extensively impacted by human trampling (b), abutted by some remaining natural dune areas with relatively less human use (c). Burrow counts of ghost crabs were made in 3 x 10 m plots arranged sequentially (A-H) in across-shore transects from the base of the seawall or dune to the seaward limit of ghost-crab distributions. Each section (i.e. impact, reference) contained 8 transects, surveyed on 15 separate occasions. (Photo credits: TA Schlacher (a), S Lucrezi (b,c))

# 1.2.2. Spatial layout and burrow counts

To test whether ghost crab densities are reduced by shore armouring and intense human trampling, we compared burrow densities between the heavily modified northernmost section of the beach (impact site) and a reference zone 40 m to the south-east (Fig. 1). Ghost crab densities were quantified by counting the number of active burrow openings on the beach surface. The impact section is the most heavily used area of the beach by humans; here all foredunes have been replaced by a seawall. By contrast, the reference section was chosen because it is the area of the beach with the fewest number of visitors and where remnant dune vegetation remains.

In each section (i.e. impact and reference), burrow counts were made across eight belt transects. Each belt transect was a continuous 10 m wide strip that extended across the shore from the base of the foredunes or seawall to the downshore limit of burrow occurrence. Individual transects within a site were interspersed by 10 m along the beach. Each transect was divided into sequential 3 m long quadrats placed continuously down the shore (Fig. 1). Thus, the basic sampling unit in this study was a 3 x 10 m quadrat, and burrow densities are expressed as the number of burrows per  $30 \text{ m}^2$ .

Burrow counts were temporally replicated on 15 days, covering one full lunar cycle between March and April 2007. The chief purpose of temporal replication was first to identify environmental factors (e.g. weather, sea conditions) that influence burrow density, and second to test whether spatial differences in burrow density linked to human disturbance are consistent over time.

On each survey day, we started burrow counts 1-2 hours after sunrise, a complete survey of all transects taking 5-6 hours. To avoid possible bias associated with the time of the day when counts were made at a specific location, the sequence of field measurements was randomised by selecting the section (i.e. impact vs. reference) to be counted first (toss of coin), and randomising the starting transect within a site (random number table). Only 'active' burrow openings were counted. Active burrows were easily recognized by either the presence of fresh tracks emanating from the opening, or evidence of recent re-working of the burrows visible as small mounds of excavated sediment next to the entrance, or both. Two species of ghost crabs, *Ocypode ceratophthalma* and *Ocypode cordimanus* occur on the beach, but their burrow openings cannot be distinguished with confidence. We therefore report all burrow counts at the genus level.

#### 1.2.3. Environmental variables

After all burrows had been counted in a quadrat, we took three replicate measurements of a) sand temperature to a depth of 5 cm (electronic thermometer Fluke 52 K/J), b) sand moisture to a depth of 8 cm (Trident microwave moisture meter), c) sand shear force resistance (field inspection vane tester Geonor H-60 with a vane size of 5 cm x 2.5 cm), and d) penetration force (Geotester penetrometer, 20 mm diameter tip); the position of replicates was randomised within each quadrat.

Morphological properties (i.e. beach profile, width, and slope) of the beach were obtained from standard theodolite surveys. We visually determined the position of the drift line (the reach of the highest swash preceding the counts marked by clearly visible deposits of detached macrophytes, carcasses and debris) and the position of the effluent line (water table outcrop) for each individual transect. The effluent line

represents the position where the water table breaches the subaerial beach; it is marked by a clearly visible transition between the zone of saturated sand (sometimes referred to as the "glassy layer") and the upper beach composed of drier, unsaturated sand. We also recorded wind speed and air temperature (Skymate SM-18 meter), wind direction (compass), wave height (visually) and wave period (counts of breaking waves over 3 min) at the start and end of each survey. Additional weather data (e.g. hourly temperature, wind speed and direction, hourly rainfall) and tidal heights were obtained from the Bureau of Meteorology (www.bom.gov.au).

Sediment properties were determined by collecting triplicate sediment cores (30 mm diameter, 100 mm deep) from every quadrat on three occasions. In the laboratory, sediment granulometry was determined by dry-sieving samples through a nested series of eight sieves arranged in decreasing order of mesh aperture size (4000  $\mu$ m, 2000  $\mu$ m, 1000  $\mu$ m, 500  $\mu$ m, 250  $\mu$ m, 200  $\mu$ m, 180  $\mu$ m, 63  $\mu$ m). Sediment parameters were calculated according to the Folk and Ward method using the Gradistat software (Blott and Pye 2001).

To determine the intensity of human disturbance by pedestrian trampling, we obtained estimates of the number of beach visitors from life guards who patrol the beach daily from 07:30 to 16:30, and count the number of people every two hours.

#### 1.2.4. Data analysis

Total variance in ghost crab burrow densities was partitioned using a Generalized Linear Model (GLM). The design included survey number as the temporal component of variation, and two spatial terms, the first being impact (reference vs. impact section), and second being shore zone (backshore above the drift line vs. foreshore below the

drift line). Count data were square-root transformed where required to achieve normality and homoscedasity (Cochran's C-test). The influence of individual environmental variables on burrow density was assessed with partial correlation analysis.

# 1.3. Results

# 1.3.1. Environmental and habitat properties

Mostly warm and dry weather conditions prevailed during the study. Temperature was 22 to  $29^{\circ}$  during the day and 17 to  $25^{\circ}$  at night, decreasing slightly over the course of the study (Fig. 2b). Wind speed was not substantially different between night (4.9-13.0 knots) and day (3.8-12.6 knots), but winds became lighter during the study (Fig. 2a). Temporal fluctuation in sand moisture (0.01-1.90%) and sand temperature (9.4-25.2°C) largely reflected weather conditions, and decreased over time as did wave height (Fig. 2). Rain was recorded on two days only (Fig. 2h).



**Figure 2** Temporal variation in weather conditions, wave height, width of the backshore, sediment properties, beach visitors and burrow densities of ghost crabs

Both beach sections were morphodynamically highly similar, being tidedominated shores of a modal intermediate to reflective state. Beach Index (McLachlan and Dorvlo 2005) values were virtually identical between impacted and reference sites (BI<sub>reference</sub> = 2.09, BI<sub>impact</sub> = 2.11); Dean's Parameter (Short 1996) also changed little between sections ( $\Omega_{\text{reference}} = 1.85$ ,  $\Omega_{\text{impact}} = 1.69$ ). Width of the beachface varied between 39 and 48 m, with mean values and ranges comparable between sites (Reference:  $\bar{x} = 41$  m, range = 39-45 m; Impact:  $\bar{x} = 42$  m, range = 39-48 m), as was the case for beach slope (Reference:  $\bar{x} = 2.58^\circ$ , se = 0.20, n = 117; Impact:  $\bar{x} = 2.66^\circ$ , se = 0.16, n = 121). No substantial differences in sediment properties were found between the impact and reference sites (Table 16). Sand temperature was only marginally (5% of reference site value) lower in the impact section, and mean values of sediment compactness were within 3-11% of measurements in the reference site (Table 16). Similarly, mean grain size differed by less than 7% between sections (Table 16). Given the close match in physical habitat properties between the impact and reference sites, it is highly unlikely that variations in environmental variables are the primary cause of spatial differences in ghost crab populations.

**Table 16** Comparison of sediment properties between impact and reference sections of the

 beach where counts of ghost crab burrows were made

Variable	Impact			Reference			ANCOVA F <sub>(1,1408)</sub>
	n	x	(se)	n	x	(se)	
Sand temperature ( ${ m C}$ )	706	21.46	(0.08)	705	22.57	(0 .09)	11.07***
Penetration force (kg/cm <sup>2</sup> )	706	5.37	(0.02)	705	5.55	(0.03)	24.40***
Compactness (KPa)	706	0.92	(0.01)	705	1.04	(0.02)	3.20 <sup>ns</sup>
Sand moisture (%)	706	0.77	(0.05)	705	1.17	(0.06)	2.68 <sup>ns</sup>
Sand grain size (µm)	131	309.26	(1.74)	124	288.60	(2.05)	20.65***

# 1.3.2. Environmental drivers of changes in crab burrow number

Significantly higher burrow counts were obtained in wetter sand after warm nights and during stronger winds (Table 17). By contrast, neither wave properties nor tidal amplitudes were correlated with crab burrow densities on the beach; sand temperature and compactness were also not correlated with the number of burrow openings (Table 17). Correlations between environmental variables and burrow densities were highly similar in both beach sections, irrespective of human disturbance intensity. In fact, no significant effect of visitor numbers was recorded in terms of a temporal concordance between burrow densities and beach visitation (Table 17). However, burrow densities decreased at the impact site during periods of heaviest beach use which peaked over the Easter Holiday (days 15 to 19 of the survey; Fig. 2d,h), and mostly remained low even after visitor numbers had reverted to the lower pre-peak intensities from day 24 onwards (Fig. 2d,h). There was no conspicuous pattern in temporal changes of burrow numbers that could unambiguously be related to lunar phases (Fig. 2h).

Table 17 Partial correlations between environmental factors and densities of ghost crab burrow

densities (n = 15 surveys)

Reference		се	Impact	
Sediment Properties				
Sand Temperature (℃)	-0.207	ns	0.003	ns
Sand Compactness (Kpa)	-0.340	ns	0.141	ns
Sand Moisture (%)	0.561	*	0.714	*
Sea Conditions and Tides				
Wave Height (m)	0.264	ns	0.160	ns
Wave Period (s)	-0.183	ns	0.003	ns
Tidal Amplitude (m)	-0.107	ns	-0.220	ns
Tidal Reach (previous night; m)	0.080	ns	0.079	ns
Tidal Reach (survey day; m)	-0.065	ns	-0.145	ns
Weather				
Air Temperature - Night (18:00-06:00; ℃)	0.603	*	0.717	*
Air Temperature Day (06:00-12:30; ℃)	-0.403	ns	-0.432	ns
Wind Speed - Night (knots)	0.666	*	0.681	*
Wind Speed - Day (knots)	0.585	*	0.597	*
Human Pressure				
Beach Visitors (daily, n)	-0.326	ns	-0.342	ns

# 1.3.3. Spatio-temporal variations in burrow densities

The spatial distribution of burrow densities varied significantly with the level of human disturbance (i.e. impact vs. reference sections) and the position across the shore (i.e. above vs. below the driftline). Importantly, both spatial sources of variation interacted significantly with temporal changes, creating a complex pattern of heterogeneity in burrow numbers in space and time (Tables 18 and 19).

**Table 18** Distribution of total burrow counts over the entire survey (n = 24290) between the upper and middle shore (separated by the drift line, DL), and between impacted and reference sections of the beach

	Reference	Impact	Both
Upper Shore (> DL)	12012	4084	16096
	(74%)	(51%)	(66%)
Middle Shore (< DL)	4234	3960	8194
	(26%)	(49%)	(34%)
Entire Beachface	16246	8044	24290

**Table 19** Summary of GLM (Generalized Linear Model) analysis contrasting burrow densityamongst: a) times, b) impact intensities, and c) shore zones (above and below the drift line, DL;\*\*\* P < 0.001, \*\* P < 0.01, \* P < 0.05)</td>

Source of variation	df	MS	F	
A – Time	13	39.61	14.77 ***	
B - Impact (Reference vs. Disturbed)	1	183.83	68.52 ***	
C - Shore Zone (>DL vs. <dl)< td=""><td>1</td><td>260.63</td><td>97.15 ***</td><td></td></dl)<>	1	260.63	97.15 ***	
A x B (time x impact)	13	12.14	4.52 ***	
A x C (time x shore zone)	13	5.73	2.14 *	
B x C (impact x shore zone)	1	30.25	11.28 ***	
A x B x C (time x impact x shore zone)	13	6.91	2.58 **	
Error	1251	2.68		

We counted a total of 24290 burrow openings. Of these, two-thirds (16096) were located on the upper shore above the drift line, compared to 8194 found on the middle section of the beach seawards of the driftline (Table 18, Fig. 3). The across-shore distribution of burrows did, however, differ markedly between the impact site and the reference site: a significantly higher proportion (74%) of burrows occurred on the backshore of the reference site, whereas in the impact site roughly equal numbers of burrows were found above and below the driftline (Table 18, Fig. 3).



**Figure 3** Distribution of ghost crab burrows across the beachface (shown as beach profiles in bottom panel) at the reference (top panel: open bars) and impact sites (top panel: solid bars); asterisks in bottom panel denote the position of the driftline (DL)

Burrow densities were substantially lower in areas intensively trampled by humans and where dunes had been replaced by a seawall (Figs. 3 and 4). Overall, the highly impacted site supported only half the number of crabs found in the less intensively disturbed areas (Table 18, Fig. 4). Although reductions in mean burrow densities between reference and impact sites were in absolute terms comparable for the upper shore (Reference<sub>upper</sub>:  $\bar{x} = 20.82$  ind. 30 m<sup>-2</sup>, se = 0.84, n = 577; Impact<sub>upper</sub>:  $\bar{x} = 7.84$  ind. 30 m<sup>-2</sup>; se = 47, n = 521) and the middle shore (Reference<sub>middle</sub>:  $\bar{x} = 33.08$  ind. 30 m<sup>-2</sup>, se = 2.07, n = 128; Impact<sub>middle</sub>:  $\bar{x} = 21.41$  ind. 30 m<sup>-2</sup>; se = 1.3, n = 185), relative decreases above the driftline (-62%) were about double that of decreases further seawards (-35%).



Figure 4 Comparison of ghost crab burrow openings between reference and impacted sites at

two heights of the shore

These spatial contrasts between heavily and less disturbed sites were, however, not necessarily consistent over time, and depended on the position across the shore where burrow counts were made (Table 20). On the upper shore, half the surveys showed significantly lower mean densities in the impacted site, and the direction of change was negative for all but a single survey (Table 20). By contrast, although burrow densities on the middle part of the beach (i.e. below the strandline) were also mostly lower in the heavily impacted areas, a significant change could only be detected in a single survey (Table 20). Thus, differences in burrow densities that could be linked to the intensity of human disturbance were detectable in half of all cases on the backshore above the driftline but not further seawards.
**Table 20** Effect sizes for spatial contrasts in burrow densities between impact and reference
 sites at two levels of the shore during individual surveys. Negative values signify lower

 densities at impacted sites and positive values higher densities in disturbed areas. Bold entries
 denote significant differences between means

	Upper S	Shore	Middle S			
Survey	Effect Size #		Р\$	Effect S	Effect Size #	
1	-21.4	(-59%)	*	12.1	(+35%)	ns
2	-25.1	(-63%)	***	-25.0	(-43%)	ns
3	-10.8	(-47%)	ns	-6.4	(-19%)	ns
4	-15.0	(-71%)	**	-0.3	(-1%)	ns
5	-20.6	(-65%)	*	-5.0	(-13%)	ns
6	-22.2	(-89%)	***	-13.0	(-33%)	ns
7	5.3	(+61%)	ns	-15.0	(-38%)	ns
8	-15.5	(-95%)	***	-27.6	(-87%)	*
9	-9.9	(-46%)	ns	-0.3	(-1%)	ns
10	-3.3	(-60%)	ns	3.0	(+32%)	ns
11	-13.8	(-52%)	**	-2.3	(-7%)	ns
12	-8.4	(-95%)	**	-24.2	(-85%)	ns
13	-9.5	(-66%)	ns	7.5	(+55%)	ns
14	-8.5	(-60%)	ns	-14.4	(-47%)	ns
No. Negative Contrasts	13			11		
No. Positive Contrasts	1			3		
	Z-statistics	Р		Z-statistics	Р	
Sign-Test	3.10	0.002		1.87	0.061	

<sup>#</sup>Effect Size = ( $\bar{x}$ -Density<sub>impact</sub> -  $\bar{x}$ -Density<sub>reference</sub>);

<sup>\$</sup> Probability values from HSD post-hoc tests following significant time x zone x impact effects in main GLM model (cf. Table 19). \*\*\* P < 0.001, \*\* P < 0.01, \* P < 0.05, <sup>ns</sup> P > 0.05

#### 1.4. Discussion

#### 1.4.1. Environmental influences on crab burrow densities

Ghost crabs are semi-terrestrial and can live in both dry and wet sediment (Fisher and Tevesz 1979); in the present study, sand moisture was positively correlated with ghost crab burrow density (Table 17). Burrows generally provide protection against dehydration, but the crabs still require access to water to moisten their gill chambers (Wolcott 1976). Also, extreme dehydration can cause the loss of body weight and impair locomotion (Weinstein 1998). Juveniles generally need to renew water in the gill chambers more frequently than adults, whose distribution can therefore extend further landward (Wolcott 1976). Conversely, the seaward limit of crab distribution is often dictated by waves and swash, because prolonged immersion in seawater can cause osmotic stress (Vinagre and others 2007).

Burrows provide a thermally stable environment, insulating crabs against temperature extremes as long as they remain fossorial (Chan and others 2006). Surface activity, mainly during the night, does expose crabs to ambient temperature conditions, and we found more active burrow openings after warmer nights (Table 17). This suggests that activity levels were influenced by metabolic responses to temperature, and consequently affected the number of active burrow openings that could be counted during the day. In fact, members of the genus *Ocypode* become less active at lower temperatures (Hughes 1966). At temperatures below ~16°C some species become dormant or migrate inland (Christoffers 1986), and upper thermal limits for activity are about 30°C (Weinstein 1998). Temperatures recorded in this study did not approach these reported limits, but temperature is clearly an important environmental variable for ghost crabs and affects the number of open, active burrow

openings. Sand surface temperature increased slightly up the shore within the impact section, possibly caused by heat radiating from the seawall or from increased trampling that allows heat to penetrate further into the sediment. Thus, coastal armouring structures may have an indirect, negative effect on ghost crabs that operates via modifications of their thermal environment; this hypothesis would merit further investigations.

We found a strong positive correlation between wind speed and burrow density (Table 17). Fewer people frequent the beach when there are strong onshore winds (S Lucrezi pers. obs.), reducing direct trampling impacts by humans. Wind strength and direction were, however, unlikely to have confounded comparisons between the heavily impacted and reference sites, because burrow densities responded equally to meteorological changes in both sections. Ghost crabs can be highly active during strong onshore winds (Wolcott 1978). Wind-driven onshore advection is the principal mechanism for delivering wrack and carrion to beaches. We observed nocturnal feeding aggregations of ghost crabs around driftlines (TA Schlacher pers. obs.), and ghost crab activity may thus respond positively to stronger winds that enhance resource availability of stranded food. However, the positive correlation between wind speed and burrow numbers measured in this study is unlikely to apply over the full spectrum of wind speeds on exposed coastlines. In fact, winds above 20 knots tend to obscure burrow openings, particularly in loose sand on the upper shore (TA Schlacher pers. obs.). Thus, burrow counts are not useful as a monitoring tool under such conditions.

#### 1.4.2. Mechanisms of impact: trampling and habitat change

Few studies have measured the impact of human trampling on the distribution and abundance of macrofauna on sandy beaches, and those that have, showed different outcomes. Recreational use could not be unequivocally linked to changes in the macrobenthos on a Chilean beach (Jaramillo and others 1996), but experimental work in South Africa demonstrated that several beach invertebrates can be sensitive to direct crushing by pedestrian trampling (Moffett and others 1998). It has been suggested that human trampling is the cause of lower ghost crab numbers on urban beaches (Barros 2001; Neves and Bemvenuti 2006). However, the actual processes that cause observed reductions in ghost crab populations in disturbed areas remain largely unresolved, except for the crushing of crabs by off-road vehicles (Schlacher and others 2007b).

In addition to direct crushing of individuals, trampling may also affect ghost crabs via several complementary mechanisms: 1) crabs simply plug their burrows, do not re-emerge, and hide within their burrows, leading to lower density estimates; 2) trampling lowers sand stability causing burrow openings to collapse; 3) crabs lower burrowing and feeding activity. Some beach visitors leave food scraps behind which may lead to shifts in crab diet, distribution and abundance (Steiner and Leatherman 1981).

Coastal armouring is increasingly being employed to combat shoreline erosion worldwide, and this trend may escalate in the face of global climate change (Feagin and others 2005). The main ecological impact of coastal armouring is the destruction of dunes (Dugan and Hubbard, 2006). Since dunes are critical refuges for ghost crabs during storms (Christoffers 1986), crabs on armoured sections of beaches may be at

greater risk during high seas. Beach armouring also alters physical properties and dimensions of beaches, particularly compressions of backshore areas, and accelerates beach loss (Fletcher and others 1997). Armoured beaches also support fewer consumers, partly as a consequence of reduced deposition rates of wrack that is a critical energy source for many beach invertebrates (Dugan and Hubbard 2006).

In the present study, the backshore of the armoured beach section was slightly higher in elevation (Fig. 3). This small rise in the beach profile could be due to changes in sediment accretion and erosion dynamics caused by the seawall. Rising of the sediment wedge could potentially make it more difficult for ghost crabs to reach the water table and could increase the energetic cost of burrowing. Further manipulative experiments are required to assess whether changes in beach elevation can significantly alter crab densities and burrowing, but this is likely to be a small effect compared to the loss of dune habitat caused by seawalls.

#### 1.4.3. Across-shore variability

Although ghost crabs can occupy a fairly broad area across the intertidal and supratidal gradient, the distribution of many species appears to be centred on the backshore, extending from the driftline to the dunes (Table 21). Ghost crab distribution may also shift in relation to tides, but evidence for such tidal migrations is often less comprehensive and conclusive (Table 21).

 Table 21 Overview of across-shore distribution of members of the genus Ocypode reported

from beaches worldwide

Species	Locality	Distribution across the beach	Evidence of active migration	Reference	
O. ceratophthalma	Moçambique	Between high water mark and extreme H.W.S.T.	Yes	Barrass 1963	
O. ceratophthalma; O. cordimanus	Seychelles	Generally above spring high water mark	Yes	Braithwaite and Talbot 1972	
O. ceratophthalma	India	Upper foreshore slope to base of dunes	No	Chakrabarti 1981	
O. ceratophthalma; O. ryderi; O. madagascariensis	South Africa	Between high tide swash line and primary dunes	Yes	McLachlan 1980	
O. ceratophthalma; O. macrocera; O. cordimanus; O. platytarsis	India	Backshore region when well developed	Yes	Chakrabarti 1993	
O. cordimanus	Australia	More burrows at the base of dunes, but extending 10-50 m into the dunes	?	Barros 2001	
O.cordimanus	Australia	Mostly around drift line	No	Moss and McPhee 2006	
O. cursor	Cyprus	A band 3 m from the water's edge extending 13 m up the beach; seasonal variation	Yes	Strachan and others 1999	
O. gaudichaudii	Chile	Most located above drift line	Yes	Quijon and others 2001	
O. quadrata	USA	Upper foreshore and lower backshore	No	Hill and Hunter 1973	
O. quadrata	USA	Backshore zone and low foredune ridge	No	Allen and Allen Curran 1974	
O. quadrata	USA	Below the drift line, close to cast-up material at high tide and inland in the day	Yes	Wolcott 1978	
O. quadrata	USA	Mostly backshore extending over 200 m inland	Yes	Fisher and Tevesz 1979	
O. quadrata	Brazil	Above medium intertidal zone, peak between 1.5 and 2 m height above water line, fewer in subterrestrial fringe 2 m above water line	Yes	Turra and others 2005	
O. quadrata	Brazil	From the highest mark of the shoreline to the foredunes	Yes	Neves and Bemvenuti 2006	

In the present study, more crab burrows were generally found on the backshore than in the lower intertidal (Table 18). However, this across-shore pattern of distribution was not the same between areas that differed in the intensity of human disturbance: in heavily impacted areas, a smaller proportion of the population occurred on the backshore (Table 18). This indicates that human disturbance both lowers the density of ghost crab burrows and shifts their distribution across the beachface. Because of this, reductions in burrow density are more severe on the backshore where the sediment is less compact, human trampling is more concentrated, and shorearmouring has destroyed the dunes.

#### 1.4.4. Implications for monitoring

Sandy beaches worldwide face escalating pressures from development and recreational use, a trend that is predicted to increase in the 21<sup>st</sup> century (Schlacher and others 2007a). Although the ecological effects caused by an increasing frequency and amplitude of human disturbance on sandy shores are becoming better known (Brown and McLachlan 2002; Schlacher and others 2007a), systematic monitoring of environmental and ecological resource states of beaches is uncommon (Schlacher and others 2006). Ghost crab densities have been employed as an ecological indicator of human impacts in urban settings (Barros 2001; Neves and Bemvenuti 2006), as well as to assess the ecological consequences of specific pressures such as off-road vehicle use on beaches (Moss and McPhee 2006; Schlacher and others 2007b). A common denominator of these monitoring studies is that crab densities are generally lower in areas subjected to human disturbance, and our data concur with this broad generalisation.

Counting ghost crab burrows can be a rapid, practical and simple tool for assessing the degree of ecological impact caused by humans in beach ecosystems (Barros 2001). Yet, the method may not be entirely without shortcomings, and it may present challenges in terms of contextualisation. We demonstrate that spatial contrasts of burrow counts are broadly useful to indicate the existence of a humaninduced disturbance effect on urban beaches, but we also highlight a number of critical, hitherto unresolved, issues in the application of this monitoring technique. These issues encompass four broad dimensions: 1) protocols need to be standardised; 2) specific causes of observed impacts are not always separated when multiple pressures act simultaneously; 3) the causal links between observed patterns and putative pressures are commonly unresolved; 4) autecological and biological responses of organisms to both natural and human factors are poorly understood.

A key requirement of all monitoring is to standardise data collections across geographic regions and programmes. Here we show that several environmental factors can significantly influence burrow numbers, including temperature, wind speed, and sand moisture (Table 17). Therefore, future monitoring using ghost crab burrow counts should either limit field surveys to defined ranges of weather conditions, or explicitly incorporate environmental conditions in both the reporting and analysis. For example, strong winds that obscure burrow openings produce a negative bias in counts or render the method impractical. Also, the time of day can alter the activity patterns of *Ocypode*, with many crabs remaining inactive during the hottest time of the day (Valero-Pacheco and others 2007). We found that many crabs had plugged their burrows by noon, making counts less reliable than in the morning. As surface layers of the sand became dryer and less cohesive due to solar radiation, many burrow openings had collapsed around noon, particularly on the upper shore. Thus, future surveys should be limited to within a few hours after sunrise.

On many urban beaches several types of human pressures can act simultaneously. For example, human trampling is often most intense in sections where the habitat has been substantially modified by shore armouring. In many real-word monitoring applications, such spatial overlap of pressures presents challenges with regards to the ability to distinguish between the ecological effects caused by individual stressors. Ideally, the best design solution would be to replicate the monitoring effort across multiple, independent sites that differ in the number, type and intensity of the pressures which are of interest. If possible, such monitoring designs should include locations with single stressors to partition the ecological effects of individual human pressures and also encompass locations with multiple stressors to assess whether additive ecological impacts operate.

Reductions in burrow counts denote a negative effect on population densities, but the actual mechanisms that cause these declines remain unknown, except for the impact of off-road vehicles that can directly crush crabs (Wolcott and Wolcott 1984; Schlacher and others 2007b). Putative causes of population declines in ghost crabs span a wide ambit such as: 1) direct crushing of crabs through trampling; 2) habitat loss and / or modifications; 3) changes to metabolic costs, reproduction, and behaviour; 4) trophic shifts and enhanced predation pressures; 5) light pollution. Measured effects will in turn depend on species-specific response to external drivers, emphasizing the need for fundamental autecological information such as reproductive cycles and recruitment, physiological climate envelopes, and trophic dynamics of ghost crabs on sandy beaches.

Mitigation measures and management interventions that seek to reduce negative ecological effects will invariably have to target the process causing the

observed impacts. In the case of ghost crabs on urban beaches, it appears logical to propose human trampling as a prime mechanism of impact (but see Jaramillo and others 1996). Robust scientific evidence to support the need for management interventions requires, however, that an unequivocal link between the level and nature of human disturbance and the biological response is demonstrated; this can only be achieved through controlled, and carefully designed manipulative experiments (Bulleri and others 2007). Thus, a major lesson from this study is that the mechanistic links between putative human pressures and biological responses need to be determined (see also Schlacher and others 2007b).

### **CHAPTER 2**

Human disturbance as a cause of bias in ecological indicators for sandy beaches: experimental evidence for the effects of human trampling on ghost crabs (*Ocypode* spp.)

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#### Abstract

Human pressures on coastlines are increasing globally, particularly on urban beaches where maintenance of sand budgets and erosion control are the main focus of current shoreline management. By contrast, biological attributes are rarely considered and few, if any, ecological indicators are routinely monitored on beaches. Abundances of ghost crabs (genus Ocypode) generally respond predictably to human stressors, and are thus a potentially suitable ecological indicator for beaches. The crabs construct burrows with a single, prominent opening at the surface, and population sizes are commonly estimated by counting the number of these burrow openings. While such 'burrow counts' are attractive as a low-cost and simple monitoring technique, they may violate a key performance criterion of indicators: not to be overly sensitive to expected sources of interference. On urban beaches such interference is human trampling and, consequently, we evaluated its influence on the performance of burrow counts. The effects of short-term, intense human trampling on numbers and sizes of crab burrows were measured in a series of impact experiments, in which pedestrian trampling was repeatedly applied over 5 hours on 4 consecutive days. Burrow counts were highly sensitive to interference from short-term trampling disturbance, which can substantially bias population estimates inferred from such counts. Importantly, burrow densities

recovered overnight and apparent shifts in entrance size structures recorded immediately after the trampling impacts were also no longer evident on the following day. Thus, short-term trampling shifted parameter estimates without significant biological effects underpinning such changes – a clear case of bias. Although crab density and size structure are susceptible to artifacts caused by human trampling, they remain valuable indicators for sandy beaches, if interference by pedestrians is small in field measurements or can be accommodated in numerical analyses.

Keywords: sandy beaches; trampling; recreation; monitoring; assessment

#### 2.1. Introduction

Rapid and widespread development, mainly fuelled by the exponential growth of coastal populations, has escalated human pressures on sandy beach ecosystems globally (Schlacher and others 2006; Schlacher and others 2007a). These developments increasingly threaten the ecological integrity of beach systems, encompassing a wide range of impacts that include the destruction of dune and beach habitats by infrastructure development (Nordstrom 2000), shoreline armouring (Dugan and others 2008), beach nourishment (Jones and others 2008), wildlife disturbance (Yasué and Dearden 2006), damage to dune vegetation (Groom and others 2007), pollution (Junoy and others 2005), beach cleaning (Gheskiere and others 2006), and impacts caused by recreation and tourism (Davenport and Davenport 2006).

Ecological indicators are widely used to assess the nature, severity and spatial ambit of human impacts, and to evaluate the efficacy of management interventions (Niemi and McDonald 2004). Ecological indicators are conventionally defined as measurable characteristics of the structure, composition, or function of ecosystems (Niemi and McDonald 2004). Numerous criteria for ecological indicators have been proposed, but the most commonly accepted include aspects of: 1) ease of measurement at low cost; 2) sensitivity to stresses and predictable response to specific pressures; 3) large insensitivity to expected sources of interference; 4) documented reaction to natural and anthropogenic disturbances in the system; 5) delivery of information at spatial and temporal scales that match management responses; 6) ability to predict changes that can, theoretically, be prevented through management (Dale and Beyeler 2001; Niemeijer and de Groot 2008).

Whilst indicators can be selected from several levels of biological and ecological organization, indicator species are the most common (Noss 1990). Concepts, applications and definitions of indicator species are diverse, including: 'keystone' species (strong interactions with other species); 'umbrella' species (large habitat range); 'dispersal-limited' species (demonstrated site fidelity); 'resource-limited' and 'process-limited' species (sensitive to changes in a specific ecological resource or process); 'flagship' species (attract public support) (Noss 1990; Lambeck 1997).

Invertebrates are efficacious ecological indicators of human stressors in a wide range of environments (Chessman 1995; Fulton and others 2005; Resh 2008; Van Dam and Van Dam 2008). They generally respond to disturbances at finer spatial scales than larger vertebrates (Carignan and Villard 2002), and their distributions and population sizes are often well correlated with environmental conditions that are, potentially, subjected to human alterations (Schoener 1986).

Ghost crabs of the genus *Ocypode* are common semi-terrestrial invertebrates on warm-temperate to tropical sandy beaches. The crabs excavate extensive burrows

on the upper shore and in the dunes, becoming surface-active mainly at night (Barras 1963). Populations of ghost crabs respond predictably to direct physical impacts (i.e. trampling, off-road vehicles) and to habitat changes in the form of reduced abundances (Barros 2001; Moss and McPhee 2006; Schlacher and others 2007b; Lucrezi and others 2009b). Also, because ghost crabs are the top invertebrate predator on sandy beaches, and are in-turn prey for a number of higher-order consumers (McLachlan 1980; Iwamoto 1986), changes in ghost crab numbers are a good proxy for impacts on whole beach food webs.

Because crab burrows have highly distinct openings on the beach surface, the 'standard method' for estimating population sizes of ghost crabs on sandy shores is to count the number of burrows in replicate plots (Barros 2001; Moss and McPhee 2006; Schlacher and others 2007b). In fact, the ease and low cost of 'burrow counts' is one of the key arguments for the use of ghost crabs as ecological indicators on sandy beaches (Barros 2001). The method may, however, produce biased results in the form of artificially low population estimates if burrow openings are merely obscured without affecting the survival of crabs inside their burrows. This situation arises most likely on urban beaches that are subjected to high volumes of pedestrian traffic: here, intense trampling by humans is likely to collapse the burrow entrances of crabs; it may also crush crabs inside their burrows. Simple 'burrow entrance counts' of ghost crabs are therefore unlikely to distinguish between actual biological impacts (i.e. individuals killed by trampling) and apparent impacts (i.e. negative bias of population sizes caused by collapsed entrances) on urban beaches. Yet, many environmental assessments using ghost crab burrow counts as ecological indicators target such urban beaches (Schlacher and others 2008b).

We tested whether short-term human trampling makes ghost crab burrow counts simply a less robust ecological indicator by introducing measurement bias, or whether it significantly lowers crab abundances by lethally crushing individuals.

#### 2.2. Material and methods

#### 2.2.1. Study area

The study was conducted on Mooloolaba Beach (26.68°S, 153.12°E; Queensland, Australia). The beach forms the southern boundary of a 1.8 km long embayment and is moderately exposed to the predominant SE-ocean swells. The beach is one of the most popular recreational areas in the region. It has a long history of human engineering interventions which have resulted in significant morphological changes over the past 60 years (Longhurst 1997). For example, dunes in the western part of the beach have been replaced with infrastructure such as seawalls, boardwalks and buildings. Some natural dune areas remain in the central and eastern part of the beach, but overall dune width is reduced. Recreational use is concentrated in the western sections of the beach that are close to infrastructure and patrols by surf life savers. Two species of ghost crabs, *Ocypode cordimanus* and *Ocypode ceratophthalma* are common on the upper beach and in the dunes, but population sizes are reduced in areas heavily trampled by humans and where shore armouring has been implemented (Lucrezi and others 2009b).

#### 2.2.2. Experimental design

The principal aim of the study was to determine the potential of pedestrian trampling to bias estimates of counts and sizes of ghost crab burrow openings. We tested the

response of burrow density and size to foot traffic in experiments where human trampling was repeatedly applied to ghost crab populations.

Experiments were conducted in four experimental plots (5 x 3 m) established in the upper intertidal zone, near the drift line and 8 m seawards from the base of the foredunes. Plots were fenced to exclude interference from the general public. Human trampling was applied to two plots and the remaining plots served as controls (i.e. human exclusion, no trampling). Human recreation is concentrated on the eastern and western end of the beach with a central area that receives fewer visitors (TA Schlacher pers. obs.). We conducted the experiments in this central area to minimize interference with public amenity values of the beach.

To prevent physically disturbing the control plots – and the impact plots before the experimental application of trampling impacts began – we used a scaffold. It consisted of a ladder lifted 30 cm above the ground by trestles placed outside the boundaries of the experimental plots. Field operators moved systematically across the ladder and measured the burrow openings below through the spaces between the rungs.

The experiments were run over four consecutive days in late April 2007. On each occasion, we counted all burrows and measured their sizes (diameter to the nearest mm using a ruler) in each plot at 07:00 (ca. 2 h after sunrise) before any disturbance was applied. The trampling treatment consisted of two people (weight: 45 and 55 kg) crossing the impact plots each 50 times in a zigzag pattern; this resulted in close to 100% coverage of footprints. The trampling treatment was applied in 5 distinct bouts at 50 min intervals over a 5 h period. Before each new trampling event, all burrows which remained intact were counted and their diameter measured.

Before each treatment event (i.e. 5 bouts separated by 50 min.) a range of environmental variables was measured at three randomly selected spots within each plot, including: a) sand temperature (5 cm deep; electronic thermometer -Fluke 52 K/J); b) sand moisture (8 cm deep; Trident microwave meter); c) sand shear force resistance (field inspection vane tester Geonor H-60, with a vane size of 5 cm length x 2.5 cm width); d) penetration force (Geotester pocket penetrometer with tips of 20 mm diameter). Air temperature and wind speed were recorded (using a Skymate SM-18 Windmeter) at the start (07:00) and end (12:00) of each experimental day. Over the course of the experiments, air temperature ranged between 22.5°C and 25.1°C in the morning (07:00) and 27.0°C to 35.9°C at noon, and w inds were light at 0-5 knots (07:00) and 2.5-16.9 knots (12:00).

#### 2.2.3. Data analysis

To examine whether the density and size of ghost crab burrow openings changed with increasing pedestrian trampling, we tested the null hypothesis that there was no difference between reference and impact plots. We did so by using a repeated measures analysis of variance (ANOVA) with a co-variate, two fixed and one repeated factors. The time the measurements were taken during each experiment (08:00-12:00) is a repeated measure, whilst experiment (1-4) and treatment (reference vs. impact) are included as fixed effect terms. To partition out the possible effect of variations in burrow densities between plots before treatments were applied at 07:00 on each day, burrow densities and sizes measured at 07:00 in each experiment before the treatments were applied are included as a co-variate. Because of possible differences in variances between impact and reference treatments that could affect the assumption of sphericity in the repeated measures ANOVA, we used Greenhouse-Geisser

corrections for all hypothesis tests (Keselman and others 2001). The same analysis was applied to environmental variables (i.e. sand moisture, temperature).

To assess whether repeated trampling (i.e. trampling impacts in 4 experiments) resulted in significant changes in population sizes in the impacted plots, we performed a simpler repeated measures ANOVA that compared the number and diameter of burrows between treatments at the start of each experiment.

#### 2.3. Results

#### 2.3.1. Habitat characteristics

Trampling did not result in significant changes to sand temperature and moisture. Sand did not became markedly hotter over the course of each experiment (Table 22; ANOVA - effect time:  $F_{(2.62,18.33)} = 0.62$ , P = 0.59), and sand surface temperature did not differ between control and trampling plots (Table 22; ANOVA - effect treatment:  $F_{(1,7)} = 0.37$ , P = 0.56). Sand temperatures (range: 22.9-23.6°C) were slightly but significantly lower during the experiments 3 and 4, but this small decrease of 0.5°C was the same for both experimental treatments (Table 22; ANOVA – experiment x treatment:  $F_{(3,7)} = 0.32$ , P = 0.81). Trampling resulted in a reduction of sand moisture (range: 0-3.6%) by between 0.46 and 0.71% in three of the four experiments, but overall, no significant effect of experimental treatment was detected (Table 22; ANOVA – effect treatment:  $F_{(1,7)} = 4.76$ , P = 0.06). The lower temperatures in experiments 3 and 4 were reflected in significantly higher moisture values at these times (Table 22; ANOVA – effect experiment:  $F_{(3,7)} = 11.49$ , P < 0.01). **Table 22** Summary of repeated measures ANOVA partitioning variation in sand moisture, sand temperature, and the density and size of ghost crab burrow openings between treatments (reference vs. impact) and between experiments (1 to 4), as well as over time (07:00-12:00). Values measured at 07:00 before the experimental application of trampling in each experiment are included as a co-variate in the analysis ( $^{ns} P > 0.05$ , \* P < 0.05, \* P < 0.01, \*\*\* P < 0.001)

ANOVA	Sand moisture (%)		Sand to	Sand temperature(°C)		Burrow	Burrow den sity (ind. m <sup>-2</sup> )			Burrow diameter (mm)		
Source of variation	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Treatment	1	0.006	4.76 <sup>ns</sup>	1	0.10	0.37 <sup>ns</sup>	1	75.05	83.72***	1	248.57	113.19***
Values at 07:00	1	0.014	11.89**	1	0.72	0.26 <sup>ns</sup>	1	10.64	11.87*	1	55.53	25.28**
Experiment	3	0.014	11.49**	3	2.23	8.01*	3	0.10	0.11 <sup>ns</sup>	3	9.03	4.11 <sup>ns</sup>
Experiment*Treatment	3	0.002	1.76 <sup>ns</sup>	3	0.09	0.32 <sup>ns</sup>	3	1.10	1.23 <sup>ns</sup>	3	14.46	6.58*
Error	7	0.001		7	0.28		7	0.90		7	2.19	
Time	1.59	0.001	1.27 <sup>ns</sup>	2.62	0.10	0.62 <sup>ns</sup>	2.28	47.81	2.58 <sup>ns</sup>	1.60	2.70	0.89 <sup>ns</sup>
Time*Values at 07:00	1.59	0.002	2.24 <sup>ns</sup>	2.62	0.06	0.37 <sup>ns</sup>	2.28	46.05	2.49 <sup>ns</sup>	1.60	2.86	0.94 <sup>ns</sup>
Time*Experiment	4.79	0.005	5.39*	7.85	0.14	0.84 <sup>ns</sup>	6.85	8.43	0.46 <sup>ns</sup>	4.80	9.53	3.15 <sup>ns</sup>
Time*Treatment	1.59	0.002	1.86 <sup>ns</sup>	2.62	0.38	2.32 <sup>ns</sup>	2.28	0.42	0.02 <sup>ns</sup>	1.60	5.81	1.92 <sup>ns</sup>
Time*Experiment*Treatment	4.79	<0.001	0.54 <sup>ns</sup>	7.85	0.10	0.62 <sup>ns</sup>	6.85	14.45	0.78 <sup>ns</sup>	4.80	17.90	5.92**
Error	11.17	0.001		18.33	0.16		15.97	18.50		9.60	3.02	

<sup>ns</sup> P > 0.05; \* P < 0.05; \*\* P < 0.01; \*\*\* P < 0.001

#### 2.3.2. Variation in burrow density and size

Pedestrian traffic substantially reduced burrow densities and sizes immediately after the trampling impacts had occurred, but it did not cause significant changes at a time scale of days. Mean burrow densities were reduced by 88% following human trampling impacts (Fig. 5). In all experiments, densities in impact plots (0.36 ind. m<sup>-2</sup>, se = 0.03) were significantly lower than in un-trampled reference plots (2.85 ind. m<sup>-2</sup>, se = 0.13; Fig. 5; Table 22; ANOVA - effect treatment:  $F_{(1,7)} = 83.72$ , P < 0.001). The first set of impacts (i.e. 100 passes) caused the greatest change to the density of ghost crab burrows; further trampling had comparatively small additional effects (Fig. 6). Time *per se* did not influence ghost crab densities irrespective of whether trampling had occurred or not (Table 22; ANOVA – time x treatment,  $F_{(2.26,15.97)} = 0.02$ , P = 0.99). There was no significant interaction between treatment and experiment (Table 22; ANOVA – experiment x treatment,  $F_{(3.7)} = 1.23$ , P = 0.37), suggesting that experimentally produced effects of trampling on burrow counts were consistent across all experiments.



**Figure 5** Variation in mean burrow counts (a) and burrow size (b) of ghost crabs in relation to experimental disturbance by human trampling. Experimental treatments consisted of 100 pedestrian passes applied five times at 50 min intervals in four separate experimental runs (days) compared with abutting control sites from which beach visitors had been excluded



**Figure 6** Relationship between changes in ghost crab burrow numbers (a) and opening diameter (b) in relation to the intensity of human disturbance. Effect size ( $\Delta$ ) is measured as: |  $(\bar{x}_{\text{Ref.}} - \bar{x}_{\text{Imp.}}) / \bar{x}_{\text{Ref.}}$ |, where  $\bar{x}$  are the mean values of burrow density or entrance diameter in the reference (Ref.) and impact (Imp.) treatments

Trampling impacts were more pronounced for larger burrows. This asymmetric impact significantly changed the size distribution of burrows not destroyed by foot traffic (Fig. 7). The mean size of burrow openings varied significantly with the time of the day, experiments and treatments (Fig. 6; Table 22; ANOVA - time x experiment x treatment,  $F_{(4.80,9.60)} = 5.92$ , P < 0.01): the average diameter of intact burrow entrances was generally smaller after trampling impacts. High-intensity foot traffic destroyed virtually all burrows >25 mm in diameter, whereas control plots contained burrows ranging up to 75 mm (Fig. 7). Conversely, the minimum size of burrows remained at 4-5 mm in both control and impact plots (Fig. 7). As was the case for burrow densities, the first set of

trampling impacts caused the greatest decrease in burrow size, with additional disturbances having much smaller additional effects (Fig. 6).



**Figure 7** Comparison of the size distribution of burrow openings between experimentally trampled (filled bars) and undisturbed control plots (open bars) before trampling treatments were applied (top row) and after each plot was repeatedly impacted by pedestrian foot traffic (bottom row)

Because experiments were run on consecutive days and the sets of trampling impacts were separated by at least 19 h between experiments, changes to the density and size of crab burrows which were measured at the start of each experiment should be indicative of short-term (i.e. days) impacts on ghost crab populations. However, we neither found a significant difference in burrow numbers nor burrow sizes between the impact and control plots before trampling commenced in each experimental run (Table 23). At the start of each experiment, mean burrow densities and sizes were similar between plots irrespective of whether trampling had been applied on the previous day or not (Table 23). This lack of significant day-to-day changes, which could not be linked to the intensity of human disturbance, suggests that crabs of all sizes repaired their burrows overnight, resulting in densities and size structures that were indistinguishable from pre-impact conditions in the short term (Fig. 6).

**Table 23** Repeated measures ANOVA contrasting ghost crab burrow density (ind. m<sup>-2</sup>) and burrow opening diameter (mm) between experiments (1-4) in the reference and impact treatments before the experimental trampling impacts were applied (Mauchly's Test of Sphericity suggested the use of Greenhouse-Geisser values; <sup>ns</sup> P > 0.05)

	Burrow density			Burrow diameter			
Source of variation	df	MS	F	df	MS	F.	
Treatment	1	0.81	0.65 <sup>ns</sup>	1	1.07	0.17 <sup>ns</sup>	
Error	2	2.50		2	6.37		
Experiment	1.07	2.47	5.22 <sup>ns</sup>	1.20	18.69	1.54 <sup>ns</sup>	
Experiment*treatment	1.07	0.13	0.27 <sup>ns</sup>	1.20	5.40	0.45 <sup>ns</sup>	
Error	2.13	0.47		2.40	12.10		

<sup>ns</sup> P > 0.05

#### 2.4. Discussion

#### 2.4.1. Environmental influences on burrow density

Environmental conditions can significantly influence the density of ghost crab burrows on sandy beaches (Lucrezi and others 2009b). We found fewer burrow entrances on hotter days and, conversely, more during cooler conditions. Ghost crabs are predominately nocturnal, generally avoiding surface activity during the day, and they prevent dehydration by plugging their burrows around noon (Barras 1963). Crabs may also not re-open a burrow after it had been trampled during the day (Neves and Bemvenuti 2006).

Burrow entrances can collapse in very dry sand, or be in-filled by wind-blown sand. By contrast, in moist sand, burrow entrances are more stable and fewer burrows become obscured by sand. Thus, both biological processes (i.e. burrow plugging) and physical mechanisms (e.g. entrance collapse) can lead to apparent decreases in density estimates of ghost crabs (Lucrezi and others 2009b). In the present study, differences between treatments were, however, consistent irrespective of variations in wind speed or the temperature and moisture of the sand.

#### 2.4.2. Disturbance effects on burrow numbers and size

Almost all benthos research on exposed sandy beaches employs mensurative designs (i.e. 'compare and contrast'), while experimental approaches that are common on rocky shores and in other sedimentary habitats are rare on beaches (Schlacher and others 2008b). Our short term trampling is one of the few experiments on the effects of human disturbance on sandy beach macrobenthos (but see Schoeman and others

2000). Disturbance is commonly defined as a distinct event in time that disrupts the structure of an ecosystem, community, or population, and that changes resources, the availability of substratum, or the physical environment (Pickett and White 1985). Disturbance events differ with respect to their frequency, duration, and intensity (Resh and others 1988), and our experiments were clearly a high-intensity, pulse event over a relatively short duration (4 days).

Intense human trampling resulted in substantially lower burrow counts, and – by implication – apparent reductions in population sizes of ghost crabs on the beach. However, the effects of the short-term trampling disturbances were mostly non-lethal to ghost crabs and did not last long. A single hit by a pedestrian suffices to cover or collapse a burrow opening, and because the crabs do not to re-open infilled burrow entrances for at least one hour (S Lucrezi pers. obs.), burrow counts fell markedly after people had walked over the plots (Fig. 5). Burrow numbers recovered, however, overnight, showing that human trampling is not necessarily lethal to most crabs. Therefore, short-term pedestrian trampling can strongly bias estimates of ghost crab densities on sandy beaches.

In the long-term, human trampling does, however, have demonstrable, negative impacts on ghost crab population sizes (Lucrezi and others 2009b), most likely as a consequence of several, additive sublethal effects related to frequent habitat disturbance. Also, other short-term trampling experiments have demonstrated direct mortalities of macrobenthic species on sandy beaches (Moffett and others 1998).

In all four experiments conducted in this study, the application of the first trampling impact (100 passes) had the largest effect on burrow numbers; subsequent trampling impacts caused much smaller additional decreases in burrow densities

(Fig. 6). Similarly, experiments that simulated typical recreational activities such as walking and volleyball games on a South African beach, also found the strongest impacts associated with the initial disturbance (Moffett and others 1998).

The most significant result with respect to burrow size was the marked decrease in the maximum burrow opening diameter measured after trampling. Intuitively, because of their larger surface area, larger burrows are more likely to be hit by footsteps. However, crabs of all sizes carry out their burrowing activities overnight (Strachan and others 1999), and every morning in the present study, burrows of both adults and juveniles were found on the beach.

This result has significant implications for interpreting changes in burrow size distributions that apparently – but falsely – indicate higher mortalities of larger individuals. Using estimates of burrow size after pedestrians have trampled a beach can lead to the false conclusion that trampling changes population age structures, preferentially killing larger, adult crabs. Yet, larger crabs simply stay within their collapsed burrows and wait to re-emerge until trampling ceases at dusk. Adult crabs are also able to withstand heat and dehydration better than juveniles, and generally can remain fossorial during the day (Chan and others 2006). Conversely, juveniles often need to feed on the beach surface during the day to avoid competition with, and predation by, adult crabs at night (Fisher and Tevesz 1979). Thus, juveniles are more likely to repair and unplug collapsed burrows following trampling impacts during the day (S Lucrezi pers. obs.). This behavioural asymmetry between adults and juveniles can further confound the interpretation of burrow size distributions.

#### 2.4.3. Consequences of recreational disturbance for ghost crabs

It has been suggested that ghost crabs can acclimatize to increasing levels of recreational beach use (Steiner and Leatherman 1981). Even positive effects of recreation have been reported when food scraps left by beach visitors provide a trophic subsidy to the scavenging crabs (Steiner and Leatherman 1981). Yet, on many beaches, pedestrian trampling is a heavy and continuous disturbance agent that causes significant negative impacts on ghost crab populations in the long term (Lucrezi and others 2009b).

Our experiments simulated heavy, short-term, trampling disturbance that did not kill significant numbers of ghost crabs over four days. Trampling is, however, likely to have a range of sublethal effects on these and other beach organisms. For example, human beach use substantially alters the physical properties of the sand matrix (Schlacher and Thompson 2008), lowering burrow stability. Recreational activities may also directly disturb crab feeding, crush more sensitive post-larval forms, and limit the duration of surface activity.

It has been suggested that ghost crabs shift into the dunes as a result of continuous disturbance on the beach (Barros 2001), which increases their metabolic costs (especially for juveniles) in the search for food and water for respiration. Shoreline armouring impedes movements of crabs into the dunes, further compounding the effects of recreational disturbance in the intertidal zone (Lucrezi and others 2009b).

Because burrows can be as deep as 1 m (Maccarone and Mathews 2007), the experimental trampling disturbance may not have completely destroyed the burrows. However, shallower burrows under construction are more susceptible. In all cases,

ghost crabs will incur energetic costs to repair burrows, whether partly or completely collapsed. Time and energy expended in repairing may impact negatively on feeding and reproductive output. Repair work does not only impose extra metabolic demands on crabs, it also exposes them to avian and mammal predators.

# 2.4.4. Implications of trampling interference for indicator performance and monitoring designs

Although evidence for widespread ecological effects linked to beach recreation is accumulating (Davenport and Davenport 2006; Moss and McPhee 2006), ecological assessments of sandy beaches are rare, and management is almost exclusively concerned with maintaining sand budgets (Schlacher and others 2008b). Part of the reason for the current lack of ecological assessments, monitoring, and management of beaches is the dearth of robust and accepted ecological indicators for these systems.

Ghost crabs are an important component of sandy beach ecosystems, occupying a pivotal trophic role as apex invertebrate predators while being also prey for vertebrate consumers (Wolcott 1978; Christoffers 1986). Frequent anthropogenic disturbance, such as human trampling and vehicles, and habitat modifications can lead to substantial declines in ghost crab population sizes on beaches (Moss and McPhee 2006; Schlacher and others 2007b; Lucrezi and others 2009b). Thus, ghost crab abundance appears to be a useful ecological indicator to measure human impacts on sandy beaches (Barros 2001; Neves and Bemvenuti 2006).

Burrow counts of ghost crabs meet two key criteria commonly used in indicator selection: 1) ease of measurement at low cost (Lucrezi and others 2009b); 2) sensitivity to stress with predictable response to stress (Schlacher and others 2007b). However,

a good indicator species must also be largely insensitive to expected sources of interference (Niemeijer and de Groot 2008). Since many applications that employ ghost crabs as indicator species are likely to take place on urban beaches, and because urban beaches experience the highest levels of human trampling, the expected interference in this instance is human trampling. Consequently, we evaluated its influence on the performance of burrow counts as ecological indicators. Our results clearly show that counts of ghost crab burrows are susceptible to short-term trampling, which can substantially bias population estimates inferred from such burrow counts.

Bias in burrow counts and sizes has consequences for using ghost crabs as ecological indicators: both counts and opening diameters are only reliable proxies for population densities and size structures if field measurements are taken when pedestrian disturbance is small. Thus, field surveys should be limited to periods when beach visitors are few - as early in the morning as possible - on weekdays rather than weekends and public holidays, and during cooler and overcast conditions rather than during sunny weather. Also, when spatial contrasts are required, measurements at different sites must be matched with respect to tides, time of the day, weather conditions, and temporal patterns of beach visitor numbers. Provided such basic design factors are explicitly incorporated into standard operating procedures for field surveys (Lucrezi and others 2009b), interference by human trampling does not constitute an insurmountable hurdle in the application of ghost crab burrows as ecological indicators of human pressures on sandy shores.

## **CHAPTER 3**

# Can storms and shore armouring exert additive effects on sandy beach habitats and biota?

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#### Abstract

Increased storminess is a likely consequence of global climate change; its effects may be most dramatic on coasts dominated by sandy beaches. This scenario demands that the impacts of storms and the role of armouring structures, constructed as storm defences, are better understood. Here we assessed how a relatively small storm impacted beach morphology and macrobenthos, and whether a seawall can modulate such impacts. The study system was a small (<1.5 km long) beach, bisected into two parts, with and without a seawall. The beach became narrower and steeper during the storm, when 26% of the subaerial sediment prism eroded from the armoured section; sand losses were five-fold smaller on the unarmoured part. Densities of ghost crabs (Ocypode) dropped significantly (36%) and were to some extent modulated by shore armouring; losses were high (62%) just seawards of the seawall where post-storm densities remained consistently lower. There was no ecological recovery in the shortterm, with most (83%) post-storm density values of crabs lower, and depressed crab counts in front of the seawall up to 3 months after the storm. Seawalls can change the resilience of beaches to storms which may result in stronger ecological effects on armoured coasts.

Keywords: storm impacts; sandy shores; recovery; erosion; climate change; ghost crabs; *Ocypode* 

#### 3.1. Introduction

Global climate change is predicted to result in more and stronger storms (Holland and Webster 2007; IPCC 2007; Elsner and others 2008), with significant impacts on coastlines worldwide, especially on sedimentary shorelines composed of sandy beaches (Slott and others 2006; Harvey and Woodroffe 2008; Inman 2009). Sandy beaches form most of the globe's coastlines and provide a wide range of irreplaceable ecosystem services to humankind (Brown and others 2008; Defeo and others 2009), including the processing of organic matter, nutrient recycling, and the provision of habitat and foraging sites for vertebrates (Weston and Elgar 2005; Peterson and others 2006; Schlacher and others 2008b). Storms can severely erode beaches, cause loss of habitat, accelerate shoreline retreat, deposit large amounts of wrack, shift sediment transport regimes, impact populations and assemblages of beach animals, and threaten coastal infrastructure (Jaramillo and others 1987; Morton and others 1994; Jones and others 2007; Ashton and others 2008; Tonisson and others 2008).

Beaches are armoured to protect human assets placed too close to the active shoreline. Common measures include hard (e.g. seawalls) and soft engineering (e.g. beach nourishment) interventions (Charlier and others 2005; Polomé and others 2005; Walker and others 2008b), all of which have negative environmental outcomes (Dugan and Hubbard 2006; Dugan and others 2008; Jones and others 2008). Paradoxically, armouring can accelerate beach erosion after the structures have been constructed (Fletcher and others 1997), and armoured beaches may be more vulnerable to storm impacts (Castelle and others 2008). If shore armouring does exacerbate the effects of

extreme events, the potential exists for additive, negative ecological effects of coastal defence structures and increased storminess.

Despite a growing body of evidence that sandy beach ecosystems are vulnerable to human stressors (Schlacher and others 2007a; Defeo and others 2009), beach management rarely extends beyond its traditional focus of protecting shoreline stability and sand budgets - it usually neglects the conservation of essential ecological structures and processes (Schlacher and others 2006; Schlacher and Thompson 2008). However, it is arguably the biggest challenge of ecologically-orientated beach management to predict environmental changes caused by climate change and to develop appropriate adaptation strategies (Jones and others 2007). Yet, information on how beach biota respond to shifts in environmental conditions caused by climate change are fragmentary at best (Jones and others 2007). Given that 1) storms are likely to increase in intensity, duration and frequency over the coming decades (Elsner and others 2008), 2) storms play a fundamental role in shaping beach habitats (Slott and others 2006), and 3) shore armouring will increasingly be used to combat the physical effects of storms on sedimentary coastlines (Polomé and others 2005), in this paper we focus on the effects of a storm event on a sandy beach and ask whether these could be modulated by coastal armouring. Our model system was a small urban beach in eastern Australia where ghost crabs (Ocypode) are a key component of the biological assemblages.

The overarching objective of this study was to measure changes in beach habitat and biota caused by a storm event. Specifically, we asked: 1) how does beach morphology respond to changes in wave regime? 2) What is the magnitude of the storm impact on the population size of ghost crabs? 3) Does shore armouring influence the susceptibility of habitats and biota to storms? 4) Can beaches and biota recover

from storm impacts in the short term (weeks to months)? 5) Is such 'recovery' influenced by shore armouring structures?

#### 3.2. Material and methods

#### 3.2.1. Study area

The study was conducted at Noosa Beach (26.38°S; 15 3.08°E) in SE Queensland, Australia. The beach forms the western boundary of Laguna Bay, is 1.4 km long and is bounded in the east by Noosa Heads and in the west by the Noosa Estuary (Fig. 8). The beach is today extensively modified by numerous human engineering interventions, past and present. In 1968, the backshore was stabilized with a rock wall to protect properties against severe erosion from cyclones. In 1978, the estuarine mouth was diverted several hundred metres to the north to its present location. The relocation works included the construction of a 260 m long rock groyne to stabilize the newly formed estuarine entrance. Furthermore, the lower sections of the estuary were extensively dredged and deepened, and the dredged material was used to create a new beach between the river mouth and the original beach (i.e. 'Spit Beach'). An additional rock groyne, 130 m long, was built in 1982 in the central part of the beach to slow erosion. This rock groyne today divides the beach into an unarmoured section to the west and an armoured section to the east. At the time of the study, the two sections of the beach were both wave-dominated shores of a modal intermediate state. with Beach Index (McLachlan and Dorvlo 2005) values of 1.12-1.87 and Dean's ( $\Omega$ ) Parameters (Short 1996) of 3.06-3.19. Maximum spring tidal range was 2.1 m.



**Figure 8** Study area, Noosa Beach, in eastern Australia, comprising an urbanized section in the south-east armoured with a seawall (b), and a north-western section not armoured and backed by natural dunes (c). Burrow counts of ghost crabs were made in 16 transects, each consisting of 9 x 10 m plots running from the base of the foredunes / walking path (Level A) to the seaward limit of burrow occurrence near the effluent line (level F). Photo Credits: a – Google Eearth; b,c – S. Lucrezi
Erosion of the armoured, eastern section of the beach is an ongoing local shoreline management issue. Since 2003, this section has been nourished with sand translocated from a borrow area located in the shallow subtidal near the estuarine entrance. The sand is pumped as slurry to the eastern section of the beach where it is deposited above and immediately seawards of the rock wall. Apparently, an objective of this nourishment program is not only to replace eroded sand but also to cover the rock wall with sand which has a much higher amenity value than the bare rocks. All the dunes in the armoured section of the beach have been replaced by urban development, with the landward boundary of the beach today formed by a pedestrian pathway. By contrast, the unarmoured section still retains natural dune areas, although these have undergone human modifications such as pathways which connect the beach to car parks. The armoured section suffers from extensive human trampling, compared to the unarmoured section which receives fewer visitors.

### 3.2.2. The storm

The morphology of the beach was changed by a storm that formed off the SE coast of Queensland and hit the shore between the  $28^{th}$  December 2007 and  $5^{th}$  of January 2008. The storm carried mainly southerly and south-easterly winds of up to 61 km h<sup>-1</sup>; relative humidity ranged between 56% and 94%, and daily precipitation was up to 40.8 mm. Sea level pressure was low, varying between 999.1 hPa and 1013.3 hPa. Mean sea surface temperature was 24.3°C, the maximu m wave height recorded was 9.3 m, and wave period ranged between 6.7 and 13.5 s. The harsher wave climate and severe weather caused substantial changes to the beach morphology which persisted for several weeks after the storm.

### 3.2.3. Abundance of ghost crabs: spatial layout and burrow counts

We used ghost crabs as the model organisms to test storm effects on beach biota. Ghost crabs are relatively large and common members of animal assemblages on warm-temperate to tropical beaches. The crabs are mainly nocturnal, spending the day in burrows that are distributed from the middle shore into the dunes (Barrass 1963). Reduced population sizes are indicators of both direct mortality (e.g. trampling, off-road vehicles) and indirect disturbance (e.g. habitat changes) by humans (Moss and McPhee 2006; Schlacher and others 2007b). Changes in ghost crab numbers are also likely to be an appropriate surrogate for impacts on whole beach food webs, because the crabs occupy the role of the top invertebrate predator on sandy beaches, but are in turn prey for a number of higher-order consumers (McLachlan 1980; Iwamoto 1986).

To test whether ghost crab populations are reduced by shoreline modifications (including the replacement of the dunes with infrastructure) and by long-term human trampling, we compared burrow densities between the heavily modified section of the beach extending 700 m south-east of the central groyne (armoured section, Fig. 8b) and the less disturbed section extending 700 m to the north-west of the central groyne (unarmoured section, Fig. 8c). Ghost crab densities were quantified by counting the number of active burrow openings on the beach surface (Lucrezi and others 2009b; Lucrezi and others 2009a).

In each beach section, burrow counts were made along eight belt transects, interspersed by 80 m along the beach. Each belt transect was a contiguous strip 10 m wide that extended from the base of the dunes (in the unarmoured section) or the pedestrian pathway (in the armoured section) to the effluent line (the water table outcrop, Fig. 8). Each transect was divided into sequential quadrats that were 9 m

wide; thus, the basic sampling units of the study were adjacent quadrats of 10 m x 9 m. Burrow counts were made during 27 surveys between November 2007 and March 2008.

On each survey day, we started burrow counts at, or soon after, sunrise; a complete survey of the entire beach taking 3-4 h to complete. To avoid possible bias caused by the time of the day when the counts were made in a particular section, transect or level, the sequence of field measurements was randomised by choosing the section to be counted first (toss of coin) and, secondly, randomly selecting the starting transect within each section. Only 'active' burrow openings were counted (Lucrezi and others 2009a). Active burrows were easily identified by either fresh tracks surrounding the openings, or by small mounds next to the entrance signalling recent burrow maintenance, or both. Two species of ghost crab are present on the beach, *Ocypode ceratophthalma* and *Ocypode cordimanus*, but their burrow openings cannot be distinguished with confidence. Therefore, we report all burrow counts at the genus level.

# 3.2.4 Environmental variables

Standard theodolite surveys of the beach face were done to measure basic morphological properties of the beach (e.g. slope, width, elevations of quadrats). Beach slope is here calculated as the angle between the base of the foredune / seawall and the low water spring tide (LWST) mark on the lower beachface. The position of the drift line (the reach of the highest swash previous to the counts) and the effluent line were identified visually. Detailed weather records (i.e. hourly air temperature, wind speed and direction, hourly rainfall) were obtained from the Bureau of Meteorology. Wave data and sea surface temperature were obtained from the nearest wave rider

buoy, operated by the EPA at Mooloolaba 32 km to the south of the study site (www.epa.qld.gov.au).

We determined sediment properties by collecting triplicate sediment cores (30 mm diameter, 100 mm deep) from every quadrat on 6 occasions. In the laboratory, we analysed sediment granulometry by dry-sieving samples through a nested series of seven sieves arranged in decreasing mesh aperture size (4000  $\mu$ m, 2000  $\mu$ m, 1000  $\mu$ m, 500  $\mu$ m, 250  $\mu$ m, 180  $\mu$ m, 63  $\mu$ m). Sediment parameters were calculated according to the Folk and Ward method using the Gradistat software (Blott and Pye 2001). The intensity of human trampling was gauged from beach visitor numbers obtained from Council's surf life saving service. Professional life guards, who patrol the beach daily from 08:00 to 16:00, count the number of people on the entire beach every two hours.

### 3.2.5. Data analysis

The fluctuations of burrow densities and environmental variables during the study were investigated for significant trends and step jumps between periods relative to the storm (before vs. during vs. after). The analysis was conducted using Trend software (Chiew and Siriwardena 2005). The non-parametric CUSUM test was performed for a step jump in the mean. We tested whether the means in two parts of a record were significantly different for a known time of change, which is the time when the storm hit.

Because the quadrats were adjacent to one another and because the same transects were sampled on repeated occasions, there was the potential for spatial and temporal correlations amongst sampling units. Hence, total variance in ghost crab burrow densities as well as sediment parameters and morphological properties of the

beach were analysed with a Mixed Linear Model, which permits the data to exhibit correlation and non-constant variability. The analysis on crab burrows included time (before vs. during vs. after the storm) as the temporal component of variation and beach section (armoured vs. unarmoured) as the spatial term. To account for variations in beach height above the low water spring tide across time and space, beach elevation was introduced as co-variate in the analysis. Count data were log<sub>10</sub>- transformed where required to achieve normality and homoscedasticity. Tukey's Honestly Significant Difference post-hoc tests on least squares marginal means were performed following significant main effects or interaction terms in the Mixed Linear Models. All univariate statistics were calculated using 'SAS' (Version 9.1.3, 2004).

To assess whether ghost crab densities recovered after the storm event, we used a control chart approach (Rocke 1989). Because absolute density values differ across the beachface, the control charts were based on density scores to enable comparison at the same scale. These density scores (d<sub>z</sub>) are studentized values where each density measurement obtained during the post-storm period from a specific level and transect (d<sub>i</sub>) was normalized in terms of the number of standard deviations (s<sub>i</sub>) it deviated from the mean pre-storm density for this level and transect ( $\bar{x}$ ): d<sub>z</sub> = (d<sub>i</sub> -  $\bar{x}$ ) / s<sub>i</sub>. Mean scores were compared for individual levels between pre- and post-storm periods with a t-test using a correction for serial correlation (Zwiers and von Storch 1995). To test whether temporal variance in mean density scores after the storm differed between the armoured and unarmoured sections of the beach, a Levene's test was run.

# 3.3. Results

# 3.3.1. Environmental conditions and habitat changes

Significant step jumps in the means of all environmental variables examined were evident during the storm (Table 24). Mean wind speed during the storm was almost twice that of the pre-storm mean (Table 24), with a maximum gust of 61 km h<sup>-1</sup>; wind speeds remained higher after the storm for several weeks (Fig. 9, Table 24). The lowest air pressure during the study period coincided with the storm event (999.3 hPa) when maximum wave height reached 9.3 m (Fig. 9).



Figure 9 Temporal variation in wind speed (a), maximum wave height (b), air pressure (c), and rainfall (d) over the study period. The shaded area indicates the time of the storm

		E	Sefore Stor	m	During Storm			After Storm		
	CUSUM Test statistic	n	x	SE	n	x	SE	n	x	SE
Sea Conditions										
Significant Wave Height (m)	2079**	4224	1.18	0.005	384	3.18	0.032	4176	1.57	0.007
Max Wave Height (m)	1899**	4224	1.99	0.009	384	5.24	0.055	4176	2.62	0.012
Wave Period (s)	854**	4224	8.42	0.030	384	10.85	0.067	4176	9.14	0.032
Weather										
Air Temperature ( $\mathfrak{C}$ )	673**	2112	22.34	0.057	192	22.46	0.108	2088	23.79	0.053
Relative Humidity (%)	174**	2112	75.01	0.256	192	83.43	0.752	2088	76.30	0.231
Wind Speed (km h <sup>-1</sup> )	555**	2112	11.72	0.143	192	21.39	0.395	2088	12.79	0.132
Maximum Wind Gust (km h <sup>-1</sup> )	610**	2112	17.96	0.208	192	35.80	0.740	2088	20.54	0.212
Hourly Rainfall (mm)	952**	2112	1.60	0.138	192	10.34	0.788	2088	2.81	0.151
Sea Level Pressure (hPa)	648**	2112	1014.89	0.086	192	1006.89	0.251	2087	1012.36	0.112

**Table 24** Comparison of environmental conditions before, during, and after the storm, including CUSUM test statistics for detection of a significant step

 change in a temporal record linked to a discrete time event (Chiew and Siriwardena 2005); \*\* P < 0.01</td>

The storm had a strong effect on the morphology of both sections of the beach (Fig. 10). Mean beach width narrowed from 63 m before the storm to 52 m during the storm (Table 24). Even though the beach widened again after the storm (55 m), it never regained its pre-storm width. In the armoured section, the beachface was compressed from a pre-storm mean width of 66 m to 57 m, whilst beach width shortened from 59 m to 47 m in the unarmoured section. By the end of the study, the width of the unarmoured section had largely recovered, whilst the armoured section had lost an additional 4 m of intertidal beachface. The beach slope also became steeper (marginally from 1.57 to 1.60° in the unarm oured section and from 1.68 to 2.09° in the armoured section) during the storm. A fter the storm, the armoured section kept getting steeper (2.12°), while the slope of the unarmoured section did not change further.



Figure 10 Changes in beach profiles in relation to the storm event

The loss of sediment caused a narrowing of the intertidal zone when the storm removed 26% of the subaerial sediment prism from the armoured section of the beach. Sand erosion on the unarmoured section was 5-fold smaller, accounting for 5% of the pre-storm subaerial beach volume. During the storm, the sediment of both sections coarsened. Sands became finer in the weeks after the event, but remained coarser on the armoured section (Tables 25 and 26). Table 25 Comparison of sand grain size (µm) before, during, and after the storm, and between beach sections (armoured vs. unarmoured).

Comparisons are made separately for six levels across the beach-face, starting at level A which abutted the dunes / walking path and progressing seawards to the lowest limit of burrow occurrence on the beach (level F, Fig. 8). n = 15 for all time x armoured combinations

Beach Level and distance from dunes / walking path		Level A: 0-9 m		Level B	Level B: 9-18 m		Level C: 18-27 m		Level D: 27-36 m		Level E: 36-45 m		Level F: 45-54 m	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Armoured	Before	502	5.98	486	5.31	519	3.86	534	0.70	531	0.74	535	0.38	
	During	660	17.01	625	4.80	650	3.19	664	0.61	661	1.95	665	0.50	
	After	598	7.20	601	4.55	594	3.47	612	0.58	612	1.59	616	0.71	
Unarmoured	Before	505	5.99	500	6.67	521	3.79	534	0.57	532	0.71	536	0.40	
	During	625	6.16	639	4.50	650	3.39	664	0.79	670	13.27	664	2.44	
	After	556	20.90	570	4.43	585	5.42	622	1.67	612	1.59	616	0.54	

**Table 26** Summary of Mixed Linear Model analysis contrasting A - sand grain size (µm) and B – burrow densities of ghost crabs amongst sections of the beach, and times in relation to the storm event (before vs. during vs. after the storm). The model includes elevation of the beach above the low water spring tide (LWST) as a co-variate. All contrasts are done separately for levels across the dune-swash gradient, starting at level A which abutted the dunes / walking path and progressing seawards to the lowest limit of burrow occurrence on the beach (level F, Fig. 8)

Beach level and distance from	Level A: 0-9 m	Level B: 9-18 m	Level C: 18-27 m	Level D: 27-36 m	Level E: 36-45 m	Level F: 45-54 m
dunes / walking path:						

#### A – Sediment Grain Size

Source of variation	$\mathrm{df},\mathrm{df}_{\mathrm{E}}$	F/sig.	df, df <sub>E</sub>	F/sig.	df, df <sub>E</sub>	F/sig.	df, df <sub>E</sub>	F/sig.	df, df <sub>E</sub>	F/sig.	df, df <sub>E</sub>	F/sig.
Section (armoured vs. unarmoured)	1,7	5.94	1,7	13.10**	1,7	1.12	1,7	28.40**	1,7	0.90	1,7	0.25
Storm (before vs. during vs. after)	1,14	5.05*	1,14	43.89***	1,14	51.39***	1,14	3221.73***	1,14	694.71***	1,14	14737.40***
Section x Storm	1,29	2.05	1,29	10.71**	1,29	0.65	1,29	27.50***	1,29	0.51	1,29	0.13
B – Ghost Crab Burrow Density												
Source of variation	$df, df_{E}$	F/sig.	df, df <sub>E</sub>	F/sig.	df, df <sub>E</sub>	F/sig.	df, df <sub>E</sub>	F/sig.	df, df <sub>E</sub>	F/sig.	df, df <sub>E</sub>	F/sig.
Section (armoured vs. unarmoured)	1,14	3.01	1,14	2.57	1,14	0.01	1,14	0.00	1,14	1.81	1,14	0.12
Storm (before vs. during vs. after)	2,28	3.45*	2,28	6.09*	2,28	13.16***	2,23	9.63*	2,18	0.01	1,11	0.01
Section x Storm	2,28	11.62***	2,28	3.20	2,28	4.20*	2,23	0.01	1,18	1.81	1,11	0.01

\* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001

## 3.3.2. Effects on ghost crab densities and distribution

Ghost crab densities were significantly depressed after the storm. For both sections of the beach, mean densities were lower by 36% (before:  $\bar{x} = 25.11$  ind. 100 m<sup>-2</sup>, se = 1.70; after:  $\bar{x} = 16.00$  ind. 100 m<sup>-2</sup>, se = 0.59). Declines were, on average, broadly comparable on the armoured (35%) and armoured (41%) section (Figs. 11 and 12). Losses of burrows were particularly dramatic in the middle part of the beachface where only a quarter of pre-storm burrows remained (Fig. 12).



**Figure 11** Temporal variation in burrow densities of ghost crabs across the armoured (solid symbols) and unarmoured (open symbol) section of the beach at four beach levels (cf. Fig. 8 for levels). The shaded area indicates the time of the storm



**Figure 12** Contrasts in the density of ghost crab burrow openings in relation to the storm event (cf. Table 26 for inferential statistics)

Although burrow densities were significantly affected by the storm in both sections of the beach, the pattern and magnitude of impact partly reflected whether an armouring structure was in place or not (Fig. 12). On the upper beach near the base of the foredunes, mean densities were halved in the unarmoured section due to erosion of the backshore (Fig. 12). There was also a marked decline (62%) just seawards of the rock wall in the armoured section; this loss was higher compared to the same shore level (Level C) in the beach section with natural dunes where mean densities only dropped by 22% (Fig. 12). The effect of the storm event on ghost crab populations was also detectable as a significant step jump in the temporal record of the armoured

section only (Fig. 11; CUSUM test statistic = 8, P = 0.05). Before the storm, densities in the lower to middle section of the beach could sometimes be higher in the beach section armoured with a seawall (Table 27). By contrast, after the storm, densities were consistently lower in the armoured section (Table 27). Table 27 Summary of spatial contrasts in ghost crab burrow density between the armoured and unarmoured section of the beach during each of 27 surveys. Significant (GLM analysis cf. Fig. 12) differences are shown for each level of burrow occurrence (A-F), with arrows facing up (♠) denoting higher mean densities in the unarmoured section, whereas arrows facing down (♣) denote higher means in the armoured section of the beach

	DAY	Level A (0-9 m from dunes)	Level B (9-18 m from dunes)	Level C (18-27 m from dunes)	Level D (27-36 m from dunes)	Level E (36-45 m from dunes)	Level F (45 - 54 m from dunes)
Before Storm	1	ተተ					
	6			Û	<b>û</b> Û	ÛÛ	
	21		Û Û	Û Û	仓仓仓	仓仓仓	
	32	ተተ	ተተ		<b>↑</b>	ተተ	
	45				↑		
During Storm	60		ተተ				
After Storm	68	ተተ	ተተ	ተተተ			
	74						
	79		↑				
	80		ተተ	ተተተ	ተተተ		
	86	↑		ተተ	ተተ		
	90			Ϋ́			
	95	ተተ	↑				
	99						
	102						
	109						
	116				1		
	121			ſ			
	122			ተተተ			
	128	1					
	132	ተተ					
	134						
	136	ûû					
	139	<b>T</b>					
	140	ተተተ					
	141	••					
	142	<b>ተተ</b>	<b>D</b> 0.04	/			
ሻቸላ/ ∜∜	₩ P < 0.00	)1, <b>ተተ/</b> ሁሁ	P < 0.01, <b>1</b>	v ₩P < 0.05			

The ghost crab population did not recover from the storm impact in the short to medium term (i.e. up to ten weeks after the storm; Fig. 13). Most (83%) density values in individual plots recorded after the storm were lower than their corresponding prestorm mean; this pattern of depressed density was slightly more pronounced in the armoured (88% of all scores) than in the unarmoured (79% of all scores) section of the beach. It was also consistent across most beach levels and lasted until the end of the study (Fig. 13). All density scores from areas seawards of the rock wall were negative after the storm. The fact that density scores were below the reference (i.e. pre-storm mean) line for many days or for the entire post-storm period also strongly suggests that the storm event caused a substantial and sustained impact on the ghost crab population. Conversely, we could not detect a consistent effect of armouring on the temporal variance of post-storm density scores, the exception being greater temporal variance at a single beach level seawards of the rock wall (ANOVA - Levene's test: Section x Level –  $F_{4.178} = 3.93$ , P = 0.004).



**Figure 13** Control charts displaying the trajectories of density scores after the storm for each beach level and section to test for recovery in the ghost crab populations. Individual density scores recorded after the storm are plotted against their corresponding pre-storm means and 95% confidence intervals. Mean scores were compared for individual levels between pre- and post-storm periods with a t-test corrected for serial correlation

### 3.4. Discussion

Although ghost crabs are highly mobile and can burrow deeply into the sediment, our data demonstrate that they are vulnerable to storms. Conversion of dune habitat to hard surfaces and the construction of shoreline defence structures had the most detrimental effect on ghost crabs, irrespective of any storm effect. A critical function of dunes is to provide refuge against extreme events (Christoffers 1986), and this was likely to have occurred in the present situation where crabs from the exposed areas of the beaches may have migrated into the dunes during the storm. This defence mechanism against storms for mobile beach species is effectively blocked by seawalls which may present physically insurmountable barriers to crabs. More significant perhaps is, however, the compounded effect of dune loss and shore armouring: access to backshore areas for intertidal species is impeded and the backshore has lost its critical habitat function as a refuge area. Natural disturbances can also have indirect, positive effects on animal populations when short-term declines are counterbalanced by longer-term increases in numbers or enhanced recruitment (Sousa 1984). For example, juvenile ghost crabs could colonize a beach when a series of hurricanes forced most of the bigger crabs into the dunes, effectively releasing competitive pressure on smaller individuals in the intertidal zone (Hobbs and others 2008).

### 3.4.1. Does shore-armouring modulate storm effects?

Seawalls have been used for centuries to protect coastal infrastructure against extreme weather events (Charlier and others 2005; Polomé and others 2005), but they may equally lower the resilience of beaches to storms (Castelle and others 2008). Armouring can accelerate erosion through the disruption of the natural sediment transport system and increased wave reflection, ultimately resulting in the loss of the

intertidal beach (Wong 2003; Dugan and others 2008). It follows that increased erosion from increased storminess is likely to be exacerbated on armoured beaches. In this study, the morphology of the armoured section of the beach was changed more by the storm and it recovered slower. For instance, the beach remained short and steep in the armoured section after the storm, whereas the profiles in the unarmoured section, which retained dunes, had recovered largely to pre-storm conditions ten weeks after the storm. Slower recovery of armoured beaches has also been observed on beaches of the Gold Coast located in the same region as our study (Castelle and others 2008).

More importantly, although ghost crab densities declined in both sections of the beach following the storm onset, there were larger losses seawards of the armouring structure. Also, after the storm, densities at all levels of the beach were always higher in the unarmoured section whereas before the storm, higher values could be observed in the armoured part of the beach. This suggests a more sustained effect of the storm in beach habitats modified by engineering structures, and the biota of armoured beaches may be more susceptible to storm impacts. Conversely, observed declines in ghost crab densities on the unvegetated beach in the unarmoured section may not necessarily translate into a real population decline when ghost crabs can seek refuge in dunes. In fact, ghost crabs that have found refuge in the dunes are available as colonizers for the beach after the storm (Hobbs and others 2008). It follows that unarmoured beaches with existing dunes should recover quicker, show less persistent effects of storm events, or both.

### 3.4.2. Is recovery possible in the short-term?

The ability of sandy beaches to rebuild after a storm event is influenced by wave regimes, rates of sediment supply, the presence of dunes, and storm succession (Regnauld and others 2004). The time for recovery of the physical environment also depends on the size of the storm, localized accretion-erosion dynamics and it can differ between parts of the beach (List and others 2006). Recovery rates range between weeks (List and others 2006), years (Morton and others 1994), and possibly decades (Tonisson and others 2008); dunes that have lost some of their complex organization may even need longer than decades for full recovery (Zhang and others 2002). While there was some recovery of the physical beach habitat, we found no evidence that ghost crab numbers recovered to pre-storm levels with three months after the storm. The vast majority of density values obtained for specific beach levels remained depressed after the storm, and this was evident in both beach sections. In fact, biological recovery of beaches after severe erosion may be lengthy, as demonstrated for the macrobenthos a New Hampshire Beach which required four years to regain pre-storm levels (Jaramillo and others 1987).

The major mechanisms for the recovery of sandy beach biota include: a) immigration of adults from undisturbed areas; b) local reproduction and subsequent short-distance dispersal and recruitment to the benthos; c) settlement by larvae or juveniles produced elsewhere (e.g. decapods, molluscs). It is likely that recovery of ghost crab populations operates via immigration from dunes in the short term (Hobbs and others 2008), and settlement of postlarvae produced by populations elsewhere less affected by storms. Because in the present situation there was no evidence for recovery in the short-term, re-invasion of the beach from the dunes was not sufficient to replenish apparent losses in the intertidal part of the population. Loss of dune habitat

in half of the beach would further retard recovery, and full recovery will therefore depend on imports of recruits from elsewhere.

Increased storminess is a predicted consequence of global climate change and likely to result in significant changes to coastlines worldwide, particularly on sedimentary shorelines dominated by ocean-exposed sandy beaches. Hence, sandy beaches are vulnerable to storms, where armouring (e.g. seawalls) is the traditional defence response against accelerated erosion. It is therefore likely that shoreline management may acquire an even stronger focus on erosion control, yet the ecological effects of such severe events are poorly understood for sandy shores.

Our data demonstrate that a storm event smaller than tropical cyclones and hurricanes can still cause significant changes to beach morphology and the animals inhabiting it. Ecological recovery is not evident in the short term – at least of the biota – and is relatively prolonged. Beaches armoured with seawalls may be physically less resilient to storms, slower to recover, and storm impacts on beach biota may be greater. Our data emphasize the need to better define how society's responses to global change on soft shorelines shape the physical and ecological fabric of sandy beaches and other ecosystems.

# **CHAPTER 4**

# Impacts of off-road vehicles (ORVs) on burrow architecture of ghost crabs (genus *Ocypode*) on sandy beaches

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## Abstract

Recreational beach use with off-road vehicles is popular, but potentially harmful from an environmental perspective. Beaches are important habitats to invertebrates such as ghost crabs of the genus *Ocyopde*, which excavate extensive and elaborate burrows. Ghost crabs are sensitive to human pressures and changes in burrow architecture may thus be a consequence of disturbance by vehicles – the predictive hypothesis of this paper. This was tested during the austral spring and summer by comparing 305 burrow casts between beaches open and closed to vehicles in eastern Australia. Traffic influenced burrow architecture: there were smaller crabs on vehicle-impacted beaches, and after the peak traffic period (Christmas and New Year holidays), these crabs had tunnelled deeper into the sediment on shores rutted by cars. Crabs constructed all types of previously described burrows, but, significantly, smaller crabs from vehicle-impacted beaches simplified their shapes following heavy traffic disturbance from four (I, J, Y, M) to only two types (I, Y). These data support a model of active behavioural responses to disturbance from vehicles, extending the known effects of beach traffic to impacts on behavioural traits of the beach fauna.

Keywords: sandy shores; invertebrates; human recreation; environmental impacts; indirect effects

### 4.1. Introduction

Sandy beaches are a valuable natural resource in the coastal zone (Houston 2008; Defeo and others 2009). Beaches deliver numerous ecosystems services - recreation being often the most prominent one (Schlacher and others 2008b), and off-road driving of vehicles has become part of the leisure activities on many ocean shores (Silberman and Andereck 2006; Schlacher and others 2007a).

While recreation using off-road vehicles has social and economic dimensions (McConnell 1977), this activity is not without environmental consequences (Wolcott and Wolcott 1984). Evidence for negative environmental impacts caused directly or indirectly by vehicle traffic on beaches and dunes is available for physical habitat changes (Thompson and Schlacher 2008), reductions in the abundance and diversity of beach invertebrates (Moss and McPhee 2006; Schlacher and Thompson 2007), damage to dune vegetation and fauna (Groom and others 2007; Van Dam and Van Dam 2008), and threats to birds and turtles (Hosier and others 1981; Buick and Paton 1989; Williams and others 2004).

The nature, intensity, spatial and temporal scope of ecological impacts of human activities on sandy beaches can be assessed with indicator species (Lucrezi and others 2009b). Ghost crabs of the genus *Ocypode* are semi-terrestrial crabs inhabiting beaches and dunes of tropical and sub-tropical regions world-wide. Their use as indicators of ecological impacts on beaches rests on them being both invertebrate apex predators and food for higher trophic levels, and having reasonably well understood responses to human pressures (Lucrezi and others 2009a). Crab abundance has been shown to be sensitive to human pressures in the form of shore armouring (Barros 2001; Lucrezi and others 2009a), urbanization (Souza and others 2008; Magalhaes and others 2009), very heavy pedestrian trampling (Neves and Bemvenuti 2006; Yong and Lim 2009), and off-road vehicles (Steiner and Leatherman 1981; Blankensteyn 2006; Moss and McPhee 2006; Maccarone and Mathews 2007; Schlacher and others 2007b; Hobbs and others 2008).

Ghost crabs excavate burrows where they spend most of the day, becoming surface-active at night (Barrass 1963). Burrows are key structures in the life of ghost crabs, providing shelter against predators, extreme weather conditions, co-specifics, and incoming tides; burrows are also critical during egg development, moulting, and mating (Vannini 1980b; Schober and Christy 1993; Chan and others 2006). Because burrowing expends considerable energy and ORVs destroy burrows, vehicles may impact on investment in reproduction and lengthen risky surface activity of crabs.

Given that burrows are a critical element in the ecology of ghost crabs, and the documented role of ghost crabs as indicators of ecological change, this study investigated whether crabs change their burrow architecture in response to physical disturbance. Physical disturbance was in the form of vehicle traffic which is known to cause substantial changes to the habitat (Anders and Leatherman 1987a). Specifically, our predictive hypothesis was that crabs would respond to greater habitat instability caused by off-road vehicles by changing the shape and dimensions of burrows.

# 4.2. Material and methods

### 4.2.1. Study area

Ghost crab burrows were investigated on four beaches on the east coast of Australia (Fig. 14). Details of these beaches are given in Schlacher and others (2008a). Briefly, all are ocean-exposed, wave-dominated beaches of the intermediate morphodynamic type. Two beaches, North Shore and Teewah Beach, are subject to vehicle traffic, while vehicles are banned from the two other beaches (Peregian Beach and Sunrise Beach). Except for vehicle traffic, there are no substantial differences in terms of beach morphology, sediment characteristics and wave regimes between beaches open and closed to vehicles (Schlacher and others 2008a).



**Figure 14** Location of study region in South-East Queensland, Australia (a), and b- beaches sampled for ghost crab burrows at two sites with vehicle impacts north of Noosa and two beaches without traffic impacts south of Noosa. Photo Credits: Google Earth

# 4.2.2. Field sampling

Burrows were measured in two belt transects per site. Transects were 3 m wide and extended from the base of the dune to the downshore limit of burrow occurrence. Transects were spaced 10 m apart along the beach, and divided into sequential 3 m long quadrats. We measured every burrow in the belt transects and recorded the distance of individual burrows and their elevation with reference to the spring tide low water mark (LWST) using a theodolite.

Burrow casts were made by pouring a mix of Cornice Cement (Gyprock<sup>tm</sup>) and water into the burrow opening until the burrow was flooded flush with the sediment surface. Cornice Cement was chosen because it is a fast-setting and non-toxic type of plaster. The plaster mix was prepared by adding 1 kg of plaster to 2 litres of freshwater until a smooth and dense blend was obtained. After the plaster had set (which took approximately 30 min), the casts were dug out by carefully removing the sediment around them by hand or with a small trowel. After measuring their depth and the angle of inclination, casts were labeled and taken back to the laboratory. In the laboratory, each cast was photographed and the following measurements made: shape; total length (length of the main shaft plus length of any secondary arms in cm); diameter of the main shaft (cm); weight (g) as a proxy for volume. A total of 305 casts, weighting 132 kg and with a total length of 150 m were made during this study.

After the casts had been excavated, sediment moisture and temperature were measured at three depths: 2 cm below the surface, in the middle, and at bottom of the hole. At each depth, triplicate readings were taken with a Trident microwave moisture meter and an electronic temperature probe (Fluke 52 K/J). We also took triplicate sediment cores (30 mm diameter, 100 mm deep) next to each burrow opening, and determined sediment granulometry by dry-sieving (details in Schlacher and others 2008a).

All four beaches were sampled at approximately monthly intervals from September 2008 to January 2009. Sampling was restricted to 3 hours either side of the time of predicted low water.

### 4.2.3. Data analysis

Total variance in burrow opening diameter, depth, length, inclination, and weight was partitioned with a Generalized Linear Model (GLM) that included the term 'human beach use' (vehicle-impacted vs. reference beaches) and 'month' (Underwood 1997); to account for possible influences on burrow metrics by the position of individual burrows across the dune-swash gradient, burrow elevation above LWST was included as a co-variate (Zar 1996). The distribution of all burrows amongst types was compared between vehicle-impacted and reference beaches using contingency analysis. Because burrow architecture is described by multiple variables (e.g. angle, width, length), we tested whether burrows from beaches open to vehicles differ in the multivariate domain from those from reference beaches using Principal Component Analysis (PCA) and Analysis of Similarities – ANOSIM (Clarke 1999).

### 4.3. Results

### 4.3.1. Beach attributes

Beaches open and closed to vehicles had very similar slopes, differing by a mere  $0.08^{\circ}$  (vehicle beaches:  $\bar{x} = 2.84^{\circ}$ , se = 0.08, n = 142; reference beaches:  $\bar{x} = 2.92^{\circ}$ , se = 0.06, n = 163; Tables 28 and 29). S imilarly, mean grain size of sediment from beaches with vehicles ( $\bar{x} = 0.48$  mm, se = 0.01, n = 142) was only finer by 0.09 mm compared with the sand from reference beaches ( $\bar{x} = 0.49$  mm, se = 0.01, n = 163; Tables 28 and 29). There was also relatively little difference in sediment sorting between beaches, all sites having poorly-sorted sand irrespective of whether being used by vehicles or not (vehicle beaches:  $\bar{x} = 1.60 \sigma$ , se = 0.01, n = 142; reference beaches:  $\bar{x} = 1.56 \sigma$ , se = 0.01, n = 163; Tables 28 and 29). **Table 28** Summary of Analysis of Co-variance (ANCOVA), contrasting sediment properties and beach slope between beaches open and closed to offroad vehicles over time (Survey 1 to 5) at monthly intervals from Sep '08 to Jan '09. The elevation of burrows above low water spring tide (LWST) was the co-variate in the analysis

		Mean Grain Size			Beach Slope				
	df	MS	F		MS	F			
Co-variate (Elevation above LWST)	1	492	4.01	***	4.06	17.83	***		
Times (5 surveys)	4	1016	8.28	***	9.85	43.30	***		
Human Use (vehicles vs. reference)	1	1087	8.85	**	5.81	25.51	***		
Times x Human Use	4	702	5.72	***	19.32	84.88	***		
Error	285	123			0.23				
		Sediment Moisture	)		Sand Temperature				
	df	MS	F		MS	F			
Co-variate (Elevation above LWST)	1	68.57	21.16		0.00	0.00	ns		
							***		
Times (5 surveys)	4	65.47	20.20		407.60	55.89	~~~		
Times (5 surveys) Human Use (vehicles vs. reference)	4 1	65.47 36.26	20.20 11.19		407.60 30.70	55.89 4.21	*		
Times (5 surveys) Human Use (vehicles vs. reference) Times x Human Use	4 1 4	65.47 36.26 10.15	20.20 11.19 3.13		407.60 30.70 219.55	55.89 4.21 30.10	*		

	Sediment Sorting								
	df	MS	F						
Co-variate (Elevation above LWST)	1	0.0001	0.03	ns					
Times (5 surveys)	4	0.0201	9.62	***					
Human Use (vehicles vs. reference)	1	0.1038	49.59	***					
Times x Human Use	4	0.0035	1.66	ns					
Error	285	0.0021							

<sup>ns</sup> P > 0.05, \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001

**Table 29** Summary of contrasts between vehicle and reference beaches from post-hoc (Student New Keuls Tests) following Analysis of Co-variance (cf. Tables 28 and 30). Cell entries denote the direction and significance of comparisons between means, with downward pointing arrows indicating lower mean values at beaches open to vehicle traffic. Conversely, upwards-pointing arrows denote higher means at vehicle beaches. Arrows in parentheses denote contrasts of means with P > 0.05. Because of significant interaction terms between time and impact, no estimate of type 1 error probability for an overall test between beaches across all surveys is given

A - Environmental Variables	Sep. '08	Oct. '08	Nov. '08	Dec. '08	Jan. '09	All surveys
Beach Slope	<b>↓</b> ***	<b>↓</b> ***	<b>①**</b> *	<b>↓</b> ***	<b>↓</b> ***	¥
Mean Grain Size	<b>↓</b> ***	<b>↓</b> *	<b>(♥)</b> <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	<b>↓</b> ***	$\mathbf{\Psi}$
Moisture	(Ѱ)	<b>(↓)</b> <sup>ns</sup>	<b>↓</b> *	(①) <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	$\mathbf{\Psi}$
Temperature	<b>①**</b> *	(①) <sup>ns</sup>	<b>↓</b> ***	<b>①**</b> *	<b>(</b> ①) <sup>ns</sup>	仓
Sorting	<b>①**</b> *	<b>압*</b>	(①) <sup>ns</sup>	(①) <sup>ns</sup>	<b>①**</b> *	仓
B - Burrow Metrics	Sep. '08	Oct. '08	Nov. '08	Dec. '08	Jan. '09	All surveys
Opening Diameter	<b>↓</b> ***	<b>(♥)</b> <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	(①) <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	$\mathbf{+}$
Depth	<b>↓</b> ***	<b>↓</b> *	(①) <sup>ns</sup>	<b>(↓)</b> <sup>ns</sup>	<b>①**</b> *	¥
Length	<b>(↓)</b> <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	(①) <sup>ns</sup>	<b>①**</b> *	$\mathbf{\Psi}$
Main Shaft Diameter	<b>↓</b> ***	<b>(♥)</b> <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	(①) <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	$\mathbf{\Psi}$
Weight	<b>↓</b> ***	<b>(♥)</b> <sup>ns</sup>	<b>(↓)</b> <sup>ns</sup>	<b>①*</b>	<b>①**</b> *	$\mathbf{\Psi}$
Angle	<b>(↓)</b> <sup>ns</sup>	(①) <sup>ns</sup>	(①) <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	<b>(</b> ①) <sup>ns</sup>	$\mathbf{\Psi}$
Length : Depth	<b>(♥)</b> <sup>ns</sup>	(①) <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	<b>(♥)</b> <sup>ns</sup>	$\mathbf{\Psi}$
Depth : Diameter	<b>①*</b>	<b>(♥)</b> <sup>ns</sup>	(①) <sup>ns</sup>	<b>(↓)</b> ns	(①) <sup>ns</sup>	仓

Key: ↓ - lower means value on vehicle beaches; û - higher mean value at vehicle beaches;

 $\Psi^{***}$ ,  $\hat{u}^{***}$ Significant (P < 0,001) differences between means of vehicle and reference beaches ( $\Psi^{*}, \hat{u}^{*} - P < 0.05$ ); ( $\Psi$ )<sup>ns</sup> ( $\hat{u}$ )<sup>ns</sup> non-significant (P > 0.05) contrasts between vehicle and reference beaches. Temperature and moisture of the sediment varied widely between sampling periods, depending on weather conditions (Fig. 15). Despite few significant differences in mean values between beaches over the study (Table 29), in most months, the sand at beaches impacted by vehicles tended to be slightly hotter and had a lower moisture content in the top layer (Fig. 15). Overall, the physical habitat of beaches with and without vehicles showed some degree of separation (Fig. 16), but differences tended to be small (ANOSIM: R = 0.145; P = 0.044) and were not consistent from month to month for several variables (Table 29).



**Figure 15** Profiles of sediment temperature (top row, a-e) and moisture (bottom row, f-j) comparing beaches open to vehicle traffic (orange dots) with nearby beaches closed to cars (blue triangles) during five surveys



**Figure 16** Ordination (PCA – principal component analysis) depicting relationship of sites based on similarity in beach slope, sand temperature, sediment moisture and the mean grain size of the sediment

### 4.3.2. Burrow shapes and metrics

Ghost crabs excavated burrows of seven principal shapes (Table 30). Half of all casts made were of the "Y" type (n = 152), and we obtained 97 simple I-shaped burrows and 35 J-shaped ones; these three burrow types made up 94% of all burrows. Less common were multi-branched burrows (n = 9), and burrows with a U-shape (n = 5), a L-shape (n = 3), or a S-shape (n = 2).

	Sep. '08 Oct. '08		Nov	. '08	Dec	. '08	Jan.	Jan. '09		rveys		
Shape	Ref. (n=41)	Veh. (n=27)	Ref. (n=34)	Veh. (n=35)	Ref. (n=36)	Veh. (n=39)	Ref. (n=23)	Veh. (n=26)	Ref. (n=26)	Veh. (n=15)	Ref. (n=160)	Veh. (n=142)
I	29%	15%	32%	34%	36%	33%	22%	54%	38%	20%	32%	32%
J	17%	11%	3%	11%	22%	0%	4%	15%	27%	0%	15%	8%
U	0%	0%	3%	3%	0%	3%	4%	0%	4%	0%	2%	1%
Y	51%	74%	50%	49%	31%	56%	70%	31%	27%	80%	45%	56%
L	3%	0%	3%	0%	0%	0%	0%	0%	4%	0%	2%	0%
М	0%	0%	9%	3%	8%	8%	0%	0%	0%	0%	3%	3%
S	0%	0%	0%	0%	3%	0%	0%	0%	0%	0%	1%	0%
Chi-square, df	4.922,	3	3.830,	5	13.568,	5	9.582,	3	12.000,	4	10.579,	6
Ρ	0.178		0.574		0.019		0.023		0.018		0.102	

Table 30 Distribution of ghost crab burrow shapes between beaches open to traffic (Veh.) and those closed to off-road vehicles (Ref.)
The occurrence of different burrow shapes was, to some degree, dependent on whether vehicles used the beach or not (Table 30). In the three months with the highest traffic volumes (November to January), the frequency of different burrow shapes differed between vehicle-free and impact beaches (Table 30). In November, 22% of burrows constructed by crabs on reference beaches were of the "J" type, but none of this type were found on vehicle beaches (Table 30). Conversely, Y-burrows were more common on vehicle beaches (56%) than on reference beaches (31%). In December, 70% of burrows on reference beaches were Y-shaped compared with only 31% on vehicle beaches (Table 30). No J-shaped burrows were found in January on vehicle beaches, but 27% of all casts on the reference beaches were of this shape (Table 30).

Burrow metrics varied substantially over time and between beaches closed and open to vehicles (Tables 29 and 31; Figs. 17 and 18). The opening diameter of burrows on vehicle-impacted beaches tended to be smaller ( $\bar{x} = 30.80$  mm, se = 1.10, n = 142) than on reference beaches ( $\bar{x} = 34.52$  mm, se = 1.02, n = 163), indicating that beach traffic had affected population structure. Differences in the mean diameter of openings between beaches were significant (P < 0.001) in the October '08 survey, where entrances on vehicle-impacted beaches ( $\bar{x} = 19.48$  mm, se = 1.22, n = 27) were only 55% the size of openings on reference beaches ( $\bar{x} = 34.80$  mm, se = 2.12, n = 41). Smaller opening diameter on vehicle beaches were observed across most burrow shapes (Fig. 17). Crabs constructed shallower burrows on vehicle-impacted beaches during the months when traffic volumes were low, but burrow depth increased significantly in Jan. '09 after the peak holiday traffic: at this time, burrows on vehicle-impacted beaches ( $\bar{x} = 43.07$  cm, se = 5.54, n = 15) were 29% deeper than those on reference beaches ( $\bar{x} = 30.67$  cm, se = 2.33, n = 26; Table 29). A similar pattern was

found for burrow length: no significant differences during the first four surveys, but distinctly longer burrows after the peak holiday traffic (Table 29). Because the crabs constructed deeper and longer burrows in Jan. '09 on beaches open to traffic, burrow weight also increased significantly during this period (vehicle beaches:  $\bar{x} = 511$  g, se = 111, n = 15; reference beaches:  $\bar{x} = 462$  g, se = 57, n = 26).

**Table 31** Summary of Analysis of Co-variance (ANCOVA), contrasting architectural features of ghost crab burrows amongst beaches open and closed to off-road vehicles over time (Survey 1 to 5) at monthly intervals from Sep '08 to Jan '09. The elevation of burrows above low water spring tide (LWST) was the co-variate in the analysis

0.73

	df	Opening Diameter MS	F		Depth (Inx +1) MS	F	
Co-variate (Elevation above LWST)	1	477.47	3.69	***	0.0022	3.87	***
Times (5 surveys)	4	384.81	2.98	*	0.0046	7.96	***
Human Use (vehicles vs. reference)	1	948.74	7.34	**	0.0050	8.82	**
Times x Human Use	4	625.14	4.84	***	0.0032	5.55	***
Error	285	129.26			0.0006		

		Length			Main Shaft Diameter			
	df	MS	F		MS	F		
Co-variate (Elevation above LWST)	1	1632.32	2.42	**	3.86	5.32	*	
Times (5 surveys)	4	2025.67	3.00	*	2.30	3.18	***	
Human Use (vehicles vs. reference)	1	2961.89	4.39	*	2.62	3.62	**	
Times x Human Use	4	2301.57	3.41	**	5.32	7.33	***	
Error	285	675.10			3.09	4.26	***	

	,			Angle		
	df	MS	F		MS	F
Co-variate (Elevation above LWST)	1	0.003	4.50	***	474.99	1.58
Times (5 surveys)	4	0.005	7.66	***	154.91	0.52
Human Use (vehicles vs. reference)	1	0.006	9.18	**	287.84	0.96
Times x Human Use	4	0.004	6.91	***	487.42	1.62
Error	285	0.001			300.51	

<sup>ns</sup> P > 0.05, \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001



**Figure 17** Comparison of key metrics of ghost crab burrows between beaches open (filled bars) and closed (open bars) to vehicle traffic for the most common shapes of burrows found. Boxes enclose the lower and upper quartile, whiskers extend to the 5 and 95% percentile and the vertical bars inside boxes denote the median



**Figure 18** Ordinations (PCA – principal component analysis) depicting relationship of sites based on similarity in burrow dimensions. R-statistics and P-values refer to Analysis of Similarities (ANOSIM) contrasting beaches with and without cars

Most contrasts in burrow metrics between beaches open and closed to cars were consistent across burrow shapes (Fig. 17). Overall, multiple metrics for burrow dimensions distinguished casts from vehicle-impacted beaches from those of reference beaches most strongly in Jan.'09 following heavy traffic during Christmas and New Year (Fig. 18). It appears that the smaller crabs on beaches affected by heavy vehicle traffic dug burrows that were deeper, longer and of greater volume during this period (Fig. 18e).

#### 4.4. Discussion

Juvenile crabs excavated shorter and shallower burrows than adults. Juveniles do not require as deep burrows as they live closer to the swash zone in moister sand (Duncan 1986; Chan and others 2006). By contrast, adult crabs can withstand longer periods without having to renew their respiratory water, and are therefore distributed on the backshore and in the dunes, probably because these areas are physically more stable and afford some protection from storms (Warburg and Shuchman 1979; Vannini 1980b; Turra and others 2005; Hobbs and others 2008). Ghost crab burrows also become deeper closer to the dunes and decrease in inclination (Duncan 1986; De 2005); this suggests that the physiological risk of desiccation is important in determining burrow morphology, and that crabs need to dig deep enough to find sand with sufficient interstitial water content to permit its extraction and thus replenish water lost to evaporation (Wolcott 1976).

Beach traffic influenced dimensions of ghost crab burrows: there were smaller crabs on vehicle-impacted beaches as suggested by smaller burrow openings. After the peak traffic period, which on local beaches is over the Christmas and New Year

holidays (Schlacher and others 2008a), crabs tunnelled deeper into the sediment on shores rutted by cars. This could have been a response of crabs to vibrations made by cars which could mimic those normally made by predators. Excavation of deeper burrows requires expenditure of more metabolic energy, possibly at the cost of lower investments into reproduction. This model assumes that burrowing is a major component in the total energy budget of crabs, but actual data are not available and feeding excursion could match burrowing in terms of energy expenditure. Crabs may also be forced to spend more time foraging outside their burrows which increases risks of predation and exposure to vehicles (Schlacher and others 2007b).

Although the pressure exerted by vehicles decreases with depth into the sediment, crabs on Australian beaches that are burrowed shallower than 30 cm get crushed by cars (Schlacher and others 2007b). In this study, 48% of burrows were shallower than 30 cm during the low-traffic months on beaches open to off-road vehicles, compared with 32% on the reference beaches. During the high traffic season (November-January), the proportion of burrows shallower than 30 cm remained the same in the traffic-free beaches, whilst it dropped considerably to 17% on vehicle-impacted beaches.

Vehicles are likely to cause more frequent collapses of burrows, and ghost crabs were expected to construct simpler burrows on vehicle-impacted beaches. We found that crabs constructed all types of previously described burrows, but – significantly – proportions of different burrows shapes changed in response to vehicle traffic. Smaller crabs from vehicle-impacted beaches changed from excavating four different types of burrows (I, J, Y, M) during periods of low traffic, to only two types (I, Y) during the high-traffic months. Similarly, larger crabs from the vehicle-impacted

beaches went from constructing J-shaped burrows during periods of low traffic to Ishaped burrows over the high traffic period.

There is now a good body of scientific evidence that vehicles driven on beaches and dunes cause environmental harm (Wolcott and Wolcott 1984; Moss and McPhee 2006; Groom and others 2007; Schlacher and Morrison 2008; Schlacher and others 2008c; Sheppard and others 2009). This presents a challenge to coastal managers who must reconcile environmental conservation with demands for beach access on social grounds. Management options usually encompass limiting the number of vehicles, restricting times of access, and excluding vehicles from beaches. For example, because ghost crabs are most vulnerable to being crushed by vehicles while feeding at the beach surface at night (Schlacher and others 2007b), banning night traffic would be beneficial.

Here we present data on using ghost crab burrows as a potential new measure for such impacts, which advances the search for ecological indicators which can detect impacts to animals populations on beaches before declines in population sizes become manifest due to mortality. Managers of beaches and dunes also frequently require measures of ecological condition and indicators of change that span more than one attribute of the biota (e.g. abundance, reproduction, behaviour) to strengthen assessments and evaluate the efficacies of interventions; to this end, burrow architecture of ghost crabs could make a useful contribution.

It is also widely recognized that dunes are highly sensitive to vehicle disturbance (Rickard and others 1994), and essentially have zero tolerance for traffic (Groom and others 2007). This would argue for restricting beach traffic to unvegetated areas shoreward of the dunes, but even in National Parks, dunes continue to be

destroyed by recreational ORV traffic (Thompson and Schlacher 2008). Ideally, traffic management on beaches should be designed within a framework of systematic conservation planning (Margules and Pressey 2000; Celliers and others 2004; Murdoch and others 2007). When properly designed and enforced, removing vehicles from beaches has clear biological returns (Williams and others 2004).

### **CHAPTER 5**

## Experimental evidence that vehicle traffic changes burrow architecture and reduces population density of ghost crabs on sandy beaches

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#### Abstract

Driving of off-road vehicles on beaches and coastal dunes is part of the recreational activity spectrum in many coastal areas. Although this practice can cause environmental harm, controlled experiments to test specific ecological impacts of vehicles are rare on high-energy shores. Here we use an experimental approach, where sections of a beach were repeatedly driven over by a vehicle, to demonstrate effects on ghost crabs (genus Ocypode) inhabiting a beach in eastern Australia. Vehicle traffic caused a significant reduction in crab burrow density by 66% and the remaining burrows were smaller by 22%, suggesting impacts on both population size and structure. Crabs also responded behaviourally to vehicle disturbance by altering their burrow architecture to simpler and deeper forms. Experimental data from this study not only add to a growing body of evidence highlighting deleterious environmental effects associated with recreational off-road vehicle (ORV) use, but clearly demonstrate that environmental harm is a direct consequence of vehicle traffic on beaches. This brings into focus the need to implement visitor management strategies that meet conservation targets without dismissing the social, cultural and economic dimensions of vehicle-based recreation.

Keywords: recreational ecology; ORV impacts; *Ocypode*; ecological indicators; pulse disturbance

#### 5.1. Introduction

The recreational use of off-road vehicles on sandy beaches increased after the Second World War when four-wheel drive vehicles became more readily available and affordable (van der Merwe and van der Merwe 1991). Driving of vehicles on beaches and dunes is today part of the recreational activity spectrum in many coastal areas and has, arguably, economic benefits for some local communities (Silberman and Andereck 2006). However, the widespread practice of four-wheel driving along coastlines around the world has repeatedly raised concerns about its environmental impacts (Hosier 1980; Wolcott and Wolcott 1984; Moss and McPhee 2006; Thompson and Schlacher 2008; Sheppard and others 2009).

Ghost crabs (genus *Ocypode*) are amongst the invertebrates most heavily affected by vehicles, because their distribution overlaps with traffic (Schlacher and Thompson 2007), and because the crabs get crushed by cars both inside their burrows and while active on the beach surface (Wolcott and Wolcott 1984; Schlacher and others 2007b). In fact, ghost crabs have been shown to be functional ecological indicators of vehicle impacts on sandy beaches, based on reductions in their density in areas open to traffic (Steiner and Leatherman 1981; Wolcott and Wolcott 1984; Moss and McPhee 2006; Foster-Smith and others 2007; Hobbs and others 2008).

Evidence for negative ecological impacts by vehicles on beach invertebrates is conventionally based on 'compare and contrast' designs, testing for differences in abundance between beaches of different traffic intensity (Moss and McPhee 2006; Schlacher and others 2008a). While such mensurative experiments (sensu Hurlbert 1984) are illustrative of changes linked to vehicle traffic at specific beach locations, robust demonstration of environmental harm usually requires controlled experiments where the putative agent of change can be isolated from potentially confounding drivers (Underwood 1997). Consequently, the chief objective of this study was to test whether experimentally controlled vehicle traffic on a sandy beach leads to significant reductions in the density of ghost crabs and results in changes to the architecture of the crabs' burrows.

#### 5.2. Material and methods

#### 5.2.1. Study area

North Stradbroke Island is a barrier island forming the eastern border of Moreton Bay (Fig. 19). The island is a popular tourist destination: most visitors come to the oceanexposed sandy beaches where recreational driving of off-road vehicles on the beaches causes considerable traffic (Schlacher and Morrison 2008). The number of cars driving on the island's eastern beaches can exceed 500 vehicles per day during peak tourist times (Schlacher and others 2007b; Schlacher and Thompson 2008).



**Figure 19** Location of the study site in eastern Australia (a), the northernmost part of the oceanexposed beach on North Stradbroke Island (b). Crab burrows were surveyed in three zones differing in vehicle traffic intensity from heavy (south of the access point marked with a star) to moderate and nil north of the access corridor cut through the dunes (c). Experimental vehicle passes were applied to a 100 x 2 m strip in the moderate traffic zone (d). Photo Credits: Google Earth Vehicles enter the beach via designated access points, and most traffic occurs on the middle and upper shore above the effluent line (Schlacher and Thompson 2007). All 34 km of Main Beach are open to vehicle traffic, except for a 600 m section at the northernmost section of the beach; this vehicle exclusion zone was designated as the '*No impact zone*' for the purpose of this study (Fig. 19). All vehicles access the beach via a corridor cut through the dunes and most cars then head south, with much fewer cars turning north. Therefore, the southern section was treated as the '*heavy traffic zone*' (Fig. 19). Some traffic is also present in the area of the beach separating the exclusion zone from the heavy traffic zone: this area was referred to as the '*moderate traffic zone*' (Fig. 19).

# 5.2.2. Experimental design for vehicle effects on burrow dimensions and crab density

In each of the three traffic zones, burrow casts were made in a 100 m long and 2 m wide strip, running parallel to the base of the dunes. Casting occurred over three days before (29–31 Jan. 2009) and after (4-6 Feb. 2009) the experimental application of vehicle passes in the moderate traffic zone (see below). Casts of every burrow in the experimental areas were obtained by pouring a mix of Cornice Cement (Gyprock<sup>tm</sup>) and water into the burrow opening. Cornice Cement was chosen because it is a fast-setting and non-toxic type of plaster. The mix was prepared by adding 1 kg of plaster to 2 liters of freshwater until a smooth blend was obtained.

After the plaster had set (approximately 30 min), the casts were dug out by carefully removing the sediment around them by hand, or with a small trowel. After measuring their depth, casts were labeled and taken back to the laboratory. Triplicate sediment moisture readings to a depth of 8 cm (Trident microwave moisture meter) and

temperature readings to a depth of 5 cm (electronic thermometer Fluke 52 K/J) were taken at three different points in the burrows (below the sand surface, in the middle, and at the bottom of the hole). In the laboratory, each cast was photographed and the following measurements were made: shape (Y, U, I, J, Spiral, Multi-branched); length of the main shaft and of any secondary arms (in cm); width of the main shaft and of any secondary arms (at the widest and narrowest point excluding chambers, in mm); angle of inclination (%; weight (proxy for volume, in gr ams).

Counts of burrow openings were made in each traffic area at sunrise on six days in the austral summer of 2009 (31<sup>st</sup> January, 1<sup>st</sup>, 3<sup>rd</sup>, 4<sup>th</sup>, 5<sup>th</sup>, 6<sup>th</sup> February). Burrow counts were made in 100 contiguous quadrats (2 x 1 m) laid in a line along the beach 3 m seawards from the base of the dune. Counts were followed by a series of vehicle passes in the moderate traffic zone: 20 vehicle passes after the first burrow count on day 1, 6 after the second, 7 after the third, 7 after the fourth, and 12 after the fifth. The number of passes was adjusted to limit environmental damage to a reasonable degree of physical disturbance of the beach surface, which was evident as deep (~20 cm) ruts that covered most of the experimental area. The total number of experimental vehicle passes done during this study is well below normal traffic levels during peak holiday periods (Schlacher and Thompson 2007). The passes were performed with Toyota Hilux (Weight 1200 kg, tyre width: 20.5 cm) which is one of the most common vehicle types on Australian beaches. No experimental traffic was applied to the vehicle exclusion zone to the north or the heavy traffic zone to the south which continued to receive normal beach traffic (Fig. 19). The potential for recovery of ghost crab populations following heavy vehicle traffic was gauged by conducting burrow counts one week after the last experimental vehicle pass on two consecutive days (11 and 12 Feb. 2009).

After the last series of experimental vehicle passes in the moderate traffic zone and following the sixth burrow count, each area where the counts had been made was divided into five transects (A-E) spaced 25 m apart along the shore (Fig. 19). Each transect extended from the base of the dunes to the low water mark, and was divided into adjacent plots, 2 m long and 1 m across. For every plot, the number of active ghost crab burrow openings, their diameter, and their position with respect to the band of tyre tracks (above, in, and below) was recorded to test for the effect of vehicle traffic on the across-shore distribution patterns of crabs.

Only 'active' burrow openings were counted. Active burrows were recognized by either the presence of fresh tracks emanating from the opening, or evidence of recent re-working of the burrows visible as small mounds of excavated sediment next to the entrance, or both. Two species of ghost crabs, *Ocypode ceratophthalma* and *Ocypode cordimanus* occur on the beach, but their burrow openings cannot be distinguished with confidence. We therefore report all burrow counts at the genus level.

#### 5.2.3. Data analysis

Correspondence Analysis was used to compare the distribution of different burrow shapes amongst beach zones before and after the experimental vehicle passes. Variation in burrow dimensions (weight, length, height, diameter, angle) and the density and diameter of burrow openings were analysed with a General Linear Model (GLM) containing the fixed factors 'Beach Traffic Zone' (heavy, moderate, none) and 'Time' in relation to experimental application of vehicle passes (before vs. after) (Zar 1996; Underwood 1997).

#### 5.3. Results

Burrows resembled the letters I, Y, J, U, M (multi-branched), and S (spiral). Over 60% of all the I-shaped burrows were found in the heavy impact zone, while the remaining beach zones were dominated by Y-shaped burrows (43.5% in the moderate traffic zone and 36.5% in the No traffic zone; Fig. 20, Table 32). J-shaped burrows were also numerous and were most abundant in the No impact zone (56%), whilst U-, M- and S-shaped burrows were the least common (Fig. 20, Table 32). U-shaped burrows were absent from the heavy impact zone and were not found in the moderate impact zone after the ORV passes (Table 32). Burrows became deeper and longer in the moderate impact zone also underwent a shift in inclination and became almost perpendicular ( $\bar{x}_{Before} = 22.26^\circ$ ,  $\bar{x}_{After} = 15.29^\circ$ , Table 34).



**Figure 20** Illustration of burrow forms and summary of Correspondence Analysis showing the distribution of frequencies of ghost crab burrow shapes (I, M, J, Y, U, S) amongst beach zones (moderate traffic (Exp.) and No traffic (Ref.)) before (1) and after (2) the experimental vehicle passes in the moderate traffic zone. Photo Credits: S Lucrezi

**Table 32** Distribution of burrow shapes in three beach sections differing in traffic intensity andbefore and after the experimental application of additional vehicle passes in the moderate trafficzone. Cell entries are number of burrow casts for each shape

	Time 1: bef	ore vehicle imp	oact	Time 2: after vehicle impacts				
Shape	Heavy Traffic	Moderate Traffic	No Traffic	Heavy Traffic	Moderate Traffic	No Traffic		
Y	15	22	26	5	21	10		
Ι	18	7	0	9	4	5		
U	0	1	1	0	0	1		
J	1	4	7	2	1	3		
М	0	0	0	1	0	2		
S	0	0	0	0	2	0		

**Table 33** Summary of general linear model (Factorial ANOVA) contrasting dimensions of ghost crab burrows between different traffic zones (No vehicle traffic, moderate traffic, and heavy traffic) before and after the experimental application of vehicle passes in the moderate traffic zone (experimental site). Values of burrow diameter (cm) and weight (g) were log-transformed and values of angle of inclination (9 square-root transformed

		Depth (o	:m)	Length	(cm)	Diameter (cm)		Weight (g)		Angle of inclination (ງໍ	
Source of variation	df	MS	F	MS	F	MS	F	MS	F	MS	F
Traffic Zone	2	3098.3	3.96*	6242.8	3.81*	0.01	0.01	3.63	3.84*	9.95	3.56*
Time	1	786.7	1.01	2083.2	1.27	0.08	0.87	0.72	0.76	28.20	10.09**
Zone x Time	2	2258.2	2.88	3539.4	2.16	0.13	1.39	2.43	2.58	25.16	9.00***
Error	162	782.7		1639.8		0.09		0.94		2.79	

\*\*\* P < 0.001, \*\*P < 0.01, \*P < 0.05

Table 34 Comparison of architectural properties of ghost crab burrows between different beach
zones (No vehicle traffic, moderate traffic, and heavy traffic) before (Time 1) and after (Time 2)
the experimental application of vehicle passes in the moderate traffic zone (experimental site)

Vehicle use zone	Tim	e	Vertica (cm)	l Height	Length	(cm)	Diameter (cm)		Weight (g)		Angle of Inclination (°)	
		Ν	x	SE	x	SE	x	SE	x	SE	x	SE
Heavy Traffic	1	34	39.35	5.85	57.72	8.76	2.81	0.13	645.76	106.74	23.79	2.21
Heavy Traffic	2	17	25.47	5.74	33.94	7.48	2.43	0.19	333.33	86.83	7.06	1.71
Moderate Traffic	1	34	42.07	4.35	62.97	7.00	2.57	0.13	638.57	100.85	22.26	2.03
Moderate Traffic	2	28	52.11	4.68	72.03	5.55	2.66	0.16	734.00	118.38	15.29	1.83
No Traffic	1	34	41.60	5.32	59.26	6.75	2.60	0.13	514.29	78.40	19.00	2.05
No Traffic	2	21	31.99	4.86	52.09	9.13	2.58	0.16	578.16	117.68	24.76	3.08

The density of ghost crab burrows was highest in the No traffic zone  $(\bar{x} = 168 \text{ ind. } 100 \text{ m}^{-2})$ , lowest at the experimental site  $(\bar{x} = 67 \text{ ind. } 100 \text{ m}^{-2})$ , and intermediate in the heavy traffic zone  $(\bar{x} = 105 \text{ ind. } 100 \text{ m}^{-2})$ . Burrow densities varied significantly over time, linked to the experimental application of ORV disturbance (Table 35; Fig. 21). After the initial 20 ORV passes, the number of burrows in the experimental zone decreased by 40%. A further 6 passes on the next day reduced the remaining burrows by 24%, and an additional 7 passes caused a further reduction by 79% (Fig. 21). By the end of the study, burrow number had recovered, but not to the pre-impact values (Fig. 21). Experimental ORV passes caused a significant decrease in the size of ghost crab burrows (Tukey HSD test P < 0.001; Fig. 21), a pattern of temporal variation that was not recorded in the other zones (Fig. 21). A week after the cessation of the experiment, mean ghost crab burrow opening diameter in the

moderate traffic zone had not recovered to its pre-impact value, but had further decreased (Tukey HSD test P < 0.001).

Source	df	SS	MS	F Value	F
Traffic Zone	1	1.488	1.488	7.79	0.0315
Time	1	0.172	0.171	0.90	0.3796
Time x Zone	1	1.744	1.744	9.13	0.0233
Error	6	1.146	0.190		

(a) 2.5 (ind.  $m^{-2}$ , mean  $\pm$  se) 2.0 **Burrow Count** 1.5 1.0 0.5 0.0 T1 **T1** T2 Т3 T2 Т3 Reference Impact 25<sub>7</sub> (b) **20**· **Opening Diameter** (mm, mean ± se) 15 10-5. 0 **T1** T2 Т3 **T1** T2 Т3 Reference Impact

**Figure 21** Comparison of burrow density (a) and burrow opening diameter (b) before (T1) during (T2) and one week after (T3) the experimental application of vehicle passes at the experimental site (impact) compared with the no-vehicle zone (reference). Arrows illustrate the vehicle passes

**Table 35** Summary results of GLM (General Linear Model) contrasting burrow counts between

 the experimental and reference area during and after the application of vehicle passes

Vehicle traffic also changed the distribution of burrows across the beach (Fig. 22). After the experimental application of traffic, burrow density was significantly lower (paired t-test, t = 4.17, df = 7, P = 0.004) where tyre tracks had substantially rutted the beach on the upper part of the shore in the experimental impact area (Fig. 22).



**Figure 22** Distribution of ghost crab burrow across the shore from the base of the dunes to the lower intertidal, compared between the reference section (no vehicle impacts) and the experimental site (illustrated by tyre tracks in the background image). Photo Credits: S Lucrezi

#### 5.4. Discussion

Burrow forms resembled the English letters I, Y, J, U, M, and S. These forms represent different transitional stages of the same burrow-making process, with increasing complexity (Chakrabarti 1981). Burrow shapes are also connected to crab age. Typical juvenile burrow shapes are I, J, U, and sometimes Y, while adult shapes include J, Y, and spiral burrows (S) or 'copulation burrows' (Vannini 1980b; Chan and others 2006). I-shaped burrows were dominant in the heavy traffic zone, whilst more complex burrow forms such as the Y and the U were more abundant in the vehicle exclusion zone and moderate traffic zone. Interestingly, U-shaped burrows were no longer present at the experimental site after the application of vehicle passes. Due to the frequent physical disruption of the sediment, crabs inhabiting heavily-driven beaches may have to regularly re-construct their burrows or repair them. Thus, the shape of crab burrows from impacted beaches is predicted to be simpler and rarely reaches more complex forms; the lack of U-shaped burrows in the moderate traffic zone after the ORV passes supports this interpretation.

Burrows became deeper and more vertical after the experimental vehicle passes. Also, burrows were substantially longer, deeper, and less inclined in the heavy traffic zone compared to the vehicle exclusion zone. Burrows only offer limited protection from crushing by vehicles, and ghost crab mortality is inversely proportional to burrow depth; individuals constructing burrows shallower than 25 cm are unlikely to survive vehicle passes (Schlacher and others 2007b). Our finding of deeper and less angled burrows appears to be a behavioural response to vehicle traffic, where crabs may react to vibrations from vehicles and shadows that mimic predators.

On the beach were we conducted the experiment, the number of tyre tracks per linear meter of beach face usually ranges between 2 and 8: more than 50% of the rutting has been recorded to be deeper than 5 cm and some ruts can be as deep as 28 cm; the total area of beach surface rutted can reach 90% (Schlacher and Thompson 2008). In the present study, tyre tracks covered the major part of the shore in the moderate and heavy traffic section, overlapping with the distribution of intertidal species such as ghost crabs. Results from our impact experiment in the moderate traffic zone show that vehicle traffic causes deep rutting of the beach and changes the across shore distribution of the crabs (Fig. 22). Reductions in density are a clear consequence of vehicle traffic (Fig. 22), but additional consequences of distributional shifts at the population level cannot be excluded.

In the preset study, ghost crab burrow densities were substantially lower in the moderate traffic zone after the experimental vehicle disturbance (Fig. 21). The experiment was a typical example of pulsed impact (Glasby and Underwood 1996; Lake 2000). It must, however, be stressed that traffic on this and other beaches in the region occurs on all days of the year (Schlacher and others 2008a), and therefore is akin to a press disturbance complemented by pulsed impacts during peak holiday periods (Schlacher and others 2007b).

Burrow opening diameter is a good proxy for body size in ghost crabs (Lucrezi and others 2009b) and it varied according to differences in traffic intensity and position across the shore. Ghost crab burrow size has previously been recorded not to differ significantly between areas varying in vehicle traffic (Maccarone and Mathews 2007). Conversely, ORV traffic might affect the survival of larger crabs: in areas where ORV traffic is chronic, the life expectancy of ghost crabs may be reduced and small ghost crabs may not mature (Steiner and Leatherman 1981). In our experiment, mean

burrow size dropped at the impact site compared with an increase at the reference site (Fig. 21b), also suggesting higher mortality or emigration of larger crabs following vehicle disturbance.

Impacts caused by four-wheel driving on sandy beaches represent a formidable challenge for environmental managers (Bird 1996). Part of this challenge arises from the multiple, often conflicting, demands that span environmental, social, economic, and cultural dimensions (Celliers and others 2004). Physical impacts to beaches and dunes are readily seen as a form of environmental degradation (Priskin 2003b), whereas environmental effects may be less obvious to the public (Schlacher and others 2006; Schlacher and others 2007a). Experimental data from this study not only add to a growing body of evidence highlighting deleterious environmental effects associated with recreational ORV use, but clearly demonstrate that environmental harm is a direct consequence of vehicle traffic on beaches. This brings into focus the need to implement visitor management strategies that meet conservation targets without dismissing the social, cultural and economic dimensions of vehicle-based recreation.

### **CHAPTER 6**

# Compression of home ranges in ghost crabs on sandy beaches impacted by vehicle traffic

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#### Abstract

Animal movement is a pivotal element of many ecological processes, and on oceanexposed sandy shores ghost crabs (genus *Ocypode*) undertake extensive nocturnal forays on the beach surface. Because ghost crab populations are also threatened by vehicle traffic, indicators that can detect sublethal effects before population declines are manifest are important. To this end we tested whether movement patterns of ghost crabs respond predictably to disturbance by vehicles, by tracking crabs at night in beach sections open and closed to traffic. Beach traffic not only halved population densities of crabs on the unvegetated beach seawards of the dunes, but it also fundamentally changed crab behaviour and movement: individuals from beach areas rutted by tyre tracks travelled shorter distances in a more erratic zigzag pattern, and they had significantly compressed home ranges. Such behavioural changes linked to human pressures are well-suited as an early warning signal for wider negative ecological impacts (as demonstrated by reduced abundances), and emphasize the need to incorporate sublethal effects in the assessment and management of ecological changes resulting from beach recreation.

Keywords: Ocypode; animal movement; tracking; behaviour; human disturbance

#### 6.1. Introduction

Animal movement is a fundamental biological and ecological process that profoundly influences population dynamics, habitat use, and transfer of materials across ecotones and levels within food webs (Pittman and McAlpine 2003; Verweij and Nagelkerken 2007). For example, introducing an organism perspective by documenting home range use, allows for an ecologically more meaningful definition of habitat that explicitly incorporates animals' daily movement patterns (Pittman and McAlpine 2003). Species-specific mobility also influences aspects of animal ecology such as the rate of habitat re-colonization, providing a fresh perspective on the magnitude of anthropogenic impacts (Breitburg and Loher 1994). Thus, understanding animal movement patterns extends beyond the study of animal ecology, to being an important element in the design of conservation strategies (Simberloff and others 1992).

On ocean-exposed sandy beaches, many invertebrates regularly switch between a fossorial lifestyle while buried in the sand and active movement on the beach surface (McLachlan and Brown 2006; Lastra and others 2009). Ghost crabs (genus *Ocypode*) are amongst the largest of beach invertebrates, being abundant and widespread on tropical and subtropical sandy beaches (Jones 1972). The crabs are highly motile (Full and Weinstein 1992) and can undertake sizeable movements during their nocturnal activity, covering distances up to 300 m; most of this activity is linked to foraging (Wolcott 1978). Ghost crabs are apex invertebrate predators, preying on shallow-buried macrobenthos (Fales 1976; Wolcott 1978), turtle hatchling (Hendrickson 1958) and the chicks of shorebirds (Sabine and others 2006). In addition, ghost crabs are prey for birds (McLachlan 1980), mammals (Barton and Roth 2008), reptiles

(Iwamoto 1986), fish foraging in the swash (S Lucrezi pers. obs.), and humans (Jackson and others 1991; Kyle and others 1997). The crabs are mainly nocturnal, emerging from their extensive burrows after dusk and retreating before dawn (Wolcott 1988).

Sandy beaches are under mounting pressure from a variety of human stressors (Defeo and others 2009), and ghost crabs are useful biological indicators of the ecological condition of beaches and dunes. They respond predictably to human stressors, with declines in population sizes having been linked to urbanization, habitat loss, armouring, trampling and vehicle traffic (Moss and McPhee 2006; Neves and Bemvenuti 2006; Lucrezi and others 2009a; Lucrezi and others 2009b; Noriega and Schlacher in press). Monitoring approaches essentially rely on numerical responses where population declines are the result of direct kills (Schlacher and others 2007b), loss of habitat integrity (Schlacher and Thompson 2008), or both (Thompson and Schlacher 2008). Arguably, if a precautionary principle is to be applied to environmental assessment and management, negative ecological impacts should be detectable before lethal effects are manifest (Gray and Bewers 1996). This places a premium on identifying and testing biological indicators that are sensitive to human stressors and are reliable in detecting impacts at the sublethal level (Sheppard and others 2009). In this paper, such sublethal indicators are assessed using ghost crabs on sandy beaches as the model system. We test movement patterns as the biological response variable and off-road vehicles as the human stressors; movement is a crucial mechanistic element in ghost crab biology (Full and Weinstein 1992) and vehicle traffic on sandy shores causes environmental harm (Moss and McPhee 2006).

#### 6.2. Material and methods

#### 6.2.1. Study area

The study was conducted on North Stradbroke Island, the southern of two large sand barrier islands that form the eastern rim of Moreton Bay in South-East Queensland, Australia. The island's ocean-exposed sandy beaches are prime recreation sites, and driving of off-road vehicles (ORVs) on the shores is a highly popular activity (Schlacher and Morrison 2008).

Main Beach is the longest (34 km) beach on the island, traversed by up to 500 cars per day which enter the beach via a cutting through the dunes at its northern end. North of this cutting is a short (600 m) stretch of beach from which vehicles are banned. We tracked crabs on the beach south of the access point that is impacted by vehicles and did the same on the beach north of the access point which is vehicle-free. Further details on the beach are provided in Schlacher and Morrison 2008, Schlacher and Thompson 2007, and Schlacher and others 2007b.

#### 6.2.1 Field measurements

Nocturnal movements of ghost crabs on the beach surface were measured using a spool-and-line tracking technique. This method entails fixing a bobbin of fine thread to an animal, which unravels as the animals moves, and tracking the thread after a specified period of time. We used lightweight (1.3 g) cocoon bobbins (dimensions: 40 x 6 x 10 mm L x H x W; thread diameter: 0. 25 mm) which unravel from the centre of the spool; this allowed us to easily fix the bobbin to the dorsal side of the crab's carapace and ensured that the thread could unravel freely. Bobbins were wrapped in a protective waterproof casing (cling wrap) to prevent snagging on vegetation and to

provide a flat surface on which the glue could be applied (Boonstra and Craine 1986; Harris and others 2006; Steinwald and others 2006; Tozetti and Martins 2007).

Spool-and-line tracking is particularly well suited for small animals (Sutherland and others 2008). It has been used to track small mammals (Miles and others 1981; Boonstra and Craine 1986; Harris and others 2006; Steinwald and others 2006; Shanahan and others 2007), reptiles (Tozetti and Martins 2007), amphibians (Tozetti and Toledo 2005), and snails (Murphy 2002).

Crabs were tracked over four consecutive days per month, between October and December 2009. Each night, two to seven (depending on crab activity) individuals were captured around the time of high tide after dusk. The capture technique was adapted from rugby, emulating the Springbok's highly efficient '*charge and slide tackle*'. The gender of each ghost crab was recorded, and its carapace width and length measured with Vernier calipers. A cocoon bobbin containing 200 m of wound thread (Sewing Thread Specialists, A Division of: McCall's Pattern Service Pty Ltd, 26-28 Clements Avenue Bankstown, NSW, 2200) was fixed to the central region of the dorsal carapace with superglue. The free end of the thread was tied to a marker flag set at the base of the dunes. Individuals were spaced 25 m apart along the beach and released within 10 min of capture near the flags. After the bobbin had been fixed, field workers withdrew quietly so crabs would not flee in any particular direction (Miles and others 1981).

Tracking began at the next low tide following their release, thus allowing the animals a full night of activity on the beach surface. The movement of each crab was traced by following the trail of thread that had unraveled as the crab moved. We recorded the position of every turning point with a Differential Global Positioning

System (DGPS) (Anderson and others 1988; Zollner 2000; Harris and others 2006; Hoare and others 2007; Shanahan and others 2007; Sutherland and others 2008; Gregory and Macdonald 2009). Turning points were also marked with ranging rods, and the distance between rods and their compass bearing recorded with reference to a DGPS-measured basepoint at the foot of the dunes (Fig. 23).



**Figure 23** Areas covered by ghost crabs (*Ocypode ceratophthalma*) during nocturnal surface activity in beach sectors open to vehicle traffic (south of the access point) and closed to cars (north of the access points). Crabs were tracked in Oct '09 (a), Nov, '09 (b) and Dec. '09 (c) using a spool-and-line tracking technique. Plotted areas are minimum convex polygons derived from GIS

Air temperature during the study ranged between 18.9 and 30.5°C, relative humidity between 21 and 96%, and wind speed between 2 and 44 km h<sup>-1</sup>. The two beach sectors were sampled on consecutive nights, and it is therefore unlikely that weather variability would have caused a directional bias to differences in crab movement between vehicle-impacted and traffic-free sections. Beach visitors and dogs were observed in both sectors after dawn, but mean densities did not differ significantly (ANOVA:  $F_{1,43} = 3.23$ , p = 0.079), and there was virtually no human disturbance during most of the night when crab movement was tracked.

Ghost crab density was quantified immediately before tracking. Densities were obtained from counts of active burrow openings made in 10 m wide belt transects that extended from the base of the dunes to the furthest seaward occurrence of burrow openings (Lucrezi and others 2009a; Lucrezi and others 2009b). In the vehicleimpacted sector, the number and depth of tyre ruts was recorded using a line-intercept method (Schlacher and Morrison 2008; Schlacher and Thompson 2008). Standard theodolite surveys of the beach face were made to obtain basic morphological properties of the shore (e.g. slope, elevation, width).

#### 6.2.3. Data analysis

Field tracking data were analysed using ArcGIS with the ABODE add-on (Laver 2005) (http://filebox.vt.edu/users/plaver/abode/download.html). The principal metrics we used were: a) the total length of the trail; b) the number turning points along the trail; c) the segment length between turning points; d) the total area covered. The latter was calculated as Minimum Convex Polygons (MCPs), which is conventionally interpreted as the space that an animal uses and traverses. For this, the first few meters of thread were excluded as this may be considered to represent a flight response (Harris and

others 2006; Hoare and others 2007; Strauβ and others 2008; Gregory and Macdonald 2009).

Because a single metric is unlikely to accurately describe the movement pattern of animals, tracking data are inherently multivariate (sensu Pittman and McAlpine 2003). Consequently, our principal analytical model operated in the multivariate domain, where the principal question of interest was whether crab surface behaviour (as represented by tracked movement) differs between beach sections with and without vehicle traffic. This comparison was made using Permutational Analysis of Variance, PERMANOVA (Anderson and Gribble 1998). The PERMANOVA design included two factors: month (random) and vehicle use (fixed, nested within month), and was run with 999 permutations on an Euclidean distance matrix using the PERMANOVA add-on in Primer 6 (Anderson and others 2008).

To ensure that the principal test of interest was not confounded, we ran three diagnostic checks that examined the putative influences of sex, body size and physical habitat properties on crab movement. For carapace width, there was neither a significant difference in the mean (Impact:  $\bar{x} = 40.1$  mm, se = 1.9; Reference:  $\bar{x} = 36.4$  mm, se = 2; t = 1.33, df = 21, P = 0.2) or median value (Impact:  $d_{50} = 40.5$  mm; Reference:  $d_{50} = 36$  mm; Mann-Whitney U test, U = 44, P = 0.2) between sections; body size was therefore considered not to have biased comparisons between sectors.

We tracked a total of 49 individuals, 13 females and 36 males; movement patterns were compared between sexes using Analysis of Similarities, ANOSIM (Clarke 1993); this diagnostic check was run independently for November and December to ensure tests for sex differences were not confounded by time. Only a single female was caught in each section during October and hence no variance estimate is available for this month to run a test. There was no significant difference in the movement patterns between males and females during either November (R = -0.19, P = 0.84) or December (R = -0.02, P = 0.48), and sexes were therefore pooled for PERMANOVA.

While it would be reasonable to assert that crab movement statistics could, theoretically, be influenced by beach width (e.g. animals cover longer distances on a wider beach and vice versa), we did not find significant correlations between beach width and movement metrics (Area:  $r_s = -0.005$ , P = 0.97; Trail Length:  $r_s = -0.135$ , P = 0.36; Distance between turns:  $r_s = 1.347$ , P = 0.356). In addition, there was also no evidence for consistent relationships between beach width and crab movement in any month or section, with a range of correlation coefficients from -0.77 to 0.82. The intertidal zone was only slightly (-12%) narrower in the vehicle-impacted section ( $\bar{x} = 30.7$  m, se = 2.6) compared with the vehicle-free zone ( $\bar{x} = 35.0$  m, se = 2.7; Fig. 24), and beach slopes were highly similar (Reference:  $\bar{x} = 3.23^\circ$ , se = 0.27; Impact:  $\bar{x} = 3.37^\circ$ , se = 0.33; ANOVA P <sub>3.53</sub> = 0.98). This strong resemblance in physical habitat attributes excludes environmental factors other than differences in human disturbance levels as the principal sources of variations in crab movement.


**Figure 24** Comparison of beach width (left column) between vehicle-impacted and reference sections of the beach and key metrics of animal movement

## 6.3. Results

Crab movement differed substantially between beach sectors closed and open to vehicles. On the beach rutted with tyre tracks, animals traversed significantly shorter distances and covered smaller areas during their nocturnal surface activity (Figs. 23 and 24). Mean trail length was shorter by 27% on the vehicle-impacted beaches over the study (Impact:  $\bar{x} = 30.4$  m, se = 5.8; Reference:  $\bar{x} = 41.6$  m, se = 7.8), but

decreases reached -49% during October (Fig. 24). The shortest ghost crab trail was recorded in the vehicle impact sector (4.5 m), while the longest trail was 160.6 m and occurred in the reference sector.

Shorter distances travelled translated into much smaller areas covered (Impact:  $\bar{x} = 109.3 \text{ m}$ , se = 35.9; Reference:  $\bar{x} = 240.8 \text{ m}$ , se = 107.2) with a loss of up to -59% during December (Fig. 24). Irrespective of total distance travelled, the crabs did not change the number of turning points along their trails in response to vehicle disturbance (Impact:  $\bar{x} = 4.38$ , se = 0.60; Reference:  $\bar{x} = 4.44$ , se = 0.83). Thus, because overall distance travelled was significantly shorter for the same number of turns, the length of segments making up the polygons was considerably shorter on the vehicle-impacted beach (Impact:  $\bar{x} = 15.22 \text{ m}$ , se = 2.90; Reference:  $\bar{x} = 20.80 \text{ m}$ , se = 3.89; Fig. 24). Overall, movement patterns of ghost crabs during their nocturnal surface activity differed significantly between beach sections open and closed to vehicle traffic (Fig. 25, Table 36).



**Figure 25** Ordination (PCO – Principal Coordinate Analysis) comparing multivariate patterns of crab movement in two beach sectors with and without vehicle traffic and during three months. Plot is based on Euclidean Matrix of normalized values for total trail length, area covered and segment length (a). Non-metric multidimensional scaling ordination plot of group centroids extracted from PCO for treatment (vehicle vs. reference) and month; arrows indicate shift in the movement pattern between the reference section (open symbols) and vehicle-impacted section (closed symbol) (b)

 Table 36 Summary of PERMANOVA results comparing movement patterns of ghost crabs

 between months and sectors open and closed to vehicles

Source	df	SS	MS	Pseudo-F	P <sub>(perm)</sub>	Unique Permutations
Month	2	21.99	10.99	4.879	0.003	999
Sector (Month)	3	25.70	8.57	3.802	0.005	999
Residual	41	92.39	2.25			
Total	46	138				

The activity of all successfully tracked crabs ceased with the construction of a burrow. The movement of 48 out of 49 ghost crabs was limited to the foreshore, from the base of the dunes where crabs had been released downshore to the effluent line (Fig. 23). Only one crab moved inland to the secondary dune ridge where its surface activity ceased. No exchange of individuals between beach sectors was recorded during the study, indicating limited longshore movement of animals.

Crab density was halved in the vehicle-impacted sector from a mean of 29.91 ind. 30 m<sup>-2</sup>, se = 1.85 in the reference sector to 14.04 ind. 30 m<sup>-2</sup>, se = 1.41 in the sector open to vehicles (ANCOVA, F <sub>1.309</sub>= 111, P < 0.001). However, densities in a particular sector did not influence surface movement of ghost crabs, indicated by no significant correlation between burrow density and trail length or area covered ( $r_s = -0.06$  and -0.16 respectively).

## 6.4. Discussion

Off-road vehicle traffic significantly changed the ghost crabs' nocturnal surface behaviour, resulting in substantial reductions in the area used by individuals. Compressions in the area used by animals as a result of human disturbance and habitat destruction have been reported for large mammals. For example, highway traffic and hunting restrict movement of bears and lead to a reduction in the area used (Manville 1983). Animals can also react to human disturbance by increasing or shifting their home range and area covered. Raptors have been shown to increase the size of the area they use when disturbed by military training activities (Andersen and others 1990).

Decapod crustaceans, including ghost crabs, have highly developed senses and great mobility, enabling them to seek alternative locations when conditions in the original habitat become unfavorable (Pittman and McAlpine 2003). We did, however, not observe a habitat shift into the dunes from the intertidal zone which is heavily disturbed by vehicles (Schlacher and others 2008a; Sheppard and others 2009). Sizeable populations of ghost crabs exist in the dunes (Thompson and Schlacher 2008), and intertidal crabs use dunes a refuge from storms (Hobbs 2008). However, the crabs scavenge mostly along the strandline, feeding on wrack cast upon the shore (TA Schlacher pers. obs.) (Cott 1930; Fisher and Tevesz 1979), and they can also be active predators in the swash zone (Wolcott 1978). The unvegetated beach and swash zone appear therefore to supply richer food resources to crabs and feeding in this zone is likely to be energetically advantageous; this must, however, be off-set against the significantly increased risk of being crushed by vehicles (Schlacher and others 2007b).

Several factors influence surface activity and movement of ghost crabs, including predators (e.g. other ghost crabs, mammals, reptiles, and birds), vehicles and humans. Human disturbance and habitat modifications can change the tracks of land crabs. On Christmas Island, breeding migration routes of the red crabs change according to whether migration starts from inhabited areas or undisturbed areas: crabs from urbanized areas travel along the side of roads, becoming diverted from their course towards the shore (Adamczewska and Morris 2001). This behaviour results in more erratic migratory routes for crabs departing from disturbed parts of the island

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(Adamczewska and Morris 2001). On sandy beaches, vehicle tracks can change the tracks of turtle hatchlings moving towards the surf: hatchlings caught inside vehicle ruts can no longer see the surf and travel inside the ruts along the beach rather than moving across the beach (Hosier 1980; Hosier and others 1981). In our study, the number and the depth of tyre tracks was not correlated to distance travelled and area used by ghost crabs. This suggests that rutting per se may not have influenced the movements of ghost crabs during their nocturnal surface activity, and that the crabs scale the apparent barriers of tyre tracks. The length of trails was, however, significantly shorter in the sector rutted by vehicles without any change to the number of turning points that the crabs made (Fig. 24). This suggests that ghost crabs not subjected to disturbance by vehicles travelled longer distances on a straight line before turning and changing their trajectory, compared to ghost crabs which had a more interrupted zigzag movement as a result of disturbance by vehicles. Interestingly, the main defensive pattern of ghost crabs against predators, vehicles and humans is a rapid escape response of running in a zigzag pattern towards the sea or their burrows (Vannini 1980a).

Ghost crabs are overwhelmingly nocturnal, becoming active on the beach surface after dusk and retreating back to their burrows around dawn. Juvenile, smaller crabs may forage during the day, and some diurnal surface activity can rarely occur in adults as well (Wolcott 1988). We recognize that our records of crab movement may have underestimated this small diurnal component, but this is likely to be very small in comparison to the nocturnal activity which represents the bulk of activity and is representative of an individual's home range (sensu Pittman and McAlpine 2003).

Because surface movement is a critical element in the biology and life-history of ghost crabs, anthropogenic changes to this behaviour may have wider ramifications. It

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is likely that crabs that cover greater areas of the beach at night are more likely to encounter more food or food of higher quality (e.g. scattered animal carcasses at the strandline). Hence, compressions in home range are hypothesized to result in reduced food intake and, possibly, slower growth, less investment in reproduction and smaller population sizes. In fact, we recorded a 53% drop in population densities in beach sections open to vehicles, consistent with earlier findings from the same area (Schlacher and others 2007b). These declines have been linked to direct mortalities when vehicles crush crabs (Schlacher and others 2007b), but it is also possible that the compressions in home range reported here can contribute to lower abundances. Overall, these findings emphasize the importance of incorporating indicators of sublethal effects into assessment and conservation initiatives to act as early warning signals for wider ecological impacts.

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## APPENDIX A

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### Monitoring human impacts on sandy shore ecosystems: a test of ghost crabs (*Ocypode* spp.) as biological indicators on an urban beach

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Abstract Sandy beaches comprise one of the most important coastal resources worldwide, providing habitats to threatened vertebrates, supporting underappreciated invertebrate biodiversity, and delivering crucial ecosystem services and economic benefits to mankind. Monitoring of the natural resource condition of sandy beaches and assessments of the ecological impacts of human disturbance are, however, rare on sandy shores. Because a crucial step in developing beach monitoring is to identify and test biological indicators, we evaluated the utility of using population densities of ghost crabs (genus Ocvpode) to measure how beach biota respond to human pressures. Densities of crabs-estimated via burrow counts-were quantified at two sites exposed to high and low levels of human disturbance on an urban beach in eastern Australia. Human disturbance consisted of pedestrian trampling and shoreline armouring which led to the loss of dune habitat. Overall, crab numbers were halved in disturbed areas, but contrasts between impact and control sites were not necessarily consistent over time and varied between different levels of the shore: stronger and more consistent effect sizes were recorded on the upper shore than further seawards. In addition to lowering crab densities, human disturbance also caused shifts in intertidal distributions, with a greater proportion of individuals occurring lower

S. Lucrezi · T. A. Schlacher (⊠) · S. Walker Faculty of Science, Health and Education, University of the Sunshine Coast, Maroochydore DC, QLD 4558, Australia e-mail: tschlach@usc.edu.au on the shore in the impacted beach sections. The number of visible burrow openings also changed in response to weather conditions (temperature and wind). We demonstrate that spatial contrasts of burrow counts are broadly useful to indicate the existence of a humaninduced disturbance effect on urban beaches; we also highlight a number of critical, hitherto unknown, issues in the application of this monitoring technique; these encompass three broad dimensions: (1) a need for standardised protocols; (2) unresolved causal links between observed patterns and putative pressures; and (3) uncertainties of how organisms responds specifically to both natural and human changes of environmental conditions on sandy shores.

Keywords Sandy beaches · Ghost crabs · Shore monitoring · Coastal management · Faunal indicators

### Introduction

Sandy beaches rank amongst the most intensively used coastal ecosystems by man, and human uses of beaches are rising sharply (Schlacher et al. 2006). Traditionally, management of beaches has almost exclusively focused on maintaining and restoring sand budgets, with scant consideration for ecological dimensions (Nordstrom 2000). Human use of beaches is, however, not without ecological consequences and can result in multiple forms of environmental degradation (Brown and McLachlan 2002; Dugan and Hubbard 2006; Schlacher et al. 2007a).

Despite the great social, economic, and environmental importance of sandy shores worldwide, environmental monitoring and assessment of sandy beach ecosystems is rare. A monitoring technique which uses ghost crabs as biological indicators to measure the effects of human disturbance on beaches has been applied on urban shores (Barros 2001; Neves and Benvenuti 2006), and to assess whether off-road vehicles driven on beaches damage the resident biota (Moss and McPhee 2006; Schlacher et al. 2007b); these studies generally report lower population densities in areas heavily disturbed by human activities.

Ghost crabs of the genus *Ocypode* are semiterrestrial invertebrates commonly found on subtropical and tropical shores. They are relatively large animals, occupying the position of apex invertebrate predator on sandy beaches (Wolcott 1978). Ghost crabs switch between surface activity at night to a fossorial lifestyle inside their burrows during the day (Barrass 1963). The crabs construct deep and complex burrows which provide shelter against climatic extremes and predators, and serve as refuges during moulting and maternity (Chan et al. 2006). The top of these burrows breaches the sand surface as a clearly visible hole, and therefore counting burrow entrances is an efficient tool to measure densities of ghost crabs on beaches (Moss and McPhee 2006).

Management interventions aimed at reducing negative ecological impacts on beach systems will need to increasingly incorporate biological information, requiring the development of beach monitoring programmes (Schlacher et al. 2006). A critical pre-requisite for such monitoring programmes is to identify appropriate indicators and to assess the scientific robustness of the technique. To this end, this paper examines to which degree population estimates of ghost crabs are influenced by external environmental factors, and whether measured responses of ghost crabs in relation to human disturbance are consistent across space and time.

### Material and methods

### Study area

The study was done on Mooloolaba Beach in southeast Queensland, Australia (Fig. 1). The beach

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is situated in a 1.8 km long embayment, bounded in the West by a rocky shore and in the East by a groyne (Fig. 1). The beach has a long history of human engineering interventions and has undergone many morphological changes over the last 60 years (Longhurst 1997). A wooden retaining wall was built in 1952 on the northern backshore area of the beach and replaced by a stone wall in 1959; this structure was the forerunner of today's seawall which is 204 m long and 2.3 m high; this part of the beach also receives the highest number of beach visitors. In 1968 the inlet of the Mooloolah Estuary was artificially stabilised with two rock walls, the northern one forming today's south-eastern boundary of the beach. All natural dune areas of the northern beach have been replaced with recreation infrastructures such as playgrounds, toilets and large buildings such as the Surf Life Saving Clubhouse. Dunes (3-4 m tall) are still present on the southern beach, although they have undergone substantial human modifications such as fencing and revegetation since 1957 (Longhurst 1997).

### Spatial layout and burrow counts

To test whether ghost crab densities are reduced by shore armouring and intense human trampling we compared burrow densities between the heavily modified northernmost section of the beach (impact site) and a reference zone 40 m to the south-east (Fig. 1). Ghost crab densities were quantified by counting the number of active burrow openings on the beach surface. The impact section is the most heavily used area of the beach by humans; here all foredunes have been replaced by a seawall. By contrast, the reference section was chosen because it is the area of the beach with the fewest number of visitors and where remnant dune vegetation remains.

In each section (i.e. impact and reference), burrow counts were made across eight belt transects. Each belt transect was a continuous 10 m wide strip that extended across the shore from the base of the foredunes or seawall to the downshore limit of burrow occurrence. Individual transects within a site were interspersed by 10 m along the beach. Each transect was divided into sequential 3 m long quadrats placed continuously down the shore (Fig. 1). Thus, the basic sampling unit in this study was a  $3 \times 10$  m quadrat, and burrow densities are expressed as the number of burrows per 30 m<sup>2</sup>.



Fig. 1 Study area, Mooloolaba Beach, in Eastern Australia (a). The urban beach has a heavily modified and armoured section that is extensively impacted by human trampling (b), abutted by some remaining natural dune areas with relatively less human use (c). Burrow counts of ghost crabs were made in  $3\times$ 

Burrow counts were temporally replicated on 15 days, covering one full lunar cycle between March and April 2007. The chief purpose of temporal replication was to (1) identify environmental factors (e.g. weather, sea conditions) that influence burrow density, and (2) test whether spatial differences in burrow density linked to human disturbance are consistent over time.

10 m plots arranged sequentially (A-H) in across-shore transects from the base of the seawall or dune to the seaward limit of ghost-crab distributions. Each section (i.e. impact, reference) contained eight transects, surveyed on 15 separate occasions (photos by TA Schlacher (a), S Lucrezi (b, c))

On each survey day, we started burrow counts 1–2 h after sunrise, a complete survey of all transects taking 5–6 h. To avoid possible bias associated with the time of the day when counts were made at a specific location, the sequence of field measurements was randomised by selecting the section (i.e. impact vs. reference) to be counted first (toss of coin), and randomising the starting

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transect within a site (random number table). Only 'active' burrow openings were counted. Active burrows were easily recognised by either the presence of fresh tracks emanating from the opening, or evidence of recent re-working of the burrows visible as small mounds of excavated sediment next to the entrance, or both. 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.

### Environmental variables

After all burrows had been counted in a quadrat, we took three replicate measurements of (1) sand temperature to a depth of 5 cm (electronic thermometer Fluke 52 K/J), (2) sand moisture to a depth of 8 cm (Trident microwave moisture meter), (3) sand shear force resistance (field inspection vane tester Geonor H-60 with a vane size of  $5 \times 2.5$  cm), and (4) penetration force (Geotester penetrometer, 20 mm diameter tip); the position of replicates was randomised within each quadrat.

Morphological properties (i.e. beach profile, width, slope) of the beach were obtained from standard theodolite surveys. We visually determined the position of the drift line (the reach of the highest swash preceding the counts marked by clearly visible deposits of detached macrophytes, carcasses and debris) and the position of the effluent line (water table outcrop) for each individual transect. The effluent line represents the position where the water table breaches the subaerial beach; it is marked by a clearly visible transition between the zone of saturated sand (sometimes referred to as the glassy layer) and the upper beach composed of drier, unsaturated sand. We also recorded wind speed and air temperature (Skymate SM-18 meter), wind direction (compass), wave height (visually) and wave period (counts of breaking waves over 3 min) at the start and end of each survey. Additional weather data (e.g. hourly temperature, wind speed and direction, hourly rainfall) and tidal heights were obtained from the Bureau of Meteorology (http://www.bom.gov.au).

Sediment properties were determined by collecting triplicate sediment cores (30 mm diameter, 100 mm deep) from every quadrat on three occasions. In the laboratory, sediment granulometry was determined by dry-sieving samples through a nested series of eight sieves arranged in decreasing order of mesh aperture

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size (4,000, 2,000, 1,000, 500, 250, 200, 180, 63  $\mu$ m). Sediment parameters were calculated according to the Folk and Ward method using the Gradistat software (Blott and Pye 2001).

To determine the intensity of human disturbance by pedestrian trampling, we obtained estimates of the number of beach visitors from life guards who patrol the beach daily from 0730 to 1630, and count the number of people every 2 h.

### Data analysis

Total variance in ghost crab burrow densities was partitioned using a generalized linear model (GLM). The design included survey number as the temporal component of variation, and two spatial terms: (1) impact (reference vs. impact section), and (2) shore zone (backshore above the drift line vs. foreshore below the drift line). Count data were square-root transformed where required to achieve normality and homoscedasticity (Cochran's *C*-test). The influence of individual environmental variables on burrow density was assessed with partial correlation analysis.

### Results

Environmental and habitat properties

Mostly warm and dry weather conditions prevailed during the study. Temperature was  $22^{\circ}$ C to  $29^{\circ}$ C during the day and  $17^{\circ}$ C to  $25^{\circ}$ C at night, decreasing slightly over the course of the study (Fig. 2b). Wind speed was not substantially different between night (4.9–13.0 knots) and day (3.8–12.6 knots), but winds became lighter during the study (Fig. 2a). Temporal fluctuation in sand moisture (0.01–1.9%) and sand temperature (9.4–25.2°C) largely reflected weather conditions, and decreased over time as did wave height (Fig. 2). Rain was recorded on two days only (Fig. 2h).

Both beach sections were morphodynamically highly similar, being tide-dominated shores of a modal intermediate to reflective state. Beach Index (McLachlan and Dorvlo 2005) values were virtually identical between impacted and reference sites (BI<sub>ref</sub>=2.09, BI<sub>impact</sub>= 2.11); Dean's Parameter (Short 1996) also changed little between sections ( $\Omega_{ref}$ =1.85, BI<sub>impact</sub>=1.69). Width of the beachface varied between 39 and 48 m, with mean values and ranges comparable between sites

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(Reference:  $\overline{x} = 41$  m, range=39-45 m; Impact:  $\overline{x} = 42$  m, range=39-48 m), as was the case for beach slope (Reference:  $\bar{x} = 2.58^{\circ}$ , SE=0.20, *n*=117; Impact:  $\overline{x} = 2.66^{\circ}$ ; SE=0.16, n=121). No substantial differences in sediment properties were found between the impact and reference sites (Table 1). Sand temperature was only marginally (5% of reference site value) lower in the impact section, and mean values of sediment compactness were within 3-11% of measurements in the reference site (Table 1). Similarly, mean grain size differed by less than 7% between sections (Table 1). Given the close match in physical habitat properties

between the impact and reference sites, it is highly unlikely that variations in environmental variables are the primary cause of spatial differences in ghost crab populations.

Environmental drivers of changes in crab burrow numbers

Significantly higher burrow counts were obtained in wetter sand after warm nights and during stronger winds (Table 2). By contrast, neither wave properties nor tidal amplitudes were correlated with crab burrow

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Table 1 Comparison of sediment properties between impact and reference sections of the beach where counts of ghost crab burrows were made

Variable	Impact			Referen	nce	ANCOVA F(1,1408	
	n	$\overline{x}$	SE	n	$\overline{x}$	SE	
Sand temperature (°C)	706	21.46	0.08	705	22.57	0.09	11.07***
Penetration force (kg/cm <sup>2</sup> )	706	5.37	0.02	705	5.55	0.03	24.40***
Compactness (kPa)	706	0.92	0.01	705	1.04	0.02	3.20 <sup>ns</sup>
Sand moisture (%)	706	0.77	0.05	705	1.17	0.06	2.68 <sup>ns</sup>
Sand grain size (µm)	131	309.26	1.74	124	288.60	2.05	20.65***

\*\*\*P<0.001, ns P>0.05

densities on the beach; sand temperature and compactness were also not correlated with the number of burrow openings (Table 2). Correlations between environmental variables and burrow densities were highly similar in both beach sections, irrespective of human disturbance intensity. In fact, no significant effect of visitor numbers was recorded in terms of a temporal concordance between burrow densities and beach visitation (Table 2). However, burrow densities decreased at the impact site during periods of heaviest beach use which peaked over the Easter Holiday (days 15 to 19 of the survey; Fig. 2d,h), and mostly remained low even after visitor numbers had reverted to the lower pre-peak intensities from day 24 onwards (Fig. 2d,h). There was no conspicuous pattern in temporal changes of burrow numbers that could unambiguously be related to lunar phases (Fig. 2h).

### Spatio-temporal variations in burrow densities

The spatial distribution of burrow densities varied significantly with the level of human disturbance (i.e. impact vs. reference sections) and the position across the shore (i.e. above vs. below the driftline). Importantly, both spatial sources of variation interacted significantly with temporal changes, creating a complex pattern of heterogeneity in burrow numbers in space and time (Tables 3 and 4).

We counted a total of 24,290 burrow openings. Of these, two-thirds (16,096) were located on the upper shore above the drift line, compared to 8,194 found on the middle section of the beach seawards of the driftline (Table 3, Fig. 3). The across-shore distribution of burrows did, however, differ markedly between the impact and reference site: a significantly higher proportion (74%) of burrows occurred on the backshore of the reference section, whereas in the

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impact site roughly equal numbers of burrows were found above and below the driftline (Table 3, Fig. 3).

Burrow densities were substantially lower in areas intensively trampled by humans and where dunes had been replaced by a seawall (Figs. 3 and 4). Overall, the highly impacted site supported only half the number of crabs found in the less intensively disturbed areas (Table 3, Fig. 4). Although reductions in mean burrow densities between reference and impact sites were in absolute terms comparable for the upper shore (Reference<sub>upper</sub>:  $\bar{x} = 20.82$  ind. 30 m<sup>-2</sup>, SE=0.84, n=577; Impact<sub>upper</sub>:  $\bar{x} = 7.84$  ind. 30 m<sup>-2</sup>; SE=47, n=521) and the middle shore (Reference<sub>middle</sub>:  $\bar{x} = 33.08$  ind. 30 m<sup>-2</sup>, SE=2.07, n=128; Impact<sub>middle</sub>:  $\bar{x} = 21.41$  ind.

 Table 2
 Partial correlations between environmental factors and densities of ghost crab burrow densities (n=15 surveys)

	Reference	Impact
Sediment properties		
Sand temperature (°C)	-0.207 <sup>ns</sup>	0.003 <sup>ns</sup>
Sand compactness (kPa)	$-0.340^{ns}$	0.141 <sup>ns</sup>
Sand moisture (%)	0.561*	0.714*
Sea conditions and tides		
Wave height (m)	0.264 <sup>ns</sup>	0.160 <sup>ns</sup>
Wave period (s)	-0.183 <sup>ns</sup>	0.003 <sup>ns</sup>
Tidal amplitude (m)	-0.107 <sup>ns</sup>	-0.220 <sup>ns</sup>
Tidal reach (previous night; m)	0.080 <sup>ns</sup>	0.079 <sup>ns</sup>
Tidal reach (survey day; m)	-0.065 <sup>ns</sup>	-0.145 <sup>ns</sup>
Weather		
Air temperature—night (1800–0600; °C)	0.603*	0.717*
Air temperature-day (0600-1230; °C)	-0.403ns	-0.432 <sup>ns</sup>
Wind speed-night (knots)	0.666*	0.681*
Wind speed-day (knots)	0.585*	0.597*
Human pressure		
Beach visitors (daily, n)	-0.326 <sup>ns</sup>	-0.342 <sup>ns</sup>

\*P<0.05, ns P>0.05

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Table 3 Distribution of total burrow counts over the entire survey (n=24,290) between the upper and middle shore (separated by the drift line, DL), and between impacted and reference sections of the beach

	Reference	Impact	Both		
Upper shore (>DL)	12,012 (74%)	4,084 (51%)	16,096 (66%)		
Middle shore ( <dl)< td=""><td>4,234 (26%)</td><td>3,960 (49%)</td><td>8,194 (34%)</td></dl)<>	4,234 (26%)	3,960 (49%)	8,194 (34%)		
Entire beachface	16,246	8,044	24,290		

 $30 \text{ m}^{-2}$ ; SE=1.3, *n*=185), relative decreases above the driftline (-62%) were about double that of decreases further seawards (-35%).

These spatial contrasts between heavily and less disturbed sites were, however, not necessarily consistent over time, and depended on the position across the shore where burrow counts were made (Table 5). On the upper shore, half the surveys showed significantly lower mean densities in the impacted site, and the direction of change was negative for all but a single survey (Table 5). By contrast, although burrow densities on the middle part of the beach (i.e. below the strandline) were also mostly lower in the heavily impacted areas, a significant change could only be detected in a single survey (Table 5). Thus, differences in burrow densities that could be linked to the intensity of human disturbance were detectable in half of all cases on the backshore above the driftline but not further seawards.

### Discussion

Environmental influences on crab burrow densities

Ghost crabs are semi-terrestrial and can live in both dry and wet sediment (Fisher and Tevesz 1979); in the present study, sand moisture was positively correlated with ghost crab burrow density (Table 2). Burrows generally provide protection against dehydration, but the crabs still require access to water to moisten their gill chambers (Wolcott 1976). Also, extreme dehydration can cause the loss of body weight and impair locomotion (Weinstein 1998). Juveniles generally need to renew water in the gill chambers more frequently than adults, whose distribution can therefore extend further landward (Wolcott 1976). Conversely, the seaward limit of crab distribution is often dictated by waves and swash, because prolonged immersion in seawater can cause osmotic stress (Vinagre et al. 2007).

Burrows provide a thermally stable environment, insulating crabs against temperature extremes as long as they remain fossorial (Chan et al. 2006). Surface activity, mainly during the night, does expose crabs to ambient temperature conditions, and we found more active burrow openings after warmer nights (Table 2). This suggests that activity levels were influenced by metabolic responses to temperature, and consequently affected the number of active burrow openings that could be counted during the day. In fact, members of the genus Ocypode become less active at lower temperatures (Hughes 1966). At temperatures below ~16°C some species become dormant or migrate inland (Christoffers 1986), and upper thermal limits for activity are about 30°C (Weinstein 1998). Temperatures recorded in this study did not approach these reported limits, but temperature is clearly an important environmental variable for ghost crabs and affects the number of open, active burrow openings. Sand surface temperature increased slightly up the shore within the impact section, possibly caused by heat radiating from the seawall or from increased trampling that allows heat to penetrate further into the sediment. Thus, coastal annouring structures may have an indirect, negative effect on ghost crabs that operates via

Table 4 Summary of generalized linear model (GLM) analysis contrasting burrow density amongst times, impact intensities, and shore zones (above and below the drift line, DL)

Source of variation	df	MS	F
A—Time	13	39.61	14.77***
B-Impact (ref. vs disturbed)	1	183.83	68.52***
C-Shore zone (>DL vs. <dl)< td=""><td>1</td><td>260.63</td><td>97.15***</td></dl)<>	1	260.63	97.15***
$A \times B$ (time × impact)	13	12.14	4.52***
$A \times C$ (time × shore zone)	13	5.73	2.14*
$B \times C$ (impact × shore zone)	1	30.25	11.28***
$A \times B \times C$ (time × impact × shore zone)	13	6.91	2.58**
Error	1,251	2.68	

\*\*\*P<0.001, \*\*P<0.01, \*P<0.05

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Fig. 3 Distribution of ghost crab burrows across the beachface (shown as beach profiles in *bottom panel*) at the reference (top panel: open bars) and impact sites (top panel: solid bars); asterisks in *bottom panel* denote the position of the driftline (DL)

modifications of their thermal environment; this hypothesis would merit further investigations.

We found a strong positive correlation between wind speed and burrow density (Table 2). Fewer people frequent the beach when there are strong onshore winds (Lucrezi, personal observation), reducing direct trampling impacts by humans. Wind strength and direction were, however, unlikely to have confounded comparisons between the heavily impacted and reference sites, because burrow densities responded equally to meteorological changes in both sections. Ghost crabs can be highly active during strong onshore winds (Wolcott 1978). Wind-driven onshore advection is the principal mechanism for delivering wrack and carrion to beaches. We observed nocturnal feeding aggregations of ghost crabs around driftlines (Schlacher, personal observation), and ghost crab activity may thus respond positively to stronger winds that enhance resource availability of stranded food. However, the positive correlation between wind speed and burrow numbers measured in this study is unlikely to apply over the full spectrum of wind speeds on exposed coastlines. In fact, winds above 20 knots tend to obscure burrow openings, particularly in loose sand on the upper shore (Schlacher, personal observation). Thus, burrow counts are not useful as a monitoring tool under such conditions.

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Mechanisms of impact: trampling and habitat change

Few studies have measured the impact of human trampling on the distribution and abundance of macrofauna on sandy beaches, and those that have, showed different outcomes. Recreational use could not be unequivocally linked to changes in the macrobenthos on a Chilean beach (Jaramillo et al. 1996), but experimental work in South Africa demonstrated that several beach invertebrates can be sensitive to direct crushing by pedestrian trampling (Moffett et al. 1998). It has been suggested that human trampling is the cause of lower ghost crab numbers on urban beaches (Barros 2001; Neves and Bemvenuti 2006). However, the actual processes that cause observed reductions in ghost crab populations in disturbed areas remains largely unresolved, except for the crushing of crabs by off-road vehicles (Schlacher et al. 2007b).

In addition to direct crushing of individuals, trampling may also affect ghost crabs via several complementary mechanisms: (1) crabs simply plug their burrows, do not re-emerge, and hide within their burrows, leading to lower density estimates; (2) trampling lowers sand stability causing burrow openings to collapse; and (3) crabs lower burrowing and feeding activity. Some beach visitors leave food scraps behind which may lead to shifts in crab diet, distribution and abundance (Steiner and Leatherman 1981).

Coastal armouring is increasingly being employed to combat shoreline erosion worldwide, and this trend may escalate in the face of global climate change (Feagin et al. 2005). The main ecological impact of coastal armouring is the destruction of dunes (Dugan



Fig. 4 Comparison of ghost crab burrow openings between reference and impacted sites at two heights of the shore

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Table 5 Effect sizes for spatial contrasts in burrow densities between impact and reference sites at two levels of the shore during individual surveys

	Upper shore	$\frac{\text{Middle shore}}{\text{Effect size}^{a}, n (\%)}$			
Survey	Effect size <sup>a</sup> , n (%)				
1	-21.4 (-59)*	12.1 (+35) <sup>ns</sup>			
2	-25.1 (-63)***	-25.0 (-43) <sup>ns</sup>			
3	-10.8 (-47) <sup>ns</sup>	$-6.4 (-19)^{ns}$			
4	-15.0 (-71)**	-0.3 (-1) <sup>ns</sup>			
5	-20.6 (-65)*	-5.0 (-13) <sup>ns</sup>			
6	-22.2 (-89)***	-13.0 (-33) <sup>ns</sup>			
7	5.3 (+61) <sup>ns</sup>	$-15.0(-38)^{ns}$			
8	-15.5 (-95)***	-27.6 (-87)*			
9	$-9.9(-46)^{ns}$	$-0.3 (-1)^{ns}$			
10	$-3.3 (-60)^{ns}$	$3.0 (+32)^{ns}$			
11	-13.8 (-52)**	$-2.3(-7)^{ns}$			
12	-8.4 (-95)**	$-24.2(-85)^{ns}$			
13	-9.5 (-66) <sup>ns</sup>	7.5 (+55) <sup>ns</sup>			
14	-8.5 (-60) <sup>ns</sup>	-14.4 (-47) <sup>ns</sup>			
No. negative contrasts	13	11			
No. positive contrasts	1	3			
Sign-test	Z-statistics=3.10; P=0.002	Z-statistics=1.87; P=0.061			

Negative values signify lower densities at impacted sites and positive values higher densities in disturbed areas. Italicized entries denote significant differences between means

<sup>a</sup> Effect size =  $\bar{x}$  – Density<sub>impact</sub> –  $\bar{x}$  – Density<sub>reference</sub> \*\*\*P<0.001, \*\*P<0.01, \*P<0.05, <sup>ns</sup>P>0.05; probability values from HSD post hoc tests following significant time× zone×impact effects in main GLM model (cf. Table 4)

and Hubbard 2006). Since dunes are critical refuges for ghost crabs during storms (Christoffers 1986), crabs on armoured sections of beaches are at greater risk during high seas (Vinagre et al. 2007). Beach armouring also alters physical properties and dimensions of beaches, particularly compressions of backshore areas, and accelerates beach loss (Fletcher et al. 1997). Armoured beaches also support fewer consumers, partly as a consequence of reduced deposition rates of wrack that is a critical energy source for many beach invertebrates (Dugan and Hubbard 2006).

In the present study, the backshore of the armoured beach section was slightly higher in elevation (Fig. 3). This small rise in the beach profile could be due to changes in sediment accretion and erosion dynamics caused by the seawall. Raising of the sediment wedge could potentially make it more difficult for ghost crabs to reach the water table and could increase the energetic cost of burrowing. Further manipulative experiments are required to assess whether changes in beach elevation can significantly alter crab densities and burrowing, but this is likely to be a small effect compared to the loss of dune habitat caused by seawalls.

### Across-shore variability

Although ghost crabs can occupy a fairly broad area across the intertidal and supratidal gradient, the distribution of many species appears to be centred on the backshore, extending from the driftline to the dunes (Table 6). Ghost crab distribution may also shift in relation to tides, but evidence for such tidal migrations is often less comprehensive and conclusive (Table 6).

In the present study, more crab burrows were generally found on the backshore than in the lower intertidal (Table 3). However, this across-shore pattern of distribution was not the same between areas that differed in the intensity of human disturbance: in heavily impacted areas, a smaller proportion of the population occurred on the backshore (Table 3). This indicates that human disturbance both lowers the density of ghost crab burrows and shifts their distribution across the beachface. Because of this, reductions in burrow density are more severe on the backshore where the sediment is less compact, human trampling is more concentrated, and shore-armouring has destroyed the dunes.

### Implications for monitoring

Sandy beaches worldwide face escalating pressures from development and recreational use, a trend that is predicted to increase in the twenty-first century (Schlacher et al. 2007a). Although the ecological effects caused by an increasing frequency and amplitude of human disturbance on sandy shores are becoming better known (Brown and McLachlan 2002; Schlacher et al. 2007a), systematic monitoring of environmental and ecological resource states of beaches is uncommon (Schlacher et al. 2006). Ghost crab densities have been employed as an ecological indicator of human impacts in urban settings (Barros 2001; Neves and Bemvenuti 2006), as well as to assess the ecological consequences of specific pressures such as off-road vehicle use on beaches (Moss

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Species	Locality	Distribution across the beach	Evidence of active migration	Reference	
O. ceratophthalma	Moçambique	Between high water mark and extreme H.W.S.T.	Yes	Barrass (1963)	
O. ceratophthalma; O. cordimana	Seychelles	Generally above spring high water mark	Yes	Braithwaite and Talbot (1972)	
O. ceratophthalma	India	Upper foreshore slope to base of dunes	No	Chakrabarti (1981)	
O. ceratophthalma; O. ryderi; O. madagascariensis	South Africa	Between high tide swash line and primary dunes	Yes	McLachlan (1980)	
O. ceratophthalma; O. macrocera; O. platytarsis	India	Backshore region when well developed	Yes	Chakrabarti (1993)	
O. cordimana	Australia	More burrows at the base of dunes, but extending 10-50 m into the dunes	?	Barros (2001)	
O. cordimana	Australia	Mostly around drift line	No	Moss and McPhee (2006)	
O. cursor	Cyprus	A band 3 m from the water's edge extending 13 m up the beach; seasonal variation	Yes	Strachan et al. (1999)	
O. gaudichaudii	Chile	Most located above drift line	Yes	Quijon et al. (2001)	
O. quadrata	USA	Upper foreshore and lower backshore	No	Hill and Hunter (1973)	
O. quadrata	USA	Backshore zone and low foredune ridge	No	Allen and Allen Curran (1974)	
O. quadrata	USA	Below the drift line, close to cast-up material at high tide and inland in the day	Yes	Wolcott (1978)	
O. quadrata	USA	Mostly backshore extending over 200 m inland	Yes	Fisher and Tevesz (1979)	
O. quadrata	Brazil	Above medium intertidal zone, peak between 1.5 and 2 m height above water line, fewer in subterrestrial fringe 2 m above water line	Yes	Turra et al. (2005)	
0. quadrata	Brazil	From the highest mark of the shoreline to the foredunes	Yes	Neves and Bemvenuti (2006)	

and McPhee 2006; Schlacher et al. 2007b). A common denominator of these monitoring studies is that crab densities are generally lower in areas subjected to human disturbance, and our data concur with this broad generalisation.

Counting ghost crab burrows can be a rapid, practical and simple tool for assessing the degree of ecological impact caused by humans in beach ecosystems (Barros 2001). Yet, the method may not be entirely without shortcomings, and it may present challenges in terms of contextualisation. We demonstrate that spatial contrasts of burrow counts are broadly useful to indicate the existence of a humaninduced disturbance effect on urban beaches, but we

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also highlight a number of critical, hitherto unresolved, issues in the application of this monitoring technique. These issues encompass four broad dimensions: (1) protocols need to be standardised; (2) specific causes of observed impacts are not always separated when multiple pressure act simultaneously, (3) the causal links between observed patterns and putative pressures are commonly unresolved; and (4) autecological and biological responses of organisms to both natural and human factors are poorly understood.

A key requirement of all monitoring is to standardise data collections across geographic regions and programmes. Here we show that several environmen-

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tal factors can significantly influence burrow numbers, including temperature, wind speed, and sand moisture (Table 2). Therefore, future monitoring using ghost crab burrow counts should either limit field surveys to defined ranges of weather conditions, or explicitly incorporate environmental conditions in both the reporting and analysis. For example, strong winds that obscure burrow openings produce a negative bias in counts or render the method impractical. Also, the time of day can alter the activity patterns of Ocypode, with many crabs remaining inactive during the hottest time of the day (Valero-Pacheco et al. 2007). We found that many crabs had plugged their burrows by noon, making counts less reliable than in the morning. As surface layers of the sand became dryer and less cohesive due to solar radiation, many burrow openings had collapsed around noon, particularly on the upper shore. Thus, future surveys should be limited to within a few hours after sunrise.

On many urban beaches several types of human pressures can act simultaneously. For example, human trampling is often most intense in sections where the habitat has been substantially modified by shore armouring. In many real-word monitoring applications such spatial overlap of pressures presents challenges with regards to the ability to distinguish between the ecological effects caused by individual stressors. Ideally, the best design solution would be to replicate the monitoring effort across multiple, independent sites that differ in the number, type and intensity of the pressures which are of interest. If possible, such monitoring designs should include locations with single stressors to partition the ecological effects of individual human pressures and also encompass locations with multiple stressor to assess whether additive ecological impacts operate.

Reductions in burrow counts denote a negative effect on population densities, but the actual mechanisms that cause these declines remain unknown, except for the impact of off-road vehicles that can directly crush crabs (Wolcott and Wolcott 1984; Schlacher et al. 2007b). Putative causes of population declines in ghost crabs span a wide ambit such as: (1) direct crushing of crabs through trampling, (2) habitat loss and/or modifications; (3) changes to metabolic costs, reproduction, and behaviour, (4) trophic shifts and enhanced predation pressures, and (5) light pollution. Measured effects will in turn depend on species-specific response to external drivers, emphasizing the need for fundamental autecological information such as reproductive cycles and recruitment, physiological climate envelopes, and trophic dynamics of ghost crabs on sandy beaches.

Mitigation measures and management interventions that seek to reduce negative ecological effects will invariably have to target the process causing the observed impacts. In the case of ghost crabs on urban beaches, it appears logical to propose human trampling as a prime mechanism of impact (but see Jaramillo et al. 1996). Robust scientific evidence to support the need for management interventions requires, however, that an unequivocal link between the level and nature of human disturbance and the biological response is demonstrated; this can only be achieved through controlled, and carefully designed manipulative experiments (Bulleri et al. 2007). Thus, a major lesson from this study is that the mechanistic links between putative human pressures and biological responses need to be determined (see also Schlacher et al. 2007b).

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# **APPENDIX B**



# Human disturbance as a cause of bias in ecological indicators for sandy beaches: Experimental evidence for the effects of human trampling on ghost crabs (Ocypode spp.)

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#### ABSTRACT

Human pressures on coastlines are increasing globally, particularly on urban beaches where maintenance of sand budgets and erosion control are the main focus of current shoreline management. By contrast, biological attributes are rarely considered and few, if any, ecological indicators are routinely monitored on beaches. Abundance of ghost crabs (genus Ocypode) generally responds predictably to human stressors, and is thus a potentially suitable ecological indicator for beaches. The crabs construct burrows with a single, prominent opening at the surface, and population sizes are commonly estimated by counting the number of these burrow openings. While such 'burrow counts' are attractive as a low-cost and simple monitoring technique, they may violate a key performance criterion of indicators: not to be overly sensitive to expected sources of interference. On urban beaches such interference is human trampling and, consequently, we evaluated its influence on the performance of burrow counts. The effects of short-term, intense human trampling on numbers and sizes of crab burrows were measured in a series of impact experiments, in which pedestrian trampling was repeatedly applied over 5 h on 4 consecutive days. Burrow counts were highly sensitive to interference from short-term trampling disturbance, which can substantially bias population estimates inferred from such counts. Importantly, burrow densities recovered overnight and apparent shifts in entrance size structures recorded immediately after the trampling impacts were also no longer evident on the following day. Thus, short-term trampling shifted parameter estimates without significant biological effects underpinning such changes-a clear case of bias. Although crab density and size structure are susceptible to artefacts caused be human trampling, they remain valuable indicators for sandy beaches, if interference by pedestrians is small in field measurements or can be accommodated in numerical analyses.

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#### 1. Introduction

Rapid and widespread development, mainly fuelled by the exponential growth of coastal populations, has escalated

human pressures on sandy beach ecosystems globally (Schlacher et al., 2006, 2007b). These developments increasingly threaten the ecological integrity of beach systems, encompassing a wide range of impacts that include the

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destruction of dune and beach habitats by infrastructure development (Nordstrom, 2000), shoreline armouring (Dugan et al., 2008), beach nourishment (Jones et al., 2008), wildlife disturbance (Yasué and Dearden, 2006), damage to dune vegetation (Groom et al., 2007), pollution (Junoy et al., 2005), beach cleaning (Gheskiere et al., 2006), and impacts caused by recreation and tourism (Davenport and Davenport, 2006).

Ecological indicators are widely used to assess the nature, severity and spatial ambit of human impacts, and to evaluate the efficacy of management interventions (Niemi and McDonald, 2004). Ecological indicators are conventionally defined as measurable characteristics of the structure, composition, or function of ecosystems (Niemi and McDonald, 2004). Numerous criteria for ecological indicators have been proposed, but the most commonly accepted include aspects of: (a) ease of measurement at low cost, (b) sensitivity to stresses and predictable response to specific pressures, (c) largely insensitive to expected sources of interference, (d) documented reaction to natural and anthropogenic disturbances in the system, (e) delivery of information at spatial and temporal scales that match management responses, and (f) ability to predict changes that can, theoretically, be prevented through management (Dale and Beyeler, 2001; Niemeijer and de Groot, 2008)

Whilst indicators can be selected from several levels of biological and ecological organisation, indicator species are the most common (Noss, 1990). Concepts, applications and definitions of indicator species are diverse, including: 'keystone' species (strong interactions with other species), 'umbrella' species (large habitat range), 'dispersal-limited' species (demonstrated site fidelity), 'resource-limited' and 'process-limited' species (sensitive to changes in a specific ecological resource or process), and 'flagship' species (attract public support; Noss, 1990; Lambeck, 1997).

Invertebrates are efficacious ecological indicators of human stressors in a wide range of environments (Chessman, 1995; Fulton et al., 2005; Resh, 2008; Van Dam and Van Dam, 2008). They generally respond to disturbances at finer spatial scales than larger vertebrates (Carignan and Villard, 2002), and their distributions and population sizes are often well correlated with environmental conditions that are, potentially, subjected to human alterations (Schoener, 1986).

Ghost crabs of the genus Ocypode are common semiterrestrial invertebrates on warm-temperate to tropical sandy beaches. The crabs excavate extensive burrows on the upper shore and in the dunes, becoming surface-active mainly at night (Barras, 1963). Populations of ghost crabs respond predictably to direct physical impacts (i.e. trampling, off-road vehicles) and to habitat changes in the form of reduced abundances (Barros, 2001; Moss and McPhee, 2006; Schlacher et al., 2007a; Lucrezi et al., 2008). Also, because ghost crabs are the top invertebrate predator on sandy beaches, and are inturn prey for a number of higher-order consumers (Christoffers, 1986), changes in ghost crab numbers are a good proxy for impacts on whole beach food webs.

Because crab burrows have highly distinct openings on the beach surface, the 'standard method' for estimating population sizes of ghost crabs on sandy shores is to count the number of burrows in replicate plots (Barros, 2001; Moss and McPhee, 2006; Schlacher et al., 2007a). In fact, the ease and low cost of 'burrow counts' is one of the key argument for the use of ghost crabs as ecological indicators on sandy beaches (Barros, 2001). The method may, however, produce biased results in the form of artificially low population estimates if burrow openings are merely obscured without affecting the survival of crabs inside their burrows. This situation arises most likely on urban beaches that are subjected to high volumes of pedestrian traffic: here, intense trampling by humans is likely to collapse the burrow entrances of crabs; it may also crush crabs inside their burrows. Simple 'burrow entrance counts' of ghost crabs are therefore unlikely to distinguish between actual biological impacts (i.e. individuals killed by trampling) and apparent impacts (i.e. negative bias of population sizes caused by collapsed entrances) on urban beaches. Yet, many environmental assessments using ghost crab burrow counts as ecological indicators target such urban beaches (Schlacher et al., 2008).

We tested whether short-term human trampling makes ghost crab burrow counts simply a less robust ecological indicator by introducing measurement bias, or whether it significantly lowers crab abundances by lethally crushing individuals.

### 2. Material and methods

### 2.1. Study area

The study was conducted on Mooloolaba Beach (26.68°S, 153.12°E; Queensland, Australia). The beach forms the southern boundary of a 1.8 km long embayment and is moderately exposed to the predominant SE-ocean swells. The beach is one of the most popular recreational areas in the region. It has a long history of human engineering interventions which have resulted in significant morphological changes over the past 60 years (Longhurst, 1997). For example, dunes in the western part of the beach have been replaced with infrastructure such as seawalls, boardwalks and buildings. Some natural dune areas remain in the central and eastern part of the beach, but overall dune width is reduced. Recreational use is concentrated in the western sections of the beach that are close to infrastructure and patrols by surf life savers. Two species of ghost crabs, Ocypode cordimana and Ocypode ceratophthalma are common on the upper beach and in the dunes, but population sizes are reduced in areas heavily trampled by humans and where shore armouring has been implemented (Lucrezi et al., 2008).

### 2.2. Experimental design

The principal aim of the study was to determine the potential of pedestrian trampling to bias estimates of counts and sizes of ghost crab burrow openings. We tested the response of burrow density and size to foot traffic in experiments where human trampling was repeatedly applied to ghost crab populations.

Experiments were conducted in four experimental plots  $(5 \text{ m} \times 3 \text{ m})$  established in the upper intertidal zone, near the drift line and 8 m seawards from the base of the foredunes.

Plots were fenced to exclude interference from the general public. Human trampling was applied to two plots and the remaining plots served as controls (i.e. human exclusion, no trampling). Human recreation is concentrated on the eastern and western end of the beach with a central area that receives fewer visitors (T.A. Schlacher pers. obs.). We conducted the experiments in this central area to minimize interference with public amenity values of the beach.

To prevent physically disturbing the control plots – and the impact plots before the experimental application of trampling impacts began – we used a scaffold. It consisted of a ladder lifted 30 cm above the ground by trestles placed outside the boundaries of the experimental plots. Field operators moved systematically across the ladder and measured the burrow openings below through the spaces between the rungs.

The experiments were run over four consecutive days in late April 2007. On each occasion, we counted all burrows and measured their sizes (diameter to the nearest mm using a ruler) in each plot at 07:00 (ca. 2 h after sunrise) before any disturbance was applied. The trampling treatment consisted of two people (weight: 45 and 55 kg) crossing the impact plots each 50 times in a zig-zag pattern; this resulted in close to 100% coverage of footprints. The trampling treatment was applied in 5 distinct bouts at 50 min intervals over a 5 h period. Before each new trampling event, all burrows which remained intact were counted and their diameter measured.

Before each treatment event (i.e. 5 bouts separated by 50 min.) a range of environmental variables was measured at three randomly selected spots within each plot, including: (a) sand temperature (5 cm deep; electronic thermometer-Fluke 52 k/J); (b) sand moisture (8 cm deep; Trident microwave meter); (c) sand shear force resistance (field inspection vane tester Geonor H-60, with a vane size of 5 cm length  $\times$  2.5 cm width); (d) penetration force (Geotester pocket penetrometer

with tips of 20 mm diameter). Air temperature and wind speed were recorded (using a Skymate SM-18 Windmeter) at the start (07:00) and end (12:00) of each experimental day. Over the course of the experiments, air temperature ranged between 22.5 and 25.1 °C in the morning (07:00) and 27.0–35.9 °C at noon, and winds were light at 0–5 knots (07:00) and 2.5–16.9 knots (12:00).

### 2.3. Data analysis

To examine whether the density and size of ghost crab burrow openings changed with increasing pedestrian trampling, we tested the null hypothesis that there was no difference between reference and impact plots. We did so by using a repeated measures analysis of variance (ANOVA) with a covariate, two fixed and one repeated factors. The time the measurements was taken during each experiment (08:00-12:00) is a repeated measure, whilst experiment (1-4) and treatment (reference vs. impact) are included as fixed effect terms. To partition out the possible effect of variations in burrow densities between plots before treatments were applied at 07:00 on each day, burrow densities and sizes measured at 07:00 in each experiment before the treatments were applied is included as a covariate. Because of possible differences in variances between impact and reference treatments that could affect the assumption of sphericity in the repeated measures ANOVA, we used Greenhouse-Geisser corrections for all hypothesis tests (Keselman et al., 2001). The same analysis was applied to environmental variables (i.e. sand moisture, temperature).

To assess whether repeated trampling (i.e. trampling impacts in 4 experiments) resulted in significant changes in population sizes in the impacted plots, we performed a simpler repeated measures ANOVA that compared the number and diameter of burrows between treatments at the start of each experiment.

Table 1 – Summary of repeated measures ANOVA partitioning variation in sand moisture, sand temperature, and the density and size of ghost crab burrow openings between treatments (reference vs. impact) and between experiments (1-4), as well as over time (07:00–12:00). Values measured at 7:00 before the experimental application of trampling in each experiment are included as a covariate in the analysis.

Source of variation	Sand moisture (%)		Sand temperature (°C)		Burrow density (ind. m <sup>-2</sup> )			Burrow diameter (mm)				
	d.f.	MS	F	d.f.	MS	F	d.f.	MS	F	d.f.	MS	F
Treatment	1	0.006	4.76 <sup>ns</sup>	1	0.10	0.37 <sup>ns</sup>	1	75.05	83.72***	1	248.57	113.19***
Values at 07:00	1	0.014	11.89**	1	0.72	0.26 <sup>ns</sup>	1	10.64	11.87*	1	55.53	25.28**
Experiment	3	0.014	11.49**	3	2.23	8.01*	3	0.10	0.11 <sup>ns</sup>	3	9.03	4.11 <sup>ns</sup>
Experiment × treatment	3	0.002	1.76 <sup>ns</sup>	3	0.09	0.32 <sup>ns</sup>	3	1.10	1.23 <sup>ns</sup>	3	14.46	6.58*
Error	7	0.001		7	0.28		7	0.90		7	2.19	
Time	1.59	0.001	1.27 <sup>ns</sup>	2.62	0.10	0.62 <sup>ns</sup>	2.28	47.81	2.58 <sup>ns</sup>	1.60	2.70	0.89 <sup>ns</sup>
Time × values at 07:00	1.59	0.002	2.24 <sup>ns</sup>	2.62	0.06	0.37 <sup>ns</sup>	2.28	46.05	2.49 <sup>ns</sup>	1.60	2.86	0.94 <sup>ns</sup>
Time × experiment	4.79	0.005	5.39*	7.85	0.14	0.84 <sup>ns</sup>	6.85	8.43	0.46 <sup>ms</sup>	4.80	9.53	3.15 <sup>ns</sup>
Time × treatment	1.59	0.002	1.86 <sup>ns</sup>	2.62	0.38	2.32 <sup>ns</sup>	2.28	0.42	0.02 <sup>ns</sup>	1.60	5.81	1.92 <sup>ns</sup>
Time × experiment × treatment	4.79	<0.001	0.54 <sup>ns</sup>	7.85	0.10	0.62 <sup>ns</sup>	6.85	14.45	0.78 <sup>ns</sup>	4.80	17.90	5.92**
Error	11.17	0.001		18.33	0.16		15.97	18.50		9.60	3.02	
$^{ns} p > 0.05; p < 0.05; p < 0.01; m p < 0.01; m p < 0.001.$												

### 3. Results

### 3.1. Habitat characteristics

Trampling did not result in significant changes to sand temperature and moisture. Sand did not became markedly hotter over the course of each experiment (Table 1; ANOVAeffect time:  $F_{(2.62,18.33)} = 0.62$ , p = 0.59), and sand surface temperature did not differ between control and trampling plots (Table 1; ANOVA—effect treatment:  $F_{(1,7)} = 0.37$ , p = 0.56). Sand temperatures (range: 22.9-23.6 °C) were slightly but significantly lower during the experiments 3 and 4, but this small decrease of 0.5 °C was the same for both experimental treatments (Table 1; ANOVA—experiment × treatment:  $F_{(3,7)} = 0.32$ , p = 0.81). Trampling resulted in a reduction of sand moisture (range: 0-3.6%) by between 0.46 and 0.71% in three of the four experiments, but overall, no significant effect of experimental treatment was detected (Table 1; ANOVAeffect treatment:  $F_{(1,7)} = 4.76$ , p = 0.06). The lower temperatures in experiments 3 and 4 were reflected in significantly higher moisture values at these times (Table 1; ANOVA-effect experiment:  $F_{(3,7)} = 11.49$ , p < 0.01).

### 3.2. Variation in burrow density and size

Pedestrian traffic substantially reduced burrow densities and sizes immediately after the trampling impacts had occurred, but it did not cause significant changes at a time scale of days. Mean burrow densities were reduced by 88% following human trampling impacts (Fig. 1). In all experiments, densities in impact plots ( $0.36 \pm 0.03$  burrows m<sup>-2</sup>) were significantly lower than in un-trampled reference plots (2.85  $\pm$  0.13 burrows  $m^{-2};$ Fig. 1; Table 1; ANOVA—effect treatment:  $F_{(1,7)} = 83.72$ , p < 0.001). The first set of impacts (i.e. 100 passes) caused the greatest change to the density of ghost crab burrows: further trampling had comparatively small additional effects (Fig. 2). Time per se did not influence ghost crab densities irrespective of whether trampling had occurred or not (Table 1; ANOVA-time × treattreatment,  $F_{(2.28,15.97)} = 0.02$ , p = 0.99). There was no significant interaction between treatment and experiment (Table 1; ANOVA—experiment × treatment,  $F_{(3,7)} = 1.23$ , p = 0.37), suggesting that experimentally produced effects of trampling on burrow counts were consistent across all experiments

Trampling impacts were more pronounced for larger burrows. This asymmetric impact significantly changed the



Fig. 1 – Variation in mean burrow counts (a) and burrow size (b) of ghost crabs in relation to experimental disturbance by human trampling. Experimental treatments consisted of 100 pedestrian passes applied five times at 50 min intervals in four separate experimental runs (days) compared with abutting control sites from which beach visitors had been excluded.



Fig. 2 – Relationship between changes in ghost crab burrow numbers (a) and opening diameter (b) in relation to the intensity of human disturbance. Effect size ( $\Delta$ ) is measured as:  $|(\vec{x}_{Ref.} - \vec{x}_{Imp.})/\vec{x}_{Ref.}|$ , where  $\vec{x}$  are the mean values of burrow density or entrance diameter in the reference (Ref.) and impact (Imp.) treatments.

size distribution of burrows not destroyed by foot traffic (Fig. 3). The mean size of burrow openings varied significantly with the time of the day, experiments and treatments (Fig. 2 and Table 1; ANOVA—time × experiment × treatment,  $F_{(4.80,9.60)} = 5.92$ , p < 0.01): the average diameter of intact burrow entrances was generally smaller after trampling impacts. High-intensity foot traffic destroyed virtually all burrows >25 mm in diameter, whereas control plots contained burrows ranging up to 75 mm (Fig. 3). Conversely, the minimum size of burrows remained at 4–5 mm in both control and impact plots (Fig. 3). As was the case for burrow densities, the first set of trampling impacts caused the greatest decrease in burrow size, with additional disturbances having much smaller additional effects (Fig. 2).

Because experiments were run on consecutive days and the sets of trampling impacts were separated by at least 19 h between experiments, changes to the density and size of crab burrows which were measured at the start of each experiment should be indicative of short-term (i.e. days) impacts on ghost crab populations. However, we neither found a significant difference in burrow numbers nor burrow sizes between the impact and control plots before trampling commenced in each experimental run (Table 2). At the start of each experiment, mean burrow densities and sizes were similar between plots irrespective of whether trampling had been applied on the previous day or not (Table 2). This lack of significant day-today changes, which could not be linked to the intensity of human disturbance, suggests that crabs of all sizes repaired their burrows overnight, resulting in densities and size structures that were indistinguishable from pre-impact conditions in the short term (Fig. 2).

### 4. Discussion

### 4.1. Environmental influences on burrow density

Environmental conditions can significantly influence the density of ghost crab burrows on sandy beaches (Lucrezi et al., 2008). We found fewer burrow entrances on hotter days and, conversely, more during cooler conditions. Ghost crabs are predominately nocturnal, generally avoiding surface activity during the day, and they prevent dehydration by plugging their burrows around noon (Barras, 1963). Crabs may also not re-open a burrow after it had been trampled during the day (Neves and Bernvenuti, 2006).

Burrow entrances can collapse in very dry sand, or be infilled by wind-blown sand. By contrast, in moist sand, burrow entrances are more stable and fewer burrows become obscured by sand. Thus, both biological processes (i.e. burrow plugging) and physical mechanisms (e.g. entrance collapse) can lead to apparent decreases in density estimates of ghost crabs (Lucrezi et al., 2008). In the present study, differences between treatments were, however, consistent irrespective of variations in wind speed or the temperature and moisture of the sand.

### 4.2. Disturbance effects on burrow numbers and size

Almost all benthos research on exposed sandy beaches employs mensurative designs (i.e. 'compare and contrast'), while experimental approaches that are common on rocky shores and in other sedimentary habitats are rare on beaches (Schlacher et al., 2008). Our short-term trampling is one of the few experiments on the effects of human disturbance on sandy beach macrobenthos (but see Schoeman et al., 2000). Disturbance is commonly defined as a distinct event in time that disrupts the structure of an ecosystem, community, or population, and that changes resources, the availability of substratum, or the physical environment (Pickett and White, 1985). Disturbance events differ with respect to their frequency, duration, and intensity (Resh et al., 1988), and our experiments were clearly a high-intensity, pulse event over a relatively short duration (4 days).

Intense, human trampling resulted in substantially lower burrow counts, and – by implication – apparent reductions in population sizes of ghost crabs on the beach. However, the effects of the short-term trampling disturbances were mostly non-lethal to ghost crabs and did not last long. A single hit by a pedestrian suffices to cover or collapse a burrow opening, and because the crabs do not to re-open infilled burrow entrances for at least one hour (S. Lucrezi, personal observation), burrow counts fell markedly after people had walked over the plots


Fig. 3 – Comparison of the size distribution of burrow openings between experimentally trampled (filled bars) and undisturbed control plots (open bars) before trampling treatments were applied (top row) and after each plot was repeatedly impacted by pedestrian foot traffic (bottom row).

(Fig. 1). Burrow numbers recovered, however, overnight, showing that human trampling is not necessarily lethal to most crabs. Therefore, short-term pedestrian trampling can strongly bias estimates of ghost crab densities on sandy beaches.

In the long-term, human trampling does, however, have demonstrable, negative impacts on ghost crab population sizes (Lucrezi et al., 2008), most likely as a consequence of several, additive sublethal effects related to frequent habitat disturbance. Also, other short-term trampling experiments have demonstrated direct mortalities of macrobenthic species on sandy beaches (Moffet et al., 1998).

In all four experiments conducted in this study, the application of the first trampling impact (100 passes) had the largest effect on burrow numbers; subsequent trampling impacts caused much smaller additional decreases in burrow densities (Fig. 2). Similarly, experiments that simulated typical recreational activities such as walking and volleyball games on a South African beach, also found the strongest impacts associated with the initial disturbance (Moffet et al., 1998).

The most significant result with respect to burrow size was the marked decrease in the maximum burrow opening diameter measured after trampling. Intuitively, because of their larger surface area, larger burrows are more likely to be hit by footsteps. However, crabs of all sizes carry out their burrowing activities overnight (Strachan et al., 1999), and, in the present study, every morning, burrows of both adults and juveniles were found on the beach.

This result has significant implications for interpreting changes in burrow size distributions that apparently – but falsely–indicate higher mortalities of larger individuals. Using estimates of burrow size after pedestrians have trampled a beach can lead to the false conclusion that trampling changes population age structures, preferentially killing larger, adult crabs. Yet, larger crabs simply stay within their collapsed burrows and wait to re-emerge until trampling ceases at dusk. Adult crabs are also able to withstand heat and dehydration better than juveniles, and generally can remain fossorial during the day (Chan et al., 2006). Conversely, juveniles often need to feed on the beach surface during the day to avoid

Source of variation		Burrow density	1	Burrow diameter			
	d.f.	MS	F	d.f.	MS	F	
Treatment	1	0.81	0.65 <sup>ns</sup>	1	1.07	0.17 <sup>m</sup>	
Error	2	2.50		2	6.37		
Experiment	1.07	2.47	5.22 <sup>ns</sup>	1.20	18.69	1.54 <sup>n</sup>	
Experiment × treatment	1.07	0.13	0.27 <sup>ns</sup>	1.20	5.40	0.45 <sup>ns</sup>	
Error	2.13	0.47		2.40	12.10		

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competition with, and predation by, adult crabs at night (Fisher and Tevesz, 1979). Thus, juveniles are more likely to repair and unplug collapsed burrows following trampling impacts during the day (S. Lucrezi, personal observation). This behavioural asymmetry between adults and juveniles can further confound the interpretation of burrow size distributions.

# 4.3. Consequences of recreational disturbance for ghost crabs

It has been suggested that ghost crabs can acclimatize to increasing levels of recreational beach use (Steiner and Leatherman, 1981). Even positive effects of recreation have been reported when food scraps left by beach visitors provide a trophic subsidy to the scavenging crabs (Steiner and Leatherman, 1981). Yet, on many beaches pedestrian trampling is a heavy and continuous disturbance agent that causes significant negative impacts on ghost crab populations in the long term (Lucrezi et al., 2008).

Our experiments simulated heavy, short-term, trampling disturbance that did not kill significant numbers of ghost crabs over four days. Trampling is, however, likely to have a range of sublethal effects on these and other beach organisms. For example, human beach use substantially alters the physical properties of the sand matrix (Schlacher and Thompson, 2008), lowering burrow stability. Recreational activities may also directly disturb crab feeding, crush more sensitive post-larval forms, and limit the duration of surface activity.

It has been suggested that ghost crabs shift into the dunes as a result of continuous disturbance on the beach (Barros, 2001), which increases their metabolic costs (especially for juveniles) in the search for food and water for respiration. Shoreline armouring impedes movements of crabs into the dunes, further compounding the effects of recreational disturbance in the intertidal zone (Lucrezi et al., 2008).

Because burrows can be as deep as 1 m (Maccarone and Mathews, 2007), the experimental trampling disturbance may not have completely destroyed the burrows. However, shallower burrows under construction are more susceptible. In all cases, ghost crabs will incur energetic costs to repair burrows, whether partly or completely collapsed. Time and energy expended in repairing may impact negatively on feeding and reproductive output. Repair work does not only impose extra metabolic demands on crabs, it also exposes them to avian and mammal predators.

#### 4.4. Implications of trampling interference for indicator performance and monitoring designs

Although evidence for widespread ecological effects linked to beach recreation is accumulating (Davenport and Davenport, 2006; Moss and McPhee, 2006), ecological assessments of sandy beaches are rare, and management is almost exclusively concerned with maintaining sand budgets (Schlacher et al., 2008). Part of the reason for the current lack of ecological assessments, monitoring, and management of beaches is the dearth of robust and accepted ecological indicators for these systems. Ghost crabs are an important component of sandy beach ecosystems, occupying a pivotal trophic role as apex invertebrate predators while being also prey for vertebrate consumers (Wolcott, 1978; Christoffers, 1986). Frequent anthropogenic disturbance, such as human trampling and vehicles, and habitat modifications can lead to substantial declines in ghost crab population sizes on beaches (Moss and McPhee, 2006; Schlacher et al., 2007a; Lucrezi et al., 2008). Thus, ghost crab abundance appears to be a useful ecological indicator to measures human impacts on sandy beaches (Barros, 2001; Neves and Bemvenuti, 2006).

Burrow counts of ghost crabs meet two key criteria commonly used in indicator selection: (1) ease of measurement at low cost (Lucrezi et al., 2008); and (2) sensitive to stress with predictable response to stress (Schlacher et al., 2007a). However, a good indicator species must also be largely insensitive to expected sources of interference (Niemeijer and de Groot, 2008). Since many applications that employ ghost crabs as indicator species are likely to take place on urban beaches, and because urban beaches experience the highest levels of human trampling, the expected interferences in this instance is human trampling. Consequently, we evaluated its influence on the performance of burrow counts as ecological indicators. Our results clearly show that counts of ghost crab burrows are susceptible to short-term trampling, which can substantially bias population estimates inferred from such burrow counts.

Bias in burrow counts and sizes has consequences for using ghost crabs as ecological indicators: both counts and opening diameters are only reliable proxies for population densities and size structures if field measurements are taken when pedestrian disturbance is small. Thus, field surveys should be limited to periods when beach visitors are few - as early in the morning as possible - on weekdays rather than weekends and public holidays, and during cooler and overcast conditions rather than during sunny weather. Also, when spatial contrasts are required, measurements at different sites must be matched with respect to tides, time of the day, weather conditions, and temporal patterns of beach visitor numbers. Provided such basic design factors are explicitly incorporated into standard operating procedures for field surveys (Lucrezi et al., 2008), interference by human trampling does not constitute an insurmountable hurdle in the application of ghost crab burrows as ecological indicators of human pressures on sandy shores.

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## **APPENDIX C**

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ENVIRONMENTAL ASSESSMENT

# Impacts of Off-Road Vehicles (ORVs) on Burrow Architecture of Ghost Crabs (Genus *Ocypode*) on Sandy Beaches

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Abstract Recreational beach use with off-road vehicles is popular, but potentially harmful from an environmental perspective. Beaches are important habitats to invertebrates such as ghost crabs of the genus Ocyopde, which excavate extensive and elaborate burrows. Ghost crabs are sensitive to human pressures and changes in burrow architecture may thus be a consequence of disturbance by vehicles-the predictive hypothesis of this article. This was tested during the austral spring and summer by comparing 305 burrow casts between beaches open and closed to vehicles in Eastern Australia. Traffic influenced burrow architecture: there were smaller crabs on vehicle-impacted beaches, and after the peak traffic period (Christmas and New Year holidays), these crabs had tunnelled deeper into the sediment on shores rutted by cars. Crabs constructed all types of previously described burrows, but, significantly, smaller crabs from vehicle-impacted beaches simplified their shapes following heavy traffic disturbance from four (I, J, Y, M) to only two types (I, Y). These data support a model of active behavioural responses to disturbance from vehicles, extending the known effects of beach traffic to impacts on behavioural traits of the beach fauna.

Keywords Sandy shores · Invertebrates · Human recreation · Environmental impacts · Indirect effects

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## Introduction

Sandy beaches are a valuable natural resource in the coastal zone (Houston 2008; Defeo and others 2009). Beaches deliver numerous ecosystems services—recreation being often the most prominent one (Schlacher and other 2008b), and off-road driving of vehicles has become part of the leisure activities on many ocean shores (Silberman and Andereck 2006; Schlacher and others 2007a).

While recreation using off-road vehicles has social and economic dimensions (McConnell 1977), this activity is not without environmental consequences (Wolcott and Wolcott 1984). Evidence for negative environmental impacts caused directly or indirectly by vehicle traffic on beaches and dunes is available for physical habitat changes (Thompson and Schlacher 2008), reductions in the abundance and diversity of beach invertebrates (Moss and McPhee 2006; Schlacher and Thompson 2007), damage to dune vegetation and fauna (Groom and others 2007; Van Dam and Van Dam 2008), and threats to birds and turtles (Hosier and others 1981; Buick and Paton 1989; Williams and others 2004).

The nature, intensity, spatial and temporal scope of ecological impacts of human activities on sandy beaches can be assessed with indicator species (Lucrezi and others 2009b). Ghost crabs of the genus *Ocypode* are semi-terrestrial crabs inhabiting beaches and dunes of tropical and sub-tropical regions world-wide. Their use as indicators of ecological impacts on beaches rests on them being both invertebrate apex predators and food for higher trophic levels, and having reasonably well understood responses to human pressures (Lucrezi and others 2009a). Crab abundance has been shown to be sensitive to human pressures in the form of shore armouring (Barros 2001; Lucrezi and others 2009a), urbanization (Souza and others 2008; Magalhaes and others 2009), very heavy pedestrian trampling (Neves and Bemvenuti

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2006; Yong and Lim 2009), and off-road vehicles (Steiner and Leatherman 1981; Blankensteyn 2006; Moss and McPhee 2006; Maccarone and Mathews 2007; Schlacher and others 2007b; Hobbs and others 2008).

Ghost crabs excavate burrows where they spend most of the day, becoming surface-active at night (Barrass 1963). Burrows are key structures in the life of ghost crabs, providing shelter against predators, extreme weather conditions, co-specifics, and incoming tides; burrows are also critical during egg development, moulting, and mating (Vannini 1980; Schober and Christy 1993; Chan and others 2006). Because burrowing expends considerable energy and ORVs destroy burrows, vehicles may impact on investment in reproduction and lengthen risky surface activity of crabs.

Given that burrows are a critical element in the ecology of ghost crabs, and the documented role of ghost crabs as indicators of ecological change, this study investigated whether crabs change their burrow architecture in response to physical disturbance. Physical disturbance was in the form of vehicle traffic which is known to cause substantial changes to the habitat (Anders and Leatherman 1987). Specifically, our predictive hypothesis was that crabs would respond to greater habitat instability caused by offroad vehicles by changing the shape and dimensions of burrows.

Fig. 1 Location of study region in south-east Queensland, Australia (a), and (b) beaches sampled for ghost crab burrows at two sites with vehicle impacts north of Noosa and two beaches without traffic impacts south of Noosa

## Materials and Methods

## Study Area

Ghost crab burrows were investigated on four beaches on the east coast of Australia (Fig. 1). Details of these beaches are given in Schlacher and others (2008a). Briefly, all are occan-exposed, wave-dominated beaches of the intermediate morphodynamic type. Two beaches, North Shore and Teewah Beach, are subject to vehicle traffic, while vehicles are banned from the two other beaches (Peregian Beach and Sunrise Beach). Except for vehicle traffic, there are no substantial differences in terms of beach morphology, sediment characteristics and wave regimes between beaches open and closed to vehicles (Schlacher and others 2008a).

#### Field Sampling

Burrows were measured in two belt transects per site. Transects were 3 m wide and extended from the base of the dune to the down-shore limit of burrow occurrence. The transects were spaced 10 m apart along the beach, and divided into sequential 3 m long quadrats. We measured every burrow in the belt transects and recorded the distance of individual burrows and their elevation with reference to the spring-tide low water mark (LWST) using a theodolite.



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Burrow casts were made by pouring a mix of Cornice Cement (Gyprock<sup>tm</sup>) and water into the burrow opening until the burrow was flooded flush with the sediment surface. Cornice Cement was chosen because it is a fast-setting and non-toxic type of plaster. The plaster mix was prepared by adding 1 kg of plaster to 2 1 of freshwater until a smooth and dense blend was obtained. After the plaster had set (which took approximately 30 min), the casts were dug out by carefully removing the sediment around them by hand or with a small trowel. After measuring their depth and the angle of inclination, casts were labeled and taken back to the laboratory. In the laboratory, each cast was photographed and the following measurements made: shape; total length (length of the main shaft plus length of any secondary arms in cm): diameter of the main shaft (cm); weight (g) as a proxy for volume. A total of 305 casts, weighting 132 kg and with a total length of 150 m were made during this study.

After the casts had been excavated, sediment moisture and temperature were measured at three depths: 2 cm below the surface, in the middle, and at bottom of the hole. At each depth, triplicate readings were taken with a Trident microwave moisture meter and an electronic temperature probe (Fluke 52 K/J). We also took triplicate sediment cores (30 mm diameter, 100 mm deep) next to each burrow opening, and determined sediment granulometry by drysieving (details in Schlacher and others 2008a).

All four beaches were sampled at approximately monthly intervals from September 2008 to January 2009. Sampling was restricted to 3 h either side of the time of predicted low water.

## Data Analysis

Total variance in burrow opening diameter, depth, length, inclination, and weight was partitioned with a GLM model that included the term 'human beach use' (vehicle-impacted vs. reference beaches) and 'month' (Underwood 1997); to account for possible influences on burrow metrics by the position of individual burrows across the dune-swash gradient, burrow elevation above LWST was included as a co-variate (Zar 1996). The distribution of all burrows amongst types was compared between vehicle-impacted and reference beaches using contingency analysis. Because

Table 1 Summary of analysis of co-variance (ANCOVA), contrasting sediment properties and beach slope between beaches open and closed to off-road vehicles over time (survey 1-5) at monthly intervals from Sep '08 to Jan '09

	df	Mean grain s	size	Beach slope	
		MS	F	MS	F
Co-variate (Elevation above LWST)	1	492	4.01***	4.06	17.83***
Times (5 surveys)	4	1,016	8.28***	9.85	43.30***
Human use (vehicles vs. ref.)	1	1,087	8.85**	5.81	25.51***
Times $\times$ human use	4	702	5.72***	19.32	84.88***
Error	285	123		0.23	
	df	Sediment Mo	oisture	Sand Temper	ature
		MS	F	MS	F
Co-variate (Elevation above LWST)	1	68.57	21.16	0.00	0.00 ns
Times (5 surveys)	4	65.47	20.20	407.60	55.89***
Human use (vehicles vs. ref.)	1	36.26	11.19	30.70	4.21*
Times × human use	4	10.15	3.13	219.55	30.10***
Error	285	3.24		7.29	
		df	Sed	iment sorting	
			MS		F
Co-variate (Elevation above LWST)		1	0.00	001	0.03 ns
Times (5 surveys)		4	0.02	201	9.62***
Human use (vehicles vs. ref.)		1	0.10	38	49.59***
Times × human use		4	0.00	35	1.66 ns
Error		285	0.00	21	

The elevation of burrows above low water spring tide (LWST) was the co-variate in the analysis

<sup>ns</sup> P > 0.05, \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001

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burrow architecture is described by multiple variables (e.g. angle, width, length etc), we tested whether burrows from beaches open to vehicles differ in the multivariate domain from those from reference beaches using Principal Component Analysis (PCA) and Analysis of Similarities—ANOSIM (Clarke 1999).

## Results

## Beach Attributes

Beaches open and closed to vehicles had very similar slopes, differing by a mere  $0.08^{\circ}$  (vehicle beaches:  $\bar{X} = 2.84 \pm 0.08^{\circ}$ ,

Table 2 Summary of contrasts between vehicle and reference beaches from post-hoc (Student New Keuls Tests) following analysis of co-variance (cf. Tables 1, 3)

A - Environmental /ariables	Sep. '08	Oct. '08	Nov. '08	Dec. '08	Jan. '09	All surveys
Beach Slope	<b>V</b> ***	<b>↓</b> ***	<b>û**</b> *	<b>↓</b> ***	<b>V</b> ***	¥
Mean Grain Size	<b>\</b> ***	<b>↓</b> *	(₩)"	(₩)	<b>↓</b> ***	¥
Moisture	(Ψ)	(₩) ^	<b>↓</b> *	(①) <sup>ns</sup>	<b>(₩)</b> <sup>ns</sup>	¥
Temperature	<b>û**</b> *	(①) <sup>ns</sup>	<b>↓</b> ***	<b>企**</b> *	(①)"	Û
Sorting	<b>①***</b>	仓*	(①) <sup>ns</sup>	(①) <sup>ns</sup>	<b>①***</b>	Û

B - Burrow Metrics	Sep. '08	Oct. '08	Nov. '08	Dec. '08	Jan. '09	All surveys
Opening Diameter	<b>\</b> ***	<b>(₩)</b> <sup>ns</sup>	(₩)"	(①) <sup>ns</sup>	<b>(₩)</b> <sup>ns</sup>	¥
Depth	<b>\</b> ***	<b>↓</b> *	(①) <sup>ns</sup>	(₩)"	<b>1</b> ***	↓
Length	<b>(₩)</b> <sup>ns</sup>	<b>(₩)</b> <sup>ns</sup>	<b>(₩)</b> <sup>ns</sup>	(①) <sup>ns</sup>	<b>1</b> ***	₩
Main Shaft Diameter	<b>\</b> ***	(₩) ^^	<b>(₩)</b> <sup>ns</sup>	(①) <sup>ns</sup>	<b>(₩)</b> <sup>ns</sup>	4
Weight	<b>\</b> ***	<b>(₩)</b> <sup>ns</sup>	(₩)**	<b>企</b> *	<b>1</b> ***	¥
Angle	<b>(₩)</b> <sup>ns</sup>	(①) <sup>ns</sup>	(①) <sup>ns</sup>	<b>(</b> ₩) <sup>ns</sup>	(①) <sup>ns</sup>	↓
Length : Depth	<b>(₩)</b> <sup>ns</sup>	(①) <sup>ns</sup>	<b>(</b> ₩) <sup>ns</sup>	<b>(₩)</b> <sup>ns</sup>	<b>(₩)</b> <sup>ns</sup>	¥
Depth : Diameter	仓*	(♥) <sup>ns</sup>	(①) <sup>ns</sup>	<b>(</b> ₩) <sup>ns</sup>	( <b>1</b> ) <sup>ns</sup>	Û

Key: V - lower means value on vehicle beaches; I - higher mean value at vehicle beaches;

\*\*\*\*, 
<sup>\*\*\*\*</sup>Significant (P<0,001) differences between means of vehicle and reference beaches (
<sup>\*</sup>, <sup>\*</sup> - P < 0.05);</p>

 $(\Psi)^{ns}$   $(\oplus)^{ns}$  non-significant (P> 0.05) contrasts between vehicle and reference beaches.

Cell entries denote the direction and significance of comparisons between means, with downward pointing arrows indicating lower mean values at beaches open to vchicle traffic. Conversely, upwards-pointing arrows denote higher means at vchicle beaches. Arrows in parentheses denote contrasts of means with P > 0.05. Because of significant interaction terms between time and impact, no estimate of type 1 error probability for an overall test between beaches across all surveys is given

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n = 142; reference beaches:  $\bar{X} = 2.92 \pm 0.06^{\circ}$ , n = 163; Tables 1 and 2). Similarly, mean grain size of sediment from beaches with vehicles ( $\bar{X} = 0.48 \pm 0.01 \text{ mm}$ , n = 142) was only finer by 0.01 mm compared with the sand from reference beaches ( $\bar{X} = 0.49 \pm 0.01 \text{ mm}$ , n = 163; Tables 1 and 2). There was also relatively little difference in sediment sorting between beaches, all sites having poorly-sorted sand, irrespective of whether being used by vehicles or not (vehicle beaches:  $\bar{X} = 1.60 \pm 0.01\sigma$ , n = 142; reference beaches:  $\bar{X} = 1.56 \pm 0.01\sigma$ , n = 163; Tables 1 and 2).

Temperature and moisture of the sediment varied widely between sampling periods, depending on weather conditions (Fig. 2). Despite few significant differences in mean values between beaches over the study (Table 2), in most months, the sand at beaches impacted by vehicles tended to be slightly hotter and had a lower moisture content in the top layer (Fig. 2). Overall, the physical habitat of beaches with and without vehicles, showed some degree of separation (Fig. 3), but differences tended to be small (ANOSIM: R = 0.145; P = 0.044) and were not consistent from month to month for several variables (Table 2).

#### Burrow Shapes and Metrics

Ghost crabs excavated burrows of seven principal shapes (Table 3). Half of all casts made were of the "Y" type (n = 152), and we obtained 97 simple I-shaped burrows and 35 J-shaped ones; these three burrow types made up 94% of all burrows. Less common were multi-branched burrows (n = 9), and burrows with a U-shape (n = 5), a L-shape (n = 3), or a S-shape (n = 2).

The occurrence of different burrow shapes was, to some degree, dependent on whether vehicles used the beach or not (Table 3). In the three months with the highest traffic volumes (November to January), the frequency of different burrow shapes differed between vehicle- and impact beaches (Table 3). In November, 22% of burrows constructed by crabs on reference beaches were of the "J" type, but none of this type were found on vehicle beaches (Table 3). Conversely, Y-burrows were more common on vehicle beaches (56%) than on reference beaches were Y-shaped compared with only 31% on reference beaches (Table 3). No J-shaped



Fig. 2 Profiles of sediment temperature (top row, a-e) and moisture (bottom row, f-j) comparing beaches open to vehicle traffic (dots) with nearby beaches closed to cars (triangles) during five surveys

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Fig. 3 Ordination (PCA—principal component analysis) depicting relationship of sites based on similarity in beach slope, sand temperature, sediment moisture and the mean grain size of the sediment

burrows were found in January on vehicle beaches, but 27% of all casts on the reference beaches were of this shape (Table 3).

Burrow metrics varied substantially over time and between beaches closed and open to vehicles (Tables 2 and 4; Figs. 4 and 5). The opening diameter of burrows on vehicle-impacted beaches tended to be smaller ( $\bar{X}$  =  $30.80 \pm 1.10 \text{ mm}, n = 142$ ) than on reference beaches  $(\bar{X} = 34.52 \pm 1.02^\circ, n = 163)$ , indicating that beach traffic had affected population structure. Differences in the mean diameter of openings between beaches were significant (P < 0.001) in the October '08 survey, where entrances on vehicle-impacted beaches ( $\bar{X} = 19.48 \pm 1.22^{\circ}$ , n = 27) were only 55% the size of openings on reference beaches  $(\bar{X} = 34.80 \pm 2.12^\circ, n = 41)$ . Smaller opening diameter on vehicle beaches were observed across most burrow shapes (Fig. 4). Crabs constructed shallower burrows on vehicleimpacted beaches during the months when traffic volumes were low, but burrow depth increased significantly in Jan. '09 after the peak holiday traffic: at this time, burrows on vehicle-impacted beaches ( $\bar{X} = 43.07 \pm 5.54$  cm, n = 15) were 29% deeper than those on reference beaches ( $\bar{X}$  =  $30.67 \pm 2.33$  cm, n = 26; Table 2). A similar pattern was found for burrow length: no significant differences during the first four surveys, but distinctly longer burrows after the peak holiday traffic (Table 2). Because the crabs constructed deeper and longer burrows in Jan. '09 on beaches open to

	Sep. '08		Oct. '08		Nov. '08		Dec. '08		Jan. '09		All surveys	
Shape	Ref. $(n = 41)$	Veh. $(n = 27)$	Ref. $(n = 34)$	Veh. $(n = 35)$	Ref. $(n = 36)$	Vch. $(n = 39)$	Ref. $(n = 23)$	Veh. $(n = 26)$	Ref. $(n = 26)$	Veh. $(n = 15)$	Ref. $(n = 160)$	Vch. $(n = 142)$
_	29%	15%	32%	34%	36%	33%	22%	54%	38%	20%	32%	32%
-	$176_{6}$	11%	3%	11%	22%	0%	4%	15%	27%	0%0	15%	8%
n	0%	9%0	3%	3%	0%	3%	4%	0%	4%	0%0	2%	1%
Y	51%	74%	50%	49%	31%	56%	70%	31%	27%	80%	45%	56%
L	3%	9%0	3%	0%	0%	0%	0%	0%0	4%	0%0	2%	0%
M	0%	0%0	9%6	3%	8%	8%	0%	9%0	0%	0%	3%	3%
S	0%	9%0	0%0	9%0	3%	0%	9%0	0%	0%	0%	1%	0%
Chi-square, df	4.922, 3		3.830, 5		13.568, 5		9.582, 3		12.000, 4		10.579, 6	
Р	0.178		0.574		0.019		0.023		0.018		0.102	

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closed to off-road vehicles over time (Surve	ey 1 to 5) at month	ily intervals from Seg	o '08 to Jan '09		
	df	Opening Diam	neter	Depth (lnx +	1)
		MS	F	MS	F
Co-variate (elevation above LWST)	1	477.47	3.69***	0.0022	3.87***
Times (5 surveys)	4	384.81	2.98*	0.0046	7.96***
Human use (vehicles vs. ref.)	1	948.74	7.34**	0.0050	8.82**
Times × human use	4	625.14	4.84***	0.0032	5.55***
Error	285	129.26		0.0006	
	df	Length		Main Shaft D	iameter
		MS	F	MS	F
Co-variate (elevation above LWST)	1	1632.32	2.42**	3.86	5.32*
Times (5 surveys)	4	2025.67	3.00*	2.30	3.18***
Human use (vehicles vs. ref.)	1	2961.89	4.39*	2.62	3.62**
Times × human use	4	2301.57	3.41**	5.32	7.33***
Error	285	675.10		3.09	4.26***
				0.73	
	df	Weight (lnx +1)		Angle	
		MS	F	MS	F
Co-variate (Elevation above LWST)	1	0.003	4.50***	474.99	1.58
Times (5 surveys)	4	0.005	7.66***	154.91	0.52
Human use (vehicles vs. ref.)	1	0.006	9.18**	287.84	0.96
Times × human use	4	0.004	6.91 <sup>****</sup>	487.42	1.62
Error	285	0.001		300.51	

Table 4 Summary of analysis of co-variance (ANCOVA), contrasting architectural features of ghost crab burrows amongst beaches open and

The elevation of burrows above low water spring tide (LWST) was the co-variate in the analysis

<sup>ns</sup> P > 0.05, \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001



Fig. 4 Comparison of key metrics of ghost crab burrows between beaches open (*filled bars*) and closed (*open bars*) to vehicle traffic for the most common shapes of burrows found. Boxes enclose the lower

and upper quartile, whiskers extend to the 5 and 95% percentile and the vertical bars inside boxes denote the median

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traffic, burrow weight also increased significantly during this period (vehicle beaches:  $\bar{X} = 511 \pm 111$  g, n = 15; reference beaches:  $\bar{X} = 462 \pm 57$  g, n = 26).

Most contrasts in burrow metrics between beaches open and closed to cars were consistent across burrow shapes (Fig. 4). Overall, multiple metrics for burrow dimensions distinguished casts from vehicle-impacted beaches from those of reference beaches most strongly in Jan. '09 following heavy traffic during Christmas and New Year (Fig. 5). It appears that the smaller crabs on beaches affected by heavy vehicle traffic dug burrows that were deeper, longer and heavier during this period (Fig. 5e).

#### Discussion

Juvenile crabs excavated shorter and shallower burrows than adults. Juveniles do not require as deep burrows as they live closer to the swash zone in moister sand (Duncan 1986; Chan and others 2006). By contrast, adult crabs can withstand longer periods without having to renew their respiratory water, and are therefore distributed on the backshore and in the dunes, probably because these areas are physically more stable and afford some protection from storms (Warburg and Shuchman 1979; Vannini 1980; Turra and others 2005; Hobbs and others 2008). Ghost crab burrows

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also become deeper closer to the dunes and decrease in inclination (Duncan 1986; De 2005); this suggests that the physiological risk of desiccation is important in determining burrow morphology, and that crabs need to dig deep enough to find sand with sufficient interstitial water content to permit its extraction and thus replenish water lost to evaporation (Wolcott 1976).

Beach traffic influenced dimensions of ghost crab burrows: there were smaller crabs on vehicle-impacted beaches as suggested by smaller burrow openings. After the peak traffic period, which on local beaches is over the Christmas and New Year holidays (Schlacher and others 2008a), crabs tunnelled deeper into the sediment on shores rutted by cars. This could have been a response of crabs to vibrations made by cars which could mimic those normally made by predators. Excavation of deeper burrows requires expenditure of more metabolic energy, possibly at the cost of lower investments into reproduction. This model assumes that burrowing is a major component in the total energy budget of crabs, but actual data are not available and feeding excursion could match burrowing in terms of energy expenditure. Crabs may, also be forced to spend more time foraging outside their burrows which increases risks of predation and exposure to vehicles (Schlacher and others 2007b).

Although the pressure exerted by vehicles decreases with depth into the sediment, on Australian beaches, crabs that are burrowed shallower than 30 cm get crushed by cars (Schlacher and others 2007b). In this study, 48% of burrows were shallower than 30 cm during the low-traffic months on beaches open to off-road vehicles, compared with 32% on the reference beaches. During the high traffic season (November–January), the proportion of burrows shallower than 30 cm remained the same in the traffic-free beaches, whilst it dropped considerably to 17% on vehicleimpacted beaches.

Vehicles are likely to cause more frequent collapses of burrows, and ghost crabs were expected to construct simpler burrows on vehicle-impacted beaches. We found that crabs constructed all types of previously described burrows, but significantly—proportions of different burrows shapes changed in response to vehicle traffic. Smaller crabs from vehicle-impacted beaches changed from excavating four different types of burrows (I, J, Y, M) during periods of low traffic, to only two types (I, Y) during the high-traffic months. Similarly, larger crabs from the vehicle-impacted beachess went from constructing J-shaped burrows during periods of low traffic to I-shaped burrows over the high traffic period.

There is now a good body of scientific evidence that vehicles driven on beaches and dunes cause environmental harm (Wolcott and Wolcott 1984; Moss and McPhee 2006; Groom and others 2007; Schlacher and Morrison 2008; Schlacher and others 2008c; Sheppard and others 2009). This

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presents a challenge to coastal managers who must reconcile environmental conservation with demands for beach access on social grounds. Management options usually encompass limiting the number of vehicles, restricting times of access and excluding vehicles from beaches. For example, because ghost crabs are most vulnerable to being crushed by vehicles while feeding at the beach surface at night (Schlacher and others 2007b), banning night traffic would be beneficial.

Here we present data on using ghost crab burrows as a potential new measures for such impacts, which advances the search for ecological indicators which can detect impacts to animals populations on beaches before declines in population sizes become manifest due to mortality. Managers of beaches and dunes also frequently require measures of ecological condition and indicators of change that span more than one attribute of the biota (e.g. abundance, reproduction, behaviour, etc.) to strengthen assessments and evaluate the efficacies of interventions; to this end, burrow architecture of ghost crabs could make a useful contribution.

It is also widely recognised that dunes are highly sensitive to vehicle disturbance (Rickard and others 1994), and essentially have zero tolerance for traffic (Groom and others 2007). This would argue for restricting beach traffic to unvegetated areas shorewards of the dunes, but even in National Parks, dunes continue to be destroyed by recreational ORV traffic (Thompson and Schlacher 2008). Ideally, traffic management on beaches should be designed within a framework of systematic conservation planning (Margules and Pressey 2000; Celliers and others 2004; Murdoch and others 2007). When properly designed and enforced, removing vehicles from beaches has clear biological returns (Williams and others 2004).

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## APPENDIX D

(1/03/2010) Thomas Schlacher - MF09259 - Submit Production Files

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Dear Thomas,

MF09259

Can storms and shore armouring exert additive effects on sandy beach habitats and biota?

Thank you for this careful revision and the details of your responses and the changes that you made as a result of the referees' comments. Your cover letter was extremely helpful in helping me see where you had made your changes, and your point by point response is clear about how you have changed the ms in response to the comments and suggestions. I also accept where you chose to disagree with comments and suggestions.

The good news is that I am pleased to now accept your ms for publication in 'Marine and Freshwater Research'. I have some further editorial suggestions for you to go through before you submit the final ms. These help reduce changes that the copyeditor will suggest later.

Comments (preceded by line number)

- 19 replace 'Here we document' with 'We assessed'
- 20 delete 'examined'
- 24, 73 delete 'Genus'
- 25 replace colon with semicolon
- 28 delete 'Arguably,' and start with 'Seawalls...'
- 32 do you want to add 'Ocypode' and 'ghost crab' to keywords?
- 48 delete 'in order'
- 58-74 combine these to form a single paragraph
- 69 delete 'that' in both cases (as you start the list before the colon with 'that')
- 73 lower case for 'Eastern'
- 77 delete 'the following questions'
- 81 insert '?' after 'months)' and delete 'and'
- 86 lower case for 'South-East'
- 88 lower case for 'East' and 'West'
- 86-102 combine these to form a single paragraph
- 94 hyphenate to read '260-m'
- 95 insert comma after 'deepened'
- 104-117 combine these to form a single paragraph
- 105 insert comma after '2003'
- 120 delete '- regionally known as a 'deep low' -'
- 121 delete hyphen
- 123, Fig 2 axis express as 'km h-1' with '-1' as superscript
- 125 is 2 decimal places warranted here?
- 130 delete 'of the Genus'
- 147 express references as 'Lucrezi et al. 2009a, 2009b)
- 153 insert space between '9' and 'm'
- 154 delete 'size'
- 155 put 'November' in full.
- 185 express in singular as 'visitor' and retain 'numbers'
- 192 delete copyright sign
- 193 delete 'distribution-free' (as you say nonparametric later)
- 205 hyphenate to read 'log10-transformed'

Page 2

- 209 express as 'SAS' (Version 9.1.3, 2004)' and delete from references
- 221 as Levene's test is well known, delete 'van Valen 2005' here and from references
- 233 delete comma
- 234 insert comma after ')'
- 240 replace 'steeping' with 'getting steeper'
- 243 insert 'zone' after 'intertidal'
- 247, 254 replace '&' with ','
- 252, 253 lower case for 'Ind.'
- 253 close brackets
- 253 delete 'and' and start new sentence with 'Declines'
- 259 replace 'was to some degree dependent on' with 'partly reflected'
- 267 replace 'in some instances' with 'sometimes'
- 283 remove brackets around df
- 290 delete '(Figs 4&5)'
- 287-303 combine these to form a single paragraph
- 307-318 combine these to form a single paragraph
- 315 delete '(Fig. 3)'
- 318 say where this example was
- 323 insert comma after 'storm'
- 324 delete '(Table 4)'
- 334-348 combine these to form a single paragraph
- 342 delete 'unambiguous'
- 344 delete '(Fig. 6)'
- 355 'affected' not 'effected'
- 371 delete 'Arguably,' and start with 'Beaches'
- 371 replace 'they may be' with 'and'
- 378 replace 'came' with 'come'
- 384 delete 'measurably'
- 408 upper case to read '(Trend/Change Detection Software)'
- 413 upper case for 'thesis' to read 'Thesis' and give location of Michigan State University at end of reference
- 419,492,499 replace '&' with 'and' in italics
- 443 give date when internet address was verified (can be when you check the references today)
- 454, 507 is '(S1)' needed?
- 471 lower case for 'Southeastern'
- 489 delete reference
- 501 move this two-authored paper to line 491 and shift rest down
- 522 delete this reference
- 544, 548 replace 'microns' with 'um'
- Table 3, last line reverse order to read '\* P < 0.05, \*\* P < 0.01; \*\*\* P < 0.001
- 561 lower case for 'Eastern'
- 565 -give source of photos
- Fig. 1 include latitude and longitude on border of top panel

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Andrew

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# **APPENDIX E**

http://www.conservationmaven.com/frontpage/the-impact-of-off-road-vehicles-on-

beach-dwelling-wildlife.html



Common ghost crab (Ocypode cordimanus) in New South Wales, Australia. Driving off-road vehicles on beaches is a popular recreational activity on many coastlines around the world. However <u>a new study in the journal Environmental Management</u> finds that off-road vehicles can impact beach-dwelling wildlife.

At beaches along the eastern coast of Australia, Serena Lucrezi and <u>Thomas Schlacher</u> conducted surveys of <u>ghost crab</u> burrows and measured characteristics such as the entrance diameter and elevation.

In an unusual attempt to see what the burrows looked like underground, they poured plaster into 305 burrows and dug out the casts, which extended as deep as 1.5 meters.

Beaches open to traffic had smaller crabs and narrower crab burrows, and the crabs living on these beaches tunneled deeper than those on beaches closed to vehicles.

The deeper tunneling was especially noticeable after the Christmas and New Year holidays, when off-road vehicle traffic hit its peak. Digging deeper burrows may leave the crabs with less energy for reproduction and less time for foraging.

The findings indicate that crabs are affected negatively by off-road vehicles even when not crushed and killed outright.

Ghost crabs in the genus Ocypode live on tropical and subtropical beaches and dunes worldwide. The crabs dig burrows into the sand to gain shelter from predators, hot weather, and other threats, and they emerge to feed at night.

Because they are major predators as well as an important prey for birds, ghost crabs represent a critical link in the beach ecosystem.

Travel by off-road vehicles on beaches and dunes has a range of well-known environmental impacts: damage to dune vegetation, harm to nesting birds and turtles, and reductions in abundance and diversity of invertebrates.

However, little is known about sublethal effects on beach-dwelling species such as ghost crabs, which may survive the traffic but change their behavior.

Given the study findings and the ecological importance of ghost crabs, Lucrezi and Schlacher suggest that resource managers could use crab burrows as an indicator of vehicle impacts on the ecosystem.

This indicator could reveal important impacts before they become evident through declines in the numbers of crabs and other beach species. The authors write,

"Managers of beaches and dunes...require measures of ecological condition and indicators of change that span more than one attribute of the biota...to strengthen assessments and evaluate the efficacies of interventions; to this end, burrow architecture of ghost crabs could make a useful contribution."

## by Peter Taylor

Lucrezi, S., & Schlacher, T. (2010). Impacts of Off-Road Vehicles (ORVs) on Burrow Architecture of Ghost Crabs (genus Ocypode) on Sandy Beaches *Environmental Management* DOI: <u>10.1007/s00267-010-9491-5</u>

# **APPENDIX F**

AMSA2009 ORAL PRESENTATIONS - Authors and Abstracts (alphabetically by author)

# Image segmentation of seabed texture homogeneity from multibeam backscatter data

## Lucieer, Vanessa

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The use of backscatter data generated by multibeam echo-sounders provides a powerful source of information to investigate marine substrate characteristics and seabed biotopes. However, the textures within these data are strongly scale dependant, and new methods integrating both physical and biological factors at various spatial scales must be developed to accurately assess how and why differences in backscatter texture indicate differences in substrate characteristics and seabed biotopes. This presentation will introduce the development of a method to characterise seafloor substrate based on object-oriented classification techniques applied to calibrated backscatter data. Object based image analysis is used to identify homogeneous regions in terms of acoustical response, which in turn enables us to map the distribution of marine biotopes. Backscatter image segmentation from colour, shape, smoothness, compactness and texture are applied at various scales across different depth strata. The object-oriented technique generates measures and maps of the classification uncertainty and segmentation reliability. The results provide an improved understanding of the utility of different marine biophysical variables as surrogates for benthic biotopes and promote the use of spatial uncertainty techniques, at local and regional scales, to assess the application of the methods for biodiversity assessment. Understanding the relationship between seafloor topography (from multibeam bathymetry) and substrate texture in marine ecosystems will eventually underpin biodiversity assessment and influence the success of ocean management in describing the biodiversity of our oceans. The methodology has the potential to be applied to seafloor types worldwide from a variety of multibeam systems, and will advance the research that aims to answer the fundamental questions relating to the role of high resolution acoustic data in explaining patterns of biodiversity.

# Canaries on the beach – the utility of ghost crabs (*Ocypode* sp.) as indicators of ecological change on sandy beaches

## Lucrezi, Serena\* and Thomas A Schlacher

Faculty of Science, Health & Education; University of the Sunshine Coast; Maroochydore DC, Q-4558, tschlach@usc.edu.au

Sandy shores are under pressure from expanding coastal populations, ribbon development in the costal strip and increasing recreational use of beaches. In Queensland and elsewhere beaches are the prime sites for human recreation and their ecosystems are being extensively modified by development and direct human use. Yet, the ecological consequences of this process, especially for urban and para-urban beaches, are poorly understood and criteria to measure the ecological health of beaches are not developed. We therefore tested the applicability of ghost crabs (Genus Ocypode) as ecological indicators on beaches. Ghost crabs offer practical advantages in that they are abundant and widespread and densities can be estimated by counting burrow openings. Because the crabs are the apex predators on beaches, their responses should also be ecologically meaningful. Densities of ghost crabs declined in areas subjected to habitat modification (i.e. seawall replacing dunes) and continuous trampling, suggesting predictable biological responses to human stressors. Crab numbers did, however, also change in response to natural variations in wave and wind regimes. This would confound the detection of impacts from human causes unless careful spatial and temporal replication is built into monitoring programs. A key feature of ghost crabs are their extensive, deep and complex burrows. Changes in burrow size, architecture and complexity thus offer the potential for a novel indicator that operates at the sublethal level via modifications to the crab's behaviour. Thus, ghost crabs can be an indicator of beach health that combines population responses that reflect mortality and emigration as well as sublethal effects manifested by changes in burrow biometrics.

## APPENDIX G

## Monitoring beach impacts: a case for ghost crabs as ecological indicators?

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## Abstract

Sandy beaches are under pressure from expanding coastal populations, ribbon development in the costal strip and increasing recreational use of beaches. In Queensland and elsewhere beaches are the prime sites for human recreation and their ecosystems are being extensively modified by development and direct human use. Yet, the ecological consequences of this process, especially for urban and peri-urban beaches, are poorly understood and criteria to measure the ecological health of beaches are not developed. We therefore tested the applicability of ghost crabs (Genus *Ocypode*) as ecological indicators on beaches. Ghost crabs offer practical advantages in that they are abundant and widespread and densities can be estimated by counting burrow openings. Because the crabs are the apex predators on beaches, their responses should also be ecologically meaningful. Densities of ghost crabs declined in areas subjected to habitat modification (i.e. seawall replacing dunes) and continuous trampling, suggesting predictable biological responses to human stressors. Crab numbers did, however, also change in response to natural variations in wave and wind regimes. This would confound the detection of impacts from human causes unless careful spatial and temporal replication is built into monitoring programs.

## 1. Introduction

Sandy beaches dominate Queensland's coastline and are the type of shoreline most intensively used by humans. In fact, significant parts of many coastal economies rely on the ecosystem services provided by beaches, most notably their role as prime areas for recreation and tourism. Rapid coastal development is also often concentrated along sandy shorelines, and population growth in coastal regions is significantly higher than elsewhere. Thus, human uses of beaches are increasing sharply (Schlacher et al. 2006; Schlacher et al. 2007a).

Beach management is, by tradition, almost exclusively focused on maintaining and restoring sand budgets, giving scant consideration for ecological dimensions (Nordstrom 2000; Schlacher et al. 2008) - environmental monitoring of beaches is rare. A monitoring technique which uses ghost crabs as biological indicators to measure the effects of human disturbance on beaches has been applied on urban shores (Barros 2001; Neves and Bemvenuti 2006), and to assess the effects of 4WD vehicles on beach biota (Moss and McPhee 2006a;

Schlacher et al. 2007b); these studies generally show reduced population densities of crabs in disturbed areas.

Ghost crabs of the genus *Ocypode* are semi-terrestrial invertebrates commonly found on subtropical and tropical shores. They are relatively large animals, occupying the position of apex invertebrate predator on sandy beaches (Wolcott 1978). Ghost crabs switch between surface activities at night to a fossorial lifestyle inside their burrows during the day (Barrass 1963). The crabs construct deep and complex burrows which provide shelter against climatic extremes and predators, and serve as refuges during moulting and maternity (Chan et al. 2006). The top of these burrows breaches the sand surface as a clearly visible hole, and therefore counting burrow entrances is an efficient tool to measure densities of ghost crabs on beaches (Moss and McPhee 2006a).

If management interventions are to reduce ecological impacts on Queensland's beach ecosystems, the development and testing of biological indicators becomes important. A critical component in this process is to assess whether the technique of using burrow counts of ghost crabs is robust in detecting human impacts on sandy shores. To this end, this paper examines three questions with respect to using ghost crabs as biological indicators on urban beaches: 1) to which degree are population estimates of ghost crabs in relation to human disturbance consistent across space and time, and 3) does short-term human trampling bias estimates of population sizes derived from burrow counts?

## 2. Material and Methods

## 2.1. Study beach

The study was done on Mooloolaba Beach in SE Queensland, Australia (Figure 1). The beach has a long history of human engineering interventions and has undergone many morphological changes over the last 60 years (Longhurst 1997). A wooden retaining wall was built in 1952 on the northern backshore area of the beach and replaced by a stone wall in 1959; this structure was the forerunner of today's seawall which is 204 m long and 2.3 m high; this part of the beach also receives the highest number of beach visitors. All natural dune areas of the northern beach have been replaced with recreation infrastructures such as playgrounds, toilets and large buildings such as the Surf Life Saving Clubhouse. Dunes (3-4 m tall) are still present on the southern beach, although they have undergone substantial human difference such as fencing and re-vegetation since 1957 (Longhurst 1997).



Figure 1 Study area, Mooloolaba Beach, in Eastern Australia (a). The urban beach has a heavily modified and armoured section that is extensively impacted by human trampling (b), abutted by some remaining natural dune areas with relatively less human use (c). Burrow counts of ghost crabs were made in  $3 \times 10$  m plots arranged sequentially (A-H) in across-shore transects from the base of the seawall or dune to the seaward limit of ghost-crab distributions. Each section (i.e. impact, reference) contained eight transects, surveyed on 15 separate occasions (photos by TA Schlacher (a), S Lucrezi (b, c))

## 2.2. Field measurements 1: impact of shore armouring on ghost crab abundance

To test whether ghost crab densities are reduced by shore armouring and intense human trampling, we compared burrow densities between the heavily modified northernmost section of the beach (impact section) and a reference zone 40 m to the south-east which is the area of the beach with the fewest number of visitors and where remnant dune vegetation remains (reference section). In each section (i.e. impact and reference), burrow counts were made across eight belt transects. Each belt transect was a continuous 10m wide strip that extended

across the shore from the base of the foredunes or seawall to the downshore limit of burrow occurrence. Each transect was divided into sequential 3m long quadrats placed continuously down the shore. Thus, the basic sampling units in this study were 3 x 10m quadrats, and burrow densities are expressed as the number of burrows per 30 m<sup>-2</sup>. Individual transects within each section were interspersed by 10 m along the beach. Burrow counts were temporally replicated on 15 days, covering a lunar cycle between March and April 2007. On each survey day, we started burrow counts 1-2 hours after sunrise; a complete survey of all transects taking 2-3 hours (the surveyors divided in two teams, one working on each section of the beach).

After all burrows had been counted in a quadrat, we took three replicate measurements of a) sand temperature to a depth of 5 cm (electronic thermometer Fluke 52 K/J), b) sand moisture to a depth of 8 cm (Trident microwave moisture meter), c) sand shear force resistance (field inspection vane tester Geonor H-60 with a vane size of 5 cm x 2.5 cm), and d) penetration force (Geotester penetrometer, 20 mm diameter tip); the position of replicates was randomised within each quadrat. We also recorded wind speed and air temperature (Skymate SM-18 meter), wind direction (compass), wave height (visually) and wave period (counts of breaking waves over 3 min) at the start and end of each survey. Additional weather data (e.g. hourly temperature, wind speed and direction, hourly rainfall) and tidal heights were obtained from the Bureau of Meteorology (www.bom.gov.au). Estimates of the number of beach visitors were obtained from life guards who patrol the beach daily from 7:30 to 16:30, and count the number of people every two hours.

## 2.3. Field measurements 2: short-term trampling bias

The response of burrow density and size to foot traffic was tested in a series of experiments where human trampling was repeatedly applied to ghost crab burrows on the beach. Experiments were conducted in four experimental plots (5 x 3 m) established in the upper intertidal zone near the drift line. Plots were fenced to exclude interference from the public. Human trampling was applied to two plots and the remaining plots served as controls (i.e. human exclusion, no trampling). To prevent physically disturbing the control plots - and the impact plots before the experimental application of trampling impacts began – we used a scaffold. It consisted of a ladder lifted 30 cm above the ground by trestles placed outside the boundaries of the experimental plots. Field operators moved systematically across the ladder and measured the burrow openings below through the spaces between the rungs.

The experiments were run over four consecutive days. On each occasion, we counted all

burrows and measured their sizes (diameter to the nearest mm using a ruler) in each plot at 07:00 (ca. 2 h after sunrise) before any disturbance was applied. The trampling treatment consisted of two people (weight: 45 & 55 kg) crossing the impact plots each 50 times in a zigzag pattern; this resulted in close to 100% coverage of footprints. The trampling treatment was applied in 5 distinct bouts at 50 min intervals over a 5 h period. Before each new trampling event, all burrows which remained intact were counted and their diameter measured.

## 3. Results

## 3.1. Environmental influence on changes in ghost crab numbers

Significantly higher burrow counts were obtained in wetter sand after warm nights and during stronger winds (Table 1). By contrast, wave properties, tidal amplitudes, sand temperature and compactness were not correlated with the number of burrow openings (Table 1). No substantial difference in sediment properties occurred between sections of the beach (Table 1). Correlations between environmental variables and burrow densities were not influenced by human disturbance intensity, and variation in environmental variables was unlikely to be the primary cause of spatial differences in ghost crab populations between sections of the beach. There was no conspicuous pattern in temporal changes of burrow numbers that could unambiguously be related to lunar phases.

## 3.2. Habitat disturbance vs. changes in burrow densities

Burrow densities were substantially lower in areas intensively trampled by humans and where dunes had been replaced by a seawall (Figure 2). Overall, the highly impacted site supported only half the number of crabs found in the less intensively disturbed areas. These spatial contrasts between heavily and less disturbed sites were, however, not necessarily consistent over time (Table 2). On the upper shore, half the surveys showed significantly lower mean densities in the impacted site, and the direction of change was negative for all but a single survey (Table 2). By contrast, although burrow densities on the middle part of the beach (i.e. below the strandline) were also mostly lower in the heavily impacted areas, a significant change could only be detected in a single survey (Table 2).

## 3.3. Trampling impacts on crab burrows

Pedestrian traffic substantially reduced burrow densities and sizes immediately after the

trampling impacts had occurred; it did, however, not cause significant changes at a time scale of days. Mean burrow densities were reduced by 88% following human trampling impacts (Figure 3). In all experiments, densities in impact plots  $(0.36 \pm 0.03 \text{ burrows m}^2)$  were significantly lower than in un- trampled reference plots  $(2.85 \pm 0.13 \text{ burrows m}^2; \text{ Fig. 2}; \text{ANOVA} - effect treatment: F(1,7) = 83.72, P < 0.001). The first set of impacts (i.e. 100 passes) caused the greatest change to the density of ghost crab burrows; further trampling had comparatively small additional effects (Figure 4). There was no significant interaction between treatment and experiment (ANOVA – experiment x treatment, F(3,7) = 1.23, P = 0.37), suggesting that experimentally produced effects of trampling on burrow counts were consistent across all experiments.$ 

Because experiments were run on consecutive days and the sets of trampling impacts were separated by at least 19 hrs between experiments, changes to the density and size of crab burrows which were measured at the start of each experiment should be indicative of short-term (i.e. days) impacts on ghost crab populations. However, we neither found a significant difference in burrow numbers nor burrow sizes between the impact and control plots before trampling commenced in each experimental run. This lack of significant day-to-day changes, which could not be linked to the intensity of human disturbance, suggests that crabs of all sizes repaired their burrows overnight, resulting in densities and size structures that were indistinguishable from pre-impact conditions in the short term.

## 4. Discussion

## 4.1. Environmental influence on changes in ghost crab numbers

We found a strong positive correlation between wind speed and burrow density (Table 1). Fewer people frequent the beach when there are strong onshore winds. Also, wind-driven onshore advection is the main mechanism for delivering wrack and carrion to beaches. This is likely to explain the higher activity of ghost crabs during strong onshore winds.

Although ghost crabs can occupy a fairly broad area across the intertidal and supratidal gradient, the distribution of many species appears to be centered on the backshore, extending from the driftline to the dune. Ghost crab distribution may also shift in relation to tides. In the present study, wave properties and tidal amplitudes were amongst the environmental variables that did not affect the number of ghost crab burrow openings. However, the surveys were carried out over one month only, providing limited tidal ranges.

<sup>2&</sup>lt;sup>nd</sup> Queensland Coastal Conference, Gold Coast, May 2009

Further studies may look at prolonging the time of sampling, in order to include phenomena such as king tides, which are possibly likely to have a substantial influence on the density and distribution of ghost crabs on the beach.

## 4.2. Trampling impacts on crab burrows

Significant decreases in burrow counts denote a negative effect on ghost crab populations, but the actual mechanisms that cause these declines remain unknown, except for the impact of off-road vehicles that can directly crush crabs (Wolcott and Wolcott 1984; Schlacher et al. 2007b). Putative causes of population declines in ghost crabs span a wide ambit such as: (a) direct crushing of crabs through trampling (but see our short-term trampling experiments), (b) habitat loss and/or modifications; (c) changes to metabolic costs, reproduction, and behavior, (d) trophic shifts and enhanced predation pressures, and (e) light pollution.

Intense, human trampling did result in lower burrow count but the effects of the short-term trampling disturbances were mostly non-lethal to ghost crabs and did not last long. A single hit by a pedestrian suffices to cover or collapse a burrow opening, and because the crabs do not to re-open filled burrow entrances for at least one hour (S. Lucrezi, personal observation), burrow counts fell markedly after people had walked over the plots (Figure 3). Burrow numbers recovered, however, overnight, showing that human trampling is not necessarily lethal to most crabs. In the long-term, human trampling does, however, have demonstrable, negative impacts on ghost crab population sizes (Figure 2), most likely as a consequence of several, additive sublethal effects related to frequent habitat disturbance. Also, other short-term trampling experiments have demonstrated direct mortalities of macrobenthic species on sandy beaches (Moffet et al. 1998).

It has been suggested that ghost crabs can acclimatize to increasing levels of recreational beach use (Steiner and Leatherman 1981). Even positive effects of recreation have been reported when food scraps left by beach visitors provide a trophic subsidy to the scavenging crabs (Steiner and Leatherman 1981). Yet, on many beaches pedestrian trampling is a heavy and continuous disturbance agent that causes significant negative impacts on ghost crab populations in the long term (Figure 2)

We found a positive correlation between wind speed and burrow density (Table 1). Fewer people frequent the beach when there are strong onshore winds (S. Lucrezi, personal observation), reducing direct trampling impacts by humans. Ghost crabs can be highly active during strong onshore winds (Wolcott 1978), and onshore winds deliver wrack and

<sup>2&</sup>lt;sup>nd</sup> Queensland Coastal Conference, Gold Coast, May 2009

carrion to beaches. We observed nocturnal feeding aggregations of ghost crabs around driftlines (TA Schlacher pers. obs.), and ghost crabs may therefore become more active when stronger winds increase the food supply of wrack. However, the positive relationship between wind speed and burrow numbers measured in this study will not apply over the full spectrum of wind speeds. In fact, winds above 20 knots tend to obscure burrow openings, particularly in loose sand on the upper shore (TA Schlacher pers. obs.). Thus, burrow counts are not useful as a monitoring tool during strong winds.

Coastal armouring has often been employed to combat shoreline erosion worldwide, and this trend may escalate in the face of global climate change (Feagin et al. 2005). The main ecological impact of coastal armouring is the destruction of dunes (Dugan and Hubbard 2006). Since dunes are critical refuges for ghost crabs during storms (Christoffers 1986), crabs on armoured sections of beaches are at greater risk during high seas (Vinagre et al. 2007).

Evidence for numerous ecological effects linked to beach recreation is accumulating (Davenport and Davenport 2006; Moss and McPhee 2006b), but ecological assessments of sandy beaches are rare (Schlacher et al. 2008). Neglect of ecological dimensions in beach management stems partly from the lack of established monitoring techniques using tested indicators for sandy shores. This paper shows that ghost crabs are useful in principle, but potential bias must be recognized and avoided.

A key requirement of all monitoring is to standardize data collections across geographic regions and programmes. Here we show that several environmental factors can significantly influence burrow numbers, including temperature, wind speed, and sand moisture. Therefore, future monitoring using ghost crab burrow counts should either limit field surveys to defined ranges of weather conditions, or explicitly incorporate environmental conditions in both the reporting and analysis.

Bias in burrow counts and sizes (Figures 2&3) has consequences for using ghost crabs as ecological indicators: both counts and opening diameters are only reliable proxies for population densities and size structures if field measurements are taken when pedestrian disturbance is small. Thus, field surveys should be limited to periods when beach visitors are expected to be few - as early in the morning as possible - on weekdays rather than weekends and public holidays, and during cooler and overcast conditions rather than during sunny weather. Provided such basic design factors are explicitly incorporated into standard operating procedures for field surveys, ghost crab burrow counts can be a rapid and cost-effective indicator to determine the extent of ecological disturbance from human uses of sandy beaches.

## Take home messages

Mitigation measures and management interventions that seek to reduce negative ecological effects will invariably have to target the process causing the observed impacts. In the case of ghost crabs on urban beaches, it appears logical to propose human trampling as a prime mechanism of impact (but see Jaramillo et al. 1996). Robust scientific evidence to support the need for management interventions requires, however, that an unequivocal link between the level and nature of human disturbance and the biological response is demonstrated; this can only be achieved through controlled, and carefully designed manipulative experiments (Bulleri et al. 2007). Thus, a major lesson from this study is that the mechanistic links between putative human pressures and biological responses need to be determined (see also Schlacher et al. 2007b).

## 5. Acknowledgments

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	Referen Section	ice n	Impac Section	:t n
Sediment Properties				
Sand Temperature ( $\mathfrak{C}$ )	-0.207	ns	0.003	ns
Sand Compactness (Kpa)	-0.340	ns	0.141	ns
Sand Moisture (%)	0.561	*	0.714	*
Sea Conditions & Tides				
Wave Height (m)	0.264	ns	0.160	ns
Wave Period (s)	-0.183	ns	0.003	ns
Tidal Amplitude (m)	-0.107	ns	-0.220	ns
Tidal Reach (previous night; m)	0.080	ns	0.079	ns
Tidal Reach (survey day; m)	-0.065	ns	-0.145	ns
Weather				
Air Temperature - Night (18:00-06:00; C)	0.603	*	0.717	*
Air Temperature Day (06:00-12:30; ℃)	-0.403	ns	-0.432	ns
Wind Speed - Night (knots)	0.666	<b>*</b>	0.681	*
Wind Speed - Day (knots)	0.585	*	0.597	*
Human Pressure				
Beach Visitors (daily, n)	-0.326	ns	-0.342	ns

 Table 1
 Partial correlations between environmental factors and densities of ghost crab

 burrow densities measured in 15 surveys on two sections of Mooloolaba Beach.

Table 2Effect sizes for spatial contrasts in the density of ghost crab burrows betweenimpact and reference sections during 15 surveys at Mooloolaba Beach.Negative valuessignify lower densities at impacted sites, whereas positive values denote higher densities inthe disturbed areas.Bold entries denote significant differences between means.

	Upper S	hore		Middle S	shore	
Survey	Effect S	ize #	P <sup>\$</sup>	Effect S	ize #	P <sup>\$</sup>
1	-21.4	(-59%)	•	12.1	(+35%)	ns
2	-25.1	(-63%)		-25.0	(-43%)	ns
3	-10.8	(-47%)	ns	-6.4	(-19%)	ns
4	-15.0	(-71%)		-0.3	(-1%)	ns
5	-20.6	(-65%)	·	-5.0	(-13%)	ns
6	-22.2	(-89%)	***	-13.0	(-33%)	ns
7	5.3	(+61%)	ns	-15.0	(-38%)	ns
8	-15.5	(-95%)		-27.6	(-87%)	
9	-9.9	(-46%)	ns	-0.3	(-1%)	ns
10	-3.3	(-60%)	ns	3.0	(+32%)	ns
11	-13.8	(-52%)	**	-2.3	(-7%)	ns
12	-8.4	(-95%)		-24.2	(-85%)	ns
13	-9.5	(-66%)	ns	7.5	(+55%)	ns
14	-8.5	(-60%)	ns	-14.4	(-47%)	ns
No. Negative Contrasts	13			11		
No. Positive Contrasts	1			3		
	Z-statistics	Ρ		Z-statistics	Р	
Sign-Test	3.10	0.002		1.87	0.061	

#Effect Size = ( -Density<sub>Impact</sub> - -Density<sub>Reference</sub>);

<sup>s</sup> Probability values from HSD post-hoc tests following significant time x zone x impact effects in the main GLM model. \*\*\* P < 0.001, \*\* P < 0.01, \* P < 0.05, <sup>ns</sup> P > 0.05.



Figure 2 Contrast in the density of ghost crab burrow openings between a beach section armoured with a seawall and heavily trampled ("impact") compared with a beach section with some remaining dunes and less impacted by pedestrians ("reference") at Mooloolaba, SE-Queensland.



Figure 3 Variation in mean burrow counts (a) and burrow size (b) of ghost crabs in relation to experimental disturbance by human trampling. Experimental treatments consisted of 100 pedestrian passes applied five times at 50 min intervals in four separate experimental runs (days) compared with abutting control sites from which beach visitors had been excluded.



## Figure 4

Relationship between changes in ghost crab burrow numbers (a) and opening diameter (b) in relation to the intensity of human disturbance through pedestrian trampling. Effect size ( $\Delta$ ) is measured as: | ( <sub>Ref.</sub> - <sub>Imp.</sub>) / <sub>Ref.</sub>|, where are the mean values of burrow density or entrance diameter in the reference (Ref.) and impact (Imp.) treatments.

2<sup>nd</sup> Queensland Coastal Conference, Gold Coast, May 2009