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Behavioral adaptations of sandy beach macrofauna in face of climate change impacts: A conceptual framework

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ABSTRACT

Sandy beaches are severely under-represented in the literature on climate-change ecology, yet different lines of evidence suggest that the macrofauna inhabiting these narrow and dynamic environments located at the land-sea interface is being reorganized under the influence of this large scale and long-lasting stressor. This is reflected in macrofaunal sensitivity to increasing sea surface temperature, sea-level rise, extreme events and erosion of the narrow physical habitat. However, evidence of behavioral responses by sandy beach macrofauna that are consistent with expectations under climate change is scarce and fragmentary. In this paper, specific hypotheses are formulated for how behavioral adaptations in sandy beach macrofauna are predicted to respond to climate change impacts. Firstly, a conceptual framework and an overview of macrofauna behavioral adaptation features are provided. Secondly, the effects of main climate change drivers on sandy beaches are summarized. Thirdly, a conceptual framework is developed giving behavioral adaptations of sandy beach macrofauna under climate change pressure. The degree to which observations on behavioral adaptations of beach animals conform to expectations under specific climate change drivers (sea level rise, sea surface temperature, winds and storminess, rainfall, acidification and eutrophication) is explored. Taking into account the empirical evidence and the theoretical framework detailed in the paper, emergent hypotheses/predictions are proposed. Climate change drivers are expected to impact habitat features and consequently the behavioral expression of macrofauna as active responses to habitat changes. Behavioral adaptations are expected to be impaired, more variable or disrupted, thus decreasing fitness, causing local population extirpations and potentially triggering a range of cascading effects of ecological change in the beach ecosystem. Biodiversity loss will be the outcome of the negative pressures driven by climate change. The specificity of sandy beaches as narrow ecotones between sea and land may be lost under climate change pressure, adversely affecting fine-tuned macrofaunal adaptations and therefore ecosystem functioning. Strictly adapted endemic sandy beach fauna will be especially subjected to local extirpations, while species with a large reaction norm (*i.e.* phenotypic and behavioral plasticity) may face changes by dispersal and exploitation of new niches. Under climate change impacts, biodiversity loss is predicted, which would hamper beach ecosystem resilience. The limits to which sandy beach macrofauna responds and can behaviorally adapt to environmental change are worthy of exploration, in view of the increasing influence of the long-lasting climate driven stressors threatening these ecosystems at risk.

1. Introduction

Sandy beaches are threatened by a variety of stressors operating at different spatial and temporal scales (McLachlan and Defeo, 2018). These perturbations translate into ecological impacts that are manifested across several dimensions, affecting the physical and biological components of the beach system (Brown and McLachlan, 2002; Defeo et al., 2009). A worrying scenario is particularly given by the increasing occurrence of press perturbations, notably climate change. A conceptual framework was recently developed to construct explanatory hypotheses and predictions in sandy beach ecology under climate change expectations (Schoeman et al., 2014). Long-term information was used to test emergent hypotheses and related predictions on population abundance, structure, individual size, body condition, and extension of reproductive and recruitment periods (Ortega et al., 2012, 2016; Celentano and Defeo, 2016), as well as in contraction/expansion

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of distributional ranges (Carstensen et al., 2010; Hubbard et al., 2014; Schoeman et al., 2015; Donelson et al., 2019). Climate change has been linked to widespread and substantial changes in the distribution, abundance, reproduction and survival of beach populations, increasing the risk of local extirpations and functional extinctions (McLachlan and Defeo, 2018). Long-term changes in species richness, ecological diversity and ecosystem-level attributes were also detected as responses to climate-driven changes in local productivity associated with climatic shifts (Lercari et al., 2018). In a climate-change context, the survival of macrofauna is related to their adaptation potential, including genetic variation and phenotypic/behavioral plasticity (O'Connor et al., 2012). Behavioral adaptations of macrofauna to the sandy beach habitat have been subjected to a large amount of observational and experimental work (Scapini, 2014; McLachlan and Defeo, 2018), yet a general conceptual framework for explanatory and predictive hypotheses is lacking, which would go beyond fragmentary evidence (Watson, 2018).

Phenotypic plasticity in sandy beach macrofauna was recognized as an adaptation to these dynamic environments, emphasizing its importance as the "adaptation to adapt" (Brown, 1996). The concept of phenotypic plasticity was developed for plants that may reproduce asexually and give progenies sharing the same genotype, but adapted to different environmental conditions (Schlichting and Pigliucci, 1998). Phenotypic plasticity is part of the concept of reaction norm and may evolve under changing environments, including also responses to anthropogenic stressors such as climate change (Kelly, 2019). Behavior is a particular case of phenotypic plasticity in animals, being expressed by individuals, which have unique genotypes and may respond to different environmental features that they encounter during development and free life (Scapini et al., 1988; Hazlett, 1995; West-Eberhard, 2003). Tolerant individuals more promptly avoid harmful stimuli or contexts through learning (negative conditioning), or they search again in the spot where they have previously found a resource (positive conditioning). In this respect, behavior is contingent (*hic et nunc*, here and now), reflecting the past and actual conditions faced by individuals. However, individuals may show peculiar behaviors, acquired through imprinting-like learning processes, defined "behavioral syndrome" or "personality", which may have evolutionary consequences (Scapini et al., 1988; Gherardi et al., 2012; Kralj-Fišer and Schuett, 2014).

Behavior is expressed by animals in response to internal needs and external stimuli, genetics underlying behavioral expression through morphological, physiological and sensorial adaptations. Behavior is an adaptation *per se,* important for survival and reproduction and, ultimately, for population and species survival (Campan and Scapini, 2002). Behavioral and physiological plasticity, which contributes to population survival, is a motor of evolution, but also a product thereof, giving rise to adaptations through processes of developmental canalization and/or genetic assimilation of gene expression (Badyaev, 2005). Inter-individual diversity is commonly observed in behavioral expression, which may provide fitness advantage to better adapted individuals, particularly in case of the colonization of new habitats, where natural selection may then establish new adaptations (O'Connor et al., 2012). Several behavioral adaptations were shown to be genetically determined, with differences within and between populations. These include rhythms, orientation, foraging behavior, parental care, mate preference and antipredator behavior (Pardi and Scapini, 1983; Scapini et al., 1985; Berthold et al., 1992; Sokolowski, 2001; Sinn et al., 2006; Kralj-Fišer and Schneider, 2012). Phenotypic plasticity and genetic variation may be considered as complementary attributes (Scapini et al., 1988; 1995). Genomic studies and molecular genetics evidence on gene expression and epigenetics offer a background for analyses of (changing) relationships between genes and environment during individual life and population evolution (Baker et al., 2001; Renn and Schumer, 2013; Clark et al., 2018).

Behavioral aspects have not been used yet in sandy beach ecology to construct hypotheses under climate change expectations. This could be due to the relatively poor understanding of how responses of individual organisms extrapolate to whole ecosystems (Schoeman et al., 2014). Hence this is an appropriate time to develop a conceptual framework of behavioral responses and flexibility in sandy beach macrofauna, in view of climate change impacts on beaches. In this paper, specific expectations are formulated for how behavioral adaptations in sandy beach macrofauna are predicted to respond to climate change related impacts. Firstly, a conceptual framework and an overview of behavioral adaptation features of sandy beach macrofauna are provided. Secondly, theory from climate change literature as applied to sandy beaches is summarized and the main drivers of change affecting the littoral active zone (LAZ) are detailed. Thirdly, a conceptual framework is developed for behavioral adaptations of sandy beach macrofauna under climate change pressure. Illustrative examples are presented for main climate change drivers that may affect behavior in beach macrofauna, based on observational data series, field and laboratory experiments. The degree to which observations on behavioral adaptations of beach macrofauna conform to expectations under specific climate change drivers is explored. Taking into account the empirical evidence and the theoretical framework detailed in the paper, a suite of emergent hypotheses/predictions is also given.

2. Behavioral adaptations in sandy beach macrofauna

Behavioral adaptations characteristic of sandy beach macrofauna are dictated by the instability of the habitat, given by unpredictable and predictable environmental changes at different temporal scales, which may impact on individual survival and population persistence (McLachlan and Defeo, 2018). Animal behavior may include various components of increasing complexity, from cue perception to behavior expression (Fig. 1). For example, tides are potentially harmful for supralittoral animals, for the risk of displacement from the suitable zone, and, at the same time, provide the "cues" that give the signal for and to orientate escape reactions, or act as *zeitgeber* (synchronizer) of tidal rhythms (Scapini, 2006; Naylor, 2010). "Responses" are reactions to single or multiple stimuli, being often innate (*i.e.* expressed at the beginning of life, without experience) and potentially shown by all individuals of the population, in many cases shared by different species inhabiting similar habitats or beach zones. Kinesis (movement with respect to environmental gradients, *e.g.* substrate temperature, humidity or salinity), taxis (movement with respect to a directional stimulus, *e.g.* shadow, light, gravity, magnetism), or more complex habitat-specific behavioral adaptations are used to find the suitable habitat or avoid a hazardous situation. "Behavioral adaptations" are functional to the habitat where the population lives and may be genetically determined (evolved through natural selection) or acquired through individual experience. In the latter process, the adaptation to adapt or learning ability may be inherited.

On sandy beaches, behavioral adaptations in mobile macrofauna are prevalently expressed to search and choose specific substrate conditions or avoid harmful ones, recover and maintain the suitable habitat in the LAZ, which lies between the outer limit of wave effects on bottom stability and the landward limit of sand transport by wind (Tinley, 1985) (Table 1S in Supplementary Material and references therein). Supralittoral species maintain or actively recover the beach zone through habitat selection, orientation and homing, tuning these behaviors to the conditions encountered (Vannini and Cannicci, 1995; Williams, 1995; Scapini, 2014). Biological rhythms contribute to express activities under optimal conditions, by synchronizing internal clocks to external cyclic variables, driven by night-day alternation, tides, lunar phases and seasons; activity rhythms are key adaptations of sandy-beach macrofauna, as they allow the anticipation of potentially stressful conditions (Naylor, 2010). Burrowing into the sediment is a common adaptation in sandy beach macrofauna to prevent hazardous conditions, such as dehydration, predation or dislocation by tides and storms, and is linked to sand granulometry and water content, which show gradients on beaches; this behavior may be greatly impaired by

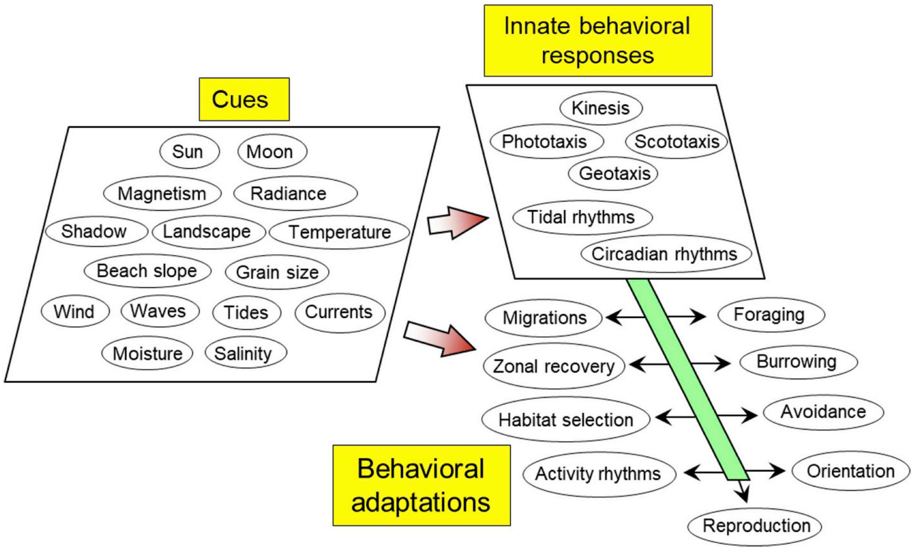

Fig. 1. Behavioral adaptation features common in sandy beach macrofauna: **Cues** are significant environmental elements to which beach individuals react with **Innate behavioral responses**, according to species physiology; **Behavioral adaptations** are expressed on the beach for functions that contribute to individual survival and reproduction and may pass on to the following generations. Modified from Campan and Scapini (2002).

direct human actions, such as beach nourishment, mechanical cleaning, car driving and trampling (Viola et al., 2014; Costa and Zalmon, 2019). In the intertidal zone, burrowing is expressed as vertical zonation change (Sassa et al., 2011; McLachlan and Defeo, 2018). Physical and chemical environmental driving forces prevail on sandy beaches, but biological ones are also relevant for behavior expression (Table 1S). In the non-vegetated zone of the beach, animals are either predators or opportunistically forage on stranded carrion and wrack, which may be abundant, but unpredictably supplied and of varying nature (Pennings et al., 2000). Cannibalism was observed under particular conditions, such as high population density under oligotrophic conditions (Duarte et al., 2010). Supralittoral animals may also forage in the foredunes and dunes, avoiding the risk of being swept away by waves, dehydration risk and predation, and at the same time exploiting a rich food supply in the case of oligotrophic coastal waters (Colombini et al., 2013; Lagar et al., 2016). Gregarious behavior may depend on the choice of the same zone (habitat selection) by several co-specifics; intraspecific competition may occur to defend resources (*e.g.* burrows, mates and food), population density being critical for the expression of competitive behavior (Gherardi et al., 2012). Behavioral adaptations may differ between species with direct development and those with larval stages. The former may express behavioral adaptations specific to the beach of origin, which are further tuned to the home beach features during life (Gambineri and Scapini, 2008). Larvae may express innate habitat selection behavior (settlement), such as taxis or kinesis to odors, sounds, salinity gradients and pressure (Stanley et al., 2012).

The expression of adaptive behaviors may be modified in response to changes of external cues and/or internal motivation and needs, as well as a consequence of individual experience. In non-homogeneous environments such as beaches, which present several land-sea physical and biological gradients, each zone of the beach may be differentially characterized; thus, animal displacement may itself cause a modification of the expressed behavior. The needs of young and small individuals and their susceptibility to stressful factors may be different than those of adult and larger ones (Williams, 1995; Scapini and Dugan, 2008); females producing eggs or carrying broods use resources for the following generation, having therefore different needs than non-reproductive females, which results in differential behavioral expression (Borgioli et al., 1999).

Genetic variation within sandy beach populations is particularly important, as their habitats are subjected to frequent changes. In some sandy beach taxa, behaviors such as site fidelity, mate choice and contrasting random mating may produce genetically differentiated subpopulations, while dispersal and migration may establish metapopulations, maintaining genetic flow (Soares et al., 1999; Bezuidenhout et al., 2014). However, populations cannot tolerate the large-scale event of habitat disappearance, which may be a consequence of climate change impacts and encroaching development from expanding human populations on land (*e.g.* coastal squeeze, Defeo et al., 2009; Hubbard et al., 2014). In such case, dispersal and successful colonization of new beaches would allow species persistence and further evolution. The expression of innate behavioral responses to the beach environmental features and gradients would favor the success of colonization. The effects of environmental change on beach macrofauna will depend firstly on behavioral adaptability, which should be included in explanatory and predictive hypotheses, subjected to *ad hoc* experimental work.

There are specific limits or constraints to the behavioral expression, which should be considered when developing predictive hypotheses. Also, specific conditions are necessary to adjust behavior to a changing environment, as the animals must actively track the environmental changes by adapting to modified and new contexts. Animal motility and the capacity of recovering a suitable beach habitat should be included in the conceptual framework. Learning is an adaptation strategy in most animals to adjust behavior to new situations, but require time, memory and a nervous system (even a simple one). Constraints for behavior adaptability depend also on the inherent characteristics of the species (life cycle, generation turnover, population abundance and genetic diversity). A certain population size and environmental temporal stability (with relation to population turnover) are necessary for adaptations to be stabilized. Prevailing climatic conditions on a sandy beach may interact with the tuning of behavioral expression, resulting in differential life-cycle and behavioral adaptations in different geographic areas (McLachlan and Defeo, 2018). The species potential for colonization of new habitats is a key factor under climate change, which implies the expression of adaptive behavior in new contexts, whereas habitat connectivity would allow shifts of species ranges (O'Connor et al., 2012; Donelson et al., 2019).

3. Sandy beach ecosystems and climate change

Climate change has added a new global dimension to modifications of sandy beach ecosystems (Schoeman et al., 2014; McLachlan and Defeo, 2018). It has been postulated that sandy beach ecosystems are at risk because of concurrent and increasing impacts of different climate change drivers (Fig. 2, Table 1). Indeed, in addition to the ecological consequences of temperature increase, sea level rise will increase erosion along sandy shores. Global warming may also be expected to cause

Table 1
Conceptual framework: emergent hypotheses for climate change impacts on behavioral adaptations in sandy beach macrofauna.

Main proximate driver	Potential effects on beaches	Implications for sandy beach macrofauna	Expected behavioral changes	Main predictions under global climate change
Sea level	Sea level rise affects the narrow land-sea interface and increases erosion rates, modifying beach morphodynamics; sediment loss diminishes beach volumes and causes a retreat of the coastline.	Habitat loss and increase in temporal instability of the environment.	**Orientation** and **migration** become more variable; complex mechanisms (*e.g.* sun compass) are disrupted and substituted by simple taxes; **foraging** becomes opportunistic.	Increasing rates of local extirpations in supralittoral invertebrates with restricted distribution and dispersal.
Temperature	Augmenting temperature ranges between superficial and deep sediments changes sediment moisture properties in the upper littoral; sustained increase in sea surface temperature changes water and sand properties and modifies local hydrodynamic conditions.	Changes in macrofaunal thermal limits; increase in the energy cost of osmoregulation.	Disruption in **activity rhythms** expression; changes in the timing of **mating** and **recruitment**; changes in **burrowing** resulting from changes in oxygen availability and moisture; decrease in burrowing depth and increase in **competition** for burrows.	Reproduction and recruitment will be affected, lowering population fitness; range shifts and distributional changes; increased competition will decrease fitness.
Onshore winds and storminess	Warmer air and water increase storminess and frequency and intensity of onshore winds; more frequent and intense onshore winds together with rising sea levels augment swash width and strength, decrease beach width and accelerate beach erosion.	Larger wind waves cause stranding and mass mortalities of intertidal species, which are carried up the beach and are unable to return to the intertidal; habitat loss for supralittoral species with restricted distribution and dispersal.	**Escape** (avoidance behavior) away from the stress source increases; changes in direction and timing of **orientation** and **migration** affect **zonation; competition behavior** increases.	Increasing population extirpations due to habitat loss, particularly under coastal squeeze scenarios.
Rainfall	Increasing freshwater flow into the marine environment decreases salinity; rise of groundwater levels increases swash run-up distances and beach erosion rates.	Decrease in salinity may alter osmoregulation and vital rates; rising groundwater and erosion may cause habitat loss for obligate beach species.	Tidal and seasonal **biorhythms** may change, due to unpredictability of synchronizing cues; changes in along- and across-shore **distribution and zonation**; disruption in **habitat recovery** and **orientation**; increase in **competition** between endemic species and invasive alien species from freshwater bodies.	Extirpations due to habitat loss for erosion/floods; recruitment failure and impaired reproduction activity; changes in community structure and function due to increasing representation of invasive species.
Acidification	Declining pH and carbonate saturation attributed to climate change are expected to alter water chemistry properties in the surf zone.	Reduced calcification rates and calcium metabolism in beach species with calcified structures in their anatomy.	Impaired **burrowing** in macrofauna with less robust shells; higher **substrate selectivity**; decreased **recruitment** for sensitive larval stages, whose motility and survival are impaired by acidification; affected **foraging** on wrack.	Increase in mortality rates and biodiversity loss; reproduction and recruitment affected in broadcast spawners with pelagic larvae; loss of fitness.
Eutrophication	Nutrient enrichment derived from climate change drivers combined with human activities increases eutrophication rates, driving to increasing frequency, intensity and periodicity of harmful algal blooms (red tides) and mass development of drifting macroalgae mats (green and golden tides), altering water and sediment properties.	Blooms of toxic algae may cause mass mortalities to suspension feeders, affecting the whole food web. Mass stranding macroalgae events decrease the diversity of intertidal benthic macrofauna, affecting some sub-surface deposit and suspension feeders.	Changes in **zonation** with species overlap; impaired specialized **foraging** and increasing representation of opportunistic species; reduced foraging rates in deposit and suspension feeders; disruption in **habitat selection** mechanisms.	Chronic changes in metabolism affecting growth and survival rates; extirpations and biodiversity loss over extended areas.

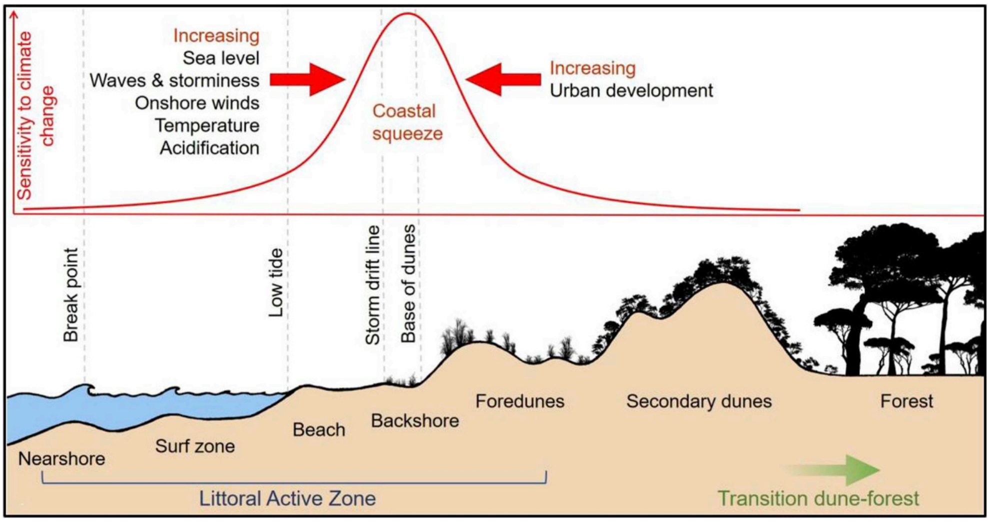

Fig. 2. The Littoral Active Zone (LAZ) and its main components from the nearshore to the foredunes: the conceptual sensitivity curve suggests that the most sensitive areas to climate change drivers are the beach, the backshore and foredunes; expanding urban development on the dry (land) side in secondary dunes and the forest nearby interacts with climate change drivers mainly acting on the wet (sea) side to produce coastal squeeze. Modified from McLachlan and Defeo (2018).

increased storminess, as well as changes in rainfall patterns. Increased storminess will also result in erosion, retreat of beaches and dune scarping with vegetation loss. Predicted increase in rainfall patterns in some regions of the world may increase freshwater flow into marine environments, decreasing salinity. Salinity will also decrease due to ice cap melting, as has been observed in the Baltic Sea (Elliott et al., 2015). Excessive precipitation and flooding may cause a rise in groundwater levels, thereby increasing swash run-up distances and erosion rates. Warmer air and water have also been accompanied by an increase in the frequency and intensity of onshore winds (Bakun, 1990; Sydeman et al., 2014), which in turn increases wave energy, moving beaches towards more erosive states (Short, 1999). It has therefore become increasingly critical to understand how sandy beach ecosystems will respond to these long-lasting and pressing changes of the environment.

The most sensitive areas of the LAZ are the beach, backshore and foredunes (Fig. 2), which together comprise a narrow stretch constrained by physical and anthropogenic limits, where impacts on sand budget and biodiversity are expected to occur. Human activities can accelerate the large-scale changes that are being generated by climate change drivers. For example, unplanned and intense urban development on land could affect the ecosystem service played by sand dunes in sand storage, increasing erosion rates. Acting together with rising sea levels, these drivers may affect the sand budget (storage and transport) across the LAZ, narrowing beaches up to the point that entire habitats could disappear, become severely restricted or move landwards, depending on the set of local conditions (Houston and Dean, 2012). Coastal squeeze is nowadays a major long-term threat that sandy beaches face worldwide (Defeo et al., 2009; McLachlan and Defeo, 2018). Particularly, climate change drivers (Table 1) are expected to affect the highly specialized sandy beach macrofauna restricted to inhabit the land-sea interface and thus lacking spatial refugia or compensatory habitats (Schoeman et al., 2014). Decreased salinity in coastal waters may affect fertility, reproduction, growth and survival rates in sandy beach macrofauna (Lima et al., 2000; Ortega et al., 2016). Predicted ocean acidification may further impact beach mollusks and crustaceans (particularly their dispersal stages), by reducing calcification rates and calcium metabolism (Jones et al., 2007). Nutrient enrichment that leads to eutrophication is another human-generated stressor in sandy beaches, driving to increasing occurrence of harmful algal blooms (Gianelli et al., 2019) and mass development of mats of drifting macro-algae (Quillien et al., 2015a), which, in turn, may affect beach macrofauna.

4. Climate change impacts on behavioral adaptations

A conceptual framework regarding behavioral adaptation to sandy beaches under climate change should consider the following aspects: i) behavioral adaptation with relation to habitat availability/variability; ii) phenotypic plasticity, including behavior, and its evolutionary role; and iii) species life-cycle traits (duration of life, dispersal, recruitment, developmental stages and intra-specific interactions).

It is expected that climate change will expose sandy beach macrofauna to significant alterations in their physical and biological environment, causing variations in behavioral expression. Under changing conditions, variability was observed in macrofaunal behavior and increase in behavioral plasticity, *i.e.* rapid adaptive behavior expressed in new contexts (Gherardi et al., 2012; Scapini, 2014). Comparative analyses of populations from different beaches showed an increase of behavioral variability and a decrease of genetic variation as a consequence of habitat loss (Scapini et al., 1995; Ketmaier et al., 2010). Behavioral plasticity may have different adaptive importance for dispersing or brooding species, with planktotrophic species showing less genetic diversity and higher phenotypic plasticity (Soares et al., 1999). The threat of global warming requires the ability to predict the differential effects of a changing environment on sandy beach species with dissimilar life cycles (Defeo and McLachlan, 2011).

Considering the importance of ambient energy variables (temperature and productivity) and local habitat conditions (beach slope and tides) as leading correlates of species richness and abundance (Defeo and McLachlan, 2013; Defeo et al., 2017) and behavioral responses as active reactions of individuals to environmental changes (Fanini and Scapini, 2008), a high priority should be given to the assessment of the effects of climate change on behavioral adaptations in beach macrofauna. Proximate drivers could impact the LAZ habitats and sandy beach macrofauna, including their behavioral adaptations and, consequently, fitness (Figs. 2 and 3).

Beach macrofauna interact with their microhabitat and respond to proximate drivers affecting the LAZ (Fig. 3). The behavior expressed by an individual may change during its life (T_0 to T_n), according to the external context (the microhabitat) and internal conditions. If individuals succeed in survival and reproduction, adaptations may eventually be passed on to the successive generations and upscaling to population level occurs. Referring to climate change impacts, caused by distal, anthropogenic drivers, the question then is to what extent macrofauna can (behaviorally, *i.e.* phenotypically) adapt to proximate drivers. Identifying constraints of behavioral plasticity is a critical issue to be explored. A direct impact of climate change drivers on behavioral adaptations has not yet been modeled. However, changes or disruptions of behavioral adaptations may represent indicators of impacts at the population level, which matters for evolution (Scapini et al., 2013; 2015; 2019). Here, some illustrative examples based on long-term

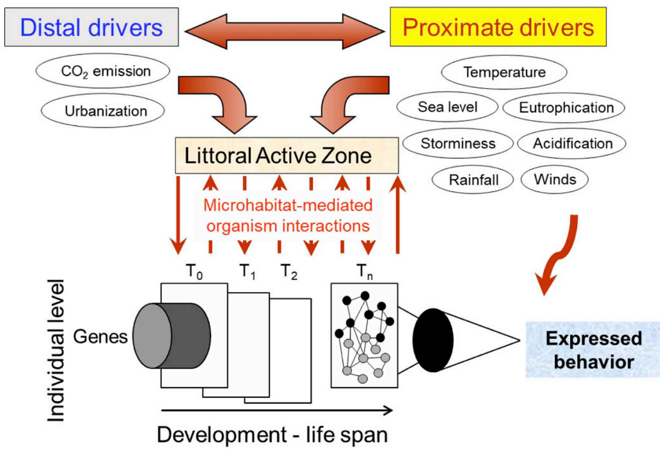

Fig. 3. Climate change distal and proximate drivers affecting the Littoral Active Zone (LAZ) and microhabitat-mediated organism interactions influencing the expressed behavior: distal drivers do not affect macrofaunal behavior directly, but the LAZ where animals find their microhabitat; macrofauna are affected by proximate drivers, which in turn influence the LAZ. At any moment, in response to specific needs and cues, individuals express behaviors developed through interactions between genes and microhabitat features. Individual development follows the time horizon from T_0 to T_n, and interactions and expressed behaviors at time T_n are different from and depend on what happened in previous life times (T_1, $T_{2, \ldots}$), as visualized by the interaction network within the organism. Modified from Campan and Scapini (2002).

observational data series, field and laboratory experiments (Table 1) are provided to explore the degree to which observations of the behavior of beach macrofauna conform to expectations under climate change. The space-for-time substitution modelling approach is also used to infer temporal trends from spatial variation in population features and ecological processes across sites that vary in environmental conditions (Blois et al., 2013; Lester et al., 2014; Celentano and Defeo, 2016).

4.1. Sea level

A projected rise in sea level will affect the narrow land-sea interface and increase erosion rates, thus modifying beach morphodynamics. Sediment loss will diminish beach volumes and cause a retreat of the coastline, which will greatly affect beach habitats, adding to the effects of coastal squeeze. Increasing human actions at the coast and shortcomings in management practices (*e.g.* nourishment, engineering structures such as groynes, revetments and breakwaters) also reduce sediment supply and therefore alter beach area, thus aggravating the scenario of concern given by sea level rise. Invertebrates with restricted distributions and dispersal inhabiting the upper zone of sandy beaches (*e.g.* crustaceans and insects) are extremely vulnerable to increasing habitat loss and fragmentation, as was documented in California and Italy on sandy beaches subjected to intense erosion and coastal squeeze (Hubbard et al., 2014; Nourisson et al., 2018; Scapini et al., 2018).

A comparison of beaches with different morphodynamic features along Mediterranean and eastern Atlantic sandy shores is used here to simulate future scenarios under climate change (Scapini et al., 2019). A strong dependence was shown of talitrid orientation on beach width and slope. On narrow and sloping beaches, higher behavioral variability was observed, indicating a disruption of the adaptation, which, under severe coastal squeeze and increasing occurrence of extreme events, will not prevent population extirpations and biodiversity loss, as was observed in pocket beaches and islands (De Matthaeis et al., 2000; Deidun, 2010). A reduced intertidal zone favors a shifting of foraging migrations of mobile macrofauna from the low shore to the vegetated sand dunes (Scapini, 1997; Colombini et al., 2013), a strategy that will not be possible with coastal squeeze. The destruction of the habitat or the reduction in organic supply from the sea will reduce adaptability of foraging behavior (Laidre, 2013).

4.2. Temperature

A sustained increase in sea surface temperature (SST) may change water and sand properties and eventually modify local hydrodynamic conditions. Beach invertebrates are sensitive to changes in their thermal limits and, therefore, they are increasingly unable to acclimate to changing temperatures, particularly at the trailing range edge of their geographical distributions (Schoeman et al., 2014). Warming has a notable influence on life history traits and processes, including changes in individual growth, population structure and the extent of reproductive and recruitment periods (Marques et al., 2003). The intensity and directionality of these responses vary according to the phylogeographic origin of the species and the intrinsic characteristics of life history (McLachlan and Defeo, 2018).

Long-term trends were observed in demographic and biological traits of sandy beach species of cool-water origin (*e.g.* the yellow clam *Mesodesma mactroides* in the Southwestern Atlantic Ocean, SAO). These were correlated with the systematic increase in SST and consistent with expectations under climate change. These are: (1) occurrence of mass mortalities in concurrence with increasing SST, and (2) lower population abundance, rates of fecundity, recruitment and adult survival, clearly reducing fitness (Herrmann et al., 2011; Ortega et al., 2012; 2016). In contrast to the trends observed for this cool-water species, increasing abundance was found in species of SAO beaches that favor warmer conditions, such as the wedge clam *Donax hanleyanus* and the mole crab *Emerita brasiliensis* (Defeo, 2003; Herrmann et al., 2009). For the mole crab, a 20-year study on an Uruguayan beach showed that with increasing SST: (1) abundance and individual growth rates increased, and (2) reproductive and recruitment periods were more extended, recruitment increased and population structure was multimodal (Celentano and Defeo, 2016). The advanced and extended breeding and recruitment seasons of *E. brasiliensis* denote a positive response of species with tropical affinities to increasing temperatures at the cold (leading) edge of its range, thus conforming to expected phenological responses to global warming (Schwartz, 2003; Parmesan, 2007; Poloczanska et al., 2013; Schoeman et al., 2014).

A main prediction of the adaptive behavior to warming in sandy beach macrofauna may be an increase in the duration and phenology of reproductive and recruitment events in species with warm-water affinities at the leading edge of their distribution, whereas species with cold-water affinities will follow the reverse trend. These changes will be accompanied by others that also reflect a trend toward tropicalization, such as an increase in growth rates and decrease in individual size and life span. The narrow range endemic species would be at greatest risk, as their rates of range extension might be outpaced by changes in temperature, making these taxa particularly vulnerable to this proximate driver. A lack of thermal “safety net” at trailing edges leaves these species vulnerable to increasing temperatures, which could lead to mass mortalities and local extirpations and therefore contractions of their distribution ranges (McLachlan and Defeo, 2018).

Activity patterns of most species in temperate areas are related to habitat variability and seasonality, which may be impacted by temperature rise; as a consequence, beach populations may face a disruption of their annual rhythms and change the seasonality of rhythm expression (Nardi et al., 2003; Nasri-Ammar and Morgan, 2006; Rossano et al., 2008; 2018). Habitat selection, feeding, mating, recruitment and larval settlement are all linked to seasonality, synchronized by various *zeitgeber* (Naylor, 2010). In a scenario of tropicalization under global warming, some synchronizers may no longer be efficient, reducing fitness, with eventual biodiversity loss.

The predicted temperature rise may affect burrowing behavior through changes in oxygen availability and water content within burrows. With increasing temperatures, the depth of burrows was observed to decrease and competition for burrows increase (Dugan et al., 2004; Sassa and Watabe, 2008; Gherardi et al., 2012). In intertidal mollusks, mean burrowing rates are expected to increase as a response to increasing temperatures (McLachlan and Defeo, 2018). In low-lying coastal areas, sea level rise could cause beach flooding, with consequent changes in groundwater level and suction-dynamics, affecting sediment compaction and, consequently, burrowing of supralittoral macrofauna (Sassa et al., 2014). The reduced fitness may cause species range shifts, distributional changes and biodiversity loss in sensitive species.

4.3. Onshore winds and storminess

Warmer air and water may increase storminess and frequency and intensity of onshore waves and winds, which in turn will impact the LAZ. More frequent and intense onshore winds, together with rising sea levels, will augment swash width and strength, decrease beach width and accelerate beach erosion rates, modifying beach morphodynamic features. The implications for the macrofauna may differ for intertidal species and supralittoral ones. Storm events in the surf can cause significant mortality in intertidal populations, which are stranded in the upper beach zones by larger waves, being unable to return to the intertidal (McLachlan et al., 1996). Supralittoral species with restricted distribution and dispersal are expected to experience habitat loss and mass mortalities with increasing storminess, particularly under coastal squeeze.

Supratidal macrofauna may anticipate extreme events by changing migration patterns, from the shoreline to the dune, where they may find a safe habitat (Scapini et al., 1992; Colombini et al., 2013). However, the loss of dune habitats may cause population mortality. Under abrupt decreases in atmospheric pressure, supratidal macrofauna was shown to anticipate storm events by changing orientation from seawards to landwards, towards a (predicted) safer zone (Scapini et al., 2002). Behavioral adaptations of marine animals appear fine-tuned to changes in pressure, yet these responses are still little studied in sandy beach macrofauna. In the intertidal zone, the motility of surfing gastropods for scavenging is driven by surf and surface currents and increasing storminess may disrupt this adaptation (Harris et al., 2017).

Habitat loss and population extirpations are the main predictions under a scenario of increasing storminess. Changes in zonation are also predicted, with increasing competition for resources, consequent decrease of fitness and population abundance and diversity.

4.4. Rainfall

Predicted rainfall increase may cause a decrease in salinity due to increased freshwater flow from land into the marine environment; at high latitudes, the melting of polar caps will add to this impact. Excessive precipitation and flooding will also raise groundwater levels, thereby increasing swash run-up distances and beach erosion rates. Sudden changes in salinity and salinity range may increase, particularly in transitional environments such as estuaries, therefore augmenting beach instability conditions (Lercari and Defeo, 1999, 2015; Colombini et al., 2006). The increase in rainfall and water transport by rivers interacts with sea level rise, impacting beach macrofauna communities. In estuarine beaches, salinity changes entrain tidal rhythms of activity, reproduction and recruitment (Naylor, 2010). Unpredictable salinity changes due to increased rainfall may disrupt the adaptation to tidal periodicity. While adult individuals will be able to counteract such changes through displacement or changes in the expression of activity rhythms, larvae settlement may fail under unsuitable salinity conditions, with negative consequences on recruitment. Habitat selection behavior (substrate choice) in mobile beach species is part of the osmoregulation process, which can affect survival rates. Sandy beach crustaceans chose the most suitable salinity within their tolerance range, independently of the salinity of their home beach (Fanini et al., 2012; 2017). Avoidance reactions of abnormal salt concentration were observed in supratidal macrofauna after submersion in unsuitable salinity (freshwater or high salt concentration) (Scapini, 1979). Many mobile beach species do not adapt physiologically (osmoregulation) but behaviorally (substrate choice and orientation), which may be critical under a scenario of decreasing salinity.

A decrease in salinity through freshwater inflow and rising groundwater will cause habitat quality to deteriorate and may cause an increase in the relative representation of freshwater species, including invasive ones, eventually competing with resident species (Persson, 2001; Herkül et al., 2006; Fanini et al., 2017). Invasive intertidal beach-hoppers, clinging to wrack, have extended their distribution range in north-eastern Baltic beaches, where increased wrack mass has been transported by storms; the invasions by osmotically-tolerant alien species (*e.g. Platorchestia platensis*) or freshwater ones (*e.g. Cryptorchestia garbinii*) are aggravated by decreasing salinity caused by polar ice melting (Herkül et al., 2006). The Asian clam *Corbicula fluminea* has been increasingly documented in estuarine sandy beaches and a spread of this invasive species is predicted under climate change (Lercari and Defeo, 2015; Reyna et al., 2018). Under a scenario of increasing freshwater run-off and polar cap melting, it is predicted that invasive species will expand their distribution range from freshwater bodies to estuarine sandy beaches. Competition for resources with endemic species is expected, decreasing endemic population fitness and affecting community composition.

4.5. Acidification

Declining pH and carbonate saturation attributed to climate change are expected to alter water chemistry properties in the surf zone. Ocean acidification might affect beach species with calcified structures in their anatomy (especially mollusks and crustaceans), reducing calcification rates and calcium metabolism. However, very large quantities of biogenic carbonate already present in beach sediments constitute a buffer system flushing through the beach system, which may counteract ocean acidification effects on beach species (Schoeman et al., 2014).

Observational and experimental evidence from other marine ecosystems (there are no examples for sandy beaches) showed that the reproductive behavior, breeding success and survival of offspring will be less affected by acidic conditions in species with parental care (brooders and direct developers) than in broadcast spawners with pelagic larval development (Byrne, 2011; Lucey et al., 2015). Thus, it is predicted that behavioral adaptations related to reproduction will be differentially affected by ocean acidification in sandy beach macrofauna as follows (in increasing order): supralittoral peracarids $<$ intertidal peracarids $<$ intertidal mollusks and crustaceans with parental care (brooders) $<$ broadcast spawners with external fertilization and planktonic larvae. Differential changes in behavior related to avoidance of stressful conditions and habitat unsuitability are also expected, particularly during larval settlement, as this phase is strongly dependent on innate behavioral and sensory adaptations (Fig. 1). Species with pelagic larval stages may also be directly affected by large scale, climate-driven changes in prevailing oceanographic systems, particularly affecting migration behavior.

Many species showed a decrease in settlement under elevated pCO_2 and reduced pH, which cause reductions in the larval sensory capacity and alter settlement substrates (Stanley et al., 2012; Espinel-Velasco et al., 2018). Reduced settlement and recruitment and increasing mortality rates are expected for species with a non-compensatory capacity (*i.e.* visual cues instead of chemical ones). Altered sensory capacity may also affect homing in sandy beach decapods, which would be more susceptible to predation and less efficient in competition for mate and space (Vannini and Cannicci, 1995; Gherardi et al., 2012).

Foraging may be altered by changes in pH. In the south-eastern Pacific littoral, *Orchestoidea tuberculata* forages on the brown algae *Durvillaea antarctica*, whose nutritive characteristics are modified by changes in CO_2 levels in seawater. Feeding preference was observed on seaweeds exposed to lower levels of CO_2, also suggesting a lower palatability of seaweed exposed to elevated CO_2 levels (Duarte et al., 2016). It is predicted that algal palatability would be affected by ocean acidification, forcing algal-consumers to display compensatory feeding (higher consumption of lower quality food), therefore increasing the feeding energetic cost. Changes in feeding behavior and/or eventual colonization of new beaches are expected to occur under the prolonged absence of good nutritional items. Therefore, food preference, consumption and absorption efficiency may be affected by ocean acidification, causing a deterioration of animal body conditions, as an estimate of foraging success, ultimately affecting fitness.

4.6. Eutrophication

Red tides, also known as harmful algal blooms (HAB), have seriously affected the health of sandy beach ecosystems and regional economies, especially as their frequency, magnitude and duration are increasing. Nutrient enrichment derived from human activities, acting together with climate change drivers (including increasing SST and onshore winds), may be main factors of the worldwide increase in frequency, intensity and periodicity of red tides (Hoagland and Scatasta, 2006; Dyson and Huppert, 2010; Rodríguez et al., 2011; Anderson et al., 2012). Several suspension feeders, including clams and mole crabs, have been increasingly affected by red tides, which can cause mass mortalities or render these suspension feeders not fit for human consumption (McLachlan et al., 1996; Defeo, 2003; Gianelli et al., 2019), thereby affecting the whole food web (Lercari et al., 2018). Large-scale changes in the composition of phytoplankton community have been documented in the surf zone of sandy beaches together with HAB, including also an increasing representation of species with warm-water affinities (Martínez et al., 2017). Therefore, it is expected that the quality and quantity of food, and thus the foraging behavior, will be affected in sandy beach suspension feeders.

In bivalves, valve activity is affected by food concentration and quality. With non-toxic food, clams maintain open valves to provide continuous ventilation and inflow through the gills and mantle cavity. However, valve closure was documented under the occurrence of toxic dinoflagellates, which may be a behavioral mechanism directed to control water inflow through the body cavity and avoid toxic cells (Basti et al., 2009). It is predicted that the increasing occurrence and magnitude of HAB will increase valve adduction activities, thus reducing the amount and quality of food and oxygen uptake, affecting body condition and fitness.

Mass occurrences of drifting macroalgae mats (green and golden tides) have been increasingly documented in sandy beaches, altering water and sediment properties (Smetacek and Zingone, 2013). Eutrophication is responsible for the increasing frequency and magnitude of green and golden tides worldwide (Charlier et al., 2008; Ye et al., 2011). Other proximate drivers related to global change (temperature, acidification), acting simultaneously, may accelerate this process (Xu et al., 2017). The production of toxic hydrogen sulphide (H_2S) from decomposition under anoxic conditions affects the physico-chemical features of the habitat and the biota. Therefore, these events may alter habitat quality and availability for the resident macrofauna and affect the beach food-web. Recent studies documented species-specific responses to green tides along the coastline of Brittany, France: herbivorous marine invertebrates and some suspension feeders benefited from the presence of *Ulva* mats, whereas large sub-surface deposit feeders and bivalve drifters, which surf up and down the shore with the tides were negatively affected (Quillien et al., 2015a). The overall diversity of intertidal benthic macrofauna decreased in the presence of green tides (Quillien et al., 2015b), but little effect was detected on subtidal communities or flatfish (Quillien et al., 2018).

It is predicted that intertidal forms will be more affected than subtidal and supralittoral ones by eutrophication because toxic compounds may accumulate in the sediment of the intertidal zone. Changes in community composition are expected under climate change driven eutrophication, with increasing occurrence of mobile supralittoral herbivorous species, which may increase their habitat and food quality and availability through adaptive changes of behavior (habitat selection, migrations, food selection) and/or exploitation of the dune habitats (Colombini et al., 2013). By contrast, the linear and narrow habitat of intertidal species will be even more restricted and could cause local extirpations.

5. Discussion and conclusions

Population size or growth rate against a background of climate change is an integrated outcome of complex interactions among fundamental biological, ecological and evolutionary traits and processes, which together comprise adaptive capacity (Dawson et al., 2011). The relevance of behavioral adaptations to changing sandy beaches has been considered mainly as a response capacity in the framework of macrofauna adaptability to changing local conditions of the habitat. Our literature review has shown the widespread behavioral responses in sandy beach macrofauna to environmental features, which were valuable to postulate specific hypotheses on potential macrofaunal adaptations to a changing climate. Biota adaptations to climate change pressure include three interlinked processes: (1) plasticity, (2) dispersal and (3) evolution (O'Connor et al., 2012). Behavioral plasticity (1) assumes a major role for survival of sandy beach macrofauna in new environments during processes (2) and (3). The evolution of new adaptations requires time to occur, but behavioral responses will allow the survival of individuals in a new habitat. Behavioral adaptations contribute to fitness and, through evolutionary time, may become more and more adapted to specific microhabitat features. Under climate change, it is predicted that strictly adapted endemic sandy beach fauna will be especially subjected to local extirpations, while species with a large reaction norm (*i.e.* euryoecious species with phenotypic - physiological and behavioral - plasticity) may face changes by dispersal and exploitation of new niches. Nevertheless, there may be species that facilitate the survival and resilience of other (more sensitive) species, even under future climate conditions (Bulleri et al., 2018). Thus, biological interactions, including behavioral ones related to interspecific and intraspecific competition, prey-predator relationships, reproduction and recruitment, may play an important role in structuring sandy beach macrofauna communities under climate change. Beach environments are inter-connected (*e.g.* by coastal continuity, longshore currents, passive transportation of organisms by stranded material or boats), and therefore the colonization of novel habitats by sandy beach macrofauna is likely, particularly, but not exclusively, for those species with pelagic larval dispersal (Bishop et al., 2017).

Our literature review regarding behavioral adaptations of macrofauna to changing environments has revealed the loss of behavioral specificity and complexity under impacts on the microhabitat (Table 1S, Supplementary Material). Under climate change, the predicted outcome will be a decrease of fitness that could eventually lead to population extirpations and biodiversity loss (Table 1; Elliott et al., 2015). In this context, rigid adaptations to a specific microhabitat may result in a constraint and behavioral plasticity may be a better strategy for population survival under climate change. An increase in behavioral variation is predicted, which may represent an early warning signal. However, increasing pressure of climate change drivers interacting with human actions on sandy beaches could lead to impaired or disrupted behavioral adaptations, threatening fitness, population survival and eventually ecosystem functioning. Sandy beach ecosystems will always exist as boundaries between sea and land, but the specificity of these ecotones, characterized by fine-tuned macrofaunal adaptations, will likely be lost under climate change pressure. The limits to which behavior can adapt to environmental changes are worthy of exploration, in view of modeling scenarios under climate change (Scapini et al., 2019).

Comparative analyses of behavioral adaptations in macrofauna populations with a wide geographic range (Table 1S, Supplementary Material) are suitable to highlight the adaptation potential under climate change impacts, also considering the large distribution range of most sandy-beach macrofauna species. On the other hand, common-garden experiments, while recommended to test specific hypotheses on the effects of microhabitat change, require time, depending on the life cycle of species (*e.g.* decades for plant populations, Germino et al., 2019). The same constraint exists for long-time series observations, which must reflect accelerating changes under climate change pressure and anthropogenic impacts (McLachlan and Defeo, 2018). Population substitution by invasive alien species, already notable and occurring in large areas in marine environments (Cardeccia et al., 2018), are also predicted for sandy beaches.

Climate change is a global process (Elliott et al., 2015), in which the sources of impact are multiple and interacting with many effects (Fig. 2, Table 1), posing novel questions on the potential adaptation of sandy beach macrofauna and its narrow habitat. The predicted scenarios under climate change may thus be complex. Degrading environmental features will impact on ecological fitness and a loss of biodiversity will be the outcome of the negative pressures originated by climate change. If sandy beaches and the ecosystem services and societal goods and benefits they provide are to be conserved, detailed insights on macrofaunal adaptations (including behavior) and the consequences of their predicted disruption by climate driven stressors, are needed to provide mechanistic explanations of changes across geographic areas. The limits to which sandy beach macrofauna responds and can behaviorally adapt to environmental change require further exploration, in view of the increasing influence of the long-lasting climate driven stressors threatening these ecosystems at risk.

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Appendix A. Supplementary data

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References

Anderson, D.M., Cembella, A.D., Hallegraeff, G.M., 2012. Progress in understanding harmful algal blooms: paradigm shifts and new technologies for research, monitoring, and management. Ann. Rev. Mar. Sci. 4, 143–176.

Badyaev, A.V., 2005. Stress-induced variation in evolution: from behavioural plasticity to genetic assimilation. Proc. Biol. Sci. 272, 877–886.

Basti, L., Nagai, K., Shimasaki, Y., Oshima, Y., Honjo, T., Segawa, S., 2009. Effects of the toxic dinoflagellate *Heterocapsa circularisquama* on the valve movement behaviour of the Manila clam *Ruditapes philippinarum*. Aquaculture 291, 41–47.

Baker, B.S., Taylor, B., Hall, J.C., 2001. Are complex behaviors specified by dedicated regulatory genes? Reasoning from *Drosophila*. Cell 105, 13–24.

Bakun, A., 1990. Global climate change and intensification of coastal ocean upwelling. Science 247, 198–201.

Berthold, P., Helbig, A.J., Mohr, G., Querner, U., 1992. Rapid microevolution of migratory behaviour in a wild bird species. Nature 360, 668–670.

Bezuidenhout, K., Nel, R., Hauser, L., 2014. Demographic history, marker variability and genetic differentiation in sandy beach fauna: what is the meaning of low FST's? Estuar. Coast. Shelf Sci. 150, 120–124.

Bishop, M.J., Mayer-Pinto, M., Airoldi, L., Firth, L.B., Morris, R.L., Loke, L.H.L., Hawkins, S.J., Naylor, L.A., Coleman, R.A., Chee, S.Y., Dafforn, K.A., 2017. Effects of ocean sprawl on ecological connectivity: impacts and solutions. J. Exp. Mar. Biol. Ecol. 492, 7–30.

Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., Ferrier, S., 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proc. Natl. Acad. Sci. U.S.A. 110, 9374–9379.

Borgioli, C., Marchetti, G.M., Scapini, F., 1999. Variation in zonal recovery in four *Talitrus saltator* populations from different coastlines: a comparison of orientation in the field and in an experimental arena. Behav. Ecol. Sociobiol. 45, 70–85.

Brown, A.C., 1996. Behavioural plasticity as a key factor in the survival and evolution of the macrofauna on exposed sandy beaches. Rev. Chil. Hist. Nat. 69, 469–474.

Brown, A.C., McLachlan, A., 2002. Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. Environ. Conserv. 29, 62–67.

Bulleri, F., Eriksson, B.K., Queirós, A., Airoldi, L., Arenas, F., Arvanitidis, C., Bouma, T.J., Crowe, T.P., Davoult, D., Guizien, K., Iveša, L., Jenkins, S.R., Michalet, R., Olabarria, C., Procaccini, G., Serrão, E.A., Wahl, M., Benedetti-Cecchi, L., 2018. Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. PLoS Biol. 16, e2006852.

Byrne, M., 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. Chapter 1. In: Gibson, R.N., Atkinson, R.J.A., Gordon, J.D.M. (Eds.), Oceanogr. Mar. Biol. Annu. Rev., vol 49. pp. 1–42.

Campan, R., Scapini, F., 2002. Ethologie: Approche Systémique du Comportement. De Boeck Supérieur, Bruxelles 742 pp.

Cardeccia, A., Marchini, A., Occhipinti-Ambrogi, A., Galil, B., Gollasch, S., Minchin, D., Narščius, A., Olenin, S., Ojaveer, H., 2018. Assessing biological invasions in European Seas: biological traits of the most widespread non-indigenous species. Estuar. Coast. Shelf Sci. 201, 17–28.

Carstensen, D., Riascos, J.M., Heilmayer, O., Arntz, W.E., Laudien, J., 2010. Recurrent, thermally-induced shifts in species distribution range in the Humboldt current upwelling system. Mar. Environ. Res. 70, 293–299.

Celentano, E., Defeo, O., 2016. Effects of climate on the mole crab *Emerita brasiliensis* on a dissipative beach in Uruguay. Mar. Ecol. Prog. Ser. 552, 211–222.

Charlier, R.H., Morand, P., Finkl, C.W., 2008. How Brittany and Florida coasts cope with green tides. Int. J. Environ. Stud. 65, 191–208.

Clark, M.S., Thorne, M.A.S., King, M., Hipperson, H., Hoffman, J.I., Peck, L.S., 2018. Life in the intertidal: cellular responses, methylation and epigenetics. Funct. Ecol. 32, 1982–1994.

Colombini, I., Chaouti, A., Fallaci, M., Gagnarli, E., Scapini, F., Bayed, A., Chelazzi, L., 2006. Effects of freshwater discharge on terrestrial arthropods in Atlantic and Mediterranean sandy shores. In: Scapini, F. (Ed.), Proceedings of the MEDCORE International Conference. Firenze University Press, Firenze, pp. 233–261.

Colombini, I., Fallaci, M., Gagnarli, E., Rossano, C., Scapini, F., Chelazzi, L., 2013. The behavioural ecology of two sympatric talitrid species, *Talitrus saltator* (Montagu) and *Orchestia gammarellus* (Pallas) on a Tyrrhenian sandy beach dune system. Estuar. Coast. Shelf Sci. 117, 37–47.

Costa, L.L., Zalmon, I.R., 2019. Sensitivity of macroinvertebrates to human impacts on sandy beaches: a case study with tiger beetles (Insecta, Cicindelidae). Estuar. Coast. Shelf Sci. 220, 142–151.

Dawson, M.N., Barber, P.H., González-Guzmán, L.I., Toonen, R.J., Dugan, J.E., Grosberg, R.K., 2011. Phylogeography of *Emerita analoga* (Crustacea, Decapoda, Hippidae), an eastern Pacific Ocean sand crab with long-lived pelagic larvae. J. Biogeogr. 38, 1600–1612.

Defeo, O., 2003. Marine invertebrate fisheries in sandy beaches: an overview. J. Coast. Res. 35, 56–65.

Defeo, O., Barboza, C.A., Barboza, F.R., Aeberhard, W.H., Cabrini, T.M., Cardoso, R.S., Ortega, L., Skinner, V., Worm, B., 2017. Aggregate patterns of macrofaunal diversity: an interocean comparison. Glob. Ecol. Biogeogr. 26, 823–834.

Defeo, O., McLachlan, A., 2011. Coupling between macrofauna community structure and beach type: a deconstructive meta-analysis. Mar. Ecol. Prog. Ser. 433, 29–41.

Defeo, O., McLachlan, A., 2013. Global patterns in sandy beach macrofauna: species richness, abundance, biomass and body size. Geomorphology 199, 106–114.

Defeo, O., McLachlan, A., Schoeman, D., Schlacher, T., Dugan, J., Jones, A., Lastra, M., Scapini, F., 2009. Threats to sandy beach ecosystems: a review. Estuar. Coast. Shelf Sci. 81, 1–12.

Deidun, A., 2010. Challenges to the conservation of biodiversity on small islands: the case of the Maltese Islands. Int. J. Arts Sci. 3, 175–187.

De Matthaeis, E., Davolos, D., Cobolli, M., Ketmaier, V., 2000. Isolation by distance in equilibrium and nonequilibrium populations of four talitrid species in the Mediterranean Sea. Evolution 54, 1606–1613.

Donelson, J.M., Sunday, J.M., Figueira, W.F., Gaitán-Espitia, J.D., Hobday, A.J., Johnson, C.R., Leis, J.M., Ling, S.D., Marshall, D., Pandolfi, J.M., Pecl, G., Rodgers, G.G., Booth, D.J., Munday, P.L., 2019. Understanding interactions between plasticity, adaptation and range shifts in response to marine environmental change. Philosoph. Trans. Roy. Soc. B 374, 20180186.

Duarte, C., Jaramillo, E., Contreras, H., Acuña, K., 2010. Cannibalism and food availability in the talitrid amphipod *Orchestoidea tuberculata*. J. Sea Res. 64, 417–421.

Duarte, C., López, J., Benítez, S., Manríquez, P.H., Navarro, J.M., Bonta, C.C., Torres, R., Quijón, P., 2016. Ocean acidification induces changes in algal palatability and herbivore feeding behavior and performance. Oecologia 180, 453–462.

Dugan, J.E., Jaramillo, E., Hubbard, D.M., Contreras, H., Duarte, C., 2004. Competitive interactions in macroinfaunal animals of exposed sandy beaches. Oecologia 139, 630–640.

Dyson, K., Huppert, D.D., 2010. Regional economic impacts of razor clam beach closures due to harmful algal blooms (HABs) on the Pacific coast of Washington. Harmful Algae 9, 264–271.

Elliott, M., Borja, Á., McQuatters-Gollop, A., Mazik, K., Birchenough, S., Andersen, J.H., Painting, S., Peck, M., 2015. *Force majeure*: will climate change affect our ability to attain Good Environmental Status for marine biodiversity? Mar. Pollut. Bull. 95, 7–27.

Espinel-Velasco, N., Hoffmann, L., Agüera, A., Byrne, M., Dupont, S., Uthicke, S., Webster, N.S., Lamare, M., 2018. Effects of ocean acidification on the settlement and metamorphosis of marine invertebrate and fish larvae: a review. Mar. Ecol. Prog. Ser. 606, 237–257.
Fanini, L., Marchetti, G.M., Baczewska, A., Sztybor, K., Scapini, F., 2012. Behavioural adaptation to different salinities in the sandhopper *Talitrus saltator* (Crustacea: Amphipoda): Mediterranean vs Baltic populations. Mar. Freshw. Res. 63, 275–281.
Fanini, L., Scapini, F., 2008. Variable orientation within a natural population of the sandhopper *Talitrus saltator* (Crustacea: Amphipoda) as a response to a variable environment: the case-study of Berkoukesh beach, Tunisia. Estuar. Coast. Shelf Sci. 77, 163–168.
Fanini, L., Zampicinini, G., Tsigenopoulos, C.S., Barboza, F.R., Lozoya, J.P., Gómez, J., Celentano, E., Lercari, D., Marchetti, G.M., Defeo, O., 2017. Life-history, substrate choice and Cytochrome Oxidase I variations in sandy beach peracaridans along the Rio de la Plata estuary. Estuar. Coast. Shelf Sci. 187, 152–159.
Gambineri, S., Scapini, F., 2008. Importance of orientation to the sun and local landscape features in young inexpert *Talitrus saltator* (Amphipoda: talitridae) from two Italian beaches differing in morphodynamics, erosion or stability. Estuar. Coast. Shelf Sci. 77, 357–368.
Germino, M.J., Moser, A.M., Sands, A.R., 2019. Adaptive variation, including local adaptation, requires decades to become evident in common gardens. Ecol. Appl. 29, e01842.
Gherardi, F., Aquiloni, L., Tricarico, E., 2012. Behavioral plasticity, behavioral syndromes and animal personality in crustacean decapods: an imperfect map is better than no map. Curr. Zool. 58, 567–579.
Gianelli, I., Ortega, L., Defeo, O., 2019. Modeling short-term fishing dynamics in a small-scale intertidal shellfishery. Fish. Res. 209, 242–250.
Harris, L.R., Abrahams, K., Bezuidenhout, K., Nel, R., 2017. The relative role of intrinsic and extrinsic factors driving alongshore movement of swash-riding smooth plough shells, *Bullia rhodostoma*. J. Exp. Mar. Biol. Ecol. 486, 77–86.
Hazlett, B.A., 1995. Behavioral plasticity in Crustacea: why not more? J. Exp. Mar. Biol. Ecol. 193, 57–66.
Herkül, K., Kotta, J., Kotta, I., 2006. Distribution and population characteristics of the alien talitrid amphipod *Orchestia cavimana* in relation to environmental conditions in the Northeastern Baltic Sea. Helgol. Mar. Res. 60, 121–126.
Herrmann, M., Alfaya, J.E.F., Lepore, M.L., Penchaszadeh, P.E., Arntz, W.E., 2011. Population structure, growth and production of the yellow clam *Mesodesma mactroides* (Bivalvia: mesodesmatidae) from a high-energy, temperate beach in northern Argentina. Helgol. Mar. Res. 65, 285–297.
Herrmann, M., Carstensen, D., Fischer, S., Laudien, J., Penchaszadeh, P.E., Arntz, W.E., 2009. Population structure, growth, and production of the wedge clam *Donax hanleyanus* (Bivalvia: donacidae) from Northern Argentinean beaches. J. Shellfish Res. 28, 511–526.
Hoagland, P., Scatasta, S., 2006. The economic effects of harmful algal blooms. In: Granéli, E., Turner, J.T. (Eds.), Ecology of Harmful Algae. Ecological Studies (Analysis and Synthesis), vol 189. Springer, Berlin, Heidelberg, pp. 391–402.
Houston, J.R., Dean, R.G., 2012. Comparisons at tide-gauge locations of glacial isostatic adjustment predictions with global positioning system measurements. J. Coast. Res. 28, 739–744.
Hubbard, D.M., Dugan, J.E., Schooler, N.K., Viola, S.M., 2014. Local extirpations and regional declines of endemic upper beach invertebrates in southern California. Estuar. Coast. Shelf Sci. 150, 67–75.
Jones, A., Gladstone, W., Hacking, N., 2007. Australian sandy-beach ecosystems and climate change: ecology and management. Aust. Zool. 34, 190–202.
Kelly, M., 2019. Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes. Philosoph. Trans. Roy. Soc. B 374, 20180176.
Ketmaier, V., De Matthaeis, E., Fanini, L., Rossano, C., Scapini, F., 2010. Variation of genetic and behavioral traits in the sandhopper *Talitrus saltator* (Crustacea Amphipoda) along a dynamic beach. Ethol. Ecol. Evol. 22, 17–35.
Kralj-Fišer, S., Schneider, J.M., 2012. Individual behavioural consistency and plasticity in an urban spider. Anim. Behav. 84, 197–204.
Kralj-Fišer, S., Schuett, W., 2014. Studying personality variation in invertebrates: why bother? Anim. Behav. 91, 41–52.
Lagar, M.C., Pazzagli, L., Cappugi, G., Giusfredi, G., Colombini, I., Fallaci, M., Chelazzi, L., Scapini, F., 2016. Enzyme activity and trophic links of macroarthropods living on an exposed Mediterranean beach–dune system. Ital. J. Zool. 83, 221–232.
Laidre, M.E., 2013. Foraging across ecosystems: diet diversity and social foraging spanning aquatic and terrestrial ecosystems by an invertebrate. Mar. Ecol. 34, 80–89.
Lercari, D., Defeo, O., 1999. Effects of freshwater discharge in sandy beach populations: the mole crab *Emerita brasiliensis* in Uruguay. Estuar. Coast. Shelf Sci. 49, 457–468.
Lercari, D., Defeo, O., 2015. Large-scale dynamics of sandy beach ecosystems in transitional waters of the Southwestern Atlantic Ocean: species turnover, stability and spatial synchrony. Estuar. Coast. Shelf Sci. 154, 184–193.
Lercari, D., Defeo, O., Ortega, L., Orlando, L., Gianelli, I., Celentano, E., 2018. Long-term structural and functional changes driven by climate variability and fishery regimes in a sandy beach ecosystem. Ecol. Model. 368, 41–51.
Lester, R.E., Close, P.G., Barton, J.L., Pope, A.J., Brown, S.C., 2014. Predicting the likely response of data-poor ecosystems to climate change using space-for-time substitution across domains. Glob. Chang. Biol. 20, 3471–3481.
Lima, M., Brazeiro, A., Defeo, O., 2000. Population dynamics of the yellow clam *Mesodesma mactroides*: recruitment variability, density-dependence and stochastic processes. Mar. Ecol. Prog. Ser. 207, 97–108.
Lucey, N.M., Lombardi, C., DeMarchi, L., Schulze, A., Gambi, M.C., Calosi, P., 2015. To brood or not to brood: are marine invertebrates that protect their offspring more resilient to ocean acidification? Sci. Rep. 5, 12009.
Marques, J., Gonçalves, S., Pardal, M., Chelazzi, L., Colombini, I., Fallaci, M., Bouslama, M., El Gtari, M., Charfi-Cheikhrouha, F., Scapini, F., 2003. Comparison of *Talitrus saltator* (Amphipoda Talitridae) biology, dynamics, and secondary production in Atlantic (Portugal) and Mediterranean (Italy and Tunisia) populations. Estuar. Coast. Shelf Sci. 58S, 127–148.
Martínez, A., Méndez, S., Fabre, A., Ortega, L., 2017. Intensificación de floraciones de dinoflagelados marinos en Uruguay. Innotec 13, 19–25.
McLachlan, A., Defeo, O., 2018. The Ecology of Sandy Shores. Elsevier, Academic Press, London 574 pp.
McLachlan, A., Dugan, J.E., Defeo, O., Ansell, A.D., Hubbard, D.M., Jaramillo, E., Penchaszadeh, P.E., 1996. Beach clam fisheries. Oceanogr. Mar. Biol. Annu. Rev. 34, 163–232.
Nardi, M., Morgan, E., Scapini, F., 2003. Seasonal variation in the free-running period in two *Talitrus saltator* populations from Italian beaches differing in morphodynamics and human disturbance. Estuar. Coast. Shelf Sci. 58S, 199–206.
Nasri-Ammar, K., Morgan, E., 2006. Seasonality of the endogenous activity rhythm in *Talitrus saltator* (Montagu) from a sandy beach in northeastern Tunisia. Biol. Rhythm Res. 37, 479–488.
Naylor, E., 2010. Chronobiology of Marine Organisms. Cambridge University Press, Cambridge, UK 242 pp.
Nourisson, D.H., Scapini, F., Milstein, A., 2018. Small-scale changes of an arthropod beach community after hard-engineering interventions on a Mediterranean beach. Region. Stud. Mar. Sci. 22, 21–30.
O'Connor, M.J., Selig, E.R., Pinsky, M.L., Altermatt, F., 2012. Toward a conceptual synthesis for climate change responses. Glob. Ecol. Biogeogr. 21, 693–703.
Ortega, L., Castilla, J.C., Espino, M., Yamashiro, C., Defeo, O., 2012. Effects of fishing, market price, and climate on two South American clam species. Mar. Ecol. Prog. Ser. 469, 71–85.
Ortega, L., Celentano, E., Delgado, E., Defeo, O., 2016. Climate change influences on abundance, individual size and body abnormalities in a sandy beach clam. Mar. Ecol. Prog. Ser. 545, 203–213.
Pardi, L., Scapini, F., 1983. Inheritance of solar direction finding in sandhoppers: mass-crossing experiments. J. Comp. Physiol. 151, 435–440.
Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob. Chang. Biol. 13, 1860–1872.
Pennings, S.C., Carefoot, T.H., Zimmer, M., Danko, J.P., Ziegler, A., 2000. Feeding preferences of supralittoral isopods and amphipods. Can. J. Zool. 78, 1918–1929.
Persson, L.E., 2001. Dispersal of *Platorchestia platensis* (Kröyer) (Amphipoda: talitridae) along Swedish coasts: a slow but successful process. Estuar. Coast. Shelf Sci. 52, 201–210.
Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., 2013. Global imprint of climate change on marine life. Nat. Clim. Change 3, 919–925.
Quillien, N., Nordström, M.C., Guyonnet, B., Maguer, M., Le Garrec, V., Bonsdorff, E., Grall, J., 2015a. Large-scale effects of green tides on macrotidal sandy beaches: habitat-specific responses of zoobenthos. Estuar. Coast. Shelf Sci. 164, 379–391.
Quillien, N., Nordström, M.C., Gauthier, O., Bonsdorff, E., Paulet, Y.M., Grall, J., 2015b. Effects of macroalgal accumulations on the variability in zoobenthos of high-energy macrotidal sandy beaches. Mar. Ecol. Prog. Ser. 522, 97–114.
Quillien, N., Nordström, M.C., Le Bris, H., Bonsdorff, E., Grall, J., 2018. Green tides on inter-and subtidal sandy shores: differential impacts on infauna and flatfish. J. Mar. Biol. Assoc. U. K. 98, 699–712.
Renn, S.C.P., Schumer, M., 2013. Genetic accommodation and behavioural evolution: insights from genomic studies. Anim. Behav. 85, 1012–1022.
Reyna, P., Nori, J., Ballesteros, M.L., Hued, A.C., Tatián, M., 2018. Targeting clams: insights into the invasive potential and current and future distribution of Asian clams. Environ. Conserv. 45, 387–395.
Rodríguez, G.R., Villasante, S., do Carme García-Negro, M., 2011. Are red tides affecting economically the commercialization of the Galician (NW Spain) mussel farming? Mar. Policy 35, 252–257.
Rossano, C., Morgan, E., Scapini, F., 2008. Variation of the locomotor activity rhythms in three species of talitrid amphipods, *Talitrus saltator, Orchestia montagui*, and *O. gammarellus*, from various habitats. Chronobiol. Int. 25, 511–532.
Rossano, C., Nourisson, D.H.,R., Scapini, F., 2018. Locomotor activity rhythm of *Talitrus saltator* (Crustacea, Amphipoda) on a progradating sandy beach. Biol. Rhythm Res. 49, 697–716.
Sassa, S., Watabe, Y., 2008. Threshold, optimum and critical geoenvironmental conditions for burrowing activity of sand bubbler crab, *Scopimera globosa*. Mar. Ecol. Prog. Ser. 354, 191–199.
Sassa, S., Watabe, Y., Yang, S., Kuwae, T., 2011. Burrowing criteria and burrowing mode adjustment in bivalves to varying geoenvironmental conditions in intertidal flats and beaches. PLoS One 6 (9), e25041.
Sassa, S., Yang, S., Watabe, Y., Kajihara, N., Takada, Y., 2014. Role of suction in sandy beach habitats and the distributions of three amphipod and isopod species. J. Sea Res. 85, 336–342.
Scapini, F., 1979. Orientation of *Talitrus saltator* Montagu (Crustacea Amphipoda) in fresh, sea and diluted sea water. Monit. Zool. Ital. 13, 71–76.
Scapini, F., 1997. Variation in scototaxis and orientation adaptation of *Talitrus saltator* populations subjected to different ecological constraints. Estuar. Coast. Shelf Sci. 44, 139–146.
Scapini, F., 2006. Keynote papers on sandhopper orientation and navigation. Mar. Freshw. Behav. Physiol. 39, 73–85.
Scapini, F., 2014. Behaviour of mobile macrofauna is a key factor in beach ecology as response to rapid environmental changes. Estuar. Coast. Shelf Sci. 150, 36–44.
Scapini, F., Aloia, A., Bouslama, M., Chelazzi, L., Colombini, I., El Gtari, M., Fallaci, M., Marchetti, G., 2002. Multiple regression analysis of the sources of variation in orientation of two sympatric sandhoppers, *Talitrus saltator* and *Talorchestia brito*, from

an exposed Mediterranean beach. Behav. Ecol. Sociobiol. 51, 403–414.
Scapini, F., Bessa, F., Gambineri, S., Bozzeda, F., 2019. Talitrid (Crustacea, Amphipoda) orientation as across scale bioindicator of sandy beaches environmental conditions: a meta-analytic approach. Estuar. Coast. Shelf Sci. 220, 25–37.
Scapini, F., Buiatti, M., De Matthaeis, E., Mattoccia, M., 1995. Orientation behaviour and heterozygosity of sandhopper populations in relation to stability of beach enviroments. J. Evol. Biol. 8, 43–52.
Scapini, F., Buiatti, M., Ottaviano, O., 1988. Phenotypic plasticity in sun orientation of sandhoppers. J. Comp. Physiol. 163, 739–747.
Scapini, F., Chelazzi, L., Colombini, I., Fallaci, M., 1992. Surface activity, zonation and migrations of *Talitrus saltator* on a Mediterranean beach. Mar. Biol. 112, 573–581.
Scapini, F., Dugan, J., 2008. Sun and landscape orientation in adult and juvenile sandhoppers *Orchestoidea tuberculata* (Amphipoda, Talitridae) from two beaches in south central Chile. Mar. Ecol. 29, 19–27.
Scapini, F., Fanini, L., Gambineri, S., Nourisson, D., Rossano, C., 2013. Monitoring changes in sandy beaches in temperate areas through sandhoppers' adaptations. Crustaceana 86, 932–954.
Scapini, F., Gambineri, S., Fanini, L., 2018. Deconstructing responses of sandy beach arthropodofauna to shoreline erosion: looking for the proper spatial scale to monitor biodiversity. Coast. Conserv. 22, 369–383.
Scapini, F., Gambineri, S., Rossano, C., ElGtari, M., Fanini, L., Nourisson, D.H., 2015. Talitrid orientation as bioindicator of shoreline stability: protected headland-bays versus exposed extended beaches. Ecol. Indicat. 53, 28–36.
Scapini, F., Ugolini, A., Pardi, L., 1985. Inheritance of solar direction finding in sandhoppers: II Differences in arcuated coastlines. J. Comp. Physiol. 156, 729–735.
Schlichting, C.D., Pigliucci, M., 1998. Phenotypic Evolution: A Reaction Norm Perspective. Sinauer Associates Incorporated, Sunderland, Massachusetts 387 pp.
Schoeman, D.S., Schlacher, T.A., Defeo, O., 2014. Climate-change impacts on sandy-beach biota: crossing a line in the sand. Glob. Chang. Biol. 20, 2383–2392.
Schoeman, D.S., Schlacher, T.A., Jones, A.R., Murray, A., Huijbers, C.M., Olds, A.D., Connolly, R.M., 2015. Edging along a warming coast: a range extension for a common sandy beach crab. PLoS One 10, e0141976.
Schwartz, M.D., 2003. Phenology: an Integrative Environmental Science. Kluwer Academic Publishers, Dordrecht, Netherlands 564 pp.
Short, A.D., 1999. Handbook of Beach and Shoreface Morphodynamics. John Wiley & Sons, Chichester 379 pp.
Sinn, D.L., Apiolaza, L.A., Moltschaniwskyj, N.A., 2006. Heritability and fitness-related consequences of squid personality traits. J. Evol. Biol. 19, 1437–1447.
Smetacek, V., Zingone, A., 2013. Green and golden seaweed tides on the rise. Nature 504, 84–88.
Soares, A.G., Scapini, F., Brown, A.C., McLachlan, A., 1999. Phenotypic plasticity, genetic similarity and evolutionary inertia in changing environments. J. Molluscan Stud. 65, 136–139.
Sokolowski, M., 2001. *Drosophila*: genetics meets behaviour. Nat. Rev. Genet. 2, 879–890.
Stanley, J.A., Radford, C.A., Jeffs, A.G., 2012. Location, location, location: finding a suitable home among the noise. Proc. Biol. Sci. 279, 3622–3631.
Sydeman, W.J., García-Reyes, M., Schoeman, D.S., Rykaczewski, R.R., Thompson, S.A., Black, B.A., Bograd, S.J., 2014. Climate change and wind intensification in coastal upwelling ecosystems. Science 345, 77–80.
Tinley, K.L., 1985. Coastal Dunes of South Africa 109. FRD, CSIR, Pretoria, South Africa 300 pp.
Vannini, M., Cannicci, S., 1995. Homing behaviour and possible cognitive maps in crustacean decapods. J. Exp. Mar. Biol. Ecol. 193, 67–91.
Viola, S.M., Hubbard, D.M., Dugan, J.E., Schooler, N.K., 2014. Burrowing inhibition by fine textured beach fill: implications for recovery of beach ecosystems. Estuar. Coast. Shelf Sci. 150, 142–148.
Watson, G.J., 2018. “Winners” and “losers” in the Anthropocene: understanding adaptation through phenotypic plasticity. Funct. Ecol. 32, 1906–1907.
West-Eberhard, M.J., 2003. Developmental Plasticity and Evolution. Oxford University Press, New York 793 pp.
Williams, J., 1995. Burrow-zone distribution of the supralittoral amphipod *Talitrus saltator* on Derbyhaven Beach, Isle of Man: a possible mechanism for regulating desiccation stress? J. Crustac. Biol. 15, 466–475.
Xu, Z., Gao, G., Xu, J., Wu, H., 2017. Physiological response of a golden tide alga (*Sargassum muticum*) to the interaction of ocean acidification and phosphorus enrichment. Biogeosciences 14, 671–681.
Ye, N.H., Zhang, X.W., Mao, Y.Z., Liang, C.W., Xu, D., Zou, J., Zhuang, Z.M., Wang, Q.Y., 2011. ‘Green tides’ are overwhelming the coastline of our blue planet: taking the world's largest example. Ecol. Res. 26, 477–485.