Herrera Acosta, César Augusto (2021) ***Biodiversity beyond species census: assessing organisms' traits and functional attributes using computer vision.*** **PhD Thesis, James Cook University.**

Biodiversity beyond species census: assessing organisms' traits and functional attributes using computer vision

Thesis submitted by

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"Until comparatively recently, ecologists were content to describe how nature "looks" (sometimes by means of fantastic terms!) and to speculate on what she might have looked like in the past or may look like in the future. Now, an equal emphasis is being placed on what nature 'does', and rightly so, because the changing face of nature can never be understood unless her metabolism is also studied. This change in approach brings the small organisms into perspective with the large, and encourages the use of experimental methods to supplement the analytic. It is evident that so long as a purely descriptive viewpoint is maintained, there is very little in common between such structurally diverse organisms as sperma-tophytes, vertebrates and bacteria. In real life, however, all these are intimately linked functionally in ecological systems, according to well-defined laws. Thus the only kind of general ecology is that which I call a 'functional ecology'..."

-- Eugene P. Odum

Fundamentals of Ecology, 1957

''New directions in science are launched by new tools much more often than by new concepts. The effect of a concept-driven revolution is to explain old things in new ways. The effect of a tool-driven revolution is to discover new things that have to be explained.''

-- Freeman Dyson

Imagined Worlds, 1997

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Abstract

Empirical and theoretical studies predict that a decrease in biodiversity will have negative impacts on the functioning of ecosystems and human well-being. Ecological and paleontological research suggests that the current extinction rate is disproportionally high in comparison to normal “background” levels. However, background and current extinction rates can be calculated only in a few well-studied and understood taxonomic groups. Concurrently, ecologists are increasingly focused on evaluating the functional characteristics of species within ecosystems, because functional diversity rather than species number fundamentally governs ecosystems. For all these reasons, it is becoming increasingly apparent that ecologists require tools that allow the extensive and intensive monitoring of species, traits, and functions across ecosystems. This is particularly true for groups that fuel important energy and matter processes in ecosystems that are already in decline, such as crabs in estuarine wetlands.

My thesis goal was to fulfil the need to develop sampling and methodological techniques that enable the collection of larger, higher quality amounts of data on species, traits and functions. I used intertidal crabs inhabiting soft sediments in estuarine wetlands as my model system, and I employed image-based sampling and computer vision algorithms to achieve this goal. Crabs living in burrows alter sediment physicochemical composition, increase plant productivity, sustain food webs and shape vegetation distribution in coastal habitats. Despite their importance, the cryptic and fossorial nature of crabs has limited our ability to study them thoroughly. Current sampling methods are invasive and destructive, or are unreliable, and conclusions drawn from these are full of uncertainty that impairs generalizations. To improve the understanding of intertidal crabs and their function within estuarine wetlands, I created a sampling and analysis workflow that uses video surveys and computer vision algorithms to assess their traits and functional attributes.

Firstly, I quantitatively compared visual census, a traditional technique to sample crabs, against video surveys to assess differences in detection, occurrence and latency to crab re-emergence for each sampling method. I used a probabilistic approach that incorporates domain knowledge, and quantifies and represents the uncertainty associated to the inference process. I found that video surveys performed consistently better in all metrics evaluated, and for most crab species. Overall, my results show that video surveys are an efficient method that can increase species detection and reduce waiting time to first crab re-emergence.

After demonstrating the advantages of using video surveys to sample intertidal crabs, I developed and implemented a workflow and software grounded on *in situ* field recordings to collect information on the movement patterns of intertidal crabs, their traits and their bioturbation activity. This software uses free and open-source computer vision and machine learning libraries to perform tasks such as motion detection, image segmentation, crab tracking and trait identification. I also employed off-the-shelf free and open-source photogrammetry software to quantify changes in the sediment volume due to crab bioturbation. I proved the utility and flexibility of computer vision algorithms to improve the study of intertidal crabs in their natural environment by extracting and characterizing movement patterns, size structure, intra-specific interactions, and bioturbation rate of 25 *Tubuca polita* individuals. This method has many advantages over traditional sampling techniques, such as low intrusiveness, greater cost-information performance, and the prospect of improvement and including additional algorithms to extract or infer crab traits and functions.

Bioturbation by burrowing crustaceans is an important ecosystem function that drives the cycle of matter and energy in soft sediments. Several techniques exist to quantify bioturbation activity of intertidal crabs. However, these are lengthy, complex and plagued with methodological flaws or assumptions. For this reason, quantitative data on crab bioturbation rates are limited. To ease these limitations and further improve the photogrammetry method used previously, I aimed to quantify the bioturbation rate of a fiddler crab species inhabiting estuarine mudflats, and its effect on sediment topography. By refining the sampling workflow, I improved the method precision to estimate bioturbation by 8-15%. I found that bioturbation rates decrease following the decline in surface activity of fiddler crabs. At its highest, crab bioturbation rate ranged from 1146 to 3108 cm^3 m^{-2} d^{-1}. Crab bioturbation increases the topographic complexity of the sediment. All these effects were spatial and time dependent, which highlights the need to conduct further observation and experiments, and take advantage of the cost effective photogrammetry method develop in this thesis.

Understanding the fine scale movement of intertidal crabs in their natural environment is fundamental to deciphering their ecology, behaviour and functional role, because crabs choose when and where to move based on their internal and external context. Thus, characterizing crabs use of space and behaviours at fine spatio-temporal resolution can inform ecologists about the underlying mechanisms driving motion and behaviour. However, the fossorial and elusive nature of intertidal crabs makes it difficult to observe them in the field, and infer their motion and activity patterns. Thus, to gain further understanding of intertidal crab movement and activity patterns, it is critical to move beyond direct visual observation to alternative tracking systems. I used the formerly developed image-based tracking method to compare and quantify variability in motion and burrow utilization pattern in 96 intertidal crabs from the superfamilies Ocypodoidea and Grapsoidea. I found that motion and burrow use were highly variable among individuals and taxonomic groups. Importantly, crabs engaged in courtship and fighting behaviour showed higher utilization areas and rate of movement than crabs engaged in feeding behaviour. These findings highlight the analytical advantages of image-based tracking methods, and the importance of simultaneously assessing motion and behaviour to understand driving factors underlying a switch in the behaviour and motion repertoire of crabs.

Computer vision is revolutionizing ecology as an emerging and effective tool to sample and retrieve biological and ecological information from images. Video surveys, computer vision analysis and algorithms have the potential to increasingly improve the amount and quality of information we can obtain from natural systems. There are several limitations that constrain the ability to extend the use of these methods to other species, habitats, and ecosystems. For instance, limited recording time, interference and occlusion of target organisms by vegetation, and the small field of observation. Recognizing these limitations is important to have a clear understanding on the capabilities and usability of new methods, and to effectively counter these limitations by developing innovations as a response to purpose-specific needs.

In this thesis, I have demonstrated how computer vision can be implemented to collect ecological data on intertidal crabs inhabiting unvegetated soft sediments. This analytical framework provides an alternative and complementary approach to the traditional and lengthy sampling techniques used to sample crabs, and it delivers a cohesive and holistic approach to evaluate traits and functional attributes of crabs. Future research should be directed to build and improve these methods, and advance their use over larger spatial and temporal scales.

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Outcomes produced during PhD candidature

Thesis Chapters

- **Herrera, C.**, Sheaves, J., Baker, R., Sheaves, M. (2020) A computer vision approach for studying fossorial and cryptic crabs. In review Ecosphere (available in *bioRxiv,* https://doi.org/10.1101/2020.05.11.085803).
- **Herrera, C.** Baker, R., Sheaves, J., Abrantes, K. and Sheaves, M. Sampling elusive intertidal crabs: leveraging video sampling for the detection of multiple taxa. In preparation, target journal Austral Ecology.
- **Herrera, C.** Baker, R., Sheaves, J., Abrantes, K. and Sheaves, M. Mapping burrows and assessing bioturbation by crabs using photogrammetry. In preparation, target journal PeerJ.
- **Herrera, C.** Baker, R., Sheaves, J., Abrantes, K. and Sheaves, M. Characterizing the fine scale movement and activity of intertidal crabs. In preparation, target journal: Journal of Animal Ecology.

Peer-reviewed papers

- Sheaves, M., Bradley, M., **Herrera, C.**, Mattone, C., Lennard, C., Sheaves, J., Konovalov, D.A. (2020) Optimizing video sampling for juvenile fish surveys: Using deep learning and evaluation of assumptions to produce critical fisheries parameters. *Fish and Fisheries*, **21**: 1259– 1276.
- Cruz-Motta, J.J., Miloslavich, P., Guerra-Castro, E., Hernández-Agreda, A., **Herrera, C.**, Barros, F., Navarrete, S.A., Sepúlveda, R.D., Glasby, T.M., Bigatti, G., Cardenas-Calle, M., Carneiro, P.B.M., Carranza, A., Flores, A.A.V., Gil-Kodaka, P., Gobin, J., Gutiérrez, J.L., Klein, E., Krull, M., Lazarus, J.F., Londoño-Cruz, E., Lotufo, T., Macaya, E.C., Mora, C., Mora, E., Palomo, G., Parragué, M., Pellizzari, F.,

Retamales, R., Rocha, R.M., Romero, L. (2020) Latitudinal patterns of species diversity on South American rocky shores: Local processes lead to contrasting trends in regional and local species diversity. *Journal of Biogeography,* **47**(9): 1966-1979.

- Hernandez-Agreda, A., Leggat, W., Bongaerts, P., **Herrera, C.**, Ainsworth, T.D. (2018) Rethinking the coral microbiome: Simplicity exits within a diverse microbial biosphere. *mBio*, **9**: e00812-18.

Book chapters

- Miloslavich, P., Cruz-Motta, J.J., Hernández, A., **Herrera, C.**, Klein, E., Barros, F., Bigatti, G., Cárdenas, M., Carranza, A., Flores, A., Gil-Kodaka, P., Gobin, J., Gutiérrez, J., Krull, M., Lazarus, J.F., Londoño, E., Lotufo, T., Macaya, E., Mora, E., Navarrete, S., Palomo, G., Parragué, M., Pellizzari, F., Rocha, R., Romero, L., Retamales, R., Sepúlveda, R., Silva, M.C., Soria, S. (2016) Benthic Assemblages in South American intertidal rocky shores: Biodiversity services and threats. *In*: Riosmena-Rodríguez R (ed) Marine Benthos: Biology, Ecosystem Functions and Environmental Impact, Chapter: 3, Publisher: Nova Science Publisher.

Conference posters and oral presentations

- **Herrera, C**., Sheaves, J., Baker, R., and Sheaves, M. (2016). Navigating ecology theories and paradigms to predict mechanisms behind the biodiversity and ecosystem functioning relationship: discovering ecology weakness. Biology in the Tropics. James Cook University, Townsville, Australia.
- **Herrera, C**., Sheaves, J., Baker, R., and Sheaves, M. (2016). Marine ecosystem functioning: what is and what really matter? Biology in the Tropics. James Cook University, Townsville, Australia.

- **Herrera, C**., Sheaves, J., Baker, R., and Sheaves, M. (2017). Computer vision for today's ecologists: an automated tool for detecting and tracking organisms in their environment. James Cook University Science Research Festival. Townsville, Australia.
- **Herrera, C**., Sheaves, J., Baker, R., and Sheaves, M. (2018). Heads no longer buried in the sand: new method for studying cryptic and fossorial crabs. Ecological Society of Australia Conference. Brisbane, Australia.

Software and scripts

- **Herrera, C.** (2020, May 11). CexyNature/Crabspy: v0.1.0-alpha.1-Tpolita (Version v0.1.0-alpha.1). Zenodo. http://doi.org/10.5281/zenodo.3820270 and https://github.com/CexyNature/Crabspy
- **Herrera, C.** (2020) https://github.com/CexyNature

Science communication pieces

- (2020) The researcher who tinkers and tailors with Crabspy. https://www.qcif.edu.au/researchimpact/the-researcher-who-tinkers-and-tailors-with-crabspy/
- Herrera, C. and Fries, J. (2018) Measuring productivity of tropical wetlands and estuaries at the ecosystem scale. https://youtu.be/DdjHp_MpmLg

Outreach

- Over 20 talks and activities in the program STEM professionals in School previously known as Scientist and Mathematicians in School, a Commonwealth Scientific and Industrial Research Organization (CSIRO) initiative. (2016-2020). Partner Schools:
    - Townsville High, Townsville, QLD Australia.
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- Over six talks and hands-on sessions in the JCU students' programming club, CodeRtsv (2019-2021). https://codertsv.github.io/

Chapter 1 - General Introduction

Biodiversity underpinning essential planetary processes

We are currently living in a time of significant planetary change (Crutzen 2002; Steffen, Crutzen & McNeill 2007). Global phenomena such as climate change, pollution, and loss of natural habitats are challenging many species' adaptive boundaries (Rockstrom *et al.* 2009; Mace *et al.* 2014). Although life on earth has flourished despite five major catastrophic events (i.e. mass extinctions), these events have responded to and triggered global transformations in the landscape, climate, and biota configuration (D'Hondt 2005; Finnegan *et al.* 2012; van de Schootbrugge *et al.* 2013; Kaiho *et al.* 2016). Thus, at present, there are major ecological concerns associated with the consequences of losing biodiversity, altering natural habitats, and changing climate at an accelerated pace (Daily *et al.* 2000; Bellard *et al.* 2012; Cardinale *et al.* 2012). The intertwined connection between biodiversity and the environment bolsters scientists to evaluate and predict the consequences of environmental changes on the future of biodiversity, and the consequences of changes in biodiversity on the environment (Winkler, Dunn & McCulloch 2002; Stenstrom & Jonsdottir 2004; Both & Visser 2005; Pankhurst & Munday 2011; Bellard *et al.* 2012; Azra *et al.* 2020; Malpeli *et al.* 2020). Consequently, an imperative goal of biological, ecological, and environmental sciences is to understand the individual and cumulative effects of losing species and habitats on the functioning of ecosystems.

Ecological, environmental, and sociological research has shown that biodiversity loss threatens ecosystem services and functions, life-support processes, and human wellbeing (Costanza *et al.* 1997; Daily *et al.* 2000; Cardinale *et al.* 2012; McInnes 2013; Taylor & Hochuli 2015; FAO 2016). In Ecology, the increased risks of species loss have aroused researchers' interest in understanding how changes in the number of species might affect essential ecosystem outcomes (Sutherland *et al.* 2013). The number of species, their identities, and life-history strategies have been found to affect ecosystem functioning (Chapin *et al.* 2000; Lavorel & Garnier 2002; Gagic *et al.* 2015; Gamfeldt *et al.* 2015). Currently, there appears to be a consensus on the positive relationship between biodiversity and ecosystem functioning across marine, aquatic and terrestrial systems (Danovaro *et al.* 2008; Cardinale 2012; Reich *et al.* 2012; Yasuhara *et al.* 2016). Thus, it is expected that biodiversity loss will diminish the functioning of the ecosystem, and subsequently reduce the benefits we receive through ecosystem goods and services. Because many of the ecosystem processes we depend upon, such as water regulation, erosion control, nutrient cycling, food production, flood protection, and recreation are underpinned by life processes, biodiversity loss jeopardizes human wellbeing and survival (Costanza *et al.* 1997; De Groot *et al.* 2010; de Groot *et al.* 2012; Costanza *et al.* 2014). Ecological models suggest that the number of species is a critical single factor predicting ecosystem functioning because number of species is positively correlated to diversity of functional traits (Danovaro *et al.* 2008; Tilman, Isbell & Cowles 2014). However, we do not have precise or accurate estimates of species diversity for many ecosystems or taxonomic groups, and when we do, we frequently fail to understand species functional roles within the ecosystem (Mlambo 2014; Bellwood *et al.* 2018; He *et al.* 2018). The biodiversity and ecosystem functioning relationship and its underlying mechanisms must be understood to predict, manage and protect ecosystems and their functions. This requires understanding the distribution of organismal traits, their life history, their functional roles, and the complex interaction and feedback loops that organisms have with other beings and the environment (Mlambo 2014).

The problem with traditional biodiversity census

Current estimates of species diversity range from tens of millions to trillions of species (Brusca & Brusca 2003; Mora *et al.* 2011; Locey & Lennon 2016; Larsen *et al.* 2017). These estimates depend on the taxa being considered. For instance, including microbial diversity skyrockets the number of species (see Locey & Lennon 2016). Regardless of the magnitude of species diversity, and even just considering the most conservative estimates, only a minute fraction of species have been described, in the most enthusiastic scenarios 1-10 % (Larsen *et al.* 2017). The current species description rate (i.e. scientific naming) is optimistically reported to be 6,200 – 18,000 species per year (Mora *et al.* 2011). Considering the most conservative number of species, at this rate, it would take at least several hundred years to describe all species (Brusca & Brusca 2003). Moreover, for the majority of those described species, we have little idea of their biologies and ecologies. For this reason, and considering we are on the verge of the sixth mass extinction (Barnosky *et al.* 2011), ecologists and biologists' are confronted to census, describe and protect as many species as possible while trying to understand their ecology and raising awareness about their importance (Renner & Ricklefs 1994; O'Dor 2004; Bickford *et al.* 2007; Costello *et al.* 2010).

Another challenge in studying biodiversity is our inclination to study ecosystems and species as discretised units (see discussions on Barmuta & Lake 1982; Butlin & Stankowski 2020; Doretto, Piano & Larson 2020; Gao & Rieseberg 2020; Mallet 2020; Wang *et al.* 2020; Wu *et al.* 2020). This vision obstructs our ability to find generalities and compare findings across the biological and ecological continuum. This is not to say that categorizing biodiversity into nominal groups is not useful or appropriate (Gao & Rieseberg 2020); but that acknowledging the continuum of genetic, organismal, and ecological diversity and in some cases coming with novel and innovative ways to categorize biodiversity (Messier, McGill & Lechowicz 2010; Cadotte, Carscadden & Mirotchnick 2011) could lead to increase our understanding of biological and ecological systems. For instance, when the only currency to compare ecosystems are species names, opportunities to understand functioning across ecosystems are minimal. Since identifying species is often easier and cheaper than describing traits and functional attributes, ecological literature regularly make biological and ecological comparisons across space and time using species lists (Ricklefs, Latham & Qian 1999; Ricklefs 2004; Pommier *et al.* 2007; Cruz-Motta *et al.* 2010; Iken *et al.* 2010; Miloslavich *et al.* 2013). Limits in our observation capabilities and the sampling cost are also an impediment to move towards better methods of assessing biodiversity. Therefore, there is an increasing need to develop surveys and methods that reduce the observation costs and gather richer information about organismal traits and functional roles, i.e. information beyond their taxonomic identity. This necessity is particularly critical for species inhabiting areas already on declining trajectories, such as wetlands and seashores (Baker *et al.* 2020).

Ecosystems and organisms at risk

Wetlands encompass a diversity of ecosystems like mangroves, saltmarshes, lakes, estuaries, rivers, and swamps that provide key functions for sustaining life at the global scales (Klaine 1993; Costanza *et al.* 1997; MA 2005; Dale & Connelly 2012; de Groot *et al.* 2012). Unfortunately, wetland conversion and degradation threaten species inhabiting these ecosystems, consequently threatening ecosystem functioning and ecosystem services. Since the 18th century, overall wetlands loss has been calculated to represent as much as 87% (Davidson 2014). With only 13 percent of the world's wetlands remaining, investigations into these ecosystems are imperative if we are to be able to predict, manage and protect them into the future. For instance, coastal and estuarine ecosystems tidal flats are among the natural systems with major areas lost in the past decades (Murray *et al.* 2019). With the increased pressure of human settlement in coastal areas, it is predicted that much of the ecosystem goods and services provide by estuaries and coastal areas will be lost (Costanza *et al.* 1997). In these ecosystems, much of the research effort for understanding change in species composition and species decline has been focused on vegetation and commercially important fish and invertebrates (Rozas, Caldwell & Minello 2005; Skilleter *et al.* 2005; Polidoro *et al.* 2010; Zhang *et al.* 2012;

Sheaves, Johnston & Baker 2016; Duke *et al.* 2017; Dunbar, Baker & Sheaves 2017; Kelleway *et al.* 2017; Queiroz *et al.* 2017). In contrast, less attention has been paid to small and cryptic invertebrates overlooked by the general public and stakeholders. The ecological consensus in estuaries and coastal ecosystem research (Fairweather 1999; Thomson *et al.* 2017) suggests we should prioritize our understanding of ecosystem metabolism, nutrient cycling and food web dynamics; all processes heavily powered by small invertebrates.

One of the most conspicuous invertebrates found in estuaries and coasts are fiddler and shore crabs. Fiddler and other ocypodoid crabs (superfamily Ocypodoidae) and shore crabs (superfamily Grapsoidea) are small brachyuran crustaceans inhabiting nearshore and intertidal areas. These animals have separate sexes and can show marked sexual dimorphism reflected in males' one or two larger claws (Vermeiren, Lennard & Trave 2020). Ocypodoid and grapsoid crabs tend to live in soft sediments, and exhibit a fossorial behavior, using burrows and crevices in the sediment (Crane 1975; Apel & Türkay 1999; Nobbs & McGuinness 1999; Hemmi 2003a; Hemmi 2003b; Kent & McGuinness 2006; Vermeiren & Sheaves 2014a; Chen *et al.* 2017). They feed on microorganisms, and organic material contained in the benthos of intertidal areas (Skov & Hartnoll 2002; Nordhaus 2003; Thongtham, Kristensen & Puangprasan 2008; Nordhaus, Diele & Wolff 2009), with cannibalistic and scavenging behavior possible (Koga *et al.* 1995; Milner *et al.* 2010). Because of reworking the intertidal sediment and feeding in decaying organic material from the terrestrial and intertidal ecosystems, ocypodoid and grapsoid crabs promote the incorporation of organic material into adjacent ecosystems (Robertson 1986; Meziane, d'Agata & Lee 2006; Thomas & Blum 2010; Fanjul *et al.* 2015; Natalio *et al.* 2017). In addition, they are a food source for terrestrial and aquatic fauna (Sheaves & Molony 2000), and they promote gas exchange in the sediment that benefits surrounding vegetation and infauna (Dye & Lasiak 1986; Smith III *et al.* 1991; Gribsholt, Kostka & Kristensen 2003; Kristensen & Alongi 2006; Fanjul *et al.* 2011; Gittman

& Keller 2013; Booth *et al.* 2019). For all these reasons, these crabs are ecosystem engineers and key species in the functioning of coastal and estuarine ecosystems.

The taxonomy of ocypodoid and grapsoid crabs has been the subject of extensive research (Crane 1975; Bliss 1982; Schubart *et al.* 2000; Rosenberg 2001; Shih *et al.* 2016). Several taxonomic and systematic revisions have produced various taxonomic and phylogenetic classifications. For instance, the previous genus *Uca*, grouping all fiddler crabs, is currently divided into more than nine genera (Rosenberg 2019). Furthermore, along with the history of fiddler and shore crab research, synonymized names have been regularly employed, making it challenging to track species-specific literature. Brachyuran crabs such as fiddler and shore crabs are widely used as model systems in behavioral, vision, and ecological studies (Backwell & Passmore 1996; Christy, Backwell & Schober 2003; Zeil, Hemmi & Backwell 2006; Booksmythe, Detto & Backwell 2008; Booksmythe, Jennions & Backwell 2010; Sanches *et al.* 2018; Gruber, Kahn & Backwell 2019). However, for most of the 105 species currently accepted, little is known about their ecology. One reason explaining this disproportional species-specific research effort is ocypodoid and grapsoid crabs cryptic and elusive nature. In addition to their similar physical appearance (i.e. the potential co-occurrence of cryptic species) and fossorial nature, these animals are very sensitive to the presence of an observer. Traditional methods to collect biological or ecological data from intertidal crab assemblages rely on the scientists direct visual observation or overcomplicated and invasive methods with a high degree of uncertainty (Colpo & Negreiros-Fransozo 2016; Schlacher *et al.* 2016). Visual observation, using only our eyes as an instrument, is likely produce imperfect data acquisition and introduce bias (Burg *et al.* 2015), affecting studies' results and conclusions (Kardish *et al.* 2015). Pitfall traps, burrow counting, excavation, and many other alternative sampling techniques are destructive, require comprehensive validation or produce skewed estimates (Nobbs & McGuinness 1999; Vermeiren & Sheaves 2014c; Schlacher *et al.* 2016).

In addition, such studies are time-consuming preventing simultaneous spatial replication or comparison. These challenges are common to other species and natural systems (Roberts *et al.* 2016; Sheaves *et al.* 2020). If scientists aim to gather better data for improving decision-making and management, novel sampling methods that reduce bias and uncertainty are therefore a critical priority.

Imperative need of new technologies in biology and ecology

The conjunction of three pressing needs motivates the innovation and development of sampling methods. Firstly, the urgency to increase the rate at which scientists census and catalog organisms and create awareness of their importance. Secondly, the need to gather more (and faster) information about organisms' traits and life history attributes to understand their functional roles within ecosystems. Lastly, and concomitant to the two previous, scientists need to modernize the sampling toolbox to reduce observation biases and uncertainty in data while reducing sampling costs. In this regard, several innovations are already taking place, as more and more scientists innovate and utilize novel methods to tackle these tasks; for instance, by using improved census methods that increase species detectability (e.g. population genetics, eDNA, 16s bacterial profiling, Remote Operated Vehicles, etc.). Importantly, as these technologies become more accessible, they can be used to research greater geographic, depth, and habitat ranges. For example, see Census of Diversity of Abyssal Marine Life (Stuart *et al.* 2008), Census of Antarctic Marine Life (Schiaparelli & Hopcroft 2011), Earth Microbiome (Thompson *et al.* 2017) and Human Microbiome Project (Turnbaugh *et al.* 2007). Continued efforts to achieve optimal sampling methods would reduce the burden on scientists' research and would facilitate efforts to better understand and protect essential processes that sustain life on our planet.

In this thesis, I leverage the power of computer vision to study intertidal crabs in estuarine wetlands. Machine vision and machine learning (MVML) are technologies that disrupt traditional ways to acquire and process data. Therefore, these advances are changing sampling and data curation paradigms in many research fields (e.g. Culibrk *et al.* 2007; Xie, Kham & Shah 2008; Mathiassen *et al.* 2011; Phinn, Roelfsema & Mumby 2011; Westoby *et al.* 2012; Zion 2012; Dell *et al.* 2014; Griffin *et al.* 2017; Weinstein 2018; Forsmoo *et al.* 2019; Piechaud *et al.* 2019; Mohamed, Nadaoka & Nakamura 2020; Hoye *et al.* 2021). The vast majority of software and computational libraries associated with these new tools have been released under some public license form. However, among the current limitations that restrict their wide adoption between biologists and ecologists are low programming literacy, unfamiliarity to imaging and processing pipelines and algorithms, and complex and costly software and hardware platforms. My thesis aims to challenge this current situation by: (1) demonstrating computer vision potential in the research of estuarine fossorial crabs, (2) improving the amount of biological and ecological information obtained from sampling events, while reducing data collection costs, and (3) creating a set of free open-source tools available for the broader community. To address these broader aims, I address the following objectives in my chapters:

1. Chapter 2 - Quantitatively assess differences in detection, occurrence, and latency to first re-emergence of intertidal crabs using two sampling methods: traditional visual census and video surveys.
2. Chapter 3 - Develop a workflow and computer vision software grounded in field video recordings to collect biological and ecological data on intertidal crabs.
3. Chapter 4 - Evaluate and quantify bioturbation rate of fiddler crabs on estuarine mudflats, and its effect on sediment topography.

4. Chapter 5 - Describe movement and burrow use patterns of intertidal crabs, and identify similarities and dissimilarities in motion across taxa and behavioral states

Thesis outline

This thesis comprises four data chapters (Figure 1-1) written for publication in peer review journals. In Chapter 2, I demonstrate that video surveys are an efficient and cost effective method to sample intertidal crabs. I examine and compare video surveys against visual census, the traditional and gold standard sampling method, in order to assess the suitability of expanding and enhancing the capabilities of video surveys. Based on Chapter 2 results, in Chapter 3, I then develop a workflow and software underpinned by video surveys to extract information on the movement, appearance and size, population structure, and bioturbation activity of intertidal crabs. In this chapter, I use computer vision libraries and off-the-shelf software to create Crabspy, a Python programming heuristic toolbox that streamline the collection of data about crabs functional biology and ecology from field video samples. In Chapter 4, I employ off-the-shelf software and Crabspy modules to quantify bioturbation activity of one species of fiddler crab. In Chapter 5, I use Crabspy to describe the movement and activity patterns of 96 intertidal crabs engaged in different behavioral states. Finally, in Chapter 6, I provide guidelines and directions on how these advances in sampling and data collection underpinned by computer vision can revolutionize the study of intertidal crabs and other similar species.

In this thesis, I describe new techniques to sample intertidal crabs in soft sediments using computer vision. Emphasis on the methodological aspects and on the quality of information generated by them is a central theme of this body of work. Designing and developing the workflow and software employed throughout this thesis was the task that required much of my effort and time. At this stage, however, many of the techniques and analysis presented can only be performed in specific environmental settings in which crab view is unobstructed, such as mudflats without vegetation. Nonetheless, current limitations can be circumvented by using alternative computer vision algorithms and by developing fit-to-purpose technology. Thus, it is my hope these new techniques, available to everyone, can continue to be utilized by others, and that they inspire others to continue to ignite a tool-driven revolution in biology and ecology.

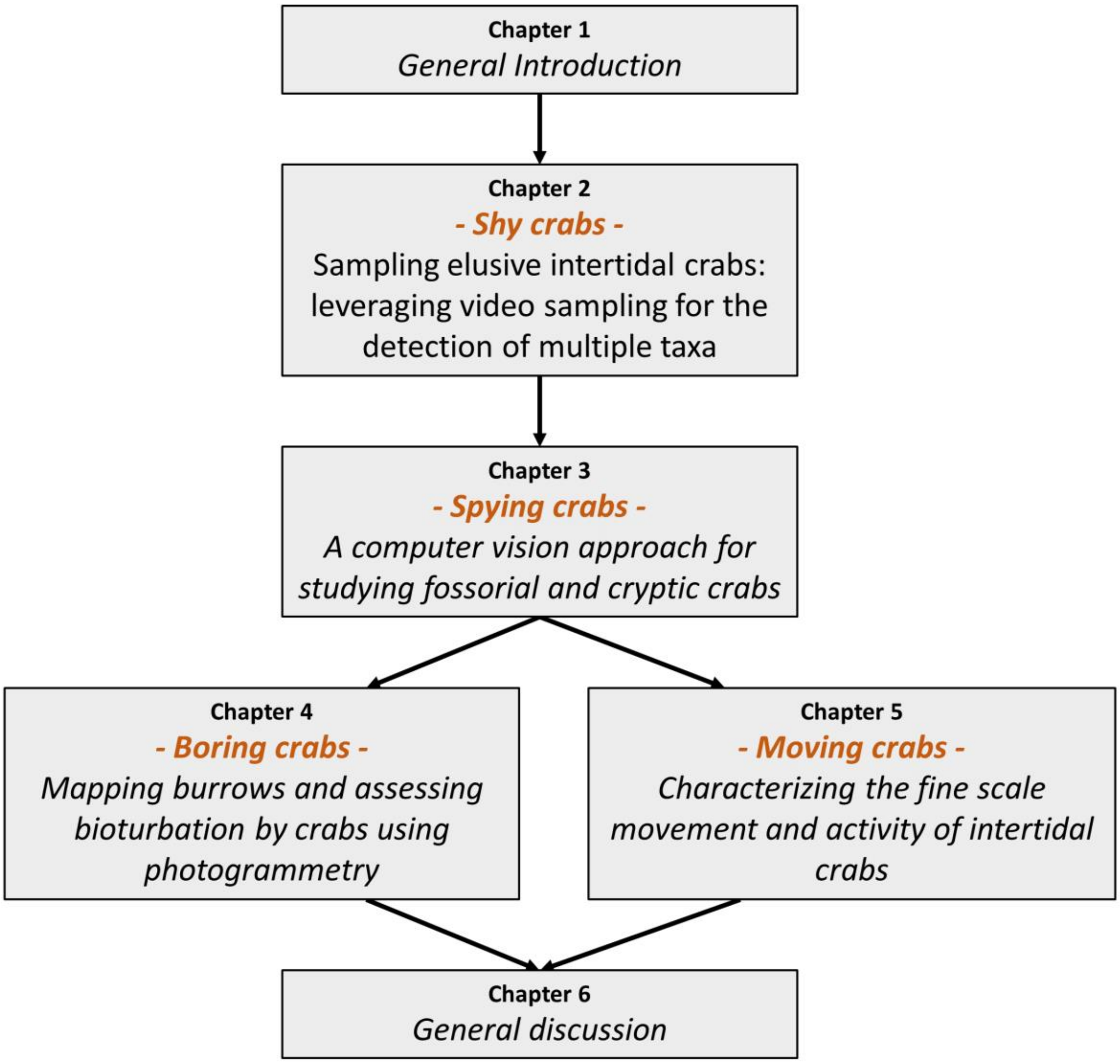
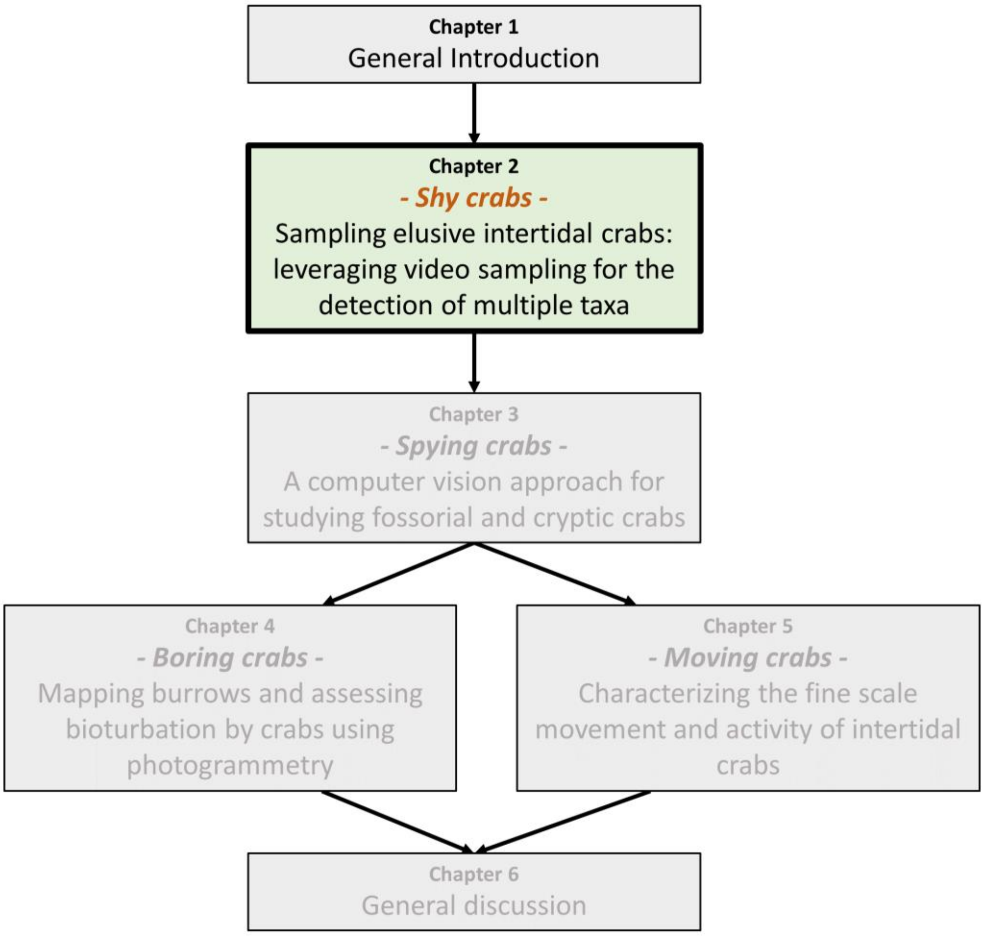


Figure 1-1: Thesis and chapters outline.

Chapter 2 - Sampling elusive intertidal crabs: leveraging video sampling for the detection of multiple taxa



Aim: Quantitatively assess differences in detection, occurrence, and latency to first re-emergence of intertidal crabs using two sampling methods: traditional visual census and video surveys.

Introduction

Assessing and monitoring species through space and time is essential for determining changes in population size, distribution, and structure (Yoccoz, Nichols & Boulinier 2001; Balmford, Green & Jenkins 2003). An essential component of species monitoring is the use of sampling methods that provide reliable estimates of spatial distribution, occupancy and other demographic and ecological metrics (Thompson 2004; MacKenzie *et al.* 2018). Organisms' life history traits and behaviours largely determine the type of sampling methods used to estimate their occurrences and densities (Unno 2008). Thus, sampling methods tend to be tailored to specific taxonomic groups. For this reason, it is often challenging to obtain abundance and distribution information from multiple species (i.e. community data), from the same sampling technique. This is the case for intertidal communities of crabs inhabiting soft sediments, which comprise several species from superfamilies Ocypodoidea Rafinesque, 1815 (e.g. fiddler crabs and other narrow-fronted crabs) and Grapsoidea MacLeay, 1838 (e.g. shore crabs and other broad-fronted crabs) with varied life styles.

Ocypodoid and grapsoid crabs from families Macrophthalmidae, Ocypodidae, Grapsidae and Sesarmidae are among the most abundant invertebrates in intertidal estuarine and soft coastal sediments (Nagelkerken *et al.* 2008). These crabs predominantly feed on fresh and decaying plant material and microorganisms, with occasional predation, scavenging, and cannibalistic feeding behaviours (Giddins *et al.* 1986; Koga *et al.* 1995; Ya, Yeo & Todd 2008; Milner *et al.* 2010; Poon, Chan & Williams 2010). They remove and compact sediment while creating and maintaining their burrows, which has been found to affect macrofauna, bacterial communities in the sediment, vegetation structure and growth, sediment properties, and stream morphology (Perillo, Minkoff & Piccolo 2005; Kristensen 2008). Ocypodoid and grapsoid crabs are critical regulators of energy and matter transfer through their feeding and fossorial activities (Werry & Lee 2005), providing key links in aquatic trophic webs (Sheaves & Molony

2000). Although we have gained detailed understanding of these crabs through careful observation of a few species, studying the biology and ecology of many other species is difficult because of their cryptic, elusive and fossorial nature. A recent taxonomic revision of these crabs (Shih *et al.* 2016; Shahdadi, Davie & Schubart 2018) has demonstrated the high level of cryptic biodiversity and the difficulties associated with species level identification given their uniform appearance (Ragionieri, Fratini & Schubart 2012; Shahdadi & Schubart 2018; Rosenberg 2019). Fiddler and shore crabs are also sensitive to the presence of an observer and will run into their burrows or climb trees to evade the perceived threat.

To overcome the elusive nature of these crabs several sampling methods are used to assess their occurrence, abundance and behaviour. Methods include visual census (Golley, Odum & Wilson 1962; Warren 1990), quadrat (Flores, Abrantes & Paula 2005) or burrow excavation (Checon & Costa 2018; Fogo, Sanches & Costa 2019), manual capture (Trave & Sheaves 2014), pitfall traps (Smith III *et al.* 1991; Schlacher, de Jager & Nielsen 2011), photographic sampling (Vermeiren & Sheaves 2014c; Vermeiren & Sheaves 2015), video surveys (Nordhaus, Diele & Wolff 2009; Smolka, Raderschall & Hemmi 2013), and burrow counts (Barros 2000; Breitfuss 2003). The sampling method selected depends on the type of information required, the method's suitability in specific environmental conditions, the budget available (i.e., time and money) and the focal taxa. Because of the many different methodological approaches, it can be difficult to quantitatively compare results from intertidal crab sampling (but see Nobbs & McGuinness 1999; Mazumder & Saintilan 2003). For instance, while some sampling methods provide direct estimates of abundance (i.e., visual census and quadrat excavation) others only quantify relative abundance (e.g. burrow counts) or crab surface activity (e.g., pitfall traps; Lee 1998; Schlacher *et al.* 2016). Thus, methods are often only qualitatively compared based on the required effort (i.e., time and cost), the type of data collected (e.g., abundance, relative abundance, activity), and the level of intervention required (i.e., destructiveness Vermeiren & Sheaves 2014c). Observer familiarity with a specific method and apprehension around methodological change could also affect method selection. When these sampling methods are employed to assess the occurrence or abundance of more than one species, we must be aware of the potential sampling biases each method could have on different taxa. Despite the recognition that studying potential methodological biases is important to evaluate the validity of our estimates (Peterson & Black 1994), relatively few studies have quantitatively evaluated the performance of different sampling techniques for a range of crab taxa (e.g. Nobbs & McGuinness 1999; Skov *et al.* 2002; Colpo & Negreiros-Fransozo 2016; Schlacher *et al.* 2016).

Here, I compare the performance of two sampling techniques, video survey and traditional visual census, to assess the occurrence and diversity of crabs from the ocypodoid and grapsoid superfamilies in an estuarine wetland. Visual census is among the most frequently used sampling methods to assess the occurrence, abundance and behaviour of crabs (e.g. Ribeiro, Daleo & Iribarne 2010). However, video surveys are increasingly used as a sampling technique to assess biodiversity and species behaviour in several taxonomic groups and habitats (Marcos *et al.* 2008; Nordhaus, Diele & Wolff 2009; Walls & Layne 2009; Crispim Junior *et al.* 2012; Sheaves, Johnston & Baker 2016; Bradley, Baker & Sheaves 2017; Sheaves *et al.* 2020). I evaluate the utility of video surveys versus visual census in three aspects: species probability of detection, latency to first crab re-emergence from its burrow after disturbance from observer, and the number of species detected.

Materials and Methods

Study area

The study was conducted in the Annandale wetland in Townsville, North Queensland, Australia, a region with semi-diurnal tides (Figure 2-1A). This intertidal wetland covers 0.41

km^2 and comprises a *Sporobolus virginicus* saltmarsh with a series of natural and human-made pools, many of which retain water throughout the tidal cycle (Figure 2-1A). These pools are interconnected, and connected to the adjacent Ross River, by a series of channels, many of which are mangrove lined (Figure 2-1A). Freshwater input is minimal, as the wetland is downstream from a series of dams that store and control the freshwater supply for Townsville. As a result, aquatic and intertidal fauna are predominantly estuarine and marine (Abrantes & Sheaves 2008; Davis *et al.* 2012b). During the wet season, and depending on the dam levels, Annandale wetland can be flooded. The intensity, volume and flow of water, and the frequency of flooding events, shape the species assemblage in this area (Sheaves *et al.* 2007; Sheaves & Johnston 2008; Davis *et al.* 2012a; Sheaves 2015). This study was carried out during the summer season September 2017 to January 2018.

Field sampling

Sampling was done using two methods, visual census and video surveys. Sampling was carried out in areas that satisfied the following requirements: (1) crab activity has been previously observed or crab occurrence was evident given the presence of recent crabs' burrows and bioturbation pellets, and (2) the sediment was not covered by salt marsh vegetation. Both requirements were necessary to maximize the exposure of crabs to both sampling techniques. Thus, these requirements (1) exposed both sampling methods to a hypothetical 100% crab occupancy, and (2) reduced factors undermining detection rate, e.g. crab occlusion by floor vegetation. Within areas that satisfied both conditions, samples were positioned haphazardly, independently, and at least separated by 15 meters, in muddy and loamy sediment, and these were observed during daytime low tides (Figure 2-1B). Each selected area was visited and sampled once during the study.

Visual censuses were conducted by an observer seated 3-4 m away from a focal quadrat that was marked out in the sediment. This is a modification from Nobbs and McGuinness

(1999), and it is a typical distance used in visual census that assurance optimal view of the focal area. One observer (CH) using Bushnell 10 X binoculars conducted all observations. A sampling event using visual census involved: approaching to the focal area, demarcation of a quadrat on the sediment, departure to observation spot, and quadrat observation during 25 minutes, commencing immediately.

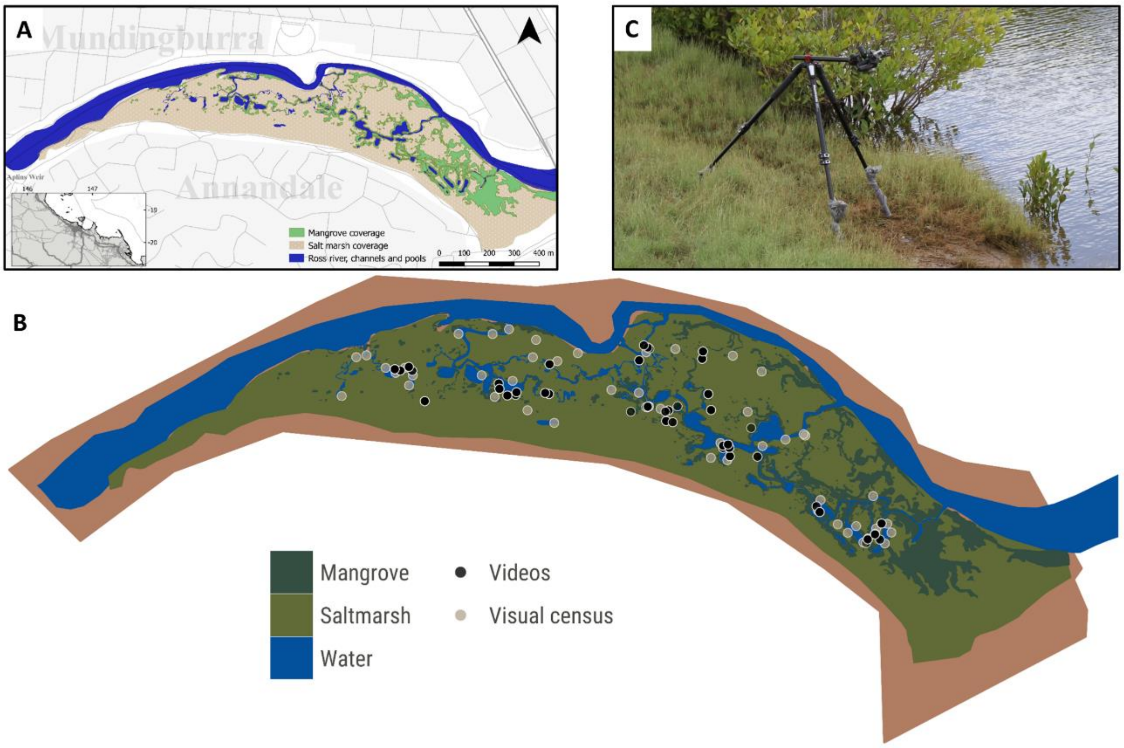


Figure 2-1: Study area and spatial distribution of visual and video surveys. A Map of the study area in Annandale wetland, located in Townsville, Queensland, Australia. B Observation positions per sample method. C Recording setup for video sruveys. i.e. action camera and tripod.

Video surveys consisted of top-down recordings of focal quadrats marked in the sediment from a distance of 0.5 to 1 m (Figure 2-1C). All recordings were conducted using action cameras (GoPro Hero 3 and Garmin VIRB XE) installed on a tripod (Manfrotto 055 MK055XPRO3-3W) or custom aluminium four-legged stand. A sampling event from video surveys involved: approaching to the focal area, demarcation of quadrat on the sediment, installation of video equipment, departure from the area to a resting spot beyond 10 m from the focal area. Video recording started immediately after installation, and the recording equipment was retrieved after 30 minutes.

The variable distances to the focal quadrat in both methods, and the use of two camera settings (i.e. stand or tripod) during video sampling, were necessary to guarantee the observer and camera were able to see the entire focal quadrat in different vegetation and spatial setups. For instance, an observer and/or video equipment needed to be positioned differently for a focal quadrat located under low hanging mangrove canopy with a tilted slope compared to a quadrat on an open and flat mudflat without overhanging vegetation. Similarly, the size of the focal quadrat was adjusted depending on the area of sediment available and to ensure it was directly observable from the observer and video position. The two quadrats sizes used were 100 by 100 centimetres and 50 by 38 centimetres.

Typically, the setup time, period from initiating the sampling event to observer departure to observation/resting spot, took less than 60 seconds in both methods. The sediment in the focal area was not disturbed during quadrat demarcation or video equipment deployment. For visual censuses, crabs were identified *in situ* during the 25 minutes of observation. For video surveys, crabs were observed and identified in the laboratory only during the first 25 minutes of the video. The 25 minute observation time is an optimal sampling period based on previous studies (Wilson 1989; Warren 1990; Nobbs & McGuinness 1999). Crabs were identified to species and genera where possible (Campbell 1967; Crane 1975; Shahdadi, Davie & Schubart 2018; Shahdadi & Schubart 2018) or were assigned as “unknown”.

Usually, crabs ran and hid in burrows or crevices of mangrove roots as the observer approached the focal area (~3-7 meters, personal observation). The latency to first crab re-emergence, i.e. the time between crabs’ response to the observer presence (i.e. run and hide) and first crab resuming its activity on the surface, was evaluated for each sampling method. For all samples, I measured latency to the first crab re-emergence in seconds. Time measurement started at the beginning of the sampling event, when the observer approached within 10 m of the focal area to demarcate the sampling quadrat. For visual censuses, the time of first crab re-emergence was noted in the field spreadsheet. In video surveys, the time from approaching and setting up the video equipment to the beginning of the recording was noted in the field spreadsheet. This time was added to the time of the first crab re-emergence observed in the video.

The total sampling effort was 48 observations for each method. These were collected in 24 days over 12 trips in the period of 5 months. Importantly, all samples regardless the method used were collected under the same tidal condition, and the number of samples collected per method each trip was equal. The observations were also paired across methods, one video survey followed by a visual census using the same quadrat size. This was required for controlling potential effects from time of the day and variable quadrat size on my response variables. Three of the video surveys were not considered due to the collapse of the recording equipment in the mud. Thus, the final sampling effort was 48 visual census and 45 video surveys. Samples where crabs were not observed (n = 7, all samples from visual census) were not considered in latency analysis.

Statistical analyses

Data were analysed using a probabilistic programming approach. I used the free and open source libraries pymc3 (Salvatier, Wiecki & Fonnesbeck 2016), Pandas (McKinney & others 2010), Numpy (Harris *et al.* 2020), Matplotlib (Hunter 2007), Theano (Team 2016) and ggplot2 (Wickham 2016), and the R and Python programming language (Python Software Foundation; R Core Team 2018). Detection probabilities were modelled using a Binomial distribution parameterized for each sample, i.e., n = 1, and probability p (Equation 1). I used the inverse logit link function to model probability p as a linear function of sampling method and crab taxon (Equation 2). I assigned Cauchy uninformative priors to intercept and slopes

(Equation 3). Species richness per method was modelled following a Poisson distribution with a rate parameter *lambda* and with a low informative prior (Equation 4 - 5). The latency for each sampling method was modelled using a Wald distribution that was parameterized using *mu* and *phi*, distribution mean and shape parameters respectively. Uniform uninformative priors were used for *mu* and *phi* (Equations 6 – 9). All models posterior distribution were sampled using Markov chain Monte Carlo No-U-Turn Sampler. Six thousand samples, from two chains, were drawn from the posterior after 1000 samples were used for tuning. Prior and posterior predictive checks were performed to verify the adequacy of models recreating the observed data (Supplementary 1).

$$Y_i^{k,\ s} \sim Binomial\left(1, p_{k,s}\right) \qquad \textbf{Equation 1}$$

$$logit(p_{k,s})\ \sim \alpha +\ \beta_k\, Method +\ \beta_s\, Taxa \qquad \textbf{Equation 2}$$

$$\alpha, \beta_k, \beta_s \sim Cauchy(0, 0.5), \qquad \textbf{Equation 3}$$

$$where\ k \begin{cases} 0 =\ method\ visual\ census \\ 1 =\ method\ video\ survey \end{cases}$$

$$where\ s\ \in \{0, \dots, 14\}: Species$$

$$Y_i^k \sim Poisson\ (\lambda_k) \qquad \textbf{Equation 4}$$

$$\lambda_k \sim Uniform\ (0, 10),\ where\ k \begin{cases} 0 =\ method\ visual\ census \\ 1 =\ method\ video\ survey \end{cases} \qquad \textbf{Equation 5}$$

$$Y_i^k \sim Wald\ (\mu, \phi) \qquad \textbf{Equation 6}$$

$$\mu_k \sim Uniform\ (0, 300),\ where\ k \begin{cases} 0 =\ method\ visual\ census \\ 1 = method\ video\ survey \end{cases} \qquad \textbf{Equation 7}$$

$$\phi_k \sim Uniform\ (0, 2000),\ where\ k \begin{cases} 0 =\ method\ visual\ census \\ 1 = method\ video\ survey \end{cases} \qquad \textbf{Equation 8}$$

$$\text{and, } \phi = \frac{\lambda}{\mu} \qquad \textbf{Equation 9}$$

Among the benefits of using a probabilistic programming approach is that probabilistic models, described in the equations above, are based on the data-generating process of latent variables (distribution parameters) that give rise to the observed data. In addition, biological and analytical assumptions can be incorporated as priors, and their credibility can be evaluated before analysing the observed data. As probabilistic models return a whole (posterior) probability distribution describing the latent variables, the uncertainty associated to the modelling assumptions and model output can be estimated. Moreover, these probabilities can be updated based on new information (i.e. data and expert knowledge). For this reason, a detailed report of the latent variables' probabilities distributions, together with a description of how well the data fit these distributions, will allow other scientist to make predictions, evaluate the plausibility of different scenarios, and update their own models.

Results

In total, I recorded 14 crab taxa in Annandale wetland. From those, 13 were identified to species and one to genus level. In addition, some crabs could not be identified and were placed in the unknown category. All 14 taxa were detected from the video surveys, and 13 were detected from visual censuses, the only exception being *Metopograpsus frontalis* Miers, 1880, which was not observed during visual censuses. Crabs were always observed on videos. In contrast, crabs were not observed in seven of the 48 visual surveys. Fiddler crab (Ocypodidae Rafinesque, 1815) was the most speciose family represented in the wetland with seven species, followed by Grapsidae MacLeay 1838 with three species, and Camptandriidae and Dotillidae Stimpson 1858, and Macrophthalmidae and Sesarmidae Dana 1851, with one taxon each (Figure 2-2). *Parasesarma* spp de Man, 1895 (in de Man, 1895-1898) was the most frequently recorded crab, regardless the sampling method, followed by *Australoplax tridentata* (A. Milne-

Edwards, 1873). *Parasesarma* spp individuals could not be identified to species in neither of the methods.

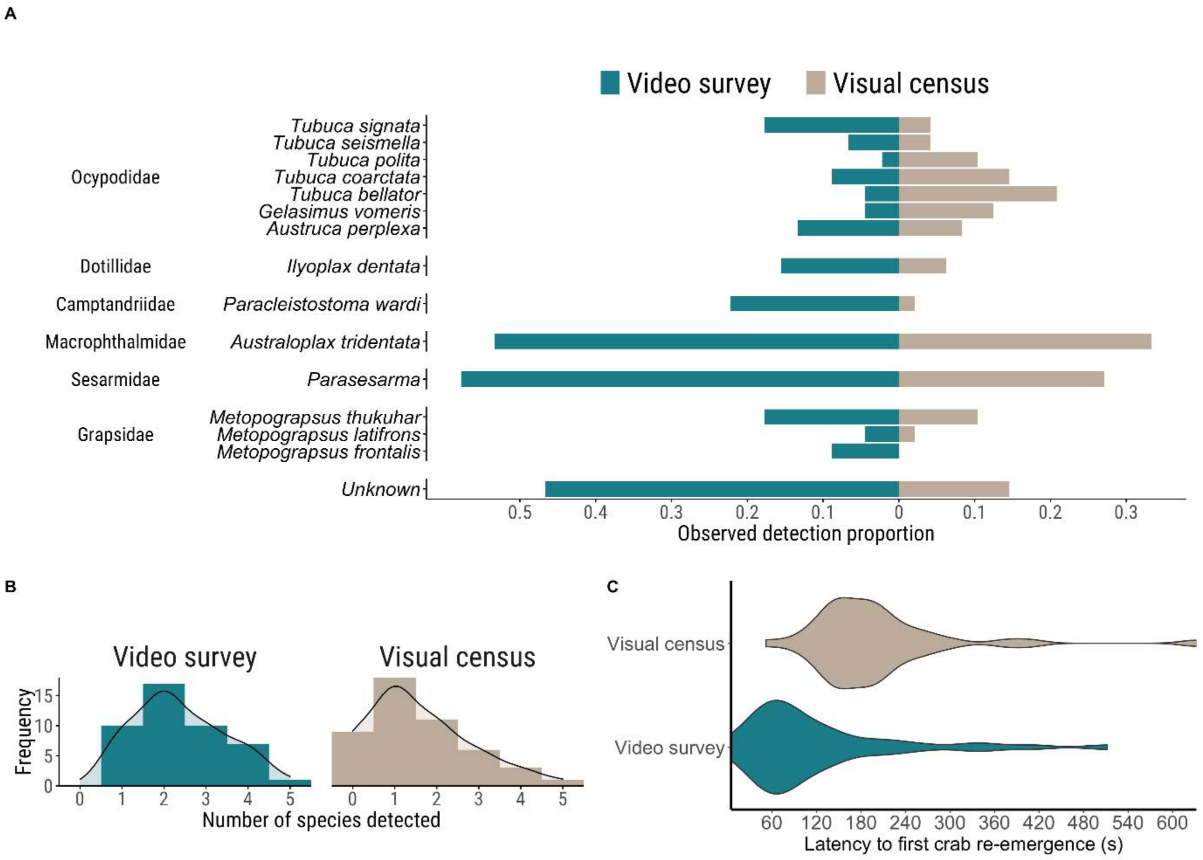


Figure 2-2: Observed data for detection proportion, species richness and latency to first crab re-emergence from the two sampling methods employed: video survey and visual census. **A** Detection proportion for each taxa and sampling method. **B** Absolute species richness frequency per sampling method. **C** Distribution of latency times to first crab re-emergence in seconds per sampling method.

Video surveys returned a higher proportion of detections. For ten taxa, individuals were recorded more frequently from videos than visual surveys (Figure 2-2A). In contrast, visual census detection proportions were only higher in four of the 14 taxa: *Tubuca polita* (Crane, 1975), *Tubuca coarctata* (H. Milne Edwards, 1852), *Tubuca bellator* (White, 1847) and *Gelasimus vomeris* (McNeill, 1920). However, the number of crabs (28) that could not be identified to species or genera was three times higher in video survey samples (21 vs 7, Figure 2-2A). The model for probability of detection successfully predicted the observed detection proportions for most combinations of sampling method and taxon (Figure 2-3). The posterior predictive distributions consistently captured the observed detection probabilities in nine taxa, including the unknown category. For all taxa, the model predicted a higher probability of detection by video than visual census, such that my model failed to capture the observed detection proportions in those taxa that exhibited higher probability of encounter in the visual census method, i.e., fiddler crabs *T. polita*, *T. coarctata*, *T. bellator* and *Gelasimus vomeris*. The model also failed to capture detection proportion in visual censuses for *Paracleistostoma wardi* (Rathbun, 1926) and *Metopograpsus frontalis* Miers, 1880. I showed that video surveys tend to increase detection probabilities for most species, and that its effect size varies according to taxon (Figure 2-3).

For both methods, the maximum number of identified taxa detected in a sample was six, but the video survey method was more likely to detect a higher number of species per sample than visual censuses (Figure 2-2B). The inference model of the Poisson *lambda* parameter for each distribution indicates that the species richness observed from these two methods came from two different distributions (Figure 2-4A-B). I compare *lambda* distributions per method against an arbitrary *lambda* point estimate of two; this value indicates a method where the theoretical species richness per sample is most likely to take a value of two species. I also calculate the difference between the two *lambda* distributions (Figure 2-4C). Both comparisons suggested that methods are different in regards of the number of species detected per sample, where video surveys in average are more likely to find one additional taxon. I use the Poisson *lambda* parameters to simulate posterior predictive cumulative distributions of richness per method (Figure 2-4D-E). I found that the probability of finding more species in a sample is higher in video surveys.

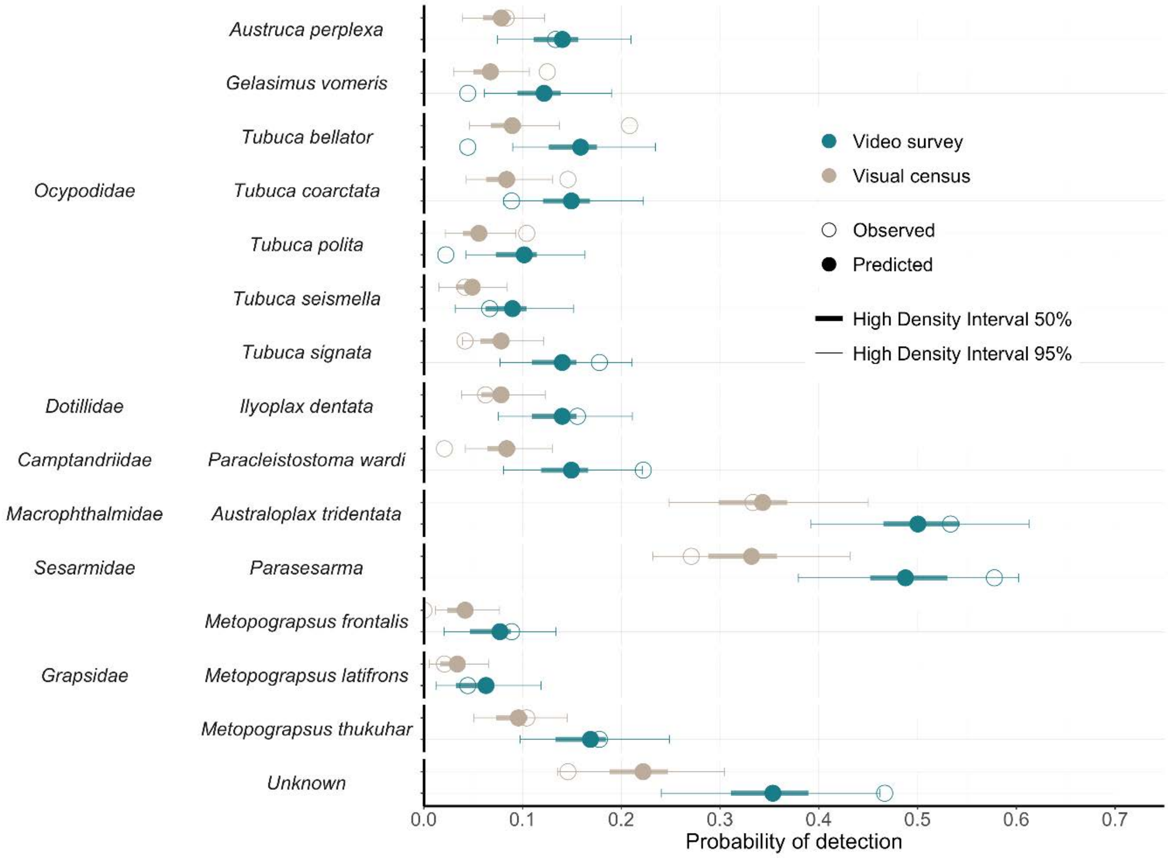


Figure 2-3: Posterior predictive probability of detection for each taxon and sampling method: video survey and visual census. Empty and filled circles indicate observed detection proportion (empty) and predicted probability (filled) of detection point estimates. Horizontal lines represent 50% and 95% Highest Density Intervals. Colours represent sampling methods: blue = video survey and sand = visual census.

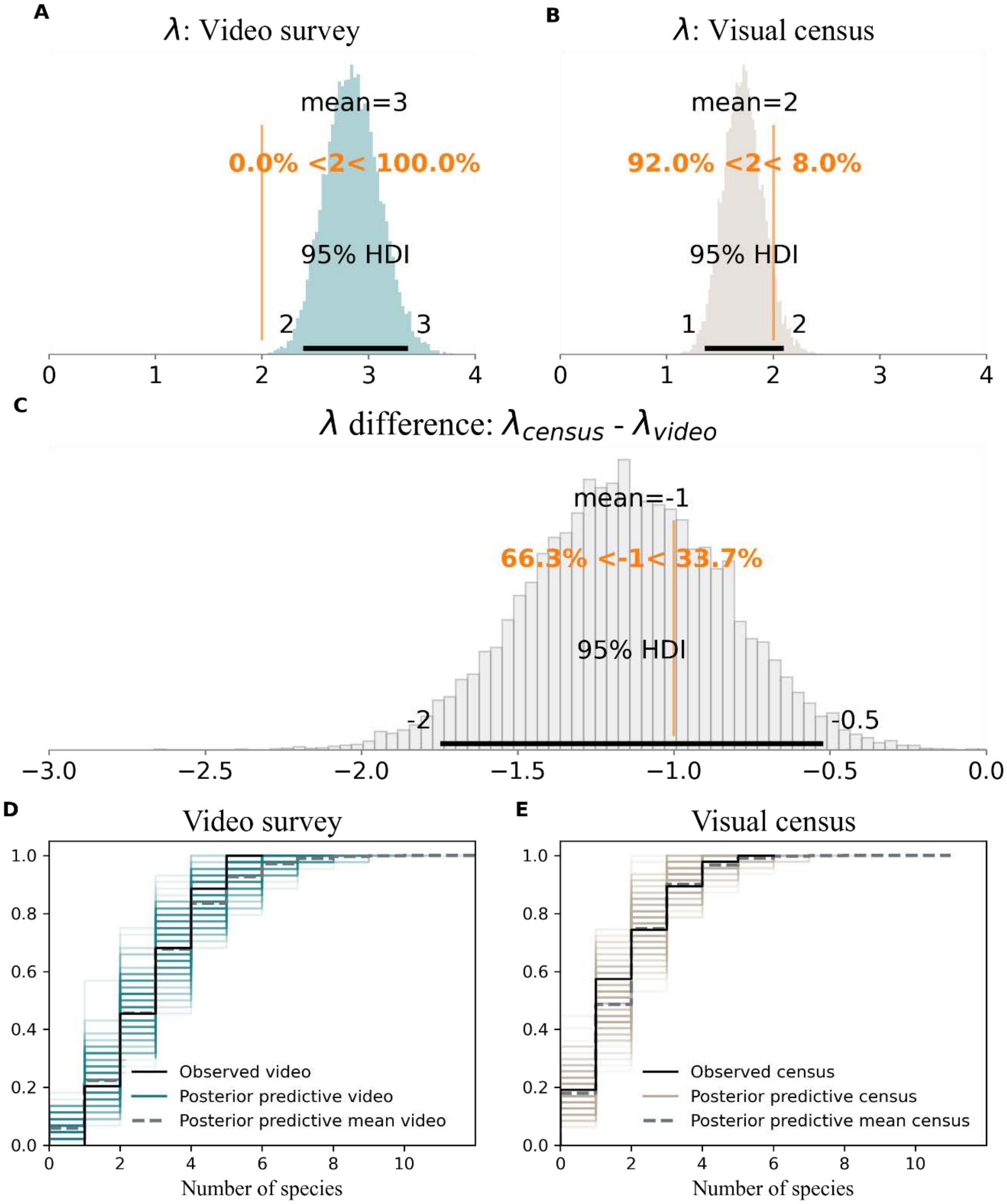


Figure 2-4: Posterior distribution and posterior predictive cumulative distribution for species richness per sampling method. **A-B** Posterior distribution of the Poisson parameter rate (λ, Equation 4) for each sampling method. **C** Posterior distribution of the difference in the Poisson parameter rates between sampling methods (i.e., λ census – λ video). **A-C** horizontal black line shows the 95% Highest Density Interval; orange vertical line indicates reference value, and orange text represents the percentage of the distribution probability mass in either region with respect to the reference value. **D-E** Species richness posterior predictive cumulative distribution per sampling method; black continuous line indicates the observed data, coloured lines represent 200 cumulative

distributions drawn from the parameter posterior distribution, and grey dashed line shows the mean of the 200 posterior predictive samples.

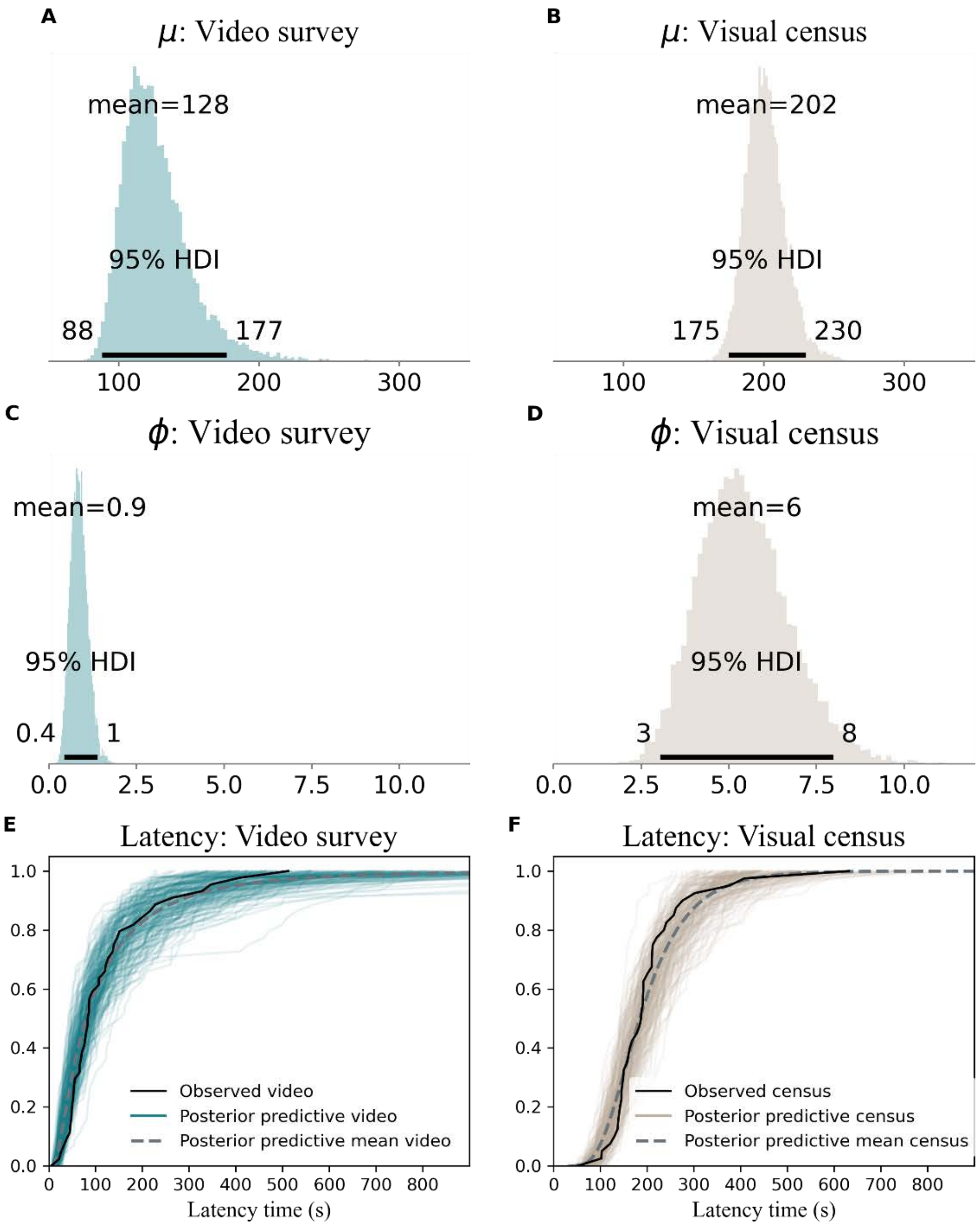


Figure 2-5: Parameters posterior distribution and posterior predictive cumulative distribution for latency to first crab re-emergence per sampling method. **A-B** Posterior distribution of the Wald distribution mean parameter (μ, Equation 6) for each sampling method. **C-D** Posterior distribution of the Wald distribution shape parameter (φ, Equation 6) for each sampling method. **A-D** horizontal black line shows the 95% Highest Density Interval. **E-F** Latency time posterior predictive cumulative distribution per sampling method; the black continuous line indicates the observed data, coloured lines represent 200 cumulative distributions drawn from the parameters posterior distributions, and the grey dashed line shows the mean of the 200 posterior predictive samples.

Latency to first crab re-emergence values were smaller (i.e. faster crab re-emergence) in video surveys than in visual censuses (Figure 2-2C). For both sampling methods the observed latency value distribution was not symmetric and longer waiting times (e.g., greater than 360 seconds) were observed, but these were not common (Figure 2-2C). The minimum and maximum latency time to first crab re-emergence were 5 and 632 seconds. On average, the observed latency for visual censuses and video surveys were 200.1 ± 95.7 and 120.9 ± 105.3 seconds, respectively. I modelled the two parameters defining the Wald distribution used to describe the latency to first crab re-emergence (Figure 2-5A-D). These parameters were different between sampling methods. In particular, the difference between the point estimates means ($\mu_{visual\ census} - \mu_{video\ survey}$) was 74 seconds, and the level of uncertainty of the mean parameter was higher for the video survey method than for visual census (wider distribution or higher spread, Figure 2-5A-B). Interestingly, the level of uncertainty associated to the shape parameter (φ) was higher for the visual census method than for video survey (Figure 2-5C-D). The posterior predictive cumulative distribution for latency shows that video surveys reduce the waiting time to the first crab re-emergence (Figure 2-5E-F). Thus, for any given latency time (abscissa), t, the probability (ordinate) of waiting t or less, $P(T \leq t)$, is smaller in video survey than in visual census.

Overall, I found that video surveys perform better than visual censuses. The video survey method exhibited higher detection probabilities, detected more species and reduced the waiting time to the first crab re-emergence. The joint posterior predictive probability for latency and richness, i.e., unobserved values simulated from the posterior probabilities, showed that video survey is more likely to find more crab taxa per sampling event while reducing waiting time to the first crab detection (Figure 2-6).

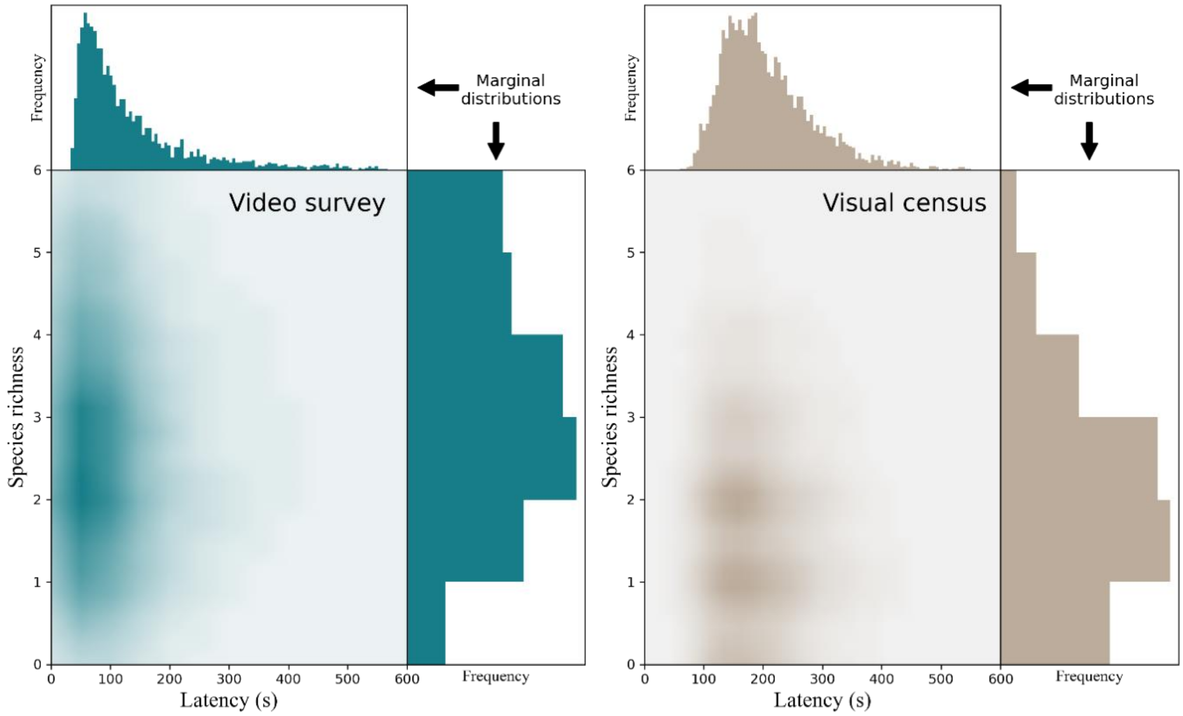


Figure 2-6: Joint posterior predictive probability distribution for latency to first crab re-emergence and species richness per method: darker coloured areas indicate higher probabilities. Joint distributions were created by sampling three thousand unobserved values from the posterior predictive distributions of latency and richness per sampling method. Marginal posterior distributions are shown for each variable and sampling method.

Discussion

In this study, I compared two non-invasive techniques to monitor intertidal ocypodoid and grapsoid species assemblages. By simultaneously using both sampling methods in a delimited wetland area, I am confident that both methods were exposed to all crab taxa occurring on the sediment surface during the day. Therefore, the results can be interpreted as direct estimates of the sampling biases associated to each method and the relatively occurrence of taxa.

Observed detection proportions were highly variable across taxa (Figure 2-2A). In our study, taxon absences can be due to a taxon not being present in the area sampled or because the taxon was not detected (Bailey, Simons & Pollock 2004). Ocypodoid and grapsoid crabs are known to have patchy distributions and occur in specific areas that fulfill their habitat requirements and preferences (Crane 1975; Reinsel & Rittschof 1995; Shin, Yiu & Cheung 2004; Vermeiren & Sheaves 2014b; Vermeiren & Sheaves 2014a). Our sampling design did not consider the potential effect of habitat or biotope (sensu Crane 1975). For this reason, the variable detection observed across taxa (Figure 2-2A) might be a reflection of the spatial heterogeneity in the Annandale wetland (e.g., sediment type, tidal level, surrounding vegetation, among others) and the adaptations each taxon requires to inhabit specific habitats within the wetland.

While observed detections across taxa might reflect environmental heterogeneity, I believe that differences in detection between methods per taxon are the result of specific biases associated to each sampling method. As part of the visual census, an observer is required to gaze over the focal area using binoculars and to take notes. These activities inherently require the observer to move. On the other hand, once the video equipment is installed it remains motionless for the remaining observation period. However, video equipment requires instillation closer to the focal crabs, where recording equipment is in direct sight of the crabs. Thus, both methods present contrasting stimulus for the target crabs: for video, motionless but in close proximity to focal crabs, and for visual census a moving observer but further from focal crabs. These features can be considered advantages or disadvantages depending on the variables considered. The opposing trend of the sampling methods in various taxa detection proportions suggest that sampling biases are taxon specific, as also suggested by Skov *et al.* (2002). That probably means that the perceived level of threat from the two sampling techniques is not homogenous across taxa. It is possible that different species could have different abilities to sense the risk of the sampling methods by using their vibratory and visual receptors (Popper, Salmon & Horch 2011).

Visual and sound/vibratory signals are the two main mechanisms that ocypodoid and grapsoid crabs use to perceive their surroundings (Salmon & Horch 1972; Von Hagen 2000;

Zeil & Hemmi 2006). For instance, ocypodoid crabs produce elaborated stridulation and percussion communication (Salmon 1967; Salmon 1983; Von Hagen 1984). Salmon (1983) found that fiddler crabs are able to detect a wide spectrum of vibrations and sounds, with different sensitivities. Similar findings have been reported for some other ocypodoid crabs (Boon, Yeo & Todd 2009). Fiddler crabs capabilities to emit and detect vibrations also depend on substrate condition (i.e. damped or not) and distance to the vibration source (Salmon & Horch 1972 as cited in Salmon 1983; Horch 1975). To our knowledge there is not direct association between the use of vibratory signals in ocypodoid and grapsoid crabs as a mechanisms of risk detection. However, it is reasonable to think that crabs can use their vibration receptors to identify potential risks (as also suggested by Popper, Salmon & Horch 2011) and as other invertebrate do (Hergenroder & Barth 1983; Castellanos & Barbosa 2006; Buscaino *et al.* 2011). Under this assumption, a seated observer four to five meters away could be recognized by some crab species, and these crabs potentially could be deterred from leaving their burrows and resuming their activities on the surface. The ability to sense substrate vibrations and air-bone vibrations (i.e. sound) vary across the family Ocypodidae, with capability of vibration detection ranging from few centimetres to 10 meters depending on the signal intensity (Salmon & Horch 1972; Popper, Salmon & Horch 2011). Detailed information about vibration detection abilities and sensitivities is not available for the species observed in this study.

The visual apparatus of grapsoid and ocypodoid crabs is very efficient in detecting and tracking other crabs and potential predators (Land & Layne 1995b; Land & Layne 1995a; Layne, Land & Zeil 1997; Cannicci, Morino & Vannini 2002). These two groups use different mechanisms to evaluate distance to a focal object (Zeil, Nalbach & Nalbach 1986). Fiddler crabs and other Ocypodoidea crabs, narrow-fronted and long stalk-eyed, use a declination system (Ooi, Wu & He 2001), where the crab's field of view horizon is used as a reference to assess conspecifics and predators (Land & Layne 1995a; Layne, Land & Zeil 1997; Hemmi & Zeil 2003). Thus, in these crabs, objects detected above the crabs' eye horizon trigger a precautionary or escape response (Layne, Land & Zeil 1997). Grapsoid crabs, broad-fronted and short stalk-eyed, use stereopsis to assess distance, and are able to visually identify shapes and predators (Zeil, Nalbach & Nalbach 1986; Cannicci, Morino & Vannini 2002). The declination system and artificial horizon used by fiddler crabs is likely to make them more susceptible to foreign objects located at their zenith. Even if the recording equipment covers a smaller absolute area than the visual area covered by a seated human observer, because recording equipment is placed closer to the crabs, its relative size would be larger and it would be perceived above the crabs' eye horizon (Land & Layne 1995a; Layne, Land & Zeil 1997). Our result seem to confirm this explanation. The four taxa with lower detection rates for video surveys are fiddler crabs (Figure 2-2A). *Tubuca signata*, *T. seismella*, and *A. perplexa* normally inhabit open areas without canopy (Crane 1975). *Tubuca coarctata* occupies the lower edge of mudflat and sandflats in the low tide zone, often in areas shaded by mangrove canopy. I cannot disregard the possibility that the use of other signals, such as olfactory cues, which could allow crabs to perceive the video equipment and an observer differently. Our results suggest that the presence of the video equipment has a negative effect in detection rates for some fiddler crabs species, in particular, those crabs that inhabit sandy and muddy open areas, where the presence of a foreign object above the crabs' eye horizon is most obvious.

For those taxa for which video surveys performed better, the detection proportion increased between two to eleven fold. Of particular significance was the detection improvement for *P. wardi* when using video surveys (Figure 2-2A). For this species detection proportion increased from 0.02 in visual censuses to 0.22 in video surveys. Little is known about the ecology and life history of *P. wardi* and other species in this genus (Kim *et al.* 2011). It has been reported that the surface activity for this species, and other species in the genus, varies across seasons and tidal cycles (Clayton 1988; Boggon 2006; Kim *et al.* 2011). I do not expect these to be a factor in our observed differences between sampling methods because sampling was carried out during the same season and on the same tides. Precautionary behaviour to perceived risk of predation has been reported in other *Paracleistostoma* species (Su & Lim 2016), and it is probable to be used by other crab species. Thus, it is likely that *P. wardi* and all other crabs taxa perceive the risk of foreign objects in their proximity differently, i.e. recording instruments and observer.

The position, distance and relative movement of an observer determine the behavioural thresholds of crabs' escape reaction (Nalbach 1990; Land & Layne 1995a; Layne, Land & Zeil 1997). An individual crab's response to a threat will also elicit a similar response in other individuals (termed "wave of panic" by Land & Layne 1995a). Given that visual censuses tended to reduce detection rates in most taxa, it is possible that to some extent the lower number of species per sample observed in this method is a consequence of the "*wave of panic*" induced by the most sensitive species to an observer. However, I also noticed that detecting crabs in videos was easier than in the field. In particular, very small and cryptic crabs that exhibited limited movement were easily detected in recordings, but much less easily in visual censuses (Skov & Hartnoll 2001). These crabs were also more difficult to identify, explaining the increased number of unidentified crabs in video surveys (Figure 2-2A).

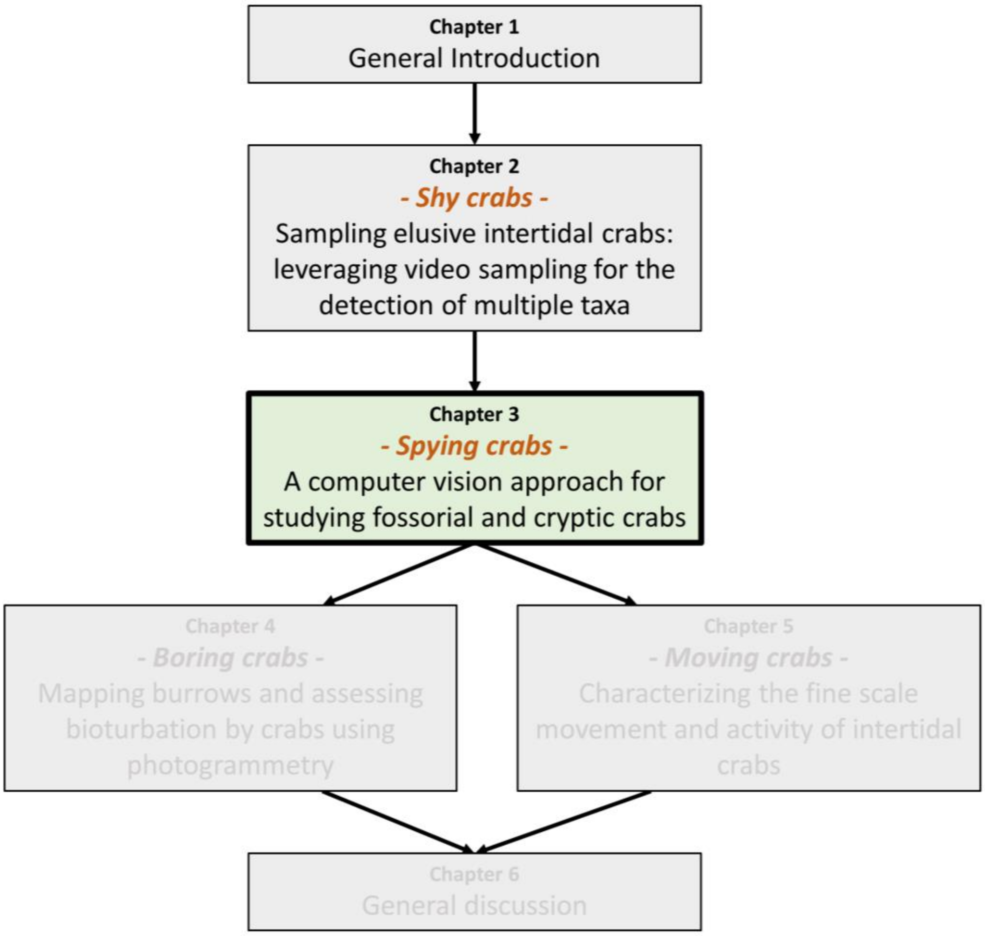
Latency to first crab re-emergence for both methods was within the expected time reported in the literature (Nobbs & McGuinness 1999). The magnitude in the latency differences of both methods were unexpected. In average, the waiting time to the first crab re-emergence was 1.65 times longer in visual censuses. Our inference model suggests that the uncertainty around the mean waiting time is higher for video surveys (Figure 2-5A-B); but uncertainty of the shape parameter is higher for visual censuses (Figure 2-5C-D). Overall, this indicates that the effect of video equipment on latency was smaller than the effect of a seated observer, but it was also more variable (Figure 2-5E-F). The apparent differences among taxa in perception of risk of the two methods could also influence the latency results. Smaller crabs often resumed activity in the surface more rapidly than larger more conspicuous individuals. Thus, lower latency values observed in video surveys may reflect the increased probability of detection of these smaller and cryptic individuals in video surveys. Therefore, differences in latency between methods could be rather a consequence of the inability to observe smaller and cryptic crabs in visual census. Unfortunately, I was not able to estimate crabs' relative size from visual censuses. For this reason, a fair comparison was not possible in regards of latency and individuals' size. Nonetheless, I believe this result is an additional argument in favour of video surveys being a more useful sampling method than visual censuses for many situations.

The negative effect of video surveys in detection rates for some fiddler crab species is an important factor to consider when selecting a sampling technique. If the main goal of a monitoring program is to obtain occurrence data of fiddler crab species, visual censuses might be the best method to employ. Importantly, in many situations overall advantages of video surveys may override this disadvantage. Alternatively, if a monitoring program aims to obtain occurrence and diversity data from a range of crab species from various higher taxonomical groups, video surveys would be a better sampling method than visual census. There is potential for making video equipment lower profile to mitigate the negative effect on some fiddler crabs. For instance, by recording the focal area from an oblique angle, further from the focal individuals but closer to the sediment, i.e. closer to the visual horizon of crabs.

Given the life history and sexual differences between species and individuals in their surface behaviour and latency (Salmon & Atsaides 1968; Hockett & Kritzler 1972; Valiela *et al.* 1974; Murai, Goshima & Nakasone 1983; Weissburg 1992), using a combination of sampling techniques, such as visual counts and video surveys is advisable to maximize accurate prediction of species richness, latency, and abundance of intertidal brachyuran crabs. A mixed sampling strategy for assessing species diversity (i.e. abundance, richness) present its own challenges, because the effect of the sampling method can be confused with variability on species behaviours and population site-specific adaptations. For instance, Skov *et al.* (2002) found that visual counts and burrow counts abundance estimates performed differently depending on species (three species considered) and locations (five sites). Schlacher *et al.* (2016) reported similar results for burrow counts on a meta-analysis (24 studies) considering several taxa (7 families). Thus, it is paramount that sampling techniques are validated and cross-validated for different species and locations (Schlacher *et al.* 2016).

Although the specific reasons driving differences in detection rates, species richness and latency between sampling methods remain unclear, overall video surveys performed better than visual census. The video survey method is both able to detect more species and to reduce latency (Figure 2-6) and to increase detection rates for most taxa (Figure 2-2A). In addition, the ability to record the focal quadrat, watch it and re-watch it several times at the lab, by a single or many observers, can reduce any effect of fatigue and bias from an individual observer, and can enable a single expert observer to, in effect, observe a large number of replicate and/or different sites simultaneously. These factors provide enormous advantages for video surveys over visual censuses. The use of videos opens the possibility to integrate computer vision and other image processing pipelines that can enhance the amount and quality of information we get from monitoring programs (Weinstein & Dray 2015; Weinstein 2018), for instance, by automating the assessment of individuals' sizes and behaviours (Sridhar, Roche & Gingins 2019). Continuous improvement of sampling methods would improve our ability to obtain reliable estimates of population and species occurrences, abundances and sizes, which would, in turn, enable better management and protection decisions. Here I have shown that video surveys advance the sampling of intertidal crabs by improving species detectability, collecting higher species numbers and reducing waiting time. Future work should focus in furthering taking advantage of the benefits of video surveys to collect more information about the biology and ecology of grapsoid and ocypodoid crabs.

Chapter 3 - A computer vision approach for studying fossorial and cryptic crabs



Aim: Develop a workflow and computer vision software grounded in field video recordings to collect biological and ecological data on intertidal crabs.

Introduction

Over the last century the rate at which species, habitats and ecosystems are being lost has become one of the most concerning challenges faced by humanity (Polidoro *et al.* 2010; Barnosky *et al.* 2011). At no other time has it been more important to describe, quantify and understand patterns of species loss, and the relationship between species loss and the functioning of ecosystems (Cardinale 2012). A primary consequence of this urgency is the necessity to scale up the volume of relevant information gathered about species and ecosystems, for instance by using Technoecology (Allan *et al.* 2018) and Ecoinformatics (Michener & Jones 2012) approaches. For biologists and ecologists with dirt under their fingernails, this is an even more challenging task, as many traditional methods of sampling and collection are logistically limited by personnel-power.

Working with cryptic and fossorial organisms, such as fiddler crabs, imposes additional challenges in achieving exhaustive biodiversity censuses and functional ecology assessments. The cryptic nature of some species makes it difficult to confirm species identities in the field. Their fossorial nature, coupled with their sensitivity to observers and fast speed, also limits our ability to study these creatures that spend a considerable proportion of the time inside burrows (Caravello & Cameron 1991; Reaney 2007). Despite these limitations, fiddler crabs as a group are among the most studied crustaceans (e.g. see references selection in Rosenberg 2001 introduction). Fiddler crabs, along with other intertidal and coastal crabs, regulate energy and matter fluxes in various ecosystems such as mangroves, salt marshes, sandy beaches and mudflats (Robertson & Daniel 1989; Sheaves & Molony 2000; Webb & Eyre 2004; Nerot *et al.* 2009; Smith, Wilcox & Lessmann 2009). For instance, crab bioturbation plays a preponderant role in shaping soil composition, texture, and microbial community, which in turns drives nutrient and soil metabolism in coastal sediments (Gribsholt, Kostka & Kristensen 2003; Wang *et al.* 2010; Fanjul *et al.* 2011; Gittman & Keller 2013; Fanjul *et al.* 2015; Booth *et al.* 2019). The importance of crab bioturbation has been hypothesized to be relative to the total burrow volume and sediment turnover rate (Katz 1980; Gribsholt, Kostka & Kristensen 2003; Wang *et al.* 2010), which is proportional to crab density and burrow behaviour. Despite substantial evidence on the ecological function of fossorial intertidal crabs, caution is necessary when generalizing their importance because precise function is likely to vary depending on environmental conditions (Michaels & Zieman 2013; Natalio *et al.* 2017).

Despite the functional role of fiddler crabs, the methods used to estimate ecological measurements, such as movement patterns, abundance, sex ratios, behaviour and bioturbation rate, among others, present some serious pitfalls and limitations (Nobbs & McGuinness 1999; Kent & McGuinness 2006; Schlacher *et al.* 2016). Invasive techniques, such as sediment excavation and digging (e.g. Colby & Fonseca 1984), installation of pitfall traps (e.g. Salmon & Hyatt 1983) and others, have the advantage of gathering the most detailed information about population structure (e.g. densities, sex ratios and size structure) and are assumed to offer the most reliable estimates (Lourenco, Paula & Henriques 2000; Macia, Quincardete & Paula 2001; Skov & Hartnoll 2001; Skov *et al.* 2002). However, these methods are time-consuming and modify the crabs' natural habitat. Moreover, given the fossorial nature of fiddler crabs, some invasive techniques, such as pitfall traps, do not guarantee accurate and precise estimates across habitats or seasons because these are designed to monitor crab activity, instead of densities (Lee 1998). Alternative and widespread non-invasive methods, such as burrow counts (e.g. Mouton & Felder 1996; Lourenco, Paula & Henriques 2000) and distant counts of active individuals (e.g. Macia, Quincardete & Paula 2001; Skov & Hartnoll 2001; Jordao & Oliveira 2003), are only reliable for specific crab species, require site-specific calibration, and are based on assumptions about species behaviour, population structure and phenology (Macia, Quincardete & Paula 2001; Skov & Hartnoll 2001; Jordao & Oliveira 2003; Schlacher *et al.* 2016). These are likely to produce a biased sample of the population. Similarly, bioturbation rates estimates often require methods such as making burrow casts or quantifying the amount of sediment moved (e.g. Katz 1980; Escapa *et al.* 2007; Wang *et al.* 2010), which are hard to apply intensively and extensively. In contrast, while non-invasive methods, such as video recordings (e.g. Nordhaus, Diele & Wolff 2009), can minimize or overcome some of these challenges, their application has been constrained because of the volume of data created and lengthy processing times. Thus, the fossorial lifestyle, behavioural habits and cryptic characteristics of fiddler crabs present an opportunity for researchers to innovate and develop fit-for-purpose sampling techniques.

New technologies offer alternatives for streamlining the collection of biological and ecological data, while automation alleviates bottlenecks in processing and analysis workflows. For instance, computer vision applications have penetrated the field of ecology and proven to be useful in extracting information from images, still or video (e.g. Zion 2012; Villon *et al.* 2018; Weinstein 2018; Schneider *et al.* 2019). Thus, computer vision is reducing the amount of time spent processing image data, so easing the bottleneck created by collecting far more data than can be processed time-effectively. Unfortunately, computer vision solutions to biological and ecological problems are not always useful for more than one purpose, because computer vision as many other statistical models are sensitive to training data sets , and can have poor generalizations capabilities. Therefore, ecology and biology require continuous development of heuristic and fit-for-purpose computer vision methods and algorithms.

Here I propose a workflow underpinned by computer vision and machine learning algorithms to collect biological and ecological metrics of intertidal crabs in mudflats and sandflats based on field video recordings. I used geometric transformation on images, motion detection, image segmentation, photogrammetry, among other algorithms to extract data on crab motion trajectories, colouration, size and bioturbation activity. A significant portion of this manuscript is devoted to describing fit-for-purpose methods, but I also list current challenges and future technological avenues to obtain additional biological and ecological metrics from image sequences. I believe that our approach can be useful for biologists and ecologists working in similar systems and taxa, regardless of the spatial and temporal scale of their work.

Materials and Methods

Tubuca polita (Crane, 1975) individuals were recorded in a mudflat of the Annandale wetland in Townsville, Australia (Figure 2- 1). A sediment area with low vegetation coverage was selected to ensure maximum visibility of crabs during recording. A virtual quadrat, 80 x 80 cm, was monitored for 30 minutes. Quadrat vertices were marked with circular coloured indicators inserted into the sediment. The coloured indicators were used as size and Cartesian coordinate references. To validate morphometric data and species identity from the videos, at the end of the recording period I manually collected as many of the observed crabs as possible. However, many crabs evaded capture and hence, individuals whose taxonomy could not be confirmed were excluded from subsequent analysis.

To track and count individuals, and assess their size and colour, a GoPro HERO3 camera was positioned to fully cover the virtual quadrat area in the field of view. I trialled three different camera positions: full top-down view perpendicular to the virtual quadrat (Figure 3-1A, mode I), an oblique recording angle relative to the virtual quadrat (Figure 3-1A, mode II), and low angle parallel to the sediment (Figure 3-1A, mode III). Mode I is ideal for movement tracking because a perpendicular view minimizes differences between the image plane and the plane of crab movement (i.e. sediment surface). However, mode I recording implies that video equipment is in the zenith of the focal crabs, and it involves stepping on the focal area of interest, both, which can increase crab burrow latency (Chapter 2, and personal observation; latency measured as the time of crab emergence from burrow after the observer abandons the area). Mode II minimizes disturbance of sediment and vegetation, slightly reduce the profile of the camera relative to the crab perspective, and if placed correctly relative to the light source (i.e. sun) it decreases equipment shadows casting over the quadrat. Camera position mode III is ideal for assessing feeding rates and behaviour (Figure 3-1A, e.g. see Figure Appx. A-1) because chelae and legs movement can be observed. Based on these aspects mode II offers the best compromise. Geographic position, sediment type, surrounding vegetation, observed tide, time of day, camera settings, and observed species composition were noted at the start of each video (Figure 3-1B). To demonstrate the capacity of the analyses presented below these were only performed in the last five minutes section of the recorded video, when all crabs appeared to have resumed normal behaviour and after the maximum crab abundance was observed. Standard data management protocols were followed, thus, multiple copies of the recording and meta-data were created and saved in local and cloud storage (Figure 3-1C).

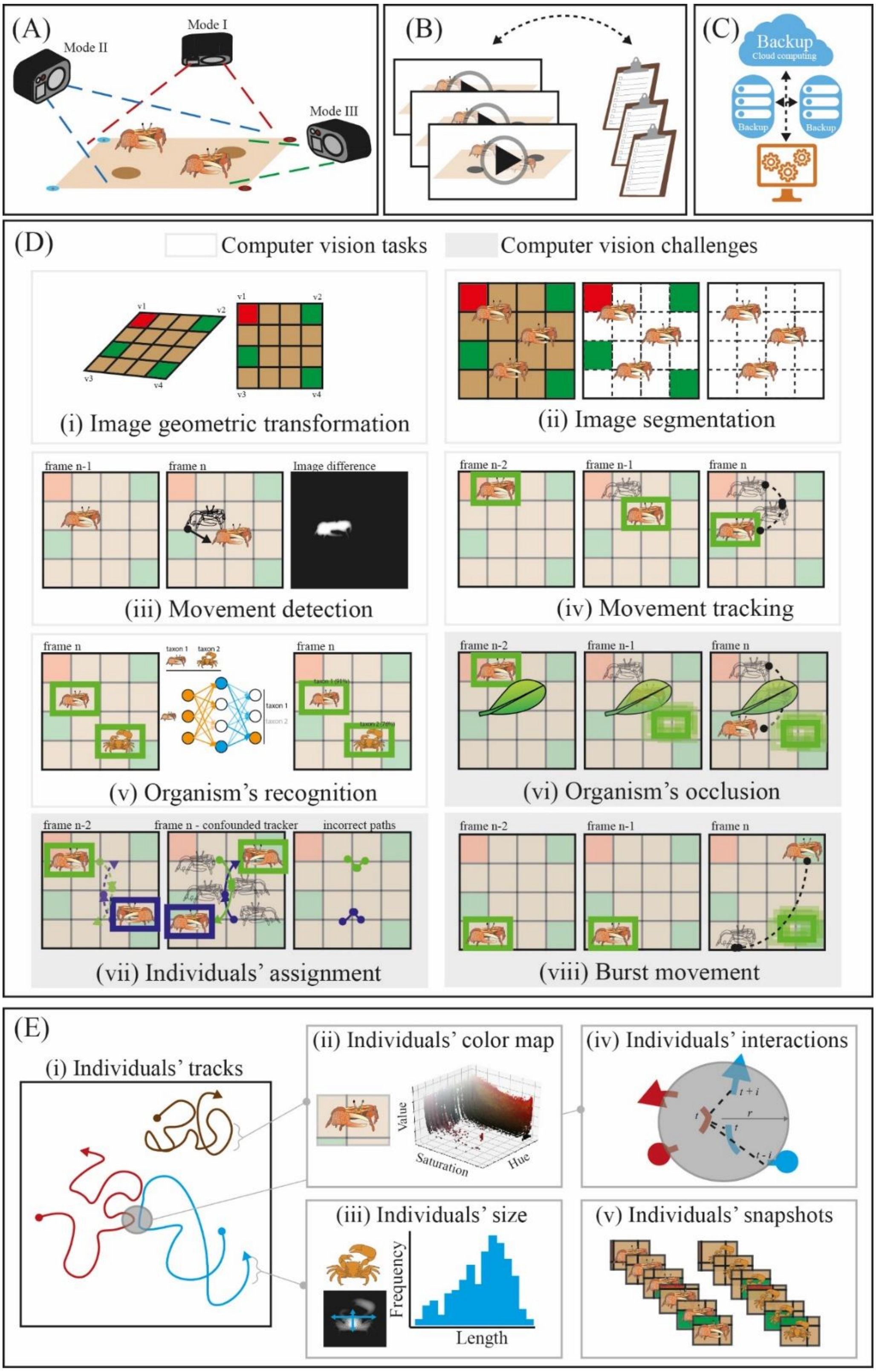


Figure 3-1: Schematic workflow for tracking, counting and measuring individuals size and colour from videos. (A) Images can be captured from different viewpoints depending on the purpose of the study: mode I and II are ideal for tracking, while mode III is convenient for observing behavioural displays. (B) Raw data and metadata are linked and cross-referenced, and (C) data is backed up to multiple local and remote locations. (D) Common

computer vision tasks applied and challenges encountered in image processing. (D-i) Image perspective transformation is useful to correct lens distortion and image composition. In natural settings foreground and background segmentation (D-ii) and movement detection (D-iii) are useful algorithms to isolate key features or organisms, and detect motion in images. Once features, objects or organisms are identified, tracking (D-iv) is done by estimating or predicting motion vectors among successive images. Furthermore, organisms' classifier and pattern recognition (D-v) can aid and improve the performance of computer vision tasks. (D-vi) Organisms' occlusion and features overlap reduce tracking success. When multiple organisms interact in close proximity, individuals' assignment during tracking is reduced potentially producing wrong track paths: individuals' identities were not preserved along the tracking period. (D-viii) Sudden and rapid motion can potentially produce loss of tracking. (E) Workflow results and products include individuals' movement paths in the field of view (E-i). Knowing an individual's position in the field of view at any time allows us to extract additional information such as individual colour and colour change (E-ii), size (E-iii) and number of close interactions with other individuals at any time (t) for a given time window (i) and minimum distance (r) (E-iv). In addition, organisms' snapshots (E-v) can be saved for training image classifiers.

A fit-for-purpose and heuristic Python programming tool was created to analyse crab videos (Herrera 2020). This free and open-source tool, Crabspy, is available on GitHub (https://github.com/CexyNature/Crabspy). Crabspy combines common image segmentation and machine learning algorithms to track crabs in videos. Firstly, an image transformation is employed to orthorectified the video, thus, the observed area maintains a constant scale (Figure 3-1D-i). Secondly, movement is detected and the foreground is isolated from the background (Figure 3-1D-ii and D-iii). Thirdly, in its current version, a tracker, define inside a bounding box, is seeded at the original position of the target individual, then the tracker position is updated based on the movement of the individual in successive frames. Tracker update can be done using any of the tracking methods available in the library OpenCV (OpenCV 2015, i.e. MIL, BOOST, and KCF) or tracking can be done manually by the user. I used the Multiple Instance Learning algorithm (MIL, Babenko, Yang & Belongie 2009). The minimum relative size of objects moving, i.e. crabs, can be set using eroding and dilation parameters (i.e. kernel size). At any given frame, the bounding box enclosing the target individual obtains its relative position, colour, size and image (Figure 3-1E). Crab images were used to create training sets for image classification (Figure 3-1D-v, Figure Appx. A-1), however, crab taxonomic recognition is beyond the scope of this study.

Several challenges were encountered during the workflow described above (Table Appx. A- 2, Figure 3-1D-vi, D-vii and D-viii). In particular, three situations trouble the tracking algorithm. When a focal crab was occluded by vegetation, the tracker was likely to lose the focal individual and provide erroneous position (Figure 3-1D-vi). When two or more organisms were interacting in close proximity sometimes the tracker could track the wrong focal crab, so tracking and individual assignment was erroneous (Figure 3-1D-vii). Finally, when a crab exhibited very fast movement a tracker could lose. In these situations, I used Crabspy manual tracking alternative.

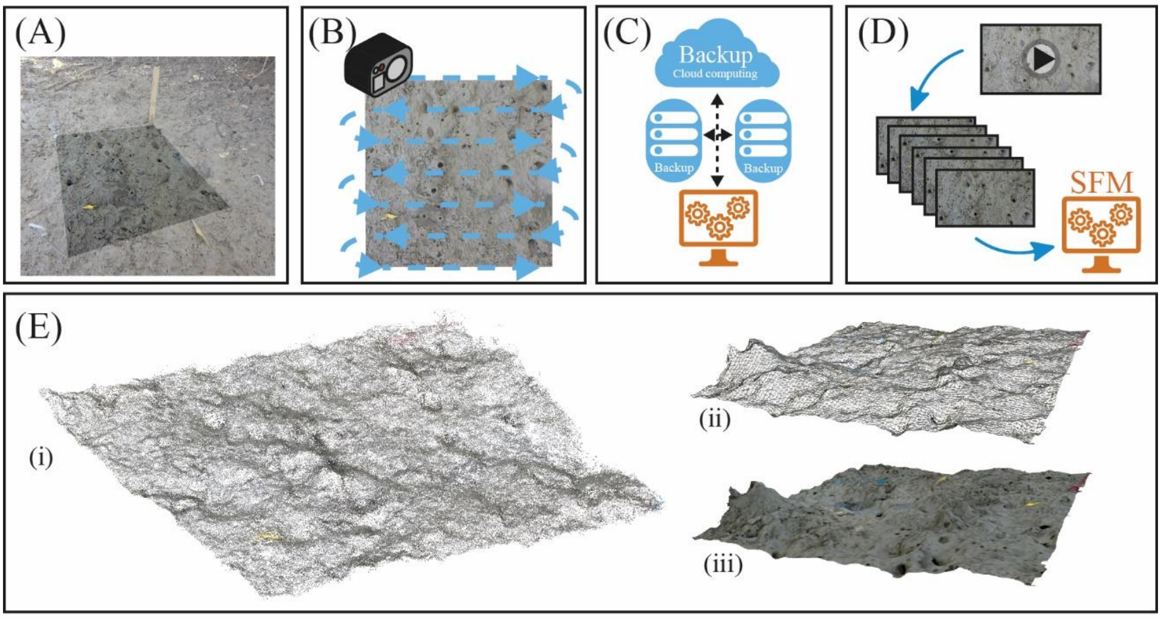


Figure 3-2: Schematic workflow for assessing sediment changes. (A) An area in the sediment is selected, and vertices were marked with coloured Ground Control Points (GCPs). (B) The area was scanned using a camera while recording a video. (C) Multiple copies from videos were created and saved in local and remote independent storage to prevent data entropy. (D) Frames from video were extracted and saved, and these were used to create photogrammetry reconstructions through Structure from Motion (SFM). From photogrammetry reconstructions three main data products can be created: dense point cloud data (E-i), mesh data (E-ii), and textured and coloured 3D models (E-iii).

During analysis, each individual was manually assigned an ID name, and its sex, handedness and species was recorded with the respective positional data (Figure 3-1E-i). This step was performed manually, but with the increasing image collection two automated models able to assign sex and handedness were developed (Table Appx. A- 1). Crabs colouration can be extracted for any individual and any given time during the recording (Figure 1-E-ii). Individual colour data is useful to study species that exhibit whitening or brightening, or other changes of colouration (e.g. Hemmi *et al.* 2006; Takeshita 2019). By using the quadrat colour indicators as ground control points, and by applying geometric transformations on images (i.e. orthorectification) I remove the effect of recording perspective and correct the scale. Thus, I was able to estimate the absolute size of crabs. The size of crabs at each frame was approximated by measuring the size of the Binary Large Objects (BLOBs) created after background removal and motion detection algorithms were applied. Each BLOB at each frame was measured along its two longer axes, which aimed to represent the width and length of the crab. As validation, the area of the BLOB was also compared with the ground truth area of the crab measured by manually segmenting individual crabs in 100 images from 10 crabs (Figure Appx. A-2). BLOB measurements resulted in a distribution of sizes per individual, from which central point estimates or confidence intervals could be estimated (Figure 3-1E-iii). For each individual crab, a file containing position and size per frame, individual ID, species, sex and handedness was created. All files were combined and analysed using R software version 3.5.0 (R Core Team 2018). Crab densities, sizes and tracks were transformed from pixel units to centimetres by scaling based on the known side dimensions of the quadrat. Using the positional data from all individuals through time I extracted events where proximity between pairs of individuals was less than 10 cm within a two second time window. Based on our observations of crabs' dynamics, this distance and time window describe well interaction between crabs. Nonetheless, the proximity distance and time window can be adjusted depending on the question and working hypothesis (Figure 3-1E-iv). The type of interaction, agonistic or non-agonistic, was also recorded by observing each interacting pair in the video. Thus, a social network analysis based on proximity was conducted to evaluate crab interaction patterns. Finally, snapshots per individual at each frame were generated (Figure 3-1E-v), and these were used to train an image classifier (Figure Appx. A-1 and Table Appx. A- 1).

I explored the bioturbation activity of *T. polita* individuals by assessing the amount of sediment moved over time. Sediment moved was measured as the volume difference between two sampling times. Volume difference was computed from 3D sediment reconstructions created using Visual Structure from Motion a photogrammetry technique (Wu 2011; Wu *et al.* 2011; Wu 2013). Visual Structure from Motion allows recovering the 3D structure from an object by computing the relative positions of object's features in relation to the image sensor in a set of overlapping images (i.e. photos or frames in videos). I monitored a permanent quadrat, 50 by 50 cm delimited with Ground Control Points (GCPs) in its vertices (Figure 3-2A). This permanent quadrat was placed in the upper intertidal area of the muddy bank where presence of *T. polita* was confirmed. Moreover, the sediment was sampled in low tide so there was no sediment transportation due to tidal change. The quadrat was independently recorded twice at two time points, namely time before and time after (7 days later), for a total of four sediment recordings. Each pair of independent video recordings at each time were filmed within minutes from each other. Thus, I assumed that there was not a significant change in sediment for these pairs, and therefore these two independent videos of the same area allow calculating the method's precision. The sediment was recorded using a camera Garmin VIRB XE by progressively moving the camera from side to side at constant speed (Figure 3-2A). As per crab recording, standard data management protocols were followed (Figure 3-2C). Every 6th frame was extracted from the videos resulting in 200 to 600 images for each video scan. These images were used to create photogrammetry reconstructions using the open-source and free software VisualSFM (Wu 2011; Wu 2013) (Figure 3-2E-i). Dense cloud data was imported in the open-source and free software CloudCompare v2.20.2 Zephyrus (CloudCompare 2019). Mesh reconstruction, as well as textured, coloured and ortho-rectified 3D models can be created in CloudCompare (Figure 3-2E-ii, E-iii). Our workflow calculations were done on dense point cloud data which preserve the inherent density of the sediment models (Figure 3-2E-i). Point cloud datasets were ortho-rectified by scaling, rotating and transforming 3D clouds based on the known dimension and distance of GCPs. Digital elevation models were generated and cloud to cloud distances among all cloud pair combinations were calculated using the quadratic function method. Furthermore, I validated the volume estimation method by calculating the volume difference using the proposed method in an experimental plot where a known amount of volume was added from the plot (Table Appx. A- 4).

Results

T. polita individuals emerged from their burrows a few minutes after the sediment was exposed to air following the receding tide. From the 25 individuals observed in the field inside the quadrat, 17 were tracked during video analysis, and from these only ten were subsequently captured after the video recording was completed, and seven escape during capture. Crab motion ranges and utilization areas overlapped among several individuals (Figure 3-3). Fourteen of the 17 tracked individuals were confirmed as males while for the remaining 3 sex was not determined. This was due to loss of one chela or because animals presented two minor chelae with some degree of hypertrophied. Ten individuals were right handed and three left handed. In four individuals, handedness could not be assessed because it was not verified in the field nor on the video. Total distance travelled per individual was variable (114.8 ± 69.16 cm), with a minimum of 24 cm (Figure 3-3, crab_6) and maximum of 240 cm (Figure 3-3, crab_3). In general, there were two types of individuals: those who wandered and those who stayed close to a burrow or territory. Some wandering individuals left the field of view during filming. *In situ* observations confirmed that at least two males, which left the field of view of the camera, moved up to four metres away from their original positions. Wandering crabs who stayed in the camera field of view travelled up to 161 cm (Figure 3-3, crab_10). For most non-wandering individuals the position of the home burrow defined the gravitational centre of the individual's utilization area. The total distance travelled was higher in crabs with adjacent neighbours. Among this subset of individuals, short distance explorations to a neighbour's burrow were observed. Burrow utilization was observed for eight individuals, and they actively defended their burrow from intruders.

The size estimate distribution per individual produced a bimodal distribution in most individuals (Figure 3-4A). This was expected as the longest two axes from each blob per frame were recorded. Various factors affected the size estimation. Firstly, the size of the kernel used for eroding and dilation during analysis constrained the possible values both axes could take. Thus, the axes' lengths are a function of the kernel sizes. This factor affects the accuracy of the estimate. Secondly, our size estimate was also affected by waving, fighting, pushing or any other behaviour which changes the apparent size of the crab. Thirdly, individual close interaction to any other moving element in the landscape such as other crabs or vegetation overestimated size. Finally, long stops (lack of motion) underestimated sizes, as the blob progressively fades away when movement is not detected. These last three factors affected the precision of the size estimate. However, the comparison between automated segmentation and manual segmentation resulted in acceptable errors (Figure Appx. A- 2, error percentage mean = 4 ± 11 %). The frequency of extreme deviations in the estimate due to the above factors is proportionally low given that a crab size estimate is generated for each frame in the video (Figure 3-4A). I explored how well this size estimate predicted the carapace width and propodus length in the ten individuals that were captured and measured in the field (Figure 3-4B). I used the mean of the crab size estimate distribution as the predictor and the measured carapace width and propodus length as response variables and surrogates of crab size. Assumptions for a linear model between size estimate and propodus length were not met. The linear model predicting carapace width based on our size estimate explained 65% of variation and this method tended to overestimate crab size (Figure 3-4B).

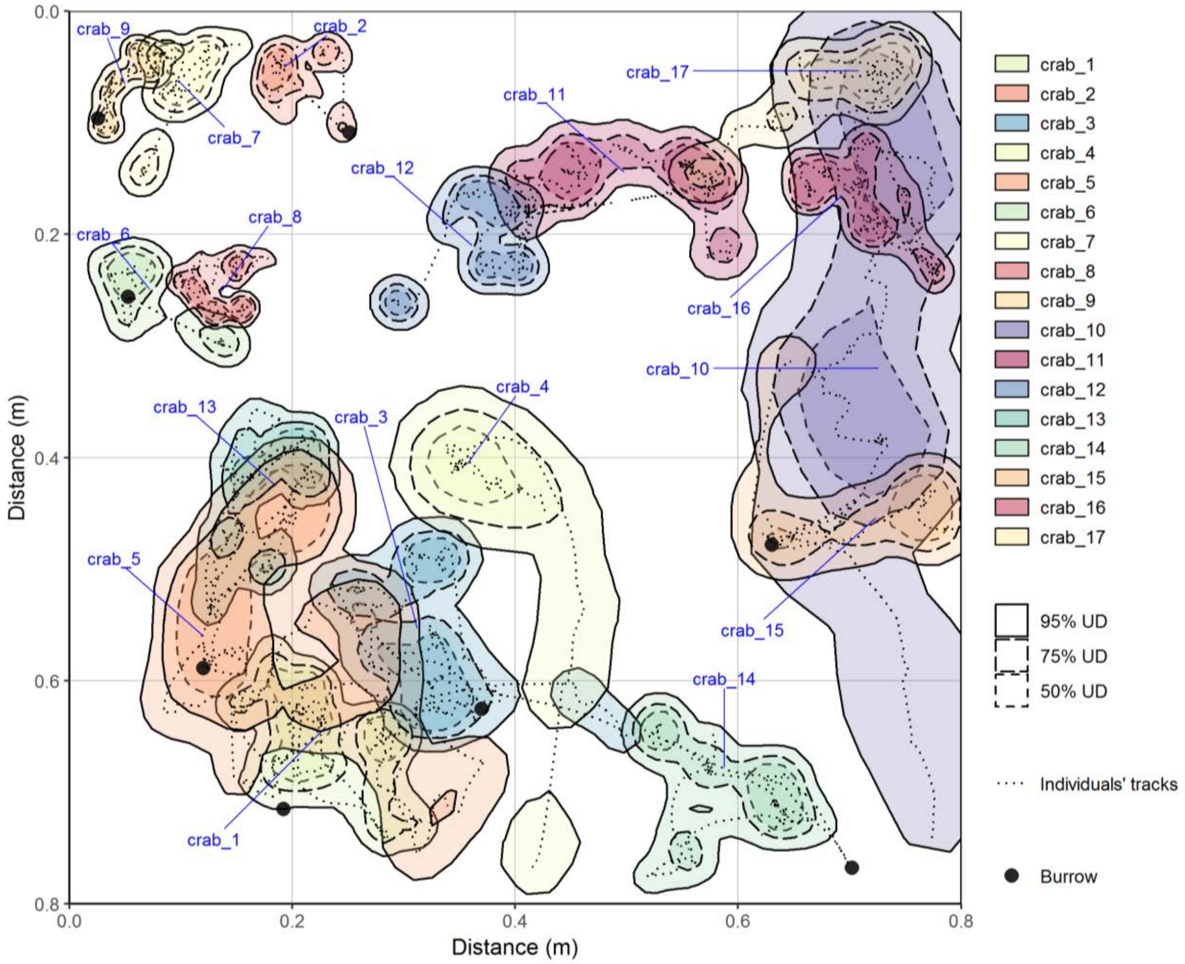


Figure 3-3: Movement tracks and kernel utilization distributions (50, 75 and 95%) for seventeen Ocypodidae crabs (*Tubuca polita*). Crabs were observed during five minutes on an intertidal mudflat fixed quadrat of 80 cm by 80 cm. Black circles represent burrows used during the observation period.

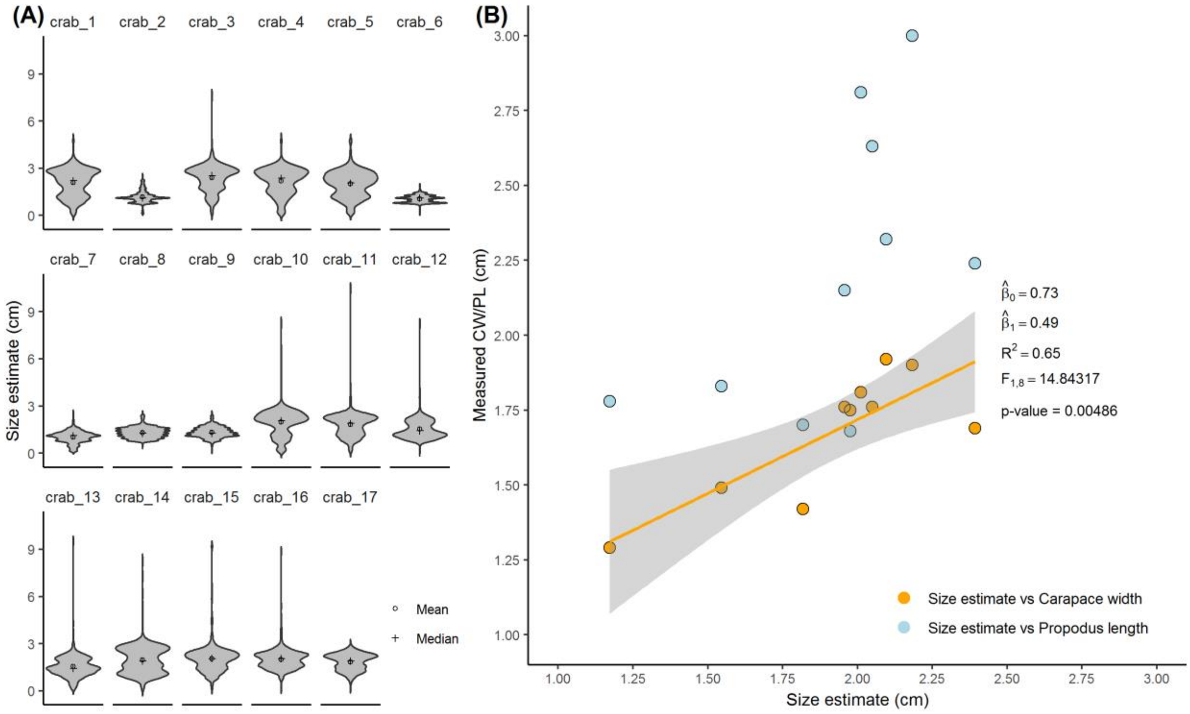


Figure 3-4: Size estimates, and size estimates and morphometric measurements relationship for *Tubuca polita* individuals. (A) Distribution of size estimates for the seventeen *Tubuca polita* individuals. Distribution is shown as violin plots. Mean and median are presented as circle and cross respectively, and these were assumed to represent the individuals' carapace width point estimates. (B) Size estimate (mean) versus morphometric measurements, i.e. Carapace Width (CW) and Propodus Length (PL), for the ten individuals measured in the field. The fitted linear model (orange continuous line) describes the relationship between the size estimate and the measured CW (95% confidence interval is shown as gray shaded area).

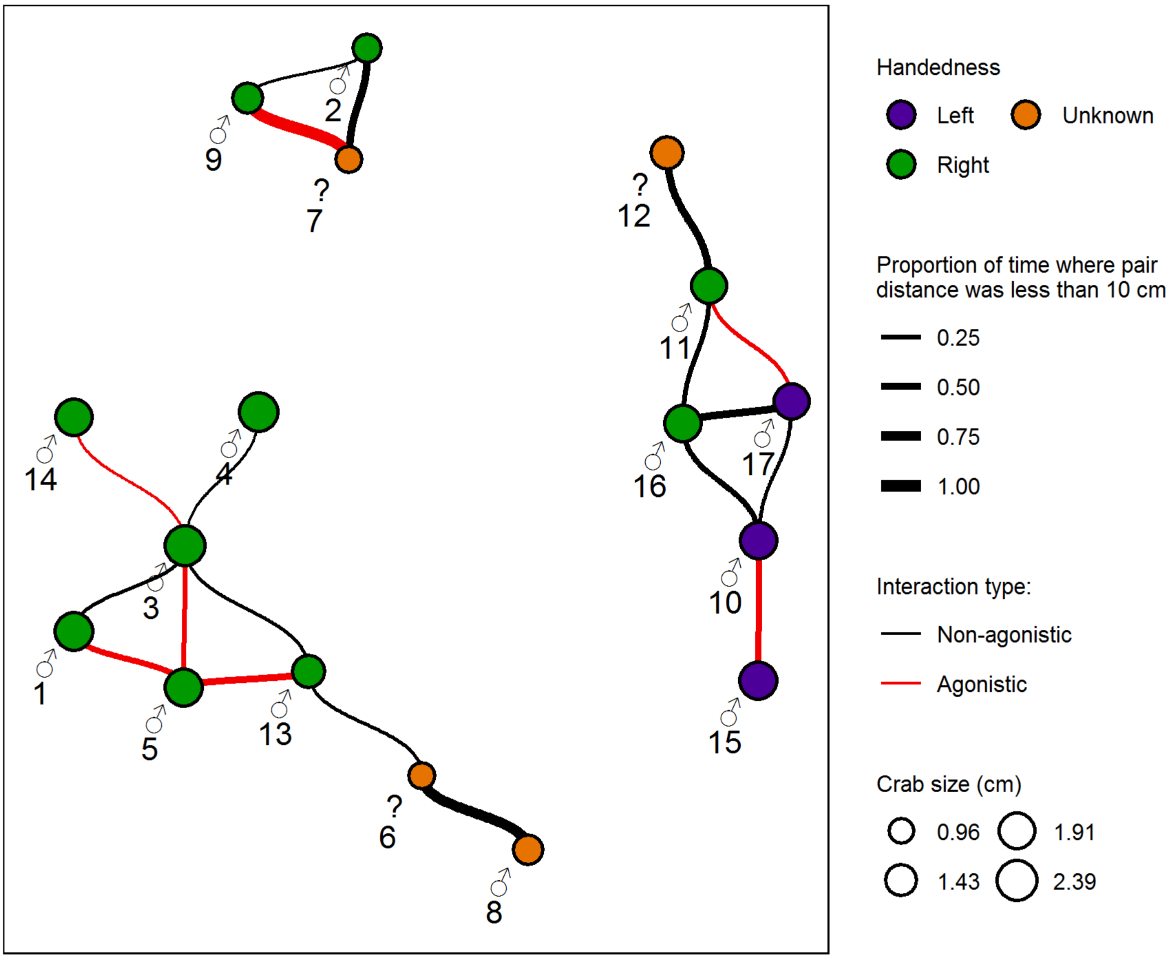


Figure 3-5: Interaction social network for *Tubuca polita* individuals (17 nodes and 19 edges). This undirected and weighted network was constructed from proximity data among pairs of individuals observed during five minutes. The node labels represent individuals ID and sex. Question marks indicate individuals for which sex was not confirmed. Node colour and size represent handedness and size estimates. Edges connecting nodes indicate that the distance between these pair of individuals was less than 10 cm in a two second window. Edge width shows the proportion of time these individuals were within 10 cm from each other. Edge colour shows the type of interaction observed: red at least one agonistic interaction; black at least one non-agonistic interaction.

The number of interactions between crabs varied on an individual basis (Figure 3-5). Most interactions occurred in the vicinity to a burrow. Crab number 3 exhibited the highest number of interactions and the highest number of agonistic interactions with different individuals (Figure 3-5). Some crab pairs kept a distance of 10 cm or less for a large proportion of the observed time, i.e. pairs 9-7, 6-8 and 12-11 (Figure 3-5). The number of edges in the network (19) is well below the possible number of edges for a proximity network with 17 individuals (i.e. 136). Size and handedness seemed to have an effect on the network structure, but this must be explored with larger data sets. As it has been observed in other systems (Barabasi & Albert 1999), some individuals acted as hubs, concentrating a higher proportion of edges (heterogeneous, scale free networks).

The calculated volume difference between before and after crab bioturbation was 1362 cm^3 ± 47 (SE) over 0.25 square metres in a seven-day period. The volume difference between time replicates were 280 cm^3 (before-before) and 171 cm^3 (after-after). This represented a 13-20% precision error. The statistical precision (i.e. similarity among time estimates) might be affected by small differences in point clouds which can be caused due to subtle differences in the image quality during capture and/or during the image analysis (Dandois, Olano & Ellis 2015; Bryson *et al.* 2017; Forsmoo *et al.* 2019). In fact, small differences were observed among the pair of digital elevation models taken a same time points (Figure 3-6A). Time replicates produced distance values predominantly equal to zero or close to zero (Figure 3-6B), with less than 5% and 10% of cloud to cloud distances being greater than 0.4 centimetre for before-before and after-after comparisons, respectively. The four possible comparisons among different time models produced similar results, and these represented sediment change between time before and time after. Furthermore, the validation measurement suggest that SfM photogrammetry is an accurate estimated of change in volume (Table Appx. A- 4).

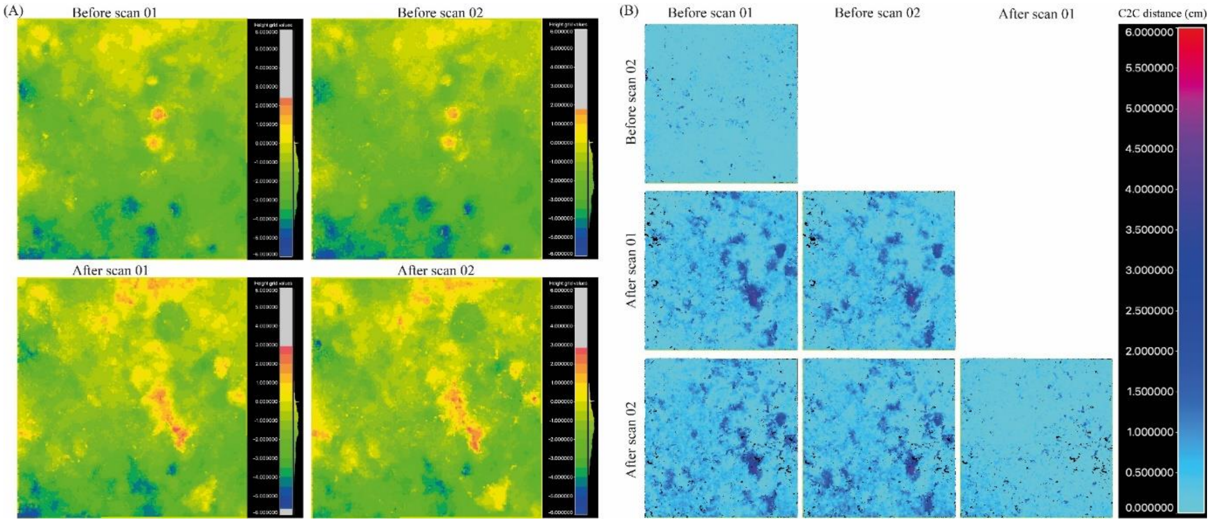


Figure 3-6: Comparison of raster generated from point cloud data for multiple sediment scans representing two times (before and after crab bioturbation). Each time was independently scanned twice. (A) Digital elevation model in centimetres. Subtle differences can be observed within time (rows), these differences can be attributed to the number of features and cloud density for each data set. (B) Raster of computed cloud to cloud (C2C) distances among four scans. Values represent the calculated distance in centimetres among clouds using a quadratic function. Within time comparisons yield values close to zero, while among time comparison shows change in sediment.

Discussion

I believe this is the first time that a non-invasive, cost- and time-efficient data workflow underpinned by computer vision has been used to gather rich data on benthic and fossorial crabs with potential scalability (Table 3-1). Our approach, using heuristic fit–for-purpose and off-the-shelf software, facilitates the rapid collection and processing of ecologically valuable data on small invertebrate organisms. For instance, here I focused on intertidal fiddler crabs, but our approach could easily be extended to include other taxa with similar modes of life. Although some of the techniques have been used before, to our knowledge they have not previously been used in combination to allow the collection of a wide range of information on an invertebrate species. Access to rich and big data overcomes issues associated with traditional sampling techniques such as hard to maintain methodological assumptions (Schlacher *et al.* 2016) and time- and labour-intensive costs. Moreover, such technological advances increase the amount of information of the species studied, thus these can accelerate our understanding of the ecology and biology of small species, which in turn can improve species and ecosystem management strategies.

Our 5-minute trial video analysis combined with 3D models demonstrates the considerable potential of employing computer vision techniques. This method allows to obtain movement patterns of several individuals of *T. polita*, estimate their size and characterize their intra-specific interactions. Few studies have tried to characterize the movement patterns of fiddler crabs (Salmon 1984; Salmon 1987; Viscido & Wethey 2002). To our knowledge, this is the first time that individual movement paths of multiple individuals of any fiddler crab species has been obtained in a natural setting. In this case, movement path information is complemented with information about the size, sex and handedness of the focal individual and neighbours. In addition, by categorizing behavioural displays throughout the video, sequential changes in behaviour can be related to specific motion and navigation changes. The need for such complementarity data, stressed by Nathan *et al.* (2008), makes this method and study system a good candidate to gather data to test mechanistic models of animal movement.

Table 3-1: Type of data obtained using the Crabspy workflow, inventory of potential uses and opportunities for improvement.

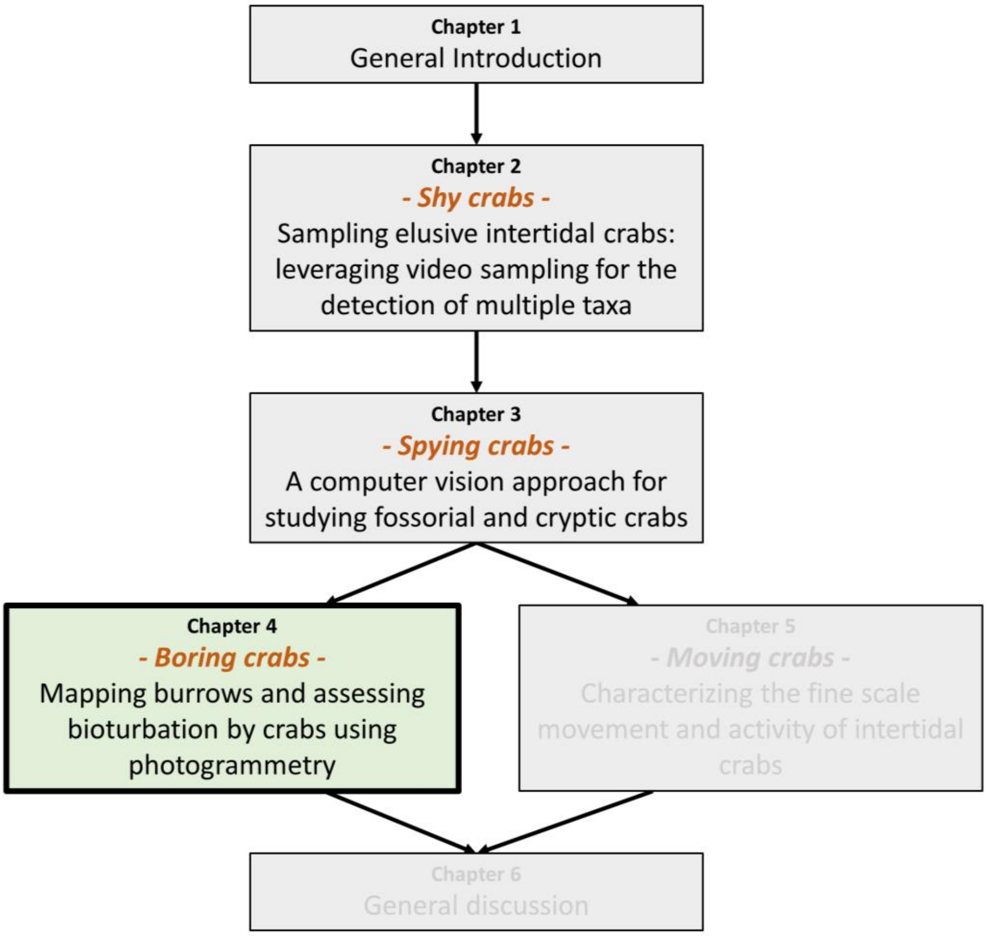
Data type	Domain knowledge	Application	Opportunity for improvement
Position, image and activity state	Animal motion	Characterize species movement.	Overcome tracking challenges described in Table Appx. A- 2. Incorporate and synchronize environmental sensors (e.g. temperature, humidity, light intensity, and other sensors) with video data.
		Study individual self-orientation mechanisms in space and time.	
		Study utilization of space.	
	Community and population ecology	Assess species abundance.	
		Assess population demographics: size structure, sex ratio and handedness ratio.	
		Characterize intra and interspecific interactions.	
	Functional ecology	Assess bioturbation and feeding rates.	
		Understand metabolic and stoichiometry processes.	
	Ecophysiology	Study thermoregulation and water loss control patterns.	
	Behavioural ecology	Characterize waving, courtship and aggression displays through time.	
		Evaluate foraging behaviour and feeding preferences.	
		Study of communication and signalling	
		Understand of phenology and activity budgets.	
Colour	Behavioural ecology	Study colour signalling.	Improve light measurement by using multispectral cameras or imaging spectrometer.
		Study crypsis.	
	Evolution	Evaluate phenotype patterns and phenotype selection.	
Sound and vibration	Ecophysiology	Study energy demands and trade-offs of stridulation at the individual level.	Incorporate sound wave recorder, phonograph, geophone or vibrometer to camera setup; and synchronize sound/vibration measurements with video.
	Behavioural ecology	Study of stridulation mechanisms, patterns and functions at population and community level.	
		Study of acoustic communication	

I have also estimated the bioturbation rate as volume change per area and time unit (778.29 cm^3 per m^2d^{-1}). Further extensive sampling is required to assess the spatial and temporal patterns of *T. polita* bioturbation. Reported bioturbation rates for another fiddler crab species, *Minuca pugnax* (324 cm^3 per m^2d^{-1}) are lower than our estimates (Katz 1980). However, Takeda and Kurihara (1987) reported greater volume change in other crab burrowing species (*Helice tridens* 11484 cm^3 per m^2d^{-1}). Our measurement assumes that no other factor than fiddler crabs contributed to volume changes, and that volume changes are a suitable surrogate to sediment turnover by crabs (i.e. mass, Table Appx. A- 3). Although crab bioturbation is inherently related to crab density, burrow volume, species size and species burrow behaviour, the method I propose can be calculated independently to these other variables. Regardless of the method used, all these assumptions (Table Appx. A- 3) must be carefully evaluated depending on the area and time of sampling. I believe the method proposed here to estimate bioturbation is reliable, reduces the potential negative impacts of destructive sampling, and allows precision to be consistently calculated and known, while relying on similar assumptions as the methods employed till now. The proportionally high error in this method (13-20%) can potentially be reduced by artificially illuminating the areas scanned, and improving orthorectification and alignment procedure during analysis.

There is a wealth of future opportunities that could be incorporated to extend the amount and type of data collected and analysed (Table 3-1). As more videos and images are collected for target species, computer vision models will likely become more robust and precise in identifying and predicting species behaviours. For instance automatically assigning sex, handedness and taxa using an image classifier can be achieve using training data obtained following workflow from this paper (Table Appx. A- 1). Furthermore, retaining the original videos or images, will allow retrospectively analyse of the data once new algorithms are available.

Computer vision is changing the nature and scope of the data collected by ecologists in two main areas. Firstly, digital sensors, digital raw data and the software used to analyse it, have the advantage of providing replicable measurements with calculable accuracy and precision (see e.g. in Weinstein 2018), thus reducing observer bias. Moreover, digital raw data in conjunction with adequate meta-information and appropriate storage is less susceptible to entropy (i.e. decay or degradation Michener 2006; Hart *et al.* 2016) and falsification than data condensations (e.g. spreadsheets). Secondly, it can create opportunities for collaborations between ecologists and other scientific disciplines (Weinstein 2018) and, with appropriate incentives, will promote and advance data sharing and open-data practices, which will strengthen ecological research. Preserving raw data from instruments is paramount so data can be revisited and reanalysed under new paradigms or tools. But, I echo the sentiment of Veiga *et al.* (2017) around concerns of using data sets beyond their intended scope and breadth and data quality recommendations. Computer vision and machine learning has the potential to revolutionize our current sampling methods and analysis in ways that allow us to rapidly and efficiently address the urgent need to sampling natural systems intensively and extensively, resulting in improved understanding of these systems and our ability to manage them. However, to avoid catastrophic consequences of misusing computer vision and machine learning (see example in Bertinetto *et al.* 2020), ecologist are encourage to understand limitations and assumptions associated to novel methods and the statistical challenges and adequate procedures to analyse rich and big data.

Chapter 4 - Mapping burrows and assessing bioturbation by crabs using photogrammetry



Aim: Evaluate and quantify bioturbation rate of fiddler crabs on estuarine mudflats, and its effect on sediment topography.

Introduction

Bioturbation is an important driver of matter and energy cycling in soft sediments of coastal and estuarine areas (Reinsel 2004; Paarlberg et al. 2005; Meysman, Middelburg & Heip 2006). In particular, reworked sediment by crabs mediate several biochemical processes (Aller & Aller 1986; Aller 1994; Kristensen 2000). For instance, crab burrows modify Oxygen availability and redox potential in the sediment and, consequentially, determine the functional composition of microbial assemblages (but see Michaels & Zieman 2013; Booth et al. 2019). Moreover, by regulating water and air flow and availability through burrow construction, crabs affect metal bioaccumulation and bioavailability (Araujo Junior et al. 2016), salt concentration (Stieglitz, Ridd & Muller 2000), Nitrogen and Carbon fluxes (Wang et al. 2010; Fanjul et al. 2011; Fanjul et al. 2015; Martinetto et al. 2016) among other effects (e.g. see Katz 1980; Dittmann 1996; Xin et al. 2009; Wang et al. 2010). In addition, burrowing crabs, directly and indirectly, affect particle size distribution and the overall geomorphology of estuarine and coastal areas (Warren & Underwood 1986; Perillo, Minkoff & Piccolo 2005). For these reasons, crabs inhabiting estuarine and coastal areas are considered ecosystem engineers (Kristensen 2008; Smith, Wilcox & Lessmann 2009). However, the magnitude of these effects are species- and environment-specific (Botto & Iribarne 2000; Fanjul et al. 2011; Martinetto et al. 2016), making generalization difficult and requiring further investigation into bioturbation effects on a species-by-species basis (Escapa et al. 2007; Aschenbroich et al. 2016; Li et al. 2018). However, one of the greatest challenges in studying bioturbation on a species-by-species basis is the elevated cost (i.e. time, investment) and complexity of current methods. Consequently, improved bioturbation estimates at lower the costs are required if substantial advances are to be achieved.

To date, studies on crab bioturbation generally fall into three categories depending on the method employed: (1) presence-absence or burrows counts (e.g. Gribsholt, Kostka &

Kristensen 2003; Gittman & Keller 2013); (2) the amount of matter translocated or compacted (e.g. Katz 1980; Takeda & Kurihara 1987); and (3) a combination of both approaches (e.g. Escapa et al. 2007). All these approaches rely on the principle that bioturbation is a function of both sediment removed and deposited elsewhere and sediment compacted (Takeda & Kurihara 1987). The presence of burrows and their abundance are qualitative and semi-quantitative indicators of bioturbation intensity, respectively. On the other hand, studies that quantify the amount of matter translocated and compacted (i.e. sediment turnover) produce quantitative estimates of bioturbation activity. Matter translocated and compacted can be estimated by measuring burrow volume (Shinn 1968; Katz 1980; Botto & Iribarne 2000; Stieglitz, Ridd & Muller 2000), or the amount of sediment dug from the burrow and deposited in the surface (Warren & Underwood 1986; Botto & Iribarne 2000). Although these methods have proven useful in increasing our understanding of crab bioturbation, each has advantages and disadvantages that need to be considered.

Bioturbation rate calculations require the measurement of the amount of matter translocated or compacted by space and time unit. However, most methods fail to account for the time consideration, preventing a specific estimate of bioturbation rate. For instance, estimating bioturbation rate by burrow volume calculation has the drawback that the burrow mean life is often unknown (e.g. temporary vs breeding burrows as per Christy 1982; but see Takeda & Kurihara 1987) preventing calculation of a bioturbation rate. These methods have several other limitations. For instance, the use of resin casts to calculate burrow volume (as per Dembowski 1926; Shinn 1968; Genoni 1991; Wang *et al.* 2015) is costly, invasive and labour intensive meaning, this method can usually only be applied to few burrows (but see effort by Lim 2006 as inspiration of what is possible). Estimating burrows volume by measuring burrow diameter and depth is an efficient and less invasive alternative. However, the variable burrow architecture in some crab species, i.e. complex and interconnected burrows and chambers (e.g.

see Hayasaka 1935; Christy 1982), make less reliable the assumption of a burrow understood as a single cylinder of known diameter and height. This applies to methods that rely on filling burrows with dried sand (Takeda & Kurihara 1987). Bioturbation rate can be estimated by measuring sediment turnover as the amount of loose sediment dug from the burrow and deposited in the surface, as it is a direct proxy of the amount of sediment reworked by crabs (Takeda & Kurihara 1987; Botto & Iribarne 2000; McCraith et al. 2003; regenerators, sensu Kristensen et al. 2012). Collecting loose sediment around a burrow opening requires little equipment and intervention. However, it depends upon mapping and monitoring burrow distribution and requires frequent sampling to identify and collect loose sediment created by burrowing activities before it is eroded or compacted (Botto & Iribarne 2000; McCraith et al. 2003; Gutierrez et al. 2006; Escapa, Perillo & Iribarne 2008; Wang et al. 2010). A less common approach to estimate bioturbation rate is to measure the overall sediment accretion due to burrowing activity. Warren and Underwood (1986) pioneered photogrammetry to estimate the change in the substratum height in areas with and without crabs by creating topographic models of the sediment. This technique relies on the assumption that most of the reworked sediment dug by crabs is translocated to the surface (as shown by Gutierrez et al. 2006; Wang et al. 2010 for one species and an assemblage of six crab species, respectively). Since then this method has not been used to estimate bioturbation activity, likely because it required specialized equipment and expertise. However, advancements in photogrammetry software, computer vision algorithms, and imaging devices offers an opportunity to re-implement this method of assessing crab bioturbation and map burrow distribution.

Photogrammetry and Structure from Motion (SfM) allow the creation of topographic and orthophotographic images from sets of overlapping images, thus allowing reconstruction of 3D models of focal areas or objects. These 3D models can then be used to assess structure and change in surfaces and volumes (Wu 2013; Wróżyński et al. 2017; Forsmoo et al. 2019).

This method is considerably cheaper and more accessible than laser scanning (e.g. LiDAR), X-ray, and computerized tomography, and it can be employed anywhere and on virtually any spatial scale (Westoby et al. 2012). Photogrammetry is becoming a standard technique to assess organisms growth (Ferrari et al. 2017; Olinger et al. 2019), benthic morphology and complexity (Sanchez, Serrano & Ballesteros 2009; Burns et al. 2015; Ferrari et al. 2016b), among many other applications (e.g. Abdo et al. 2006; Mlambo et al. 2017; Wróżyński et al. 2017; Dai et al. 2018). In regard to the study of burrowing crustaceans, some researchers have employed photogrammetry to assess the relationship between burrowing activity and geomorphology in coastal areas (Brunier et al. 2020) and assess burrow 3D structure in crayfishes (Florey & Moore 2019). As well as gaining acceptance in many scientific fields due to their accuracy and the constant improvement of the image acquisition and processing methodologies (Figueira et al. 2015; Bryson et al. 2017; Sanz-Ablanedo et al. 2018), photogrammetry and SfM offer a cheaper and potentially more precise alternative to study changes in volumes and surfaces.

This study uses SfM photogrammetry to assess bioturbation by intertidal crabs. In particular, I evaluate the method proposed in Chapter 3 to draw inferences on the bioturbation rate of a fiddler crab species. Thus, I estimate the amount of sediment turnover due to crab activity, and evaluate the relationship between bioturbation rate and burrow abundance, and study changes in the sediment surface morphology. While the importance of crab bioturbation in sediment physicochemical and biological processes is relatively well documented for some crab taxa, the cost and effort required for current methods limit researchers' ability to apply them intensively and extensively. This study demonstrates that SfM photogrammetry is a suitable and precise method for the study of bioturbation by intertidal crabs.

Methods

Study site

This study was carried out on a tidal mudflat adjacent to the Ross River in Townsville, Queensland, Australia (19.2702° S, 146.8250° E). The site was selected because the proven occurrence of fiddler crabs, and the well-known tidal regime that allows the prediction of mudflat inundation. A focal area was selected on a flat at an elevation between mean high neap tide and mean high spring tide. This area was primarily inhabited by *Tubuca signata* (Hess, 1865). However, other crab species were observed adjacent to the focal area. In particular, *Tubuca coarctata* (H. Milne Edwards, 1852) and various Sesarmidae Dana 1851 species occupied the creek bank towards the water edge. Other burrowing animals such as mudskipper, *Periophthalmus* Bloch & Schneider, 1801, and mud shrimp, Callianassidae Dana, 1852, were observed in the low intertidal. The vegetation in the focal area consisted of the mangroves *Avicennia marina* (Forssk.) Vierh and *Rhizophora stylosa* Griff. Mangrove trees were sparsely scattered in low density along the upper creek bank just below the focal area. Except for a few mangroves roots, the sediment in the focal area comprised bare mudflat.

To assess sediment turnover, burrow distribution, and sediment surface morphology, five permanent one squared meter quadrats (1 by 1 m) were installed on the sediment in areas inhabited by *T. signata* (Figure 4-1). *T. signata* is primarily active on the sediment surface during spring tides. Within this period, the peak of surface activity occurs following the high water springs during daylight (personal observation). For this reason, quadrats were monitored three times during 14 days, from the high spring tides to the next neap tide. Each of the five quadrats was assigned to a letter (A-E), and each sampling event was coded indicating the sampling time (day zero, DO; day one, D1; and day fourteen D14). Two additional quadrats were installed in the sediment as controls (Y-Z) to compare the effect of crab bioturbation on sediment surface morphology against a control treatment. These quadrats were installed in the high flat intertidal. The sediment within these two quadrats was manually flattened using a square steel bar. These two quadrats were monitored twice in two days (D0 and D1).

All quadrats were installed in areas above the tidal flood levels at the time to avoid confounding bioturbation effects with other natural processes that can modify or move matter in the sediment surface, such as tidal erosion and accretion. Thus, quadrats were not flooded during the observation period. Vertices from each quadrat were marked with Ground Control Points (GCPs, 80 mm nails topped with white expanded polystyrene spheres Figure 4-1). During the study period, only two GCPs caps were lost, i.e. white spheres – nails remained in place. Replacements were installed immediately after a loss was identified.

Data acquisition and analysis

A total of 19 sampling events were completed: the five quadrats experiencing natural variability were sampled three times to quantify burrow abundance, bioturbation and sediment surface changes, and the other two quadrats were experimentally manipulated and sampled twice. Each sampling event consisted of two independent video recordings perpendicular to the sediment within the quadrat from 50 to 60 cm height. These independent recordings allow me to calculate the statistical precision of the method. In each video, the recording followed a parallel strip pattern with high overlap to guarantee the coverage of the entire sediment area within the quadrat (Chapter 3). All videos were captured using a camera Garmin VIRB XE attached to a monopod pole during hours of high light intensity, between 10 AM and 2 PM.

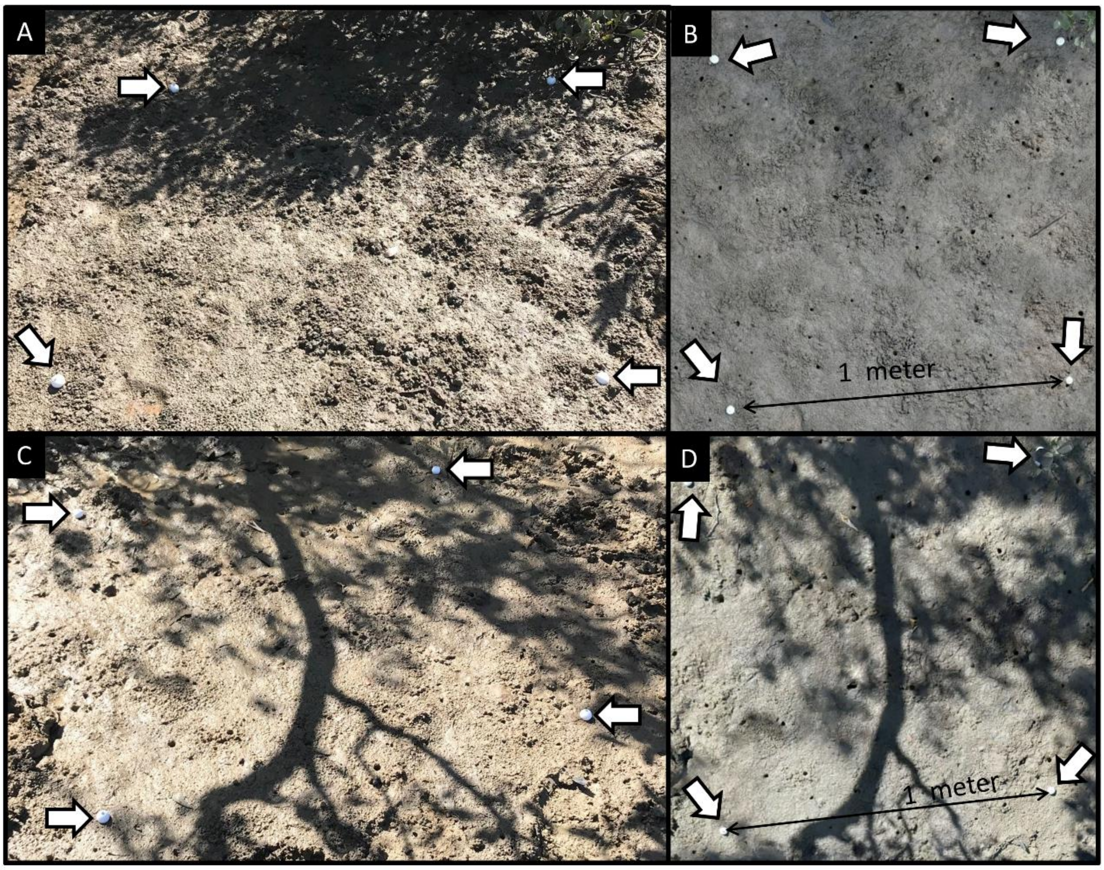


Figure 4-1: Two examples of field sites monitored using SfM photogrammetry and the two derived photo-mosaics. **A, C** Square metre quadrats (1 by 1 m) demarked in the sediment using four white spheres as Ground Control Points (GCPs, indicated by arrows). **B, D** Derived photo-mosaics used for counting crab burrows (GCPs indicated by arrows).

A total of 38 videos were captured. Each video was deconstructed into frames using a custom Python script (3.5 Python Software Foundation) and OpenCV library (OpenCV 2015). A set of images (i.e. frames) was generated from each video, and only every sixth frame was used for analysis because image overlap among consecutive frames is very high. Redundant information among consecutive frames (very high overlap) does not necessarily improve models but it does increase analysis time. Thus, each video typically consisted of 250 to 400 extracted images that were used for analysis. From each set of images, a SfM photogrammetry 3D reconstruction was created using VisualSFM (Wu 2011; Wu 2013). VisualSFM command line interface was used to create sparse and dense point cloud reconstructions using the Clustering Views for Multi-view Stereo algorithm (Furukawa et al. 2010). SfM photogrammetry models were created in batch using a Python script. All scripts used are available in the GitHub repository: https://github.com/CexyNature/bioturbation. From these models, photo-textured meshes and photo-mosaics were created using Meshlab (Figure 4-1B, D; Cignoni *et al.* 2008). A step-by-step procedure is described in the mentioned GitHub repository.

A map of burrow distributions and burrow sizes was created for each quadrat and time photo-mosaic using a custom Python script from Crabspy (Herrera 2020 source: https://github.com/CexyNature/Crabspy/blob/master/crabspy/map_burrows_from_image.py). Burrows size was approximated to the area of a circle of r radius. Burrow coordinates and radii were plotted using R (4.0.3 R Core Team 2018) and ggplot2 (Wickham 2016).

All SfM photogrammetry models were verified and prepared for analysis following a standard quality check using the software Cloud Compare (CloudCompare 2019) as follows: (1) areas outside the quadrat were trimmed, (2) model orthorectified using GCPs, (3) overhanging vegetation was removed if present, and (4) the number and density of points in the models were compared. As models presented different point densities, all models were subsampled using a 0.25 cm inter-point minimum distance. All models were ortho-rectified, and all models from the same quadrat were aligned using the four GCPs. For each quadrat, sediment turnover, the amount of volume added or removed in the sediment between successive sampling events, was calculated using Cloud Compare 2.5D Volume function over pair of aligned 3D models. I estimate the precision of the sediment turnover calculation by employing the same function between the two models from the same quadrat and time that were captured independently. As model precision was very high, I arbitrarily use models from first recordings to across sampling times. Bioturbation rate was calculated as the net difference of volume added or removed (cm^3) per quadrat (squared meter) per day.

Contours and topographic measures were calculated for 3D models from each quadrat and time combination to evaluate the effect of crab bioturbation activity on the sediment surface morphology. In particular, a Digital Terrain Model (DTM) elevation and eight 3D geometric features were calculated using a 0.5 cm kernel size. One of the outcomes of SfM Photogrammetry are 3D point clouds. Information in this 3D space can be reduce to 2D by applying methods of dimensionality reduction as Principal Component analysis. Thus, eight 3D geometric features were calculated: Principal Component 1 (PC1), Principal Component 2 (PC2), Planarity, Roughness, Sphericity, Surface Variation, Verticality, and 3rd Eigen value (Blomley et al. 2014; Weinmann, Jutzi & Mallet 2014; covariance features in Hackel, Wegner & Schindler 2016; Roughness from CloudCompare 2019). These features were selected because they summarize the relative change in 3D dimensionality, geometry, and topography. Geometric feature calculations were done in batch using Cloud Compare command line interface and a Python script, and these were exported as raster files. Raster files were plotted using R (4.0.3 R Core Team 2018) and ggplot2 (Wickham 2016).

Results

The total number of burrows and their distribution was highly variable among quadrats and times, and the total number of burrows decreased progressively over time in all quadrats (Figure 4-2A, C). At the beginning of the observation period, the mean burrow number per quadrat was 251 ± 111 burrows. Most of them were fresh and active burrows created in the last couple of days. The mean burrow number fell after one day (D1) to 169 ± 78 burrows and 82 ± 33 burrows after 14 days (D14). Variability among quadrats was also high, with quadrats B and C having the lowest number of burrows (Figure 4-2A, C). Burrow distribution was not uniform within quadrats (Figure 4-2A), and some burrows persisted in the same location after 14 days (Figure 4-2B). Total burrow area also declined over time, except for quadrat D, where the burrow area increased after one day (Figure 4-2D). The average area occupied by burrows started at 243 ± 91.5 cm^2, falling to 226 ± 122 cm^2 after one day, and 60.7 ± 26.1 cm^2 after 14 days. Proportionally, the area occupied by burrows ranged from 0.21 to 3.82 % of the total area observed (1 m^2). The total number and area of burrows were correlated ($r = 0.86$, $p = 0.000038$).

For each quadrat, the amount of volume added or removed in the sediment was calculated for each sampling time pairwise comparison (Figure 4-3A). This comparison created three time intervals: one day (DO vs D1), 13 day (D1 vs D14) and 14 days (D0 vs D14) elapsed. In most quadrats and time intervals, the volume added was higher than the amount of volume removed. Exceptions were quadrat C and E at the one-day interval, and quadrat D after 13 days. There was no clear pattern of sediment volume created as a function of the time interval (Figure 4-3A). Bioturbation rate was calculated for three different periods: one, 13 and 14 days. Bioturbation rate was consistently higher for the one-day interval (D0 vs D1 comparison), which corresponded to the peak of activity of *T. signata* (Figure 4-3B). For this interval, bioturbation rate ranged from 3108.00 ± 37.29 to 1146.85 ± 22.10 $cm^3\ m^{-2}\ d^{-1}$. After 13 and 14 days, D1 vs D14 and D0 vs D14 respectively, the bioturbation rate considerably decreased ranging from a maximum of 566.41 ± 6.45 to a minimum of 17.98 ± 1.66 $cm^3\ m^{-2}\ d^{-1}$. There was a positive relationship between the total area occupied by burrows and bioturbation rate (Figure 4-3C).

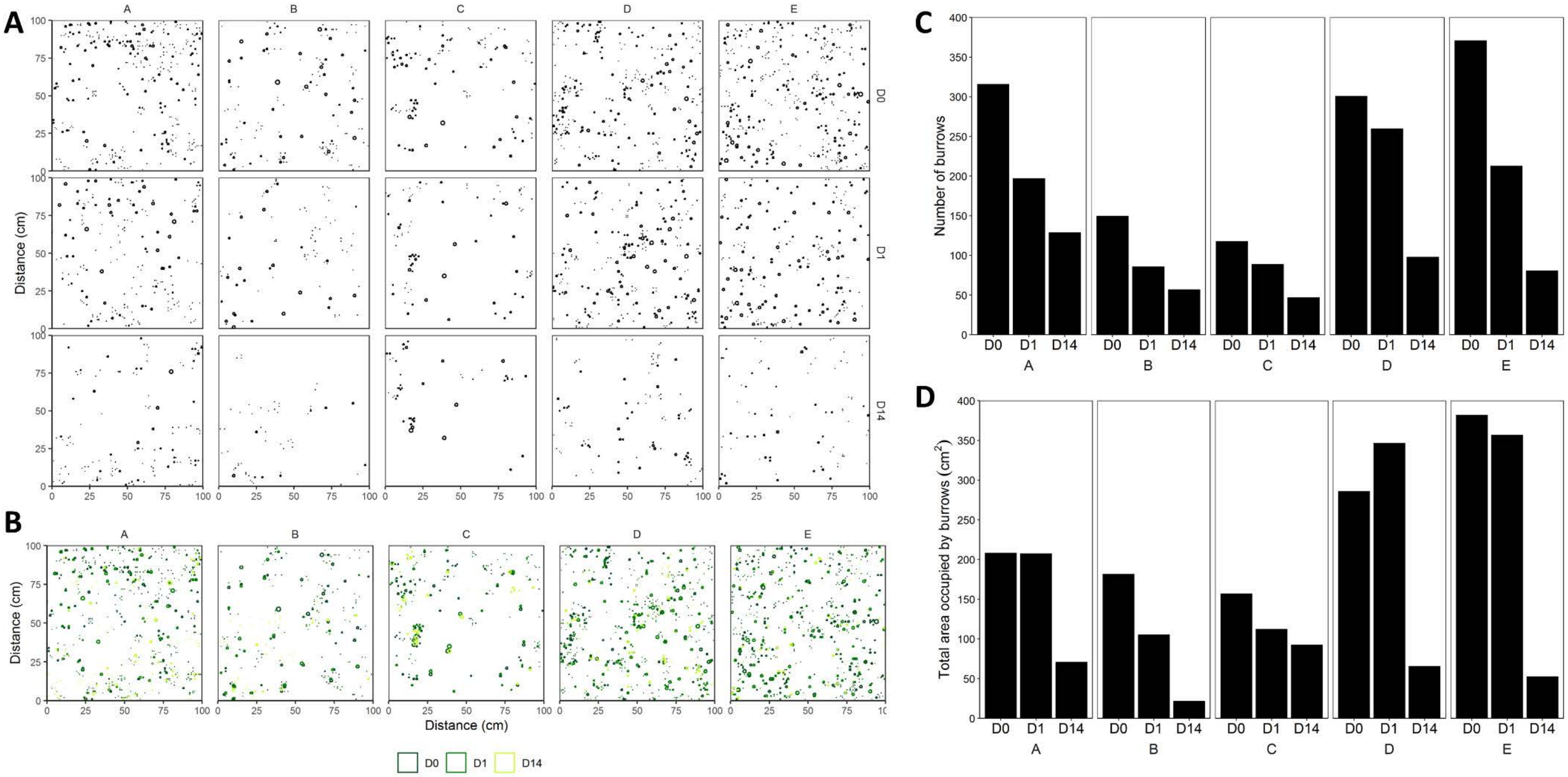


Figure 4-2: Burrow distribution and change across quadrats (i.e. A-E) and times (i.e. D0-D14). **A** Burrows maps for five quadrats (A-E) and three times (D0-D14). **B** Burrows spatial distribution for each quadrat with overlapped burrows from the three sampling times. **A, B** Each circle indicates a visible burrow mapped from photo-mosaics, and its size represents the burrow's size. **C** Total number of burrows per quadrat and time. **D** Total area occupied by burrows per quadrat and time.

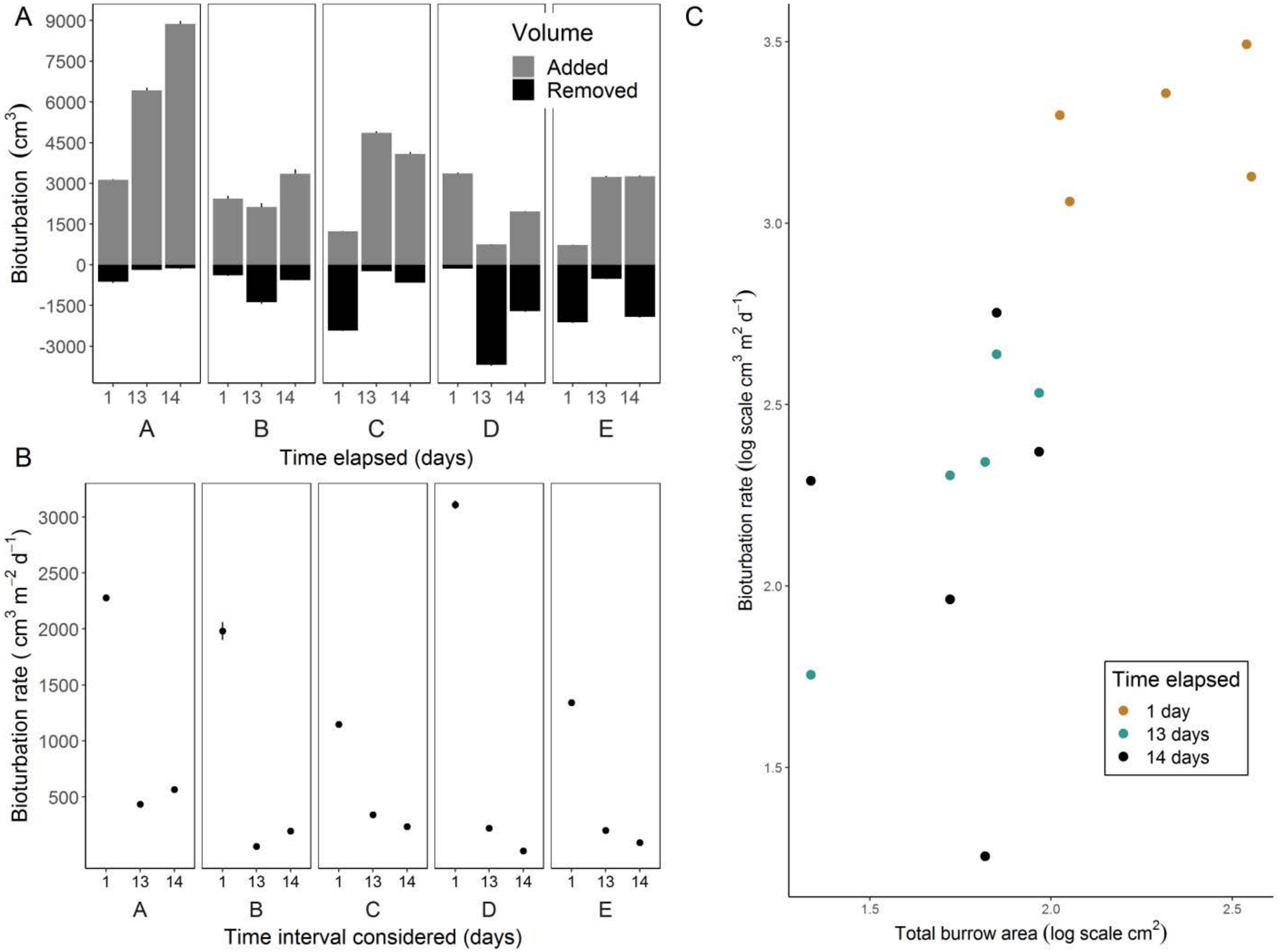


Figure 4-3: Crab bioturbation estimated from SfM Photogrammetry. **A** Bioturbation as net change of volume for each 1 m^2 quadrat (A-E) after a time span of 1, 13, and 14 days. **B** Bioturbation rate for each quadrat (A-E) and time interval (1, 13, 14 days). **A, B** Bars associated with each point represent the precision of the estimates: the standard deviation of four cross comparison measurements (see methods for details). **C** Total area of burrows and bioturbation rate relationship for each quadrat and time interval.

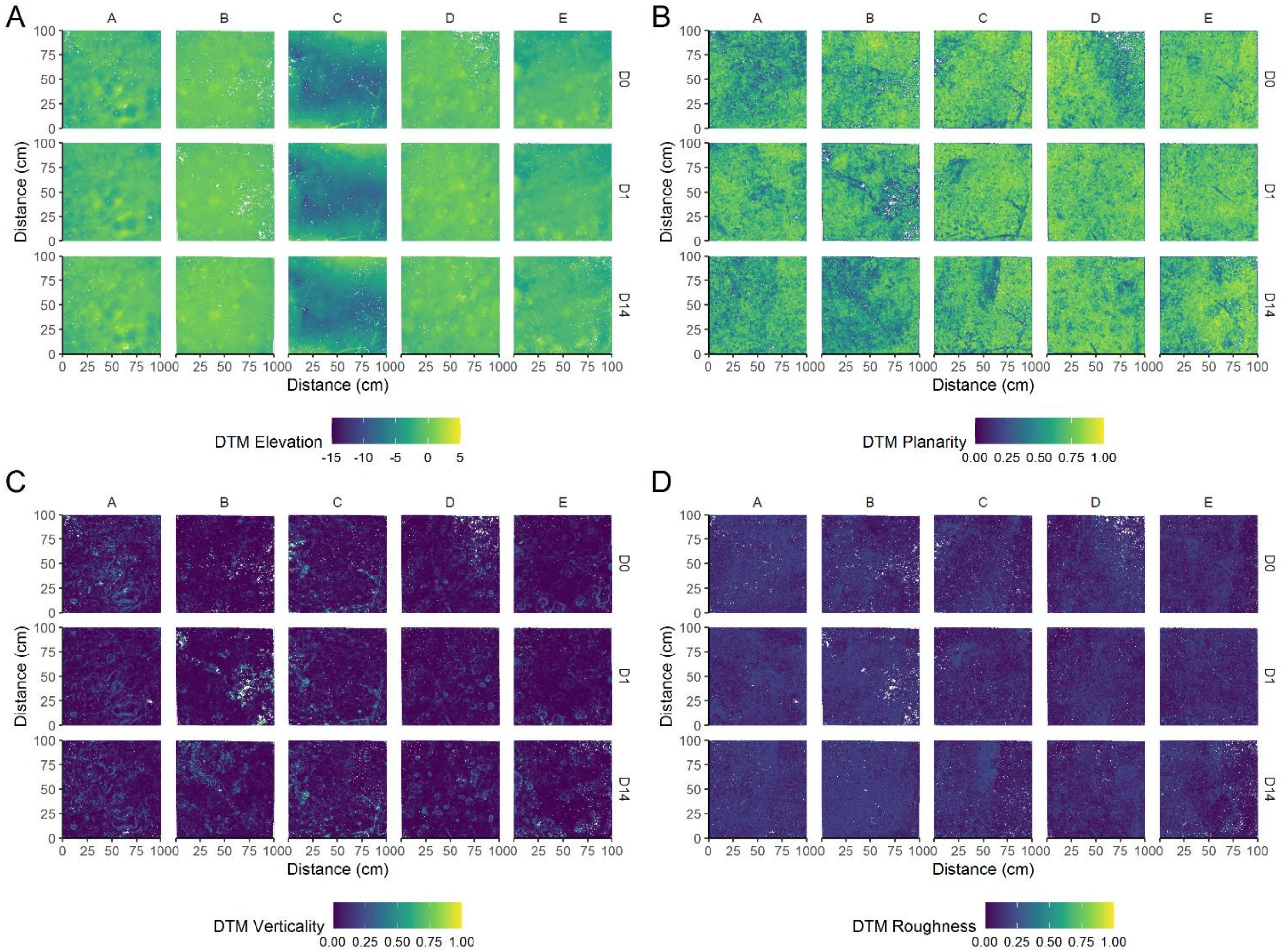


Figure 4-4: Change in sediment 3D geometric features across quadrats (A-E) and times (D0, D1, and D14). **A** Digital Terrain Model (DTM) Elevation showed in centimetres, **B** Verticality, **C** Planarity, and **D** Roughness rasters were calculated from Dense Point Clouds sediment models created by SfM Photogrammetry. Other geometric features are presented in the supplementary material (Figure Appx. B- 1-5).

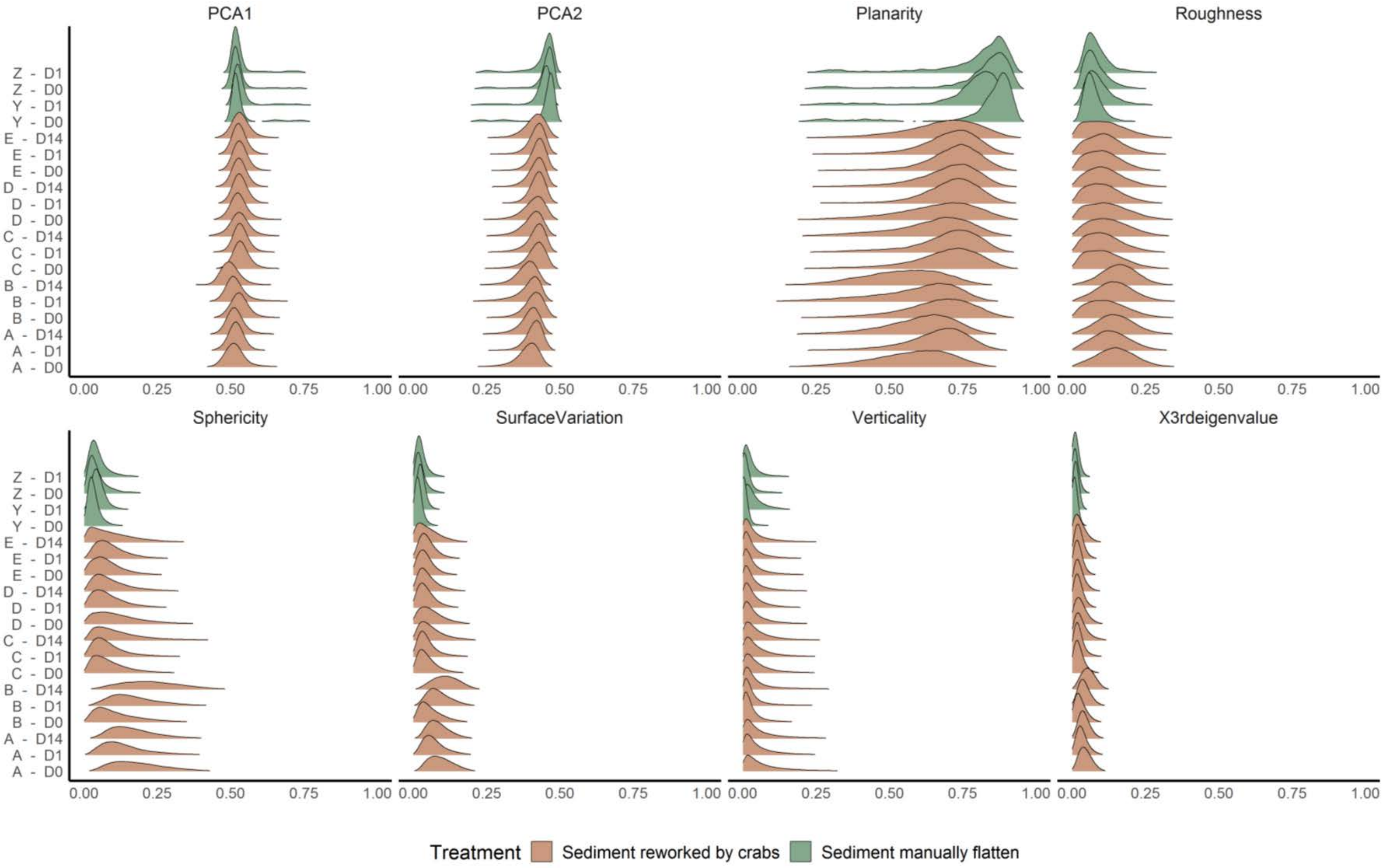


Figure 4-5: Distribution of values for all geometric features across treatments, quadrats, and times.

One hundred and twenty (120) raster images were created representing each elevation and 3D geometric feature for each quadrat and time (Figure 4-4, Figure Appx. B) to evaluate the effect of crab bioturbation effects on the sediment morphology and topography. Elevation rasters show the sediment surface height in each quadrat relative to the GCPs (Figure 4-4A). For instance, in quadrat C the GCPs were placed above a depressed area in the sediment, therefore, most of the quadrat showed a negative elevation. Sediment elevation changes through time can be observed when comparing the raster values progression for each quadrat from D0 to D14. Sediment pairwise elevation difference rasters showed the areas where most of the sediment variation occurred (Figure Appx. B- 1). Planarity, Verticality, and Roughness were among the geometric features that were more informative about sediment morphology and topography (Figure 4-4B, C, D). Planarity rasters indicate how flat or not an area is relative to the local point cloud at 0.5 cm scale (Figure 4-4B). Higher values (i.e. close to 1) designate flat areas. Planarity was the geometric feature with the most variation through time, and given the differences in sediment topography among all quadrats, it presented one of the greatest variation at any one time (Figure 4-4B). Verticality rasters showed changes in the sediment slope, indicating areas where narrow ridges occurred (Figure 4-4C). The dynamic movement of these narrow ridges is observed along the time sequence for each quadrat (brighter lines in Figure 4-4C). Roughness indicates variation in the sediment surface texture, with higher values representing areas where the sediment was not even or smooth at the local scale (0.5 cm kernel size). Sediment roughness also varied across quadrats and times (Figure 4-4D), and it was correlated to Sphericity (Figure Appx. B). Other geometric features were less informative or presented similar patterns to the ones above. PCA1, PCA2, Surface Variation, Sphericity, and 3rd Eigen Value were correlated with Planarity or Roughness (Figure Appx. B).

The value distribution for 3D geometric features was different between the sediment reworked by crabs and the sediment experimentally manipulated (Figure 4-5). Notably, the difference between treatments was detectable despite the fact that the sediment manually flatten was not perfectly smooth, due to the presence of pebble particles, roots, and sand clusters which maintained some degree of texture in the sediment. Overall, flattened sediment decreased the spread of distributions for all geometric features, thus changing the shape of the distributions. Moreover, the mean value for some geometric features distributions shifted. For instance, Roughness, Sphericity, and Surface Variation distribution mean values were lower in the sediment manually flattened. The opposite effect was observed in PCA2 and Planarity, and there was a no clear effect on the distribution mean value for PCA1, Verticality, or 3rd Eigen value. In both flattened quadrats (quadrats Y and Z), signs of crab burrowing activity (i.e. loose sediment) were observed after one day (D1). Because crab inhabited the areas experimentally manipulated, changes in the value distribution of 3D geometric features can be seen after one day in the flatted quadrats, i.e. decrease in Planarity and increase in the distribution spread of Roughness (Figure 4-5).

Discussion

In this study, I measure crab bioturbation and assess some of its effects using SfM Photogrammetry. After the pioneering work by Warren and Underwood (1986), I build on the work of Herrera et al. (2020) and use a low cost, non-invasive, and efficient method that allows monitoring crab burrows, bioturbation rate, and the sediment surface morphology and topography with high precision and low cost. This method involves using a commercial camera, open and free software, and standard photogrammetry methodologies. Notably, this technique can be employed in other soft benthic habitats where monitoring of sediment change is desired. However, prudence is advised when applying and extending this technique in similar or other contexts, as there are technical and adaptive challenges that require consideration and context-specific development.

Crab bioturbation

My results reveal important spatial and temporal differences in burrow density (Figure 4-2). In other crab species, burrow spatial variability is explained by changes in the sediment composition and vegetation root density (Bertness & Miller 1984; Skilleter & Warren 2000; McCraith et al. 2003). This could explain burrow density, and possibly crab density, differences among quadrats. However, an interesting trend observed in the current study was the reduction in burrow density through time following the peak in the spring tidal cycle when the sampling period commenced. This may be primarily attributed to the tidally driven behaviour of *T. signata*. However, it is unclear if all observed burrows were excavated by *T. signata*, as sympatric species inhabit areas close to the permanent quadrats, and fiddler crab species construct burrows that are indistinguishable from each other (a central challenge recognized by others, e.g. Nobbs 2003). Several mechanisms can explain burrow entrance disappearance over time, such as burrow collapse, surface erosion, and burrow concealment by bioturbation of neighbouring individuals. Furthermore, *T. signata* can plug their burrows with sediment (personal observation; as observed in other fiddler crab species e.g. Christy 1982). Therefore, it is important to consider that changes in burrow density does not necessarily mean changes in bioturbation activity because crabs plugging their burrows could deceptively indicate a level of crab activity (i.e. number of burrows seen by observer) that does not correspond with the true level of bioturbation activity (i.e. total number of burrows used by crabs). Thus, it is recommended that the use of burrow density or burrow area as the single estimate of bioturbation activity is avoided. Future photogrammetric analyses of burrows openings and the loose sediment near them could be of use in revealing species-specific bioturbation patterns and potentially utilized to assign burrows to specific species. While the source of variability in the number of burrows among and within quadrats could not be assigned during the current study, the substratum composition variability at site and quadrat scale should be evaluated in future studies (Icely & Jones, 1978; Wang et al 2015). The question whether the observed temporal pattern in burrow density is result of an increasing trend of burrow loss or a decreasing rate of new burrows turnover cannot be answered because I did not track individual burrow persistence through time. Further assessment of substratum composition as a possible source of spatial variability and studies of burrow persistence are needed. These could shed light on the processes explaining burrow spatial distribution at small scales.

The temporal variability of sediment turnover suggests that *T. signata* and sympatric species burrowing activity is not uniform along the tidal cycle (Figure 4-3). Fiddler and coastal crab species exhibit patchy distributions, and their surface and burrowing activities are not uniform across temporal scales (Crane 1975; Salmon & Hyatt 1983; Bertness & Miller 1984; Nobbs & Blamires 2017). Some crab species exhibit higher surface activity and concomitant bioturbation activity during spring tides and summer (Crane 1975; Murai, Goshima & Nakasone 1983). Therefore, bioturbation estimates are context and time-dependent, and so should be extrapolated with caution. This highlights the needs for methods capable of providing bioturbation estimates that improve samples sizes. Quantitative data on bioturbation rate by intertidal crabs is scarce. Katz (1980) estimated that fiddler crab Minuca pugnax (Smith, 1870) can rework approximately 18% of the top 15 cm layer of sediment over a year, with a calculated bioturbation rate of 324 cm^3 m^{-2} d^{-1}. Takeda and Kurihara (1987) reported a considerably higher bioturbation rate in the burrowing crab Helice tridens (De Haan, 1835 [in De Haan, 1833-1850]), with a calculated bioturbation rate of 11,484 cm^3 m^{-2} d^{-1} during summer, representing approximately 2.9% rework from the top 40 cm sediment layer every day. McCraith et al. (2003) found bioturbation rates ranging from 4.6 to 133 cm^3 m^{-2} d^{-1} when studying fiddler crabs reworking activity in a marsh (their estimates were calculated per month). Notably, McCraith et al. (2003) calculated rates were similar when using two independent methods (i.e. burrow casts and loose sediment). Bioturbation rate estimates in the present study ranged from 17.98

± 1.66 to 3,108.00 ± 37.29 cm^3 m^{-2} d^{-1} depending on the period considered, making it comparable to other species. However, because the architecture and maximum depth of *T. signata* burrows are unknown, the percentage of sediment layer reworked by the species is uncertain. The highest bioturbation rates were found during times of *T. signata* peak surface activity (Figure 4-3B), one-day after spring tide. Thus, the decrease in bioturbation rate in one and two orders of magnitude, when considering a broader period (i.e. 13 and 14 days), suggests a reduction in *T. signata* surface activity and bioturbation. Importantly, calculations over more extended periods increase the chances of experimental errors inherent to imagery, such as markers (GCPs) loss or position alteration, as well as exposure to erosion by wind.

The sediment in areas bioturbated by crabs showed conspicuous topography changes (Figures 4-4, 4-5). Many studies have described the importance of the habitat complexity and biodiversity relationship (Bell 1985; Kostylev et al. 2005; Kamal et al. 2014; Ferrari et al. 2016a). Areas of higher structural complexity exhibit greater individual and species abundances because of their increased surface area (MacArthur & MacArthur 1961; Torres-Pulliza et al. 2020). This effect has been documented in intertidal areas where burrows made by crabs increase sediment surface area and increase benthic species richness (but see opposite results in Dye & Lasiak 1986; Depatra & Levin 1989; Dittmann 1996; Escapa, Iribarne & Navarro 2004). In this study, I have demonstrated SfM Photogrammetry's potential to assess the effect of biological activity on the sediment surface morphology and topography. Traditionally 3D geometric features have been employed to reduce labelling costs on the classification of objects and surfaces on 3D meshes (Rouhani, Lafarge & Alliez 2017). However, SfM Photogrammetry can revolutionise sediment surface studies as a cost-effective addition to researchers' methods to evaluate surface complexity. Future efforts using this newly developed methodology can now evaluate the relationships between crab bioturbation and aspects of biodiversity and ecosystem function associated to sediment topography.

The high amount of sediment added to the surface (Figure 4-3A, Figure Appx. B- 1) indicates a high level of vertical accretion. However, the amount of sediment added and removed during this study does not appear to correspond to the study area's accretion rate. Naturally, other processes, such as erosion and substratum dispersion, must be counter-balancing vertical accretion driven by crabs over medium and long terms. For instance, while this study was conducted in the high intertidal zone, the study area can be submerged during king tides, flooding events, and spring tides during high rainfall (often 3-6 times a year). Matter translocated by crabs from deep layers to the surface is subject to passive and active erosion, transportation and deposition (Escapa, Perillo & Iribarne 2008). For instance, in sediments where mineral input is minimal, areas with a high density of burrows, and arguably higher bioturbation, accumulate less organic matter and are likely to have lower accretion rate than areas with no or few burrows (Thomas & Blum 2010). Escapa, Perillo and Iribarne (2008) found that crab bioturbation and crab burrows have different effects on the sediment erosion depending on the specific nature of the habitat and hydrodynamic conditions. Clear, further observations and experiments are needed to gain a better understanding of the relative contributions of biological, chemical, and physical processes to vertical accretion in different habitats and crab assemblages.

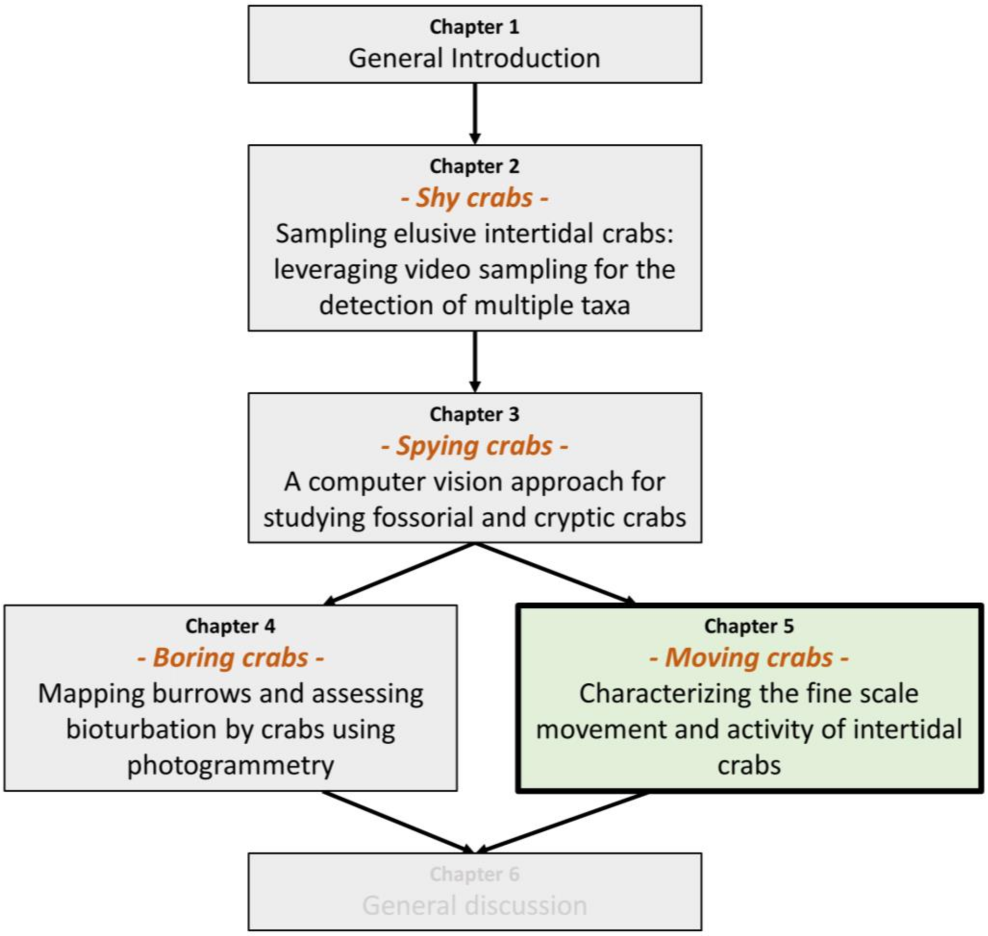
Methodological considerations

Bioturbation estimates created by SfM photogrammetric models exhibited high precision (Figure 4-3). In this study, I reduced bioturbation precision error from 13-20% reported in Chapter 3 to less than 5%. This improvement was achieved by recording videos during periods of maximum natural luminosity and using improved markers (i.e. GCPs with better 3D footprint). Variable environmental conditions during image capture affect SfM photogrammetry precision and accuracy (Figueira et al. 2015; Bryson et al. 2017; Forsmoo et al. 2019). Therefore, in assessing bioturbation by crabs, the use of artificial lights during image capture, adding more GCPs, and using photographs instead of video frames are likely to result in further improvements (Dandois, Olano & Ellis 2015; James, Robson & Smith 2017). Other factors affecting SfM photogrammetric models are the workflow and software utilized which can caused significant differences, but low effect sizes, in precision and accuracy on aerial surveys (Fraser & Congalton 2018; Forsmoo et al. 2019). The small scale and relatively low complexity of the sediment surveys would minimize errors from the software. In this study, the accuracy of 3D models was not evaluated. Nonetheless, previous studies have demonstrated that SfM photogrammetry can achieve high accuracy in assessing ground volumes (accuracy errors ranging from 0.7% to 7%, Wróżyński et al. 2017) and surface complexity (Figueira et al. 2015; Bryson et al. 2017). Such results provide confidence in the use of SfM Photogrammetry to estimate bioturbation and sediment morphology, however, accuracy should be quantified experimentally in future studies by assessing ground volumes of known amount of sediment added manually.

SfM Photogrammetry offers the possibility to study other aspects of crab behaviour. A conspicuous outcome of fiddler crabs bioturbation are biogenic sedimentary structures built on the sediment surface next to crabs burrows (Christy 1982; Christy 1988; Christy, Backwell & Schober 2003; Kim, Lee & Choe 2017; Carvalho, Pardo & Costa 2018). These above-ground sedimentary structures are believed to have diverse functions associated with movement, reproduction, intra- and inter-specific competition (Pardo et al. 2020). DTMs and 3D models created by SfM Photogrammetry offer an opportunity to characterize their size and geometry in 3D. In particular, researchers could: (1) evaluate their 3D spatial distribution, relative elevation, and orientation in relation to neighbour burrows and other above-ground structures; and (2) study the 3D progression of above-ground sedimentary structures over time. An improved 3D characterization of sedimentary crab structures and evaluation of their investment value (i.e. progression over time relative to construction and maintenance effort) can shade light into their utilities to fiddler crabs. Many other intertidal (e.g. mudskipper fish), marine (e.g. polychaetes mounds), and terrestrial organisms (e.g. ants and termites) build sedimentary structures that could be characterized and studied using SfM Photogrammetry.

Availability and accessibility to 3D reconstruction technology will likely keep improving and so become more available to biologists and ecologists' toolbox. The advancement of imaging device technologies and their cost effectivness (e.g. smartphones with LiDAR capability) would continue to promote the development of new methods to measure 3D changes in sediment and benthos. The method used in this study overcomes some of the factors that have limited from the success of many other techniques employed to evaluate bioturbation rate by crabs. Thus, it offers a promising opportunity to investigate the magnitude and effect of sediment reworking activity by crabs and other organisms, with the concomitant enhancement of researchers' ability to understand fine scale biological and ecological aspects.

Chapter 5 - Characterizing the fine scale movement and activity of intertidal crabs



Aim: Describe movement and burrow use patterns of intertidal crabs, and identify similarities and dissimilarities in motion across taxa and behavioral states.

Introduction

Studying the mechanistic basis of the organismal movement is critical to understand their ecology and evolution, because animal decisions about when and how to move, fundamentally determine populations and communities' structure and dynamics (Damschen et al. 2008; Nathan et al. 2008). Advances in biotelemetry have allowed studying of the coarse and fine spatial and temporal movement of animals, motivating innovations in the theoretical and technical approaches that scientists' employ to investigate motion and activity patterns (Cagnacci et al. 2010). Despite these advances, studying organisms' motion, their underlying drivers and causes of variability, continues to be a cornerstone area of ecological research (Holyoak et al. 2008; Sutherland et al. 2013). Interestingly, much of the research effort in animal movement ecology focuses on investigating motion and activity patterns in organisms that perform displacements over large spatial and temporal scales (i.e. vertebrates Holyoak et al. 2008). In such cases, a main analytical difficulty is establishing the relationship between the observed motion, and the behavior and traits of individuals performing movement, often not captured from biotelemetry sensors (Nathan 2008). Thus, animal movement research will benefit from studying motion and activity patterns in taxa and systems where individuals' behavior and traits can be observed simultaneously (Morales & Ellner 2002). Furthermore, an ancillary need is to observe organismal movement in the natural environment rather than in artificial settings, because a large proportion of movement research concerns how information and external stimuli from the environment affect motion and activity patterns (Morales & Ellner 2002; Nathan et al. 2008). Small mobile invertebrates living in heterogeneous and dynamic environments with relatively short spatial scale movement satisfy these needs, and could therefore be useful to advance our understanding of the mechanistic basis of movement.

Intertidal crabs from superfamilies Ocypodoidae and Grapsoidae offer an exciting opportunity to study animal movement because of their small size, social systems, relatively small home ranges, and complex interactions with con- and hetero-specific neighbors (Cannicci, Fratini & Vannini 1999a; Fratini et al. 2000; Zeil, Hemmi & Backwell 2006; Milner et al. 2010). There is a long history of behavioral research on these animals (e.g. Dembowski 1926; Seiple & Salmon 1982; Murai et al. 1995; Booksmythe, Detto & Backwell 2008; Mokhlesi et al. 2011; Peso, Curran & Backwell 2016; Backwell 2019; Gruber, Kahn & Backwell 2019). However, *in situ* research on their movement patterns has been limited due to the challenges associated with their life history (Skov et al. 2002). For instance, intertidal crabs are often elusive and cryptic, and active only during specific times of day, tidal periods, or seasons (Crane 1975; Cannicci et al. 1996). Crabs are brooder decapod crustaceans, with a pelagic larva that undergoes several metamorphoses before recruitment into the benthos (Ruppert, Barnes & Barnes 1994). Juvenile and adult intertidal crabs are often fossorial, building and using underground burrows and crevices (Breitfuss 2003; Hemmi 2003a; Breitfuss, Connolly & Dale 2004; Nordhaus, Diele & Wolff 2009; Wang, Gao & Wang 2014). Some taxa move along the sediment surface, and some of them can even climb trees, making use of trunks and canopy (Crane 1975; Cannicci, Fratini & Vannini 1999b; Cannicci, Morino & Vannini 2002).

Despite the challenges these behaviors preset for researchers, some studies have collected valuable information on their movement, for instance, through capture and recapture methods (e.g. Hockett & Kritzler 1972; Brousseau et al. 2002). From these types of studies, it is known that a large proportion of ocypodoid and grapsoid crabs tend to stay within small areas, often just a few square meters, rarely making long distance displacements greater than tens of meters (Hockett & Kritzler 1972; Cannicci et al. 1996; Cannicci, Paula & Vannini 1999). However, some grapsoid crabs can move longer distances (Brousseau et al. 2002). The range of movement of intertidal crabs have been found to differ depending on their size, sex, lifestyle, and habitat (Salmon 1984; Koga 1995; Cannicci, Paula & Vannini 1999; Brousseau et al. 2002), with variable degrees of residency, territoriality and side fidelity in different taxa (Crane 1975; Murai, Goshima & Nakasone 1983; Cannicci, Fratini & Vannini 1999b). Work on the fine-scale movement patterns of intertidal crabs is scarce. A few studies have looked at these patterns in the context of collective movement and predator response, homing and orientation, and courtship and burrowing behaviors (Salmon 1987; Viscido & Wethey 2002; Layne, Barnes & Duncan 2003). These studies have in common the use of video recording to assess crab positions over time, a process that, until recently, was very time consuming. However, new technologies such as digital cameras and computer vision algorithms are increasingly easing the burden of processing videos and extracting organisms' positions (Chapter 3).

Image-based tracking methods underpinned by computer vision algorithms are cost-effective methods that make it possible to obtain position data at high spatial and temporal resolution for one or several individuals in the field of view (Dell et al. 2014). There is a long tradition of image-based tracking to describe animals' trajectories in in vitro and confined spaces with constrained backgrounds (for instance, rodents and ants Noldus, Spink & Tegelenbosch 2001; Mersch, Crespi & Keller 2013; Hewitt et al. 2018). These conditions are ideal for image-based tracking because constant light conditions and homogeneous backgrounds facilitate isolation of individuals moving in the image foreground. *In situ* image-based tracking is increasingly difficult due to unconstrained conditions (i.e. heterogeneous background and variable light conditions). Unconstrained conditions demand more complex procedures to achieve isolation from background (and identification) of focal individuals. An important constraint of image-based tracking is that animal trajectories can only be observed while individuals are inside the camera field of view. Therefore, there is a restriction on image-based tracking methods depending on individuals' size and home range relative to the camera field of view. Nonetheless, an increasing number of studies using diverse imaging technologies have been able to study movement of several animals in semi-constrained and unconstrained conditions (Ballerini et al. 2008; Chiu et al. 2010; Butail et al. 2012; Handegard et al. 2012; Attanasi et al. 2015; Sridhar, Roche & Gingins 2019; Oleksyn et al. 2021), including intertidal crabs (Chapter 3, Herrera 2020).

With the aim of describing the movement patterns and burrow use of intertidal crabs, and to tackle challenges associated to observing crab motion *in situ*, this study used a heuristic and custom image-based tracking software to obtaining high frequency data on their fine scale motion (Chapter 3). The image-based tracking software utilized consist of a series of programming modules that allow automated and manual tracking of individuals in video recordings, manual burrow mapping on videos, and automated and manual addition of meta-information associated to animals tracked (e.g. sex, taxon, handedness, size). I take advantage of this software to explore generalities in crab movement and burrow use patterns by characterizing their use of space over time in several individuals from Ocypodoidae and Grapsoidae superfamilies engaged in two behavioral states.

Methods

Study area and video recordings

This study was conducted in mudflats adjacent to the Ross River in Annandale wetland (19.2702° S, 146.8250° E, Figure 2-1) and South Townsville (-19.2700° S, 146.8252° E), Townsville, Queensland, Australia. Six mudflat zones inhabited by different crab assemblages were selected; four in Annandale wetland and two in South Townsville. Within these zones, a focal quadrat was used to define an arbitrary area for crab observation and recording: four quadrats of 1900 cm^2 (50 x 38 cm), one quadrat of 4624 cm^2 (68 x 68 cm), and one of 6400 cm^2 (80 x 80 cm). The variable quadrat size was a response to three factors: the size of the focal individuals, overhanging vegetation, and mudflat slope. Overall, areas inhabited by small individuals, with overhanging vegetation at a low height and high slope required installing the recording equipment closed to the sediment, which reduced the observation area. This strategy was followed to maximize taxonomic identification, reduce interference from moving vegetation in videos, and increase recording equipment stability. In contrast, areas with relatively larger and easier to identify individuals, no overhanging vegetation, and flat slope, allowed observation of larger areas.

Recordings were conducted using action cameras (GoPro Hero 3 and GARMIN VIRB XE) installed in a custom four-legged stand or Manfrotto 055 (MK055XPRO3-3W head) tripod. Following Chapter 2 and 3, cameras were positioned in a top-down perpendicular or oblique angle relative to the quadrat area (Figure 2-1C, Figure 3-1A mode II). An observer seated 5-8 meters from the quadrat and equipped with Bushnell 10 X binoculars monitored all deployments. The camera field of view covered the entire quadrat area, and when possible, depending on camera height and area of observation, the camera field of view includes a buffer zone outside the focal area. Thus, the camera field of view was equal to or larger than the quadrat area. Recording started immediately after equipment installation, and cameras left to record until the battery was fully consumed. Action cameras split recordings into segments of 10 or 15 minutes. Thus, one recording typically produced several videos. Recordings from the same video deployment were combined into a single video file using the software ffmpeg (FFmpeg Developers 2017). Sections at the beginning of videos without crab activity were trimmed out. The final duration of videos used for analysis ranged from 16 to 69 minutes.

Video analysis and tracking

All videos were analysed using the Crabspy Python toolbox (Herrera 2020, Chapter 3). Depending on the video duration, videos were sped up 2x or 3x, which resulted in half or two-thirds of frames removed. Except for occasional burst movement, crabs tended to move slowly. Thus, dropping frames did not significantly impact crab position assessment over time, as most frames gave redundant information, i.e. the crab had not changed position from the previous frame. However, dropping frames improved Crabspy's motion detection algorithm and reduced processing time. Because of camera lens distortion and oblique recording angles, not every pixel in the field of view maintains a constant scale with the surface area recorded. Therefore, perspective adjustment and rectification were applied to videos to achieve a constant scale in the observation area (Brill et al. 2020). The motion of individuals was tracked over frames using an automated Multiple Instance Learning tracker (MIL, Babenko, Yang & Belongie 2009; OpenCV 2015) or manually. The MIL method was preferentially used in most cases, however, when two crabs were in close proximity this method was not always able to maintain crab identities (Chapter 3, Table Appx. A- 2). In these cases were crabs were interacting close to each other, I employed manual tracking. Both tracking strategies are available in Crabspy (Herrera 2020). An arbitrary system of coordinates in centimetre scale was employed, with origin in the top left corner vertex of the observation area. Individuals were identified to genus or species by direct observation of crabs during recording in the field or by watching videos in the laboratory; otherwise, these were categorized as unknown. When possible, sex and handedness (in the case of fiddler crabs) were noted in the field, otherwise these were noted during video analysis, using Crabspy (Table Appx. A- 1) and direct observation verification. During the tracking period, and by direct observation of the video, each individual's behaviour was categorized into two states: feeding or courtship/fighting based on Crane (1975). All burrows within the observation area were mapped and measured using Crabspy (Herrera 2020). Burrow openings were measured as the circumference circumscribing the burrow entrance.

Several individuals moved out of the observation area and the camera field of view, were occluded by vegetation, or made use of burrows. For this reason, several decisions and assumptions were made regarding individuals' identities. When an individual moved out from the observation area into the buffer zone, i.e. still within the camera field of view, the tracking continued. Thus, negative coordinates or coordinates larger than the observation areas were recorded. These values beyond the observation area were filtered out from analysis because perspective adjustment and rectification only warranted a constant scale within the observation area. When an individual completely abandoned the camera field of view, the tracking was finished. Organisms entering the camera field of view were considered a new distinct individual, thus originating a new track and tracking procedure. Individuals occluded by vegetation were manually tracked until reappearance. When one individual was occluded, it was assumed that the individual entering and exiting the occlusion area was the same individual, i.e. maintained identity. When two or more individuals were occluded, identity resolution was resolved using their size, handedness, and taxonomic group. When identity resolution was not possible using the previous criteria, individuals' speed and motion bearing were utilized to discriminate identities. It was assumed that individuals that entered and exited burrows maintain their identities because most species observed build burrows with only one entrance, and individuals tend to occupy one burrow (as observed in other species, Wolfrath 1992). Tracking for individuals making use of burrows stopped when an individual completely disappeared inside a burrow, but latent observation for this individual continued. Tracking was resumed once an individual was visible again.

Data analysis

Tracking data were analysed using adehabitat package (Calenge 2006; Calenge 2016; Calenge 2019) in the R programming language (R Core Team 2018). Tracking data were regular, meaning that relocations were obtained at a fixed and regular interval. Several R scripts were used to prepare, perform data quality checks, and analyse data (these are available in the GitHub repository https://github.com/CexyNature/crabs_moving_paper). Data quality checks verified potential errors associated to animals' positions. Thus, I verified that tracking data positions were restricted within the expected quadrat dimensions (considering the buffer zone), and that all observations contained the meta-information associated to any particular position, i.e. video recording, time absolute, time relative and animal ID. Data visualizations were prepared using packages grid, ggplot2 (Wickham 2016), scales (Wickham & Seidel 2020), ggpubr (Kassambara 2020), and viridis (Garnier 2018). Standard deviation was used to describe dispersion in the data distribution. To asses potential methodological effects of recording equipment on crab activity, the relative tracking time for each individual was calculated as the proportion of each video that the individual was observed. To evaluate individuals' residency and activity, tracking occurrence over time was plotted as an observation timeline for each individual.

Individuals' motion and use of space were described using several metrics such as distance travelled between successive relocations, the total distance travelled, Rate of Movement (ROM) and 95% kernel utilization distribution area. Distance between successive relocations was calculated using adehabitatLT package (Calenge 2016). Total distance travelled was estimated as the overall sum of distances moved between successive relocations. ROM was calculated in two ways: as the mean instantaneous ROM, and the absolute ROM. Mean instantaneous ROM was estimated as the average distance covered in successive frames divided by the time between frames (cm s^{-1}). Absolute ROM was calculated as the total distance travelled in centimetres over time in seconds (cm s^{-1}).

Burrow utilization and the area of utilization distribution were used to describe individuals' activity and space's use. Burrow visits and the proportion of time spent inside a burrow were calculated programmatically using individuals' position, burrows' position, and individuals' tracking timeline. A burrow visit was defined as an individual entering and completely disappearing inside a burrow. Burrow utilization was estimated as the number of burrow visits per minute and the relative amount of time spent inside a burrow, calculated as the proportion of time inside a burrow over the total time the individual was observed, whether in the surface or inside a burrow. The 95% utilization distribution area was calculated using the kernel methods from the adehabitatHR package. Utilization distribution areas were calculated for all individuals, except for one that did not move during the observation time and one individual that was detected in the observation areas for less than a second.

Results

From the 99 animals observed and tracked, 96 were intertidal crabs and three were mudskipper fish (*Periophthalmus*). The vast majority of crabs belong to superfamilies Ocypodoidea and Grapsoidae, with 70 and 17 individuals, respectively. Ocypodoidea was the most speciose group with seven different taxa identified (*Australoplax tridentata*, *Macrophthalmus*, *Ilyoplax dentata*, *Cleistostoma*, *Tubuca polita*, the complex *Tubuca bellator/signata*, and *Tubuca coarctata*). *T. bellator* and *T. signata* individuals could not be differentiated from field observation or videos, so these were group together. Grapsoid crabs were only identified to genus (*Parasesarma* and *Metopograpsus*), and these were mostly juveniles based on their size. Nine crabs could not be identified to species or genus, and these were assigned to the unknown category, although likely to be grapsoid crabs recruits (personal observation). During data quality check, relocations from one crab (*T. polita*) observed for less than a second, and 11 relocations from seven individuals showing errors in the tracking time stamp were removed. Relocations for one crab (unknown taxa) that did not move during the observation period (39 seconds) were maintained in the data. After data quality check, 1,413,828 relocation positions from 98 individuals were retained.

Animals tracked remained mostly within the observation area, with occasional excursions outside the observation area limits but within the camera field of view (Figure 5-1). Few transient organisms crossed through the observation area and camera field. There were differences in animal density and behaviour among videos, with between 10 and 29 animals observed in video (Figure 5-1C and Figure 5-1B). All crabs observed were mainly engaged in feeding behaviour during observation (crabs tracks in Figure 5-1A, C-F). Only one video captured courtship and fighting behaviour from 28 *T. polita* individuals (crabs tracks in Figure 5-1B). This behaviour was characterized by agonistic encounters among several individuals that included pushing, claw interlocking, claw waving and burrow defence. Therefore, the detection of these two distinct behaviours among crabs was a valuable opportunity to explore and study crab movement under these two behavioural states.

A large proportion of individuals (51%) were tracked during less than a third of the video duration, and only 39 individuals (40%) were observed for more than half of the video duration (Figure 5-2A). The average track time was 1332 ± 1292 seconds, with a minimum and maximum time of 15 and 4120 seconds, respectively. Overall, the relative tracking time was higher in Ocypodoid crabs (0.47 ± 0.32); followed by unknown crabs (0.26 ± 0.21), grapsoid crabs (0.24 ± 0.24), and mudskipper fish (0.07 ± 0.1). Although Ocypodoidae was the group with higher tracking time, some ocypodoid crabs had lower tracking times, for instance five T. coarctata were tracked for less than a quarter of the video duration. Most individuals were observed towards the end of the video (Figure 5-2B). This subtle but important bias, as noted in Chapter 2, suggests that some animals required some period of acclimation to the recording equipment. Some animals exhibited intermittent tracking timelines due to burrow use or because they exited and entered the quadrat while remaining within the field of view (Figure 5-2B).

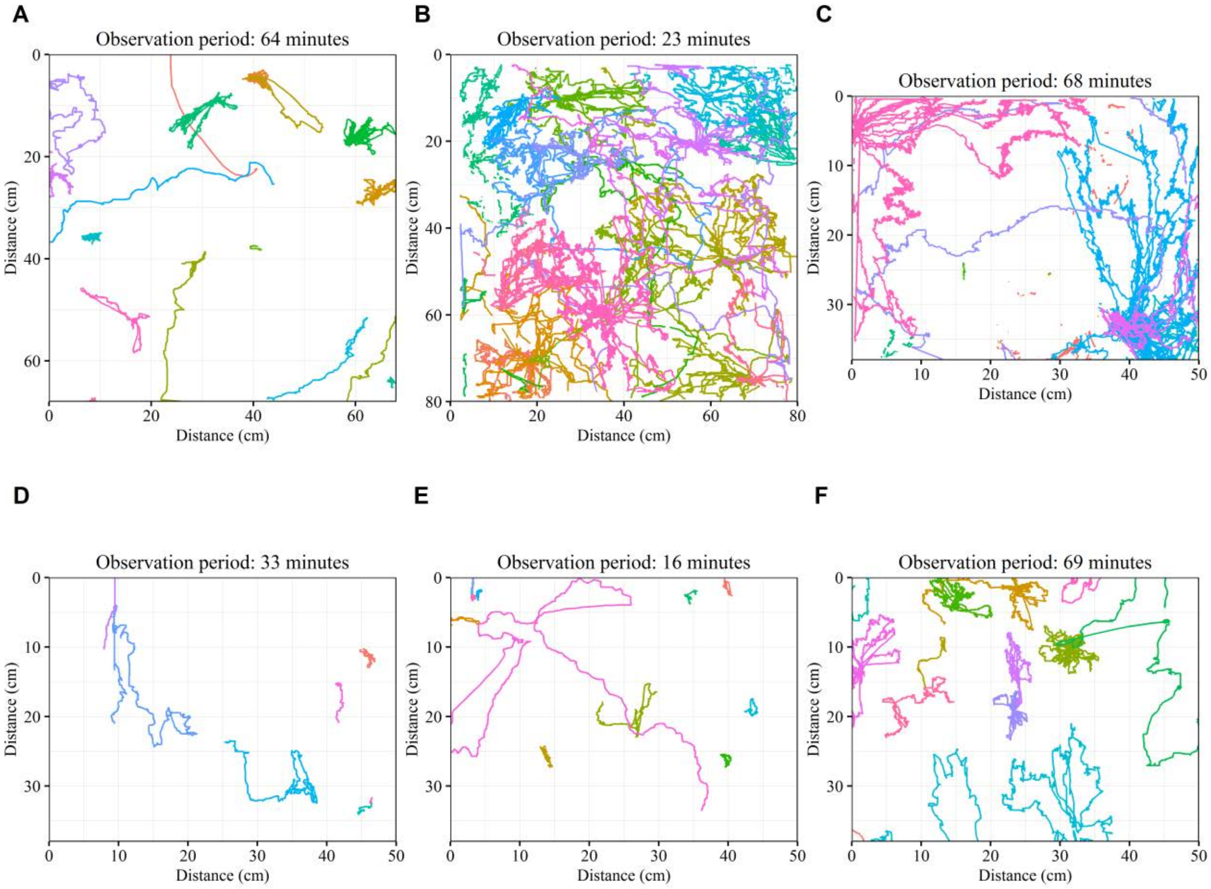


Figure 5-1: Animal trajectories per video. Movement tracks for 98 organisms (95 intertidal crabs and 3 mudskipper fish) in six videos covering areas: **A** 4624 cm^2, **B** 6400 cm^2, **C** 1900 cm^2, **D** 1900 cm^2, **E** 1900 cm^2 and **F** 1900 cm^2. Lines represent continuous movement from 1,413,828 relocation positions, and colours reflect different individuals.

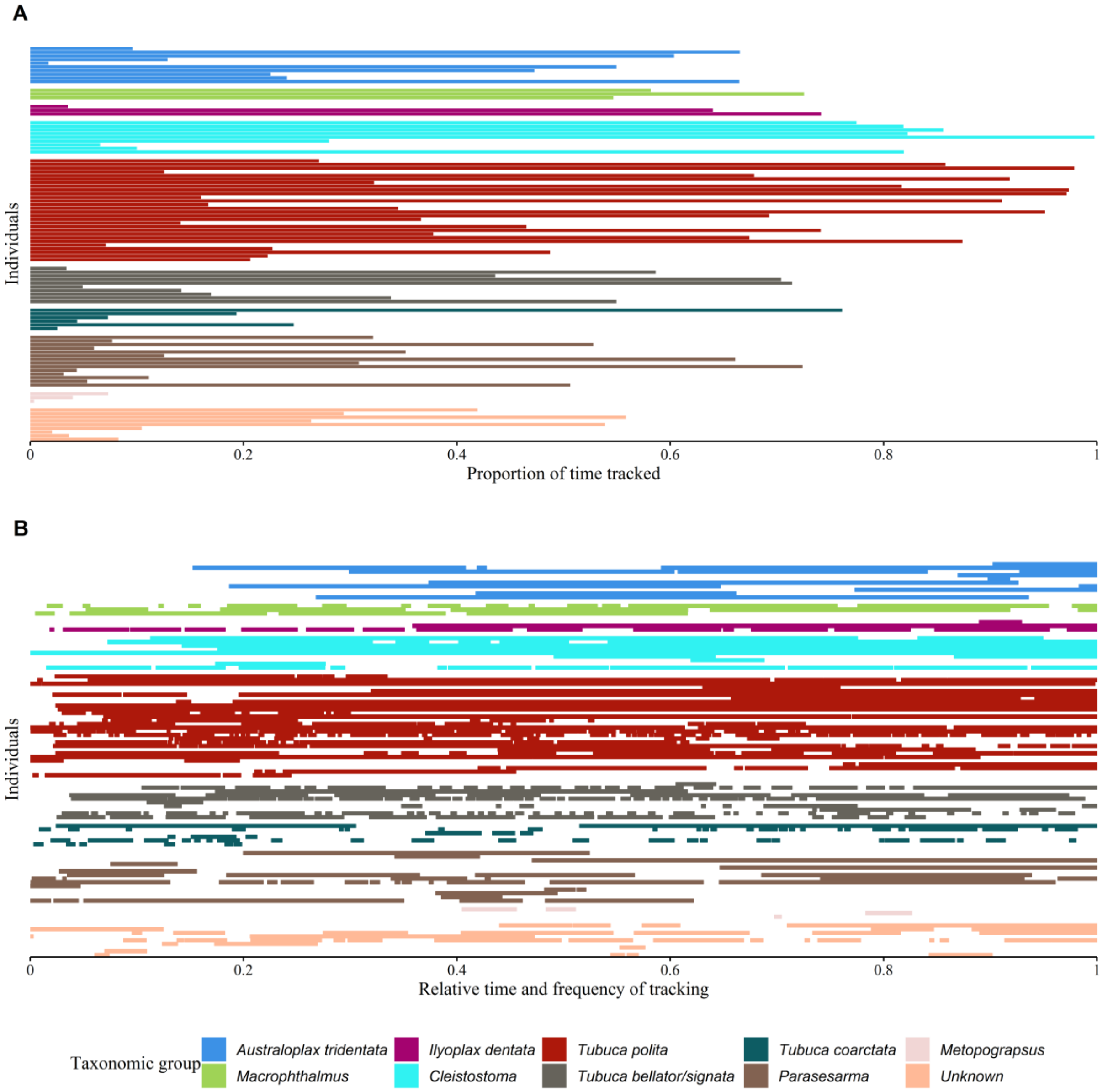


Figure 5-2: Relative proportion of time tracked and tracks timeline for 98 observed individuals in videos. **A** Proportion of time individuals were tracked relative to the length of the video. **B** Tracking timeline per individual relative to the total length of the video.

Motion and activity patterns varied among individuals and taxa. The average instantaneous ROM was 0.302 ± 0.374 cm s^{-1}. The minimum (non-zero) and maximum average instantaneous ROM were 0.004 and 1.647 cm s^{-1}, respectively. The mean instantaneous ROM and absolute ROM were significantly correlated (0.91, t = 21.008, df = 96, p-value < 0.001). The average distance travelled was 219 ± 318 cm, and only one unknown crab did not move during the observation period. The minimum (non-zero) and maximum distance covered were 2 and 2061 cm, respectively. *T. polita* crabs travelled the longest distance among all organisms (average 502 ± 423 cm, n = 28). Interestingly, longer observation times did not necessarily translate into greater distance travelled (Figure 5-3). The absolute ROM and total distance travelled exhibited a positive linear relationship (Figure 5-3, notice $\log_{10}$ scale used to improve visualization of individual points). This relationship seemed to be driven by T. polita crabs that showed the greatest absolute ROM and were among organisms that travelled the longest distances, suggesting that the behavior of crabs is tightly associated to their motion patterns.

Burrow utilization was not common across organisms, although some individuals made frequent use of burrows. Sixty organisms (61 %) did not use burrows. From these individuals that used burrows, on average organisms visit the burrow five times, and one visit was the most common number of visits, observed in thirteen animals (13 %). The average total time that animals spent inside a burrow was 481 ± 741 seconds, with an average visit duration of 129 ± 254 seconds. The highest number of visits was observed in one *Tubuca cf bellator/signata* crab that visited a burrow 34 times in a period of 3621 seconds, with an average duration of 52 ± 25 seconds per visit (Figure Appx. C- 1). The second and third highest number of visits to burrows were 28 (average visit duration 35 ± 47 seconds) and 20 (average visit duration 45 ± 13 seconds) from *Ilyoplax dentata* and *T. cf bellator/signata* crabs, respectively (Figure Appx. C-1). There was a great variability in burrow among individuals, and there was no clear relationship between the number of burrow visits per minute and the proportion of time spent inside a burrow (Figure 5-4). However, taxonomic differences seem to be important, as grapsoid crabs tended to do less burrow visits for longer times, while ocypodoid crabs exhibited a wider and more variable burrow utilization strategy (Figure 5-4, Figure Appx. C- 1).

The mean area used by animals during the observation period was 314.17 ± 601.40 cm^2, with a minimum and maximum of 0.07 and 3714.17 cm^2, respectively. *Tubuca. coarctata* and *T. polita* crabs consistently showed higher utilization areas with mean values of 807 ± 838 cm^2 and 636 ± 613 cm^2, respectively. As organisms tracked exhibited varied patterns of motion such as station keeping and transient trajectories, and given the short tracking time, utilization distribution areas do not necessarily reflect organisms' home ranges (Burt 1943). However, utilization distribution areas are an indicator of the level of crab activity. The absolute ROM and utilization area followed a positive linear relationship (Figure 5-5, once again notice $\log_{10}$ scale used to improve visualization of individual points). The observed courtship/fighting behaviour in 28 *T. polita* crabs and their corresponding level of activity, high ROM and higher utilization area, contrast with the level of activity from all other crabs engaged in feeding behaviour (Figure 5-5). This suggests that crab behaviour is a critical mechanism explaining movement patterns and level of activity (i.e. area utilized) in crabs.

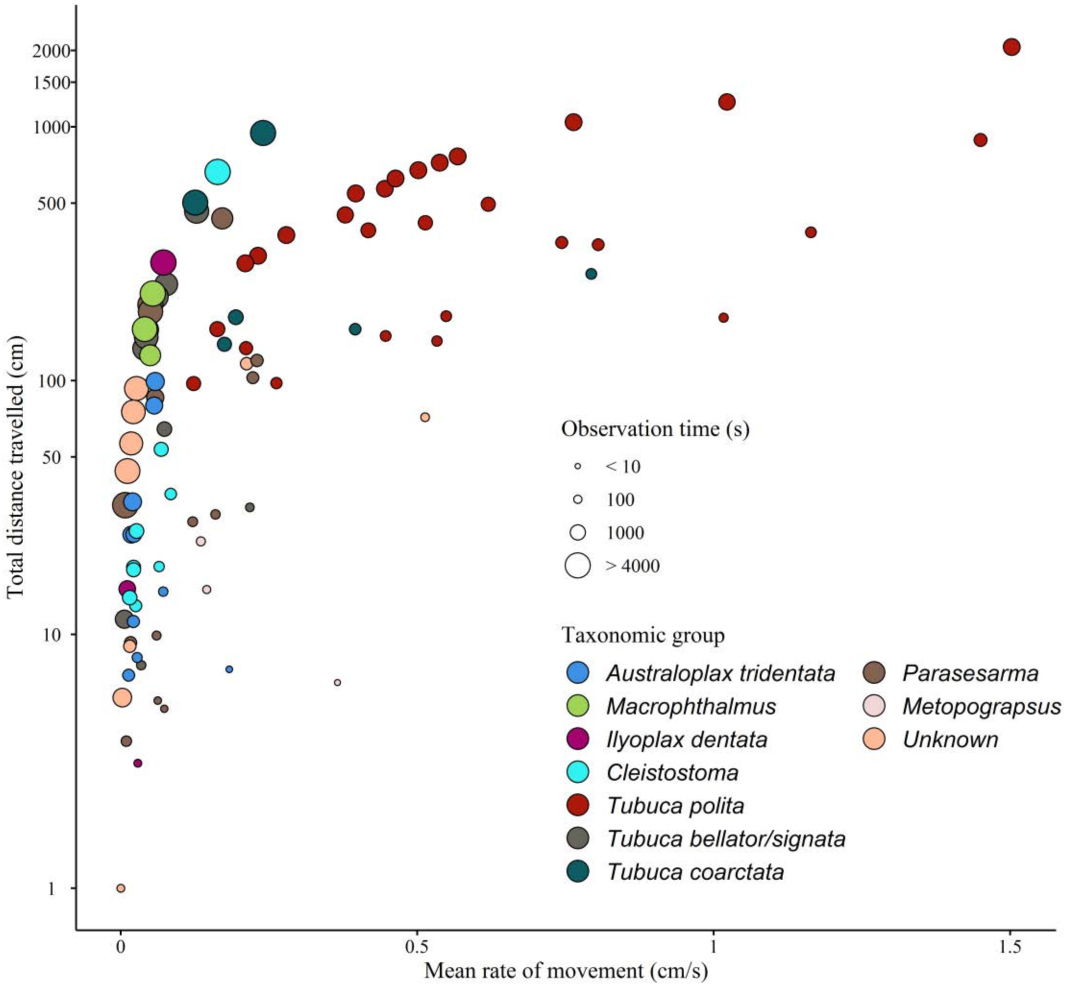


Figure 5-3: Relationship between the absolute rate of movement and total distance travelled over the variable observation period for 98 individuals. Notice $\log_{10}$ scale in ordinate.

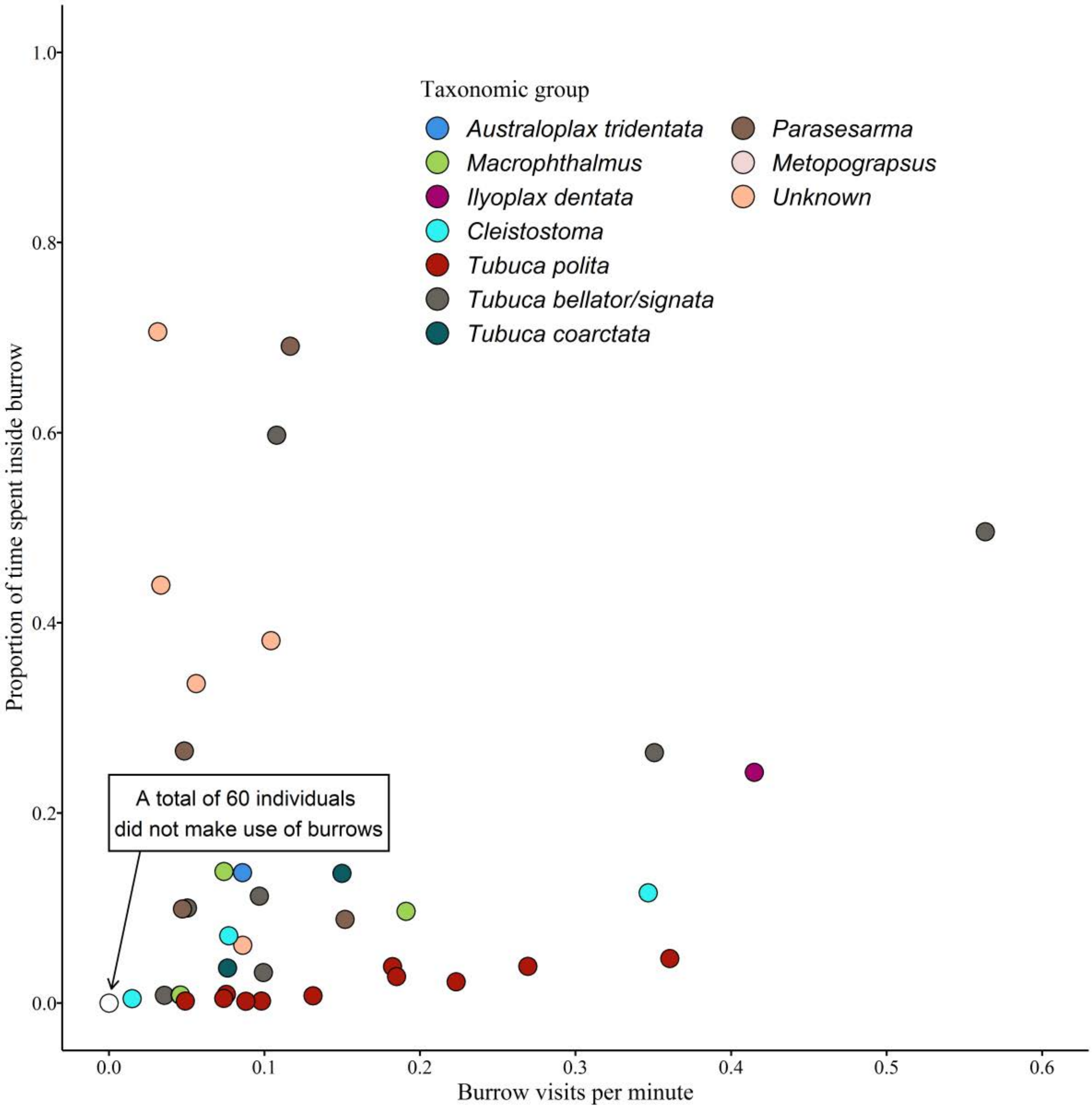


Figure 5-4: Standardized burrow utilization as number and duration of visits over the observation period.

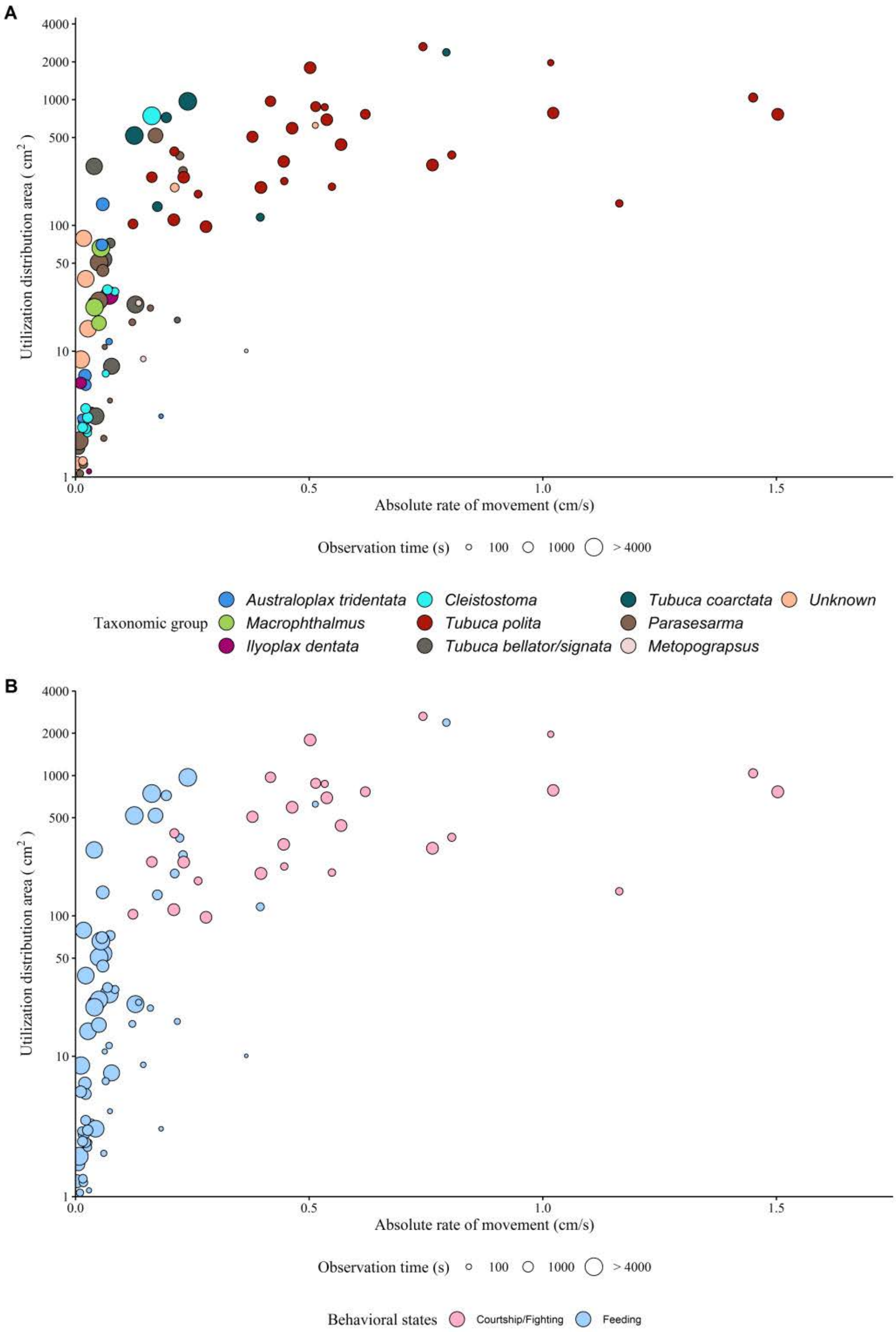


Figure 5-5: Relationship between utilization distribution areas (95%) and mean rate of movement per taxonomic group (A) and behavioural states (B). Notice the $\log_{10}$ scale in the ordinate, and that panel **B** does not contain the three observations from *Periophthalmus* mudskipper fish. In **B,** colour scale distinguishes two behavioural states: courtship/fighting (pink) and feeding (blue). Courtship/fighting behaviour was only observed in one crab species *T. polita*.

Discussion

This study advances animal movement research efforts by collecting information in animal trajectories and behaviors using image-based tracking technology in unconstrained environments. This is the first study to quantitatively characterize motion and activity levels (i.e. ROM, area utilized, burrow use, and distance travelled) of basal and excited behavioral states across multiple crab species. The fine scale movement and activity of 96 intertidal crabs were studied by analyzing and comparing motion metrics and burrow utilization in nine taxonomic groups and two behavioral states. Results showed high variability in motion patterns and burrowing activity among and within taxonomic groups. Despite this variability, a remarkable difference in motion activity was observed between behavioral states (Figure 5-5). *Tubuca polita* crabs engaged in courtship and fighting behavior exhibited higher ROM, longer total distance travelled, and bigger utilization areas than any crabs engaged in feeding behavior. From the results obtained in the present study, it is unclear whether this observation represents differences between behavioral states or differences between taxonomic groups. However, observational studies on feeding and mating behavior have reported that ocypodoid crabs show distinct movement patterns and different activity levels during courtship (Christy & Salmon 1984).

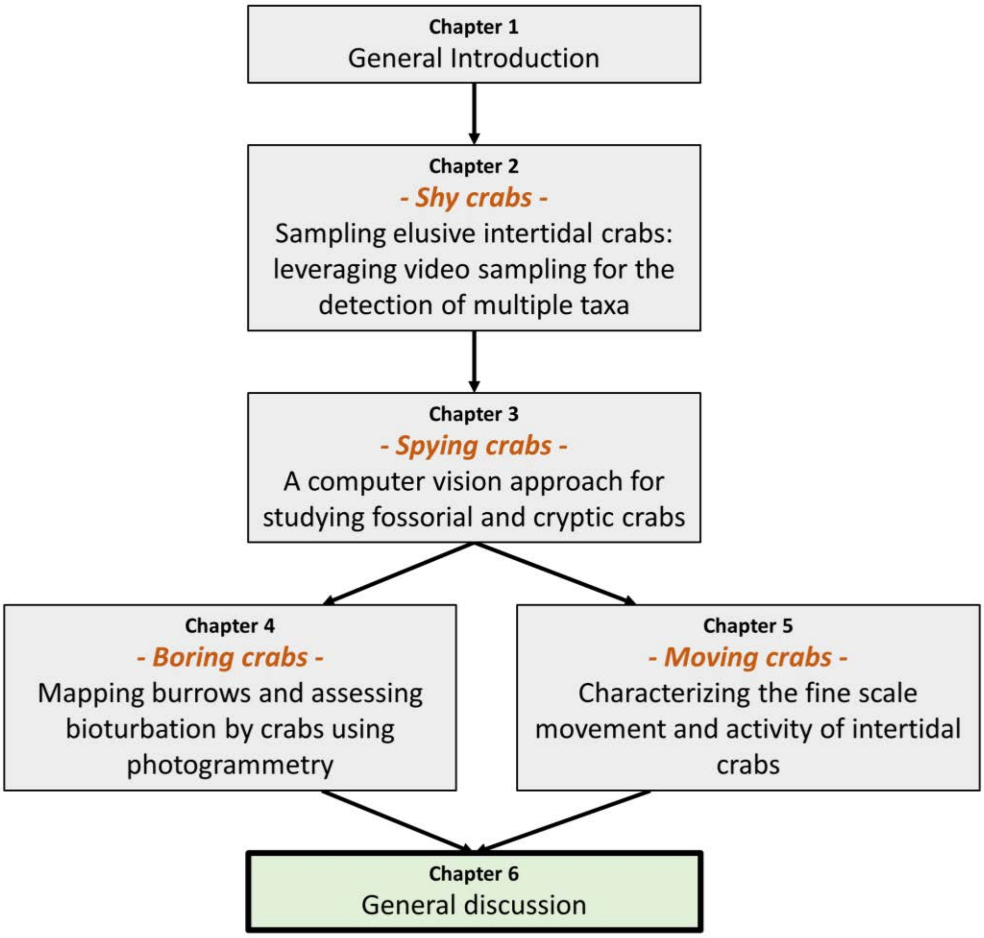
Animals continuously trade-off the cost of movement with other energy costs and physiological demands associated with feeding, reproduction, and predator avoidance (Halsey 2016). Movement and activity data collected in this study provide insights into the behavioral and physiological adaptations different taxa employ to optimize different behaviors, and overcome the environmental challenges of living in intertidal areas. The large variability in ROM and distance travelled, one and two orders of magnitude respectively, shows the range of locomotion patterns intertidal crabs display (Figure 5-3). Higher ROM and distance travelled translate into higher energetic demands from individuals. Furthermore, because ocypodoid and grapsoid crabs must keep their gills or branchiostegal chambers wet to maximize breathing (Burggren 1992), prolonged periods on the sediment surface and high energy demands can negatively impact individuals' health (Vianna et al. 2020). A common behavior utilized by intertidal crabs to reduce water loss and favor osmoregulation is to use burrows (Faria et al. 2017). This study described two different burrow utilization strategies: frequent but relatively short visits, as observed in ocypodoid crabs, and sporadic but longer visits, as in grapsoid crabs (Figure 5-4). These differences in burrow utilization are likely to reflect different life histories and physiological strategies across species. For instance, ocypodoid and grapsoid crabs have different water economies and osmoregulation (Takeda et al. 1996; Lin, Su & Su 2002; Tseng, Tsai & Lin 2020). Additional data are required to confirm if the motion and activity patterns used by crabs are species-specific traits arising from crabs' physiology and life history, and to what extent similarities exist in these patterns.

In this study, I did not observe substantial differences in the area utilized by ocypodoid and grapsoid crabs (Figure 5-5). However, it has been noted that ocypodoid crabs tend to utilize smaller areas than grapsoid crabs (Crane 1975; Cannicci et al. 1996; Cannicci, Fratini & Vannini 1999b; Cannicci, Fratini & Vannini 1999a). The discrepancy between my results and literature is likely partially explained by the life stage differences between grapsoid and ocypodoid crabs tracked. The vast majority of ocypodoid crabs were adults, yet most grapsoid crabs detected in video recordings were juveniles or recruits with short displacements. Grapsoid crabs were also the group tracked for the shortest period. With the available data, it is not possible to distinguish if grapsoid crabs were underrepresented by the sampling method, or if grapsoid relative abundance, in particular adults, was lower at the study sites. However, results from Chapter 2, where I showed that video surveys improved grapsoid crab detection (Figure 2-2), downplay the likelihood of a methodological bias. However, if grapsoid crabs exhibit large displacements (over 5-10 metres) over short time (minutes), and given the image-based tracking methods are limited to what is seen in by camera, it is unlikely that an image-based tracking method as the one used here (and Chapter 3) would be effective in collecting movement data for those crabs. Hence, image-based tracking methods' effectivity are tightly associated with the life history characteristics of the focal species.

Image-based tracking methods are constrained by the maximum area observed within the camera field of view. For this reason, the ratio between the observation area and individuals' size and home ranges are critical factors to consider when setting recording equipment for *in situ* animal tracking. In general, the larger the crab is relative to the field of view, the easier it would be to achieve an automated or manual taxonomic identification and behavioural classification because there is more information (more pixels, therefore more details). Furthermore, and regardless of their size, taxa with larger home ranges would be more difficult to track over prolonged periods because these are likely to exit the observation area. For instance, T. coarctata individuals were observed in a relatively small area compared to their size and for relatively short periods because they often exited the field of view of the camera. In this case, the observation area was deliberately small to increase the likelihood of observing and identifying other cohabitant crabs significantly smaller than T. coarctata (e.g. recruits and juvenile Metopograpsus crabs, up to four times smaller). Consequently, a compromise between observation area and distance to sediment (i.e. distance to focal species) must be considered depending on the study's purpose, and the focal species' size, behaviour and taxonomy. Thus, observational experiments like the present study are valuable in describing the distribution of movement and activities across taxa.

This study joins other projects highlighting the value of utilizing computer vision tools to sample and study the small invertebrates' movement of in their natural habitats (Chapter 3 and 4). Image-based active tracking using computer vision algorithms is a novel tool that permits high resolution tracking in space and time. There are several recognizable challenges and sources of errors associated with this technology (Chapter 3, Table Appx. A- 2, Weinstein 2018; Schneider et al. 2019; Hoye et al. 2021), however, ongoing efforts should focus on increasing observation area and time, expanding the information extracted from images (e.g. color, surrounding vegetation), and incorporating data stream from complementary technologies such as weather sensors. Structured sampling within and among populations and taxonomic groups would be ideal in future research efforts. This is not to say that observational studies in specific species and sites are not useful in their own right, but that assessing distinct locomotion and activity patterns emerging from various taxa and behaviors enables making inference of drivers of movement. Additionally, in some cases, evaluating the distribution of motion patterns in various populations and environments would reveal how some ecological and functional attributes of movement are context dependent or constrained by natural and anthropogenic pressures. Thus, longer and more frequent observation periods, coupled with environmental sensors, will shed light on the facilitative and competitive interactions among crab species and the mechanisms driving individual and collective movement.

Chapter 6 - General discussion



Ecologists are increasingly embracing the assessment and monitoring of organisms' traits and functional attributes (Violle *et al.* 2014; Asner *et al.* 2017; Cernansky 2017). Because anthropogenic pressures are shaping and driving populations and communities distributions and influencing the processes they contribute to (Steffen, Crutzen & McNeill 2007; Larsen & Ormerod 2014), the study of vulnerability and resilience of functional traits at individual, species and ecosystem level is paramount to understanding, managing and predicting the future of natural systems (Lefcheck & Duffy 2015; Greenfield *et al.* 2016). Under this approach, organisms' functional traits within ecosystems are equally as important as their taxonomic identities or the number of species occurring in the ecosystem. However, measuring organisms' functional attributes is more complex and generally requires a considerably greater effort than counting and identifying species (e.g. Pakeman & Quested 2007; Lavorel *et al.* 2008). Thus, developing new methods that lower the cost, and ease the measurement of organisms' functional traits, is of critical importance.

I have integrated concepts and tools from diverse disciplines such as computer science, engineering, videography, statistics, and ecology to address the pressing issue of increasing the pace at which natural scientists census and study species, and assess and describe their traits and functional roles. The goals of this thesis were to demonstrate the potential of computer vision to obtain biological and ecological data on intertidal invertebrates in quantities and at a level of quality unachievable using traditional approaches, as well as garnering maximal quantities of information from each sampling event, supported by the development of fit-for-purpose free and open source software. I achieved these goals by sequentially building on the work developed in previous chapters. Firstly, I demonstrated that video surveys, the underlying critical component to perform computer vision, perform better than visual census, the traditional, non-invasive and gold standard technique, to survey intertidal crabs (Chapter 2). Secondly, I developed a heuristic software and analysis workflow that greatly extended the amount of information collected from crabs observed in videos (Chapter 3, and Crabspy https://github.com/CexyNature/Crabspy). Finally, I employed this software and workflow to obtain precise crab bioturbation measurements, movement, and activity patterns (Chapters 4 and 5). In the next section, I discuss the implications and limitations of these advances, and future data and analytical avenues for intertidal crabs and biodiversity research.

Outcomes and limitations

Before embracing computer vision as a sampling tool, it was essential to identify the advantages and disadvantages of video recording over other standard sampling procedures. Compared to the visual census, in Chapter 2 I found that video recording reduces the latency to crab re-appearance and increases the number of species observed. Notably, one of the challenges associated with video recordings is data management, processing and analysis. Thus, it was essential to develop tools and pipelines that simplify video processing and analysis. Crabspy, a Python package for the analysis of crab videos, was born from this need. In Chapter 3, I used Crabspy to show how information on several traits and functional attributes of crabs can be obtained using computer vision algorithms. Many other traits and functional attributes such as feeding rate (scoops per second), carapace colour (Hue, Saturation and Value), claw waving rate (waves per second), among others not showcased in this thesis, are available from further analytical efforts assembled in Crabspy. Crabspy and methods described in Chapter 3 still rely heavily on operator supervision. As the amount of data collected and analysed increases, it will be possible to progressively incorporate more Machine and Deep Learning protocols, which would reduce the amount of supervision and ground truthing required by the operator, as long as experts can correctly label data. Nonetheless, another limitation of video recordings is that in many instances the image and behaviour of a crab are not enough to identify an individual to lower taxonomic levels. Either because key taxonomic characters cannot be observed or because the cryptic nature of some species requires a careful dissection of the specimen. When taxonomic identity is paramount, novel approaches as the ones I presented here should be combined with collection and dissection of specimens. The cryptic nature of intertidal crabs will challenge the progression of supervised learning, as labelling data to lower taxonomic levels or detailed behaviours is difficult. In Chapter 4, I measured the quantity of matter that crabs translocate per unit area and time. Implicitly, these calculations are associated with a given density of individuals. Therefore, at this stage and under the proposed method, my estimates represent the cumulative translocation of matter from several individuals. However, under continuous monitoring using recording devices with more durable batteries and larger disk storage, it would be possible to estimate bioturbation activity per individual. In Chapter 5, I described the motion and burrow activity patterns of several crabs. This is an initial step in understanding the movement capabilities of intertidal crabs and their utilization of space. Once again, recording devices that allow recording videos for longer periods would extend our understanding of crab territoriality, residency, behaviour, and space utilization over prolonged periods. Nonetheless, data already collected offer additional opportunities to evaluate collective movement, resource selection, state-space models of animal movement, and intra- and inter-specific interactions (Appendix D). Because of limitations on time, some of these analyses cannot be fully presented in this thesis. Nevertheless, to encourage the utilization of the methods I proposed, I present some of these additional outcomes in Appendix D.

I have presented a case study on the utility of computer vision algorithms for sampling crab populations and communities. I did purposely select crabs inhabiting mudflats and sand flats with low spatial complexity, this is, unvegetated and root-deprived habitats. This decision guaranteed me minimal interference or occlusion to crab view, thus, allowing me to detect and track crabs with ease. Nonetheless, many brachyuran crabs inhabit diverse habitats with higher structural complexity and denser vegetation. While the exact methods I have developed cannot be employed in these more complex habitats, these limitations do not preclude us from utilizing the same principles (i.e. computer vision) on different vision data (e.g. polarised or infrared videos), which could distinguish (i.e. detect and track) a crab in areas with dense vegetation and roots. The amount and variety of sensing devices can spur innovations that deal with specific limitations associated to the observation of crab in complex natural settings. Furthermore, current constraints are likely to inspire and drive the evolution of new sensing devices, algorithms, and analysis.

Leveraging computer vision for animal movement research

The capacity to extract animals' position and behavior, and the environmental conditions during observation for one or multiple individuals simultaneously is an enormous benefit in understanding how behavioral and environmental factors shape animal movement (Nathan *et al.* 2008). Empirical movement data from traditional tracking and telemetry methods, such as acoustic and GPS tags, often only consists of a series of positions (2D or 3D) over time. Several motion and utilization metrics can be calculated (e.g. speed, rate of movement, home range) from this type of time series. These descriptive metrics can help ecologists to understand organisms' utilization of space over time (when and where organisms move). When evaluated in conjunction with environmental variables, these can shine a light on the mechanistic drivers underlying animal movement (i.e. why organisms move). However, one limitation of traditional tracking and telemetry methods is the inability or difficulty to infer the behavior and physiological condition (what organisms do and sense) and type of locomotion employed by animals over time (how organisms move). Analytical state-space methods such as Hidden Markov chain Models (HMM) deal with these limitations by attempting to extract and describe organisms' conditions (behavior and physiology) at each time step (Langrock *et al.* 2012; Leos-Barajas *et al.* 2017; Goodall *et al.* 2019). However, these sophisticated analyses require regular relocation data with low spatial error (Michelot, Langrock & Patterson 2016). Ideally, the underlying conditions of organisms inferred by state-space models must be ground truthed to validate these methods. Activity tags provide an alternative way to gain access to organisms' behavior, as they provide ancillary data to organisms' position using accelerometer, gyroscope, magnetometer, and heart rate sensors, among others (Clark *et al.* 2010; Bestley *et al.* 2016; Williams *et al.* 2017).

Innovations in the analytical and technical aspects of animal movement telemetry and biologging are reducing the challenges associated with extracting animals' positions and inferring their behavior and physiological condition (Halsey *et al.* 2009; Rutz & Hays 2009; Wilmers *et al.* 2015). Species- and system-specific challenges faced by ecologists drive several of these innovations (e.g. McKinnon & Love 2018). However, the field of animal movement research is intimately interconnected regardless of species or system of interest, i.e. there is an increasing high prevalence and infectivity of methodological approaches and ideas across species and systems, although sometimes analysis and ideas are independently reinvented (Nathan 2008; Nathan & Giuggioli 2013; Joo *et al.* 2019). For this reason, it is important to evaluate the effectiveness and holistic nature of analytical approaches, models, and conclusions in various species and systems. The methods, software, and workflow presented in this thesis provide unique opportunities to advance animal movement research's theoretical and analytical concepts. In particular, because image-based tracking allows collecting comprehensive information about crabs' movement in their natural environment (Chapter 3 and 5). Behavior, size, interactions, among other data, can be extracted for one or multiple focal individuals. The value of such a comprehensive dataset is high, as it could serve as a case study in the revision and assessment of assumptions, statistical properties, and outcomes of well-established and novel analytical methods. The overarching goal now is to improve image-based tracking methods to the point where we can accomplish their extensive and intensive use.

Computer vision in Ecology: What does the future hold?

From here, further technical challenges remain, including improving organismal segmentation in unconstrained environments, better organismal recognition, superior tracking performance, improving identity assignment in situations with multiple interacting individuals, and increasing capability to fully automate these tasks. Technologies such as "You Only Look Once" (YOLO) and Deep Simple Online Realtime Tracking (SORT) are already tackling some of these challenges (Xu *et al.* 2019; Azhar *et al.* 2020). Implementing these advances in the biological and ecological domain and overcoming challenges species- and system-specific will require close collaboration from domain knowledge experts from diverse disciplines (computing science, engineering, IT, biology, and ecology). Synergy from those collaborations produce tangible data and literature outcomes (Villon *et al.* 2018; Konovalov *et al.* 2019; Piechaud *et al.* 2019; Mohamed, Nadaoka & Nakamura 2020; Saleh *et al.* 2020; Sheaves *et al.* 2020), and it is likely to trigger the born of new academic disciplines (Michener & Jones 2012; Allan *et al.* 2018). Importantly, although bottom-up collaborations can trigger positive initiatives that advance ecological and biological knowledge, medium to the long-term vision and strategic plans from institutions and academic societies would be key in determining how fast and effectively ecology and biology would benefit from image-based sampling and other novel technologies. Therefore, academic and research institutions and societies' commitment to create or enhance spaces for cross- and multi-disciplinary collaboration would be critical in propelling synergy between natural and computer scientists.

The possibilities of leveraging the power of computer vision, machine learning, and ecological sampling are that every observation event is likely to produce a vast amount of data, which can be analyzed to answer old questions or to discover questions that need to be answered. Collecting more information, and in some cases of better quality, at a faster pace, will support the progress of ecology in the next decades. As it has happened in other research fields (e.g. genetics, astrophysics), a tool driven revolution producing greatly increased volumes of data will prompt analytical and conceptual innovations. New disciplines as technoecology (Allan *et al.* 2018) and ecoinformatics (Michener & Jones 2012) are already leading new approaches to transform data acquisition and assimilate data in pipelines that generate knowledge. Big data will also challenge the local storing capacity of scientists and institutions. This could enable and encourage the creation (or use) of public databases or data aggregations in curated and well-maintained repositories. Several initiatives already perform this function, for instance: Movebank (Kranstauber *et al.* 2011), Ocean Biodiversity Information System (OBIS 2021), World Register of Marine Species (Horton *et al.* 2019), and iNaturalist (Van Horn *et al.* 2018). These, and future, public databases and data aggregations are a gigantic asset for Ecology and humanity because anyone can access observations and information. Whether these databases are used as long-term research archives, for learning and training, for testing new hypotheses or for challenging old paradigms, public data promotes scientific transparency and reproducibility. In particular, curated databases and data aggregations can increase the public understanding of science, allow scientists to gain greater systematic insight of ecological patterns, increase the life cycle of data and sustain a healthy scientific accountability.

Conclusions and future research

I have demonstrated the benefits of using video surveys for sampling intertidal crabs in soft sediments (Chapter 2), and I developed methods and software (Chapter 3) that can harvest ecological data from crab recordings (Chapter 4 and 5, and Appendix C). This work proposes and impulses the use of a computer vision framework to assess intertidal crabs' traits and functional attributes. Although in relatively small instances, I demonstrated the capabilities of this novel and innovative approach in identifying and documenting important biological and ecological aspects of intertidal crabs' life history, such as bioturbation activity (Chapter 3 and

4) and movement (Chapter 3 and 5). The amount of time and effort invested in developing these methods and software precluded me from using them extensively. However, I expect this work lays the ground for future innovations and improvements in the image-based sampling of intertidal crabs and serves other biologists and ecologists researching intertidal crabs. Computer vision offers several strategic opportunities to study intertidal crabs over traditional methods; for instance, easy scalability in space and time, reduction in bias and data uncertainty, the ability to revisit and re-analyze raw data with improved algorithms, and decrease in sampling costs. Incorporating video surveys and computer vision analyses in biologists and ecologists' toolbox and effectively combining them with traditional sample techniques will be pivotal to their ability to study species diversity, traits and functional roles of intertidal crabs, and to investigate the interacting effects of species, traits and functional attributes variability across populations and environmental conditions on the functioning of ecosystems.

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Appendix A: Chapter 3 - A computer vision approach for studying fossorial and cryptic crabs

Figure Appx. A- 1: Photogram example from video reel showing recording type mode III, parallel to ground, and crab detection and recognition. This type of recording angle is useful for observing behavioural displays and accessing feeding rates. The video reel shows tracking and classification possibilities from convolutional neural network models. The full video can be obtained from Figshare (https://doi.org/10.6084/m9.figshare.12284435.v1).

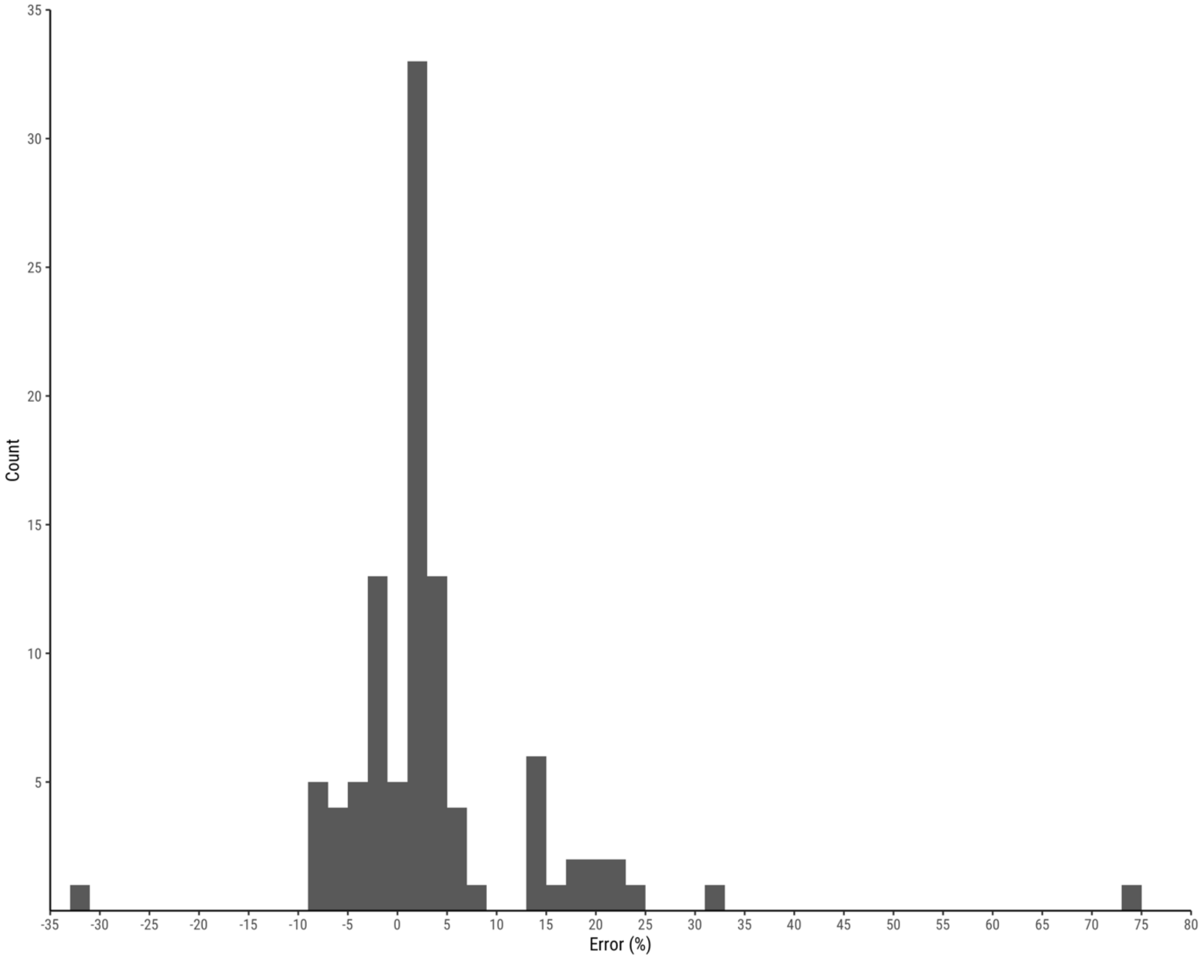


Figure Appx. A- 2: Validation of crab segmentation by Crabspy. One hundred images from 10 individuals were manually segmented and used as ground truth. The pixel area was calculated and compared with the area segmented by Crabspy. Results from this comparison are presented as error percentage.

Table Appx. A- 1: Classification performance metrics for machine learning models trained with images following the proposed sampling workflow in this paper and Crabspy. Three models were employed in two classification problems. For assessing male fiddler crabs handedness a Support Vector Machine (SVM) on Histogram of Oriented Gradients (HOG) and a Convolutional Neural Network (CNN) were used. For classifying crabs images within two labels, fiddler crab and no fiddler crab, an off the shelf CNN was employed by applying transferring learning on crabs images. Label, represents the two possible categories in the binary classifiers. Metrics presented follow definitions from the Python package Scikit-learn: support, is the total number of images per category; precision, is a ratio from the amount of images correctly classified in the category divided by the total images from the category; recall, is a ratio from the amount of images correctly classified in a category divided by the total images classified in the category; overall accuracy, is the average precision of both categories/labels. Models available at:

https://github.com/CexyNature/CrabsHandedness;
https://github.com/CexyNature/CrabsHandedness/blob/master/handedness_crabs_NN.ipynb ; and
https://github.com/CexyNature/Crabspy

Problem	Model type	Label	Support	Precision	Recall	Overall accuracy
Binary classification of handedness in male fiddler crabs	CNN	Left	385	0.96	0.99	0.98
		Right	539	0.99	0.97	
	SVM	Left	400	0.91	0.93	0.93
		Right	599	0.95	0.93	
Binary classification of intertidal crabs	CNN (transferring learning)	Fiddler crab	497	0.86	0.9	0.84
		No fiddler crab	262	0.77	0.77	

Table Appx. A- 2: Challenges associated with identifying and tracking crabs in their environment: causes, effects and mitigation actions.

Challenge	Cause	Effect	Mitigation action
Identify and track organisms in unconstrained environments. This is, environments with sudden and variable change in contrast and in illumination conditions.	Sunlight casting through canopy and understory foliage can produce hard contrast between fully illuminated and dark patches of sediment. This effect is exacerbated when moderate and strong winds moved the canopy and understory foliage, producing a frequent shift of these contrast shades in the sediment.	Increase inability to detect organismal motion and reduce successful identification and tracking. It can bias scientist's decision about where and when to sample.	Sample in areas where this effect is absent, or sample at times when light intensity and illumination levels minimize this challenge. Explicitly acknowledge sampling bias and assumptions. Use more robust models to describe the background and foreground, such as cluster background models, texturized models, models based on neural networks, and others (e.g. Culibrk *et al.* 2007; Guo, Dai & Hoiem 2011; Zhu, Guo & Ma 2012; Kumar & Agarwal 2013). These models are often more computationally intensive. Track organisms manually under unfavourable light conditions.
Maintain correspondence and consistency in organisms tracking ID when:		Reduce the success of tracking one or multiple individuals.	
Organisms are occluded behind vegetation or other objects in the landscape (Fig 1-D-vi).	Camera, equipment configuration, and heterogeneous landscape prevents a direct view of		Position camera and equipment to minimise blind spots in the field of view (e.g. mode I Fig 1-A).

	the organism at any given time.		
Two or more organisms were interacting adjacent to each other (Fig 1-D-vii).	The correspondence between organisms and their trackers is normally established only using distance information between current and previous time.		Include additional information to resolve organism and tracker assignment. For instance, colour, size, texture, speed and direction, among other variables, can be explicitly added and considered in the tracking model and assignment algorithm.
Organisms moves rapidly (Fig 1-D-viii).	Crabs exhibit burst motion which increase tracking ID mismatch.		Avoid skipping or dropping frames during analysis.

Table Appx. A- 3: Assumptions underpinning bioturbation rates estimates.

Assumption	Basis	Uncertainties	Uncertainty level
Volume change in the sediment surface is a good surrogate of mass turnover.	Fossorial crabs create burrows by removing and compacting sediment. Burrow volume has been long used as an estimate of sedimend removed (Katz 1980; Takeda & Kurihara 1987; Gutierrez et al. 2006; Escapa et al. 2007; Wang et al. 2010; Fanjul et al. 2011; Fanjul et al. 2015).	Sediment deposited inside the burrow is not accounted in this method.	Medium
No other factor (other than the species observed) contributed to volume changes.	Area was only occupied by target species.	Some grapsid species exhibit nocturnal and crepuscular activity. Thus, potentially these species (and others) could been active during time periods when the researchers were absent. However, these species were not observed, and their bioturbation capabilities are low.	Low
	The sampled area (upper intertidal) was out of reach from other crab species and mud skipper fish, which are also bioturbators (lower intertidal).	Some individuals from lower intertidal species could have wandered to the upper intertidal area. This behaviour has not been observed.	Low
	The area was not exposed to flooding during the sampling period.	Tides and tidal range (i.e. flooding regime) is well known in the area.	Low
	Birds were not observed visiting the area.	While the apparent level of uncertainty of these assumptions is high, the muddy sediment guarantees that any incursion in the sampling area would be recorded in the sediment. No footprints from animals (except the researchers' ones) were observed during the sampling period.	Low
	People and other mammals (e.g. wild cats and dogs) were not observed in the sampling area.		Low
	Vegetation growth and senescence were negligible.	Bioturbation was calculated for a relatively short time scale (days) where root growth and sediment vertical accretion were not observed. The amount of fallen leaves in the sampling plots was low.	Low

Table Appx. A- 4: Validation results for volume difference estimated by SfM photogrammetry. Following the technique described in Chapter 4, the known volume difference in three samples was estimated using SfM photogrammetry. These three samples were made of: addition of 120 ml of sediment in two scoops of 60 ml each, addition of 370 ml of sediment in two scoops of 60 ml and one scoop of 250 ml, and addition of 60 ml of sediment in 12 scoops of 5 ml. The accuracy is presented as error percentage relative to the ground truth volume.

Experiment description	**Total volume difference (ml)**	**SfM Photogrammetry volume difference (ml)**	**Error (%)**
Two scoops of 60 ml	120.00	114.63	4.47
Two scoops of 60 ml + one scoop of 250 ml	370.00	368.13	0.51
Twelve scoops of 5 ml	60.00	56.78	5.37

Appendix B: Chapter 4 - Mapping burrows and assessing bioturbation by crabs using photogrammetry

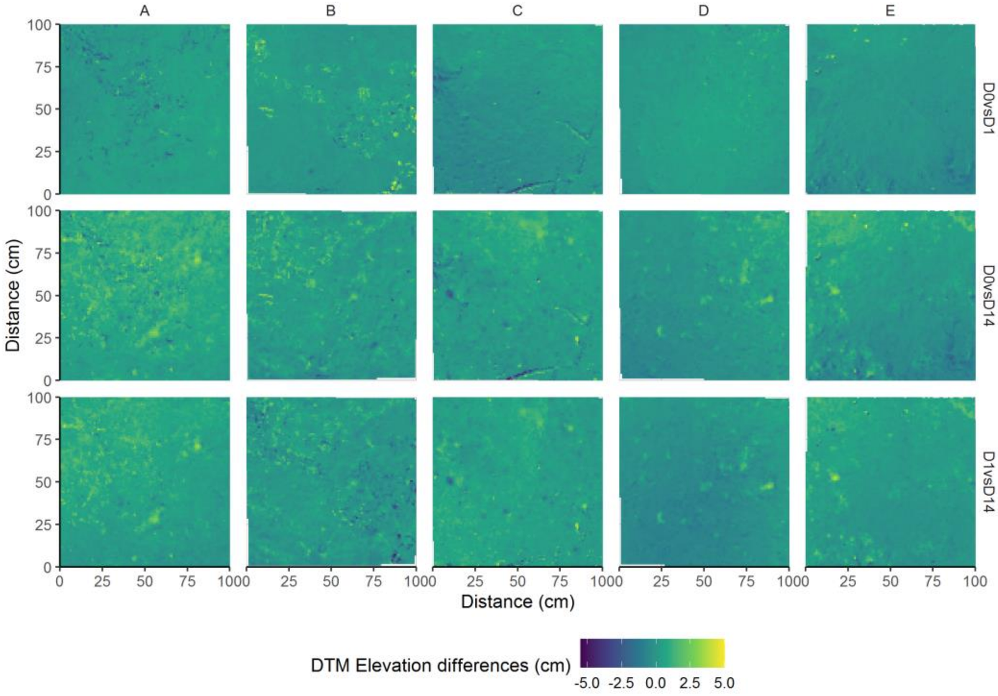


Figure Appx. B- 1: Change in sediment elevation across quadrats (A-E) and time intervals.

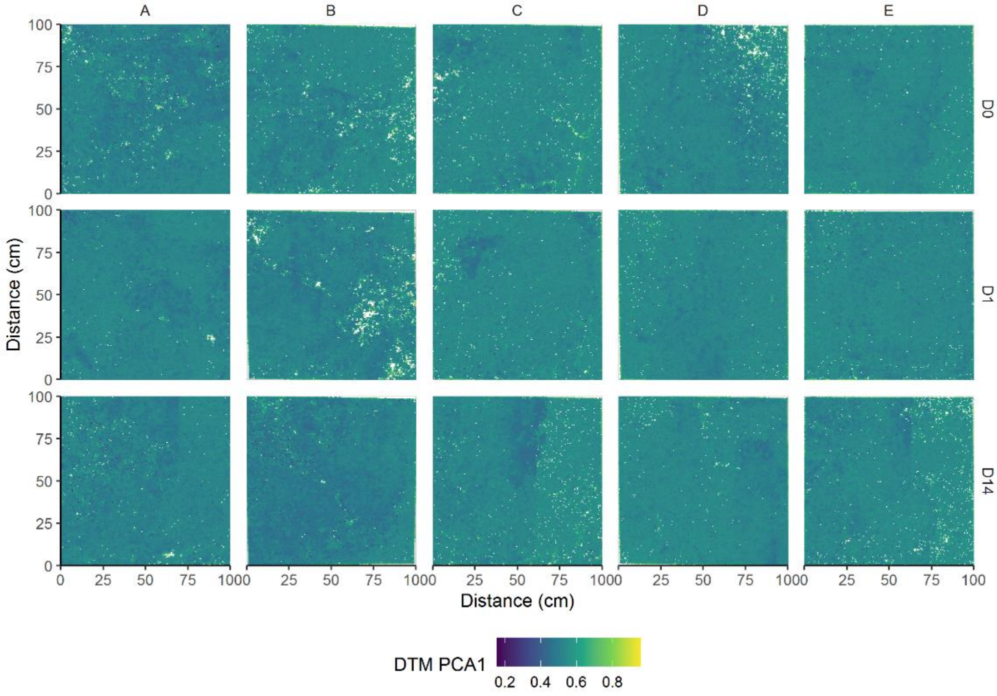


Figure Appx. B- 2: Change in Principal Component 1 (PC1) derived from sediment 3D data across quadrats (A-E) and times (D0, D1, D14).

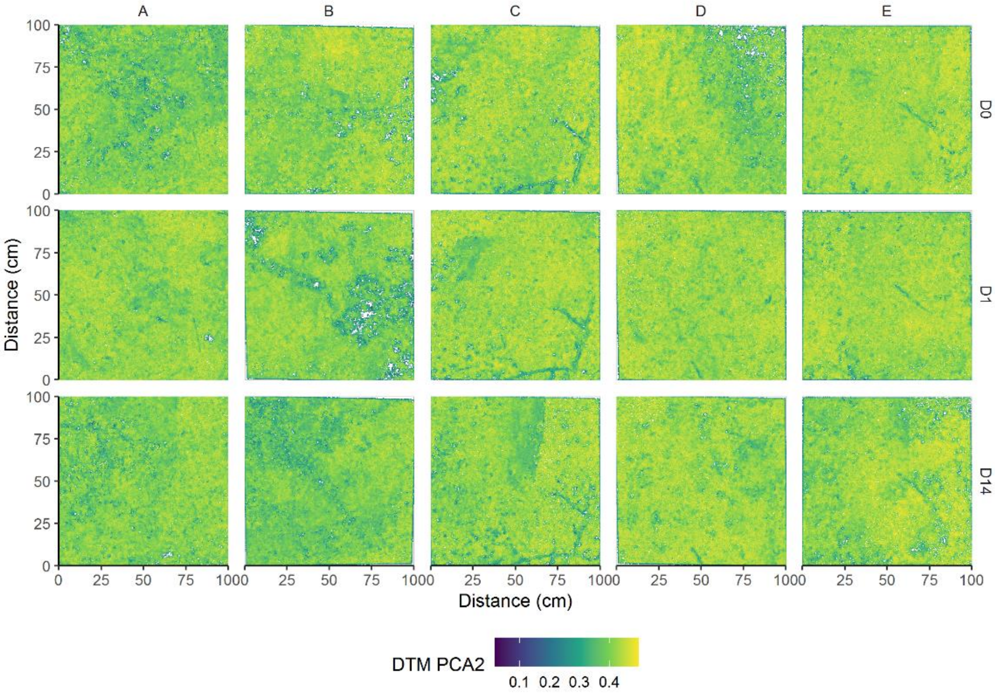


Figure Appx. B- 3: Change in Principal Component 2 (PC2) derived from sediment 3D data across quadrats (A-E) and times (D0, D1, D14).

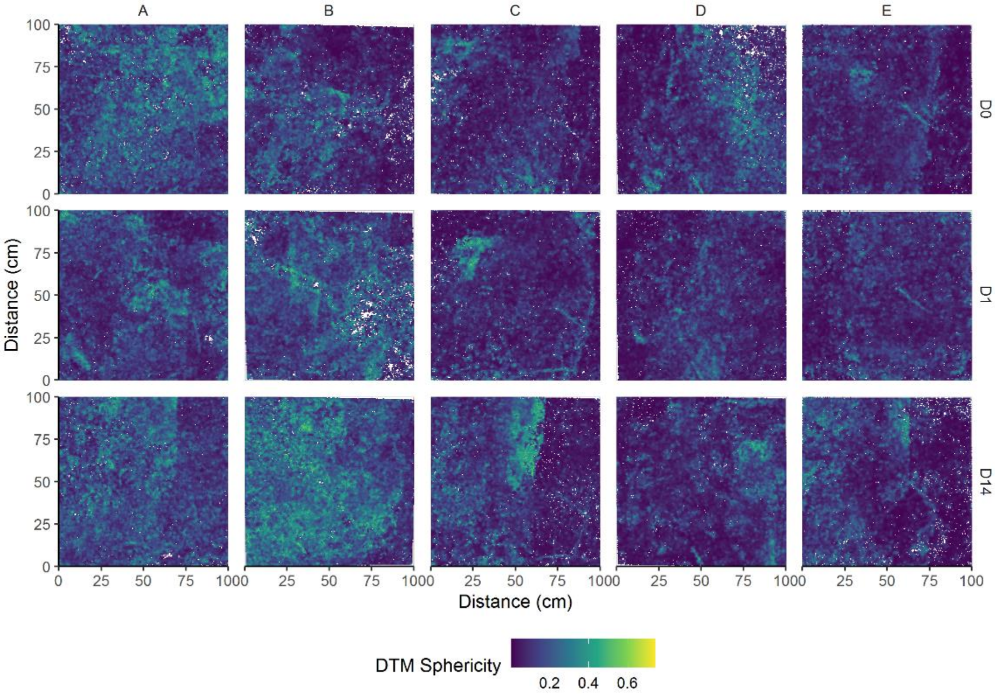


Figure Appx. B- 4: Change in Sphericity derived from sediment 3D data across quadrats (A-E) and times (D0, D1, D14).

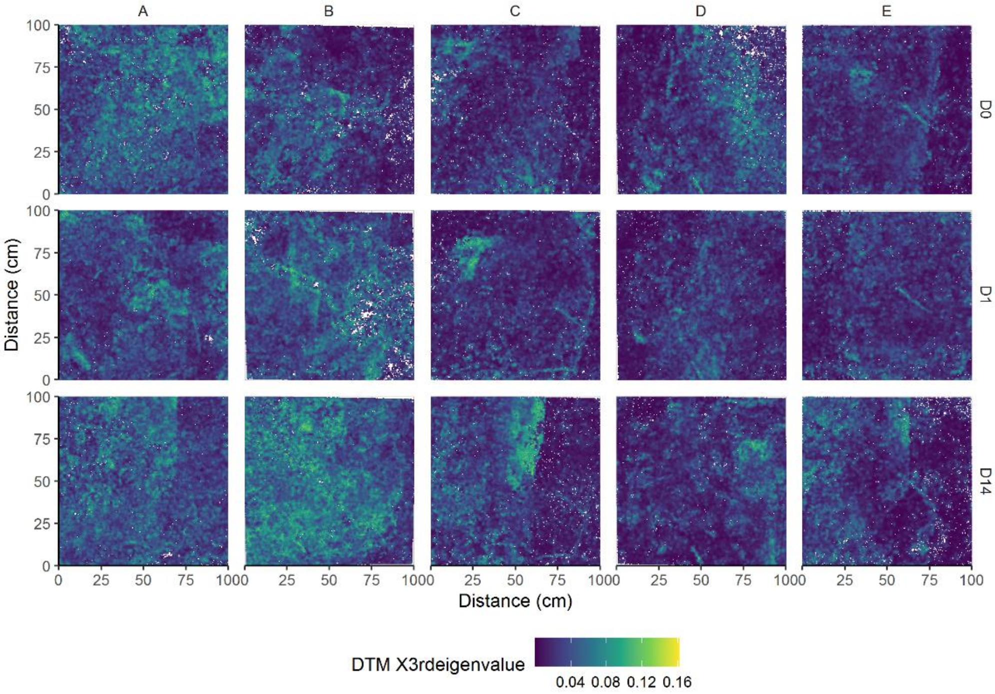


Figure Appx. B- 5: Change in 3rd eigenvalue (X3rdeigenvalue) derived from sediment 3D data across quadrats (A-E) and times (D0, D1, D14).

Appendix C: Chapter 5 - Characterizing the fine scale movement and activity of intertidal crabs

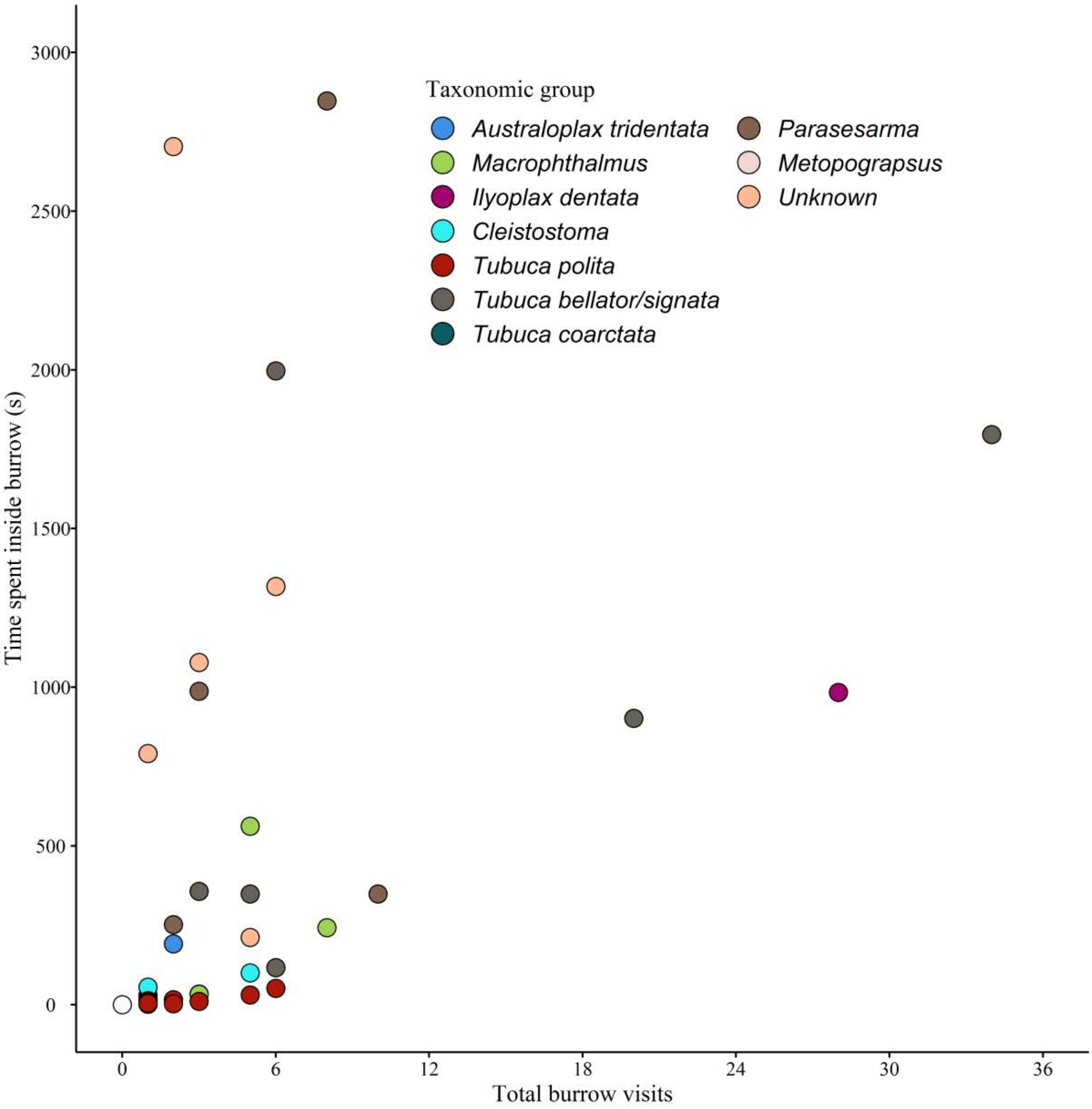


Figure Appx. C- 1: Burrow utilization as number and duration of visits over the observation period. The colour scale distinguishes between ocypodoid crabs (superfamily Ocypodoidea, Purple-Blue scale), grapsoid crabs (superfamily Grapsoidae, green scale), and mudskipper fish (yellow).

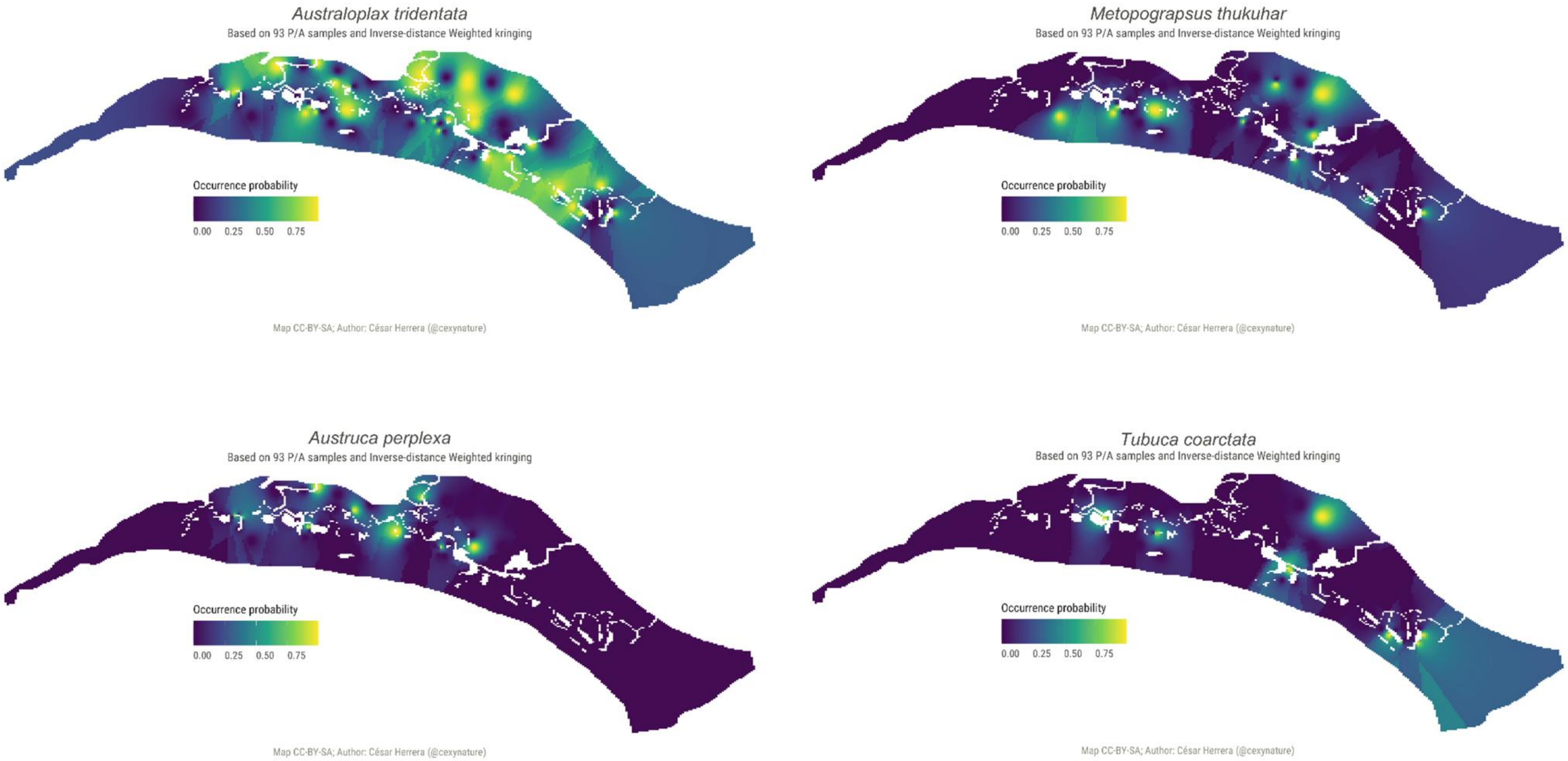
Appendix D: Biodiversity of traits and functions

In this appendix, it is not my intention to comprehensively review additional outcomes resulted from using video surveys and computer vision algorithms; I rather outline them to demonstrate additional research and analytical avenues, and their relevance for applying a functional ecology approach to intertidal crab research.

One of the advantages of using video surveys is that an increase in sampling effort does not necessarily imply an increase in field personnel or labour. In fact, as crabs exhibit semi predictable patterns of activity in the surface, one person equipped with several video cameras can deploy and collect data over relatively large scales enabling synchronous data collection across a number of sites, and/or simultaneous spatial replication. This higher deployment and data collection rate is useful in some circumstances such as comparison among sites and the rapid assessment of crab species distribution (Figure Appx. D- 1). If cameras are deployed considering the advice in Chapter 3, additional information can be extracted from videos (e.g. Chapter 5). Once individual trajectories are calculated per individual crab, the collective behaviour of crabs can be studied. Social network analysis permit study of the nature of interactions between pairs of individuals (Figure Appx. D- 2A). Studying the frequency distribution of interacting crab pairs based on taxa, size, handedness or other traits, is useful to describe and understand the social patterns and structure on intertidal crabs (Figure Appx. D-2B). Taken together, the tools and analyses I propose present an exciting opportunity to describe unknown aspects of the ecology of intertidal crabs. By bridging the gap between the ecology of crabs and computer vision, and I have started to describe basic aspects of the crab life history. After the basic descriptive analysis and knowledge are generated by these methods, deeper and more complex questions are expected to arise. In the future, and given the composite nature of data and the vast amount of information produced, bridging the gap between ecology and big data analysis will be required.

Most ecologists intuitively understand the difference between a statistical population and sample. A population describe the entire group of interest, for instance, all individual from a species. While a sample refers to a subgroup of the population that was observed or measured, for instance, few individuals within a species. Routinely, we ecologists use samples to infer properties of a population (statistics). For instance, when collecting measurements on the morphometric from individuals within a species (statistical sample) to infer the morphometric of the species (statistical population). However, because of natural selection, genetic drift and gene flow, the variability of traits (alleles) and likely functional roles, in a population (ecological) or meta-population are under constant change (Futuyma 1998). Thus, random and non-random events, either selective or non-selective, change the frequency and distribution of traits. As ecosystem functioning is underpinned by the composition of species and their functional attributes and traits, it is paramount to study their variability and the forces that shape their distribution and alter their frequency. I join other scientists that stressed this idea (Tilman 1999; Duffy 2009; Lefcheck, Bastazini & Griffin 2015; Asner *et al.* 2017). I believe we, ecologists, must make a greater effort in understanding and measuring the variability of traits and functional attributes in the natural world. For this reason, a great emphasis in my research is to enable observation of traits at the individual level. In particular, traits and functional attributes related to the movement and transformation of matter and energy (ecosystem functions, sensu Odum 1962).

One could imagine that with the right technology ecologists could solely assess the distribution of traits and functional attributes from individual organisms inhabiting an ecosystem, without necessarily needing to recover their taxonomic identities (Figure Appx. D-3A). This type of information would provide a description of the functional makeup of the ecosystem. Arguably, if enough of these traits and functional attributes were measured in each individual, it would be possible to recover guild, taxonomic or phylogenetic groups because, over one individual trait/function or over sets of traits/functions within a group, variability will tend to be smaller than among group variability (Figure Appx. D- 3B, Chiarucci, Bacaro & Scheiner 2011). Furthermore, the trait and functional makeup of an ecosystem can be compare among locations or times (Figure Appx. D- 3C), making it possible to detect functional enhancement or deficiencies across space or time. Although simplistic, this outcome has been historically difficult to achieve because the complexity of assessing traits and functions at the individual level. I am proposing biodiversity should be measured as the distribution of traits and functional attributes within a given space and time. It might appear that in some systems or for some species this will not be possible, indeed until recently this was the case for intertidal crabs. Yet, data presented in Figure 3, represent the standardized variability of traits and functional attributes of 100 individual crabs modelled from empirical data. These data are presented here merely to illustrate how biodiversity of traits and functions can be used. I expect to continue to collect more information on crabs that provide additional support to this idea. By combining different methods of sampling, such as mark and recapture, tissue and chemical analysis, a more exhaustive description of traits and functional attributes can be achieved (Figure Appx. D- 4). Of course, I must mention that some or several of the organism's characters I have denominated traits and functional attributes could be biologically or ecological meaningless (Price & Schmitz 2016). Identifying these worthless characters would be by itself an interesting ecological endeavour. Certainly, a more enticing enterprise is to study how the distribution of traits and functional attributes change in space and time responding the natural and anthropogenic changes.



Australoplax tridentata

Based on 93 P/A samples and Inverse-distance Weighted kringing

Map CC-BY-SA; Author: César Herrera (@cexynature)

Metopograpsus thukuhar

Based on 93 P/A samples and Inverse-distance Weighted kringing

Map CC-BY-SA; Author: César Herrera (@cexynature)

Austruca perplexa

Based on 93 P/A samples and Inverse-distance Weighted kringing

Map CC-BY-SA; Author: César Herrera (@cexynature)

Tubuca coarctata

Based on 93 P/A samples and Inverse-distance Weighted kringing

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Figure Appx. D- 1: Example of advantage of using video surveys and computer vision to increase sampling effort and rapid assessment of crab species. Probability and distribution of occurrences for four crab species in Annandale wetland, Townsville, Queensland, Australia. Occurrence probability was calculated from detections in video surveys and visual census.

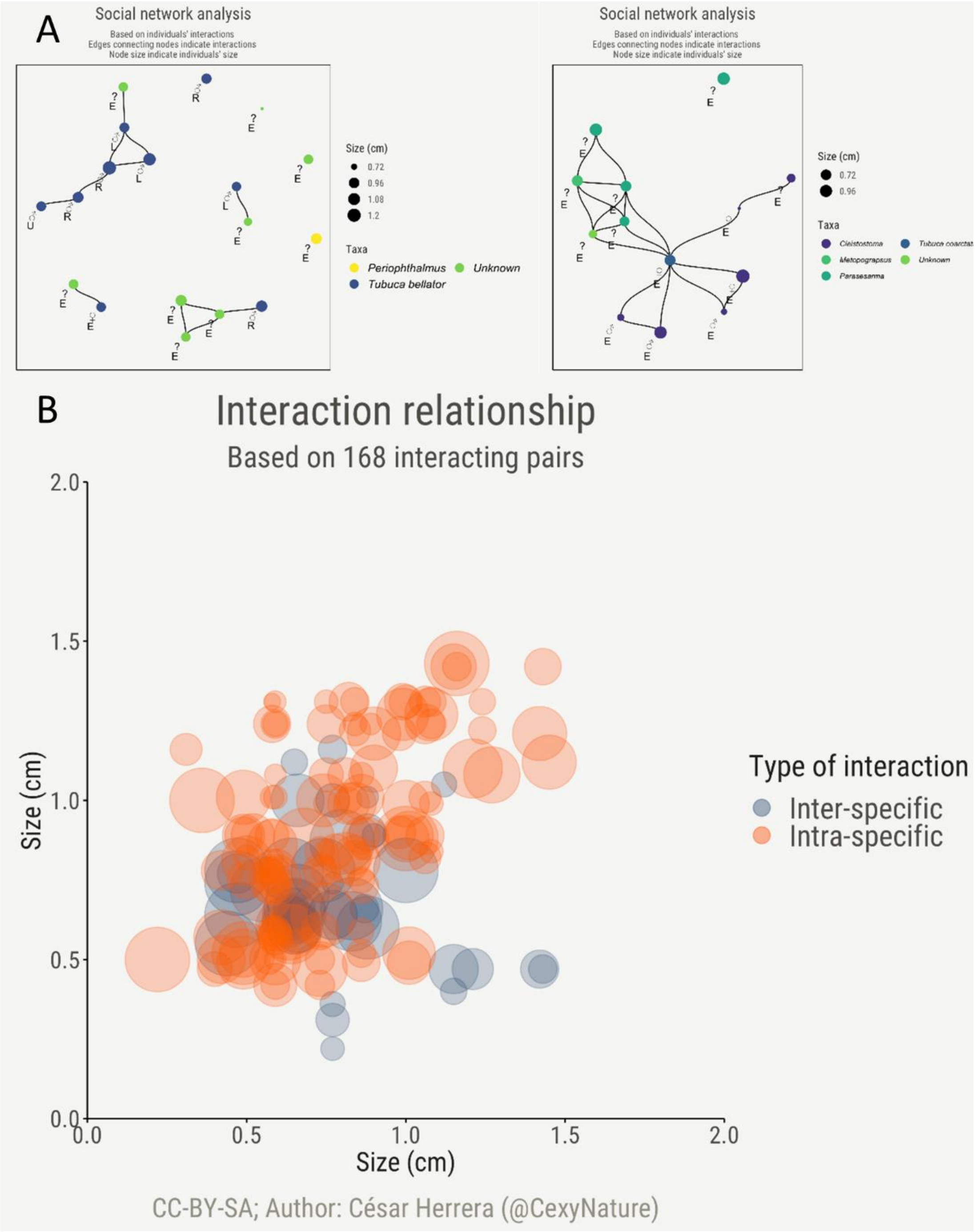

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Figure Appx. D- 2: Example of social networks analyses that are possible after obtaining individual crab movement trajectories. **A** Two social networks created from two video recordings showing crabs as nodes, and interactions among them as edges connecting nodes When available, size, chela handedness, sex and taxa for each crab is presented. **B** Allometric relationships of interacting pairs of crabs depending of type of interaction: intra- (orange) and inter-specific (blue).

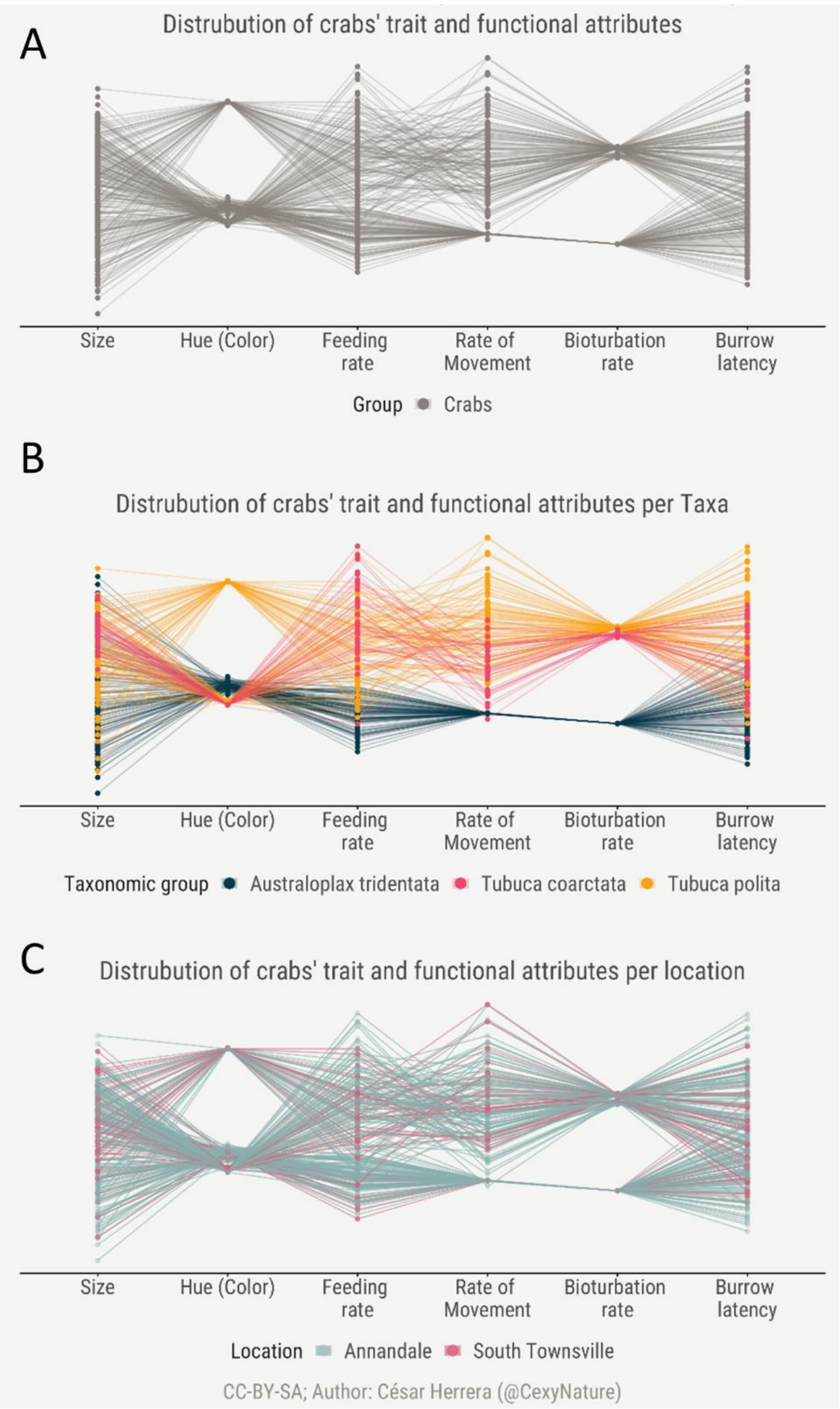

Figure Appx. D- 3: A new model for assessing and studying functional biodiversity. Parallel coordinate graphic with standardized scale showing variability in traits and functional attributes for one hundred individual crabs. Abscissa shows different traits and functional attributes in crabs, such as organisms' size, colour, rate of feeding, movement and bioturbation, and burrow latency. These traits and functional attributes, along with many others, can be obtained using Crabspy and other computer vision algorithms. Ordinate (axis not shown) displays standardized values for each trait/functional attribute and organisms. The assemblage and variability of traits and functional attributes is shown for all 100 individuals without taxonomic distinction (**A**), by taxa (**B**), and by location (**C**).

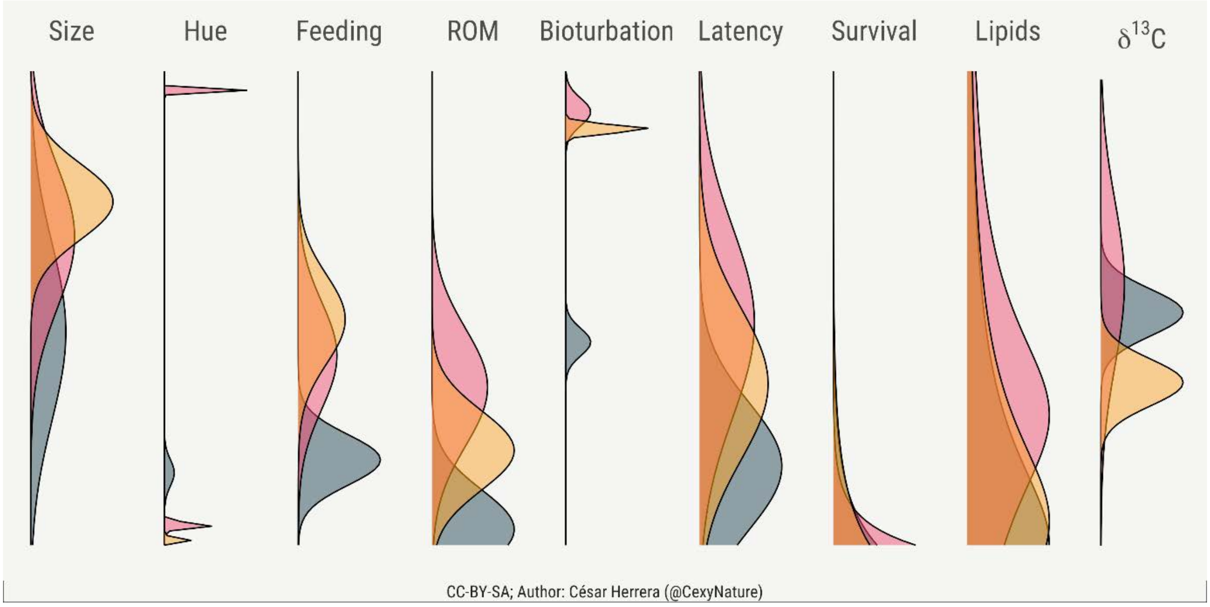

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Figure Appx. D- 4: Probability distribution of traits, functional attributes and other ecological and physiological characteristics for three distinct groups of organisms. Abscissa shows different metrics and ordinate (axis not shown) displays standardized values for each metric and group. Measurable traits, functional attributes, and eco- and physio-logical characteristics can be obtained from complementary sampling methods.