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Investigating the effects of climatic variability on long term behavioural activity budgets of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia

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University of Bristol

Abstract

Extreme climatic events (ECEs) can alter key animal behaviours. Understanding how animals are likely to respond behaviourally to ECEs will help inform conservation decisions in the face of climate change. However, upon reviewing the literature on animal behavioural responses to ECEs, it is clear that there remains a large gap in our understanding. This study aims to address this research gap by investigating the effects of climatic variability, including the Southern Oscillation Index and sea surface temperatures, on the behavioural activity budgets of Shark Bay's Indo-Pacific bottlenose dolphin population. An individual level approach was used for two study sites, including the eastern gulf, with a sample size of 198 males and 164 females from 1991-2020, and the western gulf, with a sample size of 86 males and 51 females from 2009-2019. A population level approach was also taken in the eastern gulf and included 2,055 individuals from 2009-2020. Foraging and socialising activity were significantly affected by extreme Southern Oscillation events, including La Niña and El Niño. Focusing on a 2011 marine heatwave event, individual foraging budgets dropped significantly immediately after this ECE, and then increased to peak levels in 2016. Prey availability likely peaked immediately post-heatwave as seagrass cover declined, then became scarce thereafter, requiring greater foraging effort. In contrast, individual socialising budgets increased immediately after the ECE and then dropped in subsequent years. Between sex differences in behavioural response were also detected, including lower foraging activity budgets and higher socialising activity budgets for male dolphins, likely due to sex-differences in reproductive strategies. Differences in activity budgets of tool-users vs non-tool-users were also investigated, with tool-using dolphins spending more time foraging than non-tool-using dolphins, which confirms previous research. This work indicates that ECEs can have a significant and long-lasting impact on the key behaviours of even behaviourally flexible marine predators.

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Author’s declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: ....Natalie Klepacova... DATE:......02/11/21....................

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Chapter 1 – Behavioural responses to extreme climatic events: an introductory review

1.1 Introduction

One of the consequences of the anthropogenic climate change is the proliferation of extreme climatic events (ECEs) (Jarraud & Steiner, 2012; Oliver et al., 2018), which can be defined as unusual climatic events that alter ecosystem structure and function beyond what would be considered typical (Smale et al., 2019; Smith, 2011). ECEs can include severe droughts, floods, heatwaves and hurricanes (Solomon et al., 2007), to which direct and indirect negative effects on species and communities have often been attributed (Nowicki et al., 2019; Piatt et al., 2020; Santora et al., 2020; Smale et al., 2019; Von Biela et al., 2018; Wernberg et al., 2013). ECEs are predicted to become more frequent and severe as a result of ongoing climate change, with potentially deleterious consequences for vulnerable ecosystems (Jarraud & Steiner, 2012; Mitchell et al., 2006; Oliver et al., 2018). In order to establish effective conservation measures and minimise the impacts of future ECEs, it is important to understand how animals respond to them (Buchholz et al., 2019; Pecl et al., 2017).

Understanding how animals respond to climate change has been a primary focus for biologists in recent years (Cohen et al., 2018; Schleuning et al., 2020). However, many of our modelling predictions for animal responses still concentrate on climatic trends, such as projected mean temperatures, instead of acute climatic events (Cheung et al., 2012; Jentsch et al., 2007; Wernberg et al., 2013). Currently, there remains a lack of evidence regarding animal responses to ECEs, in particular behavioural responses (Beever et al., 2017; Buchholz et al., 2019; Nowicki et al., 2019). The majority of evidence regarding behavioural responses to ECEs has been classified as either anecdotal or incidental to studies focusing on animal physiology (Buchholz et al., 2019). In this introductory review, I have compiled recent studies focusing on behavioural responses to ECEs. I examine studies that explore the effects of ECEs on key behaviours, including foraging and socialising, then discuss how behavioural flexibility, as well as life-history trade-offs, may play a role in species responses to climatic events.

1.2 Extreme climatic events and foraging behaviour

Animals forage to find food and meet their energetic demands, but finding these resources can be challenging when the foraging landscape changes dramatically, for example, in response to a climatic event (Rosenblatt & Schmitz, 2016; Sato et al., 2014). In the examples below, I look at the effects of

ECEs on primary producers to top level consumers and discuss how climatic events can disrupt the energy transfer in previously stable food webs. The changes in the abundance and nutritional value of forage or prey species described in the studies below may help to elucidate why we see differing foraging behaviours in higher trophic levels following an ECE. These studies also show how changes in prey distribution due to mass mortalities or emigrations in response to ECEs can have further negative effects on consumer species and may explain breeding failures of top predators. Overall, these studies illustrate how ECEs can have significant indirect effects on higher trophic levels.

Marine heatwaves (MHWs), in which sea temperatures rise to abnormally high levels for a period of time, are just one example of an ECE. MHWs can impact marine ecosystems for days or, in some cases, for many years after the initial event (Nowicki et al., 2019; Oliver et al., 2018; Wernberg et al., 2016). From 2013-2016, a MHW known as ‘the Blob’ occurred in the North Pacific Ocean. Von Biela et al. (2018) investigated how this ECE affected energy transfer from lower to higher trophic levels in the Gulf of Alaska by studying a key forage fish species. The Pacific sand lance (*Amodytes personatus*) is one of the most important prey species for a variety of consumers in the Gulf of Alaska, including predatory fish, sea birds, and marine mammals (Piatt et al., 2018). Von Biela et al. (2018) examined the nutritional value of the Pacific sand lance during the years encompassing ‘the Blob’ and found an 89% decrease in nutritional value by 2016, as well as a decrease in its abundance. This significant decrease in nutritional value, as well as the likely effects on predatory species, were explained with regards to a disruption in energy transfer (Von Biela et al. 2018). Lower trophic level species such as zooplankton are primary prey sources for Pacific sand lance. In warmer weather, communities of zooplankton in the study area tend to be dominated by smaller and less nutritious species (Piatt et al., 2018; Von Biela et al., 2018). Von Biela et al. (2018) suggested that, during the MHW, sand lances were still consuming zooplankton but receiving less energy in doing so, likely explaining the significant decrease in nutritional value and abundance of sand lances. The decrease in energetic transfer may have impacted higher level consumers that feed on sand lances, such as the common murre (*Uria aalge*), which experienced high mortality and breeding failure following the MHW (Piatt et al., 2020).

As food chains in the North Pacific altered following the Blob, some predators altered their foraging behaviour in response. Black legged kittiwakes (*Rissa tridactyla*), for example, are also reliant on fish as a prey source and were found to increase their foraging ranges and change their foraging behaviour following the MHW, flying further and faster to find food and spending less time resting (Osborne et al. 2020). These changes were attributed to a decrease in fish abundance and nutritional value following the ECE and, significantly, were shown to persist for many years after the MHW, indicating that ECEs can have long lasting effects on animal behaviour (Osborne et al. 2020). King penguins (*Aptenodytes patagonicus*) are another example of a predator altering its foraging behaviour in response to climatic events. Bost et al. (2015) suggested that decreases in prey abundance at lower trophic levels following large-scale climatic events may explain changes in foraging habitat and diving behaviour of king penguins. These examples suggest that ECEs can have indirect and potentially long-lasting effects on the foraging behaviour of higher trophic predators. As these species alter their foraging ranges in response to ECEs, they may be met with unforeseen challenges.

A recent study by Santora et al. (2020) investigated the potential link between changes in the foraging behaviour of North Pacific humpback whales (*Megaptera novaeangliae*) and increased rates of entanglement off the coast of California in the years following the Blob. In the studies referred to above, the potential mechanism driving changes in foraging behaviour was the disruption of energy transfer in food chains due to changes in the abundance of lower trophic levels (Bost et al., 2015; Osborne et al., 2020; Piatt et al., 2020; Von Biela et al., 2018). The same mechanisms likely impacted whale foraging behaviour (Santora et al. 2020). Whale entanglements were found to increase steadily from 2014 to 2016, as the MHW continued to affect the ecosystem. Santora et al. (2020) suggests that, due to changes in prey distribution and foraging areas, whales were more likely to be in areas of high fishing activity and therefore fishing gear, leading to entanglements. It is important to note that ECEs, such as the Blob, will have a large impact on fisheries. Santora et al. (2020) indicated that crab fisheries had to delay opening in the 2015/2016 season because of the MHW. When the fisheries opened, it coincided with the arrival of whales into the area, likely leading to increased whale entanglements. This example illustrates that species changing their foraging behaviour in response to an ECE may be further challenged by interacting with humans dealing with the impacts of the same event.

The studies above highlight the significant and long-lasting impact that a single ECE, such as the Blob, can have on a wide variety of species and trophic levels. Foraging is obviously vital for survival and understanding how ECEs are likely to alter this behaviour across taxa might help us make more informed conservation decisions in order to buffer the known negative consequences of these events. There are other behaviours that are crucial for survival and fitness, such as socialising, which may also be impacted by ECEs.

1.3 Extreme climatic events and socialising behaviour

Socialising is another critical behavioural category in many animals and includes cooperative behaviour to gain food resources (Samuni et al., 2018), affiliations with conspecifics for mating (Connor et al., 2000; King et al., 2021) and aggressive behaviour to defend resources (Baxter & Dukas, 2017). Socialising behaviours can be extremely important for individual survival and reproductive success (Archie et al., 2014; Silk, 2007). While studies investigating the effects of ECEs on animal behaviour have focused primarily on foraging, it remains largely unknown how ECEs will impact the social landscape of animal populations.

A recent study by Testard et al. (2020) investigated the social dynamics of a population of rhesus macaques (*Macaca mulatta*) following a catastrophic climatic event. This population resides on Cayo Santiago Island, Puerto Rico, which was devastated by Hurricane Maria in 2017. Green vegetation declined by 63% following the hurricane, and the macaques were left with little shelter or resources. Interestingly, Testard et al. (2020) found that the macaques formed new social connections and actively sought social contact following this ECE. Furthermore, individuals who were more isolated previously were found to make the most effort in socialising following the hurricane. A possible explanation suggested was the need for a larger number of social partners to call upon in times of resource scarcity. Interesting parallels were also made between the social response of these gregarious monkeys and humans following an ECE in regard to the importance of social relationships in times of stress (Testard et al. 2020). Another plausible explanation for the increase in social connections referred to a lack of shelter following the destruction of vegetation on the island, the authors suggesting that habitat compression may have led to individuals spending more time in closer proximity, leading to increased grooming behaviour which helps to form and strengthen social bonds. This study provides evidence of flexible social behaviour following an ECE in monkeys but Testard et al. (2020) advocate for furthering our understanding of the effects of ECEs on social behaviour in order to explain why some animals are more resilient than others following such an event.

In contrast to these primates increasing their social connections, Rat et al. (2020) found that social structure of a passerine bird became more fragmented and less cohesive during times of extreme and variable environmental temperatures. This study investigated the behaviour of three social weaver (*Philetairus socius*) colonies in the Kalahari Desert in response to extreme temperatures. As temperatures increased to above average levels, social weavers spent more time performing heat dissipation behaviour in order to keep their body temperatures at a viable level (Rat et al. 2020).

Furthermore, while individuals were performing heat dissipation behaviours, such as panting, they would associate less with conspecifics. This decrease in affiliative behaviour may have contributed to the fragmented social structure seen in these colonies. Rat et al. (2020) suggested that there may have been a trade-off between heat dissipation behaviour and socialising behaviour, leading to a less cohesive social network during times of extreme temperatures. The authors go on to discuss how social cohesiveness can be important in protecting against predators or finding food, and that a breakdown in these social colonies may significantly decrease fitness. It is therefore important to understand how ECEs can affect the social behaviour of animals, as climatic changes may impact individual fitness by reducing social cohesion.

Earlier in this introduction, the bottom-up effects of changes in prey distribution and energy transfer were discussed with regards to foraging behaviour. However, changes in the abundance and distribution of lower trophic levels have also been found to effect the social structure of some species. Lusseau et al. (2004) found that Atlantic bottlenose dolphins (*Tursiops truncatus*) and Pacific killer whales (*Orcinus orca*) tended to associate in smaller groups during times of low prey abundance associated with the Atlantic Multidecadal Oscillation. This decrease in group size could influence the choices that individuals make in interacting with other members of the group, potentially driving changes in overall social structure (Lusseau et al. 2004). The long-term repercussions of such a behavioural change have yet to be explored. A decrease in group size following resource distribution changes due to an ECE was also detected in zebra finches (*Taeniopygia guttata*) in New South Wales, Australia (Funghi et al. 2019). Zebra finches tended to forage in smaller groups following extreme increases in air temperature. The consequences of this change in social structure are not yet fully understood but it is possible that smaller group sizes render zebra finches more vulnerable to predation. This research reveals that ECEs can have indirect effects on the social structure of animals, and that more research is needed to determine whether there are subsequent impacts on fitness.

1.4 Behavioural flexibility and trade-offs

The aforementioned studies describe examples of behavioural flexibility, which can be defined as an adaptive change in behaviour in response to a changing environment (Brown & Tait, 2010; Uddin, 2021): Black legged kittiwakes altering their foraging behaviour in response to 'the Blob' and rhesus macaques showing flexibility in their social behaviour following a hurricane, for example (Osborne et al., 2020; Testard et al., 2020). It is now widely accepted that flexibility in such key behaviours will determine how well a community, population or species might adapt to the consequences of climate change (Beever et al., 2017; Buchholz et al., 2019; Sih, 2013).

An example of behavioural flexibility determining the resilience of a population can be seen in the American pikas (*Ochotona princeps*) of the Great Basin, North America. Pikas suffered sharp population declines related to climate change (Beever et al., 2016), but some populations within the Great Basin fared better than others, with a behaviourally unique, low-elevation population even thriving (Beever et al., 2017; Varner et al., 2016). Beever et al. (2017) suggest that this low-elevation population were able to thrive due to flexibility in their foraging behaviour, thermoregulatory behaviour and habitat use. This included spending more time in forested habitat and consuming more moss than their high-elevation counterparts. Behavioural flexibility in this pika population led to increased resilience in the face of climate change. However, these pikas showed flexibility in response to gradual climatic change, and not in response to an ECE. ECEs are acute and severe in nature, and only animals that can adapt their behaviour in a much shorter time span following such sudden changes to their environment will persist. Furthermore, ECEs are predicted to become more frequent, meaning that recovery times for animals between events will decrease, and may be too short to allow for successful changes in behaviour in order to make a recovery (Buchholz et al., 2019).

Beever et al. (2017) stress the importance of understanding the limitations of behavioural flexibility, as well as the fitness implications, when including behaviour in conservation management decisions. In order to understand potential fitness implications following changes in behaviour, we need to recognize fitness trade-offs. In regards to animal behaviour, a trade-off can occur when the increase in one behaviour means a decrease in another, and vice versa (Garland, 2014) - the trade-off between heat dissipation behaviour and socialising in social weavers, for example (Rat et al., 2020). These trade-offs may involve fitness costs if behaviours important for survival are reduced or otherwise compromised. Low prey abundance following an ECE may lead to increased foraging behaviour in consumer species which may, in turn, lead to a reduced predator vigilance trade-off, potentially increasing predation risk. Fitness costs, such as reduced reproductive success or survival, further reveal that climate-related behavioural change may not be sufficient in ensuring the long-term viability of a population or species following an ECE.

Although flexibility in key behaviours is important in an animal's response to climate change, fitness costs and the nature of ECEs themselves may diminish the effectiveness of these adaptations.

Understanding these behavioural responses and their implications on fitness is vital if we are to identify which populations and species are more vulnerable or, indeed, more resilient to ECEs.

1.5 Conclusion

The research introduced here highlights the complexity of animal behavioural responses to ECEs. Using various ECEs as case studies, the sometimes far-reaching and long-lasting impacts of singular climatic events can be seen. The foraging behaviour of many consumer species has been altered in association with such events, including that of black-legged kittiwakes and king penguins, with the potential drivers of this behavioural change being the disruption of food chains and energy transfers (Bost et al., 2015; Osborne et al., 2020; Piatt et al., 2020; Von Biela et al., 2018). Unforeseen challenges following behavioural adaptations in foraging behaviour were also highlighted, with increased whale entanglements from commercial fisheries illustrating the continued threat that anthropogenic activities have on animal survival, and how an ECE can exacerbate this relationship (Santora et al., 2020). Though not well-studied, the impacts of ECEs on socialising behaviour were also discussed, with contrasting outcomes of social cohesion in rhesus macaques and social fragmentation in weavers (Rat et al., 2020; Testard et al., 2020). ECEs were also found to effect social group sizes in animals, from zebra finches to killer whales (Funghi et al., 2019; Lusseau et al., 2004). The importance of behavioural flexibility in buffering the negative impacts of climate change was also highlighted, using studies on American pika as an example (Beever et al., 2017; Varner et al., 2016). Limitations of behavioural flexibility, however, were also noted, touching upon potential fitness trade-offs and the nature of ECEs themselves potentially diminishing the effectiveness of behavioural adaptation. There remain large gaps in our understanding of how ECEs effect animal behaviour. The studies introduced here have a common aim, to encourage further research into this field, with the goal of better informing conservation and management policies in the face of further ECEs associated with climate change.

Chapter 2 – Investigating the effects of climatic variability on long term behavioural activity budgets of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia

2.1 Introduction

2.1.1 Climate events not trends

As we come out of the hottest decade on record (NOAA, 2021), with current atmospheric carbon dioxide at record levels (Global Monitoring Laboratory, NOAA, 2021), it is clear that the climate crisis is not a distant eventuality, but a present day threat. Extreme climatic events (ECEs), introduced in Chapter 1, have received more attention in recent years as agents of change, altering ecosystem structure and function beyond typical margins (Smale et al., 2019; Smith, 2011). This increased attention on climate events, rather than climate trends, is justified considering the rapid and often violent nature of ECEs, allowing little room for organisms to adapt (Babcock et al., 2019).

Assessing the impacts of ECEs on ecosystems and species is a challenging but necessary task. In recent years, there has been impetus to collect more animal response data as climate change continues to alter the environment (Beever et al., 2017; Buchholz et al., 2019; Nagelkerken & Munday, 2016; Oliver et al., 2018). By understanding how animals respond to ECEs, we may be better able to predict what our natural world will look like in a climatically further-altered future. This may enable policy makers and wildlife managers to establish effective conservation measures in order to limit the known impacts of climate change. Given that ECEs are becoming more frequent and severe, understanding species responses is increasingly important (Jarraud & Steiner, 2012; Oliver et al., 2018; Wu et al., 2012).

There remains a gap in our understanding of animal behavioural responses to ECEs for several reasons. Firstly, to accurately assess behavioural responses to ECEs, we need long term behavioural data that encompasses an ECE, the occurrence of which can be difficult to predict. Secondly, long term data collection can be financially and logistically challenging, particularly for long-lived or inaccessible taxa. In regards to published literature, of the studies that have addressed behavioural responses to ECEs, fewer than 25% took place in aquatic environments, and only 7% of studies overall occurred over multiple years (Beever et al., 2017). This may, however, be an artifact of the lack of behavioural research in marine environments compared to terrestrial environments due to the increased difficulty of data collection (Beever et al., 2017; Brakes & Dall, 2016; Buchholz et al., 2019). Nonetheless, there is cause to focus research efforts on understanding behavioural responses to ECEs in aquatic environments over a substantial time frame.

2.1.2 Ningaloo Niño and Shark Bay

One recent example of an ECE that impacted aquatic environments was the 'Ningaloo Niño', a marine heatwave (MHW) that occurred in 2011 off the coast of Western Australia. During this time, sea surface temperatures (SSTs) increased by up to 4°C above long term averages for more than two months (Feng et al., 2013; Nowicki et al., 2019). A combination of factors contributed to this ECE, including the El Niño Southern Oscillation (ENSO) and the Leeuwin Current (Kendrick et al., 2019). ENSO is an atmospheric-oceanic cycle with periodic fluctuations in SSTs and wind that occurs in the tropical Pacific Ocean (Hanley et al., 2003). ENSO has three phases, El Niño, La Niña and neutral, categorized using the Southern Oscillation Index (SOI). For Western Australia, La Niña years typically signify increased precipitation and warmer SSTs (Power et al., 2006), and it was during such a phase that the 2011 MHW occurred. The Leeuwin Current, one of the dominant oceanographic features of Western Australian coastal waters, transports warm tropical waters southwards. It flows with greater strength during La Niña phases and contributed to increased ocean temperatures during the 2011 MHW (Feng et al., 2013). The final factor contributing to the Ningaloo Niño was a reversal of southerly winds that typically help to mediate increased ocean temperatures (Kendrick et al., 2019). The combination of these environmental factors resulted in an intense MHW that had devastating effects on ecosystems along the Western Australian coast (Pearce et al., 2014).

An area particularly affected by the Ningaloo Niño was Shark Bay, a marine embayment located 800km north of Perth. Shark Bay is a Marine Protected Area and World Heritage Area famous for its vast, diverse seagrass beds that provide a benthic habitat for a multitude of species and megafauna (Thomson et al., 2015). Shark Bay also lies on a tropical-temperate boundary and the temperate species that inhabit the area are therefore particularly vulnerable to warming and climatic change. The Ningaloo Niño consequently caused a multitude of cascading ecological effects in this area (Kendrick et al., 2019; Nowicki et al., 2019; Pearce et al., 2014; Wild et al., 2019). Widespread seagrass mortality occurred as a result of the MHW, with *Amphibolis antarctica*, a temperate seagrass species that typically dominates the embayment experiencing a dieback of over 90% in some areas (Thomson et al., 2015). As a result of this seagrass dieback, many benthic species that relied upon this habitat to seek shelter or find prey experienced mass mortalities (Pearce et al., 2014). Further effects included significant population reductions in marine megafauna such as sharks (*Chondrichthians)*, turtles (*Testudines)*, sea snakes (*Hydrophiinae)* and dugongs (*Dugong dugon)* (Nowicki et al., 2019). There was also an immediate and long-term decline in reproduction and survival of Shark Bay's dolphin population (Wild et al., 2019).

2.1.3 Shark Bay dolphins

Shark Bay is characterised by vast shallow areas of sand and seagrass beds (predominantly 0-6m depth), interspersed with deeper (>8m) channels and open embayment plains (Heithaus & Dill, 2002; Tyne et al., 2012). The bay is home to an iconic population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) which has been the subject of long-term research, spanning almost 40 years (Connor and Smolker 1985). There are two gulfs within Shark Bay, western and eastern, each with resident dolphin communities under study by Shark Bay Dolphin Research. Although the communities are separated by only tens of kilometres, there is no exchange between the two communities studied, due to bisexual philopatry whereby individuals of both sexes stay within their natal home ranges (Bacher et al., 2010; Krützen et al., 2004; Tsai & Mann, 2013). These dolphins are highly social and exhibit a fission-fusion grouping pattern, where individuals associate in small groups that frequently change in composition and behaviour, much like humans (*Homo sapiens sapiens*) and chimpanzees (*Pan troglodytes*) (Connor et al., 2000; Smolker et al., 1992).

Within this open social network, the male dolphins in Shark Bay are famously known to form multi-level, cooperative alliances among unrelated individuals (Connor et al., 1992, 2000; Connor & Whitehead, 2005; King et al., 2021). These alliances are thought to be the most complex outside of those formed by humans, and are vital for each male's reproductive success (Connor & Krützen, 2015). Within these multi-level alliances, first-order alliances are formed by pairs or trios of males that work together in order to 'herd' single oestrous females for mating purposes (Connor et al., 1992). These pairs or trios also cooperate with other pairs and trios from within larger, second-order alliances in the pursuit and defence of females (Connor et al., 1992). Second-order alliances are the core unit of male social organisation in Shark Bay and can last decades (Connor & Krützen, 2015). Some second-order alliances also form third-order alliances, which are significant association preferences among two or more second-order alliances that may support each other in the capture and defense of females from other alliances (King et al., 2021). The formation and maintenance of alliances is specific to males, while female associations are weaker and more variable, based on home range overlap, matrilineal and biparental kinship (Connor et al., 2000; Frère et al., 2010; Smolker et al., 1992).

Male and female dolphins in Shark Bay thereby differ markedly in their social affiliations, as they tend to in foraging behaviour. This dolphin population exhibits a wide array of foraging tactics, including two different types of tool use (Allen et al., 2011; Krützen et al., 2014; Mann et al., 2008; Tyne et al., 2012; Wild et al., 2020).The most well studied form of tool use in this population of dolphins is referred to as 'sponging' (Smolker et al., 1997; Krützen et al., 2005; Wild et al., 2019). A conical sponge is carried over the individual's rostrum as a protective 'glove' when seeking prey in benthic habitat (Smolker et al., 1997). This behaviour is predominantly exhibited by females (but see Bizzozzero et al., 2019), and is vertically, socially transmitted down the matriline (Wild et al., 2019). Shelling is the second example of tool use, whereby an individual will chase prey into an empty trumpet (*Syrinx aruanus*) or bailer (*Melo amphora*) shell (Wild et al., 2020). Following the MHW in 2011, sponging dolphins saw less of a decline in survival than did non-sponging individuals in the same habitat, suggesting that perhaps sponging dolphins were able to access a less affected foraging niche (Wild et al., 2019). To better understand the decline in survival and reproduction of Shark Bay's dolphins following the MHW, we can examine the long-term dataset on specific behavioural states over time, before-, during- and after-MHW.

2.1.4 Study aims and objectives

This study aims to address research gaps in behavioural responses to ECEs in marine environments. Using long-term data, collected by the team at Shark Bay Dolphin Research, I will investigate how MHWs effect the behavioural activity of Shark Bay's iconic population of Indo-Pacific bottlenose dolphins. Understanding how specific behaviours fluctuate over the long-term and, more specifically, following the marine heatwave could provide insight into why a decline in reproduction and survival was detected in this dolphin population. The robust behavioural data set from Shark Bay Dolphin Research encompasses the years of the Ningaloo Niño. Using this long-term data set, I will assess whether dolphin behavioural activity budgets (i.e., the proportion of time spent performing behavioural activities including foraging and socialising) were significantly affected by ENSO, as well as SSTs. I will also examine the difference in behavioural activity budgets between males and females, as well as sponging and non-sponging individuals to assess whether tool-users responded differently following the MHW. Furthermore, the two ecologically differing gulfs within Shark Bay provide the opportunity to investigate how the eastern and western dolphin communities may have responded differently to the same marine heatwave.

I hypothesise that an increase in foraging activity could occur as resources become scarce during or after La Niña phases and when SSTs are high. This is based on previous literature describing mass mortalities of prey in the Shark Bay area following a MHW during a La Niña phase (Pearce et al., 2014). Furthermore, I hypothesise differing behavioural responses between males and females regarding socialising behaviour. This could include general increased socialising behaviour in males compared to females due to distinct reproductive strategies, including the formation and maintenance of male alliances involving increased male socialising behaviour (Connor et al., 1992, 2000; Frère et al., 2010; King et al., 2021; Smolker et. al., 1992). I also predict that there will be differing foraging behavioural responses between males and females due to sex differences in foraging behaviours, for example sponging behaviour, that is predominantly exhibited by females (Wild et al., 2019). I also hypothesise a difference in the behavioural changes of individuals in the eastern compared to the western gulf of Shark Bay due to the ecological differences between the two study sites. The western gulf study area contains a larger percentage of favourable habitat for 'sponging' behaviour due to its deep channels, and also less seagrass habitat (Tyne et al. 2012). Seagrass was the major habitat affected by this ECE (Thomson et al., 2015), consequently affecting fish and invertebrate communities in the area (Pearce et al., 2014). I hypothesis that foraging behaviour in general would therefore be expected to be less affected post-heatwave in the western gulf compared to the eastern gulf due to the relative lack of seagrass habitat and more favourable sponging habitat. Furthermore, sponging dolphins can access a different foraging niche (Krützen et al., 2014) and exhibited less precipitous declines in survivorship compared to non-sponging dolphins following the 2011 MHW (Wild et al., 2019). Therefore, I predict that we may see differences in foraging activity budgets of spongers and non-spongers after MHWs.

The main questions to be addressed in this study are as follows: Do activity budgets differ (i) among El Niño, La Niña and neutral years or (ii) according to SSTs? And, if so, are there behavioural differences between (iii) sexes, (iv) eastern and western gulf communities or (v) sponging vs non-sponging dolphins?

In my analysis chapter, I will explain in detail how I use a traditional hypothesis testing approach using ANOVA, to test whether a number of linear mixed-effects models I created explained significantly more variance than null models. In my linear mixed-effects models I will include variables such as behavioural activity budget, sex, ENSO, SST and tool-use for both the eastern and western gulfs. This will allow me to test whether socialising and foraging behavioural activity budgets significantly differ due to environmental variables related to ENSO, sex, and tool-use, and not just due to random chance, therefore addressing the main questions outlined in this study.

2.2 Methods

2.2.1 Study subjects and survey method

Behavioural, demographic and genetic data were collected as part of a long-term study on the population of Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia. Standardised behavioural surveys have been conducted on a near-annual, seasonal basis (typically austral winter–spring) since 1982 off Monkey Mia (in the eastern gulf) and 2007 off Useless Loop (in the western gulf). The timeframe of my study covers the years 1991-2020 for the eastern gulf, and 2009-2019 for the western gulf. Few data were collected in the western gulf in 2020 because of COVID-19.

Behavioural data were collected via boat-based surveys from both gulfs. A ‘survey’ is a minimum five-min observation of dolphin group composition (as defined by the 10m chain rule, where each dolphin in the group is within 10m of any other dolphin; Smolker et al., 1992) and behavioural activity. During these surveys, researchers in a small (<7m) research vessel identify individual dolphins using standard photo-identification techniques, including unique body markings and dorsal fin shape (Bichell et al., 2018; Würsig & Würsig, 1977). Behavioural activity data were collected for all individuals encountered within the first five mins (i.e., predominant group activity) and included four mutually exclusive categories: foraging, socialising, resting or travelling (Table 1.).

The sex of individual dolphins within the study was determined through genetic sexing, observations of genitals, or the presence of a dependent calf (Krützen et al., 2002; Smolker et al., 1992). This enabled assessment of whether there were differences in the ways males and females responded to climatic variability. In order to investigate whether tool users may have responded differently to non-tool users following the MHW, I included an individual level variable of ‘sponger’ or ‘non-sponger’. An individual is considered a sponger if they have been seen sponging on two or more occasions (Mann et al., 2008).

Table 1. Definition of behavioural activities (taken from the Shark Bay Dolphin Research Ethogram).

Behaviour	Description
Foraging	This includes behaviours that indicate the dolphins are seeking prey. Dive types and inter-individual geometry are important in assessing whether the dolphins are foraging. Foraging is generally performed by a single dolphin or in an assemblage of dolphins more than 2 metres apart from each other.
Socialising	Socialising behaviour includes five categories: affiliative, aggressive, sexual, non-contact displays and miscellaneous. Behaviours such as petting, rubbing and synchronous movements are used to determine which category a behaviour falls in.
Resting	When the dolphins are in a tight group, moving slowly in a straight line or meandering, they are resting. There is also no evidence of socialising or foraging during resting behaviour.
Travelling	This occurs when individuals are moving in one general direction in a parallel orientation through two surfacing periods or for at least a minute.

2.2.2 Environmental data

In order to assess the effects of climatic variability on behavioural activity budgets, I used two forms of environmental data. These included the Southern Oscillation Index (SOI) and sea surface temperatures (SST), which were collected from the Australian Bureau of Meteorology and the National Oceanic and Atmospheric Association, respectively (NOAA) (Bureau of Meteorology, 2021; Hirahara et al., 2014). The SOI is used to assess the intensity of an El Niño or La Niña event. An index >8 indicates a La Niña, <-8 indicates an El Niño, and anything in-between is characterized as neutral (Bureau of Meteorology, 2021). This SOI data is collected on a monthly scale. The SST data from the NOAA has a spatial coverage of 1.0 degree latitude x 1.0 degree longitude and covers all the years of this study on a monthly scale. I used an average SST from three coordinates that cover our study site (25°82’S, 113°31’E; 25°46’S, 113°72’E; 25°37’S, 113°39’E) in order to represent the extent of the bay.

2.2.3 Foraging behaviour

For additional information on how foraging behaviour was specifically affected by the 2011 MHW as an ECE case study, I extracted data on the frequency of new foraging types. Any newly observed foraging behaviours were recorded during the standard boat-based surveys. The foraging types used for this analysis were “prawn feeding” and “shelling” across both gulfs. As previously mentioned, shelling is a type of tool use whereby an individual chases pray into an empty trumpet or bailer shell (Wild et al., 2020). Looking at number of observations of these two different foraging behaviours over time may reveal a strategic preference for different types of prey following the MHW.

2.3 Analysis

All analyses were conducted in R Studio (version 1.2.5).

2.3.1 Individual level analysis

For this approach, behavioural activity budgets were calculated for each individual on a yearly scale. A yearly scale was chosen as there were not enough surveys per individual per month to assess monthly budgets. Behavioural activity budgets were calculated using the number of times an individual was sighted engaging in a certain behavioural activity over a year as a proportion of all behavioural sightings for that individual in that year. Only individuals that had been seen 50 times or more over the chosen timeframe were used to ensure a sufficient number of sightings over the study period with which to calculate accurate activity budgets. In the eastern gulf, activity budgets were calculated each year from 1991-2020 for 198 males and 164 females, excluding the years 2007 and 2008 where no survey data were collected. For the western gulf, activity budgets were calculated from 2009-2019 for 86 males and 51 females. Individual level variables included behavioural activity budget, sex and tool use (whether the individual was a sponger or a non-sponger). The environmental variable included for the individual level approach was the Southern Oscillation Index (SOI). Using SOI data, I characterized each year as El Niño, La Niña, or neutral based on whether the majority of months within that year fell under one of those categories. This enabled me to investigate whether behavioural activity budgets differed during El Niño, La Niña or neutral years.

I built four linear mixed-effect models for which the dependent variable was activity budget. For each model, my fixed effects were sex (categorical variable of male or female), Southern Oscillation (categorical variable of El Niño, La Niña, or neutral based on SOI values) and tool use (categorical variable of sponger or non-sponger). Finally, I included individual identity as a random effect (to account for repeated measures). The first two models were run for the eastern gulf, one for foraging and the second for socialising. The other two models were run for the western gulf, again one for foraging and the other for socialising. I used variance inflation factors (VIF) to check for collinearity and ensure our predictor variables were not correlated (VIF < 3 indicated no correlation (Zuur et al., 2010)).

I employed a traditional hypothesis testing approach where I used ANOVA to test whether the full model (containing all our fixed effects) explained significantly more variance than the null model (intercept only model). I checked the assumption for normality of model residuals by plotting a histogram and a quantile-quantile plot of the residuals to see whether they were normally distributed. Homogeneity of variance was also tested by comparing fitted values to residuals in our models.

2.3.2 Population level analysis

For this approach, monthly activity budgets were calculated for the whole population in the eastern gulf. I was able to create monthly activity budgets at the population level due to greater sample size compared to the individual level analysis. Only months with >100 surveys from the years 1991-2020 were included in the analysis. The population activity budgets were calculated by counting the number of times all individuals were documented engaged in one behavioural state within a month, divided by the total number of behavioural records that month. To assess whether tool-users responded differently to non-tool users, the focal population was also split into spongers and non-spongers, and monthly activity budgets were calculated separately for these groups. There were 74 spongers and 1,981 non-spongers overall. The environmental variables included for the population level approach included SSTs and SOI, both on a monthly scale. Months were categorized as El Niño, La Niña or neutral using the same SOI values described previously.

I built two linear models for which the dependent variable was activity budget. For each model, my independent variables were SOI (categorical variable of El Niño, La Niña, or neutral based on SOI values) and SSTs (numerical values of sea surface in degrees Celsius). Both models were run for the whole population in the eastern gulf, the first for foraging and the second for socialising. A third linear model was built, this time using the activity budgets calculated separately for spongers and non-spongers. For this linear model, the dependent variable was activity budget, and the independent variables were Southern Oscillation, SST and tool use (categorical variable of sponger or non-sponger). I also used variance inflation factors (VIF) to check for collinearity and make sure our predictor variables were not correlated (VIF < 3 indicated no correlation).

I again employed a traditional hypothesis testing approach where I used ANOVA to test whether the full model (containing all our independent variables) explained significantly more variance than the null model (intercept only model). As with my individual level analysis, I checked the assumption for normality of model residuals by plotting a histogram and a quantile-quantile plot of the residuals to see whether they were normally distributed. Homogeneity of variance was also tested by comparing fitted values to residuals in our models.

2.4 Results

2.4.1 Individual level

Foraging

Models for foraging activity in the eastern and western gulf explained significantly more variance than the null models (Table 1) and our fixed effects were not correlated (eastern gulf: vif-sex = 1.02, vif-Southern Oscillation = 1.00, vif-sponging = 1.01, western gulf: vif-sex = 1.03, vif-Southern Oscillation = 1.00, vif-sponging = 1.03). In the eastern gulf, males foraged significantly less than females (lmer estimate: -0.05, 97.5% confidence interval (CI) = -0.03, $t = -3.97$, $p < 0.0001$; Figure 1). The Southern Oscillation had a significant effect on foraging budgets with dolphins foraging significantly less during La Niña years (lmer estimate: -0.02, CI = -0.01, $t = -2.67$, $p = 0.008$). Foraging activity budgets were also significantly different between spongers and non-spongers, with spongers spending significantly more time foraging (lmer estimate: 0.11, CI = 0.15, $t = 4.81$, $p < 0.0001$).

In the western gulf, males foraged less than females, but the difference was not significant (lmer estimate: -0.03, CI = 0.02, $t = -1.20$, $p = 0.23$). The Southern Oscillation significantly affected foraging budgets in the western gulf also, with dolphins foraging significantly less during El Niño years (lmer estimate: -0.07, CI = -0.03, $t = -3.55$, $p = 0.004$). Foraging activity budgets were significantly different between spongers and non-spongers, with spongers spending significantly more time foraging (lmer estimate: 0.12, CI = 0.18, $t = 4.05$, $p < 0.0001$).

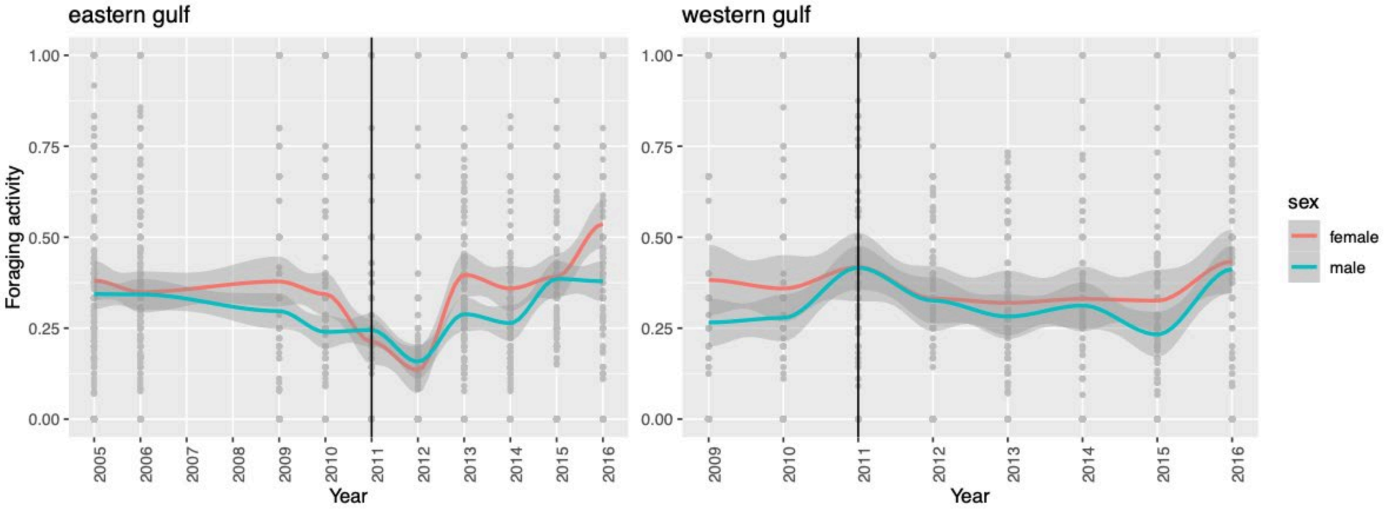

Figure 1. A snapshot of foraging activity budgets before, during and after the Ningaloo Niño. Yearly individual foraging activity budgets of dolphins in Shark Bay, Western Australia. Only data from 2005-2016 in the eastern gulf, and 2009-2016 in the western gulf are shown to present a focused snapshot of foraging activity before, during and after the 2011 marine heatwave. No data were collected in the eastern gulf in 2007 and 2008. Data included 198 males and 164 females in the eastern gulf, 86 males and 51 females in the west. The vertical line indicates the focal 2011 La Niña event, known as the Ningaloo Niño. Points on the graph represent raw data with a smooth local regression line created using a loess method (local polynomial regression fitting) within R Studio (version 1.2.5), with variation shown as shading around the line.

Socialising

Our models for socialising in both the eastern and western gulf explained significantly more variance than the null models (Table 1) and our fixed effects were not correlated (eastern gulf: vif-sex = 1.01, vif-Southern Oscillation = 1.00, vif-sponging = 1.01, western gulf: vif-sex = 1.03, vif-Southern Oscillation = 1.00, vif-sponging = 1.03). In the eastern gulf, socialising activity budgets were significantly different between males and females, with males spending significantly more time socialising (lmer estimate: 0.06, CI = 0.08, $t = 8.10$ $p < 0.0001$; Figure 2.). The Southern Oscillation had a significant effect on socialising budgets, with dolphins socialising significantly less during El Niño years (lmer estimate: -0.02, CI = -0.005, $t = -2.76$, $p = 0.006$). There was no significant difference in socialising activity budgets between spongers and non-spongers in the eastern gulf (lmer estimate: 0.009, CI = 0.034, $t = 0.72$, $p = 0.470$).

In the western gulf, our linear mixed effects models found no significant effect for sex (lmer estimate: 0.035, CI = 0.07, $t = 1.78$, $p = 0.08$), Southern Oscillation (lmer estimate: 0.01, CI = 0.04, $t = 1.03$, $p = 0.3$) or tool-use (lmer estimate: -0.04, CI = 0.005, $t = -1.71$, $p = 0.09$) on socialising activity budgets.

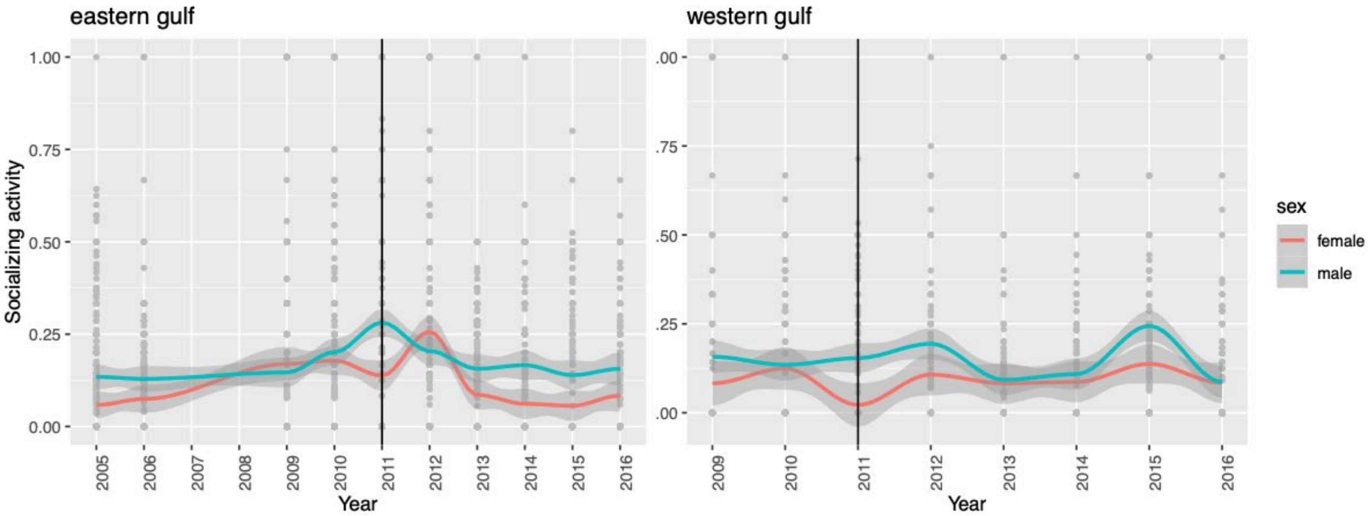

Figure 2. A snapshot of socialising activity budgets before, during and after the Ningaloo Niño. Yearly individual socialising activity budgets of dolphins in Shark Bay, Western Australia. Only data from 2005-2016 in the eastern gulf, and 2009-2016 in the western gulf are shown to present a focused snapshot of socialising activity before, during and after the 2011 marine heatwave. Data included 198 males and 164 females in the eastern gulf, 86 males and 51 females in the west. The vertical line indicates the focal 2011 La Niña event, known as the Ningaloo Niño. Points on the graph represent raw data with a smooth local regression line created using a loess method (local polynomial regression fitting) within R Studio (version 1.2.5), with variation shown as shading around the line.

2.4.2 Population level

The predictor variables were not correlated (vif-Southern Oscillation = 1.03, vif-SST = 1.03). Foraging activity budgets calculated for the eastern gulf population were not significantly affected by the Southern Oscillation (lm estimate: 0.00008, CI = 0.002, $t = 0.11$, $p = 0.91$) or SSTs (lm estimate: -0.004, CI = 0.006, $t = -0.78$, $p = 0.44$). Socialising activity budgets were also not significantly affected by the Southern Oscillation (lm estimate: 0.0007, CI = 0.002, $t = 1.53$, $p = 0.13$), or SSTs (lm estimate: -0.006, CI = 0.0004, $t = -1.863$, $p = 0.06$). However, activity budgets calculated separately for spongers and non-spongers revealed that spongers spent significantly more time foraging than non-spongers in the eastern gulf (lm estimate: 0.12, CI = 0.15, $t = 8.25$, $p < 0.0001$) (Figure 3). Spongers also foraged significantly more as SSTs increased (lm estimate: 0.027, CI = 0.008, $t = 3.3$, $p = 0.00108$).

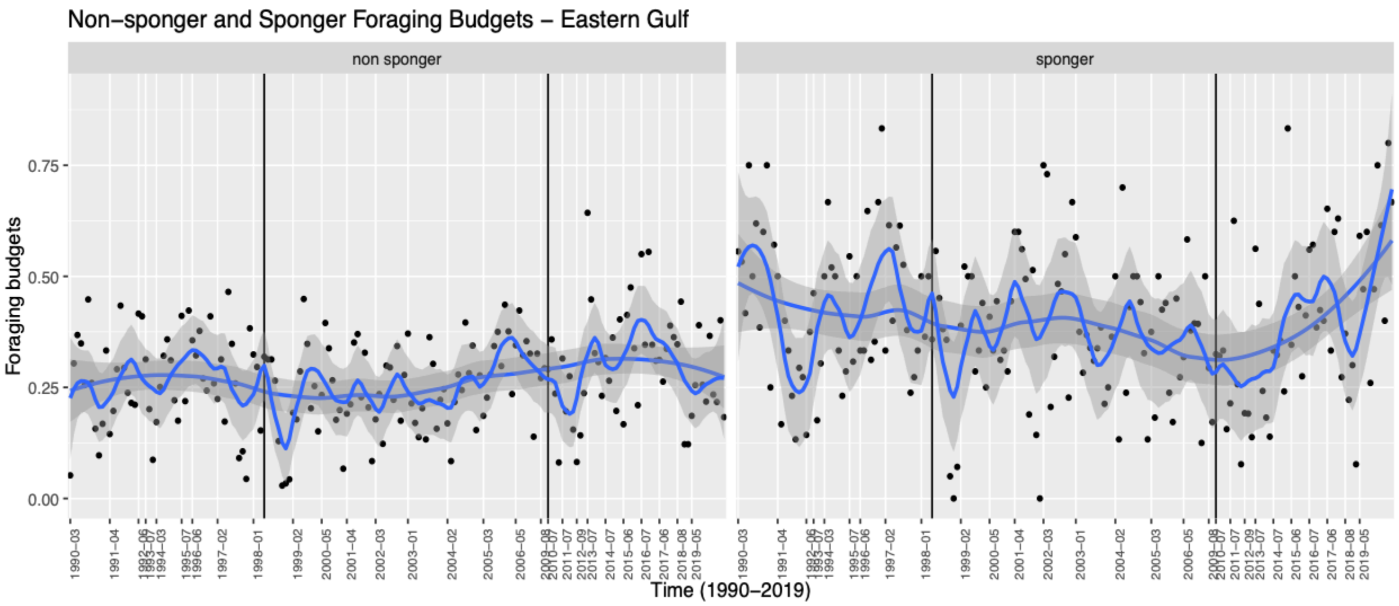

Figure 3. Foraging budgets for non-spongers and spongers in the eastern gulf. Monthly foraging activity budgets calculated separately for non-sponging (N = 1,984) and sponging (N = 74) dolphins in Shark Bay, Western Australia, against time (1990-2019). Vertical lines indicate two strong La Niña events, the first in 1998 and the second in late 2010. Note that the number of months where data was collected varied each year, and that only the first month of data collection in each year is labelled. Points on the graph represent raw data with 2 smooth local regression lines, one with a greater degree of smoothing, created using a loess method (local polynomial regression fitting) within R Studio (version 1.2.5). Variation is also shown as shading for both the raw data and line of best fit.

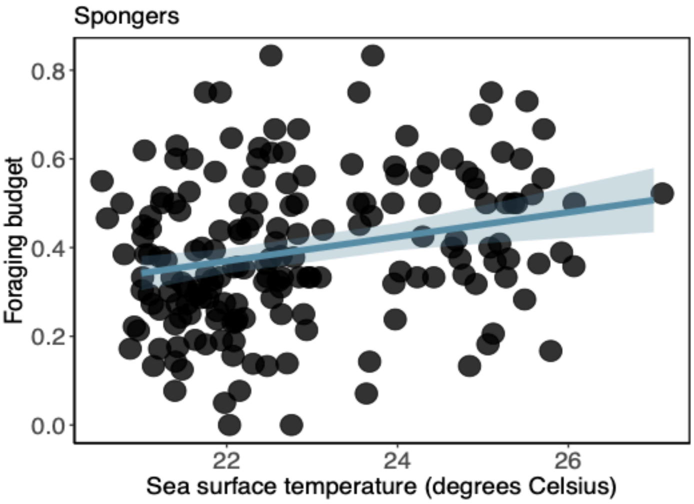

Figure 4a. Sponger foraging budgets and linear model estimates against sea surface temperatures. Foraging activity budgets calculated monthly from 1990-2019 plotted against sea

surface temperatures (SST) for sponging (N = 74) dolphins in Shark Bay, Western Australia. Blue line indicates linear model estimates of SST effects on foraging budgets (*lm (budgets ~ SST + SOI)*).

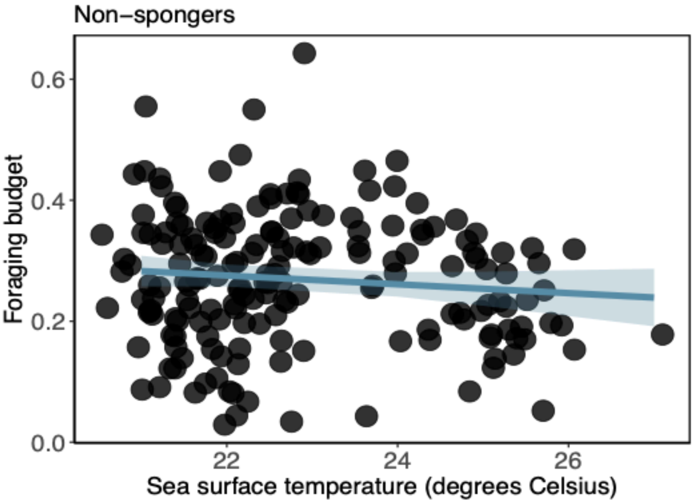

Figure 4b. Non-sponger foraging budgets and linear model estimates against sea surface temperatures. Foraging activity budgets calculated monthly from 1990-2019 plotted against sea surface temperatures (SST) for non-sponging (N = 1,984) dolphins in Shark Bay, Western Australia. Blue line indicates linear model estimates of SST effects on foraging budgets (*lm (budgets ~ SST + SOI)*).

2.4.3 Foraging behaviour

Interestingly, foraging techniques prawn feeding and shelling increased after the MHW (Figure 5.)

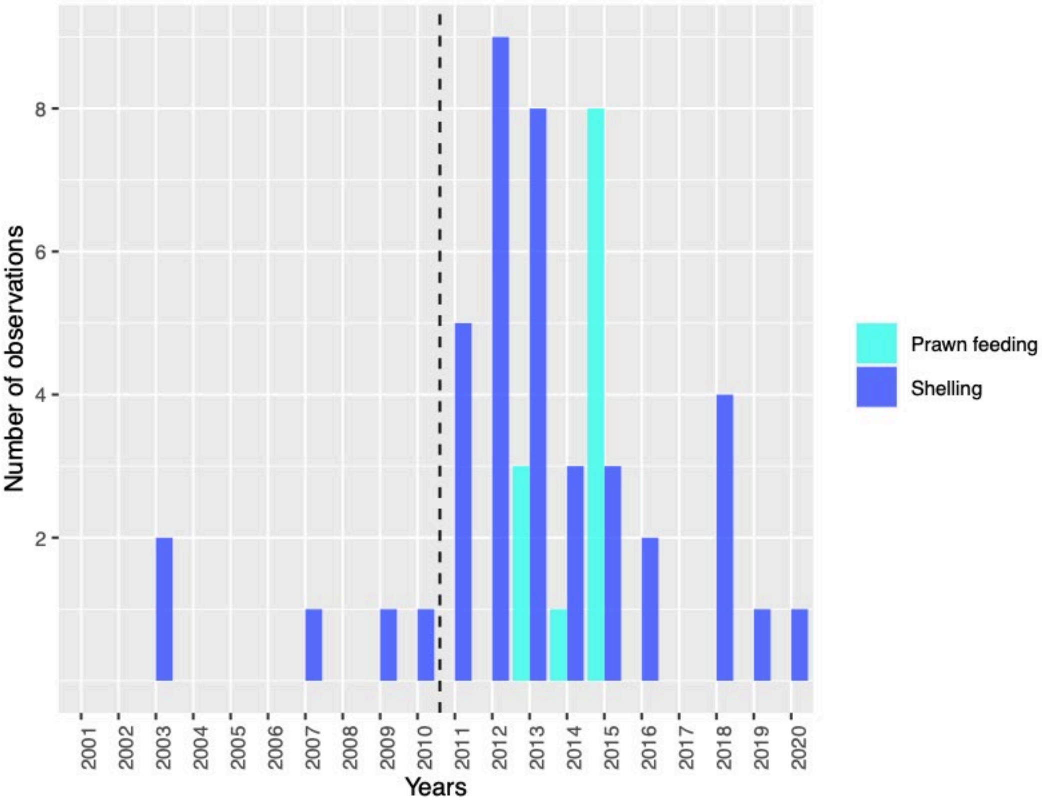

Figure 5. Observations of prawn feeding and shelling foraging types over time. The number of shelling and prawn feeding events observed for dolphins in Shark Bay, Western Australia. Western and eastern gulf data combined. Dashed line indicates the late 2010/early 2011 marine heatwave.

2.5 Discussion

Both foraging and socialising activity budgets of Shark Bay's bottlenose dolphins, at an individual level, were significantly affected by extreme Southern Oscillation events, either El Niño or La Niña, indicating that ECEs can alter the behaviour of even behaviourally flexible high trophic level marine predators. Focusing specifically on the 2011 Ningaloo Niño in the eastern gulf, my individual level analysis revealed that there was a sharp drop in foraging activity immediately after the MHW, reaching a minimum in 2012 (Figure 1, eastern gulf). Foraging budgets then rose sharply and continued to increase in the following years, reaching their highest level in 2016. In contrast to foraging behaviour, individual socialising activity budgets in the eastern gulf peaked immediately after the MHW and then dropped to pre-MHW levels in the following years (Figure 2, eastern gulf). The individual level analysis also showed between-sex behavioural differences, with males foraging less than females in both eastern and western gulfs. Males also socialised more than females at an individual level, but only in the eastern gulf. Furthermore, sponging dolphins in both gulfs were found to spend more time foraging than non-spongers at both the individual and population levels of analyses.

At the population level in the eastern gulf, spongers also foraged significantly more as SSTs increased. My population level analysis and in contrast to the individual level analysis, however, found that there was no significant effect of SOI on foraging and socialising activity budgets. The benefits of the population level approach included an increased sample size, enabling me to analyse behavioural activity budgets on a monthly scale. This was beneficial when including SSTs as an environmental variable, as they are measured on a monthly scale. In my individual level analysis, there were not enough surveys to create monthly activity budgets, so they were calculated on a yearly scale. The benefits of individual level analysis, however, included the ability to separate males and females, enabling me to investigate sex differences in activity budgets. I was also able to exclude individuals that had not been seen 50 times or more, ensuring a sufficient number of sightings over the time frame of the study.

To understand why we see these changes in foraging and socialising activity budgets, we need to explore potential changes in predator-prey interactions, as well as the general ecology of Shark Bay following the 2011 MHW. An ECE is defined by its ability to change the structure and function of an ecosystem in a short time frame. The Ningaloo Niño was no exception, causing cascading ecological effects within Shark Bay, impacting primary producers to top level consumers (Nowicki et al., 2019; Pearce et al., 2014; Strydom et al., 2020; Thomson et al., 2015; Wild et al., 2019). The immediate drop in foraging activity following the Ningaloo Niño is indicative of dolphins being able to find prey more easily, enabling them to spend less time foraging whilst still meeting their necessary food intake. Although prey may have been easier to find initially, the subsequent sharp increase in foraging, sustained for multiple years after the MHW, suggests that prey became increasingly difficult to find. Shark Bay lies on a tropical-temperate boundary, leaving temperate species particularly vulnerable to increased temperatures. The temperate seagrass species *Amphibolis antarctica,* which typically dominated seagrass beds in Shark Bay, experienced a dieback of over 90% due to the sustained, abnormally high SSTs (Thomson et al., 2015). The absence of this seagrass habitat, providing benthic species with vital cover and protection from predators, may have changed the foraging landscape for the Shark Bay dolphins.

To help explain why foraging may have been easier in a degraded seagrass habitat, we need to look at the mechanisms of dolphin foraging behaviour. Dolphins are known to use echolocation, producing high-frequency clicks in order to detect and capture prey (Au, 1993; Au & Snyder, 1980). Vegetated aquatic environments including seagrass beds attenuate these high-frequency clicks, reducing the effectiveness of echolocation (Nowacek, 2005; Wilson et al., 2013). As these clicks travel deeper into the seagrass bed, sound attenuation occurs and, the healthier the seagrass tissue, the more effective it may be at attenuating the sound (Wilson et al., 2013). These seagrass beds may therefore act as vital acoustic refuges for benthic species, minimising detection from echolocating marine predators (Nowicki et al., 2019; Wilson et al., 2013). Large scale seagrass dieback following the MHW in Shark Bay would thus have reduced the area of acoustic refuges, as well as the quality of the refuge itself. In this newly denuded habitat, with fewer acoustic refuges, echolocation would be uninhibited, prey search times would be reduced and prey encounter rates would likely increase (Nowicki et al., 2019). Therefore, individuals could afford to spend less time foraging whilst still finding enough food, explaining the sharp drop in foraging activity budgets immediately after the heatwave. This significant drop in foraging behaviour can also be seen following a 1998 La Niña event in Shark Bay (Figure 3), indicative of a similar situation prior to the 2011 MHW, where prey was easier to find immediately after an ECE.

The degradation of seagrass beds may have initially been beneficial for the dolphins, but the absence of this habitat ultimately led to the emigration and/or mortality of many fish and invertebrate communities in the area. A Department of Fisheries report (Pearce et al., 2014) describes mass mortalities of fish and invertebrates in Shark Bay, as well as changes in species distributions and mass emigrations in the years following the MHW. Increased prey encounter rates in denuded seagrass habitats would therefore have lasted only a short while before the number of prey available to the dolphins decreased substantially. This lack of available prey is reflected in the sustained increase in dolphin foraging activity budgets in years following the MHW (Figure 1). Foraging activity budgets continued to increase until 2016 (Figure 1). This could be due to the fact that it took a long time for many species to recover from the direct and indirect effects of the MHW. For example, it took up to five years for seagrass habitats in Shark Bay to make a recovery, with tropical species of seagrass replacing the temperate *A. antarctica* (Kendrick et al., 2019; Thomson et al., 2015). Fish and invertebrate communities that emigrated following the MHW may have taken years to return and some may not have returned at all. As the abundance and distribution of prey species changed, dolphins may have been required to alter their foraging methods in response. The number of shelling events observed increased substantially after the Ningaloo Niño, peaking in 2012, and prawn feeding observations were noted after the MHW (Figure 5). These different foraging methods likely reflect dolphins taking advantage of novel sources of prey to meet their daily food intake requirements.

Dolphins spending less time foraging immediately after the MHW meant more time and energy for other behaviours, such as socialising. Overall, males spent more time socialising than females, likely due to sex-differences in reproductive strategies (Connor et al., 1992; Connor & Krützen, 2015; Smolker et al., 1992). Males form multi-level, cooperative alliances that are vital for reproductive success (Connor et al., 2000; Connor & Krützen, 2015; King et al., 2021). The maintenance and formation of these alliances is specific to males, with females forming weaker and more variable associations (Connor et al., 2000; Smolker et al., 1992). The importance of social relationships for male dolphins may therefore explain the overall increased time spent socialising compared to females in this study. Socialising activity budgets peaked immediately after the Ningaloo Niño and then dropped in the following years (Figure 2, eastern gulf). Shark Bay dolphins are highly social and exhibit fission-fusion grouping patterns like those of humans (Connor & Krützen, 2015). It is possible that, during times when food is easily found and daily energy intake is met quickly, individuals are able to spend more time performing important social behaviours such as playing, partaking in affiliative behaviour or mating. Similarly, if dolphins are spending significantly more time foraging, as seen in the years after the MHW (Figure 1), the amount of time performing other behavioural activities will likely decrease in order to balance energy budgets. This can be seen in the drop in socialising behaviour in 2012 (Figure 2, eastern gulf).

The fluctuating behavioural activity budgets reported here may help explain the long-term decline in survival and reproduction of the Shark Bay dolphins following the 2011 MHW (Nowicki et al., 2019; Wild et al., 2019). A female dolphin with a calf, for example, would normally need to spend more time foraging in order to meet the high energetic demands of lactation and parental care (Clutton-Brock et al., 1982; Speakman, 2008). If there was less prey available after an ECE, this female would have to work even harder to find food, spending more time foraging to meet the energetic demands for herself and her calf. The calf may receive fewer resources from its mother due to the lack of food available and, furthermore, the female may be less vigilant, with both the mother and calf thereby being exposed to a greater risk of predation. This hypothesis, proposed by Wild et al. (2019), would help to explain the decline in survival and reproduction of the Shark Bay dolphins after the 2011 MHW, with individuals spending more time foraging for many years after the MHW.

Wild et al. (2019) also found that the decline in dolphin survival following the Ningaloo Niño was less severe for sponging dolphins compared to non-sponging dolphins, perhaps because spongers were able to access a foraging niche less impacted by the MHW. In the present study, both individual and population level analyses suggested that spongers overall have higher foraging activity budgets than non-spongers. This supports previous studies on the behaviour of Shark Bay dolphins, indicating that spongers spend more time foraging than non-sponging individuals (Bizzozzero et al., 2019; Kopps et al., 2014; Mann et al., 2008). I also found females spent more time foraging than males. As above, females, especially those with calves, generally have higher energy requirements than males, which likely explains why females were found to forage more. Furthermore, sponging behaviour is predominantly exhibited by females (but see Bizzozzero et al., 2019). Therefore, the finding that females forage more than males may also be an artifact of spongers foraging more than non-spongers, as sponging is female-biased.

Differing foraging niches may also help to explain the opposing trends in foraging behaviour for sponging and non-sponging dolphins following a rise in SST. I looked into the effects of SST on foraging activity budgets of the Shark Bay dolphins, as SST fluctuations typically accompany MHWs. As SST in Shark Bay increased, foraging budgets increased for spongers but decreased for non-spongers (Figure 4a and 4b). As above, spongers tend to have higher foraging activity budgets in general, but this only explains the higher baseline foraging budget compared to non-spongers, not the increase in foraging as SSTs rise. Although the foraging activity of sponging dolphins increased as SSTs rose (Figure 4a and 4b), their survival and reproduction was less impacted by the MHW than those of non-spongers (Wild et al., 2019). Within Shark Bay, female spongers were found to spend 95% of their foraging time sponging (Bizzozzero et al., 2019; Mann et al., 2008). If only 5% of foraging time is devoted to other foraging methods, then sponging individuals, so specialised to their primary foraging technique, may be less able to adapt if sponging becomes less effective in their environment. ECEs or increases in SSTs may alter the ecology of Shark Bay in a way that impacts certain foraging niches more than others and requires novel foraging methods to be immediately adopted. For example, shelling and prawn feeding observations increased following the 2011 MHW (Figure 5), likely in response to changing prey distributions and the availability of gastropod shells, suggesting the importance of alternative foraging behaviours following an ECE. As ECEs become more frequent and foraging landscapes change as a result, the flexibility of foraging behaviours will likely play a vital role in the ability of individuals to adapt.

This study shows ECEs can significantly alter the behavioural activity budgets of even behaviourally flexible and cognitively advanced marine predators. These findings are in accord with some previous literature, describing the ways in which ECEs can affect foraging and socialising behaviours. For example, Indian Ocean Dipole events altered foraging habitat choice and diving behaviour of king penguins, and changes in social grouping behaviour of killer whales was documented in response to the Pacific decadal oscillation (Bost et al., 2015; Lusseau et al., 2004). The trends I detected in foraging and socialising activity budgets also support prior hypotheses as to why lower reproductive success and survival was documented in Shark Bay's dolphin population (Wild et al., 2019). Furthermore, the cascading ecological effects of the Ningaloo Niño, from the destruction of seagrass habitat and acoustic refuges to the mortality of fish and invertebrate communities, correlate with the trends detected in this study. Between sex differences in activity budgets were found and explained by sex-biased foraging methods and differing reproductive strategies. Differences between spongers and non-spongers were also found, and the importance of flexibility in foraging behaviour considered. This study aimed to fill a gap in our knowledge of long term behavioural responses to ECEs in marine environments. As the climate crisis continues, and habitats across the globe face further change and uncertainty, long term behavioural research is crucial in understanding how species will respond.

Concluding remarks and future work

This work aims to draw attention to the ways in which animals respond behaviourally to ECEs, and how this information can be used to understand why certain species or communities may be more or less resilient. It is important to note that this research was only possible through access to long term data that encompassed ECEs. Moving forward, it will be important to continue long term behavioural research projects, for a variety of taxa and in a variety of environments, in order to better understand how biodiversity across the world will respond to our changing climate. Through understanding how key behaviours such as foraging and socialising are likely to be affected, we may be better able to formulate conservation and management plans to buffer the potential negative consequences of ECEs.

Appendix

Table A1. Results of linear mixed effect models, linear models and their corresponding null models.

		Model	Deviance	Pr(>Chi)
Individual analysis				
Eastern Gulf				
Model 1 - Forage	Full	lmer (budgets ~ sex + so + sponging + (1|id.individual)	1258.3	< 0.0001
	Null	lmer (budgets ~ 1 + (1|id.individual)	1307.6	
Model 2 - Socialise	Full	lmer (budgets ~ sex + so + sponging + (1|id.individual)	-2776.4	< 0.0001
	Null	lmer (budgets ~ 1 + (1|id.individual)	-2707.2	
Western Gulf				
Model 3 - Forage	Full	lmer (budgets ~ sex + so + sponging + (1|id.individual)	423.48	< 0.0001
	Null	lmer (budgets ~ 1 + (1|id.individual)	456.64	
Model 4 - Socialise	Full	lmer (budgets ~ sex + so + sponging + (1|id.individual)	-444.66	0.02
	Null	lmer (budgets ~ 1 + (1|id.individual)	-432.59	
Population analysis			**SSE**	**Pr(>F)**
Model 1 - Forage	Full	lm (budgets ~ SOI + SST)	1.99	0.72
	Null	lm (budgets ~ 1)	2.00	
Model 2 - Socialise	Full	lm (budget s~ SST + SOI)	0.84	0.03
		lm (budgets ~ 1)	0.87	
Spongers and non-spongers				
Model 3 - Forage		lm (budgets ~ sponging + SST + SOI)	7.13	< 0.0001
		lm (budgets ~ 1)	8.58	

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