Assessing the effects of trampling and bait-collecting on population, morphological and reproductive metrics of a key ecosystem engineer in Langebaan Lagoon

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1. ABSTRACT

Coastal sedimentary habitats, like Langebaan Lagoon, provide vital ecological and economic services that many human livelihoods rely upon. However, they are vulnerable to multiple human-related disturbances such as intense bait collection and trampling, that compromise ecosystem resilience and functionality. Research on how human disturbance impacts keystone species, such as the endobenthic sandprawn *Kraussilichirus kraussi*, an important ecosystem engineer, has proven to be valuable and effective in monitoring ecosystem health and improving ecosystem management. Knowledge of how human disturbance impacts these sandprawns is however, limited as it is primarily focused on population-level metrics such as abundance and morphology. Therefore, this study aimed to advance our understanding of how human disturbance impacts sandprawn populations, their reproduction, and the potential implications for the essential services they provide, across a spatial putative human disturbance gradient in Zone A, Langebaan Lagoon. Moreover, I aim to determine whether the reproductive responses of sandprawns can serve as novel, ecological indicators of benthic stress in intertidal sedimentary systems. The results demonstrate that sandprawn reproductive responses effectively indicate ecological stress. Increased human numbers correlate with increased sediment compaction and reduced dissolved oxygen concentrations. As an indirect result of these changes, there were significantly high percentages of sandprawn embryos which displayed abnormalities and arrested development in these sites with increased human numbers. However, at a sandprawn population-level, increased human numbers had no significant difference in sandprawn catch per unit effort and sandprawns had better body conditions at these sites. These findings suggest resource trade-offs as a response to low sediment oxygen, in which sandprawns in highly disturbed sites shift resources from reproduction to prioritise self-maintenance and survival. Recent literature has shown a growing

interest in using keystone sandprawns as ecological stress indicators and this study further expands on this idea by linking human recreational disturbance to their reproductive biology of sandprawns. Adverse effects on sandprawn reproductive outputs are a cause of great concern, as chronic legacy effects of recreational disturbance may lead to population-level consequences, and thus compromise the vital ecological functions that these crustaceans provide. These effects are likely further exacerbated in intertidal systems with high frequencies of human disturbance and lack of management/regulation of human numbers. Overall, further research which links human disturbance to sandprawn reproduction in other coastal ecosystems is crucial to improving our understanding of this phenomenon and our future management of these systems.

2. INTRODUCTION

2.1 Coastal Ecosystems and Human Disturbance

Coastal biotopes are among the world's most ecologically significant habitats (Barbier et al., 2011; Mead et al., 2013; Nagelkerken et al., 2015). These environments are characterised by their high productivity and are biodiversity hotspots for both marine and terrestrial fauna (Crain et al., 2009; Mead et al., 2013; Nagelkerken et al., 2015). In addition, coastal biotopes facilitate vital trophic and nutrient transfers to offshore ecosystems (Heck et al., 2008; Sink et al., 2019a). As a result, a multitude of resident and migratory species rely upon these environments as crucial nursery and feeding grounds (Sink et al., 2019a). These habitats have enormous economic value, providing essential goods and services that many numerous human livelihoods and economies rely upon (Crain et al., 2009; Barbier et al., 2011). Such functions and services include the provision of water, food, raw resources, climate regulation, storm flood and erosion control, waste detoxification, recreational and cultural uses, and nutrient cycling (Crain et al., 2009).

The ease of access and proximity of coastal environments to human settlement make them some of the world's most degraded and threatened habitats (Lotze et al., 2006; Crain et al., 2009; Barbier et al., 2011; Mead et al., 2013). Such degradation arises from cumulative environmental and anthropogenic pressures placed on these systems (Harley et al., 2006; Mead et al., 2013). The intensity and frequency of these stressors often correlate with the extent of human presence and activity (Dale & Beyeler, 2001; Lotze et al., 2006). Anthropogenic stressors compromise ecosystem resilience, impair ecosystem multifunctionality, and diminish the quality and quantity of vital goods and services they provide (Dale & Beyeler, 2001; Lotze et al., 2006). Furthermore, the severity of these stressors is escalating, primarily driven by large-scale habitat transformation, the introduction of non-native species, nutrient enrichment, and intense resource harvesting, collectively contributing to the global deterioration of coastal systems (Harley et al., 2006; Lotze et al., 2006; Crain et al., 2009; Barbier et al., 2011).

At a global scale, nearly half (43%) of coastal habitats are estimated to be affected by multiple anthropogenic pressures, with sedimentary ecosystems being particularly susceptible to ecosystem degradation (Lotze et al., 2006; Halpern et al., 2008). Sedimentary ecosystems frequently experience direct and indirect human disturbance due to their increasing popularity for recreational activities (Lotze et al., 2006). Within these soft sediment habitats, human disturbance associated with recreational activity can significantly alter sediment biogeochemistry and granulometric structure, ultimately impacting entire benthic assemblages (Wynberg & Branch, 1994; Wynberg & Branch, 1997; Contessa & Bird, 2004). As a result, recreational disturbance has gained recognition as a major influence in structuring marine soft sediment communities, prompting further research on this process (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Contessa & Bird, 2004; Nel & Branch, 2013; Nel & Branch, 2014; Gül & Griffen, 2020; Chumsri et al., 2023). However, understanding the ecological consequences of recreational disturbance is complicated by the highly dynamic and heterogeneous nature of coastal sedimentary systems, which poses challenges for study designs, data collection, and hypothesis testing, principally regarding establishing control conditions in which disturbance is absent but under similar abiotic contexts (Schenone & Thrush, 2022).

Bait collection and trampling are the primary forms of recreational disturbances that occur in coastal sedimentary ecosystems (Wynberg & Branch, 1997). Bait collection causes physical damage to benthic organisms, which can impact entire benthic communities upon their removal (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Contessa & Bird, 2004). Moreover, trampling compacts the sediment, indirectly altering sediment biogeochemistry, associated benthic community composition, and organismal distribution and densities (Wynberg & Branch, 1997). For example, trampling has been reported to decrease porosity in sediment and substantially decrease sediment oxygen levels (Skilleter et al., 2005). The latter, in turn, adversely affects benthic community structure, complexity, and diversity (Rosenberg et al., 2001). Bait collection and trampling have been argued to be equally impactful and can have important consequences for the benthos (Wynberg & Branch, 1997).

2.2 *Kraussillichirus kraussi*: The Ecosystem Engineer

The consequences of recreational bait collecting and sediment trampling can have severe consequences for ecosystem processes and keystone species functions are impacted. *Kraussillichirus kraussi,* commonly known as the sandprawn is a keystone engineer (Jones et al. 1994) that has been impacted by recreational disturbance associated with bait collecting and trampling (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997). These crustaceans, formally classified as thalassinidean shrimp, are among the most influential organisms in marine soft-sediment habitats (Pillay & Branch, 2011; Poore et al. 2014). Sandprawns are recognised as ecosystem engineers due to the significant alterations of their surrounding environment they induce through highly complex non-trophic and trophic interactions (Wynberg & Branch, 1991; Siebert & Branch 2007; Pillay & Branch, 2011). Endobenthic sandprawns construct burrows that create micro-niches, providing refuge from predation and shelter from extreme environmental changes such as tidal mixing (Pillay, 2010; Pillay & Branch, 2011; Pillay et al., 2012). Additionally, these ecosystem engineers regulate resource flows to other coexisting species via bioturbation (Jones et al., 1994; Pillay et al., 2012).

Figure 1. *Dorsal view of the female sandprawn* <u>*Kraussillichirus kraussi*</u> *(5.5cm) in Langebaan Lagoon.*

Bioturbation is the process of sediment reworking, leading to subsequent alterations in the physical state and biogeochemistry of sediment (Ziebis et al. 1996; Bertics et al. 2010; Pillay & Branch, 2011). Bioturbating organisms, such as sandprawns, can also bioirrigate, a process in which burrows are actively flushed with overlying water (Bouma et al., 2009; Pillay & Branch, 2011; Venter et al., 2020). These activities have a significant impact on interactions among co-existing species and resource availability (Wilson, 1991; Volkenborn et al., 2008; Bouma et al., 2009). Furthermore, sandprawn bioturbation activities increase sediment oxygenation, porosity, granulometry, and erodibility (Wynberg & Branch, 1997; Contessa & Bird, 2004). This sediment mixing increases sediment biochemical heterogeneity, impacting the distribution and densities of other benthic species (Pillay et al., 2008; Pillay, 2010). For example, a study in the Japanese Ariake Sound System observed that an increase in *Neotrypaea harmandi* densities (formally known as *Nihonotrypaea harmandi*) coincided with the extinction of the coexisting grazing gastropod *Umbonium moniliferum* (Tamaki, 1994). Additionally, an experimental study conducted by Pillay et al. (2012) demonstrated that sandprawn exclusion led to improved biomass, physiological condition, and size of *Liza richardsonii*, a local co-existing fish species.

Axiidean crustaceans (deposit-feeders from the former Thalassinidea) are globally distributed; with majority of southern hemisphere research occuring in South America, Africa and Australia (Pillay & Branch, 2011). These studies have contributed greatly to the overall understanding of endobenthic crustaceans; however, there is a lack of studies specifically, focusing on sandprawns (Pillay & Branch, 2011). Despite recognition of the crucial roles sandprawns play in marine sedimentary habitats, there is a limited understanding of how human disturbance impacts these organisms. Table 1 summarises research focusing on the effects of how human recreational disturbance, such as bait collection and trampling, impact endobenthic crustaceans. What is evident from Table 1 is that research on human disturbance impacts on these organisms has focused predominantly on population-level metrics such as abundances and morphological changes, with little attention given to reproduction (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Nel & Branch, 2013; Nel & Branch, 2014).

Table 1. *Review of studies that have investigated the effect of bait collection and trampling on axiidean populations.*

Reference	Axiidean	Methodology	Location	Outcome
Wynberg & Branch (1991)	*Kraussillichirus kraussi*	Experimental	South Africa	Intense bait collected areas exhibited decreased population density and modal body sizes in comparison to areas unexploited areas
Wynberg & Branch (1994)	*Kraussillichirus kraussi*	Experimental	South Africa	Bait collected sites displayed decreased prawn population density and increased recovery time post-disturbance (up to 18 months)
Wynberg & Branch (1997)	*Kraussillichirus kraussi*	Experimental	South Africa	Sites exploited by bait collection and trampling exhibited decreased population density. Recognised that trampling has an equal impact on sandprawn populations as their removal
Souza & Borzone (2003)	*Callichirus corruptus*	Comparative	Brazil	Areas of bait collection by a local fishery were assessed before and after intense extraction exhibited decreased population density and body sizes of shrimp
Contessa & Bird (2004)	*Trypaea australiensis*	Experimental	Australia	Decreased population density with trampling resulting in the greatest mortality
Skilleter et al. (2005)	*Trypaea australiensis*	Experimental	Australia	Decreased shrimp patchiness; however, no impact on population densities and body sizes
Nel & Branch (2014)	*Kraussillichirus kraussi*	Comparative	South Africa	Estimated that at least 0.12% of sandprawn stock in Langebaan Lagoon is annually removed; population stock appears to be sustainably harvested
Moschetto, et al. (2020)	*Callichirus corruptus*	Comparative	Brazil	Decreased population density and modal body sizes
Costa et al. (2020)	*Callichirus corruptus*	Comparative	Brazil	Decreased body sizes, fecundity, and percentage of ovigerous females
Kalberg-Normark et al. (2022)	*Kraussillichirus kraussi*	Comparative	South Africa	Sandprawn isotope niche sizes showed variation; however, this did not relate to the putative human disturbance gradient. Better body conditions were reported at highly disturbed sites, which suggests a diverse feeding strategy is beneficial
Hernáez et al. (2019)	*Callichirus corruptus*	Comparative	Brazil	Reduced burrow density and female carapace length size in disturbed sites. Additionally, more disturbed sites had a reduced number of females present than less disturbed sites.

2.3 Reproduction

Reproduction is the process by which new individuals in a population are formed from the parent stock (Richmond et al., 2018). The production and survival of high-quality individuals capable of successful recruitment are essential for population sustainability (Richmond et al., 2018; Manlik, 2019). This highly complex process includes biological signals, hormonal and behavioural factors, and morphogenesis (Jackson, 1985; Strasser & Felder 1998).

Reproductive success is greatly influenced by environmental conditions that affect populations and their ecosystems (Hernáez et al. 2008; Hernáez et al. 2012; Peiró et al., 2014; Manlik, 2019). These environmental conditions include resource availability, resource quality, biotic and enemy pressures, and space (Cothran & Jeyasingh, 2010; Merkling et al., 2017). Within this framework, it is plausible for human disturbances to exacerbate environmentally stressed organisms and induce challenging resource trade-offs (Harley et al., 2006; Mead et al., 2013; Kelly et al., 2016; Merkling et al., 2017). Under stressful conditions, organisms may adapt their physiological and behavioural processes to prioritise survival and self-maintenance at the expense of reproduction (Cote et al., 2006; Kelly et al., 2016; Merkling et al., 2017).

2.3.1 Sexual Dimorphism and Embryonic Development

Changes to reproductive traits and processes, such as sexual dimorphism and embryonic development, can have a significant impact on reproductive success and juvenile performance (Jackson, 1985; Correa & Thiel 2003; Shimoda et al., 2004). Sexual dimorphism refers to the condition in which sexes of the same species display differing morphological characteristics aside from those directly involved in gamete exchange and production (Raven et al., 2017; Hodgson, 2018). Sexual dimorphism is primarily driven by sexual selection, as originally proposed by Darwin (1859). According to this theory, one sex of a species may undergo modifications in response to competition among males seeking access to females for reproduction (Darwin, 1859; Cuervo & Moller, 1999; Allen & Levinton, 2007). Interactions between and within sexes, including mate searching, combat, and courtship displays, result in the evolution of structures that persuade potential mating partners and therefore increase an individual's reproductive success (Shimoda et al., 2004; Raven et al., 2017). These secondary sexual traits serve as signals of individual quality to potential opponents or picky partners (Allen & Levinton, 2007). Additionally, larger body sizes in males of numerous species have evolved because they provide advantages in male-male combat and access to potential mates (Shine, 1989). However, it should be noted that it is not always the case as reported by Baeza and Asorey (2012) for porcelian crabs.

Many endobenthic crustaceans, including sandprawns, exhibit sexual dimorphism in their chelipeds (Mariappan et al., 2000; Shimoda et al., 2004; Hernáez 2018; Hernáez et al., 2018; Rio et al., 2019). These specialised appendages, often referred to as 'weapons', serve multiple purposes, including aggressive and courtship displays (Mariappan et al., 2000). The sexual dimorphism in chelipeds is characterised by the presence of heterochelous chelipeds, where the major chela is significantly larger (major) and more robust than the minor (Shimoda et al., 2004; Hernáez 2018). This dimorphism is believed to have evolved through sexual selection, with males engaging in antagonistic interactions such as male-male combat and courtship displays to gain access to females (Mariappan et al., 2000; Shimoda et al., 2004; Yoshino et al., 2011). As a result, males typically possess disproportionately larger major chelipeds compared to females (Yoshino et al., 2011).

In addition to sexual dimorphism, embryogenesis greatly impacts an organism's reproductive success (Sundelin & Eriksson, 1998). This process is a critical, highly sensitive stage in the biological life cycle and is essential for population resilience and persistence (Jackson, 1985; Sundelin & Eriksson, 1998; Jackson et al., 2005; Richmond et al., 2018). To contextualise the importance of embryonic development, Birge et al. (1980) proposed that even a 10% reduction in embryo survivorship could have substantial ramifications for population dynamics and severely compromise population success. Due to eggs and embryos being hypersensitive, unfavourable shifts in environmental conditions or exposure to stressors during specific developmental stages may result in embryo malformations, aberrations, and atypical phenotypes, as seen in studies by Jackson (1985), Sundelin & Eriksson (1998), and Karlson et al. (2018).

While sexual dimorphism and embryo development in endobenthic sandprawns have been documented in previous studies (Forbes, 1973; Forbes, 1976; Hodgson, 2018), there is a noticeable gap in our understanding of how human recreational disturbance affects these reproductive components of sandprawns. Existing research has shown that human disturbance can have adverse effects on the claw morphological variability of some crustaceans, as observed in the ghost crab *Ocypode quadrata* (Gül & Griffen, 2020). However, to my knowledge, there is a lack of equivalent research on the reproductive components of endobenthic sandprawns.

Most research on the impact of stressors on marine invertebrate embryos has largely focused on survival and growth rates as indicators of ecological stress (Sundelin & Eriksson, 1998). However, Sheehan (1984) suggested that monitoring the frequency of malformed larvae and embryos in highly disturbed marine ecosystems may prove to be more effective. Sundelin &

Eriksson (1998) agreed, adding that investigating the frequency of malformed embryos across a disturbance gradient would be highly insightful in estimating the severity of human-induced stress. Currently, research by Jackson (1985) and Jackson et al. (2005) remains the only studies that demonstrate how human-induced stress impacts sandprawn embryonic development. The Jackson (1985) experimental study showed that sandprawn eggs and larvae exposed to large quantities of Qatar crude oil had increased embryonic malformations, interrupted development, and high percentages of mortality (Jackson, 1985). In the Jackson et al. (2005) study, sandprawn embryos exposed to heavy trace metal levels exhibited significant reductions in brood development and increased embryo mortality.

The production and maintenance of sexually selected traits, as well as embryonic development, impose substantial resource and energic demands on adults (Shimoda et al., 2004; Cothran & Jeyasingh, 2010; Yoshino et al., 2011; Kelly et al., 2016; Merkling et al., 2017). Sexually selected traits exhibit high phenotypic variation and require great resource trade-offs essential for reproductive success (Cothran & Jeyasingh, 2010). Unlike facultative traits that are expressed occasionally, sexually selected traits are permanent morphological structures with continuous resource requirements over the lifespan of organisms (Allen & Levinton, 2007). Male sexually selected traits, such as the major chelae of crustaceans, incur substantial production and maintenance costs and are thus often referred to as resource sinks (Shimoda et al., 2004; Cothran & Jeyasingh, 2010; Yoshino et al., 2011). Similarly, the production and development of embryos demand considerable resources and energy, leading many sexually reproducing species to prioritise reproduction (Kelly et al., 2016; Merkling et al., 2017). However, resource trade-offs in stressed ecosystems can become constraining, hindering an organism’s ability to simultaneously prioritise multiple functions (Mariappan et al., 2000; Kelly et al., 2016). Therefore, under stressful conditions, many organisms prioritise survival and self-maintenance at the expense of reproduction (Mariappan et al., 2000; Kelly et al., 2016). Sexual dimorphism has the potential to serve as an effective ecological indicator of stress, as these secondary traits are highly sensitive to environmental perturbations (Shine, 1989; Leung et al., 2000; Cothran & Jeyasingh, 2010). Additionally, the use of embryonic quality and development as sensitive indicators of ecological stress is well documented and has proven to be highly insightful (Sundelin & Eriksson, 1998; Oh & Hartnoll, 1999; O'Brien et al., 2017; Karlson et al., 2018). For example, the embryonic responses of the amphipod *Monopereria affinis* (Baltic Sea) have received significant attention as an ecological indicator (Sundelin & Eriksson, 1998; Reutgard & Furuhagen, 2016; Karlson et al., 2018; Luo et al., 2019). Prior research demonstrated that *M. Affinis* embryos located near industrial discharges displayed a higher frequency of malformations and aberrations or were deceased compared to those located further away from the discharges (Sundelin & Eriksson, 1998; Karlson et al., 2018). Similar embryonic responses were observed in a study by Karlson et al. (2018), where copepod body mass, fecundity, and viable embryo percentage in broods were all reduced in females exposed to stress.

2.4 Ecosystem Management

Given the ecological and economic importance of coastal habitats globally, there is substantial interest in understanding the consequences of anthropogenic activities on these environments (Harley et al., 2006). Local and international government initiatives have invested considerably in identifying and implementing measures to mitigate human pressures and address the ongoing loss of marine biodiversity and resources (Crain et al., 2009). Unfortunately, sedimentary habitats often lack the aesthetic appeal of other coastal marine habitats such as coral reefs and kelp forests, leading to comparatively little conservation attention and effort (Lotze et al., 2006). Moreover, advocating for marine conservation can be challenging in developing countries, where addressing basic human needs takes precedence over ecological conservation (Lotze et al., 2006). South Africa's rich and diverse marine ecosystems have been recognised to play a crucial role in supporting human livelihoods, improving food security, increasing tourism, and providing medical resources (Sink et al., 2019b). However, damaging activities such as poor agricultural practises, large-scale habitat transformation and urbanisation, and nesting within the context of growing human populations have posed significant challenges that impact the dynamics of coastal areas (Sink et al., 2019b). Nevertheless, management authorities of coastal sedimentary habitats must remain vigilant to emerging stressors, including increasing recreational disturbances, and their potential impact on key ecological processes.

The use of biological organisms as ecological indicators to detect, signal, and mitigate ecosystem degradation has become increasingly popular (Dale & Beyeler, 2001; Teixeira, 2010; Venter et al., 2020). One major reason for this trend is the sustainability of using biological organisms for nature-based solutions, bioremediation, and/or biomanipulation (Teixeira, 2010; Venter et al., 2020). Ecological indicators play a vital role in assessing environmental conditions and can provide early warning signals of ecosystem degradation (Dale & Beyeler, 2001). Effective ecological indicators should account for the complexity of the ecological system, be easily measured and monitored, exhibit a predictable response to stressors, and demonstrate low variability in their responses (Dale & Beyeler, 2001).

2.5 Problem Statement

Endobenthic sandprawns, ubiquitous in soft sedimentary habitats in Southern Africa, exert a significant influence on their surrounding benthic environment (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997). These crustaceans are resilient and have a wide distribution along the coast, implying that these organisms may be valuable and effective ecological indicators of stress, including that arising from recreational disturbance. Existing research primarily focuses on how recreational disturbance impacts sandprawn abundance and morphology; however, there is a large knowledge gap regarding potential effects on arguably one of the most crucial biological processes, their reproduction (Jackson, 1985; Abrunhosa et al., 2008; Peiró et al., 2014). The utilisation of *K. kraussi* as an ecological tool for detecting human disturbance in coastal ecosystems has only recently gained interest in the literature (Kallberg-Normark et al., 2022). Therefore, furthering our understanding of how human disturbance may impact the reproductive components of sandprawns, may be crucial for assessing the long-term ecological consequences of recreational human disturbance on this species, their essential services, and its associated ecosystems. Moreover, recognising the importance and sensitivity of sexual dimorphism and embryonic quality and development in organismal reproductive success when applied to sandprawns, highlights these components as promising ecological indicators of recreational disturbance effects.

2.6 Project Objectives

This study contributes to advancing our understanding of how human recreational disturbance affects the population, morphological, and reproductive biology of *K. kraussi*, a key ecosystem engineer, across a spatial gradient of human disturbance in Langebaan Lagoon, South Africa. Specifically, this study aims to determine whether sandprawn reproductive responses can serve as novel ecological indicators of benthic stress in intertidal sedimentary systems. To achieve this goal, sandprawn sexual dimorphism variability between males and females, as well as their embryonic quality and development, was assessed across a putative gradient of human disturbance. Simultaneously, sandprawn abundance (as catch per unit; CPUE) and physical body condition was measured.

2.7 Hypothesis

I hypothesise that increased human numbers and associated trampling will result in sediment compaction, subsequently reducing sediment oxygenation. These changes in sediment biogeochemistry are expected to adversely affect sandprawn reproductive responses, resulting in reduced sexual dimorphism variability between male and female sandprawns, as well as increased embryonic malformations and arrested development. Such changes are expected due to compaction incurring energetic costs to burrowing and low oxygen and increased hydrogen sulphide levels physiologically stressing embryos. Furthermore, changes in sediment biogeochemistry due to increased human numbers as well as direct harvesting are expected to reduce sandprawn population sizes and lead to a reduction in their body conditions. These hypotheses are illustrated in Figure 2.

2.8 Project Significance

Understanding the impact of human recreational disturbance on sandprawn reproductive biology provides valuable insights that extend beyond the specific context of Langebaan Lagoon. The insights gained from this study have the potential to significantly contribute to the conservation and management of coastal sedimentary ecosystems and inform policies related to human recreational activities in these areas. This knowledge is particularly relevant for urban sedimentary ecosystems lacking managed or regulated human presence, as implications are likely magnified in the absence of human disturbance management. If human disturbance is found to adversely affect sandprawn reproductive success, it underscores the importance of considering sandprawns as novel and effective bioindicators of benthic intertidal stress.

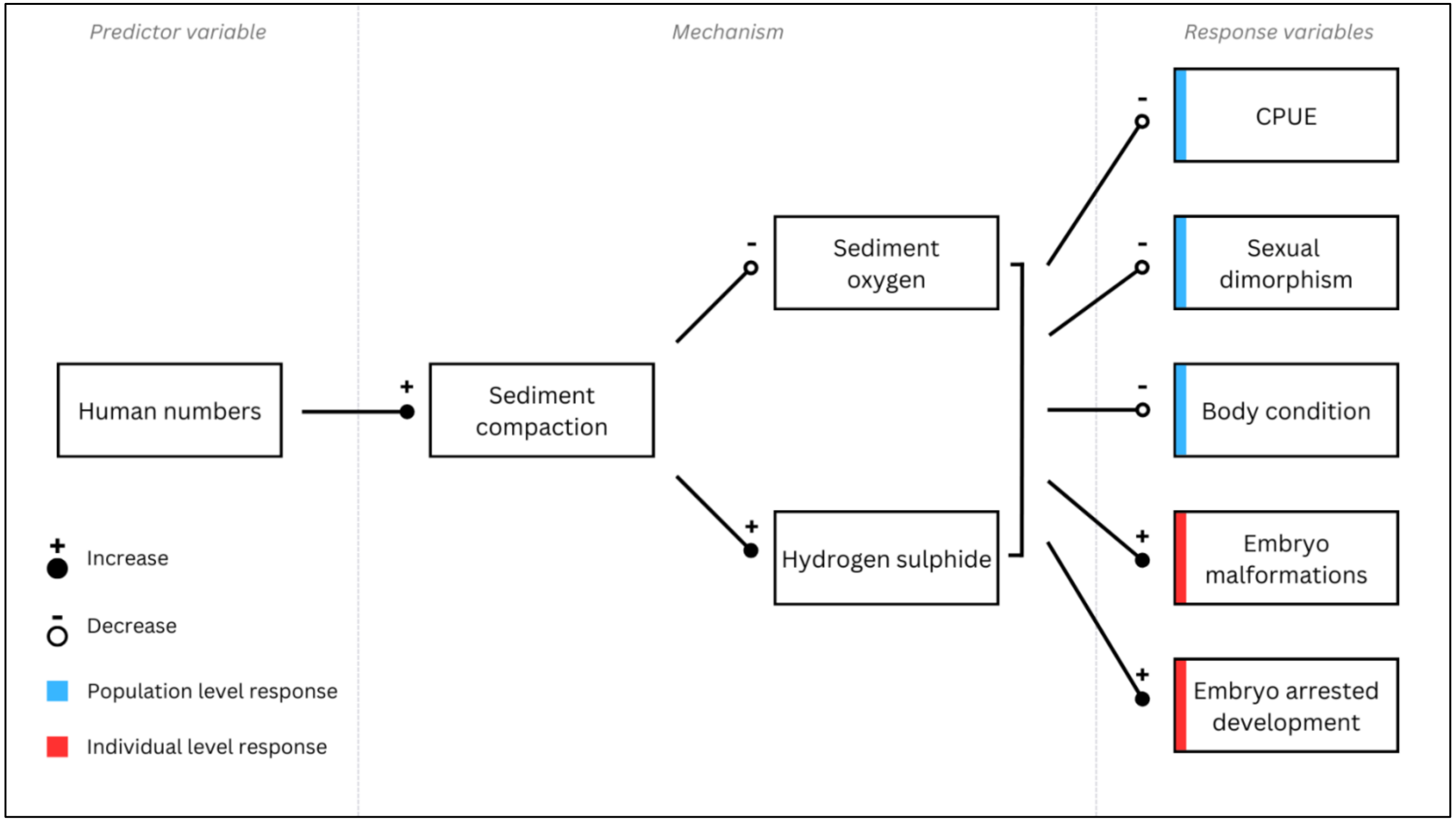

Figure 2. Diagrammatic overview of the hypothesis tested in this study. Increasing human numbers is expected to result in increased sediment compaction, decreased oxygenation and increased hydrogen sulphide. These effects were hypothesized to increase the frequency of sandprawn embryo malformations and arrested development, while causing declines in body condition and sexual dimorphism. These effects along with direct harvesting were also hypothesised to decrease sandprawn CPUE.

3. METHODOLOGY

3.1 Ethical Clearance and Sampling Permits

This study's methodology was approved by the University of Cape Town (UCT) Science Faculty Animal Ethics Committee (SFAEC; 2022/V5/DP). Additionally, a permit to collect sandprawns and other benthic samples from Langebaan Lagoon was approved by South African National Parks (SANParks; CRC/2022-2023/008—2022/V1).

3.2 Study Area

Langebaan Lagoon (33°10'S, 18°05'E) is a permanently open, marine-dominated embayment (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Kallberg-Normark et al., 2022). It is located on the west coast of South Africa and supports highly diverse marine and estuarine assemblages (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997). The lagoon is located within the West Coast National Park and is approximately 15 km long and 4 km wide (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997). This system is a priority conservation area and the common sandprawn, *Kraussillichirus kraussi,* alongside another endobenthic crustacean, *Upogebia africana* accounts for approximately 48% of the total benthic biomass of the lagoon (Christie & Moldan, 1977; Wynberg & Branch, 1994). In 1973, the Sea Fisheries Act 58 resulted in the division of Langebaan Lagoon into three distinct zones (Wynberg & Branch, 1991). These spatially exclusive zones permit contrasting levels of human presence and activities as shown in Figure 3. The northernmost zone (Zone A) is a multipurpose recreational area that permits human presence and bait collection from the benthos (Wynberg & Branch, 1991). Bait harvesting is typically carried out with hand-operated suction pumps, and targets organisms such as sandprawns, mudprawns, polychaetes and amphipods (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Kallberg-Normark et al., 2022). Zone B permits limited human presence and recreational activities; however, bait collecting is prohibited (Wynberg & Branch, 1991). Zone C is a sanctuary and does not permit human presence, activities, or bait collection (Wynberg & Branch, 1991). The lagoon does not receive riverine inputs and the salinity and temperature variability are low, especially in the intertidal (Shannon & Stander 1977). Since the three distinct zones have different degrees of human presence, there is a putative human disturbance gradient in the lagoon, with Zone A experiencing the greatest degree of human disturbance and Zone C the least. In this study, Zone A was the focal area, since sampling of Zones B and C was not permitted by park management. Additionally, sandprawns are gravimetrically dominant in Zone A (likely due to the sandy sediment), and the main benthic organism collected as bait. Although the sampling was been restricted to Zone A, this did minimise spatial co-variance associated with sampling at larger scales. For example, sediment particle size has been noted to change across zones in the lagoon, which can greatly influence sandprawn populations and potentially confound the interpretation of recreational effects. (Nel & Branch 2013).

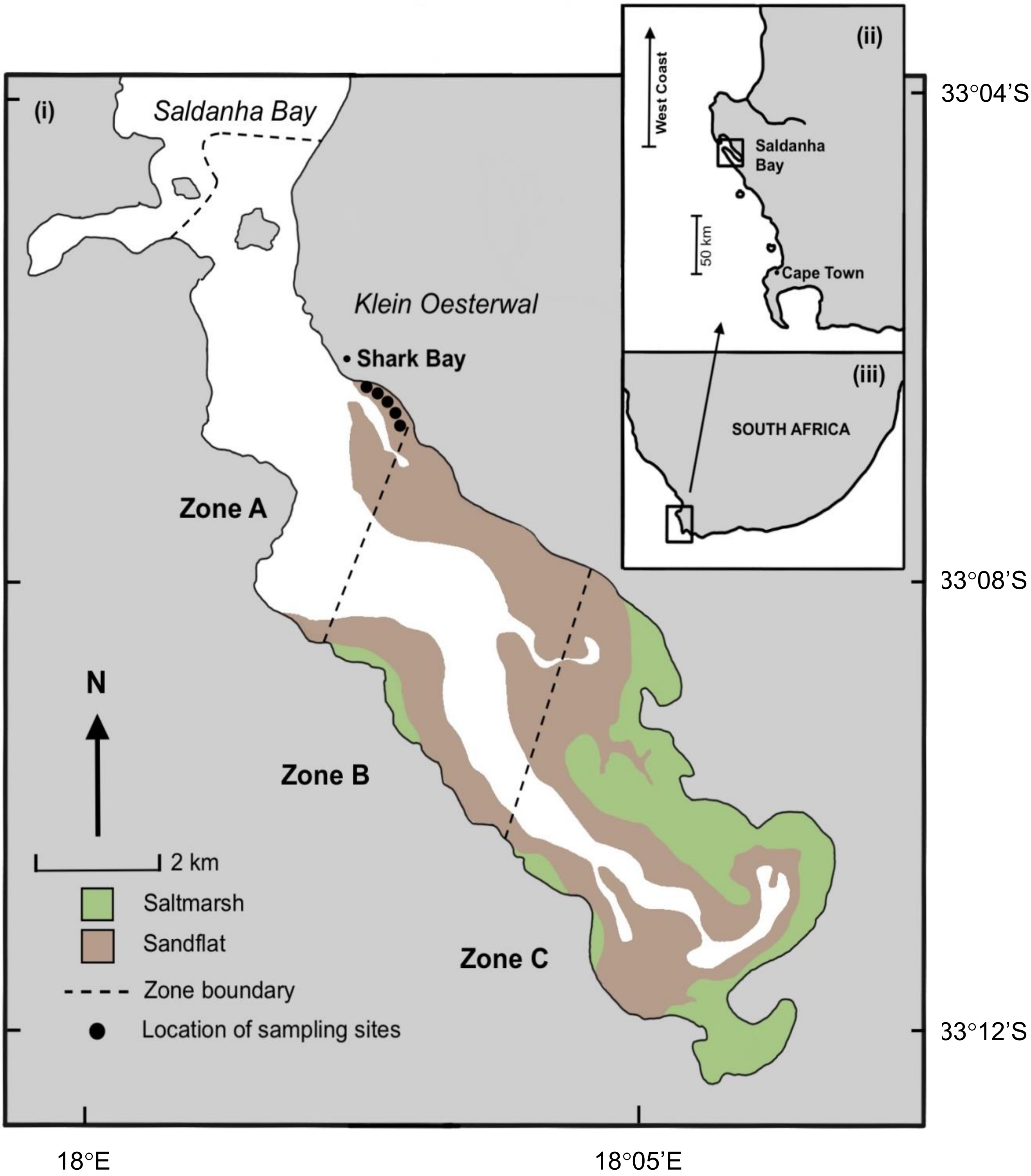

Figure 3. *Map of Langebaan Lagoon (i) located near Saldanha Bay (ii), on the west coast of South Africa (iii). The red circles denote the five sampling sites which are located near the start of Shark Bay, within Zone A, Klein Oesterwal, Langebaan Lagoon. All sampling sites were intertidal.*

3.3 Sampling Procedure

Sampling was undertaken in winter (July/August 2022) and summer (January 2023) within Zone A in Klein Oesterwal (Figure 3). This study focused on the putative human disturbance gradient in only Zone A as, at a larger scale, the environment may become heterogeneous. The likelihood of abiotic variance confounding the effect of human disturbance on the lagoon increases with the increase of sample area. Additionally, there are logistical constraints with sampling a larger area such as resources and time. Therefore, five intertidal sites were sampled starting from Shark Bay (Site 1) and extending 1 km parallel to the shoreline, approximately 950 m from the end of Zone A (Site 5; Figure 3). Each site was approximately 200 m apart and was divided into subsites (20 m apart), from which replicate samples were collected. Sample collection occurred at the start of low spring tide (benthic microalgae, sediment particle size and organic matter content, redox conditions) and progressed over incoming tide (all sandprawn data) towards high tide (water parameters and phytoplankton).

3.4 Environmental Variables

3.4.1 Benthic Microalgae

During low tide, microphytobenthic algal biomass (green algae, cyanobacteria, and diatoms) was measured with a BenthoTorch (BBE Moldaenke) at 10 subsites per site. This rapid, portable device is capable of measuring benthic microalgae biomass in situ (Harris & Graham, 2015). More specifically, the BenthoTorch measures the fluorescence of photosynthetic pigments of microalgal cells by casting light onto a substratum and thereafter measuring the amount of light that is reflected or absorbed to calculate algal concentrations (Harris & Graham, 2015). Stagnant water patches and newly turned-over sediment as a result of bait collecting were avoided during data collection. Measurements were made between sandprawn mounds for consistency. Microalgal biomass data provides essential information on benthic productivity across the 5 sampling sites.

3.4.2 Sediment Particle Size and Organic Matter Content

Three sediment cores (diameter = 2 cm, depth = 1 cm) were randomly collected from three of the ten subsites per site for organic matter content and sediment particle size analysis (n = 3 per variable per site per season). These cores were placed in 30 ml glass polytop vials and stored in the laboratory refrigerator at -20°C. For particle size analysis, sediment cores were oven-dried at 100°C for 48 hours. Once cooled, a Malvern Mastersizer 2000 SM Auto-analyser was utilised to obtain sediment granulometric data. The Auto-analyser quantified the number of sediment particles within the range of 0.02-2000 µm (Wang et al., 2021). The remaining sediment cores were subjected to organic material analysis following the methodology of Contessa and Bird (2004). This involved oven drying the sediment cores at 100°C for 48 hours, followed by the samples being weighed (A&D GR-202 balance; precision: 0.00000g). Thereafter, samples were combusted in a muffle furnace at 600°C for 3 hours, cooled and weighed again. Organic matter content was computed as the change in mass between pre- and post-combusted sediment and expressed as a percentage of the total sediment weight (dry mass) (Contessa & Bird, 2004).

3.4.3 Redox Conditions

Due to funding and equipment limitations, sediment redox potential could not be measured directly. Rather, sediment colour was used as a proxy for sediment redox conditions. Surface sediment cores (diameter = 3.2 cm, depth = 19 cm) were collected at three subsites per site per season using a clear Perspex corer. Each extracted core while in the Perspex corer was photographed (iPhone 13 mini; 2340 x 1080 pixel resolution) and thereafter analysed using image processing software GNU Image Manipulation Program (GIMP; The GIMP Development Team, 2023). The path tool in GIMP was utilised to crop sediment cores from images followed by the application of auto-colour correction. Pixels were set on a grayscale range from 0 (black) to 255 (white) and grayscale pixel value frequency was recorded. Thereafter, pixel frequency histograms with a bin width of 5 pixels were created from which modal peaks per histogram were determined. The mean, median, and standard deviation for pixels of each histogram were calculated by GIMP.

3.4.4 Water Parameters and Phytoplankton

At high tide, water temperature, dissolved oxygen concentration, pH and salinity were measured at three subsites per site using a CTD profiler (Conductivity temperature and depth; YSI 6600 multi-parameter probe). Phytoplankton biomass (as chlorophyll-*a*; a proxy for pelagic trophic resource availability) was determined from 1 water sample per site, collected in black 100 ml bottles. Samples were stored in a cooler box, and transported to the laboratory, where chl-*a* biomass (µg/l) was measured fluorometrically (Turner Designs Trilogy fluorometer).

3.4.5 Human Numbers

Human numbers per site were determined following the scan-sampling method (Gilby et al., 2010). This involved the number of people present per site being counted at 30-minute intervals for approximately 6 hours (from low tide) for two days. Human counts were averaged across days and 30-minute intervals to obtain values per site per season.

3.5 Sandprawn Data

3.5.1 Catch Per Unit Effort

Sandprawn catch per unit effort (CPUE) was estimated during the incoming tide (50 cm water depth), from ten sediment cores collected from 5 subsites per site (n = 50 pumps per site per season). Cores were collected using standard prawn pumps (total length = 90 cm; diameter = 5 cm) in areas devoid of obvious signs of recent sediment disturbance caused by bait collecting and sieved (30 cm x 30 cm x 30 cm box sieve; mesh size = 2 mm). Retained sandprawns were measured (carapace length; CL) with a vernier calliper; individuals with a CL < 5 mm were classified as juveniles while the rest were classed as adults; and sexed via the examination of the first pleopods (swimmerets). These appendages are reduced, short and stout in males and more elongated and slender in females (Barnard, 1950). After the number of juveniles, males and females were recorded, they were released back into the environment.

3.5.2 Sandprawn Sexual Dimorphism

For sexual dimorphism analysis, sandprawns were collected as described in 1.4.1 but with minor modifications. Sediment cores were collected randomly from the start of a site towards its end. After sieving, sandprawns with a CL greater than 6.5 mm were selected, as below this size, sexual dimorphism is not evident due to individuals being sexually immature (Hodgson, 2018). Sandprawns were placed in jars on ice (to slow metabolism before preservation) in a cooler box for 20 min followed by males being placed within labelled plastic jars containing 70% ethanol (per site). Females were individually stored in 15 ml polytop jars containing 70% ethanol to ensure that all eggs or embryos were preserved with the corresponding female. Juvenile sandprawns and other benthic organisms caught within the box sieve during sampling were released. In the laboratory, sandprawn CL, and the total length of major chela (MCL) were measured with a digital calliper (0.1 mm, Mitutoyo 500 Absolute Digimatic Calliper). The total length of the major chela was determined by laterally flattening the appendage and measuring from the start of the merus to the tip of the dactyl (See Appendix Figure A 1).

3.5.3 Sandprawn Egg and Embryo Analysis

Eggs and embryos were quantitatively and qualitatively analysed using a stereomicroscope (Nikon SMZ800N). With the use of forceps, sandprawns were removed from their vials and placed in petri dishes. Thereafter, all eggs and embryos were carefully removed from the sandprawns abdomen and placed in separate petri dishes using forceps and pipettes (3 ml) to prevent damage to the eggs. Any eggs that fell off females that were found within the vials were picked and added to their respective petri dishes. Fecundity was determined by counting the number of eggs and embryos per female. Following the methodology of Forbes (1973) and the schematics of Jackson (1985), sandprawn embryo development stages and any malformation type were identified and classified (Figure 4; See Appendix Figure A 2). Criteria used to score eggs and embryos are shown in Table 2 and Figure 4. Additionally, the biomass of all eggs and embryos was measured. Eggs and embryos were carefully dried on paper towels (10 min per female), placed in petri dishes, and thereafter weighed to quantify total egg biomass per female (A&D GR-202 balance, precision = 0.0000g). Female egg and embryo dry biomass data were averaged per female.

Table 2. *Descriptions of sandprawn embryo developmental stages and malformation types following Jackson (1985).*

Classification	Description
Development Stage 1	Cell division but no cell differentiation
Development Stage 2	Partial differentiation of the embryo
Development Stage 3	Complete differentiation with visible eyes
Development Stage 4	Large visible eyes, receding yolk, immature telson
Development Stage 5	Well-developed telson, large eyes fully formed
Malformation type 1	Ruptured/broken egg casing
Malformation type 2	Opaque/discoloured egg casing
Malformation type 3	Ruptured/damaged and discoloured egg casing

3.5.4 Sandprawn Body Condition

The body condition of sandprawns was determined following methodology by Kallberg-Normark et al. (2022). Sandprawns were individually dried at 60°C for 48 hours and then weighed (A&D GR-202 balance, precision = 0.00000g). Body condition was determined as the ratio of sandprawn dry weight to corresponding CL.

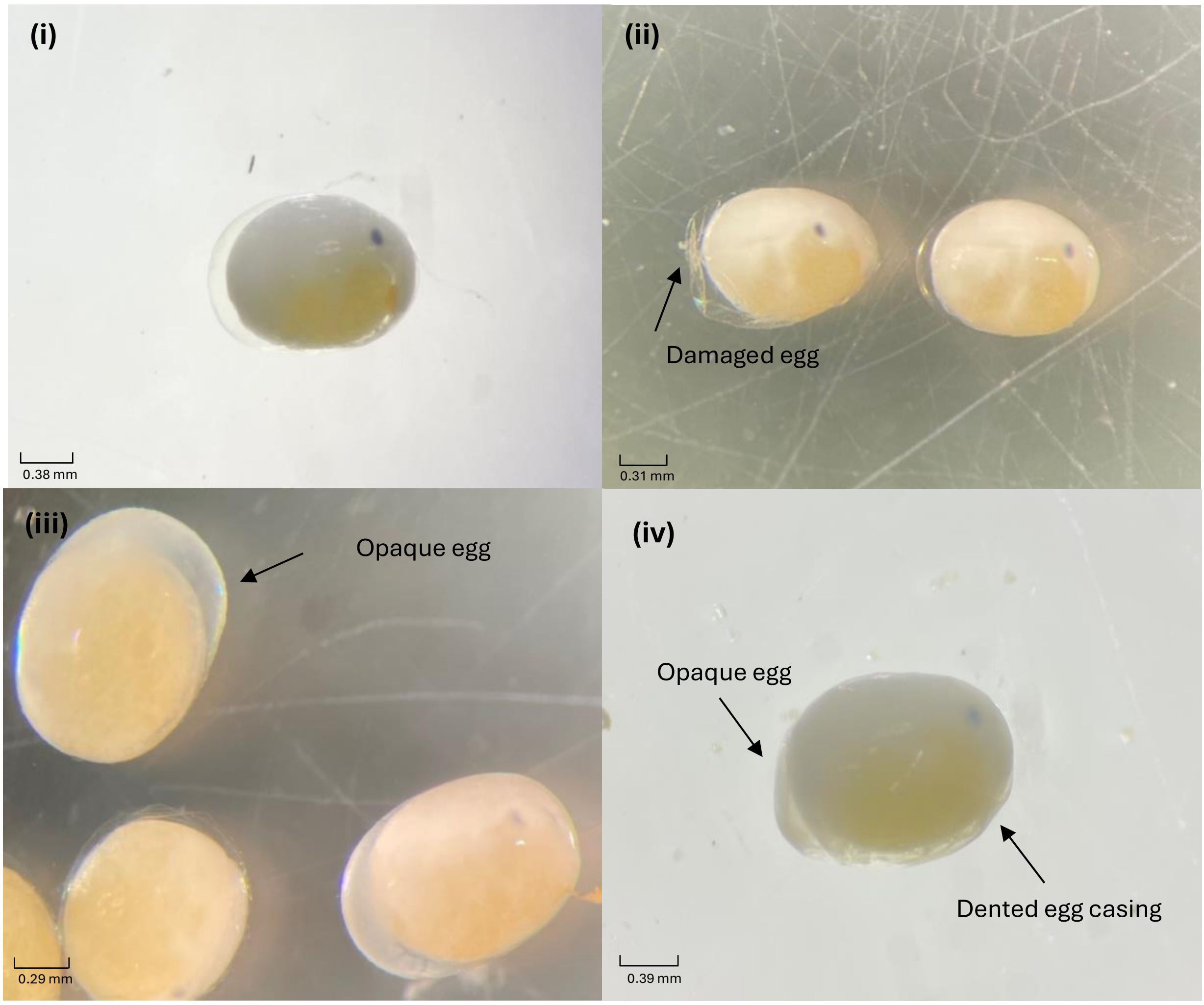

Figure 4. *Embryonic developmental stages and malformation types expressed in the sandprawn Kraussillichirus kraussi. (i) Development stage 4; (ii) Development stage 4, malformation type 1; (iii) Development stage 4, malformation type 2; (iv) Development stage 4, with malformation type 3. Explanations for the different stages of development and malformation type are provided in Table 1.*

3.6 Statistical Analysis

All statistical analysis for this study was performed in R (R Core Team, 2023). Before parametric analysis, data were assessed for normality and homogeneity of variance using the Shapiro-Wilk test, Levene's test and by plotting the model residuals and QQ plots. Where data violated the assumptions of parametric testing, data were transformed, and parametric testing was applied (See Appendix Table A 1 for a list of transformations applied).

Sediment particle size, sediment organic matter content, sandprawn major chela length and body condition data were all log-transformed. Two-factor ANOVAs (Analysis of Variance) were performed using the 'anova' function in RStudio with the 'stats' and 'car' packages to determine whether abiotic (sediment particle size; sediment organic matter content; human numbers; mean pixel values for redox potential images) and biotic (sandprawn body condition) response variables varied significantly among sites, seasons, and their interaction (Fox & Weisberg, 2019; R Core Team, 2023). For sandprawn sexual dimorphism data, once major chela lengths were log-transformed, a three-way ANCOVA (Analysis of Covariance) was performed with carapace length as the covariate to determine whether major chela length (as an indicator of sexual dimorphism) varied significantly among sexes, sites, seasons, and their interaction. Additionally, scatterplots of log (major chela length) vs carapace length were plotted and the 'forecast' function in Microsoft Excel was applied to project trendlines for carapace lengths of 6.5mm to 11.5 mm to visualise relationships between the variables over a standardised carapace length. Sandprawn CPUE data were square root transformed and three two-factor ANOVAs performed to determine whether total CPUE, and those of males, females and juveniles were affected by sites, seasons, and their interactions.

Sandprawn egg and embryo data consisted of fecundity, egg biomass, malformation, and development stage datasets. All data was collected during the winter sample as no gravid female sandprawns were recorded in the summer. One-factor ANCOVAs were performed with carapace length as the covariate to determine whether fecundity and egg biomass differed significantly among the sites. Since egg and embryo malformation data was expressed as a percentage (per female), data was logit transformed and a one-factor ANOVA was performed to determine whether egg and embryo malformation occurrence differed among the sites. Additionally, one-factor ANOVAs were performed on each type of malformation occurrence (malformation types 1-3) to determine whether the different types of malformation occurrence varied among the sites. Egg and embryo development stage data were not normally distributed, and data transformation was ineffective in addressing this. Therefore, a Kruskal-Wallis Rank Sum Test from the 'coin' package was performed for each development stage (1-5) to determine whether development stages differed across the five sites (Hothorn et al., 2006). The 'dunn.test' package was utilised to run a Dunn's test with Bonferroni correction to determine within-site variability (Dinno, 2017).

For all ANOVAs and ANCOVAs performed, when p-values were significant ($p < 0.05$), a Tukey post hoc ('lsmeans' package) was used to identify within site and season variation (Lenth, 2016).

4. RESULTS

4.1 Environmental Variables

Generally, spatial variation in temperature, dissolved oxygen, salinity, and phytoplankton biomass was minimal among the study sites. However, seasonal variation was evident for temperature, which ranged between 14.56°C - 16.97°C and 24.81°C - 26.38°C for winter and summer, respectively (Table 3). Sediment organic matter content was not significantly different between the five sites (ANOVA, $F = 1.922$, $df = 4$, $p = 0.146$) and between seasons (ANOVA $F = 0.713$, $df = 1$, $p = 0.4084$; Table 4; Table 5). However, sediment particle size did significantly differ between the sites (ANOVA, $F = 6.462$, $df = 4$, $p = 0.0017$; Table 5), with Sites 1 and 2 generally having finer sediment than the other sites (post hoc Tukey, $p < 0.05$; Table 4). Human numbers were significantly different among sites (ANOVA, $F = 57.542$, $df = 4$, $p < 0.001$) and seasons (ANOVA, $F = 167.302$, $df = 1$, $p < 0.001$; Table 5). There was also a significant interaction for human numbers between site x season (ANOVA, $F = 25.560$, $df = 4$, $p < 0.001$; Table 5). Human numbers were significantly different (post hoc Tukey $p < 0.001$) and greatest at Site 1 for both seasons (8.30 ± 0.92 SE and 86.8 ± 14.64 SE in winter and summer respectively). In both seasons, virtually no human numbers were recorded in Sites 3 to 5 (Table 4).

Table 3. *Physico-chemical variables measured at each of the five sampling sites for summer and winter in Zone A, Langebaan Lagoon.*

Season	Site	Temperature (°C)	Dissolved Oxygen (µg/l)	Salinity (ppt)	Phytoplankton (µg/l)
Winter	1	14.56	8.91	33.48	3.88
	2	16.05	8.62	32.60	3.42
	3	15.85	10.02	33.96	3.52
	4	16.97	9.01	33.50	3.68
	5	16.08	9.30	33.57	5.38
Summer	1	24.81	10.40	33.58	5.09
	2	26.38	9.43	35.80	4.92
	3	25.60	9.20	35.80	5.21
	4	26.30	9.30	36.10	5.30
	5	25.20	7.90	35.90	5.04

Table 4. *Mean (±SE) of human numbers, sediment particle size and organic matter content at each of the five sampling sites for both seasons in Zone A, Langebaan Lagoon.*

Season	Site	Human numbers	Sediment particle size (µm)	Organic matter (%)
Winter	1	8.30 ± 0.92	173.24 ± 6.37	0.88 ± 0.21
	2	0.10 ± 0.85	180.34 ± 4.75	0.75 ± 0.01
	3	0.00 ± 0.00	246.66 ± 30.94	1.24 ± 0.13
	4	0.00 ± 0.00	313.17 ± 27.85	0.94 ± 0.04
	5	0.00 ± 0.00	220.09 ± 16.26	0.70 ± 0.09
Summer	1	86.79 ± 14.64	169.96 ± 1.02	0.65 ± 0.03
	2	2.50 ± 0.85	189.22 ± 12.67	0.43 ± 0.15
	3	0.20 ± 0.20	210.61 ± 2.99	0.69 ± 0.06
	4	0.00 ± 0.00	266.69 ± 13.67	0.83 ± 0.25
	5	0.00 ± 0.00	210.12 ± 16.91	0.61 ± 0.12

***Table 5**. Results of two-factor ANOVAs which tested the main and interactive effects of site and season on sediment particle size, organic matter content, human numbers and mean pixel values for summer and winter. The table reports the degrees of freedom (df) and sum of squares (Sum Sq) for each predictor, along with the resulting F statistic (F value) and significance (p-value). Statistically significant outcomes are denoted by *.*

	Predictor	**df**	**Sum Sq**	**F value**	**p-value**
Sediment particle size	Site	4	0.333	6.462	0.0017 *
	Season	1	0.000	0.037	0.8476
	Site x Season	2	0.043	0.842	0.5146
	Residuals	20	0.257		
Organic matter	Site	4	1.013	1.922	0.1460
	Season	1	0.094	0.713	0.4084
	Site x Season	2	0.390	0.739	0.5762
	Residuals	20	2.635		
Human numbers	Site	4	70730	57.542	<0.0001*
	Season	1	51412	167.302	<0.0001*
	Site x Season	4	31418	25.560	<0.0001*
	Residuals	111	34110		
Mean pixel values	Site	4	634	3.082	0.0395*
	Season	1	103	1.999	0.1728
	Site x Season	4	858	4.171	0.0129*
	Residuals	20	1028		

Qualitative histograms indicated spatial shifts in sediment pixel frequency across sites. At Site 1, the mode grayscale intensity was darker (near pixel values closer to 0) but shifted to lighter shades (near pixel values closer to 255) towards Site 5 (Figures 5 & 6). This magnitude of difference in modes from Sites 1 to 5 appeared greater in summer (Figure 6). Results of a two-factor ANOVA indicated that the mean pixel values differed among the sites (ANOVA, F = 3.082, df = 4, p = 0.0395), with a significant site x season interaction (ANOVA, F = 4.171, df = 4, p = 0.0129; Table 5). Pixel values for Site 1 did not vary significantly between summer and winter but were different from Sites 3, 4 and 5 in both seasons (post hoc Tukey, $p < 0.01$; Figures 5 & 6).

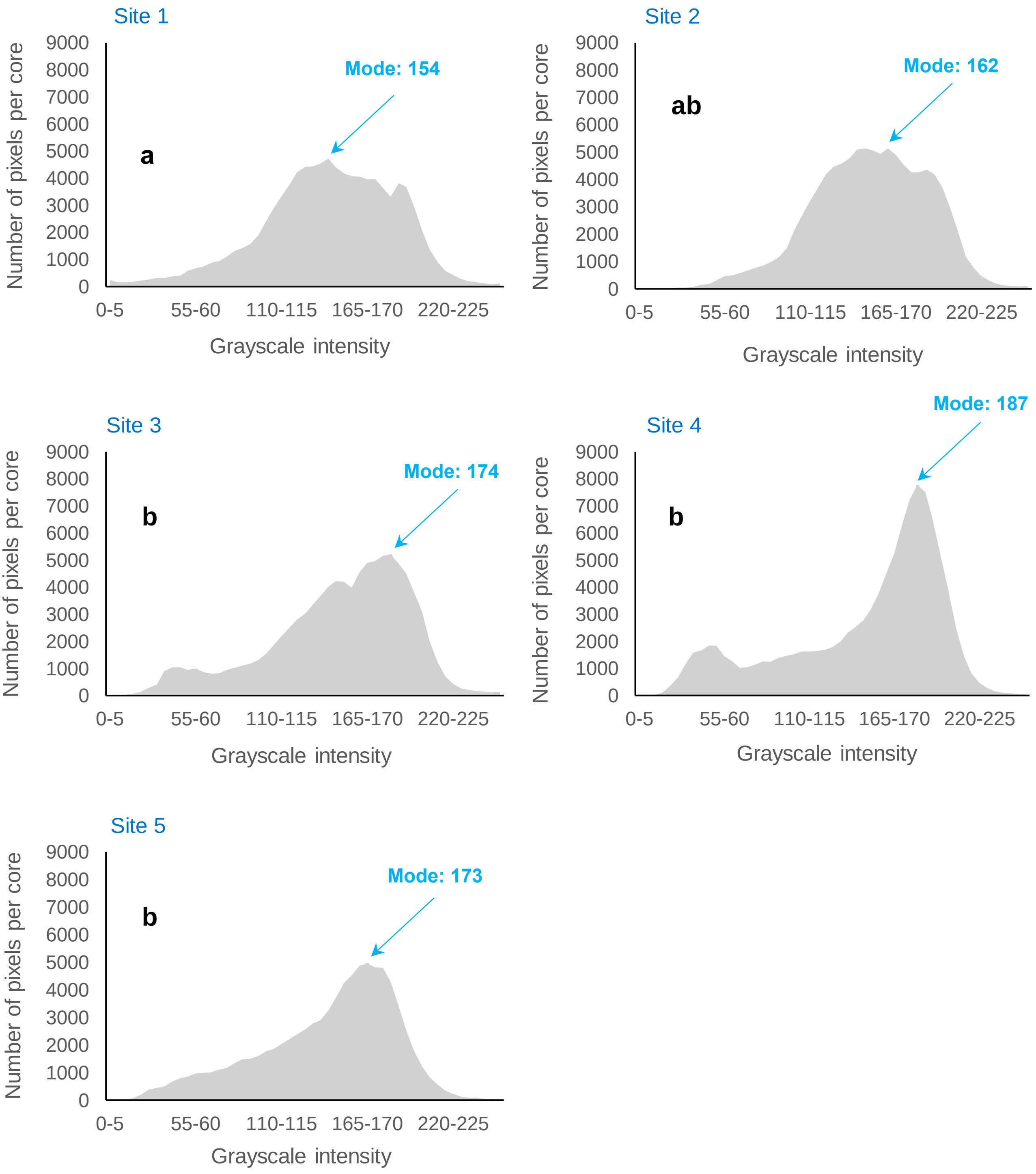

Figure 5. *The number of pixels in each grayscale intensity range (0 = black and 225= white) with a bin width of 5 pixels. Values have been extracted from grayscale images taken in each of the five sampling sites in winter in Zone A, Langebaan Lagoon. Bold arrow indicates modal peak for each histogram. Shared letters denote a lack of statistical difference among sites (post hoc Tukey p > 0.05). Histograms are composite curves for each of the 3 cores.*

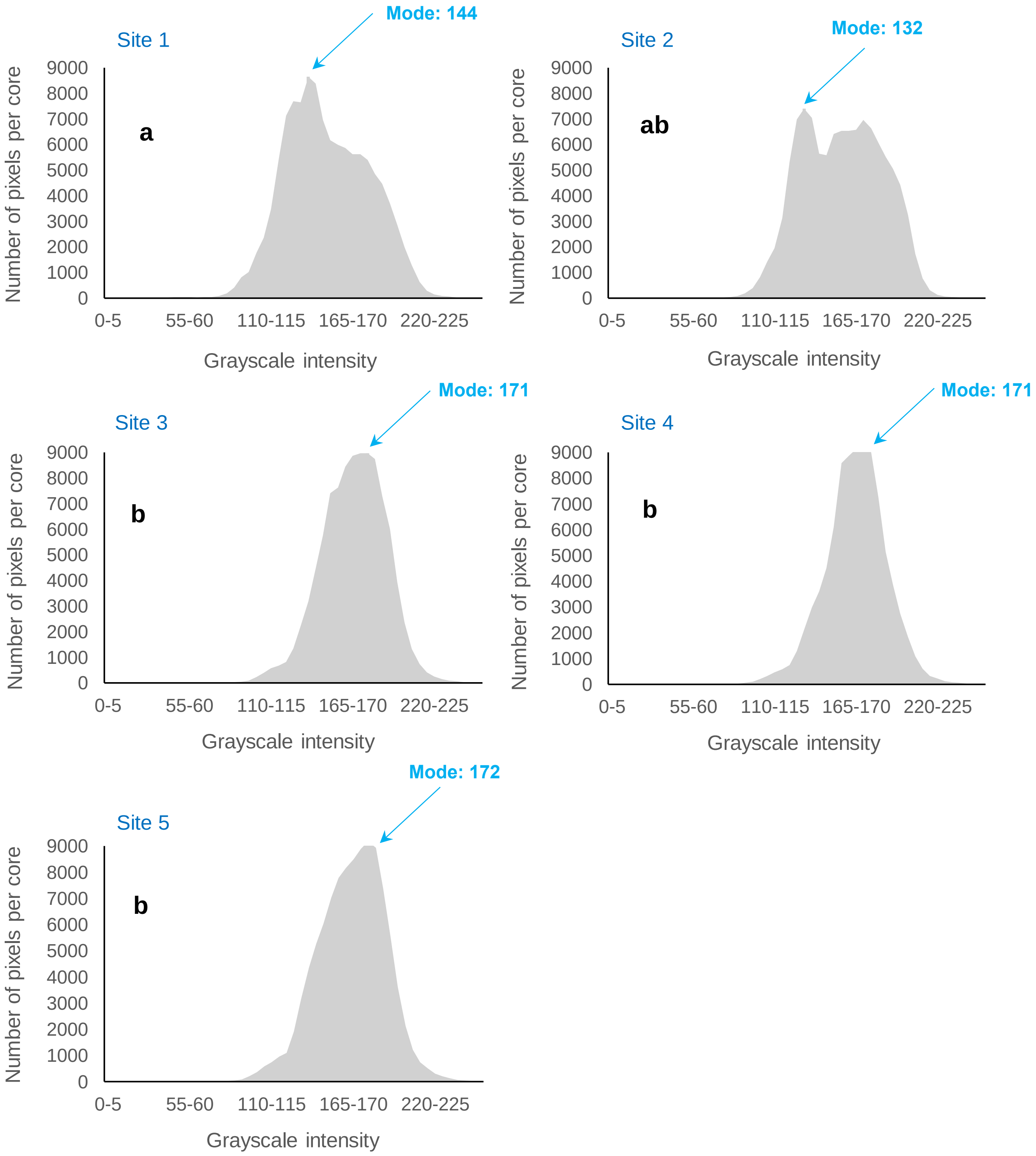

***Figure 6**. The number of pixels in each grayscale intensity range (0 = black and 225= white) with a bin width of 5 pixels. Values have been extracted from grayscale images taken in each of the five sampling sites in summer in Zone A, Langebaan Lagoon. Bold arrow indicates modal peak for each histogram. Shared letters denote a lack of statistical difference among sites (post hoc Tukey p > 0.05). Histograms are composite curves for each of the 3 cores.*

4.2 Sandprawn Population Metrics

A total of 789 sandprawns were collected from sampling sites in both seasons, of which, 384 were male and 405 were female. 178 (46.35%) of males and 202 (49.88%) of females were collected during the winter.

4.2.1 Sandprawn CPUE

There was no significant difference in the total CPUE across the five sites (ANOVA, F = 1.983, df = 4, p = 0.1157), but seasonal variation was significant (ANOVA, F = 19.174, df = 1, $p < 0.001$), with mean summer values being greater than winter (post-hoc Tukey, $p < 0.001$; Table 6). Individually, male (ANOVA, F = 2.182, df = 4, p = 0.0884), female (ANOVA, F = 1.704, df = 4, p = 0.1682) and juvenile (ANOVA, F = 1.491, df = 4, p = 0.2233) CPUE were not significantly different across the five sites (Table 6). Male CPUE did not significantly differ between seasons (ANOVA, F = 1.919, df = 1, p = 0.1737), in opposition to both female (ANOVA, F = 10.733, df = 1, p = 0.0023) and juvenile CPUE (ANOVA, F = 7.808, df = 1, p = 0.0080; Table 6). Generally, female and juvenile CPUE values were greater in summer than in winter (female post-hoc Tukey p = 0.001; juvenile post-hoc Tukey p = 0.028; Figure 7).

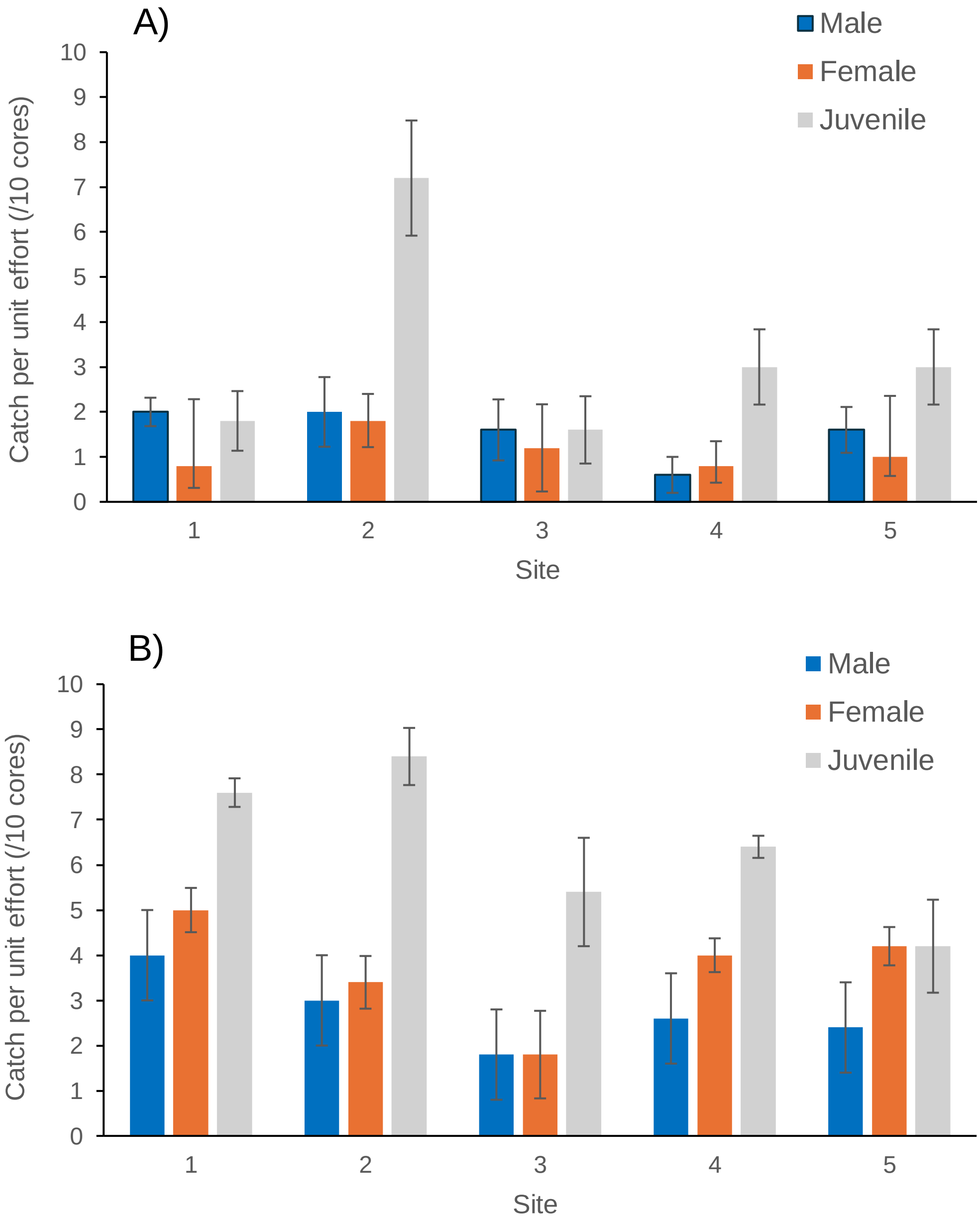

Figure 7. *Mean (±SE) CPUE for male, female and juvenile sandprawns collected per 10 cores in each of the five sites in winter (A) and summer (B), in Zone A, Langebaan Lagoon.*

Table 6. *Results of three two-factor ANOVAs which tested the main and interactive effects of total sandprawn catch per unit effort (CPUE), Male CPUE, Female CPUE and Juvenile CPUE for the five sampling sites for summer and winter. The table reports the degrees of freedom (df) and sums of squares (Sum Sq) for each predictor, along with the resulting F statistic (F value) and significance (p-value). Statistically significant outcomes are denoted by *.*

	Predictor	**df**	**Sum Sq**	**F value**	**p-value**
Total CPUE	Site	4	3.666	1.983	0.1157
	Season	1	8.863	19.174	< 0.001*
	Site x Season	4	3.011	1.629	0.1859
	Residuals	40	18.490		
Male CPUE	Site	4	4.077	2.182	0.0884
	Season	1	0.896	1.919	0.1737
	Site x Season	4	2.702	1.446	0.2366
	Residuals	49	18.681		
Female CPUE	Site	4	3.891	1.704	0.1682
	Season	1	6.128	10.733	0.0023*
	Site x Season	4	2.624	1.1487	0.3471
	Residuals	40	22.840		
Juvenile CPUE	Site	4	4.276	1.491	0.2233
	Season	1	5.599	7.808	0.0080*
	Site x Season	4	2.625	0.915	0.4647
	Residuals	40	28.687		

4.2.2 Sandprawn Sexual Dimorphism

With sandprawn carapace length as a covariate, site (ANCOVA, F = 0.197, df = 4, p = 0.9400) and season (ANCOVA, F = 0.036, df = 1, p = 0.8491) did not individually predict variance in major chela length (Table 7). Additionally, there was no significant interaction between sex, site, and season on the major chela length (ANCOVA, F = 0.742, p = 0.5636; Table 7). Sandprawn sex was the only predictor of major chela length (ANCOVA, F = 17.389, df = 1, p

< 0.001; Table 7), with values for males being greater than females (post hoc Tukey $p < 0.001$; Figures 8 & 9). Adjusted means of major chela lengths (log) from the ANCOVA indicated that for both seasons, differences in chela lengths between males and females were smallest at Site 1 and increased towards Site 5 (Table 8). This trend was also visually evident when major chela length was standardised by projecting to a consistent lower and upper limit per season (Figures 8 & 9). Additionally, female major chela length is greatest in Site 1 and decreased to Site 5 for both seasons and the opposite occurs for males (Table 8). In Site 1, differentials in projected maximum male and female major chela lengths were generally smallest at, with an increasing trend towards Site 5 for both summer and winter (Figures 8 & 9). Furthermore, projected differentials between male and female major chela lengths were almost doubled from Sites 1 to 5 in winter (projected difference = 0.66 in Site 1, 1.20 in Site 5; Figure 8). In summer, the sex differential was less prominent (projected difference = 0.47 in Site 1, 0.75 in Site 5; Figure 9).

Table 7. *Results of a three-factor ANCOVA which tested the effect of carapace length, sex, site, season and their interactions on the major chela length of sandprawn from the five sampling sites for summer and winter. Bold text refers to results in which carapace length was controlled for. Non-bold text denotes outcomes when carapace length is not controlled; these results are provided as part of the output of ANCOVA analysis for comparative purposes. The table reports the degrees of freedom (df) and sums of squares (Sum Sq) for each predictor, along with the resulting F statistic (F value) and significance (p-value). Statistically significant outcomes are denoted by *.*

Predictor	**df**	**Sum Sq**	**F value**	**p-value**
Carapace length (mm)	1	0.034	5.619	0.0180*
Sex	1	0.084	13.832	< 0.0002*
Site	4	0.006	0.231	0.9209
Season	1	0.000	0.005	0.0053
Sex: Site	4	0.001	0.389	0.9431
Sex: Season	1	0.008	1.385	0.8169
Site: Season	4	0.013	0.531	0.7133
Sex: Site: Season	4	0.020	0.838	0.5012
Sex	**1**	**0.106**	**17.389**	**< 0.0001***
Site	**4**	**0.005**	**0.197**	**0.9400**
Season	**1**	**0.000**	**0.036**	**0.8491**
Sex x Site	**4**	**0.016**	**0.640**	**0.6345**
Site x Season	**4**	**0.013**	**0.513**	**0.7264**
Sex x Season	**1**	**0.015**	**2.486**	**0.1153**
Sex x Site x Season	**4**	**0.018**	**0.742**	**0.5636**
Residuals	**737**	**4.488**		

Table 8. *Adjusted means (±SE) of major chela length (log) for male and female sandprawns (with carapace length held constant) at each of the five sampling sites for summer and winter in Zone A, Langebaan Lagoon.*

Season	**Site**	**Male (mm)**	**Female (mm)**
Winter	1	3.24 ± 0.02	3.10 ± 0.01
	2	3.32 ± 0.01	3.10 ± 0.01
	3	3.29 ± 0.02	3.02 ± 0.03
	4	3.34 ± 0.01	3.04 ± 0.02
	5	3.36 ± 0.01	3.01 ± 0.02
Summer	1	3.17 ± 0.02	3.13 ± 0.02
	2	3.29 ± 0.01	3.02 ± 0.01
	3	3.23 ± 0.01	3.09 ± 0.01
	4	3.25 ± 0.01	3.04 ± 0.02
	5	3.24 ± 0.01	3.02 ± 0.02

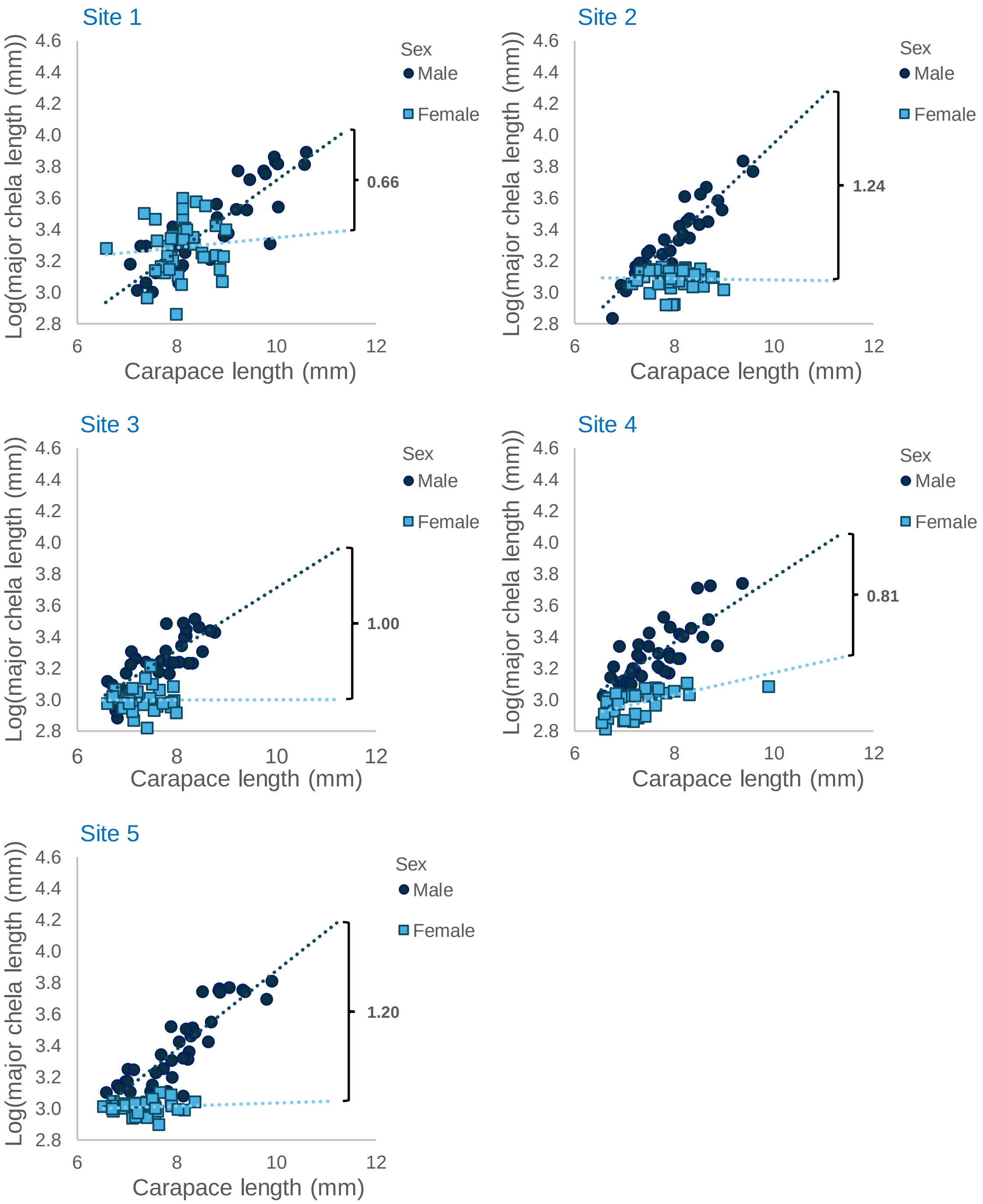

Figure 8. *The relationship between the carapace length and major chela length (log) of male and female sandprawns from the five sampling sites during winter located in Zone A, Langebaan Lagoon. Trend lines start at a standardised carapace length of 6.5 mm and are projected towards a maximum carapace length of 11.5 mm. Predicted maximum differentials between male and female major chela length (log) are indicated by a bracket.*

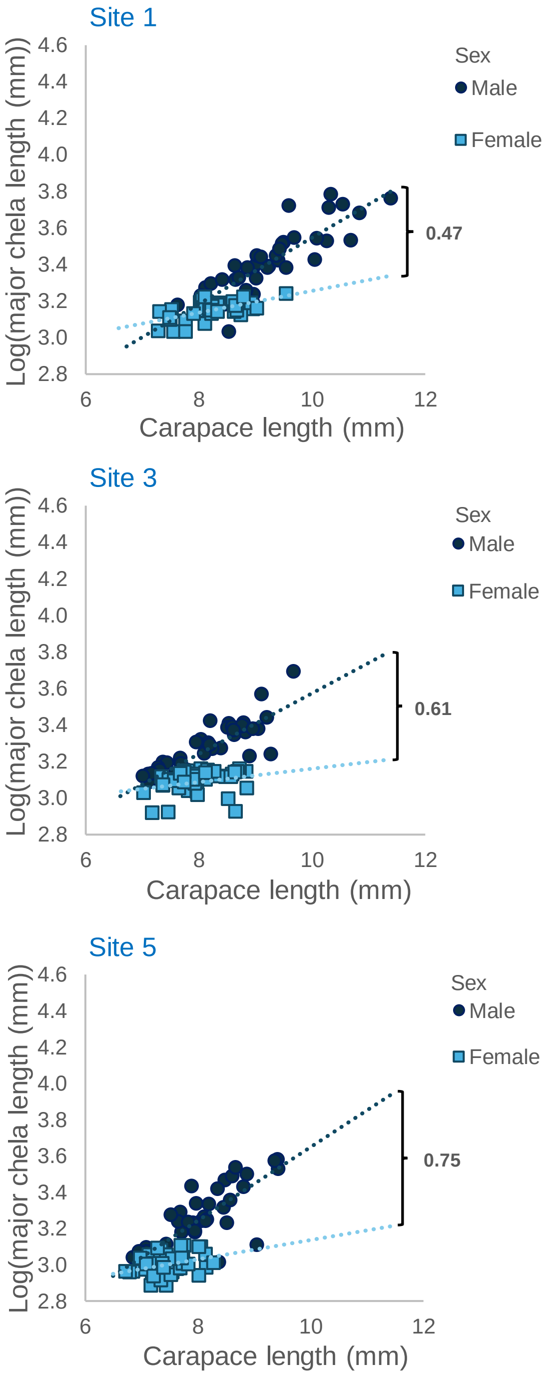

Figure 9. *The relationship between the carapace length and major chela length (log) of male and female sandprawns from the five sampling sites during summer located in Zone A, Langebaan Lagoon. Trend lines start at a standardised carapace length of 6.5 mm and are projected towards a maximum carapace length of 11.5 mm. Predicted maximum differentials between male and female major chela length (log) are indicated by a bracket.*

4.2.3 Sandprawn Body Condition

Sandprawn body condition was not significantly different between sexes (ANOVA, F = 1.581, df = 1, p = 0.2089) and between seasons (ANOVA, F = 2.866, df = 1, p = 0.1049; Table 9). However, it was significantly different among the five sampling sites (ANOVA, F = 26.434, df = 4, p < 0.001) and was significantly affected by the sex x site interaction (ANOVA, F = 2.671, df = 1, p = 0.0312; Table 9). Additional interactive predictors included the (1) site x season interaction (ANOVA, F = 15.563, df = 4, p < 0.001) and (2) sex x site x season interaction (ANOVA, F = 3.299, df = 4, p = 0.0108; Table 9). Generally, sandprawn body condition in Site 1 was significantly greater than values at all other sites (post hoc Tukey p < 0.01) for both seasons (Figure 10). Male sandprawns had greater body condition values than females and this difference was greatest in summer (Figure 10).

Table 9. *Results of a two-factor ANOVA which tested the main and interactive effects of sandprawn body condition (mm/mg) for the five sampling sites for winter and summer and the associated interactions. The table reports the degrees of freedom (df) and sums of squares (Sum Sq) for each predictor, along with the resulting F statistic (F value) and significance (p-value). Statistically significant outcomes are denoted by *.*

Predictor	**df**	**Sum Sq**	**F value**	**p-value**
Sex	1	0.110	1.581	0.2089
Site	4	7.800	27.729	< 0.0001*
Season	1	0.190	2.637	0.1049
Sex x Site	4	0.750	2.671	0.0312*
Sex x Season	1	0.010	0.161	0.6881
Site x Season	4	4.380	15.563	< 0.0001*
Sex x Site x Season	4	0.930	3.299	0.0108*
Residuals	744	52.290		

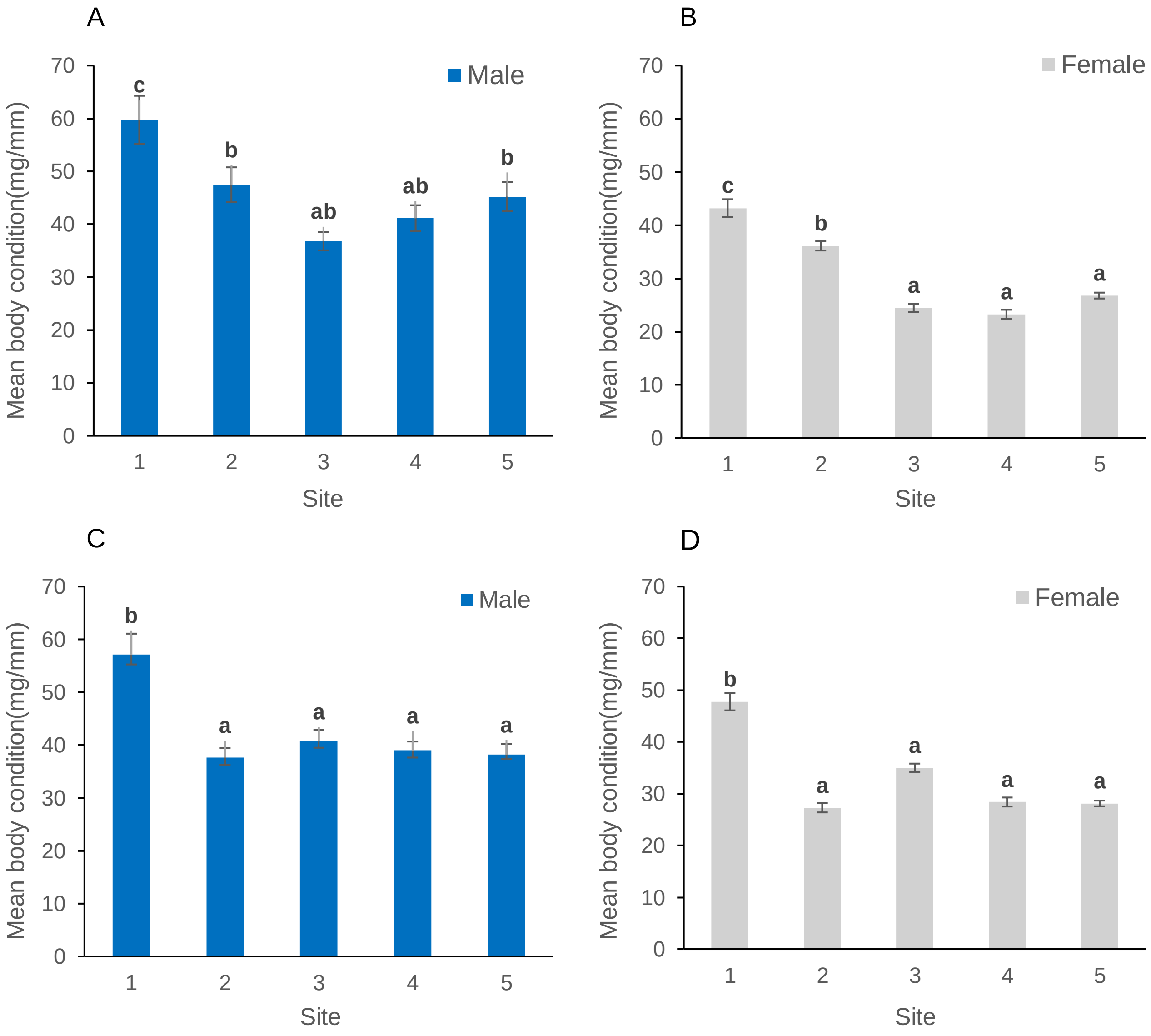

Figure 10*. Mean (±SE) body condition (mg/mm) of male and female sandprawns collected in the five sampling sites (A and B) for winter and (C and D) for summer in Zone A, Langebaan Lagoon. Shared letters denote a lack of statistical difference among sites (post hoc Tukey p > 0.05).*

4.3 Sandprawn Egg and Embryo Variability

No female sandprawns collected in summer were gravid. Therefore, all 8495 eggs and embryos analysed were obtained during winter. 33.33% (135 of 405) of females were ovigerous. Sites

3 and 5 had the greatest percentage of ovigerous females (75.00% each), followed by Site 4 (64.71%), Site 2 (63.83%) and Site 1 (48.65%).

4.3.1 Female Fecundity

When adjusting for female carapace length, fecundity was found to be significantly different across the sampling sites (ANCOVA, F = 3.2715, df = 4, p = 0.0113; Table 10). Site 2 had the largest adjusted mean ± SE fecundity (15.02 ± 2.09 eggs and embryos) and Site 4 had the lowest (8.11 ± 2.41 eggs and embryos; Table 11). A Tukey post hoc test indicated that female fecundity in Site 2 was significantly different to all other sites (Table 11). Sites 3, 4 and 5 were not significantly different (Table 11).

Table 10. *Results of a one-factor ANCOVA which tested the main and interactive effect of carapace length and site on the number of eggs and embryos per female sandprawn from the five sampling sites for winter. Bold text refers to results in which carapace length was controlled. Non-bold text denotes outcomes when carapace length is not controlled; these results are provided as part of the output of ANCOVA analysis for comparative purposes. The table reports the degrees of freedom (df) and sums of squares (Sum Sq) for each predictor, along with the resulting F statistic (F value) and significance (p-value). Statistically significant outcomes are denoted by *.*

Predictor	df	Sum Sq	F value	p-value
Carapace length	1	1571	2.277	0.1317
Site	4	8660	3.138	0.0142*
Site	**4**	**9029**	**3.272**	**0.0113***
Residuals	**754**	**520258**		

Table 11. *Adjusted means (±SE) number of eggs and embryos for female sandprawns (with carapace length held constant) at each of the five sampling sites for winter in Zone A, Langebaan Lagoon. The table reports post hoc Tukey letters where shared letters denote a lack of statistical difference among sites ($p > 0.05$).*

Site	**Adjusted mean (±SE) number of eggs and embryos**	**post hoc Tukey ($p > 0.05$)**
1	10.65 ± 2.72	ab
2	15.02 ± 2.09	a
3	8.47 ± 2.15	b
4	8.11 ± 2.41	b
5	8.74 ± 2.15	b

4.3.2 Egg and Embryo Biomass

When adjusting for female carapace length, egg and embryo biomass was not significantly different across the sampling sites (ANCOVA, $F = 0.243$, $df = 4$, $p = 0.9134$; Table 12). The largest adjusted mean ± SE egg and embryo biomass is found in Site 4 (1.87 ± 0.33 mg) and Site 5 (1.81 ± 0.35 mg) (Table 13), followed by Site 2 (1.37 ± 0.38 mg), Site 1 (1.06 ± 0.78 mg) and Site 3 (1.02 ± 0.38 mg) (Table 13).

Table 12. *Results of a one-factor ANCOVA which tested the main and interactive effect of carapace length and site on the egg and embryo biomass per female sandprawn from the five sampling sites for winter. Bold text refers to results in which carapace length was controlled. Non-bold text denotes outcomes when carapace length is not controlled; these results are provided as part of the output of ANCOVA analysis for comparative purposes. The table reports the degrees of freedom (df) and sums of squares (Sum Sq) for each predictor, along with the resulting F statistic (F value) and significance (p-value). Statistically significant outcomes are denoted by a *.*

Predictor	**df**	**Sum Sq**	**F value**	**p-value**
Carapace length	1	1.102	0.489	0.4860
Site	4	2.534	0.281	0.8900
Site	**4**	**2.193**	**0.243**	**0.9134**
Residuals	**116**	**261.779**		

Table 13. *Adjusted means (±SE) dry biomass (mg) of eggs and embryos for female sandprawns (with carapace length held constant) at each of the five sampling sites for winter in Zone A, Langebaan Lagoon. The table reports post hoc Tukey letters where shared letters denote a lack of statistical difference among sites (p > 0.05).*

Site	**Adjusted mean (±SE) dry biomass of eggs and embryo**	**post hoc Tukey (p > 0.05)**
1	1.06 ± 0.78	a
2	1.37 ± 0.38	a
3	1.02 ± 0.38	a
4	1.87 ± 0.33	a
5	1.81 ± 0.35	a

4.3.3 Egg and Embryo Malformations

A total of 946 (11.14%) eggs and embryos displayed malformation type 1, 344 (4.05%) displayed malformation type 2 and 134 (1.58%) had malformation type 3. The percentage of eggs and embryos that were malformed was significantly different between the five sites (ANOVA, F = 4.633, df = 4, p = 0.0017; Table 14). The mean malformation percentage declined from Site 1 (26.60 ± 6.70 SE %) to 5 (11.03 ± 5.18 %), with Site 5 having significantly reduced malformation percentages compared to other sites (post hoc Tukey $p < 0.05$; Figure 11). Generally, Site 1 had the largest mean number of eggs and embryos which displayed malformations of all types (Figure 12). The most common type of egg deformation, malformation type 1, was significantly different among the sites (ANOVA, F = 4.597, df = 4, p = 0.0017; Table 14; Figure 12). A Tukey post hoc test revealed that Site 2 had a significantly greater mean number of eggs and embryos which displayed malformation type 1 compared to Site 5 (Figure 12). Sites 3, 4 and 5 had similar mean numbers of eggs and embryos which had malformation type 1, but with a declining trend (Figure 12). Malformation type 2 was not significantly different among the sites (ANOVA, F = 0.951, df = 4, p = 0.4370; Table 14). The prevalence of malformation type 3 was significantly different among the sites (ANOVA, F = 2.865, df = 4, p = 0.0258; Table 14; Figure 12). A Tukey post hoc test revealed that Site 2 had significantly different numbers of eggs and embryos with malformation type 3 relative to Sites 3 and 5 (Figure 12). Overall, malformation type 3 was the least common malformation for sandprawn eggs and embryos (Figure 12).

***Table 14**. Results of four one-factor ANOVAs which tested the main and interactive effect of total egg and embryo malformation, malformation type 1, malformation type 2 and malformation type 3 occurrence percentage (%) for the five sampling sites during winter. The table displays the degrees of freedom (df) and sums of squares (Sum Sq) for each source, along with the resulting F statistic (F value) and p-value. Significance is denoted by a *.*

	Predictor	**df**	**Sum Sq**	**F value**	**p-value**
Total malformations	Site	4	9.13	4.633	0.0016*****
	Residuals	124	60.94		
Malformation type 1	Site	4	1081	4.597	0.0017*****
	Residuals	130	7640		
Malformation type 2	Site	4	157	0.951	0.4370
	Residuals	130	5353		
Malformation type 3	Site	4	33.1	2.865	0.0258*****
	Residuals	130	375.9		

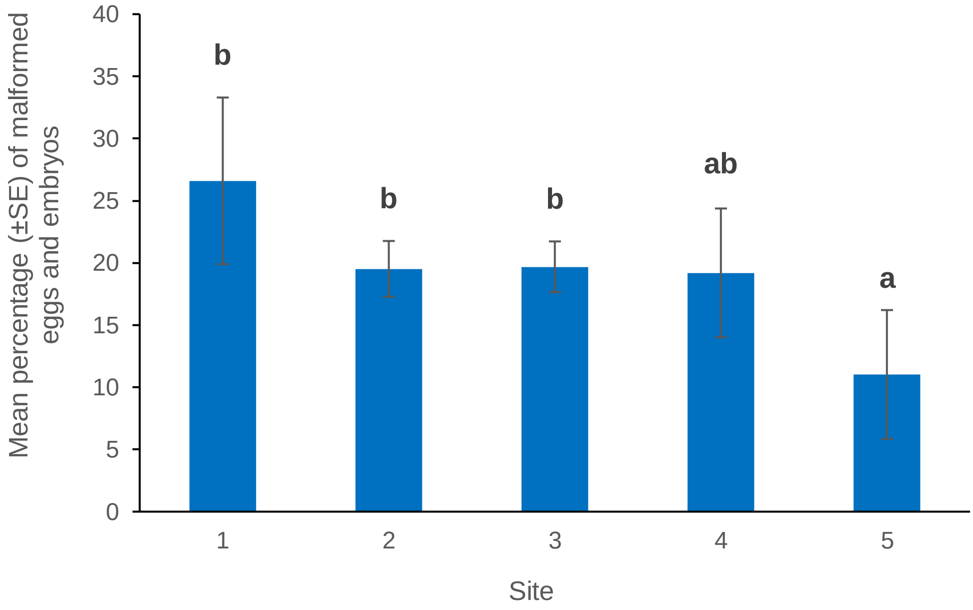

Figure 11. *Mean percentage (±SE) of malformed eggs and embryos for the five sampling sites collected during winter located in Zone A, Langebaan Lagoon. Shared letters denote a lack of statistical difference among sites (post hoc Tukey p > 0.05).*

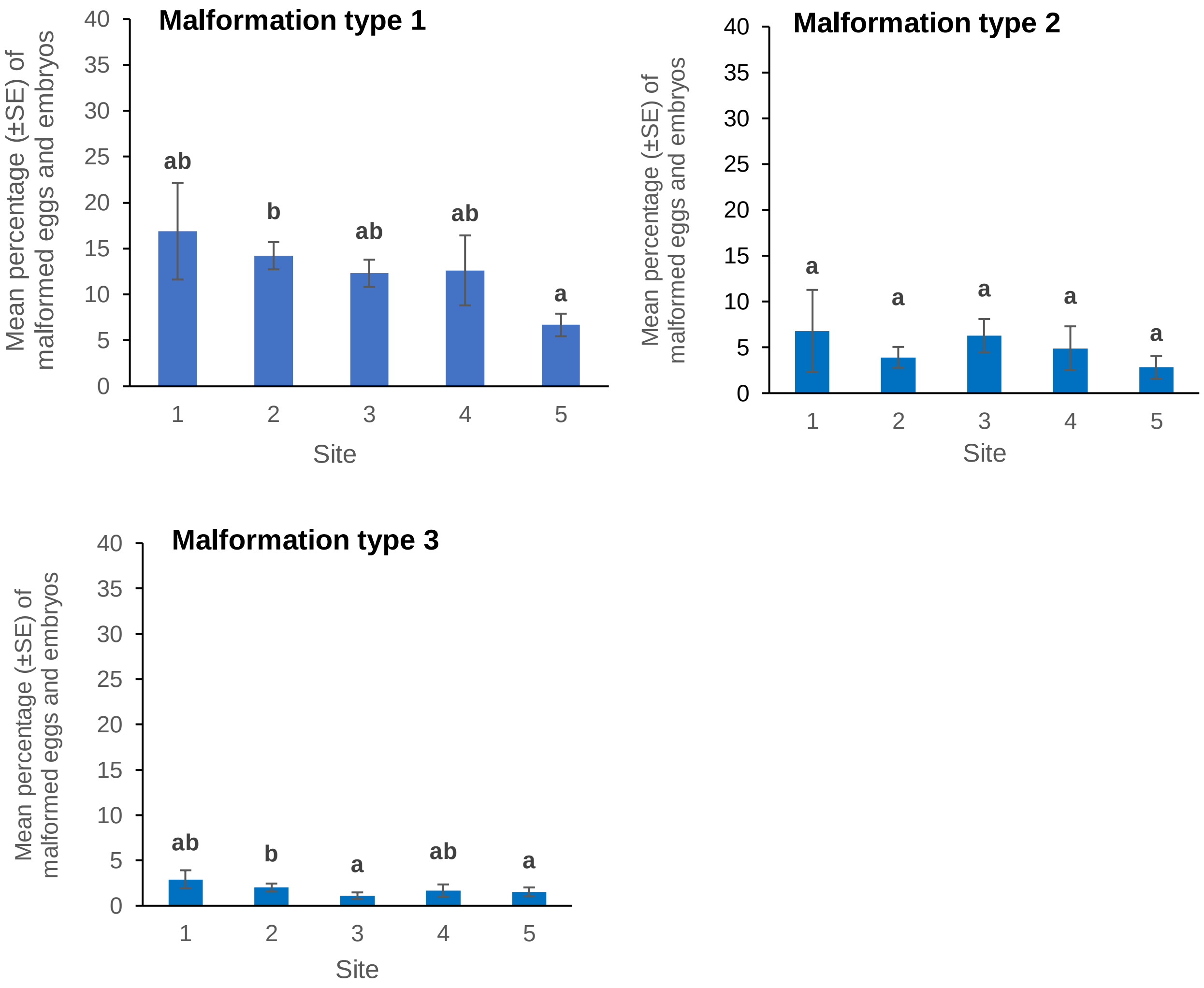

Figure 12. *Mean percentage (±SE) of malformed eggs and embryos for each malformation type (1-3) for the five sampling sites collected during winter located in Zone A, Langebaan Lagoon. Shared letters denote a lack of statistical difference among sites (post hoc Tukey p > 0.05).*

4.3.4 Egg and Embryo Developmental Stage

The percentage of eggs and embryos at development stages 1(Kruskal-Wallis, χ^2 = 18.847, p = 0.0008), 2 (Kruskal-Wallis, χ^2 = 12.772, p = 0.0125), 3 (Kruskal-Wallis, χ^2 = 17.378, p = 0.0016) and 4 (Kruskal-Wallis, χ^2 = 15.049, p = 0.0046) were significantly different among the five sampling sites (Table 15). The percentage of eggs and embryos at development stage 5 did not significantly differ between the five sites (Kruskal-Wallis, χ^2 = 4.958, df = 4, p = 0.2916; Table 15). This is likely due to the low number of eggs at stage 5 of development (Site 2: 0.07 ± 0.07 SE, Site 3: 0.52 ± 0.45 SE, Site 4: 0.26 ± 0.19 SE). The majority of eggs and embryos from Site 1 were in earlier development stages (stages 1 – 3; Figure 13). In contrast, most of the eggs and embryos from Sites 3, 4 and 5 showed later developmental stages (stages 3 – 4; Figure 13).

Table 15. *Results of five Kruskal-Wallis one-way analysis of variance which tested the differences in egg and embryo developmental stages (1-5) between the five sampling sites during winter. The table displays the Chi-squared statistic values (χ^2), degrees of freedom(df) and p-value. Significance is denoted by a *.*

Development Stage	χ^2	**df**	**p-value**
1	18.847	4	0.0008*
2	12.772	4	0.0125*
3	17.378	4	0.0016*
4	15.049	4	0.0046*
5	4.958	4	0.2916

The majority of malformed eggs and embryos identified in development stage 1 displayed malformation type 1 deformities (Figure 14). Malformation type 2 was the most prevalent in development stage 2, followed by malformation type 1 and lastly malformation type 3 (Figure 14). More advanced developed eggs and embryos (stages 3 – 4) had the largest percentage of malformation type 1 deformities (68.52% and 68.55% respectively; Figure 14). More developed eggs and embryos (compared to earlier developed) had the lowest percentage occurrence for malformation type 3 (Figure 14).

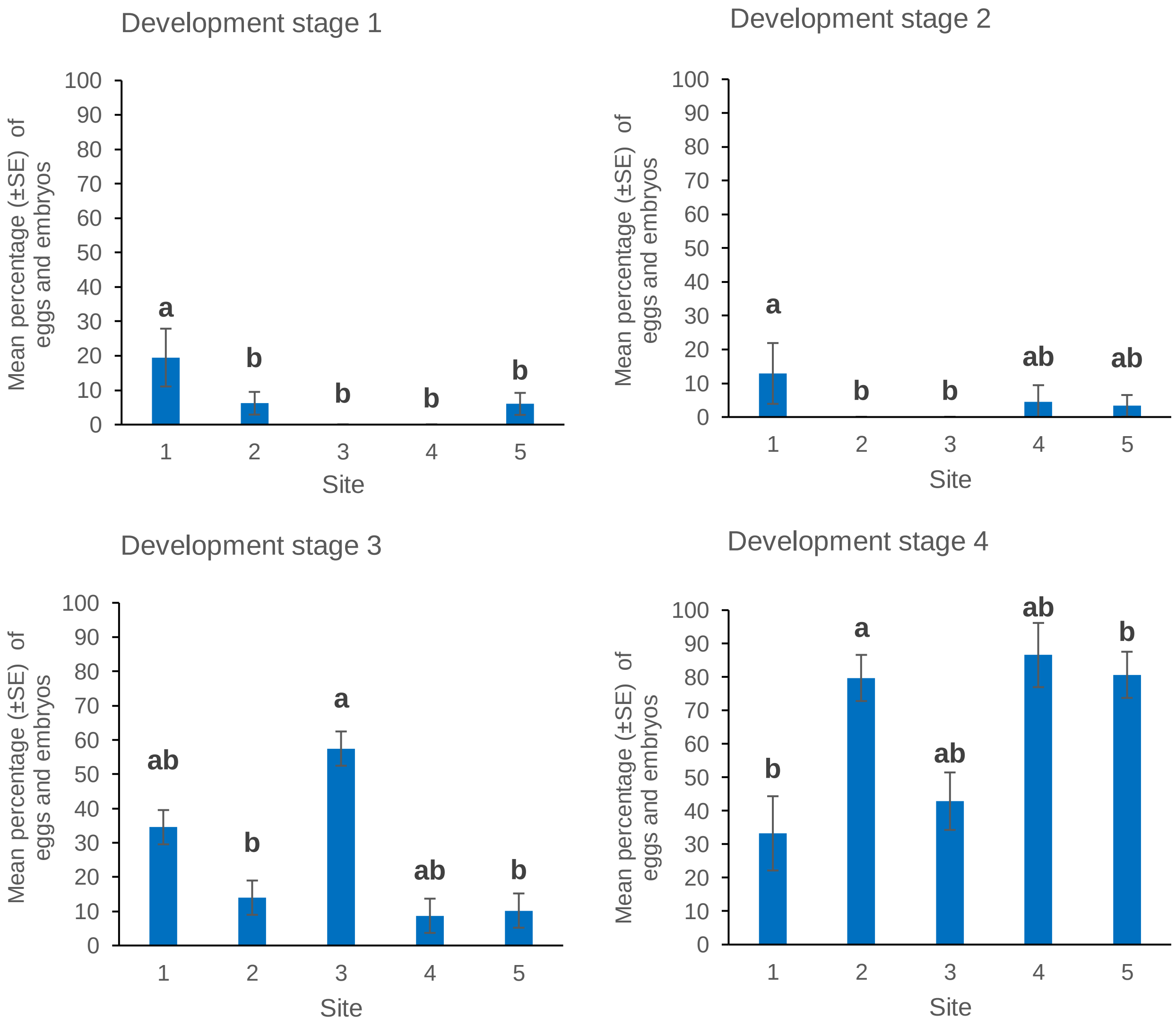

Figure 13*. Mean percentage (±SE) of eggs and embryos per female sandprawn for the first four embryonic development stages collected in the five sampling sites during winter located in Zone A, Langebaan Lagoon. Shared letters denote a lack of statistical difference among sites (Dunn's test > 0.05). Development stage 5 not shown due to low-frequency variability in the sites.*

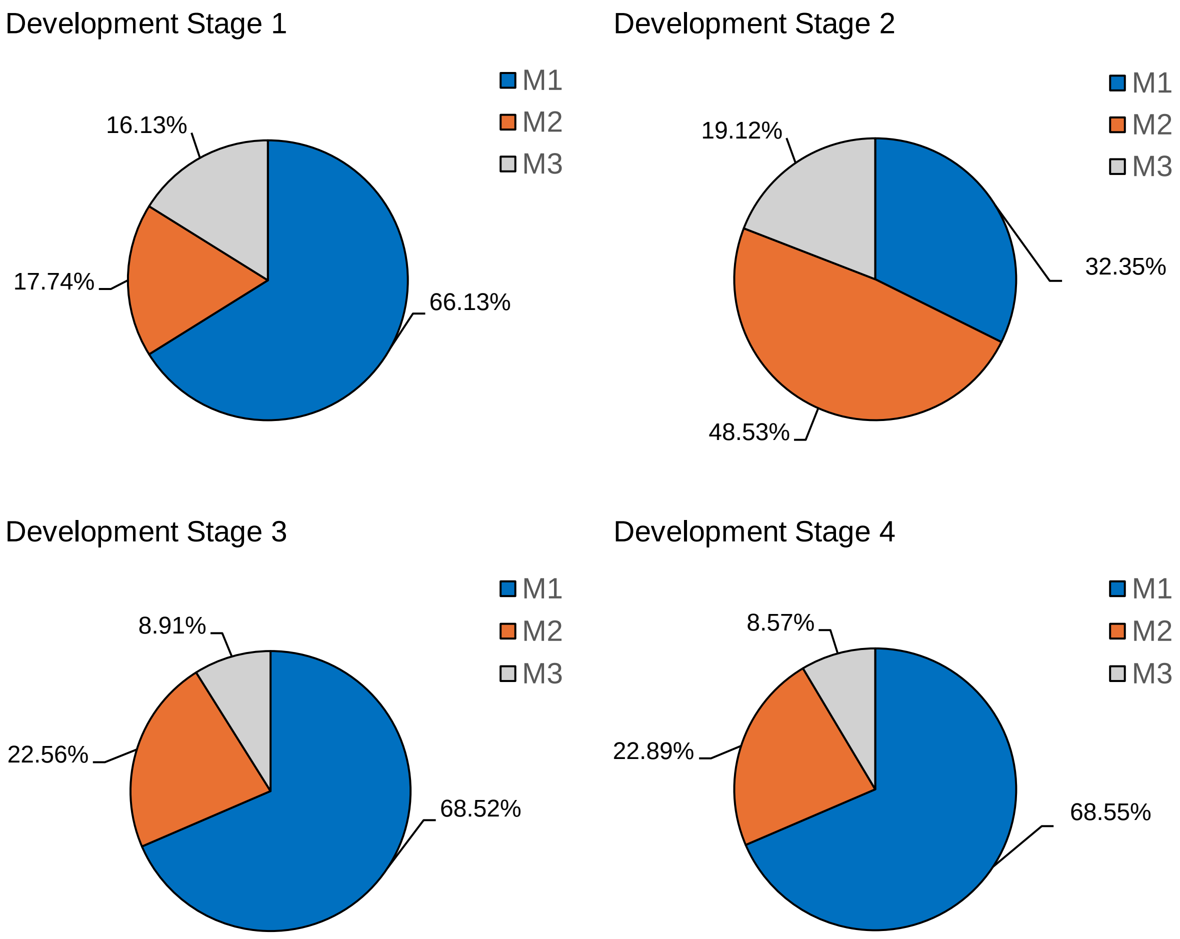

Figure 14. *Proportion of eggs and embryos which displayed the different malformation types (1 - 3) in the first four embryonic development stages collected in the five sampling sites during winter located in Zone A, Langebaan Lagoon. Development stage 5 not shown due to low-frequency variability in the sites.*

5. DISCUSSION

Coastal habitats hold immense ecological and economic importance; however, they have experienced a surge in human-related disturbances (Dale & Beyeler, 2001; Barbier et al., 2011; Chumsri et al., 2023). These disturbances have triggered various adverse responses from coastal marine macroinvertebrates and such responses have established them as effective bioindicators (Gul & Griffen, 2019; Gül & Griffen, 2020; Chumsri et al., 2023). However, in numerous developing countries, South Africa included, essential resources such as finances, capacity, and infrastructure are often lacking; these ultimately lead to knowledge gaps on ecosystem responses to disturbances and management thereof (Sink et al., 2019a). With these ideas in mind, this study contributes to improving our understanding of how trampling and bait collection impact intertidal sedimentary ecosystems in South Africa, and a key ecosystem engineer inhabiting these systems (*Kraussilichirus kraussi*; sandprawn). This study also introduces a novel, tool that can be used for signalling benthic stress in intertidal sedimentary systems. This research study has revealed significant differences in the reproductive aspects of sandprawns along a human disturbance gradient in Zone A of Langebaan Lagoon, South Africa. At the population level, findings indicate little impact of human disturbance on sandprawn abundance (as CPUE; catch per unit effort). However, the degree of development and malformation of eggs and embryos, which are critical reproductive parameters were adversely affected at sites with maximum human numbers (Sundelin & Eriksson, 1998; Du et al., 2020). Beyond this study, the reproductive consequences of trampling and bait-collecting by recreational visitors may have implications for the keystone functions sandprawns provide.

5.1 Human Numbers and Abiotic Variables

Results of this study indicate a distinct localised human presence in Site 1 relative to the remaining sites within Zone A, Langebaan Lagoon. Notably, human numbers were tenfold greater in summer than in winter. In contrast, Sites 3, 4, and 5 experienced little to no human visitors in both seasons. These results align with the findings of Nel and Branch (2014) who noted seasonal variability in human numbers, with the highest values occurring in summer and spring and the lowest in winter. The increased human numbers in Sites 1 and 2 (to a much lesser degree), can likely be attributed to their ease of accessibility by foot as well as their proximity to Shark Bay and Langebaan Village (Siebert & Branch, 2005; Nel & Branch, 2013; Nel & Branch, 2014). Conversely, the lower human numbers in Sites 3, 4, and 5 are likely due to their greater distance from the main access point. Thus, accessibility establishes a sharp human disturbance spatial gradient across the sites in Zone A, which forms the foundation of this study.

Water temperature, dissolved oxygen concentration, salinity, and phytoplankton biomass, exhibited limited variability among the sampling sites. This is consistent with Shannon and Stander's (1977) findings that the lagoon's water column physicochemical variables such as temperature and salinity exhibit minimal variation. This study further observed no significant spatial differences in sediment organic matter. However, sediment particle size varied among the sites, with a general increase from Site 1 to 5. This variation could be attributed to disturbance-induced changes in sandprawn bioturbation and bio-irrigation activities, which are influential ecosystem engineering processes that are known to alter sediment granulometry (Suchanek & Colin, 1986; Wynberg & Branch, 1994; Nel & Branch, 2013). In particular, sandprawn activities mobilise finer particles to the surface and typically result in the formation of mounds around their burrow openings (Suchanek & Colin, 1986; Wynberg & Branch, 1994; Nel & Branch, 2013). Additionally, studies have established a strong connection between sediment particle sizes and the effects of bait collecting and trampling (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Contessa & Bird, 2004; Siebert & Branch, 2005). The collection and removal of endobenthic sandprawns result in the deposition of finer sediment on the surface while simultaneously causing the accumulation of coarser sediment at greater depths (Wynberg & Branch, 1994; Contessa & Bird, 2004; Siebert & Branch, 2005). Finer sediment characteristics, including increased surface area, cohesion, and smaller pore spaces, contribute to increasing compaction though this is likely exacerbated by decadal-scale trampling by people (Scarlatos & Kim, 2002; Li et al., 2023). During sampling, the sediment of Site 1 was consistently firmer than other sites, indicating greater compaction. Fine sediment and compaction also limit dissolved oxygen penetration (Skilleter et al., 2005; Kemp et al., 2011; Jones et al., 2012). At extremes, low oxygen levels can severely compromise benthic ecosystem functioning by hindering the regulation of benthic geochemical cycles, benthic community structure, complexity, and diversity (Rosenberg et al., 2001).

Sediment redox conditions measured in this study based on sediment core colour changes, appear to reflect the gradient in human numbers across the sampling sites, with sediment colouration shifting from being darker at Site 1 to lighter at Site 5. Previous studies in Langebaan Lagoon (Wynberg & Branch, 1994) and Coronet Bay, Australia (Contessa & Bird, 2004), have highlighted reduced sediment oxygen levels due to the removal of ghost shrimp and associated benthic trampling. These activities lead to the collapse of burrows and hinder the mobility of benthic organisms, thereby limiting their capacity to fulfil crucial ecological roles (Wynberg & Branch, 1994; Contessa & Bird, 2004). Burrowing organisms are essential for bioturbation and bio-irrigation processes that oxygenate sediment at greater depths

(Wynberg & Branch, 1994; Contessa & Bird, 2004). These processes greatly impact the distribution and complexity of sympatric assemblages (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997). Although this study did not directly measure hydrogen sulphide concentrations, sediment colouration is an indicator of its redox state (Rosenberg et al., 2001). The darker, grey sediment at Site 1 likely indicates the presence of iron sulphide and hypoxic/anoxic conditions, while the lighter sediment at Site 5 suggests a more oxygenated benthic environment (Rosenberg et al., 2001). Iron sulphide poses a significant threat to benthic organisms, especially with prolonged exposure (Rosenberg et al., 2001; Choi et al., 2023). It is plausible that the substantial number of human visitors in Site 1, and the associated disturbance caused, leads to a benthic shift in finer-grained sediment, benthic compaction and a reduction of essential biogeochemical processes based on low oxygen levels (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Nel & Branch, 2013; Nel & Branch, 2014). At Sites 3, 4 and 5, where people are virtually absent, the sediment is more porous (based on observations during sampling) and lighter in colour, suggesting little evidence for oxygen depletion.

5.2 Sandprawn Population Responses

Contrary to my hypothesis, sandprawn population-level metrics (CPUE), were not significantly lower at Site 1 and did not vary among the sites. The effects of bait collection and trampling on sandprawn populations in Langebaan Lagoon have been extensively studied (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Nel & Branch, 2013; Nel & Branch, 2014). Wynberg and Branch (1991) reported a notable reduction in sandprawn densities and modal body sizes in highly disturbed sites across the whole lagoon, attributed to harvesting intensity. Subsequent studies conducted in 1994 and 1997 further emphasised that sandprawn densities required well over 6 weeks post-disturbance to fully (Wynberg & Branch, 1997). Similar declines in population densities and sizes were observed in Brazil for *Callichirus corruptus* (Botter-Carvalho et al., 2007; Hernáez et al. 2019; Moschetto et al., 2020). Another study further noted that intense bait collection of the ghost shrimp, *Trypaea australiensis*, adversely affected its distribution in an Australian coastal embayment (Skilleter et al., 2005). However, in my study, CPUE showed no significant variation across the sites. While it may be initially presumed that human visitors at Site 1 limit quantities of sandprawns collected, this seems unlikely. This is because Nel and Branch (2014) reported that bait collectors on average removed 86 sandprawns per collection event, which exceeds the legal daily limit by 36 sandprawns. Instead, a more plausible explanation is that within the sites sampled in Zone A, harvesting was probably restricted to Site 1 (based on human numbers) with Sites 2, 3, 4, and 5 largely having virtually unharvested sandprawn populations. Expressed differently, 80% of the sampling sites had sandprawn populations that were largely unaffected by harvesting. Thus, these undisturbed sites could have served as a viable source population from which individuals could colonise Site 1. This is possible due to the proximity of the sites which are only separated by 200m and the known ability of sandprawns to a construct highly extensive burrowing network (Pillay & Branch, 2011).

The findings of this study indicate significant variation in sandprawn body conditions among the sampling sites, with sandprawns at Site 1 (greatest human numbers) displaying better body conditions than those at other sites. These findings are similar to research conducted by Kallberg Normark et al. (2022), who reported greater sandprawn condition in Zone A of Langebaan Lagoon compared with Zone C. While providing a mechanistic explanation for these observations is challenging, one possible explanation is that higher body conditions are an adaptive response of sandprawns to the abiotic environment. The compacted, firm, and poorly oxygenated sediment recorded in Site 1, especially during summer, may necessitate sandprawns to maintain better physical conditions, potentially involving increased body mass for a given body length, to cope with these sedimentary conditions. Alternatively, improved body conditions could result from resource trade-offs, with body conditions being prioritised at the expense of reproduction (Shine, 1989; Shimoda et al., 2004; O'Brien et al., 2017; Chumsri et al., 2023). This aspect regarding potential trade-offs among sandprawns will be addressed in more detail later in the discussion.

5.2.1 Reproductive Responses: Sexual Dimorphism

Previous research on endobenthic burrowing prawns, conducted both locally and internationally, has focused on general biology and anatomy (Forbes, 1976; Tamaki, 1994; Botter-Carvalho et al., 2007; Peiró et al., 2014; Hernáez et al., 2018). However, while sexual dimorphism in endobenthic burrowing prawns has been noted, changes in response to stressors have rarely been quantified (Peiró et al., 2014). Notably, research on how human disturbance impacts sexually selected traits of other crustaceans is gaining popularity (Gül & Griffen, 2020; Costa et al., 2022). Contrary to my hypothesis, sexual dimorphism variability in sandprawns was not impacted by spatial variance in human numbers. However, examination of the predicted maximum differentials and the adjusted means of major chela length for male and female sandprawns, revealed evidence of spatial variance, although without statistical support. Female adjusted mean major chela lengths were greatest at Site 1 and decreased to Site 5, while the opposite trend was evident for males. Additionally, when chela length was standardised to a maximum sandprawn carapace length, sexual dimorphism was reduced at Site 1 in both seasons, driven by female chela length increasing and secondarily by male chela length decreasing. Sexually selected traits, such as sandprawn major chelae, are significantly influenced by environmental conditions, including the availability and quality of resources, biotic pressures, and predatory interactions (Cothran & Jeyasingh, 2010; Gül & Griffen, 2020; Costa et al., 2022). Consequently, habitats exposed to stress may indirectly impact the success and variability of sexually selected traits (Cothran & Jeyasingh, 2010; Iglesias-Carrasco et al., 2016; Gül & Griffen, 2020; Costa et al., 2022; Potter et al., 2022). These traits are known to be resource-intensive, requiring substantial production and maintenance costs (Shimoda et al., 2004; Cothran & Jeyasingh, 2010; Yoshino et al., 2011; Gül & Griffen, 2020). As a result, the qualitative reduction in sexual dimorphism exhibited in Site 1 (greatest human numbers) is likely a consequence of resource trade-offs which will be elaborated upon later in this discussion.

5.2.2 Reproductive Responses: Embryonic Variability

Embryogenesis, the developmental changes an embryo undergoes, is considered one of the most crucial and sensitive phases in the biological life cycle (Jackson, 1985; Sundelin & Eriksson, 1998; Jackson et al., 2005; Richmond et al., 2018). The hypersensitivity of embryos makes them susceptible to unfavourable environmental conditions or stressors during specific developmental stages, leading to malformations, and atypical phenotypes in some cases (Jackson, 1985; Parsons, 1992; Sundelin & Eriksson, 1998; Koopman et al., 2015; Karlson et al., 2018; Du et al., 2020; Torres et al., 2020).

As hypothesised, the highest percentage of abnormalities in sandprawn eggs and embryos were recorded in Site 1, which had the greatest number of human visitors in winter and summer within Zone A. Moreover, eggs and embryos from Sites 1 and 2 were in earlier developmental stages compared to those from the other sites, suggesting arrested development (Kast-

Hutcheson et al., 2001; Mu & LeBlanc, 2002; Rosa et al., 2012; Koopman et al., 2015; Gravinese, 2018; Du et al., 2020). Stress during prenatal development can profoundly impact the development of embryos and offspring (O'Brien et al., 2017). This stress can originate maternally (applied indirectly to reproducing females), embryonically (applied directly to developing embryos) or in combination (O'Brien et al., 2017). While prenatal stress has been extensively researched in various species, it remains uncertain whether the observed consequences stem from stress responses in the embryos and offspring or are instead transmitted maternally (Weinstock, 2008; Favreau-Peigné et al., 2014; O'Brien et al., 2017). A plausible mechanism for the effects of prenatal stress on offspring involves the transmission of stress hormones, such as glucocorticoids and catecholamines, from the mother to the developing embryo via the egg yolk (O'Brien et al., 2017). Although on a population level, adult sandprawns seem unaffected by site differences, it is possible that adults are affected physiologically to low oxygen concentrations and sediment compaction levels at Site 1 and are subsequently transmitting stress compounds to eggs and embryos. Therefore, these embryos may become more vulnerable to low oxygen levels and potentially hydrogen sulphide at Site 1, potentially resulting in the increased frequency of abnormalities and arrested development.

As far as I am aware, Jackson (1985) and Jackson et al. (2004) are the only studies that have investigated developmental changes in *Kraussilichirus kraussi* embryos when exposed to stressors (crude oils and metal contaminants). Unfortunately, there is a notable knowledge gap on the influences of other human disturbances on the reproductive biology of burrowing shrimp. Nonetheless, various studies have reported embryonic responses in other crustacea when exposed to stressors such as sediment contaminants (Sundelin & Eriksson, 1998; Coiro et al., 2000; Karlson et al., 2018; Sun et al., 2020; Choi et al., 2023) and environmental perturbations such as fluctuating temperature, pH and salinity (Koopman et al., 2015; Pardo &

Costa, 2021). In line with my findings, the frequency of malformed eggs in the deposit-feeding Baltic Sea amphipod *Monoporeia affinis* was highest in areas near kraft pulp mills that discharge chlorinated guaiacols (Sundelin & Eriksson, 1998). These amphipods displayed embryonic abnormalities including enlarged eggs, and eggs with aberrated cleavages (Sundelin & Eriksson, 1998). Moreover, amphipods found in areas closest to discharge exhibited a similar feature to the one described in this study, viz. damaged egg membranes. These embryos had membranes described as fragile and prone to bursting (Sundelin & Eriksson, 1998).

Damaged egg membranes (Malformation type 1) were the most frequently recorded malformation in my study, being statistically more frequent at Site 2, followed by Site 1, relative to the other sites. The incidence of malformation type 2 (opaque/discoloured egg membrane) did not vary statistically among sites; however, Site 1 had twice as many eggs and embryos exhibiting this abnormality relative to the remaining sites. Malformation type 3 (ruptured and discoloured egg membrane) was most frequently recorded in Site 1 followed by Site 2. The discolouration of the sandprawn egg membrane may indicate inhibition of its functionality. An experiment conducted by Jackson (1985) revealed that all sandprawn larvae that hatched from opaque egg membranes did not survive past the first moult. These hatched larvae were less mobile, as they remained in a “curled up” position, with their tails bent and their “heads” appearing rounded (Jackson, 1985). Egg membranes serve to protect embryos from harsh environmental stressors such as unfavourable salinity, pH, and temperature (Bas et al., 2022). They are also essential for embryonic osmoregulation, by regulating selective ion transfer to an intramembrane area (Bas et al., 2022). Since hydrogen sulphide can increase the permeability of cell membranes, sandprawn egg membrane discolouration in Sites 1 and 2 may be indicative of impaired functionality, probably in response to low oxygen conditions and exposure to hydrogen sulphide (Riahi & Rowley, 2014). Hydrogen sulphide also induces oxidative stress, which could be detrimental to developing embryos (Riahi & Rowley, 2014; Bas et al., 2022). Therefore, it is plausible that the observed arrested development in this study in the sites with the greatest human numbers is also a consequence of exposure to low oxygen conditions. Numerous studies have highlighted the adverse effects of anoxic and hypoxic conditions on the embryonic development in various marine crustaceans including copepods (Marcus et al., 2004; Choi et al., 2023), the blue crab *Callinectes sapidus* (Tomasetti et al., 2018), the marsh grass shrimp *Palaemon vulgaris* (Coiro et al., 2000), and the oriental river prawn *Macrobrachium nipponense* (Sun et al., 2020). In response to anoxia, embryos of the squid *Loligo vulgaris* showing arrested development were reported to have decreased oxygen consumption rates and exhibited active metabolic suppression (Rosa et al., 2012). Metabolic demands such as cell division and vital organ formation in early embryonic development are suppressed to allow the embryos to conserve energy/resources and prioritise survival (Rosa et al., 2012; Choi et al., 2023). Under oxidative stress, invertebrate eggs sometimes maximise oxygen diffusion by swelling to increase their surface area and decrease egg membrane thickness (Rosa et al., 2012).

Exposure to hydrogen sulphide has been known to induce other notable reproductive responses. For instance, hypoxic conditions were found to inhibit the endocrine system and induce metabolic abnormalities in the oriental river prawn (Sun et al., 2020). In this study, male prawns exposed to hypoxia displayed significantly reduced testicular germ cell quality, delayed testicular development and a hormone imbalance, particularly between testosterone and oestradiol (Sun et al., 2020). Notably, Sun et al. (2020) reported that the F1 generation (first filial generation of offspring) of male prawns exposed to hypoxia exhibited abnormal embryonic development, decreased hatching success and larval development, even though the F1 generation was not directly exposed to hypoxic conditions. Given the increased frequency of darker sediment at Site 1, the higher levels of embryonic malformations and eggs showing arrested development likely arise from exposure to hydrogen sulphide. In turn, the arrested development of sandprawn embryos could be a result of a reduction in egg membrane thickness as well as metabolic suppression. Furthermore, hydrogen sulphide effects that cause embryonic malformations likely incur developmental resource costs, thereby inducing arrested development (Jackson, 1985; Kast-Hutcheson et al., 2001; Rosa et al., 2012; Du et al., 2020).

The fecundity of macroinvertebrates is often used as an indicator of stress (Stockwell et al., 2003; Peiró et al., 2014; Foo & Byrne, 2017). Fecundity determines a population's reproductive capacity and sheds light on its adaptive strategies in response to environmental conditions (Peiró et al., 2014). Factors like larval survival, altered behaviour, and prolonged exposure to stressors can influence fecundity (Li et al., 2011; Koopman et al., 2015; Costa et al., 2020). Conversely to what was hypothesised, significantly higher female sandprawn fecundity was observed at Site 2. However, the pattern across sites was not consistently strong, as values at Sites 1, 3, 4 and 5 were similar. In contrast, research has shown that female fecundity tends to decrease under stressful conditions, as observed by studies such as Costa et al. (2020) and Karlson et al. (2018). For instance, Costa et al. (2020) reported reduced female prawn fecundity in areas subject to burrowing shrimp fisheries compared to unexploited sites. While egg and embryo biomass did not significantly differ across the sites in this study, the adjusted means for egg and embryo dry biomass were highest at Sites 4 and 5. This variation in biomass may be attributed to more embryos in these sites being in advanced developmental stages, compared to those from Sites 1, 2, and 3, aligning with observations made by Forbes (1973) that sandprawn embryos grow larger as they develop.

It is important to note that the results obtained for embryo malformations and development originate from a single winter sample since females were not gravid in summer. Furthermore, human numbers recorded in this study were lower during winter than summer, and lower in winter than previously recorded by Nel and Branch (2014) in Langebaan Lagoon. Despite the low human numbers, clear effects on sandprawn embryonic quality and development were detected, suggesting that even under low human numbers, egg and embryo metrics may be sensitive and robust indicators that can signal bait collection and trampling stress. Notably, human numbers peak during the summer season in the lagoon, with spikes occurring on weekends, public holidays, and especially during festive occasions like Christmas, New Year's, and Easter (Nel & Branch, 2014). Thus, it is plausible that the observed embryonic responses in sandprawns may be attributed to a legacy effect stemming from greater human numbers that occur during summer. This is because during summer, intense bait collection and trampling have severe implications on sediment, and these effects are likely carried over to the following winter season and maintained by smaller numbers of people.

5.3 Resource Trade-offs

Activities with high energy demands, including growth, maintenance, foraging for food, and reproduction, rely on a finite number of resources in the environment (Merkling et al., 2017). Consequently, individuals are required to make energetic trade-offs to optimise their overall fitness (Merkling et al., 2017). These trade-offs often involve prioritising between survival and reproduction (Kelly et al., 2016; Merkling et al., 2017; Gül & Griffen, 2020; Costa et al., 2022). This becomes particularly challenging under stressful conditions, where individuals are required to prioritise one aspect at the expense of the other (Kelly et al., 2016; Gül & Griffen, 2020; Costa et al., 2022).

At sexual maturity, males, including sandprawns, allocate resources towards the production and maintenance of disproportionally large major chela, whilst females, including sandprawns, prioritise resource allocation for egg production (Shine, 1989; Sundelin & Eriksson, 1998). Simultaneously, sandprawns rework the sediment at high rates which likely demands substantial resources (Pillay & Branch, 2011; Hodgson, 2018). Therefore, the high human numbers at Site 1, and the associated observed sediment compaction and low oxygenation, likely necessitate prioritisation of self-maintenance, stomatic growth and overall survival in sandprawns over reproduction. This resource shift is exemplified by the larger, and improved body conditions of individuals recorded at Site 1, in contrast to the remaining sites. Moreover, the reduction in sexual dimorphism at Site 1 (albeit unsupported statistically) suggests a shift away from investment in reproduction. Thus, the increase in the frequency of abnormalities and arrested development in eggs and embryos at Site 1 further suggests a reduction in investment in reproduction. Recent research has highlighted shifts in resource trade-offs in response to human disturbances, for the Atlantic ghost crab *Ocypode quadrata* (Gül & Griffen, 2020; Costa et al., 2022). However, there remains a noticeable gap in the literature regarding the consequences of bait collection and trampling as stressors on sandprawn resource allocation shifts in the context of reproduction.

5.4 Study Implications

Based on CPUE, sandprawn populations within this study's sampling area in Langebaan Lagoon appear to be robust and minimally affected by human disturbance. However, a closer examination of egg and embryo malformations and development changes reveals that increasing human numbers and associated sedimentary changes may negatively impact reproduction. Beyond my study, these findings flag a concern, regarding the potential for high human numbers to impact reproduction and potentially sandprawn populations, given the pivotal role sandprawns play as ecosystem engineers and in sedimentary ecosystems (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Venter et al., 2020). Sandprawns significantly alter sediment biogeochemistry and structure at a remarkable rate, thereby influencing the distribution and abundance of co-existing organisms (Pillay & Branch, 2011). These ecosystem engineers replenish their burrows and adjacent sediment with oxygen and nutrients while flushing out harmful toxins and faecal matter (Pillay, 2010; Pillay & Branch, 2011; Venter et al., 2020). Recent research by Venter, Pillay, and Prayag (2020) further demonstrated the significant role of sandprawns in improving coastal ecosystems by improving water quality through filtrations associated with bi-directional water pumping.

The persistence of marine invertebrate populations, including sandprawns, relies on successful reproductive and recruitment processes (Richmond et al., 2018). The production of offspring becomes trivial unless larvae can successfully recruit and reproduce, and contribute to sustaining the population (Richmond et al., 2018). The adverse effects of human disturbance on sandprawn embryos are likely to result from resource trade-offs, as these organisms prioritise survival/maintenance over reproduction. In the context of Langebaan Lagoon, its division into three distinct zones facilitates effective management, particularly in regulating human presence and activity (Wynberg & Branch, 1991). Sampling for this study occurred over a linear distance of 1km across a gradient of increasing human numbers in Zone A, to reduce the influence of confounding abiotic variables and processes that can mask human disturbance, and to avoid sampling disturbance in the protected sanctuary area (Zone C). Notably, this study’s findings showed localised human disturbance within a 200m area closest to the main public access point (Site 1).

To the best of my knowledge, there are few similar coastal sedimentary habitats in South Africa that simultaneously regulate human numbers and exhibit minimal environmental variation. Most other South African estuarine systems typically exhibit strong longitudinal gradients, particularly salinity (Day, 1959; Wynberg & Branch, 1991). It is thus plausible that the adverse embryonic responses detected in sites from this study with high human numbers could be significantly magnified in other coastal habitats which lack human spatial management and probably experience greater foot traffic, harvesting and recreation that has persisted over decadal timescales. The increase in egg malformations and arrested development with increasing human numbers, as evident at Site 1, flags a broad concern that expected increases in recreation demand in future, may generate negative consequences for sandprawn juveniles and populations, with further ramifications for key ecosystem functions (sediment oxygenation, water filtration) they provide.

Prior research investigating the impact of human disturbance on sandprawns has primarily relied on burrow counting to estimate population densities (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Nel & Branch, 2013). However, these methods have yielded inconsistent results, leaving uncertainties about the consequences of recreational activities for sandprawn populations (Wynberg & Branch, 1991; Wynberg & Branch, 1994; Wynberg & Branch, 1997; Nel & Branch, 2013). This inconsistency raises concerns, as effective ecosystem management necessitates accurate, early detection of ecosystem health deterioration before irreversible changes occur, including loss of biodiversity and/or functionally important species (Dale & Beyeler, 2001; Coleman & Williams, 2002). To the best of my knowledge, sandprawn eggs and embryos have not previously been utilised as indicators for recreational disturbance. However, based on the findings of this study, the embryonic responses detected can act as useful sentinels of recreational disturbances and potentially other stressors. The embryonic responses recorded can be attributed to sediment compaction, low sediment oxygen levels and exposure to hydrogen sulphide. These stressors; however, are not exclusive to human trampling and bait collection. Other environmental stressors that induce similar sediment biogeochemical changes are likely to yield comparable embryonic responses. Thus, in theory, these eggs and embryos can serve as indicators of various stressors including impairment of bioturbation, climate change, pollutants, and exposure to trace metals, as observed by Jackson (1985) and Jackson et al. (2004). The caveat though is that further testing of embryonic responses to diverse stressors is required in future.

The utilisation of embryonic responses to identify and signal ecological stress is well-recognised (Sundelin & Eriksson, 1998; Oh & Hartnoll, 1999; O'Brien et al., 2017; Karlson et al., 2018). However, equivalent research for burrowing shrimps has rarely been carried out previously. Burrowing shrimps are known for their resilience, adaptability, and wide distribution regionally and globally (Pillay & Branch, 2011). The ubiquitous sandprawn distribution along South Africa’s coastline allows these organisms to serve as an effective bioindicator in coastal sedimentary habitats locally. This is crucial because bioindicators that are applicable across several habitats provide a valuable opportunity for comparative research into stressor effects across large spatial scales (Reutgard & Furuhagen, 2016). Adding to the utility of sandprawns as bioindicators, especially in the context of eggs and embryos, is the fact that these organisms lack a planktonic stage and undergo direct development, implying that monitoring of eggs and embryos may provide important information on the stress applied to adult populations and trade-offs in resource allocation that occur consequently. Lastly, the retention of eggs and embryos by female sandprawns throughout embryogenesis implies that these embryos reflect local conditions and stressors, and that they could be valuable monitoring tools at a local level. Overall, this study shows the potential for sandprawn embryonic responses to provide a novel and sensitive tool for detecting ecosystem stress, primarily in response to trampling and bait collecting.

5.5 Conclusion

This study has shed light on the effect of human recreation and associated disturbance on a key ecosystem engineer, *Kraussilichirus kraussi* (sandprawn), in Langebaan Lagoon, South Africa. Coastal sedimentary habitats, like the one under investigation, are of immense ecological and economic importance. However, human-related disturbances, such as trampling and bait collection, which have severe ecological consequences, are increasing in such habitats. This study therefore aimed to further our understanding of how human disturbance impacts sandprawn populations, their reproduction, and the potential implications for the ecological services they provide.

The findings from this research highlight several key insights. Sediment compaction and low oxygen levels in Site 1 likely stemmed from the substantial number of human visitors. At a population level, no significant differences in sandprawn CPUE were detected across the sites, suggesting that the sandprawn population across the sampling sites were minimally influenced by changes in human numbers and associated disturbance. Additionally, sandprawns in Site 1 exhibited better body conditions than those from the other sites. This finding likely reflects resource trade-offs in which sandprawns at Site 1 have shifted resources away from reproduction to prioritise self-maintenance and survival. This idea is supported by the notably high percentages of sandprawn eggs and embryos exhibiting abnormalities and arrested development in sites with increased human numbers. Overall, while recent research has shown a growing interest in using sandprawns as indicators of ecological stress, the findings of this study expand on this idea, by linking human recreational disturbances with the reproductive biology of sandprawns (Venter et al., 2020; Kallberg-Normark et al., 2022). While the sandprawn population itself appears negligibly impacted by human disturbance, adverse effects on reproductive outputs, particularly the high embryonic abnormalities and arrested development, are cause for concern, especially for systems in which human numbers are not managed/regulated. In particular, chronic legacy effects of recreational disturbance may lead to population-level consequences, which in turn may compromise essential ecological functions provided. Further research linking human disturbance to sandprawn reproduction in other coastal ecosystems can advance understanding of this phenomenon and its management in the future. Additionally, data collection over longer time frames and larger spatial areas would be greatly insightful.

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7. APPENDIX

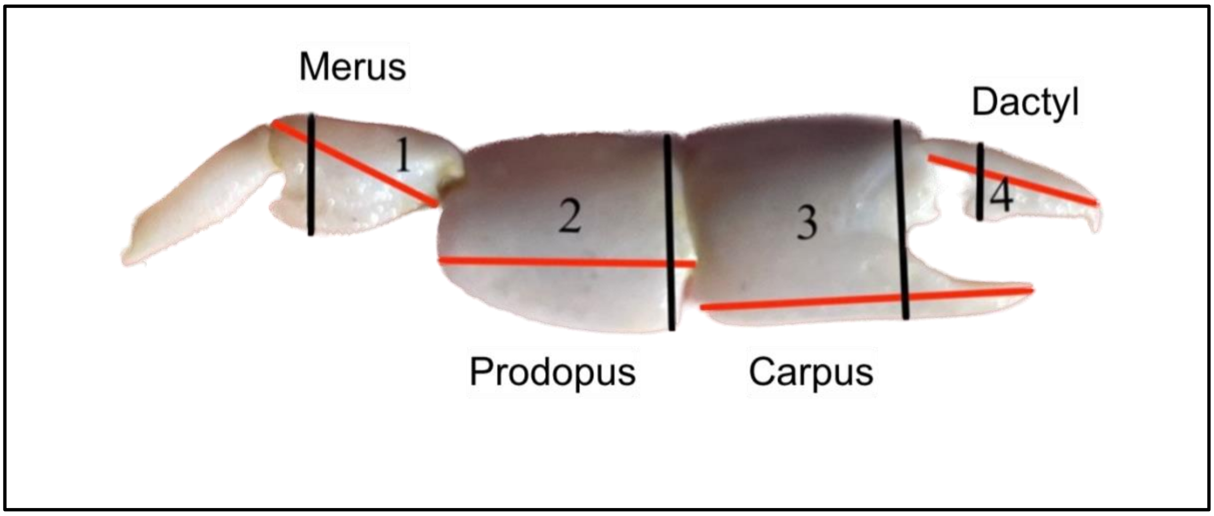

Figure A 1. *Diagram of the sandprawn major chela. The numbers indicate the segment label; 1 = Merus; 2 = Prodopus; 3 = Carpus; 4 = Dactyl. Total major chela length for this study was measured from the start of the merus to the end of the dactyl.*

Table A 1. *Statistical transformations applied to each response variable.*

Transformation	Response variable
Log	Sediment particle size; Sediment organic matter content; Sandprawn major chela length; Body condition; Sexual Dimorphism
Square root	Total CPUE; Male CPUE; Female CPUE; Juvenile CPUE
Logit	Egg and embryo malformation percentage occurrence
n/a	Fecundity; Egg and embryo biomass; Egg and embryo development stage

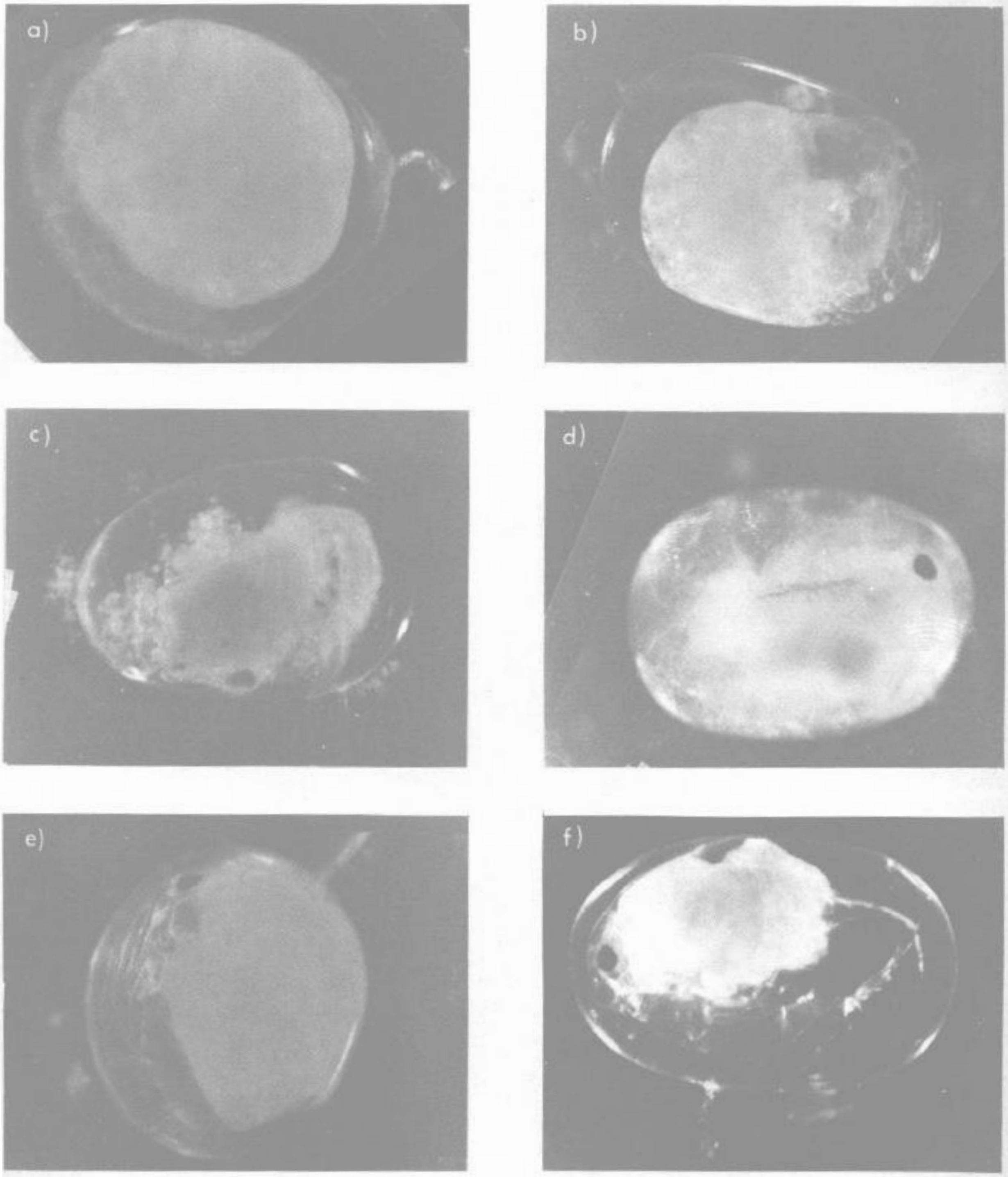

Figure A 2. *Embryonic developmental staged and malformation types expressed in the sandprawn* <u>*Kraussillichirus kraussi*</u>. *(a) Development stage 1; (b) Development stage 2; (c) Development stage 3, Malformation type 1; (d) Development stage 4, with Malformation type 2; (e) Development stage 5; (f) Development stage 5, advanced. Image source: Jackson (1985).*