Modelling the spatial and genetic response of the endemic sparid: *Polysteganus praeorbitalis* (Pisces: Sparidae) to climate change in the Agulhas Current system

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Abstract

The Scotsman Seabream, *Polysteganus praeorbitalis*, is one of several large, slow-growing members of the Sparidae family of fishes endemic to the Agulhas Current system in the Western Indian Ocean (WIO). Relatively little research has been conducted on this species despite its importance to both recreational and commercial line fisheries in South Africa and the drastic decline in catch per unit effort (CPUE) that has been recorded since the 1940s. Changing sea temperatures as a result of global climate change are further expected to affect the distribution and abundance of many fish species based on their thermal tolerances, life histories and population structures. The ability of these species to shift their distribution and adapt to new environments and thermal conditions will depend to some degree on the levels of genetic variation and gene flow, within and between populations. A combined approach using species distribution modelling and genetic analyses may prove to be a useful tool in investigating the potential effects of climate change on the distribution and genetic diversity of species.

An ensemble species distribution model (SDM) based on 205 occurrence records and 30 years of Reynolds Optimum Interpolated (OI) sea surface temperature data was constructed to predict the distributional response of *P. praeorbitalis* to climate change in the Agulhas Current system. The ensemble SDM displayed a true skill statistic (TSS) of 0.975 and an area under the receiver operating curve (ROC) of 0.999, indicating good model fit. Autumn and winter minimum temperatures, as well as bathymetry, were the most important predictor variables in the majority of models, indicating that these variables may directly constrain the distribution of *P. praeorbitalis*. In particular, the southern range edge of this species appeared to be constrained by autumn and winter minima, with high model agreement on this range edge. Conversely, the northern range limit showed poor model agreement leading to a gradual reduction in occurrence. This indicates that this range edge may be constrained by other factors not included in the models such as species interactions. The ensemble SDM projected the current range of *P. praeorbitalis* to be 1500 km^2, smaller than the published range for this species. The model underestimated the northern range edge of this species by approximately 5° latitude when binary transformed. This is probably due to the rarity of this species in the landings of the Mozambican linefishery, which was assumed to be an indication of low abundance of *P. praeorbitalis* in these waters. The absence of a specimen to verify the published northern range edge of this species indicates that the northern range edge produced by this model is likely to be closer to the actual range limit of the species. A range contraction of 30% occurring at both the northern and southern edge of *P.*

praeorbitalis' range and range fragmentation occurring, towards its northern range edge by 2030, was predicted. These changes are modelled to be the results of cooling related to the intensification of the Port Alfred upwelling cell and of warming predicted north of the Natal Bight and in southern Mozambique.

Genetic analyses of the nuclear DNA (nDNA) S7 intron 1 and mitochondrial DNA (mtDNA) control region genes were carried out using 118 tissue samples of *P. praeorbitalis* collected at four main localities: the Eastern Cape, Transkei, southern KwaZulu-Natal and northern KwaZulu-Natal. Analyses of genetic diversity levels revealed relatively low diversity in the mtDNA dataset (*Hd* = 0.488; π = 0.004) and moderate levels of diversity in the nDNA dataset (*Ad* = 0.922; π = 0.005). The low levels of diversity observed in the mtDNA dataset might be explained by a number of factors, including high variation in spawning success, the negative effects of over-harvesting, or a recent population bottleneck. The last explanation is supported by characteristic star-shaped haplotype networks and unimodal mismatch distributions displayed by both datasets. These results, in conjunction with a significant (p = 0.005) negative Tajimas D value (-2.029) in the mtDNA dataset and significant (p = 0.0005) negative Fu's F statistic in both the nDNA (F = -26.5) and mtDNA (F = -11.9) datasets, provide strong evidence for a recent population expansion after a bottleneck event in this species. Spatially, mtDNA diversity was highest in the Eastern Cape and lowest in the middle localities, while nDNA diversity showed the opposite pattern. These results may be indicative of differences in the sex ratio between localities, possibly as a result of the protogynous hermaphroditism that has been postulated for this species.

Although pairwise comparisons and exact tests of population differentiation revealed no significant geneticdifferentiation between populations in the mtDNA dataset, there was some evidence of low levels of differentiation in the nDNA dataset. This occurred for comparisons between the Eastern Cape and Transkei (F_{st} = 0.039; p <0.05), and the northern KwaZulu-Natal (F_{st} = 0.045; p < 0.05).. This might be the result of one or a combination of factors including the effects of the Port Alfred upwelling cell on dispersal and gene flow, or the possibility of more than one spawning ground for this species promoting sub-structuring. A SAMOVA analyses run on the nDNA dataset maximised variance by grouping the Eastern Cape and southern KwaZulu-Natal together and Transkei and northern KwaZulu-Natal together in two groups. This revealed no evidence of spatial structure (p = 0.36), with only 3.30% of variation explained by this grouping. The removal of individuals below the estimated length at 50% maturity in the nDNA dataset, in order to test for temporal structure, resulted in stronger evidence of differentiation between the Eastern Cape and all other localities: Transkei (F_{st} = 0.081; p< 0.05), southern KwaZulu-Natal (F_{st} = 0.031; p<0.05), and

northern KwaZulu-Natal (F_{st} = 0.078; p< 0.05). This indicates that some temporal genetic structure may exist between age classes within this species.

The differentiation observed between the Eastern Cape and other localities, coupled with the high percentage of private haplotypes in the mtDNA dataset in this locality, indicates that this area is where *P. praeorbitalis* is most vulnerable to the potential negative effects of climate change on its genetic diversity. However, the vast majority of this species genetic diversity appears to reside towards the centre of its range where it is most abundant and the lack of strong genetic structure indicates high levels of gene flow. In conclusion, while *P. praeorbitalis* is vulnerable to range loss as a result of climate change, its genetic diversity is unlikely to be greatly affected.

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Chapter 1
General Introduction

1.1) Global climate change and marine environments

Warming of the global climate system is now widely accepted in both public and scientific circles, predominantly because of observed increases in the magnitude and variability of global atmospheric and ocean temperatures (Bindoff *et al.* 2007; Trenberth *et al.* 2007), rising sea levels (Bindoff *et al.* 2007) and reductions in glacial ice (Lemke *et al.* 2007). An increase in global mean surface temperature of 0.74 °C (±0.18 °C) has been observed over the 100 years between 1906 and 2005. This trend appears to be growing in magnitude, with an average increase of 0.13 °C (±0.3 °C) per decade observed in the 50-year period between 1956 and 2005 (Trenberth *et al.* 2007). Furthermore, Fussel (2009) reports that the eight warmest years ever recorded have all occurred since 1998 and the 14 warmest since 1990. The observed warming has been widespread globally, but not evenly distributed, with northern hemisphere polar latitudes displaying the most rapid warming (almost double the global average) and terrestrial systems warming faster than marine systems (Trenberth *et al.* 2007). While terrestrial systems have been observed to warm faster than oceans, Levitus *et al.* (2005) note that the world's oceans are taking up approximately 20 times more of the heat added by warming than terrestrial systems. This has resulted in and continues to result in a number of physical changes to marine environments.

The changes to the marine environment caused by global climate change have already begun to affect marine species and ecosystems and can be expected to continue to do so (Roessig *et al.* 2004). Increases in oceanic temperature have manifested as increases in both average sea temperature and spatial and temporal temperature variability. These changes have occurred at depths of up to 3000 m, although most changes have occurred in depths less than 700 m (Bindoff *et al.* 2007). Other changes include reductions in the extent of sea ice (Lemke *et al.* 2007), an increase in sea level of 1.8 mm (±0.5 mm) per annum between 1961 and 2003 (Bindoff *et al.* 2007), a freshening of sub-polar latitudes and salinification of shallow tropical and subtropical seas (Levitus *et al.* 2005), and an increase in the inorganic carbon content of the ocean (Sabine *et al.* 2004). While each of these factors is likely to contribute to changes in marine ecosystems, changes in sea temperature have the most obvious effect and have already been observed to affect the distribution and abundance of marine species (e.g. Perry *et al.* 2005). Furthermore, marine ectotherms are

considered to occupy a greater proportion of their thermal niche than other organisms as a result of their narrow temperature tolerances, and there being fewer geographic barriers to dispersal in marine environments (Sunday *et al.* 2012). This makes changes in sea temperature one of the most important factors affecting the future distribution of marine fishes.

Climate change has been predicted and observed to have a number of effects on species distribution and abundance in both marine and terrestrial ecosystems (Parmesan and Yohe 2003; Parmesan 2006). The magnitude of these impacts on a species is thought to be determined by its spatial distribution and life-history characteristics, as well as the synergistic effects of other anthropogenic factors (Harley *et al.* 2006). The ability of marine species to evolve and adapt to new conditions and habitats will, to some extent, determine the likelihood of their survival in the face of environmental and ecological changes (Berteaux *et al.* 2004; Stockwell *et al.* 2003). The speed at which a marine species is able to adapt to changing conditions is determined by its phenotypic plasticity, generation time, genetic diversity and gene flow (Harley *et al.* 2006). Gene flow is, in turn, affected by several life-history characteristics such as larval dispersion and migratory behaviour (Harley *et al.* 2006; Stockwell *et al.* 2003). Species which are endemic with limited distributions (Thomas *et al.* 2004), long life spans (Perry *et al.* 2005) and those already negatively affected by anthropogenic factors (Harley *et. al.* 2006), have been predicted and observed to be more vulnerable to the negative effects of climate change. Considering that many economically and biologically valuable marine species display the traits listed above, the potential effects of climate change on these species should be considered when planning the conservation and management of marine ecosystems and living resources.

1.2) Marine capture fisheries

Marine capture fisheries remain the last major wild-harvested living resources on the planet. The Food and Agriculture Organisation of the United Nations (FAO) reports that in 2010, marine capture fisheries produced approximately 77.4 million tons of fish, making up a large fraction of the 128 million tons of fish consumed that year (FAO 2012). Fisheries provide an important source of dietary protein and made up approximately 6% of the global total protein intake in 2010 and make up almost 20% of total protein intake for an estimated 3.0 billion people (FAO 2012). Despite their obvious importance, marine capture fisheries have suffered from mismanagement from their inception. A trend of industrialisation, intensification of effort and spatial expansion of marine fisheries in the face of declining catch returns has continued unchecked on a global scale. This is despite the collapse of important pelagic

(Clark 1977; Radovich 1982) and subsequently demersal (Hutchings and Myers 1995) stocks, and a plateau in total global landings being reached in the 1990's (Pauly *et al.* 2005; FAO 2012). Continued declines in catch returns have, in more recent times, led to an increase in the number of papers highlighting the need to curb effort to sustainable levels (Pauly *et al.* 2005; FAO 2012). The FAO (2012) reports that, on a global scale, approximately 57% of marine fish stocks were fully exploited in 2009, with an additional 29% considered over-exploited and in need of drastic management. A number of authors have also highlighted the extensive negative effects of commercial fishing on the ecosystems that support the resource itself.

The status of the multi-species inshore fishery shared by South Africa and Mozambique in the sub-tropical South Western Indian Ocean (SWIO) also reflects this history of mismanagement and over-exploitation. In South Africa, 68% of commercially important stocks have collapsed, 11% are considered over-exploited and 16% are considered optimally exploited (WWF 2011). The status of this fishery in southern Mozambique is less certain due to the artisanal nature of most of its participants and the relatively young age of the commercial linefishery (van der Elst *et al.* 2005). Although less than 17% of Mozambican fishermen are involved in commercial fisheries, artisanal and subsistence fisheries are important to this developing country and provide employment and food security (fish makes up roughly 50% of the average person's total animal protein intake in Mozambique) and should not be under-estimated (van der Elst *et al.* 2005). The economic and social importance of these fisheries makes their management a complex social and political problem as well as an environmental one. The potential effects of external physical factors such as climate change on marine environments and fisheries, add to this complexity and therefore warrant investigation.

The importance of climate variability to fisheries management has been highlighted by Lehodey *et al.* (2006), who noted that both long- and short-term fluctuations in the distribution and abundance of marine species are often forced by climate-related processes. This applies not only to seasonal and annual cycles, but also to decadal and inter-decadal cycles. In light of these correlations, it is expected that global climate change has affected, and will continue to affect the abundance and distribution of many marine species. The results of Perry *et al.* (2005) and Hsieh *et al.* (2008) support this hypothesis. Perry *et al.* (2005) reported distribution shifts in almost two-thirds of both exploited and non-exploited fishes in the North Sea over a 25-year period, and concluded that these shifts correlate with observed increases in mean sea surface temperature in this area. In addition to this, the results of Hsieh *et al.* (2008) indicate that fully exploited and over-exploited species are more

sensitive to the effects of climate change, showing more pronounced shifts in distribution than non-exploited and under-exploited species.

Harley *et al.* (2006) highlight the fact that the effects of climate change and other anthropogenic factors (such as exploitation) on species may often work synergistically, thereby enhancing their negative impact. In the case of marine fisheries, Hsieh *et al* (2008) hypothesised that the reduction in spatial heterogeneity and geographic distribution (e.g. MacCall 1990; Berkely *et al.* 2004) and age/size truncation of populations (e.g. Conover and Munch 2002; Berkely *et al.* 2004; Hutchings and Reynolds 2004) often associated with high fishing pressure, may reduce the resilience of these species to the negative effects of climate change. Furthermore, the loss of genetic diversity and changes in genetic population structure associated with exploitation (Smith 1994), may greatly reduce the raw materials available to fish populations to adapt to changing environments (Berteaux *et al.* 2004; Harley *et al.* 2006). The over-exploited status of many fish stocks indicates that global climate change may have a pronounced effect on these stocks and that climate variability should therefore be included in models used for their management under the ecosystem-based approach to fisheries (Botsford *et al.* 1997; Pikitch *et al.* 2004).

1.3) Species outline

The Scotsman *Polysteganus praeorbitalis* is a member of the family Sparidae and is endemic to the sub-tropical Western Indian Ocean (WIO), being distributed from Algoa Bay in South Africa to Beira in Mozambique (Heemstra and Heemstra 2004). Adults occur mainly on offshore rocky reefs between 50 and 120 m (Heemstra and Heemstra 2004). While considered to be relatively sedentary and solitary during most of the year, this slow-growing reef predator is known to congregate in spawning aggregations off the KwaZulu-Natal (KZN) coast during winter months, making it vulnerable to fishing pressure at this time (van der Elst 1997).

In South Africa, *P. praeorbitalis* is harvested by the boat-based KwaZulu-Natal recreational and commercial linefishery (Garrat *et al.* 1994). Beginning in Durban Harbour in 1905 and spreading to other areas of KwaZulu-Natal as technological and logistical advances allowed, the KwaZulu-Natal commercial linefishery initially targeted large, slow-growing endemic sparids, such as red steenbras (*Petrus rupestris*), poenskop (*Cymatoceps nasatus*), Scotsman (*P. praeorbitalis*) and seventy-four (*Polysteganus undulosus*) (Penney *et al.* 1999). However, their complex life histories did not allow these species to withstand intense fishing pressure and the contribution of these endemic species to commercial catches

declined from approximately 50% in the 1920s to approximately 5% by 1983 (van der Elst 1989). The decline in their contribution to catches reflects large-scale declines in abundance of these vulnerable species due to prolonged and severe over-exploitation. One of the main reasons for the vulnerability of these species is the limited availability of reef habitat along the KwaZulu-Natal coastline. The KwaZulu-Natal linefishery targets two main reef areas: scattered shallow-water reefs which are mainly located in a narrow strip along the 50 m isobath, and deep-water reefs between 100 and 200 m occurring south of Durban (the south coast) and also in an approximately 150 km strip near Richards Bay (opposite the mouth of the Thukela River) in an area referred to as the Thukela Banks (Lamberth *et al.* 2009; Sauer *et al.* 2003).

In terms of participants, the fishery peaked in 1995 with an estimated 140 commercial and 2 009 recreational boats operational at the time and approximately 10 000 fishers (Lamberth *et al.* 2009). Continued declines in catches led to a declaration of a state of emergency in the South African linefishery in 2000 (Notice no. 4727 of 2000, *Government Gazette* no. 21949), resulting in drastic cuts in effort (Hutton *et al.* 2001). As a result of these declines in catches and new regulations, commercial boats operating in KwaZulu-Natal in 2001 numbered 108 and employed approximately 600 people (Sauer *et al.* 2003). These boats are almost evenly split between launch sites on either side of Durban, with at least 50% accessing the Thukela Banks while the remainder access reefs on the south coast (Lamberth *et al.* 2009).

Today the recreational linefishery is managed on species-specific bag and minimum size limits while the commercial fishery is currently managed mainly through a total allowable effort (TAE) allocation, together with species-specific size limits and bag limits for a few species, including *P. praeorbitalis* (DAFF 2012). This is in accordance with the Marine Living Resources Act (Act. no. 18 of 1998, *Government Gazette* no. 18930). In the case of *P. praeorbitalis*, stocks have been severely depleted in South African waters through overfishing (Branch *et al.* 1994, van der Elst 1997) with a >90% decline in catch per unit effort (CPUE) for *P. praeorbitalis* recorded in KwaZulu-Natal between 1941 and 1992. This is reflected in the fact that *P. praeorbitalis* comprised less than 1.2% of the total KwaZulu-Natal catch by 1992 (Garrat *et al.* 1994). Lamberth *et al.* (2009) reported that *P. praeorbitalis* comprised only 0.17% of commercial landings taken from north of Durban (Thukela Banks) and 1.15% of total landings in the KwaZulu-Natal Linefishery between 1985 and 2001, and estimated the stock to be at 10% of pristine levels. Despite this decrease in abundance, Fennessy *et al.* (2003) found that *P. praeorbitalus* still comprised 4.6% and 4.2% of the commercial and recreational ski-boat landings, respectively, in the northern Transkei region.

P. praeorbitalis appears infrequently in the catches of the semi-industrial and industrial linefishery in southern Mozambique, where reef species are targeted mainly using hook and line, and sometimes traps (A. Guissamulo, pers. comm.; van der Elst *et al.* 1995). It is also likely that *P. praeorbitalis* has appeared infrequently in the catches of the artisanal linefishery which uses handlines, traps and spears. While recreational linefisheries are present in Mozambique, these target mainly pelagic species (van der Elst *et al.* 1995). The semi-industrial linefishery encompasses port-based vessels of 10 m–20 m which hold 10–15 crew members and keep their catch on ice. Industrial vessels are greater than 20 m and can freeze their catch (van der Elst *et al.* 1995). This allows them to spend a longer time at sea and therefore fish further from port than semi-industrial vessels. Together, these two sectors were estimated to support approximately 550 fishers in 2011 (Fennessy *et al.* 2012).

Historically, the semi-industrial linefishery in Mozambique has mainly operated south of 24°S, but more recently, there has been increased effort north of 21°S on the Sofala Banks (Fennessy *et al.* 2012). It is in the area south of 24°S that *P. praeorbitalis* is most likely to feature in catches as the catch composition in this area is dominated by three other sparid species: slinger *Chrysoblepus puniceus*, santer *Chrysoblephus anglicus* and the blueskin seabream *Polysteganus coeruleopunctatus* which together made up more than 70% of the semi-industrial linefishery catch in 2000 (van der Elst *et al.* 2003). These species are commonly caught alongside *P. praeorbitalis* in KwaZulu-Natal and are known to share similar habitats (Penney *et al.* 1999). Because of the civil war between 1977 and 1990, Mozambican fisheries have, historically, grown more slowly than those in South Africa; however, Fennessy *et al.* (2012) report that these fisheries grew substantially after 1990 and recent growth in the semi-industrial linefishery operating south of 24°S has been extremely rapid, with a 50% increase in effort (recorded as total annual days at sea) recorded between 2008 and 2010. This rapid increase in effort appears to have resulted in over-exploitation in this area with a 70% decline in catch per unit effort (CPUE) for large sparids recorded between 1991 and 2010, as well as a decline in the mean sizes of *C. puniceus* and *C. anglicus* (Fennessy *et al.* 2012).

1.4) Study area

1.4.1) *Oceanography*

The Agulhas Current carries warm water from the tropical Western Indian Ocean southward into subtropical and temperate latitudes (Lutjeharms 2006a). This western boundary current is driven by wind stress over the subtropical Indian Ocean basin and, like other western

boundary currents, forms the western part of an anti-cyclonic subtropical gyre (Lutjeharms 2006a). The current develops somewhere between the city of Durban and the mouth of the Mozambique Channel and is fed by three main sources: flow through the Mozambique Channel, flow from east of Madagascar, and re-circulation in an anti-cyclonic sub-gyre situated in the south-west Indian Ocean (Lutjeharms 2006a). The contributions of the flow from eastern Madagascar and the re-circulation of the anti-cyclonic sub-gyre to the Agulhas Current are substantial, while flow through the Mozambique Channel is relatively small (Lutjeharms 2006a). The current continues south-west from its inception, increasing in volume and speed along the eastern coast of South Africa before terminating in the Agulhas Current retroflection off the southernmost tip of Africa and feeding into the Southern Ocean, Southern Atlantic Ocean and Southern Indian Ocean (Lutjeharms and van Ballegooyen 1988; Lutjeharms and Cooper 1996).

Lutjeharms (2006a) describes the section of the Agulhas Current between approximately 27°S and 34°S latitude as the Northern Agulhas Current. This region is characterised by a smooth, narrow, steep continental shelf along which the Agulhas Current accelerates, growing in size and strength as it flows southwards. This sheer, narrow shelf has a stabilising effect on both the speed and trajectory of the current (De Ruijter *et al.* 1999). Direct current measurements in this region have shown a high annual mean flow rate of1.5 $m.s^{-1}$, with monthly standard deviations of 0.5 $m.s^{-1}$ and very little evidence of seasonal variation (Pearce and Gründlingh 1982). Hydrographic sections conducted between St Lucia and Port Elizabeth by Gründlingh (1983) indicate that, on average, the current meanders by less than 15 km to either side of its central position.

Despite the relative stability of the current, the difference in temperature between the warm current waters and the cooler waters of the continental shelf results in large fluctuations in regional inshore sea surface temperatures (SST) over a timescale of days (Lutjeharms *et al.* 2000a). These fluctuations are due to seasonal upwelling events which occur predominantly in the waters off the Western Cape (Schumann *et al.* 1982). This upwelling is caused by north-easterly trade winds which push warm surface water offshore through Eckman transport, pulling up the cold shelf water beneath it. In addition to these seasonal upwelling events, upwelling also occurs at upwelling cells, which are driven kinematically by the Agulhas Current, as a result of downstream widening of the continental shelf and are intensified by north-easterly trade winds (Lutjeharms *et al.* 2000a). This occurs at the northern corner of the Natal Bight between St Lucia and Richards Bay and between the Mbashe Estuary and the eastern edge of Algoa Bay. The core of the latter upwelling cell is found at Port Alfred (Lutjeharms *et al.* 2000a).

The sheer edge of the continental shelf also causes some lateral circulation, the most notable and persistent feature of which is the Durban Eddy. The Durban Eddy is a cyclonic eddy which exists off Durban, directly downstream from the St Lucia-Richards Bay upwelling cell (Lutjeharms 2006a). Here the widening of the continental shelf and the slight inflection of the coastline which form the Natal Bight result in a persistent counter-current, forming a vortex of cooler water which is periodically shed downstream in what is referred to as a Natal Pulse (Lutjeharms *et al.* 2000b). This phenomenon is thought to be the result of instability in the Durban Eddy caused by peaks in the flow rate of the Agulhas Current. Its progress downstream causes the current to move further offshore and results in fluctuations in SST and inshore counter-currents as far south at Port Elizabeth (Lutjeharms *et al.* 2001; Lutjeharms 2006a). South of Port Elizabeth, the continental shelf widens into the Agulhas Bank, causing the current to destabilise and meander; this is the beginning of the more complex Southern Agulhas Current system (Lutjeharms 2006a).

1.4.2) *Biogeography*

Three main biogeographic provinces have been defined in the Agulhas Current system based on species assemblages in different habitats: warm-temperate, subtropical, and tropical provinces (e.g. Harrison 2002). The positions of the boundaries between these provinces have been investigated in rocky shore biota (Stephenson and Stephenson 1972; Bustamante and Branch 1996), marine invertebrates (Emanuel *et al.* 1992), intertidal fishes (Prochazka 1994) and estuarine fishes (Maree *et al.* 2000; Harrison 2002). These provinces tend to shift and overlap depending on season and the habitats of the taxa investigated. In the case of shelf-associated fishes, Turpie *et al.* (2000) hypothesised a warm-temperate province occurring south of Port Edward, a subtropical province between Port Edward and Kosi Bay and a tropical region extending north of Kosi Bay into Mozambique. Species richness in shelf-associated fishes in this system has been observed to decrease from north to south. However, a peak in the number of species endemic to the South African coastline occurs near Algoa Bay (Turpie *et al.* 2000).

1.5) Climate change and the Agulhas Current system

Climate change is predicted to result in a pole-ward shift of westerly winds, translating into an increase in the frequency and intensity of north-easterly trade winds in the southern Indian Ocean (Lutjeharms *et al.* 2001). In turn, this change is expected to intensify the Agulhas Current through increases in the wind stress that drive the current (Lutjeharms *et al.* 2001; Lutjeharms 2006b). The intensification of the Agulhas Current has been predicted to

result in an increase in SST in the southern and northern Agulhas Current system as well as an increase in the frequency of Natal Pulse events. Also predicted is an increase in the intensity of both the Port Alfred and St Lucia–Richards Bay upwelling cells, a pattern likely to be exacerbated by increases in the frequency and intensity of upwelling-favourable easterly winds (Lutjeharms *et al.* 2001).

The results of Rouault *et al.* (2009) support these hypotheses, showing seasonal warming in the southern Agulhas Current, some cooling in the northern Agulhas Current and increased kinetic energy in the Agulhas Current retroflection, as well as intensification of the Port Alfred upwelling cell. Optimum Interpolated Reynolds SST data (a combination of remotely sensed and in-situ data) recorded between 1982 and 2009 shows that since the 1980s, the SST of the Agulhas Current has warmed by up to 0.7 °C per decade with a mean decadal increase in SST of approximately 0.5 °C observed between 1982 and 2009 (Rouault *et al.* 2009). In coastal areas, warming of up to 0.55 °C has been recorded in summer along the east coast of South Africa. However, this trend is not uniform and there are several areas along the west, south and southeast coasts where seasonal (autumn and winter) cooling has been observed (Rouault *et al.* 2009, 2010).

1.6) Evaluating species vulnerability to climate change

Current spatial distribution and levels of genetic diversity and spatial structure can both be used in combination with life-history characteristics to help predict the response of a species to future climate change. Species distribution models or bioclimatic envelope models constructed using occurrence and environmental data have been used to predict the future distribution of both terrestrial and marine species (e.g. Cheung *et al.* 2009; Albouy *et al.* 2012) under future climate scenarios. These models are, however, sensitive to slight changes in their assumptions and show high levels of uncertainty due to many unknown variables including the evolutionary and behavioural response of the species and whether or not the population is currently in equilibrium with its environment (Pearson and Dawson 2003). Despite their perceived inaccuracies, bioclimatic envelope models provide one of few means available to predict the extent and direction of species distribution shifts in response to climate change and are thus a valuable tool for providng a first cut risk assesment to those who wish to conserve and manage living resources in the face of climate change (Guisan and Zimmermann 2000; Austin 2002; Elith and Leathwick 2009).

While the pace of anthropogenic-induced climate change may be rapid in geographic terms, most authors agree that many species will be able to adapt to these changes on a genotypic

level through contemporary evolution (Harley *et al.* 2006; Berteaux *et al.* 2004). In many marine organisms, survival may depend on the variation present at very specific loci such as those coding for the production of the heat shock protein HSP70, which is important in response to thermal stress (Harley *et al.* 2006; Hoffmann and Sorte 2005). The interaction between gene flow and genetic diversity can have varied effects on the speed of adaptation of a species. Stockwell *et al.* (2003) note that low levels of gene flow can favour rapid local adaption in genetically diverse populations, but can in some cases, lead to genetic drift, resulting in a loss of genetic diversity and thus a reduced ability to adapt to changing conditions on a genotypic level. It is therefore important to understand the genetic structure and connectivity of a fishery when attempting to manage it in a changing environment. From the current genetic structure of a species or taxa in relation to its distribution, one can infer much about the response of these species to past environmental changes which helps predict the response to similar shifts in the future (Bermingham and Moritz 1998). Thus genetic stock assessments may provide a useful tool in combination with species distribution modelling to evaluate the potential of a species to adapt to and survive the effects of climate change on its environment.

1.7) Research aims and objectives

This study aims to combine species distribution modelling and genetic analysis with available life history information to predict the effects of climate change on the commercially and recreationally exploited *P. praeorbitalis* in the Agulhas Current system off the east coast of southern Africa. Research objectives include:

- to predict whether or not the current range of *P. praeorbitalis* will shift in response to climate change and in which direction;
- to predict whether the overall range of *P. praeorbitalis* will expand or contract in response to climate change;
- to determine the current genetic structure and diversity of *P. praeorbitalis* throughout its range with reference to historical demographics and distribution patterns.

By achieving these objectives, it is hoped that this study will provide an assessment of the vulnerability of *P. praeorbitalis* to the negative effects of climate change on its distribution and genetic diversity. This will, in turn, allow the estimation of the ability of this and other similar WIO species to adapt to changing environmental conditions through contemporary evolution.

Chapter 2

Species distribution modelling: predicting the distributional response of *Polysteganus praeorbitalis* to climate change in the Agulhas Current system.

2.1) Introduction

A global meta-analysis of 1 700 species by Parmesan and Yohe (2003) found that many terrestrial and aquatic species are already responding to the effects of climate change through pole-ward shifts in distribution averaging 6.1 km per decade. Another global study by Cheung *et al.* (2009), using a dynamic bioclimatic envelope model, predicted a global pole-ward shift in marine fishes and invertebrates at a median rate of 45–49 km per decade. The rate of species distribution changes may thus be more rapid in marine environments. Parmesan and Yohe (2003) note that species distributions are often more strongly limited by localised geographic and environmental factors than by regional climate. In ecosystems where this is the case, these localised geographic and environmental factors may restrict species distributional responses to climate change, causing reductions in range (Parmesan 2006). This is exemplified by the plight of mountain butterfly species which are restricted by altitude and localised temperatures and are therefore unable to expand their range pole-wards in response to climate change (Wilson *et al.* 2005). In these ecosystems the risk of climate change-induced decreases in distribution and abundance, and extinctions are increased (Thomas *et al.* 2004).

The importance of different climatic and environmental variables in limiting the distribution of species, and the possible effects of climate change on this can, to some extent, be predicted using species distribution models (SDM's) (Guisan and Zimmermann 2000; Austin 2002; Elith and Leathwick 2009). Correlative species distribution models relate natural distribution data to a combination of environmental and/or geographical gradients on a spatial scale in order to estimate the probability of occurrence of a given species in an area as a function of environmental conditions (Elith and Leathwick 2009). Despite concerns that they do not consider ecological factors such as biotic interactions, dispersal rates and species evolutionary responses (Pearson and Dawson 2003), SDM's have proved useful in predicting the extent of species ranges and, more recently, have been projected over geographical and environmental space to provide a first cut risk assessment of the invasion potential of species and responses of indigenious species to climate change (e.g. Guisan

and Zimmermann 2000; Pearson and Dawson 2003; Elith and Leathwick 2009). In the latter application, the use of a multi-model 'ensemble' approach has gained popularity (Buisson *et al.* 2010) and is recommended in order to reduce the effects of model uncertainty (Thuiller 2003, 2004; Araújo *et al.* 2005; Araújo and New 2007).

While climate change studies using SDM's initially focused on terrestrial plant distributions, (e.g. Huntley 1995; Huntley *et al.* 1995; Bakkenes *et al.* 2002), recent studies have focused on animals, including marine fishes (e.g. Cheung *et al.* 2009; Albouy *et al.* 2012). These methods however, remain under-utilized in the marine environment largely due to a paucity of appropriate environmental and occurrence data for many marine ecosystems (Lam *et al.* 2008; Robinson *et al.* 2011). The use of remotely-sensed data presents new opportunities to investigate the potential effects of climate change on species in marine ecosystems to which SDM's have yet to be applied (Robinson *et al.* 2011), such as the Agulhas Current system.

Important in producing useful SDM's is the choice of environmental variables that directly or indirectly limit the distribution of the species in question and for which long-term data exists (Austin 2002). Because of the relatively few physical barriers to dispersal in marine environments, marine ectotherms are considered to occupy a greater proportion of their thermal niche than their terrestrial counterparts (Sunday *et al.* 2012). Thermal tolerance limits fish distribution directly by decreasing aerobic scope at thermal limits (Pörtner and Knust 2007), affecting growth and survival of adults, and particularly, of larvae (Houde 1989; Munday *et al.* 2008). Furthermore, because many fish species rely on thermal cues to synchronise reproduction and migration (Humston *et al.* 2000; Sims *et al.* 2001; Hilder and Pankhurst 2003; Sims *et al.* 2004), these would be directly affected by changes in thermal conditions (Munday *et al.* 2008). Marine fishes are also likely to be indirectly affected by changes in sea surface temperature (SST) through effects on other environmental factors and trophic levels (Rijnsdorp *et al.* 2009). Thermal gradients, therefore, play an important role in limiting marine fish distributions, and as a result, distribution modelling of marine fish species based on SST may be a useful tool. Due to the fact that SST only represents surface temperatures and fails to consider the effects of thermal stratification with depth, models based on this type of data must be interpreted with caution, taking into account this potentially confounding factor. The Agulhas Current system off the east coast of southern Africa is a good model as it is considered to be climate change 'hotspot', with regard to changes in SST (refer to Chapter 1).

Although the Agulhas Current system is not highly productive, Griffiths *et al.* (2010) consider that it has high levels of biodiversity and endemism with a meta-analysis listing of 4 233

species endemic to the South African exclusive economic zone (EEZ) (although this does include some West Coast species from the Benguela Current system). Griffiths *et al.* (2010) list species distribution shifts caused by the effects of climate change as one of the main future threats to South African marine biodiversity. Heileman *et al.* (2008) also note that the living resources of coastal environments within the Agulhas Current system are highly vulnerable to the negative effects of climate change, citing the widespread temperature-related bleaching of coral reefs in this system during the 1998 El Niño event. Despite these indications of the potential effects of climate change on the environmental parameters and biodiversity of this system, and the value of this biodiversity to South Africa and Mozambique, there are few studies on the possible ecological effects of climate change on species within this current system.

Rijnsdorp *et al.* (2009), in attempting to elucidate the effects of climate change on marine fishes, made several key predictions based on fisheries studies, including:

1) Range-restricted species and endemic species with small ranges will be more vulnerable to the effects of climate change, as will demersal species, because of the fixed geographic nature of their habitat requirements.
2) Over-exploited species will be more vulnerable to the effects of climate change than non-exploited or under-exploited species.
3) Long-lived, slow-maturing species with low population turnover rates will be less equipped to deal with environmental changes and therefore will be more vulnerable to the effects of climate change than short-lived species.

These assumptions suggest that *Polysteganus praeorbitalis* as a long-lived, slow-growing and over-exploited reef species, endemic to the Agulhas Current system, would be particularly vulnerable to reductions in range and abundance as a result of the effects of climate change. This study therefore aimed to estimate the current range of *P. praeorbitalis* and to investigate the potential effects of climate change-induced SST changes in the Agulhas system on the future range of this species. The key research questions were:

1) What is the current realised distribution of *P. praeorbitalis*?
2) Is the current distribution of *P. praeorbitalis* likely to show a pole-ward shift as a result of the effects of climate change?
3) If historical trends in SST change continue, is the overall range of *P. praeorbitalis* likely to expand or contract?

that, despite regional warming, *P. praeorbitalis* is unlikely to show a pole-ward shift in distribution. Instead, due to cooling at its southern range edge as a result of the intensification of the Port Alfred upwelling cell, a reduction in range was hypothesised.

2.2) Materials and Methods

2.2.1) Occurrence data

A total of 203 occurrence records were obtained from three main sources. The National Marine Linefish System (NMLS) catch database includes catch records obtained through shore patrols, inspections and observer records of commercial operators, as well as voluntary submissions and competition records from recreational anglers in South Africa. The Oceanographic Research Institute (ORI) / World Wildlife Fund (WWF) South Africa tagging database consists of tag-recapture data submitted by anglers and scientists, while the National Fish Collection maintained by the South African Institute for Aquatic Biodiversity (SAIAB) features occurrence records of voucher specimens positively identified and recorded by scientists. A paucity of occurrence records north of the South African-Mozambican border remains, due in part, to a lack of fisheries infrastructure in Mozambique, but also to the relative rarity of this species in Mozambican catches (A. Guissamulo, pers. comm.), an indication of its low abundance in these waters.

2.2.2) Environmental Data (historic)

Sea surface temperature data were extracted from the Reynolds Optimum Interpolation (OI) SST dataset (http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.htm) (Reynolds *et al.* 2002). This is a 1°×1° resolution SST monthly mean dataset (30 years monthly means: 1971-2000) generated from satellite and in-situ SST data corrected for biases using the methods of Reynolds (1988) and Reynolds and Marisco (1993). This dataset has been shown to provide adequate representation of the Agulhas system at a regional scale (Rouault *et al.* 2003) and was chosen in preference to the more fine-scale Moderate Resolution Imaging Spectroradiometers (MODIS) and Advanced Very High Resolution Radiometer (AVHRR) SST datasets available, because of its relatively long timeframe and lack of missing data caused by cloud cover. Rouault *et al.* (2010) however, warn that this data should be used with caution at a regional scale because of its low resolution, which poorly defines some key features of the Agulhas system. Twelve mean monthly SST datasets were downloaded for the years 1971-2000 within coordinates 20W, 60E, -39S and 35N.

Eight minimum and maximum composite GIS layers were prepared from the monthly means to give a minimum and maximum layer for each season (summer: January-March, autumn: April-June, winter: July-September and spring: October–December) using ArcMap™ 10.0 (ESRI Inc. California, USA). Seasonal minimum and maximum SSTs were chosen in

preference to means, because of the high level of daily variation in SST within the Agulhas system, a result of frequent upwelling events (Lutjeharms 2006a). This was informed by the conclusions of Sunday *et al.* (2012) that fish distributions are more likely to be constrained by thermal extremes than averages. Bathymetry was also considered important in light of the reef-dwelling nature of the species (van der Elst 1997). Bathymetry data used in the study are a blend of Smith and Sandwell (1977) and GEBCO (General Bathymetric Chart of the Oceans) bathymetries at a 0.0167° resolution and were extracted from <http://omap.africanmarineatlas.org/index.html>.All layers were re-sampled to a 0.05° resolution using a distance weighted average between points and clipped to the area between the 0 m and 1000 m depth contour in order to exclude areas where the species does not occur.

Scatterplots calculated between variables revealed a high correlation between summer minimum and maximum temperatures, as well as between winter minimum and maximum temperatures. In order to reduce the negative effects of correlated variables on model performance, summer minimum and winter maximum temperatures were excluded from the modelling process.

2.2.3) Environmental Data (Predicted)

Similar SDM studies have used temperature predictions derived from general circulation models (GCM's) such as the Intergovernmental Panel on Climate Change (IPCC) AR4 model. However, these models often lack the resolution necessary for finer scale predictions at regional levels (Redfern *et al.* 2006), and fail in particular, to resolve adequately the main features of the Agulhas Current system. This may result in significant underestimations of heat fluxes within the system (Rouault, *et al.* 2003). For this reason, a strategy of 'persistence is the best forecast' was adopted and predicted SST layers were constructed by extending temperature trends in time (M. Rouault, pers. comm.). Monthly OI-SST data were used to calculate linear regressions of SST (°C per decade) over the period January 1982 to December 2010, after which seasonal trends were calculated in IDRISI Selva (Clark Labs, Worcester, USA). These layers were used to predict SST for 2020 and 2030.

2.2.4) Distribution Modelling

The package Biomod 2 v1.0 (Thuiller *et al.* 2009) run in R 2.15.1 statistical software (R Development Core Team 2011) was used to model the environmental niche occupied by *P. praeorbitalis* and to predict how that niche might change in relation to future climate change

scenarios. In order to account for modelling uncertainty (Thuiller 2004; Elith *et al.* 2006), recent studies recommend an ensemble approach to modelling when projecting models into future climate scenarios (Araújo and New 2007; Buisson *et al.* 2010). This approach weights the contributions of several algorithms according to a statistic describing accuracy. Seven models (described below) were chosen for inclusion in a probability weighted means ensemble model.

Generalised Linear Models (GLMs) (McCullagh and Nelder 1989; Austin and Meyers 1996) provide a more flexible form of multiple linear regression models by allowing for the inclusion of response curves with error distributions other than normal, through the use of a link function. Generalised Additive Models (GAMs) (Hastie and Tibshirani 1990; Austin and Meyers 19966) use equations called 'smoothers' to fit many localised smooth response curves to subsections of the data and calculate a single smoothed curve for each predictor, maximising parsimony and fit. This allows them to fit more complex response curves than GLMs. Classification tree analyses (CTA) (Breiman *et al.* 1984; De'Ath and Fabricius 2000) create a decision tree by repeatedly splitting the data based on a single explanatory variable into exclusive groups, maximizing homogeneity with regard to the response variable. Boosted Regression Trees (BRTs) (Friedman 2001; Austin and Meyers 19966) combine a number of simple decision trees in a modified regression model while Random Forest (RF) (Breiman 2001; Elith *et al.* 2006) generates and takes the mode from a large number of decision trees through the implementation of Breiman's random forest algorithm. Multivariate Adaptive Regression Splines (MARS) (Elith *et al.* 2006) is a non-parametric regression method, particularly effective at including the effects of complex interactions between explanatory variables on the response variable. Maximum Entropy Models (MaxEnt) (Phillips and Dudik 2008; Elith *et al.* 2006) work by minimising the relative entropy between probability densities created for the response and explanatory variables in space. All models were calibrated using 70% of the total dataset while the remaining 30% was used for evaluation.

The lack of absence data available for *P. praeorbitalis* and other marine fishes necessitated the creation of pseudo-absences in order to apply most of the available modelling algorithms. Pseudo-absences were generated over the same area and at the same resolution used for the environmental variables. This area includes the entire range of the species, with margins on all sides except for the western range limit which is constrained by the coastline. Model performance as a function of pseudo-absence selection strategy differs between algorithms and therefore different algorithms require different pseudo-absence datasets for optimum performance (Barbet-Massin *et al.* 2012). The use of different pseudo-

absence datasets in different models, however, would introduce bias into the comparisons of accuracy necessary for weighting models in an ensemble. This necessitated selecting a single strategy midway between the optimums for all models. Because of the climatically biased nature of occurrence data used in this study as a result of the scarcity of *P. praeorbitalis* in Mozambican waters, a Surface Range Envelope (SRE) model was used when generating a pseudo-absence dataset (Barbet-Massin *et al.* 2012), excluding points which exceeded a similarity-to-presence-data threshold of 0.025. From this dataset ten pseudo-absence datasets of n = 203 were randomly selected with replacement and weighted equally to the presence dataset. This number was chosen to cater to models such as GLM, GAM and MaxEnt which perform best with a large pseudo-absence dataset (n = 1000) while preventing under-predictions of range in machine learning methods such as RF and CTA, which perform better with multiple, smaller (n = 100) pseudo-absence datasets (Barbet-Massin *et al.* 2012).

Models were evaluated through a confusion matrix calculating the number of true positives (a), false positives (b), true negatives (c) and false negatives (d), from which sensitivity $\left(\frac{a}{a+c}\right)$, specificity $\left(\frac{d}{b+d}\right)$ and overall accuracy $\left(\frac{a+d}{n}\right)$ were calculated. In the ensemble model, all models were weighted according to their accuracy as calculated by the True Skill Statistic (TSS) $\left(\frac{ad-bc}{(a+c)(b+d)}\right)$, which is considered a reliable measure of model accuracy independent of prevalence (Allouche *et al.* 2006). A maximum score of 1 indicates a perfect model fit, and a minimum of 0 indicates a fit no better than random. Threshold values for binary transformation of model outputs were calculated to maximise the TSS.

In order to provide a measure of accuracy independent of threshold, models were also evaluated using the area under the receiver operating characteristic (ROC) curve (Fielding and Bell 1997). This method plots sensitivity vs. 1 – specificity for all possible thresholds calculated using multiple confusion matrixes and taking the area under the curve as an independent measure of accuracy. A maximum score of 1 indicates a perfect fit. Variable importance was evaluated by comparing the original prediction of each calibrated model with a prediction made using the same variables but with one variable randomised. The correlation score produced inversely represents the importance of the randomised variable in the model relative to the scores obtained for other variables in the same model, but cannot be compared between models. This procedure was repeated three times per variable for each model and the mean inverse of the correlation was taken as a proportion of the total to represent the variable importance. The probability weighted ensemble model generated was

projected using the mean of the historical conditions to represent current conditions, while future predicted SST values were generated for 2020 and 2030. Projections were visualised in ArcMap™ 10.0

2.3) Results

2.3.1) Present and future climates

A map of mean seasonal SSTs shows a gradual decrease in SSTs from north-east to south-west (Fig 2.1). The coolest areas are south-west of the Port Alfred upwelling cell, dropping as low as 15.97 °C in winter, while the waters of northern Mozambique represent the warmest areas and reach temperatures of up to 29.25 °C in summer.

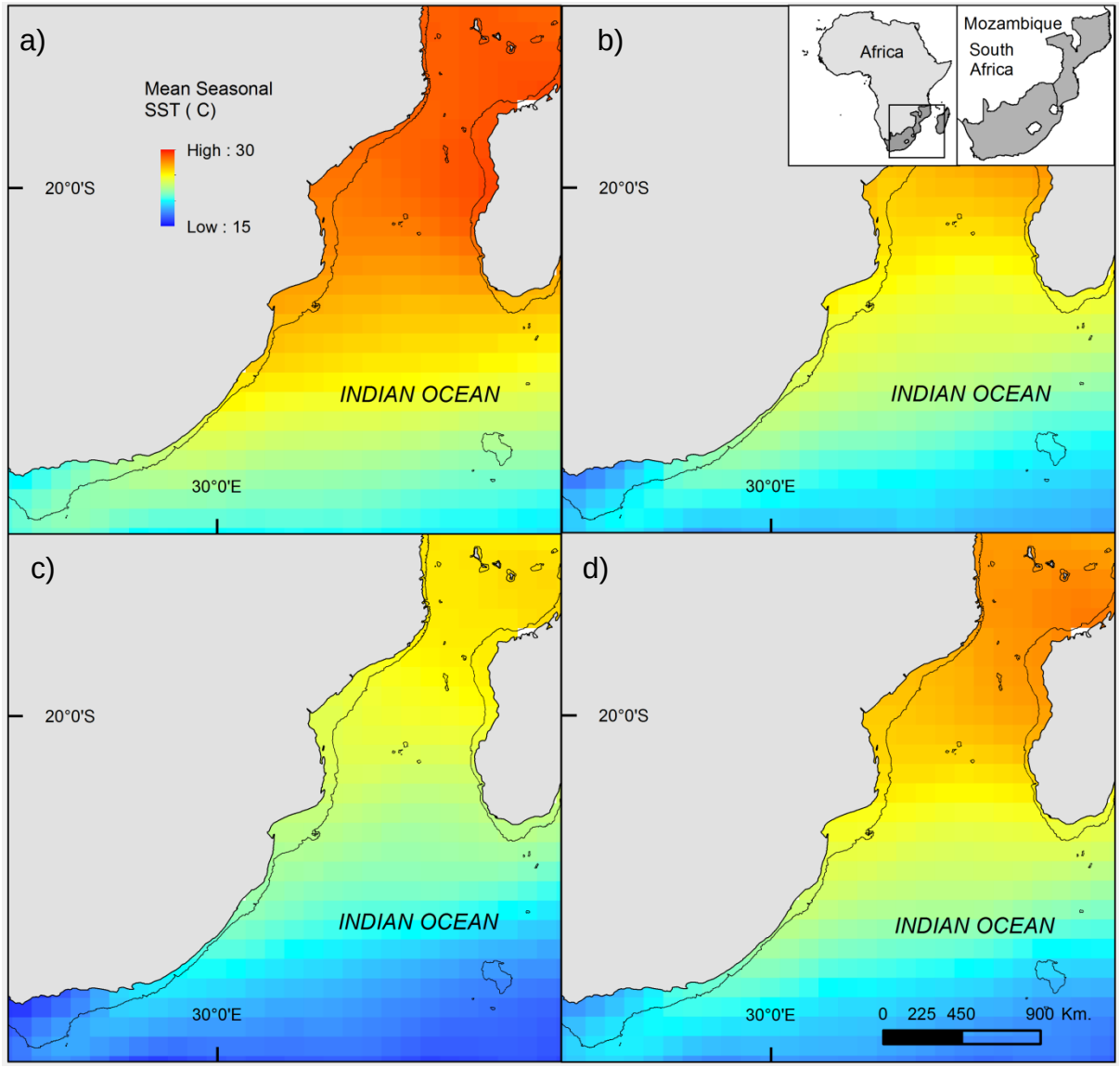

Figure 2.1: Mean seasonal SST's for the Agulhas Current system calculated using Reynolds OI SST data between 1980 and 2010. Shown are: summer (a), autumn (b), winter (c) and spring (d).

A seasonal linear trend plotted for Reynolds SST (1982-2010) revealed coastal warming occurring throughout the year along the east coast of South Africa, with a peak in warming of up to 0.52 °C per decade occurring in summer (Fig 2.2a). Cooling trends were observed during the autumn and winter months in a narrow strip south-west of Algoa Bay, South Africa, with temperatures decreasing by up to 0.31 °C per decade in winter and autumn (Fig 2.2b and 2.2c). Coastal warming was observed along the Mozambique coast during summer (up to 0.39 °C) and spring (Fig 2.2a), with small pockets of cooling observed in southern Mozambique in spring (cooling around Maputo) and winter (Beira and Maputo) by as much as 0.23 °C per decade (Fig 2.2c and 2.2d).

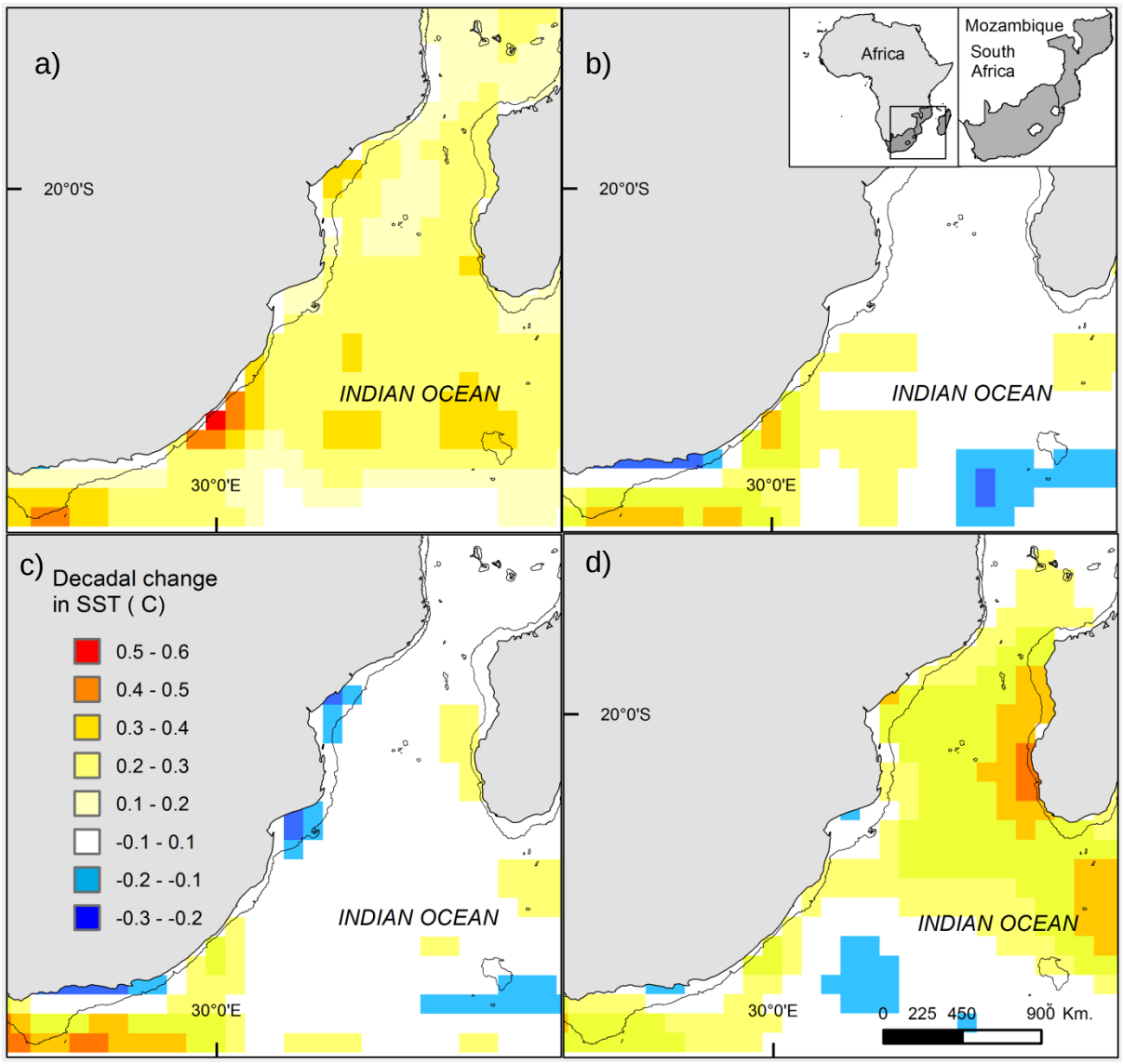

Figure 2.2: Observed mean decadal change in seasonal SST in the Agulhas Current system calculated using a linear regression applied to 30 years of Reynolds OI SST data (1980-2010). Shown are: summer (a), autumn (b), winter (c), and spring (d).

2.3.2) Model prediction accuracies and environmental variable contributions

The 203 occurrence records obtained adequately cover the centre and southern half of *P. praeorbitalis'* published range (Fig 2.3). However, there are few records north of the South Africa–Mozambique border and this is likely to hinder model representation of the northern edge of this species range.

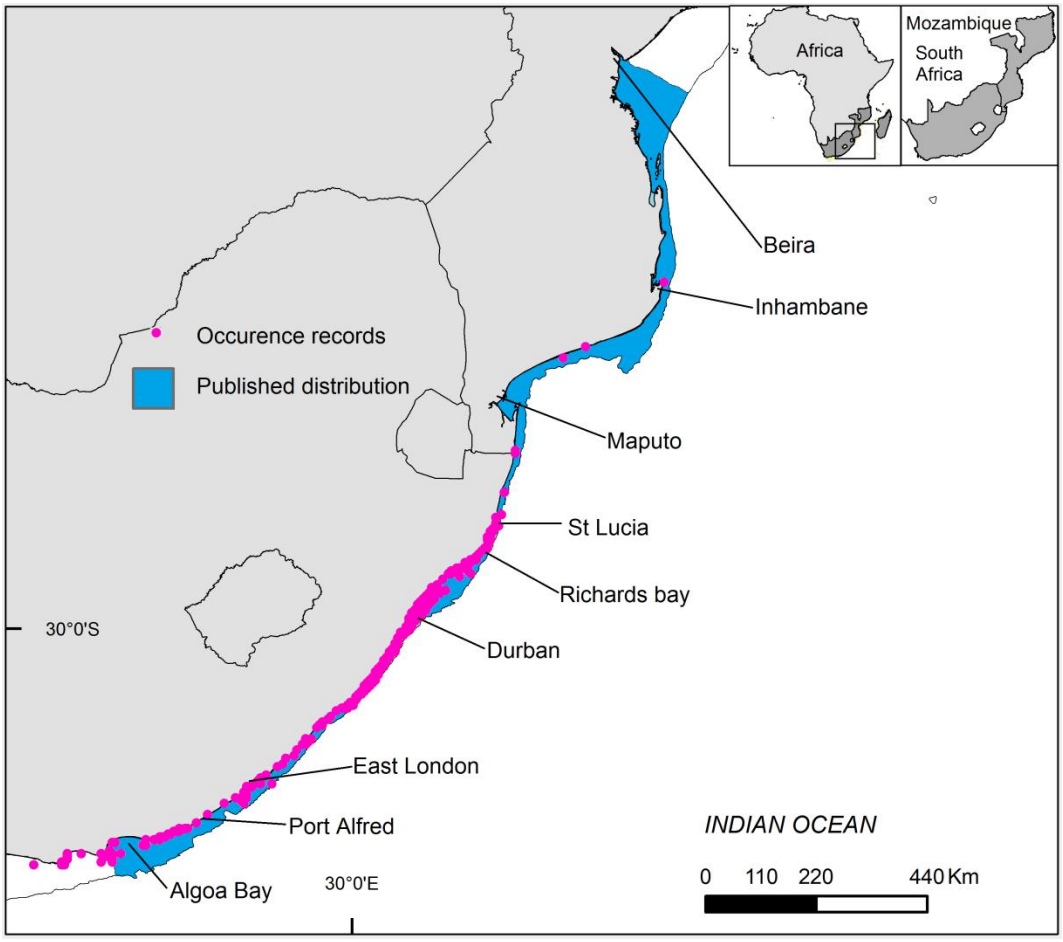

Figure 2.3: Map showing occurrence records obtained for *P praeorbitalis* (n=203) and its distribution listed by Heemstra and Heemstra (2004).

Variable importances calculated and expressed as proportions of total importance for each model are depicted in Table 2.1. Winter minimum, autumn minimum and bathymetry were found to be the three most important environmental variables overall. In light of *P. praeorbitalis'* dependence on reef habitats, the importance of bathymetry is to be expected,

while winter and autumn minimum SST's are likely to determine the southern range edge of *P. praeorbitalis*.

Table 2.1: Variable importances of seven environmental variables to seven species distribution models for *P. praeorbitalis*, calculated in Biomod 2 and expressed as a proportion of total importance for each model. The most important variable to each model is shaded.

Variable	Model							
	GAM	GLM	MaxEnt	GBM	MARS	CTA	RF	Mean.
Winter min.	0.155	0.165	0.000	0.635	0.380	0.842	0.106	0.326
Autumn min.	0.036	0.243	0.582	0.014	0.399	0.001	0.064	0.191
Bathymetry	0.100	0.055	0.199	0.056	0.086	0.154	0.553	0.172
Summer max.	0.002	0.069	0.218	0.254	0.135	0.001	0.043	0.103
Spring min.	0.246	0.243	0.000	0.012	0.000	0.001	0.085	0.084
Spring max.	0.460	0.000	0.000	0.018	0.000	0.001	0.085	0.081
Autumn max.	0.002	0.224	0.000	0.012	0.000	0.001	0.064	0.043

Model evaluation using TSS and ROC showed all models fitted the dataset well with no result for either statistic falling below 0.94 (Table 2.2).

Table 2.2: Model evaluations with current and future range predictions and comparisons for seven binary transformed species distribution models and an ensemble model constructed from them, for *P. praeorbitalis* in the Agulhas Current system.

Model	Evaluation		Results				
	TSS	ROC	Current range (km^2)	2020 range (km^2)	2030 range (km^2)	20 year change (%)	30 year change (%)
GAM	0.961	0.998	1534	1441	1369	-6.063	-10.756
GLM	0.975	0.999	2503	2010	1561	-19.696	-37.635
MaxEnt	0.970	0.999	1539	1197	960	-22.222	-37.622
GBM	0.946	0.996	2399	2214	2051	-7.712	-14.506
MARS	0.961	0.998	1926	1979	2012	2.752	4.465
CTA	0.966	0.989	1493	1544	1543	3.416	3.349
RF	0.98	1.000	1750	1439	1368	-17.771	-21.829
PMW	0.975	0.999	1550	1351	1085	-12.839	-30.000

2.3.3) *Current distribution*

Predictions of suitable habitats for *P. praeorbitalis* differ substantially between models, with range size varying between 1 493 and 2 503 km^2. The ensemble model predicts a relatively small current range size of 1 500 km^2 (Table 2.2). *Polysteganus praeorbitalis* is listed as occurring from Algoa Bay in the south to Beira in the north (Heemstra and Heemstra, 2004). The ensemble model projects *P. praeorbitalis* occurring from Cape St Francis in the south to Maputo in the north (Figs 2.4, 2.5). Although there is general agreement among models on the position of the southern range edge, there is less agreement on the northern range edge

(Appendix 2). This has led the ensemble model to show a gradual reduction in probability of occurrence at the northern edge between Ponta do' Ouro and Maputo (Fig 2.4).

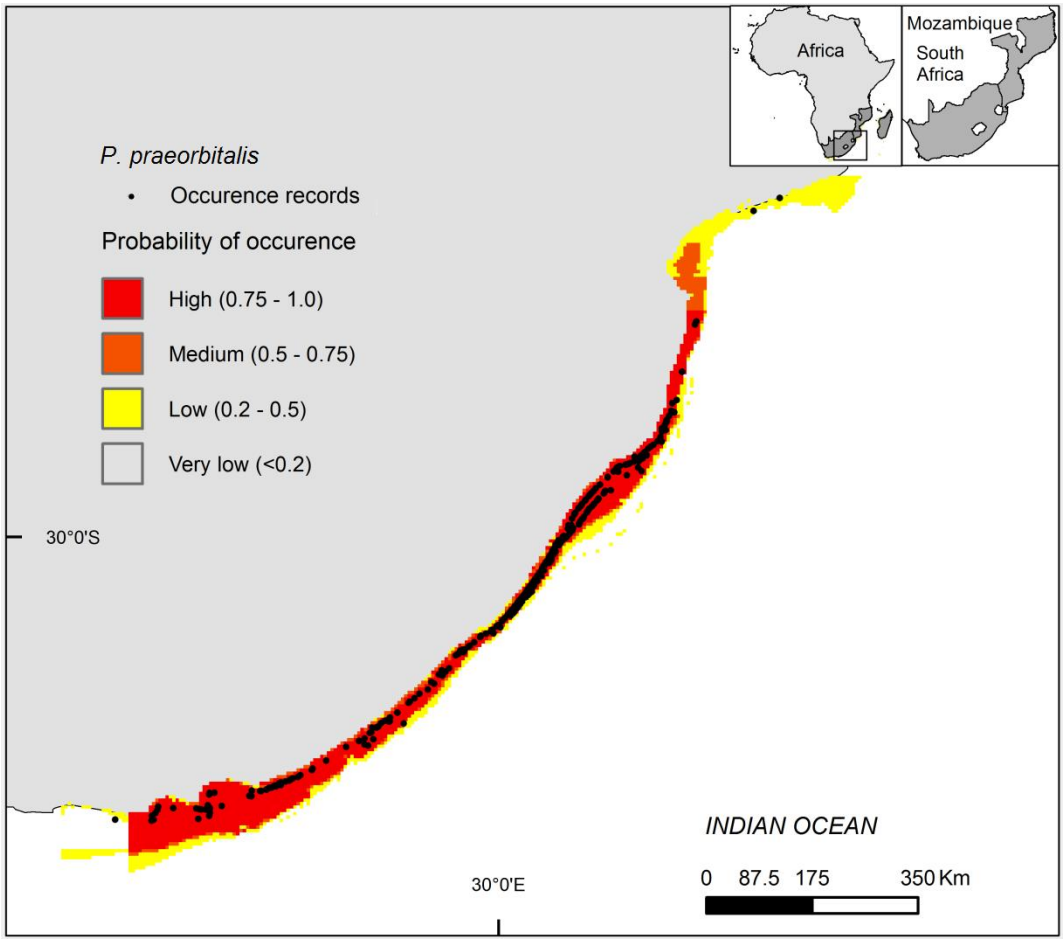

Figure 2.4: Probability of occurrence map of PMW ensemble model projections for *P. praeorbitalis* showing occurrence records obtained (n=203) and current predictions**.**

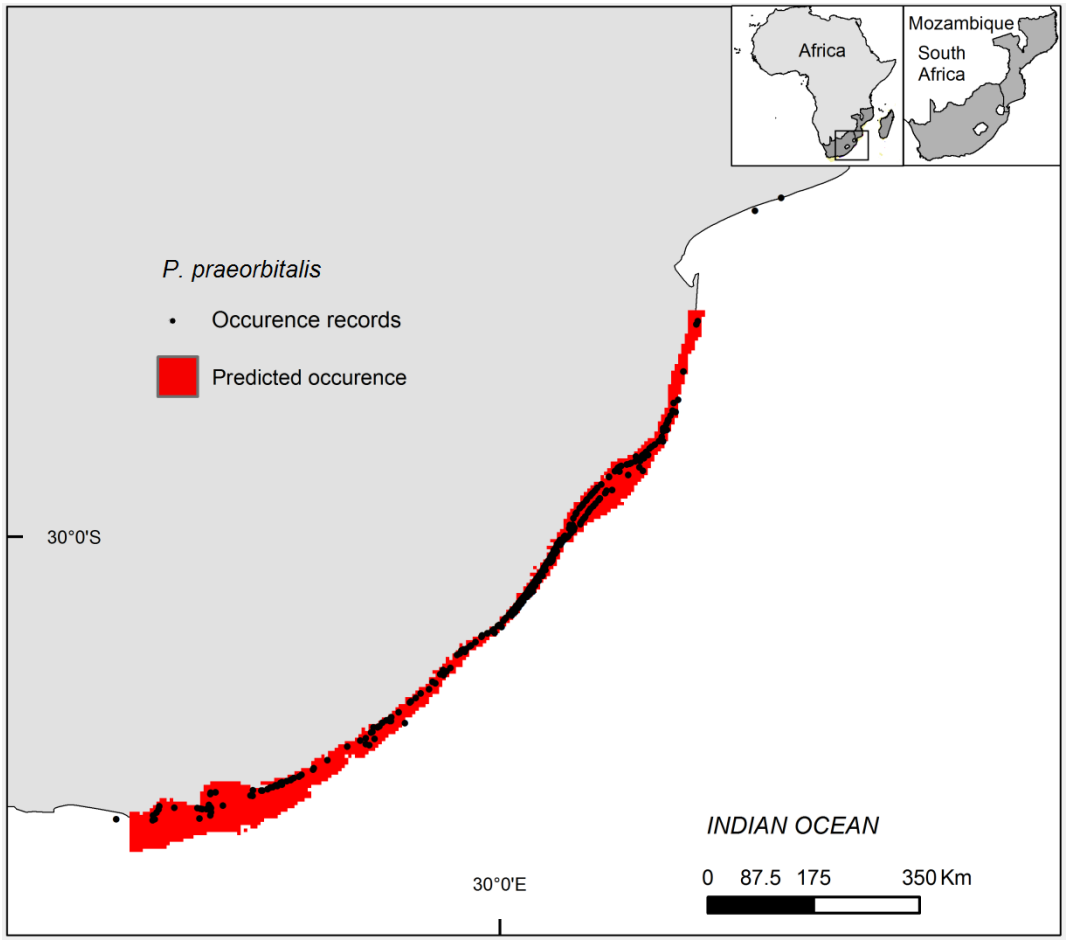

Figure 2.5: Binary transformed occurrence map of PMW ensemble model projections for *P. praeorbitalis* showing occurrence records *P. praeorbitalis* (n=203) and current predictions.

2.3.4) Predicted future range

Variations were observed between models for the 2030 projected geographic range of *P. praeorbitalis* after binary transformation, with both range expansions (up to a 2.8% expansion) and range contractions (up to a 22.2% contraction) predicted by different models (Table 2.2). Similarly, the 2030 projected geographic range also differed between models, with range contractions of up 37.6% and range expansions of up to 4.5% predicted (Table 2.2). Despite these differences, the majority of models suggested range contractions and were in agreement on the spatial distribution of these contractions. This was reflected in the ensemble model.

2.3.5) Ensemble model predictions

The PMW ensemble model projected that the probability of *P. praeorbitalis* occurring would decrease south of Algoa Bay, as well as off Durban and Richards Bay by 2020, with this trend becoming more pronounced in 2030 (Fig 2.6 and Fig 2.8). Predictions after binary transformation of these results are that *P. praeorbitalis* will lose 12.8% and 30% of its

geographic range by 2020 and 2030, respectively (Table 2.2; Fig 2.7 and Fig 2.9). The model projects range contraction at both the northern and southern edges of *P. praeorbitalis'* geographic range. The range is also predicted to become more fragmented by 2030, with a small break in the distribution of this species predicted just north of Richards Bay (Fig 2.9).

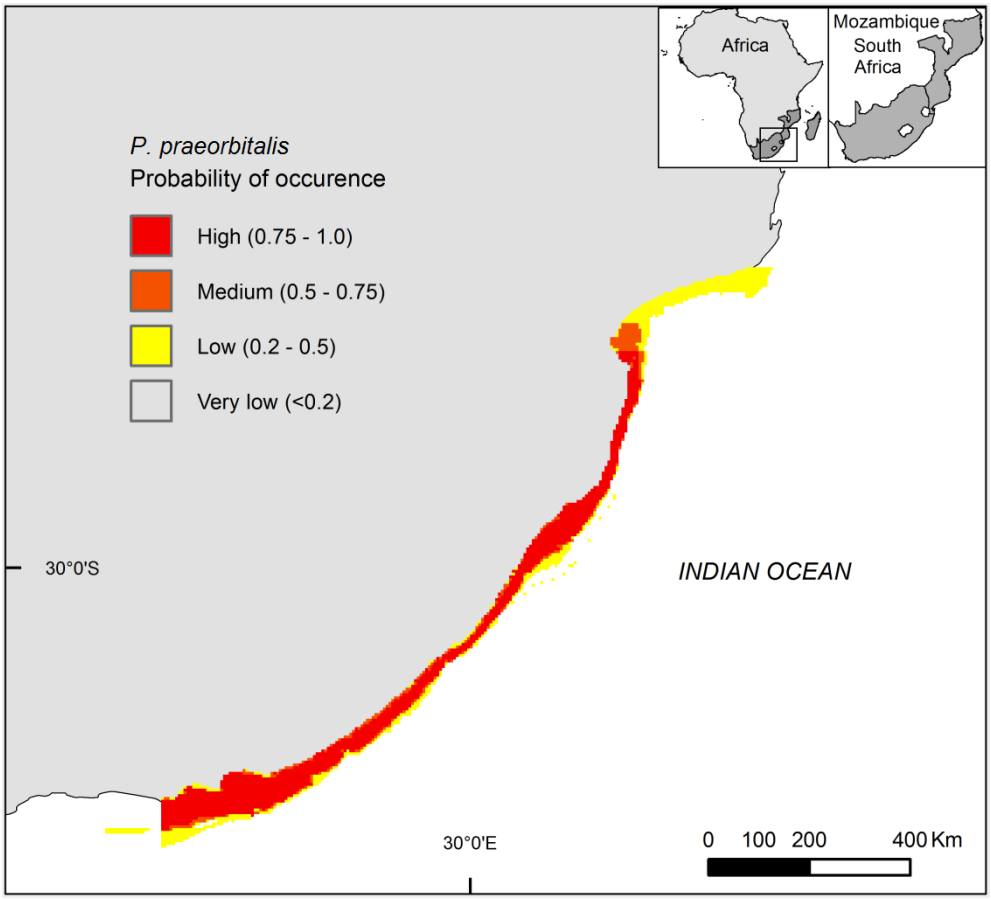

Figure 2.6: Probability of occurrence map of PMW ensemble model projections for *P. praeorbitalis* showing 20-year future predictions.

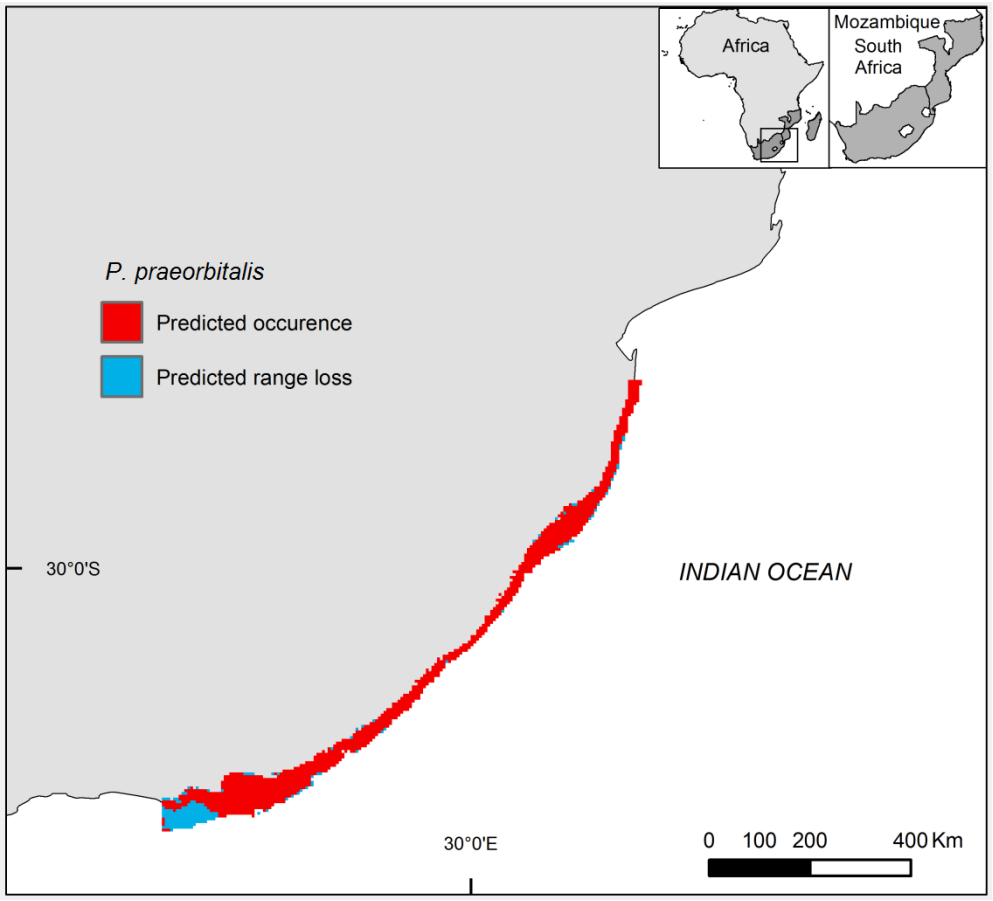

Figure 2.7: Binary transformed occurrence maps of PMW ensemble model projections for *P. praeorbitalis* showing 20-year future predictions.

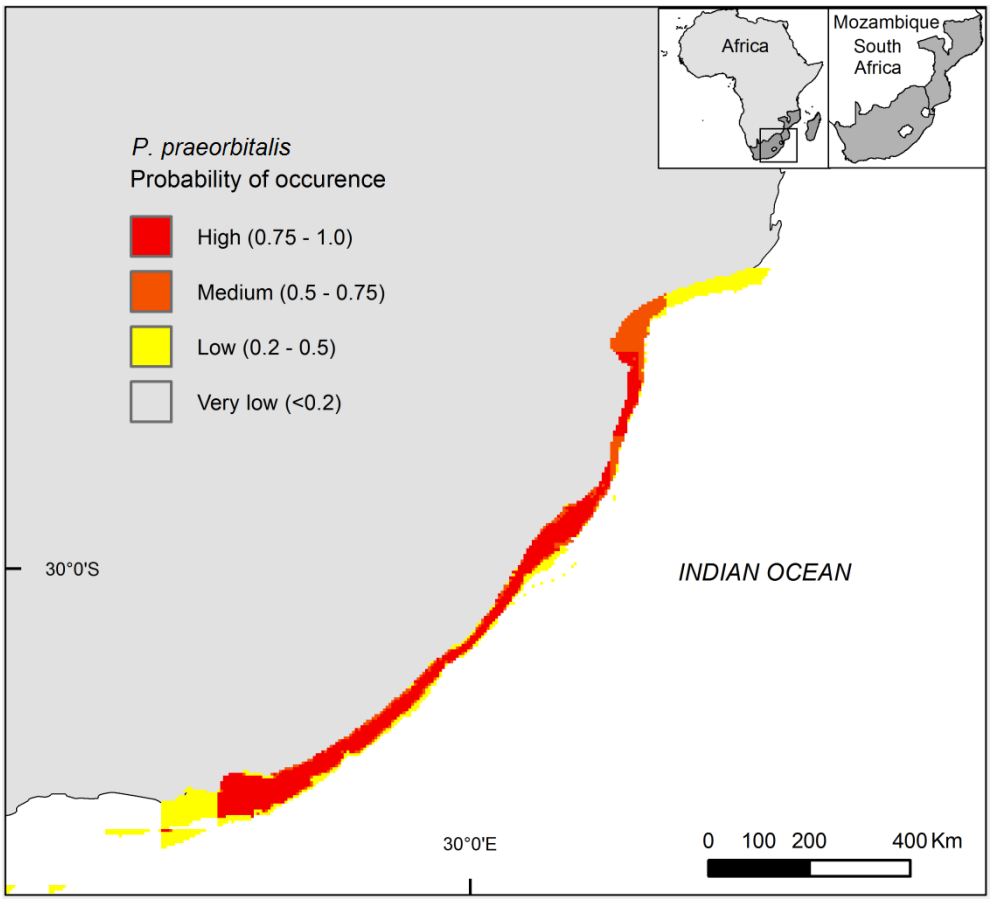

Figure 2.8: Probability of occurrence map of PMW ensemble model projections for *P. praeorbitalis* showing 30-year future predictions.

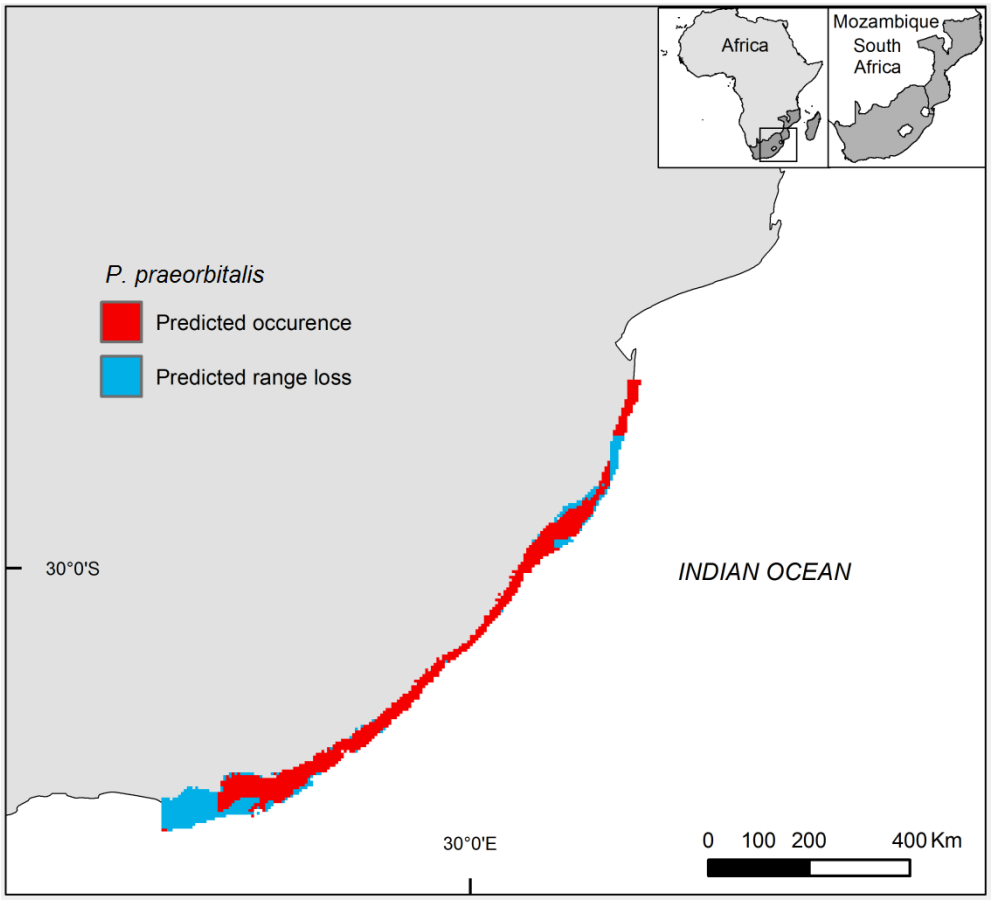

Figure 2.9: Binary transformed occurrence maps of PMW ensemble model projections for *P. praeorbitalis* showing 30-year future predictions.

2.4) Discussion

Twenty- and thirty-year projections showed an overall reduction in the range of *P. praeorbitalis* and of habitat fragmentation. Habitat fragmentation, combined with continued contraction at the southern range edge, is predicted to result in a total range loss up to 30% by 2030. This result supports the hypothesis of Rijnsdorp *et al.* (2009) that endemic fish species with limited distributions will be vulnerable to reductions in range and abundance due to the effects of climate change. Cheung *et al.* (2009) obtained a similar result for the Australian ruff (*Arripis georgianus*), an endemic Australian species which was predicted to show fragmentation in its range due to climate change. Similarly, the results of Albouy *et al.* (2012) predicted reductions in overall species richness and range reductions in range-restricted species in the Mediterranean Sea due to warming. The combination of cooling and warming predicted in the Agulhas system makes the response of *P. praeorbitalis* more complex. In order to understand which factors explain the predicted response, it is important to first understand which factors restrict the current distribution of *P. praeorbitalis*.

2.4.1) Current predictions

The southern range edge of *P. praeorbitalis* is recorded as Algoa Bay in the literature (Heemstra and Heemstra 2004). However, occurrence records were obtained south of Algoa Bay such that there was a strong model agreement for the southern range edge occurring at Cape St Francis. This clear delineation of the southern edge is probably the result of the sudden latitudinal drop in SST caused by the widening of the continental shelf in this area, which moves the warm Agulhas Current further offshore (Lutjeharms 2006a). This drop in temperature is particularly evident in winter and autumn and results from this study indicate that winter and autumn SST minima are the factors most likely to constrain *P. praeorbitalis* at its southern range edge. This region also constitutes the southern range edge for a number of marine fish species, including other sparids that occupy similar habitats and ranges as *P. praeorbitalis*, such as *Chrysoblephus anglicus*, *Polysteganus undulosus* and *Argyrops spinifer* (Heemstra and Heemstra 2004). Maree *et al.* (2000) note a high coincidence of species southern range edges in the vicinity of Algoa Bay and suggest that this is the result of the divergence of the Agulhas Current in this region. The persistent thermal front associated with the upstream Port Alfred upwelling cell may also contribute to reduced temperatures. In the nearby Benguela Current system, the coincidence of a number of species range edges, and observations of genetic and morphological differentiation between species on either side of the Lüderitz upwelling cell, have similarly led to this feature being labelled as a biogeographic barrier to pelagic fish and larvae, and have highlighted its importance in limiting the range of many marine fish and invertebrate species (O'Toole 1977; Agenbag 1980; Boyd and Cruickshank 1983; Barange *et al.* 1992).

In comparison to the south, the northern range edge of *P. praeorbitalis* predicted by the ensemble SDM shows a much weaker model agreement. The model underestimates the range of the species in the North [compared to the range listed by Heemstra and Heemstra (2004)] by approximately 5° latitude when binary transformed. Without binary transformation the ensemble model does not predict *P. praeorbitalis* occurring as far north as Inhambane but rather predicts its northern range edge to lie between Maputo and Inhambane, with a gradual decline in probability of occurrence beginning at Maputo. The modelled range edge coincides very closely with the range of the closely related *Polysteganus undulosus*. No specimen exists to confirm the published northern range edge for this species. Occurrence records obtained for this study indicate that *P. praeorbitalis* occurs (albeit at very low prevalence) as far north as Inhambane, Mozambique. Its contribution to Mozambican semi-industrial and artisanal catches, with fishers mainly fishing north of Maputo (Pereira 2000), is miniscule (A. Guisamallo, pers. comm). The Mozambican semi-industrial linefishery is relatively young and targets many of the same demersal linefish species found off the

KwaZulu-Natal coast, using similar methods as the older South African commercial and recreational linefishery (Pereira 2000; FAO 2006). It is therefore highly unlikely that the rarity of *P. praeorbitalis* in Mozambican catches is the result of differences in gear or overfishing, but instead reflects an extremely low abundance of this species in Mozambican waters.

MacArthur (1984), and later Brown *et al.* (1996), note that species ranges across environmental gradients are often constrained by environmental pressures at one end, and biological pressures (such as competition and predation) at the other. With regard to latitudinal gradients, the gradient of increasing species diversity with decreasing latitude (Dobzhansky 1950), has been linked to increased evolutionary importance of biological factors towards the tropics (Stevens 1989). It is therefore possible that the northern distribution of *P. praeorbitalis* is constrained more by biological stresses than environmental ones, a hypothesis supported by the low level of agreement between models at this range edge and the fact that summer maximum SST was of less importance to the models than either winter or autumn minima. If this is the case, seasonal SST may be more likely to affect the northern distribution of *P. praeorbitalis* indirectly through its effects on the distribution of tropical and sub-tropical predator, prey and competitor species (Austin 2002). This possibility should be considered in predictions about the effects of future climate change on this and other subtropical species in the Agulhas Current system based on SST data, as it may explain future projections which make little biological sense.

2.4.2) Future predictions

The future climatic niches projected for *P. praeorbitalis* do not reflect pole-ward range shifts in response to increasing temperatures which have been predicted and observed for marine species in other systems (Perry *et al.* 2005) and on a global scale (Cheung *et al.* 2009). The probability of occurrence north of Maputo increases in both the 2020 and 2030 projections. These expansions are most likely due to winter and spring cooling trends observed around Maputo. It is possible that these cooling trends reflect the effects of the intensification of the Agulhas Current on its interaction with the Delagoa Bight. The widening of the continental shelf in this area to form the Delagoa Bight results in increased upwelling frequency and the presence of lee eddies, factors of biological importance (Lutjeharms 2006a).

Range reductions in the north (as reflected in the binary transformed results) are caused by range fragmentation. Considering that the northern range edge of *P. praeorbitalis* may be more dependent on biological than environmental factors, and given the fact that this species has been recorded further north than the current model predicts, the future

fragmentation predicted at the northern range edge is difficult to validate from an ecological point of view. In light of this, this result should be treated with caution.

In contrast, the future contractions in range predicted at the southern range edge are more plausible, given that minimum temperatures determine the southern limit of *P. praeorbitalis'* distribution. These contractions correlate well with observed patterns of cooling south of Port Alfred. This cooling is believed to be the result of intensification of the Port Alfred upwelling cell caused by increases in the strength and frequency of upwelling, favourable easterly winds and an increase in the strength of the Agulhas Current (Rouault *et al.* 2009; 2010). Climate change-induced increases in the frequency of wind-driven upwelling events are by no means unique to the Agulhas system; they have been predicted and recorded in eastern boundary currents such as the California Current (Bakun 1990; Snyder *et al.* 2003).

While frequent upwelling may noticeably reduce mean monthly SST in this region, it is on a daily timescale that this phenomenon is likely to affect species distribution. Upwelling events within the Port Alfred upwelling zone cause this region to show the most temperature variability of any area in the Agulhas Current system (Lutjeharms *et al.* 2000b) and have been observed to cause shelf water temperature to cool by more than 10 °C over a timescale of days (Lutjeharms 2006a; Lutjeharms *et al.* 2000b). Such rapid temperature shifts have been observed to drive deep-water species close inshore and into estuaries and, in some cases, have resulted in fish kills in other parts of the Agulhas Current system (Hanekom *et al.* 1989). Furthermore, studies on the Lüderitz upwelling zone in the Benguela Current system indicate that, while temperature fluctuations may partially explain its role as a biogeographic boundary, other factors, such as turbidity, may play an even greater role (Agenbag and Shannon 1988). Given that neither these factors nor the daily thermal fluctuations are defined in the mean monthly SST minima and maxima used to construct these models, the possible range reduction of *P. praeorbitalis* as a result of the effects of intensification of this upwelling cell may be more severe than the ensemble model predicts.

2.4.3) *Vulnerability of P. praeorbitalis to future climate change*

Brook *et al.* (2008) note that extinctions are often caused not by a single factor, but by a number of synergistic processes which feed back to one another, altering the trajectory of a population. In the context of climate change, it is therefore important to consider the effects of climate change on the factors which already threaten a species, because it is in combination with these factors that climate change may pose the greatest risk (Brook *et al.* 2008). Three factors indicate that *P. praeorbitalis* may be particularly vulnerable to the negative effects of climate change, providing further cause for concern in the light of the

predictions of the ensemble model used in this study. These factors are: 1) the relatively small range size of this species (Thomas *et al.* 2004; Ohlemüller *et al.* 2008), 2) its status as an overexploited species, and 3) its slow growth rate (Mann *et al.* 2005; Brander 2007; Hsieh *et al.* 2008).

The results of this study indicate the range of *P. praeorbitalis* is even smaller than that defined in the literature. Endemic species with small range sizes are often restricted due to environmental tolerances which evolved to suit past climates (Jansson 2003). Past climate changes caused these environments become rare or shrink, trapping species in small ranges (Ohlemüller *et al.* 2008). The negative impact of climate fluctuations on species with limited distributions is evident in their rarity within regions with a history of high amplitude climatic shifts such as the temperate and polar seas (Jansson 2003). This is because, as a result of their narrow environmental tolerances, species with small range sizes stand to lose a disproportionate amount of their habitat under climatic change in comparison to species with larger ranges (Ohlemüller *et al.* 2008).

The over-exploited status of this species is likely to further compound the negative effects of climate change on its distribution. Over-exploitation is likely to make species more vulnerable to climate change because of its negative effects on age and size diversity (Brander 2007), and on spatial heterogeneity (Hsieh *et al.* 2008). Brander (2007) notes that by selectively removing certain size classes (usually larger fish), overfishing can reduce the ability of populations to respond to climate change, usually leaving a higher proportion of smaller individuals which are more vulnerable to environmental factors. Long-lived, slow-growing species such as *P. praeorbitalis* are particularly vulnerable to this effect (Brander 2007). Conversely, the effects of climate change may reduce the ability of populations to withstand exploitative pressure (Jennings and Blanchard 2004). This is supported by Brander (2007), who notes that the effects of climate change may reduce reproductive success in some fisheries species, making them unable to sustain levels of exploitation previously considered sustainable. He cites the negative effects of short-term environmental changes on the recruitment of Atlantic cod (*Gadus morhua*) as an example.

2.4.4) Implications

The results of the current and future projections of the ensemble models produced have implications for the conservation and management of both *P. praeorbitalis* and subtropical marine biodiversity in the Agulhas Current system as a whole. The current prediction indicates that, although *P. praeorbitalis* has a theoretical range which stretches into Mozambique, most of its realised niche appears to fall within the South African exclusive

economic zone (EEZ). This result is important to the management of this fishery indicating, a) that the size of this stock is likely smaller than initially estimated and probably receives no recruitment from Mozambique, and b) that declines in abundance are the result of overharvesting by South African fisheries alone. Predicted range contractions and possible fragmentation as a result of climate change are a cause for concern, particularly in light of *P. praeorbitalis'* status as an overexploited, slow-growing, and endemic species. These results should, however, be interpreted with caution because of the assumptions and uncertainty associated with species distribution modelling in general, and climate change projections in particular.

The decline in CPUE (Garrat *et al.* 1994) and subsequent declaration of the stock as collapsed by Mann *et al.* (2005), indicate that *P. praeorbitalis* has already been placed under severe pressure by overexploitation. The effects of overexploitation and climate change on a species are often compounding (Rijnsdorp *et al.* 2009). Unfortunately, the predicted gap in the future distribution of *P. praeorbitalis* north of Richards Bay occurs within an area which the results of Mann *et al.* (2005) and Hutchings *et al.* (2002) indicate might be important to spawning for this and a host of other linefish species. Similarly, slight contractions around the Natal Blight area predicted to occur by 2030 may have negative effects on recruitment for this species as this area is also considered a nursery area for many species and is an area in which juvenile *P. praeorbitalis* have been recorded (Garrat *et al.* 1994; Hutchings *et al.* 2002). While the results of the ensemble model predictions for this edge of *P. praeorbitalis'* range should be treated with caution (see *2.4.2 Future predictions*), the vulnerability of larval and juvenile phases to environmental stress, such as that caused by increasing SST, is greater than that of adult fishes (Foster 1971, Harley *et al.* 2006), and these results remain therefore, a cause for concern.

Of equal concern is the contraction in range predicted to occur at the southern range edge of *P. praeorbitalis*. According to Rijnsdorp *et al.* (2009), populations at the limits of their latitudinal distribution are likely to be more vulnerable to the negative effects of climate change than those towards the centre. While this area does not have the high abundances recorded off the Transkei and KwaZulu-Natal coasts, *P. praeorbitalis* still features with some regularity in the catches of ski-boat fishermen here, indicating that it does occur in reasonable abundance (G. Marchland, pers. comm.). The loss of this habitat might cause more individuals to move into the KwaZulu-Natal area where they will be accessible to the larger KwaZulu-Natal linefishery (Penney *et al.* 1999). While this shift might temporarily boost CPUE off KwaZulu-Natal, in the long term this means that this already over-exploited stock will be harvested over a greater proportion of its range.

2.4.5) Model limitations

All models achieved high TSS and ROC scores, indicating good fit. These high scores are likely to be partially linked to the small range of *P. praeorbitalis* and the high sample size within that range (Venter *et al.* 1999: Manel *et al.* 2001, Stockwell and Peterson 2002, McPherson *et al*. 2004). They may also indicate that the available presence data and pseudo-absences generated for *P. praeorbitalis* correspond well with environmental data. In addition, the elongated shape of the study area, combined with the latitudinal gradients observed in the SST variables used, limits the amount of unoccupied, suitable thermal and bathymetric habitat available to the models, while still capturing the entire response curves for these variables. This reduces false positives in model predictions and is likely to have contributed to the high scores obtained (Thuiller *et al.* 2004). Despite these high scores, the results of these and any other SDM should be interpreted with caution and with reference to their limitations.

Species distribution models are based on the hypothesis that a species distribution is controlled by a particular set of environmental factors and assume that a species distribution is static and in equilibrium (or pseudo-equilibrium) with its environment (Guisan and Zimmermann 2000; Lischke *et al.* 1998). While the static nature of these models has been criticised in favour of more mechanistic, process-based models based on ecological and environmental data, the paucity of studies detailing the dynamic responses of species to climate change has ensured their continued use in this field (Elith and Leathwick 2009; Guisan and Zimmermann 2000). In the role of predicting species distributional response to climate change, SDMs have been criticised because their results cannot be adequately validated due to the dual uncertainty of both the model predictions (different models give conflicting results) and future climate predictions (Thuiller 2004; Araújo *et al.* 2005). Despite the increasing popularity of a multi-model 'ensemble' approach used in order to reduce model uncertainty, this criticism remains valid (Buisson *et al.* 2010). Also of concern is the fact that the distribution data used represents the realised (as opposed to potential) niche of a species, thereby potentially underestimating its environmental tolerances (Guisan and Zimmermann 2000). In light of this, the predictions of SDMs based on future climate change scenarios should be seen as a tool to help understand the potential effects of climate change on species distribution rather than an accurate portrayal of future events. In addition, the results of these models should always be interpreted from an ecological perspective in order ensure that the predictions represent real ecological processes and risks as opposed to statistical artefacts (Elith and Leathwick 2009).

2.4.6) Conclusions and further research opportunities

Given the pole-ward shifts predicted and observed by large-scale studies, such as Parmesan and Yohe's (2003), of mostly terrestrial and freshwater species and the often perceived lack of biogeographic boundaries in marine environments, one might assume that the response of marine fishes to climate change is likely to be simpler than that of terrestrial and freshwater species. Observations and models of pelagic and demersal species have produced evidence of simple shifts in latitude (Perry *et al.* 2005; Lam *et al.* 2008) and depth (Dulvy *et al.* 2008). The results of this study, however, support those of Lam *et al.* (2008), Albouy *et al.* (2012) and Cheung *et al.* (2009) which reveal that, when viewed at a higher resolution, coastal and inshore species may produce more complex distributional responses due to fine scale variation in localised environmental, geographical and ecological factors. In many cases, these factors are predicted to limit the distributional response of these species to the effects of climate change, resulting in increased vulnerability to range reductions and declines in abundance (Cheung *et al.* 2009, Thomas *et al.* 2004). While the previously mentioned studies focused on mainly geographic factors such as peninsulas and partially closed seas, the importance of current-shelf interactions, as indicated in this study, suggests that finer scale localised oceanographic features and shelf topography should not be overlooked. An opportunity exists to test the results of this study through long term monitoring of the abundance of *P. praeorbitlalis* around both of the range limits defined in this study. Such a study would prove useful in validating the accuracy of this and similar models on shelf-associated species in the Agulhas Current system.

The failure of the Reynolds OI SST data used in this study to fully define the features of the Port Alfred upwelling cell (Rouault*et al.* 2010), highlights the difficulties of attempting to model localised oceanographic features with low resolution global data. Future projects should investigate the use of higher spatial resolution datasets such as Advanced Very High Resolution Radiometer (AVHRR) SST data. Opportunities for further research in this region also include the application of species distribution models to a variety of species within the Agulhas Current system, particularly those whose southern or northern range edges lie in or around the Port Alfred upwelling region.

Chapter 3
Genetic analyses: Investigating the population genetics of *Polysteganus praeorbitalis* using mitochondrial and nuclear DNA markers.

3.1) Introduction

Marine environments are open systems that have relatively few physical barriers and thus favour the dispersal of marine organisms over large areas (Palumbi 1992; Palumbi 1994; Waples 1998). In particular, organisms with planktonic larval phases such as the Scotsman *Polysteganus praeorbitalis* tend to be high-dispersal species characterised by high levels of gene flow. This often results in limited genetic structuring, even between widely separated populations (Palumbi 1992). Strong genetic structure and breaks in distribution between semi-isolated populations have nonetheless been observed in some high-dispersal species, including marine fishes off southern Africa (e.g. Barber *et al.* 2002; Teske *et al.* 2005; Waters *et al.* 2005). This is because differences in the selective pressure placed upon semi-isolated populations by environmental and ecological gradients promote genetic differentiation (e.g. Koehn *et al.* 1980; Hilbish and Koehn 1985; Teske *et al.* 2008). The existence of structure is not rare in marine organisms and has been attributed to both allopatric and sympatric mechanisms of divergence, including the effects of past and present geographical and oceanographic barriers to dispersal or gene flow (e.g. Teske *et al.* 2005; Waters *et al.* 2005; Waters 2008).

The Agulhas Current system, to which *P. praeorbitalis* is endemic, can be divided into three often overlapping biogeographic provinces based on abiotic and biotic differences between areas (refer to Chapter 1) (Turpie *et al.* 2000). However, interaction between the warm Agulhas Current and cooler shelf waters influenced by shelf topography and prevailing coastal winds, means that this system holds a large number of unique spatial and temporal habitats within these biogeographic provinces (Lutjeharms 2006a; b). As a result of this, patterns of connectivity, dispersal, biodiversity and abundance are likely to be more complex. It is possible that *P. praeorbitalis* exists in semi-isolated populations or separate stocks as a result of historical and current oceanographic and geographic features of this complex system.

Marine fish and invertebrate species are the last extensively harvested, wild, living resources. However, the patterns of genetic structure of most fisheries species are generally unclear. A marine stock has been defined as a randomly interbreeding group of animals confined within spatial and temporal boundaries (Ihssen *et al.* 1981). Understanding and delineating the spatial genetic structure of marine stocks is useful in defining the maximum sustainable levels of localised harvesting that can inform conservation strategies and result in ecological, economic and social impacts (Carvalho and Hauser 1994). Applying genetic methods to fisheries science has in recent years become commonplace, particularly for the identification and definition of unique stocks (Ward 2000; Hauser and Carvalho 2008; Hauser and Seeb 2008). Initial fisheries studies used allozyme electrophoresis and mitochondrial DNA (mtDNA) fragments sequenced using restriction fragment length polymorphisms (RFLP) (Carvalho and Hauser 1994; Hauser and Seeb 2008). The advent of polymerase chain reaction (PCR) amplification allowed the relatively rapid sequencing of nuclear DNA (nDNA) and mtDNA sequences in large numbers. These techniques revealed strong spatial genetic structure in many widespread marine species previously assumed to exist in single, homogenous populations. This resulted in a paradigm shift in fisheries biology towards the idea of smaller, locally-adapted stocks in dynamic equilibrium with local conditions (Carvalho and Hauser 1994; Hauser and Carvalho 2008; Hauser and Seeb 2008). The ability to sequence nDNA was a precursor to the discovery of more rapidly evolving neutral nDNA markers such as microsatellites, and subsequently, single nucleotide polymorphisms (SNPs) making it possible to resolve more recently diverged populations (Ward 2000; Hauser and Seeb 2008). The cost of these techniques, however, often prohibits their use in developing countries or on less valuable stocks and thus studies using mtDNA and nDNA sequences remain relevant.

Mitochondrial DNA, and in particular the control region located adjacent to the 3' end of the cytochrome-*b* protein coding region, has been used in a number of studies on the genetic structure of commercially important marine fishes (e.g. Dahle 1991; Martin *et al.* 1992; Aboim *et al.* 2005). The fact that mtDNA is haploid (effectively halving population size) and unaffected by recombination (because it is predominantly maternally inherited), allows for relatively rapid genetic drift in this genome (Hecht *et al.* 1984; Shacklee and Bentzen 1998). In combination with the high substitution rate often observed in the control region (Shacklee and Bentzen 1998), these factors tend to result in relatively rapid genetic divergence at these loci under conditions of reduced gene flow, making them very useful in detecting spatial genetic structure (Ferris and Berg 1987; Billington and Herbert 1991). Using the mitochondrial control region has, however, been criticised by authors because of its diversity levels which, in some species, may be either too high (e.g. Rocha-Olivares *et al.* 2000) or to

low (e.g. Lundy *et al.* 2000; von der Heyden *et al.* 2010) to display genetic structure. In particular, von der Heyden *et al.* (2010) note that mtDNA diversity is particularly low for many Agulhas Current species and advise using more rapidly evolving markers on taxa from this area. It is therefore good practice to analyse an additional gene region in order to provide comparative results, should this be the case.

While mtDNA studies have dominated fisheries biology, the use of nDNA gene regions is far less common in this field (Park and Moran 1994; Ward 2000). Initially, this was due to the difficulty associated with working with nDNA, but since the advent of PCR technology, the slower mutation rate of nDNA gene regions and the non-neutral status of much of this genome have seen them mostly used in phylogenetic studies in marine and freshwater fishes (e.g. Ward 2000; Bernardi *et al.* 2004; He *et al.* 2008; Craig *et al.* 2009). However, the results of Chow and Takeyama (1998) indicated that introns such as the first intron of the S7 ribosomal protein coding gene (RP1) may accumulate enough variation to be useful in population genetics studies in fishes. This intron was amplified by Chow and Takeyama (1998) in the swordfish *Xiphias gladius* with results indicating that this marker displays enough neutral variability to be used in intraspecific genetics studies. Craig *et al.* (2009) used the S7 gene in conjunction with mtDNA to investigate cryptic speciation and population structure in exploited marine fishes and provided strong evidence of genetic structure. This, and similar nDNA gene regions, may thus provide an alternative for population genetics studies in fishes where mtDNA variation is too high or too low for analysis, and financial constraints prevent the use of microsatellites or SNPs.

In South Africa, genetic studies have been conducted on a number of commercially important fish species, including those making up the bulk of its two most economically important fisheries on the west coast: the pelagic sardine *Sardinops ocellata* (Grant 1985a; Grant and Bowen 1998) and anchovy *Engraulis capensis* (Grant 1985b; Grant and Bowen 1998), and the Cape hakes *Merluccius capensis* and *Merluccius paradoxus* (von der Heyden *et al.* 2007; von der Heyden *et al.* 2010). There has also been increased research into the less economically important, but arguably more socially important commercial and recreational inshore linefish species of the Agulhas Current system, of which *P. praeorbitalis* is one. This has included genetic stock assessments of the dusky kob *Argyrosomus japonicus* (Klopper 2005), spotted grunter *Pomadasys commersonnii* (Klopper 2005), red roman *Chrysoblephus laticeps* (Teske *et al.* 2010), white steenbras *Lithognathus lithognathus* (Bennettt 2012) and poenskop *Cymatoceps nasutus* (Murray 2012). These studies were carried out in response to declines in CPUE in this multispecies linefishery

which culminated in it being declared in a state of crisis in 2000, with drastic cuts in effort enforced (Griffiths *et al.* 1999; Hutton *et al.* 2001).

As one of the linefish species more severely affected by overharvesting before 2000, *P. praeorbitalis* displays several life-history characteristics typical of large sparids in the Agulhas Current system, including slow growth rates, residency, pelagic larval phases and protogynous hermaphroditism (unconfirmed but strongly suspected) (Garret *et al.* 1994; Mann *et al.* 2005). The declaration of this stock as collapsed five years after the declaration of a state of emergency in the linefishery in 2000 warrants investigation of the genetic diversity and spatial structure of this stock. This study should help to evaluate its current status and inform future management decisions. Furthermore, *P. praeorbitalis* inhabits a wide range of different environmental and ecological conditions from Algoa Bay in South Africa to Beira in Mozambique, with three biogeographic provinces defined within its relatively small distribution (Turpie *et al.* 2000). This indicates that it may show adaptive genetic divergence between areas, especially in light of its observed residency.

This study therefore aimed to investigate spatial and temporal patterns in the genetic diversity of *P. praeorbitalis* in order to inform fisheries management about conservation and sustainable use for this species. Specific questions were:

1) Does *P. praeorbitalis* occur as a single stock or more than one discreet population?
2) If more than one population does exist, what are the levels of connectivity between populations and what biogeographical barriers affect connectivity?
3) What historical and present demographic patterns are displayed by this species?

By answering these questions, it is hoped that this study will contribute to marine policy affecting this and other similar species in the Agulhas Current system.

3.2) Materials and Methods

3.2.1) Sampling and localities

Tissue samples of *P. praeorbitalis* in the form of fin clips and muscle tissue (1–3 cm) were collected from fish at landing sites, from those caught by volunteer anglers, and fish purchased from fish markets; they were preserved in 95% ethanol and stored at -20 °C. Date of capture, landing site, locality (coordinates or description) and fork length (mm) were recorded where available. Because anglers were reluctant to disclose the locations of their reefs, GPS coordinates were obtained for approximately only 36% of the samples, while the remaining localities were verified from anglers' or trader's descriptions and published data of relevant fishing areas (Penney *et al.* 1999). This level of accuracy was considered

acceptable for the inference of genetic structure due to the large geographic distances between landing sites.

Samples were grouped according to the known reef structure within the areas in which they were caught (Penney *et al.* 1999; Fennessy *et al.* 2003) on the basis of spatial proximity and possible biogeographic barriers. This was required in order to produce statistically significant results and also because of the small sample sizes obtained for some sampling sites, as well as the fact that some landing sites provided specimens from the same fishing areas. Sampling sites were therefore grouped into four localities. Port Alfred and Kenton-on-Sea were combined to represent the southern sites (Eastern Cape) because of their small sample sizes and close proximity to each other in relation to the other sites. Despite their close proximity, Shelly Beach and Pumula landing sites were separated from the Mkambati, Mnyameni and Xhora landing sites, creating two localities: southern KwaZulu-Natal (southern KZN) and Transkei. This was informed by the study of Penney *et al.* (1999) which indicated that the former two landing sites provide fishing access to the same area of rocky reefs along the southern KwaZulu-Natal coast between Port St Johns and Durban. Mkambati, Mnyameni and Xhora landing sites, on the other hand, provide access to reefs within the Transkei, south of Port Edward. The grouping of Richards Bay and Maputo into the northern KwaZulu-Natal locality (northern KZN), in spite of the great distance between them, was necessitated by the small sample sizes obtained from these sites, both of which represent areas near the northern range edge of this species. This locality is separated from others to the south by the St Lucia–Richards Bay upwelling cell and represents the northern edge, not of the species distribution, but rather of its occurrence at abundances that made sampling feasible for this study.

3.2.2) Mitochondrial and nuclear DNA amplification

Genomic DNA extractions were performed using the Wizard® Genomic DNA purification kit (Promega, USA) and stored at -20 °C in 100 µl DNA rehydration solution. An approximately 700 bp fragment of the mitochondrial control region was amplified using the forward primer, ChrysoCytbF (5'- GCA GCA GCA YTA GCA GAG AAC -3'), and reverse primer, Sparid12SR1 (5'-TGC TSR CGG RGC TTT TTA GGG-3'), designed for the related sparid, *Chrysoblephus cristiceps* (Teske *et al.* 2010). Amplifications were performed using a protocol modified from Teske *et al.* (2010) in 50 µL PCR reactions. Each reaction solution contained 5–10 µL DNA, 5 µL of 10× PCR buffer, 2.5 nM of $MgCl_2$, 0.8 mM DNTPs (Kapa Biosystems, Cape Town, RSA), 0.1 mM of each primer and 1 unit of Super-Therm Taq DNA Polymerase (JMR Holdings, Kent, UK). The PCR thermal cycling profile began with a denaturation step (3 min at 94 °C) followed by 35 cycles that included: denaturation (50 sec

at 94 °C), annealing (1 min at 53 °C) and extension (1 min at 72 °C) before final elongation (10 min at 72 °C) and holding steps (4 °C).

Amplification of a 720 bp fragment of the first intron of the S7 ribosomal protein gene (RP1) was performed using the universal primers, S7RPEX1F (5'- TGG CCT CTT CCT TGG CCG TC-3') and S7RPEX2R (5'-AAC TCG TCT GGC TTT TCG CC - 3') designed to anneal to the 3' end of exon 1 and the 5' end of exon 2 of this gene, respectively (Chow and Hazama 1998). Amplifications were performed using a protocol modified from Chow and Hazama (1998) in a 25 µL reaction mixture containing: 1–5 µL DNA, 2.5 µL of 10× PCR buffer, 1.5 nM of $MgCl_2$, 0.4 mM DNTPs, 0.05 mM of each primer and 1 unit of Super-Therm Taq DNA Polymerase. The PCR thermal cycling profile began with a denaturation step (3 min at 95 °C) followed by 35 cycles of denaturation (1 min at 95 °C), annealing (1 min at 55 °C) and extension (1:30 min at 72 °C), before final elongation (7 min at 72 °C) and a holding step (4 °C).

PCR products were screened using agarose gel electrophoresis (viewed under UV light using Ethidium bromide) and the forward (5'–3') sequences sequenced by Macrogen Inc. (Seoul, Korea). Five reverse sequences were also run for each dataset to verify sequence quality. Mitochondrial and nuclear DNA sequence chromatograms of *P. praeorbitalis* were screened using the program Chromas 2.01 (Technelysium Pty Ltd., Queensland, Australia). Both mtDNA and nDNA sequences were checked, aligned by eye and trimmed to 320 bp and 540 bp respectively in Seqman Pro™ (DNASTAR® Inc., Madison, USA). The sequence fasta files exported from Seqman Pro™ were then re-aligned with ClustalW multiple alignment (Thomson *et al.* 1994) in BioEdit Sequence Alignment Editor® (Hall 1999). The programme DNA Sequence Polymorphism® (DnaSP) v5.10.01 (Librado and Rozas 2009) was used to phase polymorphic sites in the nDNA sequences.

3.2.3) Analysis of neutrality

Non-neutral selection is a potential confounding factor in genetic studies because directional selection influences the frequency of alleles within populations thereby confounding the results of tests which assume that differences in allele frequencies between populations are solely the result of genetic drift. In order to test the assumption of neutral selection, analyses of neutrality (Tajima's D and Fu's F) were conducted in Arlequin® 3.5.1.2 (Excoffier and Lischer 2010). These tests can also investigate the demographic history of species. Tajima's D considers the difference between mean nucleotide diversity and the number of segregating sites in relation to their variance, in order to test the null hypotheses of constant

population size and the equilibrium between mutation and drift (Tajima 1989). The test produces a p-value corresponding to the significance ($p< 0.05$) of a D-value between -2 and 2. Negative D-values indicate an excess of unique alleles and are considered indicative of purifying selection or a recent population expansion (Aris-Brosou and Excoffier 1996). In contrast, positive values reflect a low number of unique alleles indicating that unique alleles may have been removed by a recent population expansion or over-dominance selection, while values close to zero indicate that the population is in equilibrium with its environment (Tajima 1989). Fu's F considers the probability of an equal or smaller number of alleles than those observed, occurring in a random sample assuming neutrality and the same level of diversity (Fu 1997). The F-value produced can be positive or negative, signifying a deficiency or excess of alleles respectively, and corresponds to a p-value at a significance level of ($p< 0.02$). The deficiency in alleles revealed by a positive F is considered evidence of purifying selection, while a negative value is indicative of recent population expansion, and an F close to zero implies neutral selection.

A mismatch distribution (Harpending 1994, Schneider and Excoffier 1999) was also calculated for both datasets in DnaSP by comparing the number of observed pairwise differences to the number of pairwise differences expected under a model of population expansion and contraction (Harpending 1994). This allows one to investigate whether the population in question is at mutation-drift equilibrium (indicated by a multimodal mismatch distribution) or has undergone recent expansion (indicated by a unimodal distribution). The fit of the mismatch distribution to a unimodal distribution (H_o) predicted under a sudden expansion model (Rogers 1995) was evaluated using a raggedness index (Harpending 1994) and sum of squared deviations (Rogers and Harpending 1992).

3.2.4) Tests for genetic differentiation and structure

Investigation began with examinations of nucleotide (π) and haplotype (*Hd)* diversity (Tajima 1989; Nei and Tajima 1981) for the whole population as well as the four localities (Eastern Cape, Transkei, southern KZN and northern KZN) in order understand the distribution of genetic diversity within the population using Arlequin® 3.5.1.2 (Excoffier and Lischer 2010). This was followed by the calculation of a haplotype network in NETWORK 4.2.0.1 using a median-joining algorithm (Bandelt *et al.* 1999) in order to illustrate the mutational steps between haplotypes and their distribution between different localities.

In order to investigate the existence of genetic differentiation and identify barriers to gene flow, the available localities were compared using a number or statistical techniques. The genetic differentiation between localities was tested in Arlequin® using Wright's F statistics

(Wright 1951). While Wright (1978) suggested F_{st} values greater than 0.05 indicated moderate or greater genetic differentiation between subpopulations, Waples (1998) noted that the median F_{st} calculated for marine fish subpopulations was lower (F_{st} = 0.02) because of larger population sizes and fewer barriers to gene flow in marine environments. In light of this, the author decided that F_{st} values greater than 0.02 would indicate moderate genetic differentiation in this study. Pairwise locality differentiation was also investigated using Exact Tests of population differentiation (Raymond and Rousset 1995) in order to provide an alternative to methods dependant on F_{st}. This method tests the null hypothesis that haplotype distribution between populations is random, using a Markov chain (length: 100 000 steps).

Pairwise differences were also used by grouping the four localities to perform an analysis of molecular variance (AMOVA) (Weir and Cockerham 1984), comparing the proportion of genetic variance explained at group, locality and sampling site levels. This method was also used in conjunction with geographic coordinate data to detect possible barriers to gene flow by applying the spatial analysis of molecular variance (SAMOVA) algorithm in the programme SAMOVA (Dupanloup *et al.* 2002). This algorithm defines a set number of geographically distinct groups by maximising the proportion of total variance explained by differences between them. SAMOVA was run for K=2 population groups, specifying 100 initial conditions.

Wright's F statistic and exact tests of population differentiation were re-run with juveniles separated from sexually mature fish informed by the length at first maturity (405 mm FL) as estimated by Mann *et al.* (2005). This was only performed on the nDNA dataset because of the smaller sample size of the mtDNA dataset. This was done to test the assumption that some potentially confounding temporal structure may exist in the population, due to evidence of juveniles occupying different habitats (Garrat *et al.* 1994; Mann *et al.* 2005).

3.3) Results

3.3.1) Samples

A total of 125 tissue samples were collected from nine landing sites (Table 3.1) which were pooled into four localities: Eastern Cape (*n* = 23), Transkei (*n* = 36), southern KwaZulu-Natal (*n* = 39) and northern KwaZulu-Natal (*n* = 27). This resulted in 115 DNA sequences of the mitochondrial control region and 118 of the Nuclear (nDNA) S7 intron 1 regions being successfully amplified (Table 3.1). The approximately 700 bp of amplified mtDNA sequence had regions of poor quality. Only 325 bp of the control region was useful for analysis, with

nucleotide polymorphisms at 23 sites. The poor quality amplification may be the result of non-specific binding as the sparid primers used were developed for the genus *Chrysoblephus* (Teske *et al.* 2010) and not *Polysteganus*. The quality of nDNA sequences was of a higher standard and a 499 bp fragment, from approximately 720 bp amplified sequence, was considered useful for analyses after alignment. This fragment displayed nuclear polymorphisms at 20 sites. Due to the diploid nature of nDNA, two sequence alleles were produced per PCR reaction by phasing the sequences in DNASp, resulting in a larger sample size (approximately double) in the nDNA dataset than in the mtDNA dataset.

Table 3.1: Sample sizes of mitochondrial D-loop and Nuclear S7 intron 1 sequences obtained from nine sampling sites for *P. praeorbitalis* showing coordinates and the grouping into four localities.

Site	Coordinates	Locality	Tissue samples	mtDNA	nDNA	nDNA (>405 mm FL)
Port Elizabeth	34°12'42"S, 25°68'83"E	Eastern Cape	4	19	36	34
Kenton-on-Sea	33°77'60"S, 26°76'61"E	Eastern Cape	19	5	10	6
Xhora	32°07'03"S, 29°12'11"E	Transkei	3	2	6	6
Mkambati	31°27'73"S, 30°11'19"E	Transkei	28	29	58	42
Mnyameni	31°18'08"S, 30°19'03"E	Transkei	5	5	10	2
Shelly Beach	30°80'26"S, 30°46'78"E	southern KZN	35	33	70	40
Pumula	30°66'15"S, 30°58'95"E	southern KZN	4	4	8	8
Richards Bay	28°86'90"S, 32°18'79"E	northern KZN	25	16	34	22
Maputo	25°98'63"S, 33°01'90"E	northern KZN	2	2	4	4
Total Population			125	115	236	164

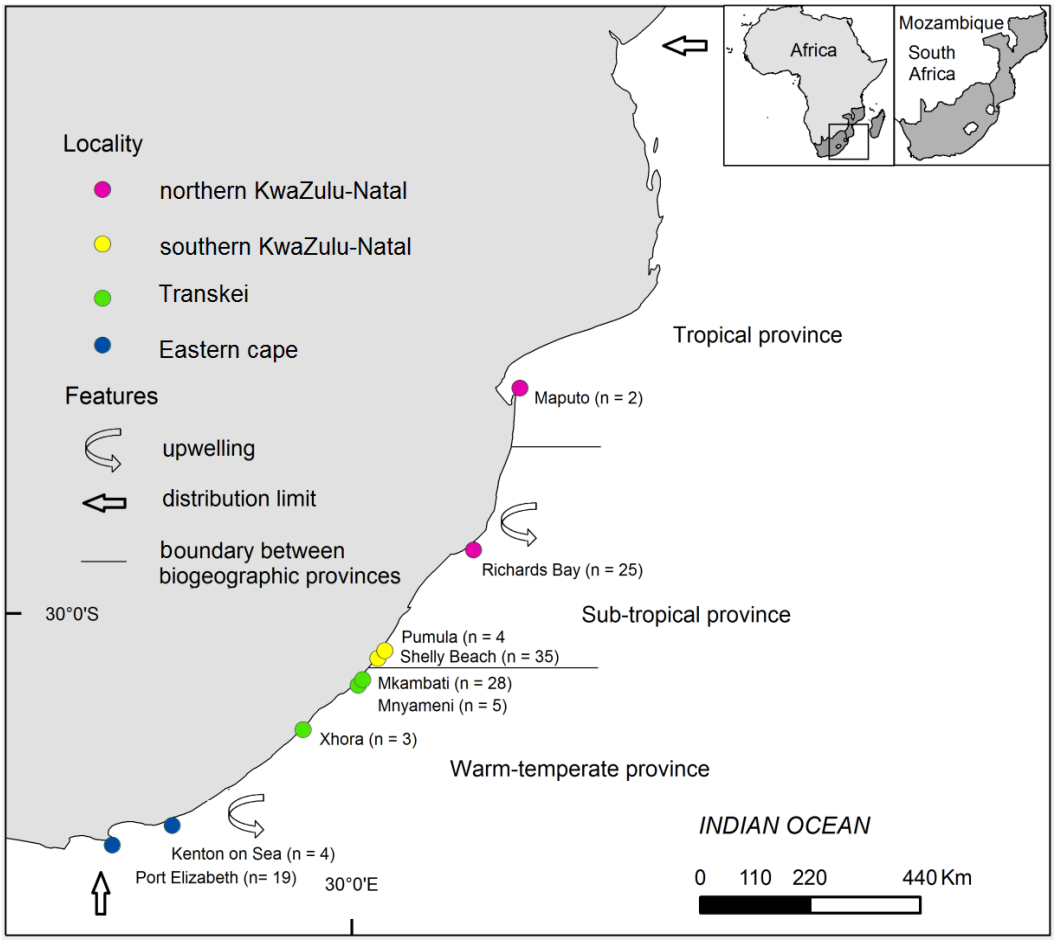

Figure 3.1: Map of the Agulhas Current system showing the sampling sites from which tissue samples of *P. praeorbitalis* were collected as well as the number of samples obtained from each site. Also shown are the Port Alfred and St Lucia–Richards Bay upwelling cells, the theoretical distribution range of *P. praeorbitalis* (Heemstra and Heemstra 2004) and the biogeographic province boundaries for shelf biota as proposed by Turpie *et al.* (2000).

3.3.2) Population demography

An analysis of neutrality for the total population indicated a significant (p = 0.005) Tajima's D value of -2.029 for the mtDNA dataset and significant (p = 0.0005) Fu's FS values of -11.928 and -26.506 for the mtDNA and nDNA datasets respectively. Both these results imply an excess of unique alleles and, in isolation, could be explained by purifying selection at the loci tested or a recent population expansion (Fu 1997; Innan and Stephan 2000). The fact that both genes are in agreement however, makes the former explanation unlikely. More likely is that these results represent the signature of a recent population expansion (Tajima 1989). Furthermore, Tajima's D-values for the nDNA dataset were negative (-0.599) but not significant (p = 0.324).

Mismatch distributions (Fig 3.2) calculated for both the nDNA and mtDNA datasets were unimodal. The low value obtained for the Harpending's raggedness index (r = 0.036) in the nDNA dataset, while not significant (*p*= 0.26) does indicate a good fit to the expansion-contraction model (Harpending 1994). This result supports the results of the Tajima's D and Fu's F statistics, indicating a recent population expansion. In contrast, the higher value of the raggedness index in the mtDNA dataset (r = 0.114), not significant (*p* = 1), provides little support for these results.

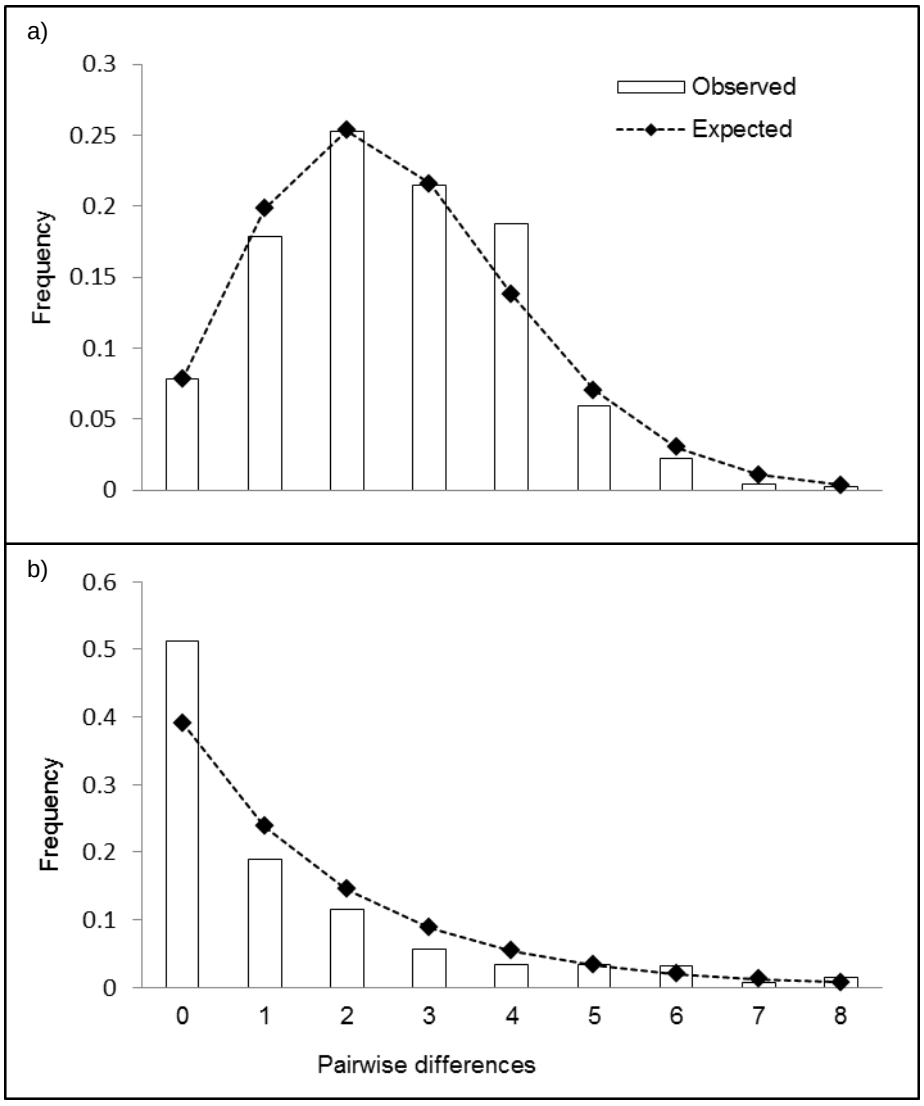

Figure 3.2: Mismatch distributions calculated for: (a) 499 bp nuclear S7 intron 1 ribosomal protein coding region sequences (*n* = 236, *r* = 0.036, *p* = 0.26, S.S.D = 0.002, *p* = 0.058) and (b) 325 bp mitochondrial control region sequences (*n* = 115, *r* = 0.114, *p* = 1, S.S.D = 0.294, *p* = 0.002) for *P. praeorbitalis*, in relation to frequencies expected under a population expansion-contraction model calculated in Arlequin® 3.5.1.2.

3.3.3) Indices of molecular diversity

Analyses of genetic diversity (Table 3.2) revealed differences between the mtDNA and nDNA genes in *P. praeorbitalis*. Haplotype diversity (*Hd*) was relatively low in the mtDNA dataset (0.504 to 0.549) when compared to the allelic diversity (*Ad*) of the nDNA dataset (0.910 to 0.926). Genetic diversity indices in the mtDNA dataset (Table 3.2, Fig. 3.3a and b) reveal haplotype and nucleotide diversities to be lowest in the two central localities (Transkei and southern KZN), while the two edge localities (Eastern Cape and northern KZN) display higher levels of genetic diversity. In particular, the Transkei displays the lowest values for both nucleotide diversity (π = 0.006 ±0.002) and haplotype diversity (*Hd*= 0.504 ±0.123) in this dataset. A pattern of decreasing diversity from north to south is also observed from northern KZN to the Transkei. With regard to the number of private haplotypes (%*Hp*), a decreasing trend in number is evident from south to north, with the Eastern Cape displaying the highest (57.1% *Hp*) and northern KZN the lowest (25% *Hp*) values (Table 3.2, Fig. 3.3c).

The pattern observed in diversity indices within the mtDNA dataset is reversed in the nDNA dataset, where the Eastern Cape displays the lowest *Ad* and π scores and only one private haplotype, whilst the northern KZN had only three private haplotypes. The diversity indices in this dataset appeared more similar amongst all localities showing less disparity between them. With regard to the percentage of private alleles (% *Ap*), this dataset shows an almost identical trend to that of the mtDNA dataset, with the notable exception of the Eastern Cape, which displays the highest percentage of private alleles as opposed to the mtDNA dataset where this locality displayed the lowest percentage.

Table 3.2: Summary of genetic diversity indices of *P. praeorbitalis* from mitochondrial control region and nuclear S7 intron 1 sequences. The table includes the number of haplotypes (*H*), number of private haplotypes (*Hp*), haplotype diversity (*Hd*), allelic diversity (*Ad*), nucleotide diversity (π), percentage of private haplotypes (%*Hp*) and the percentage of private alleles (*% Ap*).

	mtDNA						nDNA					
Locality	*n*	*H*	*Hp*	*Hd*	π	% *Hp*	*n*	Alleles	*Ap*	*Ad*	π	% *Ap*
Eastern Cape	24	7	4	0.504 ±0.123	0.006 ±0.002	57.1	46	14	1	0.910 ±0.021	0.004 ±0.000	7.1
Transkei	36	8	3	0.440 ±0.103	0.002 ±0.001	37.5	74	25	9	0.919 ±0.016	0.005 ±0.000	36.0
southern KZN	37	9	4	0.506 ±0.099	0.004 ±0.001	44.4	78	29	11	0.926 ±0.015	0.005 ±0.000	37.9
northern KZN	18	4	1	0.549 ±0.126	0.005 ±0.002	25.0	38	18	3	0.919 ±0.026	0.005 ±0.001	16.7
Total	115	18		0.488 ±0.058	0.004 ±0.001		236	45		0.922 ±0.000	0.005 ±0.000	

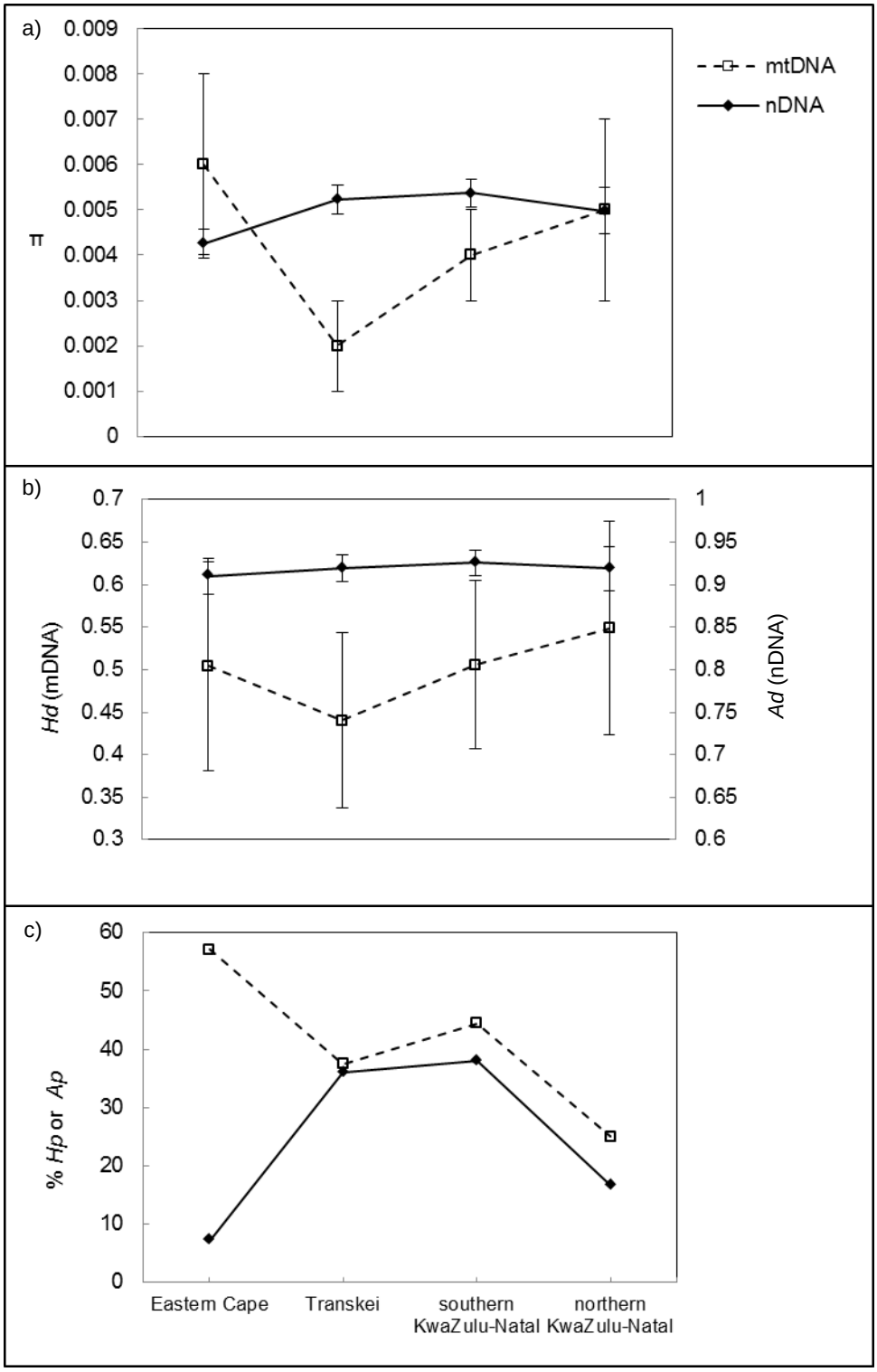

Figure 3.3: The nucleotide diversity (π) (a), haplotype (*Hd*) and allelic diversity (*Ad*) (b) and percentage of private haplotypes or alleles (%*Hp* or *Ap*) (c) of mitochondrial D-loop and nuclear S7 intron 1 sequence datasets for *P. praeorbitalis* among the four localities. The standard deviations for the two genes are also indicated in figures a) and b).

3.3.4) Haplotype network

A median-joining haplotype network generated from mtDNA sequences (Fig 3.4a) showed a star-like shape with a single, central high frequency haplotype from which a number of low frequency haplotypes were separated by few mutational steps (mostly one step). This star-like shape indicates/could indicate a possible recent population expansion (Bargelloni *et al.* 2005). This network indicated no clear evidence of a relationship between haplotype genealogy and geographic location. This figure does, however, show that two private haplotypes from the Eastern Cape were divergent in this dataset, being separated by two and four steps, respectively, from the network. A similar network constructed using the nDNA sequence dataset is more revealing (Fig 3.4b). The enclosed subset of the network (clade 1) delineates a branch from which the two range southern and northern edges (Eastern Cape and northern KZN) are almost excluded. The Eastern Cape is represented by only two alleles from three individuals in this clade, while northern KZN displays only two from two. This clade is dominated by Transkei (13 alleles from 12 individuals) and southern KZN (16 alleles from 13 individuals). This may provide some evidence of a relationship between geographic position and haplotype genealogy, suggesting high diversity in the central two localities, which appear well mixed, flanked by less diverse and smaller populations to the south and north (Eastern Cape and northern KZN).

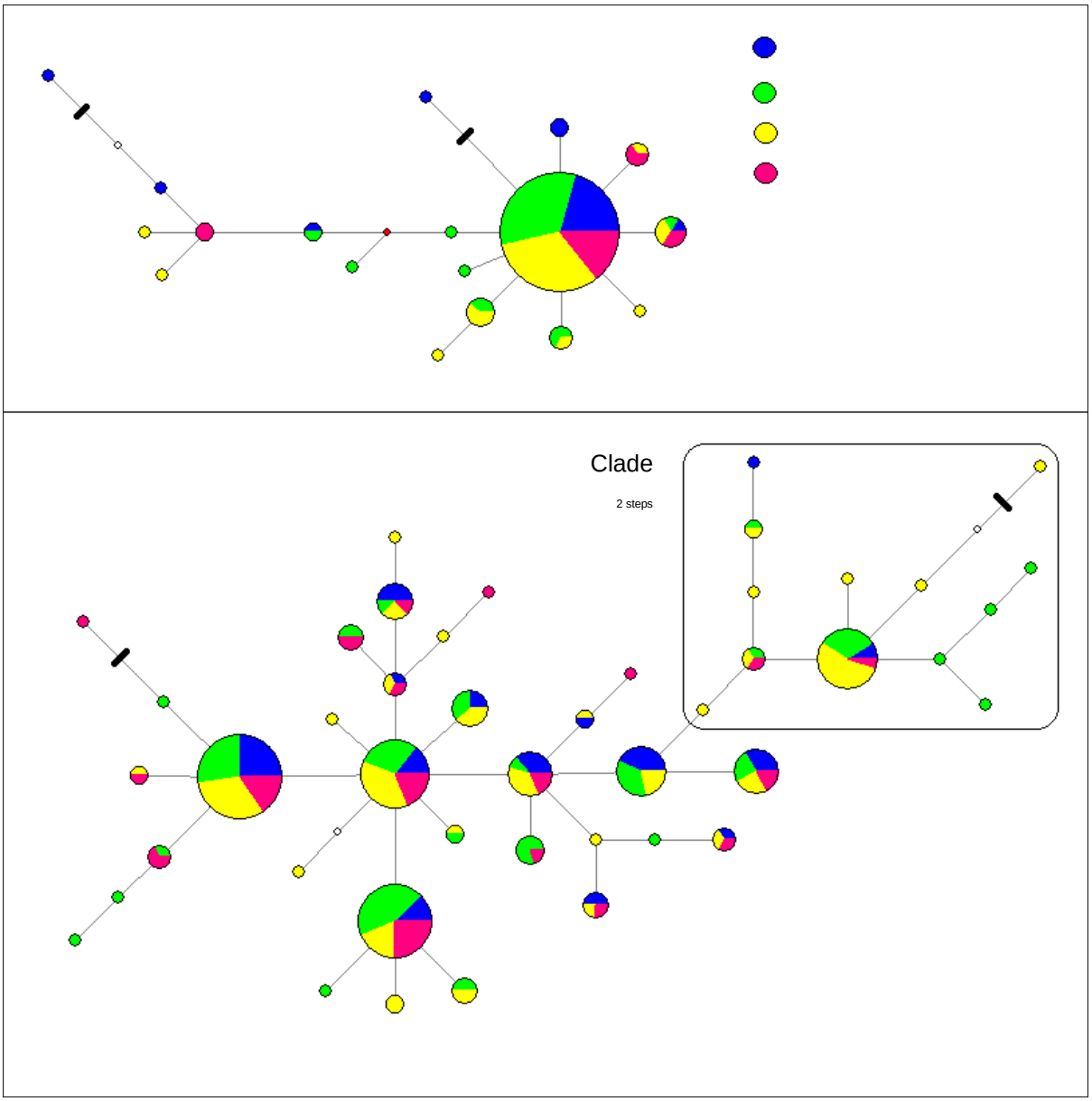

Figure 3.4: Median-joining haplotype network (with maximum parsimony) constructed using mitochondrial control region (a) and nuclear S7 intron 1 (b) gene datasets for *P. praeorbitalis*. Connecting lines indicate one mutational step between haplotypes (unless otherwise stated) while the size of each circle is proportional to haplotype or allele frequency within the dataset. The smallest circles represent one haplotype or allele. Small clear nodes represent hypothetical median vector haplotypes absent from the samples. The enclosed Fig 3.5b(1) is a clade considered to be partially restricted to the Transkei and southern KZN.

3.3.5) Genetic differentiation and structure

Pairwise comparisons between localities (Table 3.3) provided no evidence of genetic differentiation in the mtDNA dataset. However, significant ($p < 0.05$) genetic differentiation was evident in the nDNA dataset. In particular, the Eastern Cape displayed significant (p

<0.05) F_{st} values of 0.039 and 0.045 when compared to the Transkei and northern KZN respectively. This provides evidence of low to moderate levels of differentiation between the southern and northern range edges of *P. praeorbitalis* (northern KZN) as well as the adjacent Transkei region. A significant ($p < 0.05$) F_{st} value of 0.025 obtained when comparing southern and northern KZN indicates that some differentiation may also exist between these localities. The lack of evidence for differentiation between the southern KZN and Eastern Cape localities is noteworthy considering the differentiation observed between the Eastern Cape and the other two localities and may be the result of a confounding factor. One such factor may be the fact that the majority of samples collected from sites within southern KZN were collected during the month of July when *P. praeorbitalis* has been observed to aggregate in this area (and further north) in what are thought to be spawning aggregations (van der Elst 1997). This sample might therefore include a number of migrants from other localities and particularly from localities further south. Temporal structure might also be a confounding factor in this case since a large proportion of the samples collected in southern KZN were from juvenile fish.

Table 3.3: F_{st} values generated from pairwise comparisons of mitochondrial control region (below diagonal) and nuclear S7 intron 1 (above diagonal) sequences from four localities for *P. praeorbitalis*. Significant ($p < 0.05$) results are in bold.

	nDNA			
mtDNA	Eastern Cape	Transkei	southern KZN	northern KZN
Eastern Cape		**0.039**	0.015	**0.045**
Transkei	0.011		**0.016**	-0.01
southern KZN	0.004	-0.007		**0.025**
northern KZN	-0.022	0.023	-0.009	

Exact tests of population differentiation (Table 3.4) did not show any significant ($p < 0.05$) evidence of differentiation between localities in both the mtDNA and nDNA dataset.

Table 3.4: Results (*p*-values) of exact tests of population differentiation of mitochondrial D-loop (below diagonal) and nuclear S7 intron 1 (above diagonal) sequences from four geographic groups for *P. praeorbitalis*.

	nDNA			
mtDNA	Eastern Cape	Transkei	southern KZN	northern KZN
Eastern Cape	-	0.119 ±0.017	0.738 ±0.012	0.131 ±0.012
Transkei	0.309 ±0.012	-	0.437 ±0.017	0.519 ±0.022
southern KZN	0.223 ±0.007	1.000 ±0.000	-	0.259 ±0.025
northern KZN	0.231 ±0.005	0.112 ±0.011	0.365 ±0.006	-

Pairwise F_{st} performed on the nDNA dataset after the removal of juvenile fish (less than 405 mm FL), produced significant F_{st} values between all localities, unlike the full dataset (Table 3.5). In particular, F_{st} comparison values between the Eastern Cape and all three other localities were higher and significant ($p < 0.01$). For example, F_{st} values of 0.081 and 0.078 were obtained for comparisons with Transkei and northern KZN respectively. These results provide evidence of moderate genetic differentiation between these localities. Evidence of significant ($p < 0.05$) but low genetic differentiation was also found for southern KZN versus the Eastern Cape (F_{st}=0.031), Transkei (F_{st}=0.022) and northern KZN (F_{st}=0.029).

Table 3.5: F_{st} values of the pairwise comparisons of nuclear S7 intron 1 sequences of *P. praeorbitalis* from four localities. Indicated are values from the full dataset (below diagonal) and the reduced dataset with fish below 405 mm FL removed (above diagonal). Significant ($p < 0.05$) values are in bold.

	<405mm FL removed			
Full Dataset	Eastern Cape	Transkei	southern KZN	northern KZN
Eastern Cape		**0.081**	**0.031**	**0.078**
Transkei	**0.039**		**0.022**	-0.016
southern KZN	0.015	0.016		**0.029**
northern KZN	**0.045**	-0.01	**0.025**	

An exact test of population differentiation done when fish below 405 mm FL were removed from the dataset (Table 3.6) revealed a significant (p = 0.0123 ±0.003) difference shown between Eastern Cape and Transkei. These results support the hypothesis that behavioural differences between different age classes might be a confounding factor in tests for spatial genetic differentiation in this species.

Table 3.6: Results (p-values) of exact tests of population differentiation on nuclear S7 intron 1 sequences of *P. praeorbitalis* from four localities. Presented are values from the full dataset (below diagonal) and the reduced dataset with fish below 405 mm FL removed (above diagonal). Significant ($p < 0.05$) values are shown in bold.

	<405mm FL removed			
Full Dataset	Eastern Cape	Transkei	southern KZN	northern KZN
Eastern Cape		**0.0126 ±0.003**	0.195 ±0.012	0.114 ±0.006
Transkei	0.119 ±0.017		0.162 ±0.010	0.739 ±0.013
southern KZN	0.738 ±0.012	0.437 ±0.017		0.330 ±0.016
northern KZN	0.131 ±0.012	0.519 ±0.022	0.259 ±0.025	

A spatial analysis of molecular variance was run on both datasets using the program SAMOVA, in order to group localities in a manner which maximised variance between

groups. In the mtDNA dataset, variance was maximised by separating the Eastern Cape and grouping the remaining three localities. Despite this, a *p*-value of 0.25 ± 0.01 provided no evidence of spatial structure in this dataset with only 1.14% of variation explained between the groups. In the nDNA dataset, variance was maximised by grouping the Eastern Cape and southern KZN localities and the Transkei and northern KwaZulu-Natal localities together into two groups. This produced a *p*-value of 0.36 ± 0.00, explaining only 3.30% of the variation present.

3.4) Discussion

3.4.1) Genetic diversity

Levels of both haplotype (*Hd* = 0.488 ± 0.058) and nucleotide (π = 0.004 ± 0.001) diversity observed in the mtDNA dataset of *P. praeorbitalis* were low compared with those observed for this gene in other sparids within the Agulhas Current system (Oosthuizen 2006; Teske *et al.* 2010; Murray 2012; Bennetttt 2012). However, these values were well within the range of diversity indices calculated for the mitochondrial control region of a number of sparids in the Atlantic and Mediterranean (Bargelloni *et al.* 2003). In comparison to the mtDNA dataset, haplotype diversity was higher in the nDNA dataset (*Ad* = 0.922 ± 0.000), while nucleotide diversity was similar (π = 0.005 ± 0.000). The differences between the mtDNA and nDNA datasets were reflected in the median-joining haplotype networks constructed, with nDNA displaying a more complex network with more common haplotypes separated by more mutations than the simpler, star-like network calculated for mtDNA. Grant and Bowen (1998) note that many marine fish species display low levels of mtDNA diversity. Several possible reasons are given for this, including large variation in reproductive success between individuals (e.g. Shields and Gust 1995), overharvesting (e.g. Camper *et al.* 1993), and previous population bottlenecks or selective sweeps (e.g. Dodson *et al.* 1991; Gold *et al.* 1994). According to Grant and Bowen (1998), the combination of low *Hd* and π observed in the mtDNA dataset is indicative of a recent population bottleneck or founder event. Similarly, the high *Ad* and low π observed in the nDNA dataset is also possibly the result of a population bottleneck followed by rapid population growth. The differences in the diversity observed between the mtDNA and nDNA datasets in this study may be the result of one or a combination of factors, including differences in mutation rates between loci (Shaklee and Bentzen 1998) and maternal inheritance of mtDNA (Hecht *et al.* 1984).

Spatial patterns in diversity show interesting trends, especially when nDNA and mtDNA datasets are compared. In particular, the Eastern Cape showed the lowest levels of π in the nDNA dataset and the highest in the mtDNA dataset. Similarly, the mtDNA dataset had the

highest percentage of private haplotypes, while the nDNA dataset had the lowest. This large difference in the percentages of private haplotypes was recorded in the Eastern Cape, while the results were similar between datasets within the other localities. These disparities may be indicative of differences in sex ratios between the Eastern Cape and other localities, or may reflect differences in selection pressures on populations. Because it has been suggested that this species is a protogynous hermaphrodite (Garrat *et al.* 1994; Mann *et al.* 2005), differences in size structure might represent differences in sex ratios between localities as a higher proportion of larger fishes might be males, reducing the effective population size of the maternally-inherited mtDNA in areas with a higher proportion of large fish. Future genetic studies on this species might therefore benefit from recording the sex of the fish from which samples are taken. These differences in diversity indices between the Eastern Cape and other localities are supported by the results of the pairwise comparisons, providing further evidence of genetic divergence between this locality and the others.

3.4.2) Demographic history

The significant negative Fu's F values and unimodal mismatch distributions obtained for both datasets and the significant negative Tajima's-D obtained for the mtDNA dataset indicate that *P. praeorbitalis* underwent a recent population expansion subsequent to a bottleneck or selective sweep (Tajima 1989; Harpendinger 1994; Fu 1997; Innan and Stephan 2000). This result is also supported by the mtDNA haplotype network which displays the star-like shape (Bargelloni 2005) with few mutational steps separating several low frequency haplotypes from a dominant one. Similar signatures of recent population expansion have been observed in the Cape hake *Merluccius paradoxus* (von der Heyden 2009) and members of the sparid family such as the poenskop *Cymatoceps nasatus* (Murray 2012), within the Agulhas Current system. Murray (2012) calculated that the expansion of *C. nasatus* occurred between 130 000 and 35 000 years ago and hypothesised that this may have been facilitated by increases in sea level and temperature, opening up the shelf environment within the Agulhas Current system. Given the similarities in habitat and behaviour between this species and *P. praeorbitalis*, it is possible that *P. praeorbitalis* was affected by the same factors, resulting in a similar genetic signature of population expansion.

3.4.3) Genetic differentiation and structure

The results of nDNA analyses for *P. praeorbitalis* provide some evidence of weak genetic differentiation between the Eastern Cape and two localities (Transkei and northern KwaZulu-Natal). This genetic differentiation was strengthened by the removal of fish below the estimated length at 50% maturity (Mann *et al.* 2005) which indicated that the most differentiation between localities occurs in sexually mature fishes and provided evidence of

temporal structuring. This result may be due to behavioural differences between adult and juvenile fishes such as an ontogenetic shift towards more territorial or sedentary behaviour with the onset of sexual maturity, or possibly linked to a sex change later on. This explanation is supported by the fact that ontogenetic changes in aggregation behaviour and habitat usage have been observed in other sparids (Macpherson 1998) and the differences in aggregation and depth preference reported for *P. praeorbitalis* by Garrat *et al.* (1994). Another possible explanation for this is natal homing, a phenomenon where, at the onset of sexual maturity or during spawning events, juvenile fishes return to the area in which they were spawned or hatched (Bradbury and Laurel 2007). This has been hypothesised to occur in some marine demersal and reef species (e.g. Thorrold *et al.* 2001; Svedäng *et al.* 2007), but is difficult to prove (Bradbury and Laurel 2007).

The results of mtDNA analyses however, revealed no evidence of any genetic differentiation between localities. Similar studies using mtDNA, performed on sparids in the Agulhas Current system have mostly observed zero to weak genetic structure. These include studies on the Cape stumpnose, *Rhabdosargus holubi* (Oosthuizen 2006), red roman *Chrysoblephus laticeps* (Teske *et al.* 2010) and white steenbras, *Lithognathus lithognathus* (Bennettt 2012). However, Murray's results (2012) did provide some evidence of genetic differentiation between localities for the poenskop *Cymatoceps nasutus* with the southern range edge of this species off the Western Cape displaying significant Φ_{st} values (>0.1) when compared with most of the more northerly localities. While the magnitude of the F_{st} values obtained for the nDNA dataset in this study is far lower, the similarities in the results (evidence of genetic variation between the southern range edges and the rest of the localities), and similarities in the life history of these two species, indicate that further investigation using more sensitive markers or larger sample sizes, might reveal stronger evidence of genetic differentiation between localities in *P. praeorbitalis*.

3.4.4) Factors influencing gene flow

The lack of evidence for genetic structuring observed over much of *P. praeorbitalis'* range indicates that the stock is likely to have high levels of gene flow. This was expected because of the high dispersal rates of marine species with planktonic larval phases in general (Palumbi 1992), and in particular, the effects of the complex currents within the Agulhas Current system on larval dispersal (Hutchings *et al.* 2002). *Polysteganus praeorbitalis* has been observed to display varying degrees of residency in adult individuals (Maggs 2012), indicating that genetic connectivity between localities is most likely maintained through egg, larval and juvenile dispersal. Egg and larval dispersal appears to be important to a number of similarly distributed sparids, including the slinger, *Chrysoblephus puniceus,* and santer,

Cheimerius nufar, (Connell *et al.* 1999) as their small buoyant eggs maximise dispersal potential within this system. Although it was noted that *P. praeorbitalis*, *C. puniceus* and *C. nufar* did not display the seasonal spawning migrations observed in other coastal linefish species (Garrat 1988), it was later suggested (Garrat *et al.* 1994) that *P. praeorbitalis* may aggregate at certain times of year. While one might intuitively assume that larval dispersal in the Agulhas Current would take place in a south-westerly direction only, Beckley (1995) indicated that the larvae of many coastal linefish species in this system tend to be retained on the coastal shelf by inshore boundary current phenomena. Indeed the results of a number of regional studies estimate larval dispersal occurs in both westerly and easterly directions at rates of over 200 km per week, depending on the prevailing conditions and locality (Tilney *et al.* 1996; Hutchings *et al.* 2002; Brouwer *et al.* 2003; Attwood and Cowley 2005).

3.4.5) Explaining spatial genetic differentiation

The presence of weak to moderate genetic differentiation between the Eastern Cape and the other three localities indicated by F_{st} values in the nDNA dataset and the higher percentage of private haplotypes in the mtDNA dataset was unexpected, given the patterns of larval dispersal described above. However, Palumbi (1994) notes that while many marine species have the potential for high dispersal, a number of factors can still lead to or maintain genetic divergence. These include diversifying selection, behavioural limits to dispersal and the effects of small and large-scale oceanic features on gene flow. In the Agulhas Current system, sparid larvae have been observed to be able to swim at rates exceeding shelf current speeds and thereby potentially contribute to, or mitigate their own dispersal (Pattrick 2008). Juvenile *P. praeorbitalis* have been observed residing in shallow coastal waters (10 m–30 m) while larger specimens are known to inhabit deeper reefs (30 m–120 m) (Garrat *et al.* 1994). In addition to this, Maggs (2012) indicated a northward movement of large adult male fishes in *P. praeorbitalis*. In combination, these factors highlight the potential for larval, juvenile and even adult dispersal in *P. praeorbitalis* and indicate that behavioural factors might contribute substantially to gene flow and hence the low levels of genetic differentiation observed in this study. In particular, the increase in significant F_{st} comparisons after the exclusion of individuals below 50% maturity (Mann *et al.* 2005) in both the nDNA and mtDNA datasets indicates that *P. praeorbitalis* might show higher levels of residency in older, sexually mature fishes or possibly differential levels of residency between sexes. This result also provides some evidence of natal homing in *P. praeorbitalis*, a phenomenon known to occur in marine demersal fishes with pelagic larval phases (Swearer *et al.* 2002). The presence of genetic differentiation between the Eastern Cape and other localities also indicates that *P. praeorbitalis* might not undergo a spawning migration to a single specific spawning site as has been previously suggested (Garrat 1988). Such a

spawning migration would increase mixing and prevent genetic divergence between localities. These results indicate that it is more likely that *P. praeorbitalis* spawns at more than one locality, thereby allowing incomplete barriers to gene flow such as oceanographic features, and possibly diversifying selection to result in weak genetic differentiation.

The dynamic Port Alfred upwelling cell represents a persistent, near-shore oceanographic discontinuity due to the effects of frequent upwelling events in this region on the temperature and turbidity of the local shelf waters (Lutjeharms 2006a, b). While the waters directly off Port Alfred appear to form the centre of this upwelling cell, the process of kinematically driven upwelling begins with the widening of the continental shelf further north near the mouth of the Mbashe River (Lutjeharms 2006a, b). Upwelling cells have been observed to form biogeographic barriers between populations of marine fishes and invertebrates in the Agulhas (Teske *et al.* 2011) and other systems (e.g. Crawford *et al.* 1987; Wares *et al.* 2001) through both abrupt spatial discontinuities in temperature variability and the physical effects of upwelling and counter-currents on larval dispersal (Gaylord and Gaines 2000). Turpie *et al.* (2000) note that the coincidence of the southern range edges of many species of shallow water (Penrith 1976) and intertidal fishes (Prochazka 1994) and rocky shore invertebrates (Emanuel *at al.* 1992) between Port Alfred and the Mbashe River Mouth may be the result of this persistent upwelling and the resultant thermal front in this area. These results highlight the potential importance of the Port Alfred upwelling cell as a biogeographic barrier and might explain the weak genetic differentiation observed in this study between the southern populations of *P. praeorbitalis* (locality: Eastern Cape) and the central and northern populations.

The range of *P. praeorbitalis*, spans at least three biogeographic provinces (refer to Chapter 1). It is likely that the differences in biotic and abiotic factors between and within these regions subject *P. praeorbitalis* to different selection pressures. While it is assumed that the mtDNA and nDNA markers used in this study are neutral, Palumbi (1994) notes that adaptive divergence is likely to contribute to genetic divergence between semi-isolated populations and help to maintain existing genetic structure in previously isolated populations. More recent studies have indicated that adaptive divergence in marine environments may exist on a finer scale than previously thought, affected by localised selection pressures (Conover *et al.* 2006). It is therefore not unlikely that the genetic differences between the Eastern Cape (warm temperate) and Transkei (warm temperate–subtropical), southern KwaZulu-Natal (subtropical) and northern KwaZulu-Natal (subtropical–tropical) localities, might be partly the result of different selection pressures between and within biogeographic provinces.

One factor which may exert considerable differential selection pressure between the provinces is water temperature. Water temperature, in particular, is known to affect larval development and survival in marine fishes (Houde 1989; Pepin 1991). In addition to this, some fishes have been observed to display temperature-dependent sex determination (Conover 1984). This may occur in one of two ways: either sex is directly determined by temperature during larval development, or temperature indirectly determines sex by influencing growth rate, affecting the size of the fish as it reaches sexual maturity and thereby the probability of it being male or female (Ospina-A'lvares and Piferrer 2008). In fishes which display temperature-dependent sex determination, colder temperatures have been observed to result in a higher probability of fish maturing into females (Conover 1984; Ospina-Alvares and Piferrer 2008). Such a phenomenon would explain the high diversity of the maternally inherited mtDNA dataset of *P. praeorbitalis* individuals from the Eastern Cape (warm temperate) in relation to the other localities sampled. Exposure of larvae and/or juvenile fishes to lower temperatures in this warm temperate region might cause sex ratios of the Eastern Cape population to be skewed in favour of females, increasing the effective population size with regard to maternally inherited mtDNA while leaving nDNA diversity unaffected. This would also explain the patterns of increasing mean size and proportion of male fish with decreasing latitude observed by Garrat *et al.* (1994). Such a hypothesis however, could only be verified with laboratory experiments.

Chapter 4

General discussion

Polysteganus praeorbitalis is an important species for both the commercial and recreational linefishery in South Africa. It is a favourite of recreational anglers because of its unique colouration and fighting ability (van der Elst 1983), and makes up a not insignificant proportion (>4%) of commercial landings off of the Transkei coast (Fennessy *et al.* 2003) and approximately 1.15% of KwaZulu-Natal commercial boat catches (Lamberth *et al.* 2009). It has been suggested that this proportion was far higher off the KwaZulu-Natal coastline at the advent of the KwaZulu-Natal linefishery, when this species and other large sparids made up approximately 50% of the catch (van der Elst 1997; Penney *et al.* 1999), indicating that *P. praeorbitalis* could, at one time, have been considered a major fisheries species. While *P. praeorbitalis* has been researched as a part of multi-species studies by Garrat *et al.* (1994), Mann *et al.* (2005) and Maggs (2012), there has yet to be a study conducted solely on this species and, as such, a paucity of vital species information remains. This is due mostly to the difficulty of obtaining adequate sample sizes of *P. praeorbitalis* as a result of its solitary behaviour (Heemstra and Heemstra 2004), and more recently, the negative effects of severe over-exploitation on its abundance (Garrat *et al.* 1994). Indeed both Garrat *et al.* (1994) and Mann *et al.* (2005) failed to determine conclusively the spawning season or age at 50% maturity and were unable to verify whether this species undergoes protogynous hermaphroditism due to insufficient sample sizes of reproductively active fish. Mann *et al.* (2005) expressed frustration at the fact that observers stationed off Richards Bay managed only 42 measurements of *P. praeorbitalis* over the course of three years.

This study was therefore the first to focus on *P. praeorbitalis* and aimed to contribute to the available information on this species by using genetic analyses of mtDNA and nDNA, and species distribution models based on occurrence records and remotely sensed SST data. These methods were used to investigate the genetic structure, distribution ranges and the current status of this stock to predict how this might change in response to the effects of global climate change. By using genetic analysis which requires fewer samples than other fisheries methods, and historical occurrence records collected over a long timeframe, this study was able to draw conclusions, despite the difficulties inherent in obtaining samples for this species.

4.1) Potential impacts of climate change on genetic diversity

Combining the results of species distribution models (SDMs) and genetic analyses has been shown to provide an effective tool for evaluating the potential for losing genetic diversity due to future climate change in plant species (Alsos *et al.* 2011). In the case of *P. praeorbitalis* in this study, all of the sites from which samples were collected were included in the range of this species in the 2020 and 2030 predictions of the SDM. Although there were no genetic samples obtained from areas south of Algoa, samples obtained from sites (Port Elizabeth and Kenton-on-Sea) within the Eastern Cape locality provide some indication of the levels of genetic diversity at the southern range edge of the distribution of *P. praeorbitalis*.

The Eastern Cape was low to moderately differentiated from other localities and had a relatively high number of private haplotypes in the mtDNA dataset. In the mtDNA dataset, four out of seven (57.1%) haplotypes from this locality were private while only one out of 14 (7.1%) alleles were private in the nDNA dataset. The range contraction predicted at this edge of the *P. praeorbitalis* distribution might place these unique alleles at risk. Given the number of private alleles/haplotypes observed in the Eastern Cape locality, the loss of this habitat would potentially threaten 22.2% and 2.2%, respectively, of the total number of unique haplotypes and alleles observed in the mtDNA and nDNA datasets of this study. Similarly, the fragmentation predicted north of Richards Bay might directly affect individuals from northern KwaZulu-Natal, placing at risk 5.6% and 6.7%, respectively, of the total diversity observed in the mtDNA and nDNA datasets. These results provide little evidence to suggest that climate change is likely to have a great impact on the observed genetic diversity of *P. praeorbitalis,* but do indicate that the Eastern Cape and northern KwaZulu-Natal localities might be affected, resulting in some risk to the unique alleles at these localities. This is particularly relevant to the Eastern Cape which displays some evidence of moderate genetic differentiation in the nDNA dataset and a high percentage of private alleles in the mtDNA dataset (refer to Chapter 3).

The ‘centre periphery hypothesis’ predicts that peripheral populations hold less genetic diversity than those towards the centre of a species range and are therefore more vulnerable to extinction (Lawton 1993). This is because these populations often occur in habitats which are closer to the limits of the species environmental and ecological tolerances (Lawton 1993; Vucetich and Waite 2003). This hypothesis is generally accepted at localised geographic scales but has been shown to be less important at scales broader than regional scales because spatial patterns of genetic diversity at broader than regional scales often reflect past climatic changes rather than dispersal patterns (Hewitt 2004; Hampe and Petit 2005).

This may result in most of the genetic diversity displayed in marginal populations as opposed to central populations (e.g. Petit *et al.* 2002; Hewitt 2004). In the case of *P. praeorbitalis,* its occurrence at a localised scale only (over three biogeographic provinces) and the higher levels of genetic diversity observed in the two central populations indicate that this species may fit the 'centre periphery hypothesis'. In terms of this hypothesis, the peripheral populations of the Eastern Cape and northern KwaZulu-Natal would be expected to be highly vulnerable to the negative effects of climate change. However, the two central localities are less likely to be negatively affected and hold most of this species' genetic diversity, possibly as a result of its high abundance in these areas (Garrat *et al.* 1994; Penney *et al.* 1995; G. Marchland, pers. comm.). This indicates that the more direct effects of climate change on the genetic diversity of this species are likely to be minimal.

Results of similar genetic studies on sparids in the Agulhas Current system have all revealed little to no genetic structure and well-mixed populations (e.g. Klopper 2005; Teske *et al.* 2010; Bennettt 2012; Murray 2012), with the only sub-structuring observed between the southern edges of species ranges and the rest of their distribution (e.g. Teske *et al.* 2010; Murray 2012). In the light of all these results and this study, it appears that sparids with similar distributions in this system face a low risk to loss of genetic diversity caused by the predicted effects of climate change on their distribution. Most genetic studies attribute the lack of genetic spatial structure displayed by sparids in this system to their life history which tends to consist of group spawning and high larval dispersal, resulting in panmixia in many cases (e.g. Teske *et al.* 2010; Bennettt 2012, Murray 2012). However, the dependence of many Agulhas Current system species on specific spawning sites (Hutchings *et al.* 2002) within this system might place them at risk to the localised effects of climate change on the environmental conditions at those sites.

4.2) Potential effects of climate change on life history.

Three major spawning sites of importance to shelf-associated fish species in South Africa have been identified within the Agulhas Current system (Hutchings *et al.* 2002), two of which fall within the range of *P. praeorbitalis* (Figure 4.1). One of these sites lies north of Richards Bay and St Lucia, while the other is in the Transkei region. A third site lies southwest of Cape St Francis, on the southern edge of this species' range and is unlikely to be used by *P. praeorbitalis*. All sites occur on a narrow section of the continental shelf and lie upstream from a potential enrichment mechanism (in the form of an upwelling cell) and shelf widening that is associated with a nursery area.

The spawning site north of Richards Bay and St Lucia lies directly upstream of the St Lucia–Richards Bay upwelling cell (providing enrichment) and Natal Bight nursery ground (shelf widening providing larval retention) (Hutchings *et al.* 2002). This spawning site is important for several shelf-associated species including slinger, *Chrysoblephus puniceus* (Hutchings *et al.* 2002), geelbek, *Atractoscion aequidens* (Griffiths and Hecht 1995), red steenbras, *Petrus rupestrus,* and seventy-four, *Polysteganus undulosus* (Garrat 1988), some of which are thought to also use spawning grounds further south in the Transkei and even south of Cape St Francis. The observed high abundances of large adult *P. praeorbitalis* in this area (Mann *et al.* 2005), the hypothesised gradual northward migration of large *P. praeorbitalis* from the southern KwaZulu-Natal and northern Transkei areas (Mann *et al.* 2005; Maggs 2012), and the observation of spawning aggregations in the Natal Bight area during the winter months of July and August (van der Elst 1997), indicate that this site is most likely the main spawning site of *P. praeorbitalis* (Garret *et al.* 1994, Mann *et al.* 2005). The effects of climate change on this important spawning ground are therefore likely to affect crucial life-history stages of important species in the multispecies South African linefishery.

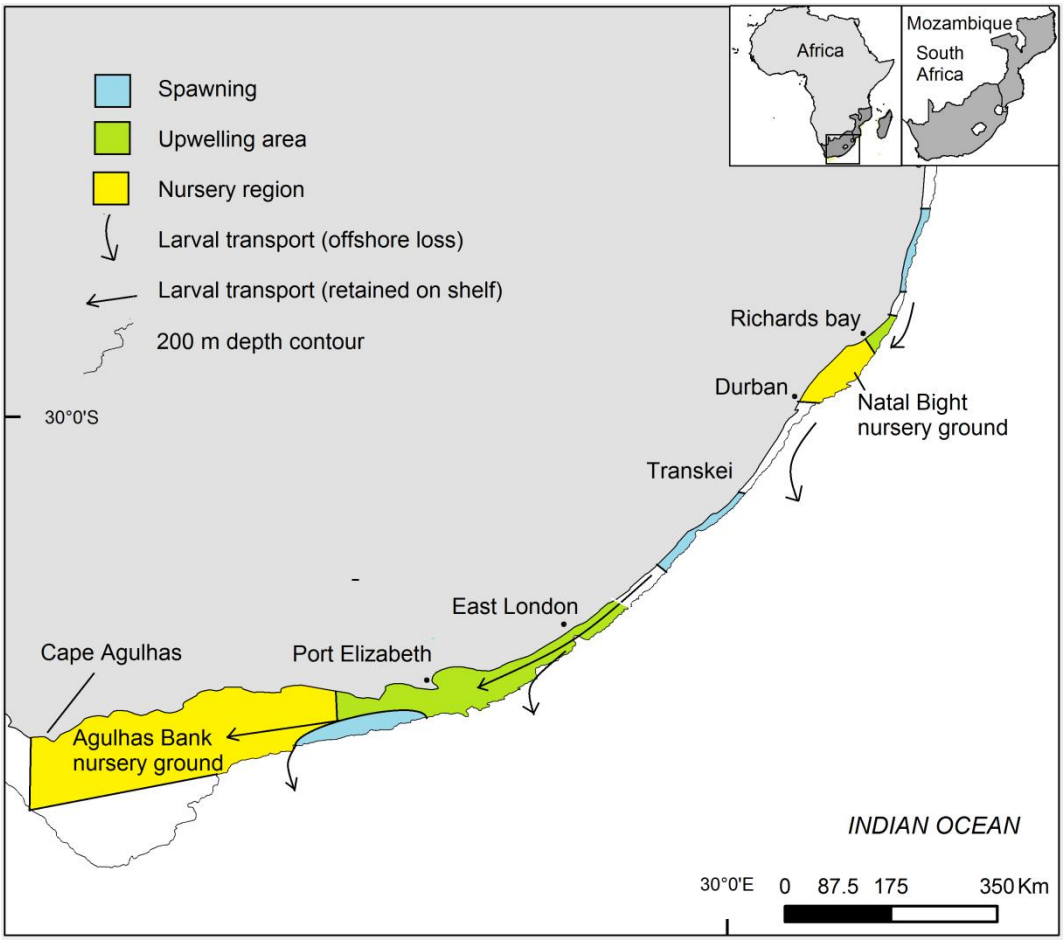

Figure 4.1: Map showing the three main reproductive habitats of shelf-associated fishes in the Agulhas Current system (after Hutchings *et al.* 2002). Spawning tends to take place on narrow shelf areas directly upstream of areas where the shelf widens. This makes use of the enrichment (through upwelling) and larval retention (through inshore counter currents) associated with these areas which act as nursery grounds.

The genetic differentiation observed in this study indicates that *P. praeorbitalis* might also use the second site located off the Transkei coast. This spawning site lies directly upstream from the Port Alfred upwelling cell (providing enrichment) and is also utilised by other shelf-associated species such as white steenbras, *Lithognathus lithognathus,* and geelbek, *Atractoscion aequidens* (Bennettt 1993; Griffiths and Hecht 1995). White steenbras has been observed to also use the spawning grounds southwest of Port Elizabeth (Bennettt 1993; Hutchings *et al.* 2002). The nursery grounds of these species lie on the Agulhas Bank south of Cape St Francis, where low temperatures would prevent survival of *P. praeorbitalis* (Hutchings *et al.* 2002). More likely is the possibility that the eggs and larvae of *P. praeorbitalis* are retained in low numbers by the inshore counter currents and divergence-driven upwelling south of the Mbashe estuary, with nursery areas as far south as Port

Elizabeth. A similar hypothesis was proposed for the related sparid, the poenskop (*Cymatoceps nasutus*), by Murray (2012) who noted that the eggs of many sparid species (including the closely related *Polysteganus undulosus*) hatch within 48 hours (Connell 2007). Furthermore, larvae of sparid species have been shown to possess enough mobility to influence their dispersal within the Agulhas Current system, thereby increasing their chances of settling on inshore reefs (Pattrick 2008). The high potential for loss of larvae to both offshore dispersal and the Agulhas Bank would, however, make the success of spawning of *P. praeorbitalis* on this second spawning ground lower than that of the more northerly Natal Bight one. This may partly explain the observed lower abundances of *P. praeorbitalis* towards its southern range edge despite historically lower levels of exploitation in these areas (Garrat *et al.* 1994; Penney *et al.* 1995; G. Marchland, pers. comm.).

The fragmentation predicted by the ensemble SDM to occur north of Richards Bay near St Lucia by 2030, is most likely caused by spring, summer and autumn warming in this area (refer to Chapter 2). The spring, summer and autumn warming of this area might be mitigated by the seasonality of spawning of *P. praeorbitalis* in winter at this site. However, if future warming does affect the reproductive success of this species (either directly or indirectly), this would place increased pressure on this already vulnerable species and (if it does indeed spawn at a second site) increase the importance of its second spawning site.

4.3) Synergistic effects of climate change and exploitation on *P. praeorbitalis*

Harley *et al.* (2006) noted that climate change poses the largest threat to species when its effects work synergistically with other negative anthropogenic pressures, thereby compounding their negative impacts. This project has highlighted key potential negative effects of climate change on the range (Chapter 2), genetic diversity and reproductive success of *P. praeorbitalis*. These factors are likely to work synergistically with continued exploitation of this over-exploited species (Mann *et al.* 2005), amplifying the effects of climate change on its range and reducing its resilience to the negative effects on genetic diversity and reproductive success (Hsieh *et al.* 2008).

Over-exploitation of marine fish species may lead to range reduction as individuals move from less favourable habitats (usually towards the edges of their range) into the space created by the removal of individuals from the most favourable habitats (usually towards the centre of their range) (MacCall 1990; Swain and Wade 1993). This is likely to be particularly true of range-restricted, reef-dwelling species such as *P. praeorbitalis* for which suitable reef habitats are limited (e.g. Penney *et al.* 1999). Furthermore, the solitary nature of *P.*

praeorbitalis (van der Elst 1997) and its observed high site fidelity (Maggs 2012) indicate that this species might display territorial behaviour which would make it even more vulnerable to range contraction from over-exploitation (MacCall 1990). The high abundances (Garrat *et al.* 1994) and levels of genetic diversity (Chapter 3) observed in southern KwaZulu-Natal indicate that this region may contain some of the most favourable habitat for this species, while also displaying some of the highest levels of exploitation (Penney *et al.* 1999). Over-exploitation of this species by the KwaZulu-Natal linefishery might, therefore, cause the northern and southern edges of *P. Praeorbitalis'* range to contract as individuals move from marginal habitats into the spaces made available by the removal of individuals from the more favourable habitats off of the KwaZulu-Natal coastline. As its range contracts, an ever-greater proportion of the population will be exposed to the high levels of exploitation which occur in this area, resulting in a negative feedback loop. Range reduction from over-exploitation would compound the contractions and fragmentation predicted by the ensemble SDM used in this study. The resultant range reduction due to the combined effects of climate change and over-exploitation would also increase the vulnerability of this species to mortality from extreme environmental events due to disproportionately large proportions of the population residing in small areas (Hutchings and Reynolds 2004). These events are likely to become more frequent as a result of the increase in oceanic environmental variability caused by climate change (Bindoff *et al.* 2007; Trenberth *et al.* 2007).

Over-exploitation has also been observed to negatively affect the reproductive success of marine fish species through reductions in the density of spawning aggregations. The effects of reduced density of spawning aggregations may include reduced fertilization rates, reduced mate availability and reduced intensity of social spawning cues (Rowe and Hutchings 2003). Rowe and Hutchings (2003) also note that in species which show sequential hermaphroditism (as *P. praeorbitalis* is suspected to), the age/size truncation often associated with over-exploitation (Conover and Munch 2002; Berkely *et al.* 2004; Hutchings and Reynolds 2004) may result in changes in sex ratios that further reduce reproductive success. These reductions in reproductive success are likely to exacerbate the negative effects of the potential loss of spawning habitat predicted for *P. praeorbitalis* by the ensemble SDM in this study (Chapter 2). Here again, the initial pressures placed upon the species by climate change and over-exploitation are likely to feed back with reduced reproductive success resulting in lower abundances, causing increased sensitivity to range reductions, reduced resilience to extreme environmental events and further reductions in reproductive success.

This study predicts the effects of range contraction due to climate change on the genetic diversity of this species to be relatively minor (refer to section 4.2). However, range contraction in combination with the negative effects of over-exploitation on genetic diversity and population structure, is a cause for concern. The low levels of genetic diversity observed in the mtDNA dataset (refer to Chapter 3), though indicative of a previous population bottleneck or selective sweep, are however, low in comparison to other shelf-associated sparids in the Agulhas Current system (e.g. Klopper 2005; Bennettt 2012; Murray 2012). Other possible reasons for this low level include over-exploitation and high variation in reproductive success (Camper *et al.* 1993; Shields and Gust 1995). The fact that these low levels are only displayed in the maternally inherited mtDNA dataset while levels in the nDNA dataset are higher, suggests that high variation in the reproductive success of females might be responsible. This is particularly likely if *P. praeorbitalis* undergoes protogynous hermaphroditism (Garrat *et al.* 1994; Mann *et al.* 2005) which would indicate a disproportionate genetic contribution from a small proportion of the total population made up of large male fish. Species with this type of life history are highly vulnerable to loss of genetic diversity through overfishing which tends to remove large individuals first (e.g. Buxton 1993). It is therefore likely that *P. praeorbitalis* has already experienced some loss of genetic diversity due to over-exploitation.

4.4) Implications and management recommendations

The results of this study have indicated that *P. praeorbitalis* is likely to come under increasing pressure from climate change, in addition to the pressure already placed on this species from continued exploitation by both the commercial and recreational linefishery in South Africa. While there is no local solution to the problem of climate change, efficient management of the commercial and recreational linefisheries harvesting this species would reduce the overall pressure placed upon it. This would reduce the synergistic impact of exploitation and climate change on the species and might aid in the recovery of the stock in a changing environment.

Polysteganus praeorbitalis is currently managed in both the recreational and commercial linefishery in South Africa by a bag limit of one fish per person per day and a minimum size limit of 400 mm FL (Act no. 18 of 1998, *Government Gazette* no. 18930). The minimum size limit lies just below the observed length at first maturity (405 mm FL) (Mann *et al.* 2005). While this measure is likely to provide some protection to juvenile *P. praeorbitalis,* it provides none to the spawner biomass of this stock and fails to take into account this species' suspected protogynous hermaphroditism. Protecting juveniles is important to preventing growth overfishing where juveniles enter the fishery before they grow large enough to

contribute to the next generation, reducing maximum sustainable yield (Pauly 1983). However, it is also important to protect older fish due to their higher fecundity, spawning success rates and larvae quality (Berkely *et al.* 2004; Birkeland and Dayton 2005), and to prevent negative evolutionary changes caused by the selection against larger, older fish (Pérez-Ruzafa *et al.* 2006). In species which display sequential hermaphroditism, it becomes particularly important to protect the age structure of the population in order to maintain sex ratios. For these reasons, a slot limit (limiting both the maximum and minimum size of fish which may be removed) might provide an appropriate management measure to control negative effects of exploitation on the age and sex structure of this stock (e.g. Gengerke and Moen 1989), thereby protecting genetic diversity. In order to determine the most effective slot limit for this species, further research is needed to: a) determine the age at 50% maturity for this species; b) determine conclusively whether or not this species is a protogynous hermaphrodite, and c) determine the age/length at which this species changes sex if it is a hermaphrodite. With such information, a slot limit which best protects both juvenile and older male fish, while allowing removal of more abundant female fish of intermediate size could be determined.

While the enforcement of a slot limit might have a positive effect on the fishery, such a measure might prove ineffective in the face of continued over-exploitation by both the recreational and commercial linefishery. Considering the collapsed status of this species stock (Mann *et al.* 2005), it is surprising that it has not yet been de-commercialised. The fishery for the closely related seventy-four, *Polysteganus undulosus,* was closed to both recreational and commercial fishers in 1998 (Act no. 18 of 1998, *Government Gazette* no. 18930) due to its stock having collapsed (Chale-Matsau *et al.* 2001). Similarly, the red steenbras, *Petrus rupesterus,* was de-commercialised in 1998 and the fishery closed entirely in 2012 (Notice no. R959 of 2012, *Government Gazette* no. 35903). Both these species share some life-history characteristics with *P. praeorbitalis*. While de-commercialisation should only technically remove fishing pressure by the commercial linefishery, many recreational anglers in South Africa illegally sell their catches to cover the costs of fuel and tackle, and in some cases, to supplement their incomes. Sauer *et al.* (1997) reports that, in the Eastern Cape and Kwazulu-Natal, 58% and 54% respectively, of boat-based recreational fishermen surveyed admitted to selling their catch, and notes that this percentage is probably higher in reality due the reluctance of fishermen to admit to breaking the law. De-commercialising a species therefore has the potential to reduce both commercial and recreational fishing pressure as, by making the sale of the species illegal, the wholesaler and consumers are held accountable as well as the fisher. It is the recommendation of this study that *P. praeorbitalis* be de-commercialised in order to remove some of the fishing pressure

placed upon it by the commercial and recreational linefisheries and to allow the stock to recover enough to a) adapt to the stress placed upon it by climate change (Chapter 2), and b) withstand reduced and better controlled exploitation by the recreational linefishery. Such a measure might prevent this species from declining further and ultimately prevent the full closure of the fishery in the future.

Another measure that is in place to protect this and other linefish species along the South African coast is the demarcation of no-take Marine Protected Areas (MPAs). Attwood *et al.* (1997) advocated the use of no-take MPAs along the South African coastline as effective tools to help recovering stocks and ensure against stock collapse, noting that enforcement of MPAs is easier than enforcing size and bag limits. In theory, MPAs should protect the spawner biomass of species with resident life-history stages, enhancing the fisheries yield of surrounding areas through spill-over of juveniles and adults, and boosting recruitment through the export of eggs, larvae and pre-recruits (Attwood *et al.* 1997; Kleczkowski *et al.* 2008). In South Africa, MPAs have been shown to allow the recovery of local populations of shelf-associated reef fishes with resident life history stages (e.g. Buxton and Smale 1989; Götz *et al.* 2012; Maggs *et al.* 2012), but have been less effective on migrant species (Bennetttt and Attwood 1991; Kerwath *et al.* 2009). Furthermore, Buxton and Smale (1989) observed improvement in sex ratios of the protogynous hermaphrodite sparid species, *Chrysoblephus laticeps* and *C. cristiceps,* within the Tsitsikamma MPA indicating that MPAs can relieve the negative effects of fishing pressure on sex ratios in sequential hermaphrodites such as *P. praeorbitalis*. This was supported by the results of Buxton (1993) and Chan *et al.* (2012). However, Chan *et al.* (2012) caution that, in the case of protogynous hermaphrodites, MPAs are effective in rebuilding and preserving collapsed stocks but may reduce the maximum sustainable yield due to an uneven spatial distribution of larger male fish (due to uneven distribution of fishing effort) resulting in reduced reproductive success outside of the reserves.

Marine Protected Areas have been observed to protect genetic diversity and integrity in some species, acting as sanctuaries for rare alleles and removing fisheries-induced selection pressure (Pérez-Ruzafa *et al.* 2006, von der Heyden 2009). In order to provide maximum protection of genetic diversity for a species, a network of MPAs should be spaced so as to provide connectivity through larval dispersal as well as adult and juvenile movement (von der Heyden 2009; Christie *et al.* 2010). Furthermore, reserves which are self-seeding, or which seed or are seeded by other reserves, should theoretically amplify the positive effects of MPAs on recruitment and yield (Palumbi 2003). Gaines *et al.* (2003) note that ocean currents can create complex patterns of dispersal and structure which do not

necessarily correspond with habitat suitability. It is therefore difficult to determine the importance of an area to the continued survival of a species such as *P. praeorbitalis* which most likely has high larval dispersal but which are restricted to rocky reef habitats. Von der Heyden (2009) noted these difficulties and highlighted the potential for genetic studies to inform the placement of MPAs by providing information on the levels of connectivity between areas and highlighting areas of high genetic diversity.

At present, eight MPAs are demarcated within the current distribution of *P. praeorbitalis* as predicted by the ensemble SDM used in this study (Figure 4.2). However, the preference of this species for deep-water, rocky-reef habitats means that not all of these reserves will provide it with protection. Furthermore, von der Heyden (2009) notes that it is incorrect to assume connectivity between networks of reserves which are separated by areas where genetic breaks have been observed. One such section of coastline highlighted by von der Heyden (2009) lies between Kenton-on-Sea and the southern Transkei coast. Here, genetic breaks have been identified for the brown mussel *Perna perna* (Zardi *et al.* 2007) and the prawn *Upogebia africana* (Teske *et al.* 2006). It is therefore likely that the genetic differentiation between similar localities found in this study may impact on the effectiveness of MPAs in South Africa with regard to *P. praeorbitalis*.

The results of genetic analyses in this study (Chapter 3) provided evidence of genetic differentiation between the Eastern Cape and more northerly localities. This region also displayed a relatively high proportion of private alleles. These results indicate limited connectivity between this locality and those further to the north. It would therefore be incorrect to assume that this region benefits from the demarcation of MPAs along the Transkei and KwaZulu-Natal coastlines. Furthermore, while this area is unlikely to export larvae to any of the other localities because of a lack of documented spawning aggregations and the fact that it lies downstream in the Agulhas Current, these results also indicate that this area might act as a reservoir for rare alleles. Therefore, its importance to the genetic diversity of *P. praeorbitalis* should not be underestimated, and warrants protection.

At present the the Pondoland, Hluleka and Dwesa-Cwebe MPAs provide some protection for this species in the northern Transkei and southern KwaZulu-Natal, while the St Lucia MPA is likely to provide protection to *P. praeorbitalis* during its spawning aggregations in that area. However, because this species does not occur as far south as the Tsitsikamma MPA, there are not enough MPAs towards its southern range edge (with the exception of Bird Island MPA). The demarcation of further MPAs in this area might therefore greatly aid in the

connectivity of the current network of MPAs along the South African coastline with regard to this and similar species.

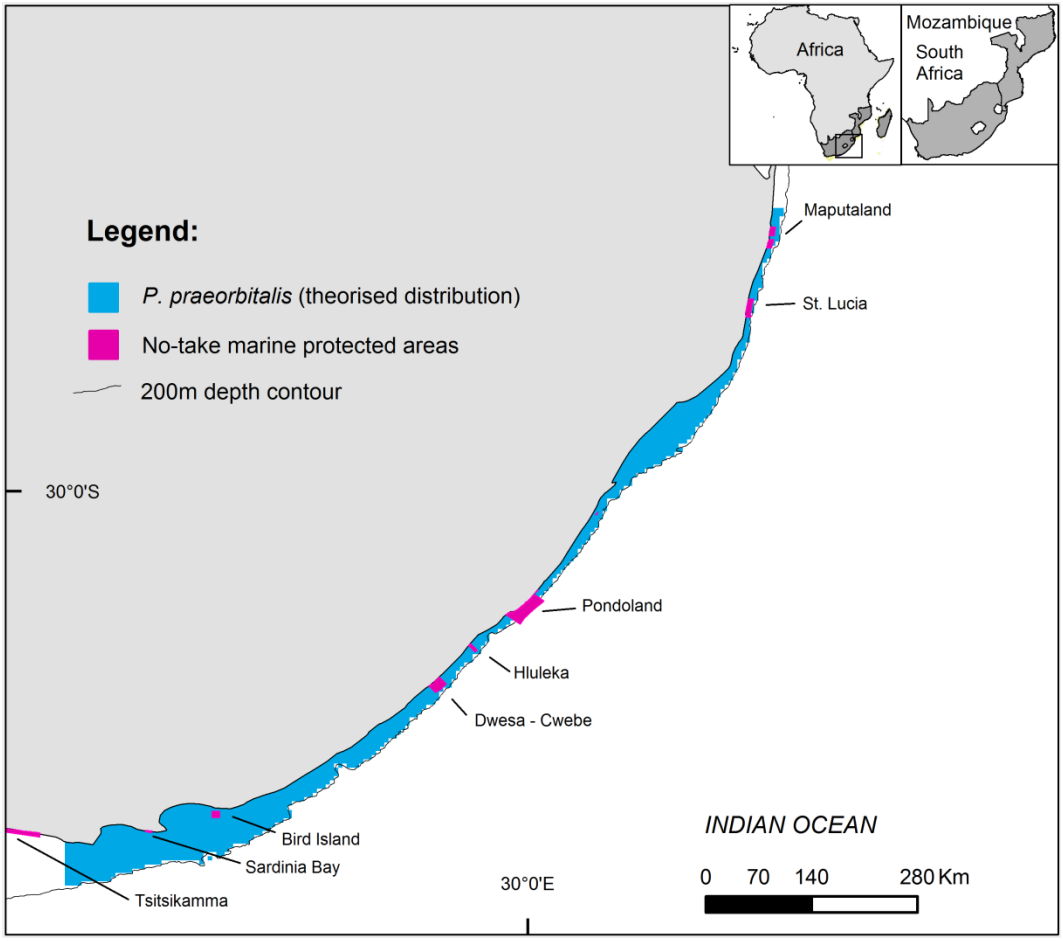

Figure 4.2: Map showing the size and position of no-take marine protected areas (after Sink 2011) in the Agulhas Current system and the distribution of *P. praeorbitalis* as predicted by a PMW ensemble model.

4.5) Opportunities for further research

The difficulties in sampling *P. praeorbitalis* have resulted in a paucity of information on this species, and as such, opportunities exist for further research, making use of new methods which do not require large sample sizes. A more thorough genetic analysis of this species using microsatellite markers would allow full investigation of the level of genetic differentiation between localities and, with further collaborative sampling, might be used to investigate the population dynamics of this species north of the South Africa–Mozambique border. Several aspects of this species' life history remain unconfirmed, including details of its spawning, age at 50% maturity, and the possibility that it is a protogynous hermaphrodite (Garrat *et al.* 1994; Mann *et al* 2005). While evidence suggests that *P. praeorbitalis* might be a protogynous hermaphrodite, this remains unconfirmed. This aspect of this species' life

history is likely to have a significant effect on its vulnerability to fishing and environmental pressures as well as the interpretation of genetic results, and could be confirmed with a relatively small sample size through histological analysis (Sadovy and Shapiro 1987).

Because of the availability of long-term occurrence data on endemic South African linefish species from the NMMLS and ORI/WWF tagging databases, there is an opportunity for a similar study on the potential effects of climate change on endemic linefish species from the warm-temperate region of the Agulhas Current system, similar to that conducted by Albouy *et al.* (2012) in the Mediterranean sea. The Agulhas Current region has the largest proportion South African endemic shelf-associated species (Turpie *et al.* 2000), and might therefore provide an informative picture of the potential effects of climate change on the fisheries and biodiversity of the South African east coast. Such a study should take into account species turnover and allow for the investigation of the potential effects of climate change on species with different life histories in the Agulhas Current system in southern Africa. Given the recovering status of this country's multi-species fishery, such a study might be of great importance in informing its management in a changing environment.

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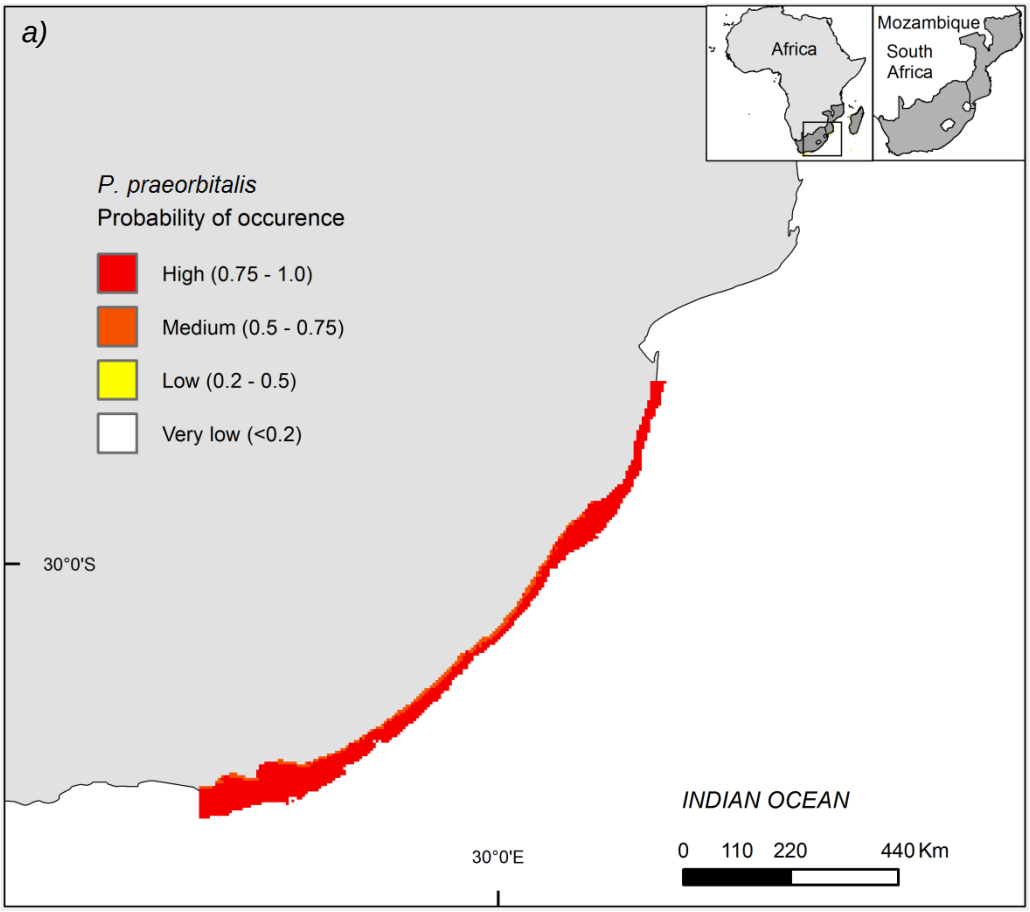
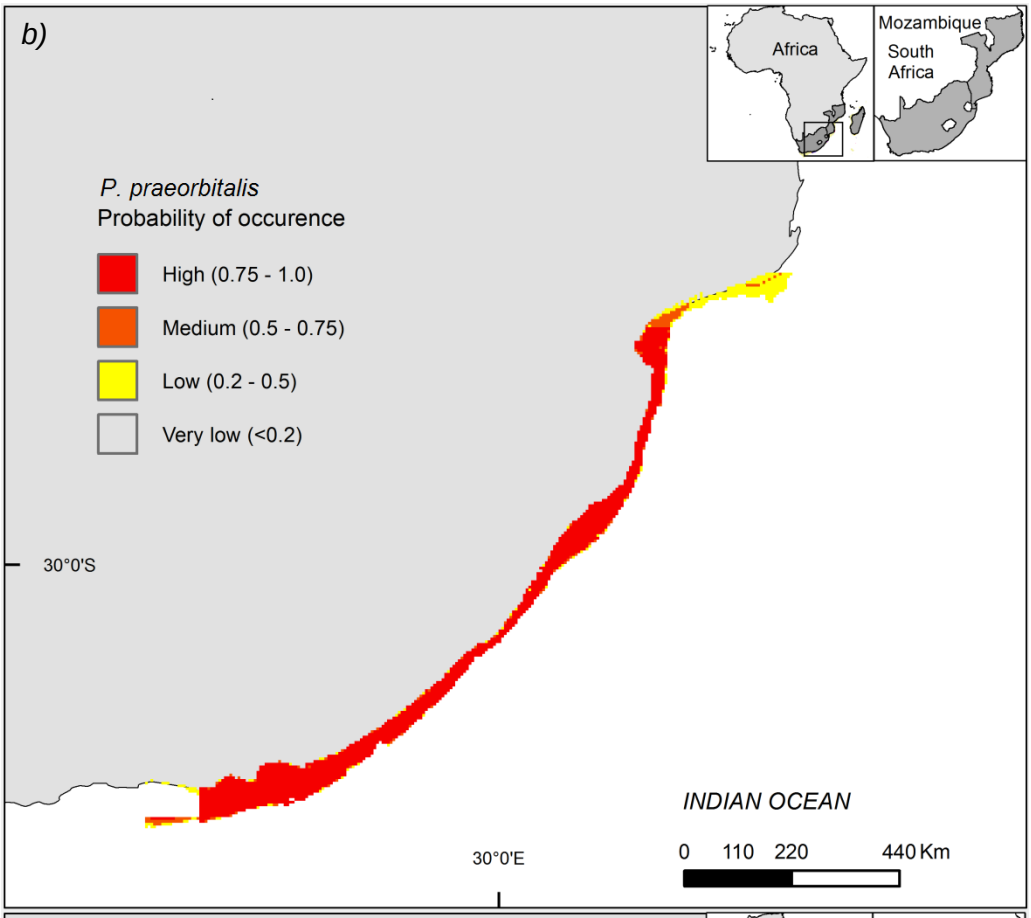
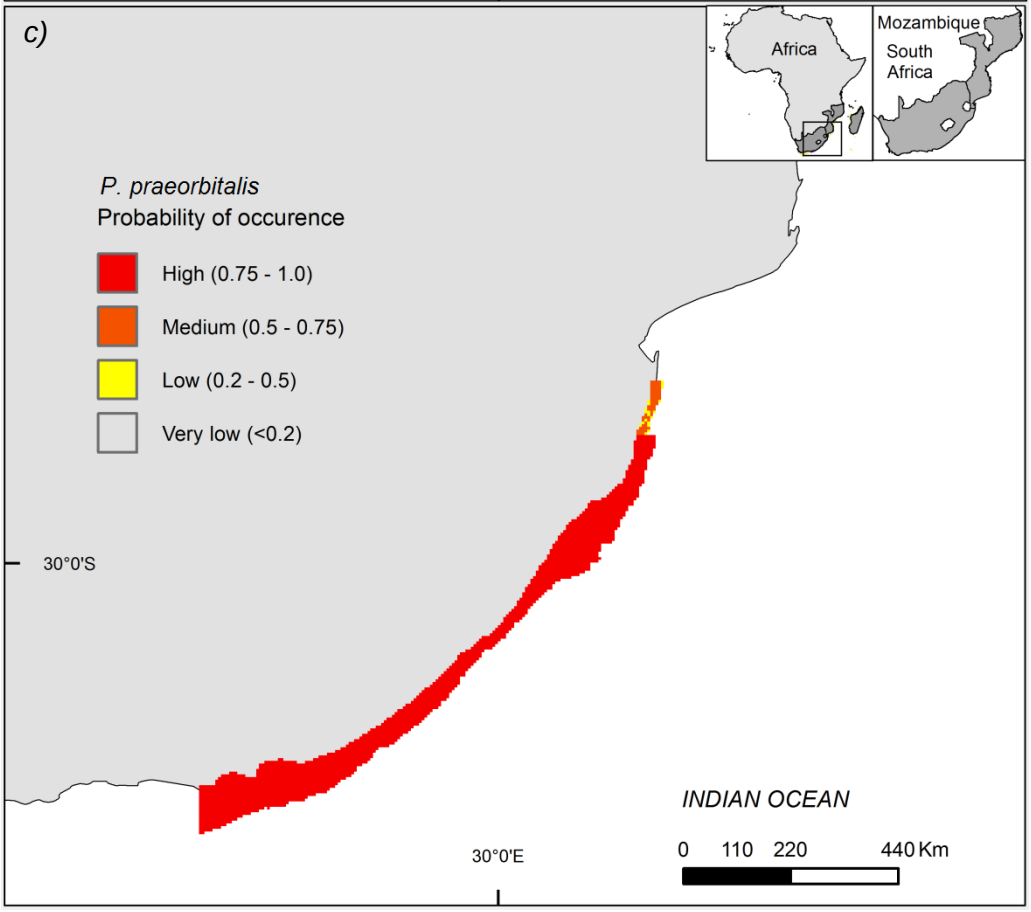
Appendices

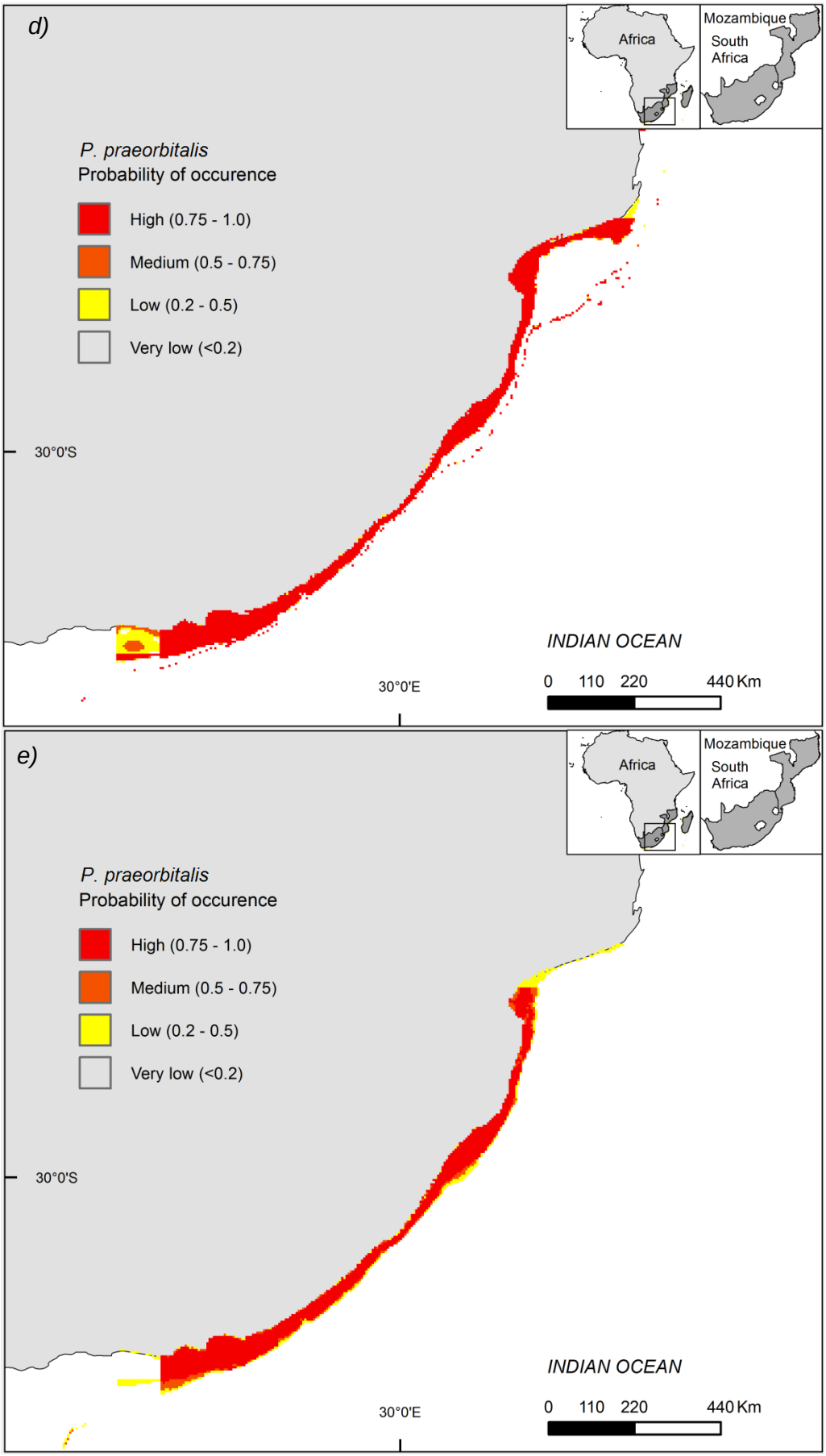
Appendix 1

Probability of occurrence maps of model projections for *P. praeorbitalis* showing current distribution as predicted by seven different models. Models shown are: a) CTA, b) GAM, c) GBM, d) GLM, e) MARS, f) Maxent, and g) RF.

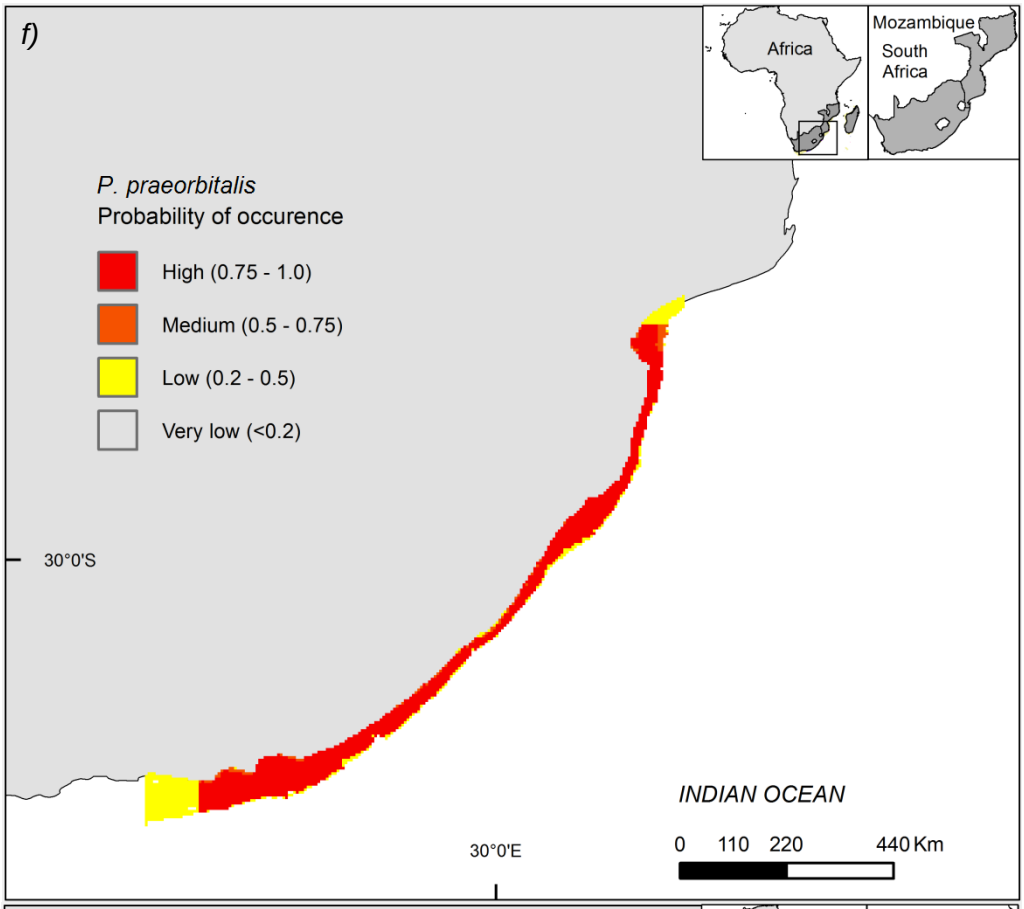



b)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km

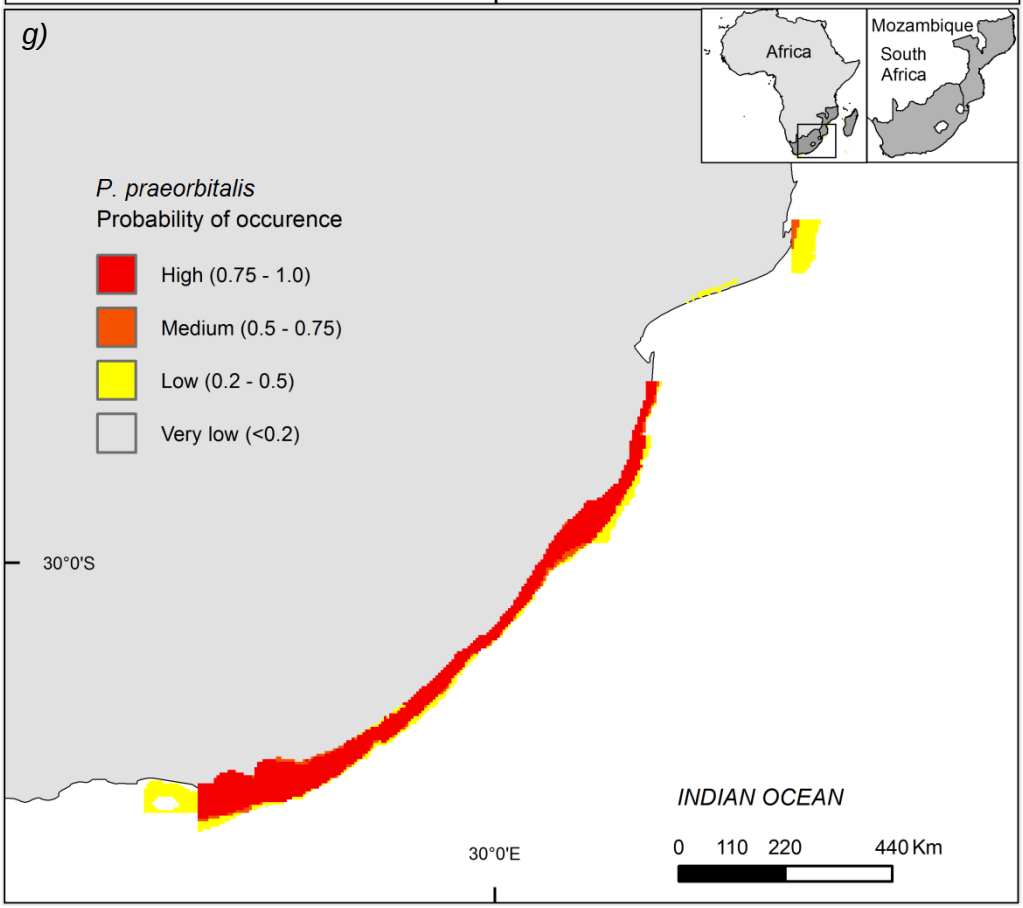

c)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km


d)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km
e)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km

f)

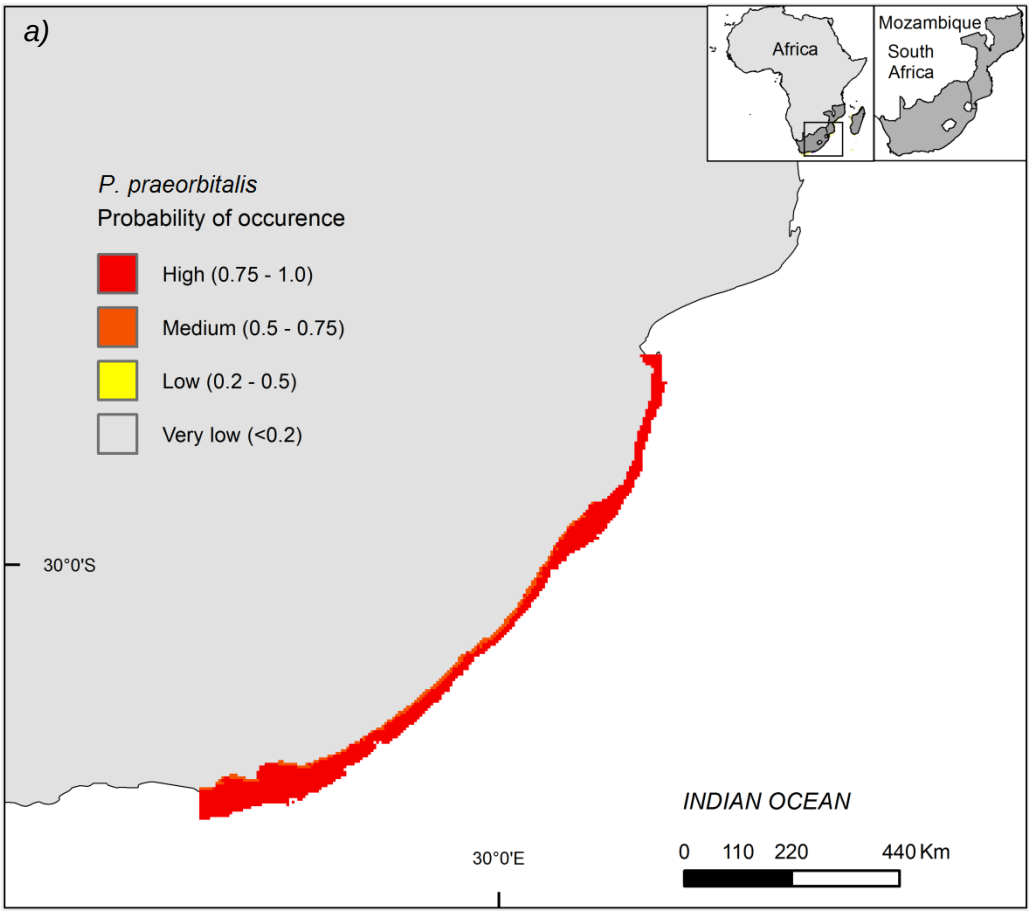

f)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km

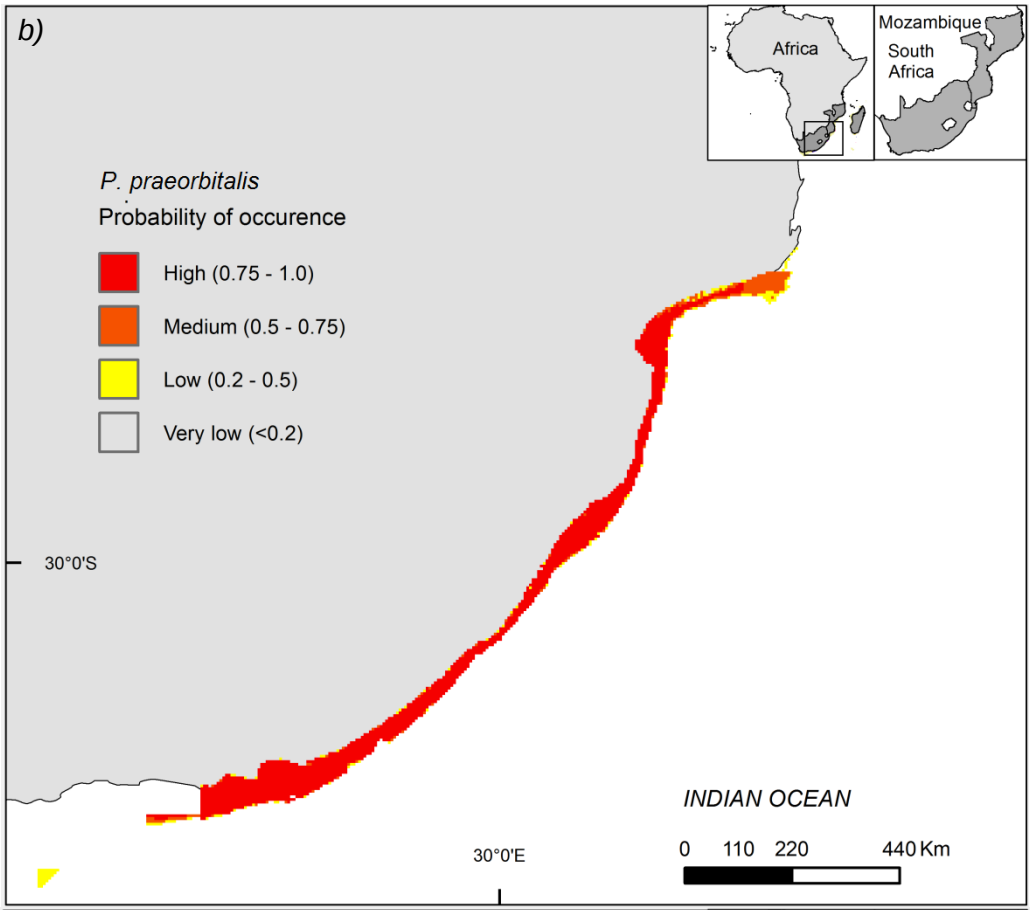
g)

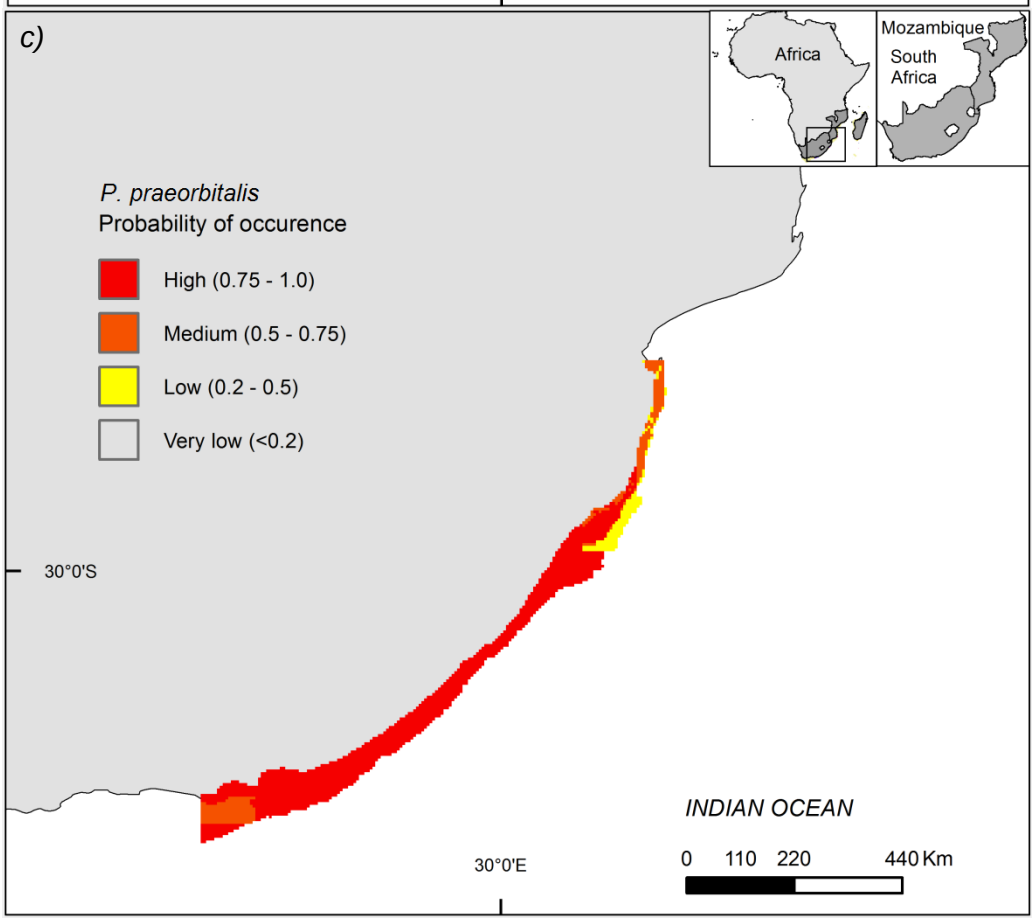

g)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km

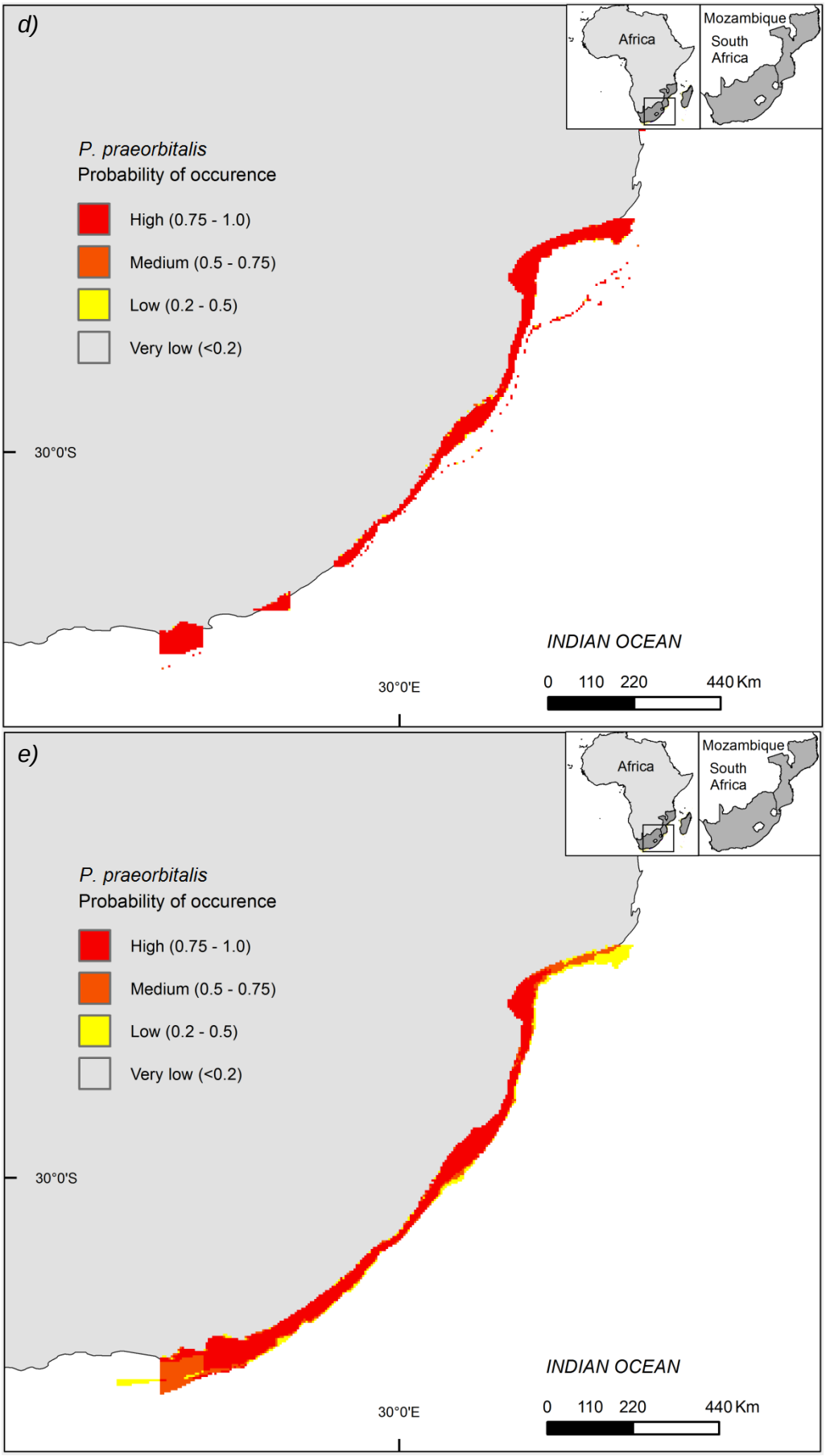
Appendix 2

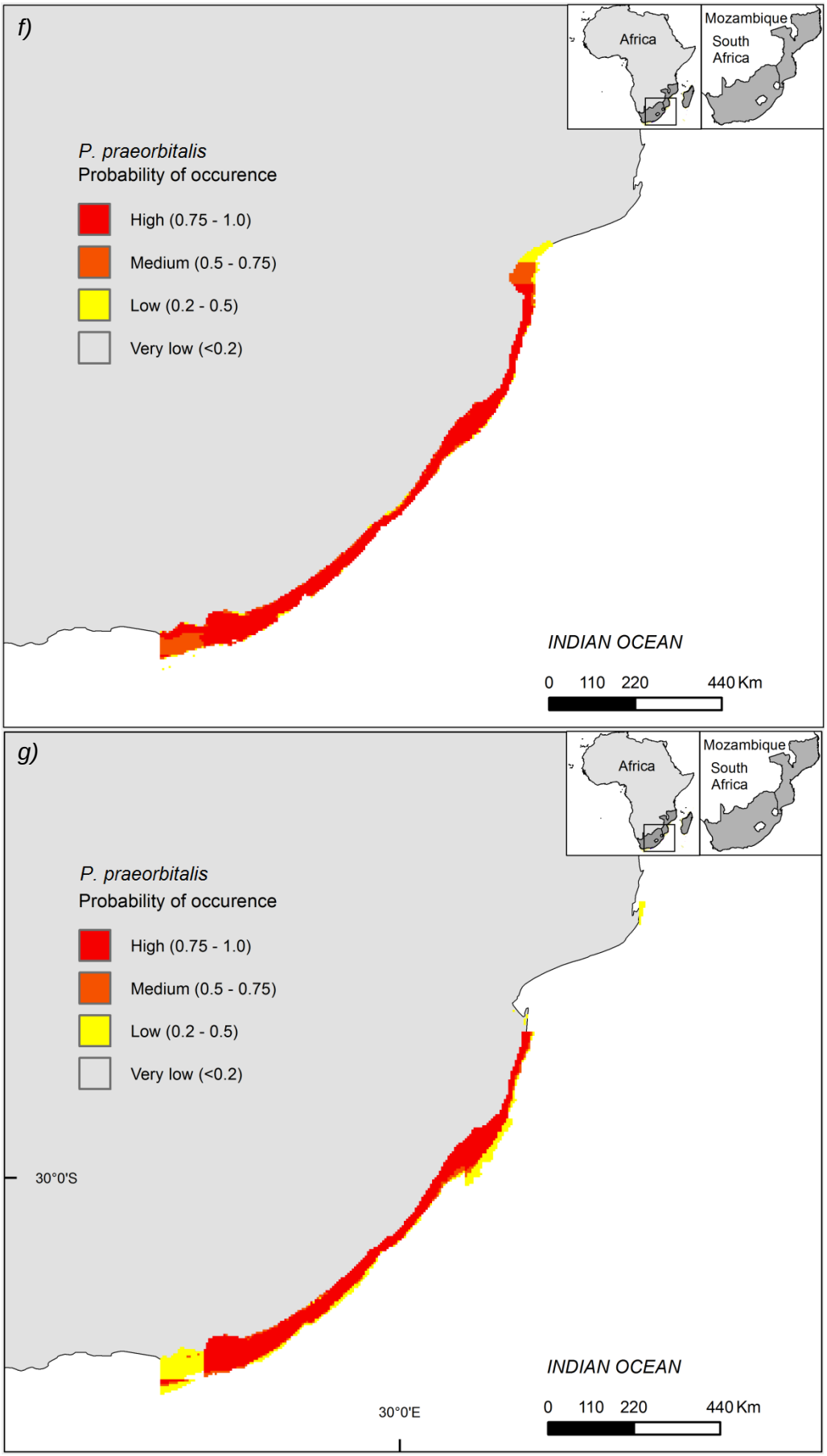
Probability of occurrence maps of model projections for *P. praeorbitalis* showing twenty-year future distribution as predicted by seven different models. Models shown are: a) CTA, b) GAM, c) GBM, d) GLM, e) MARS, f) Maxent, and g) RF.




b)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km

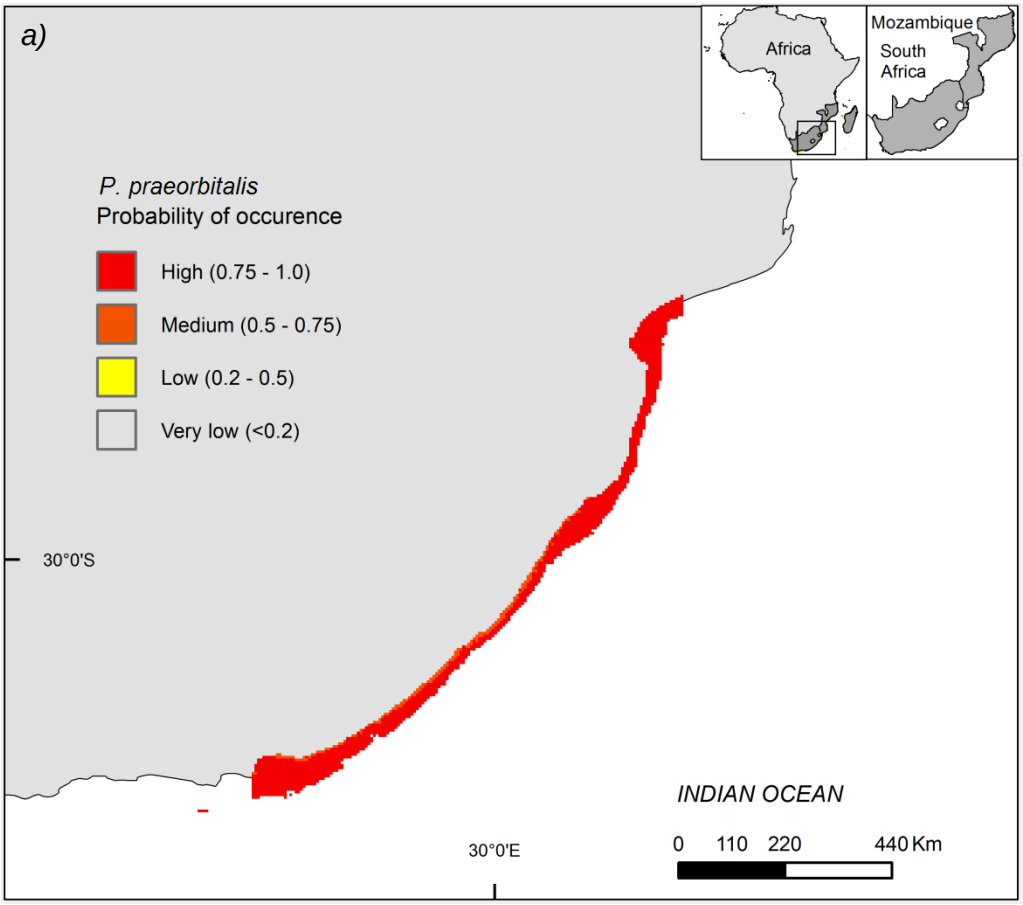

c)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km

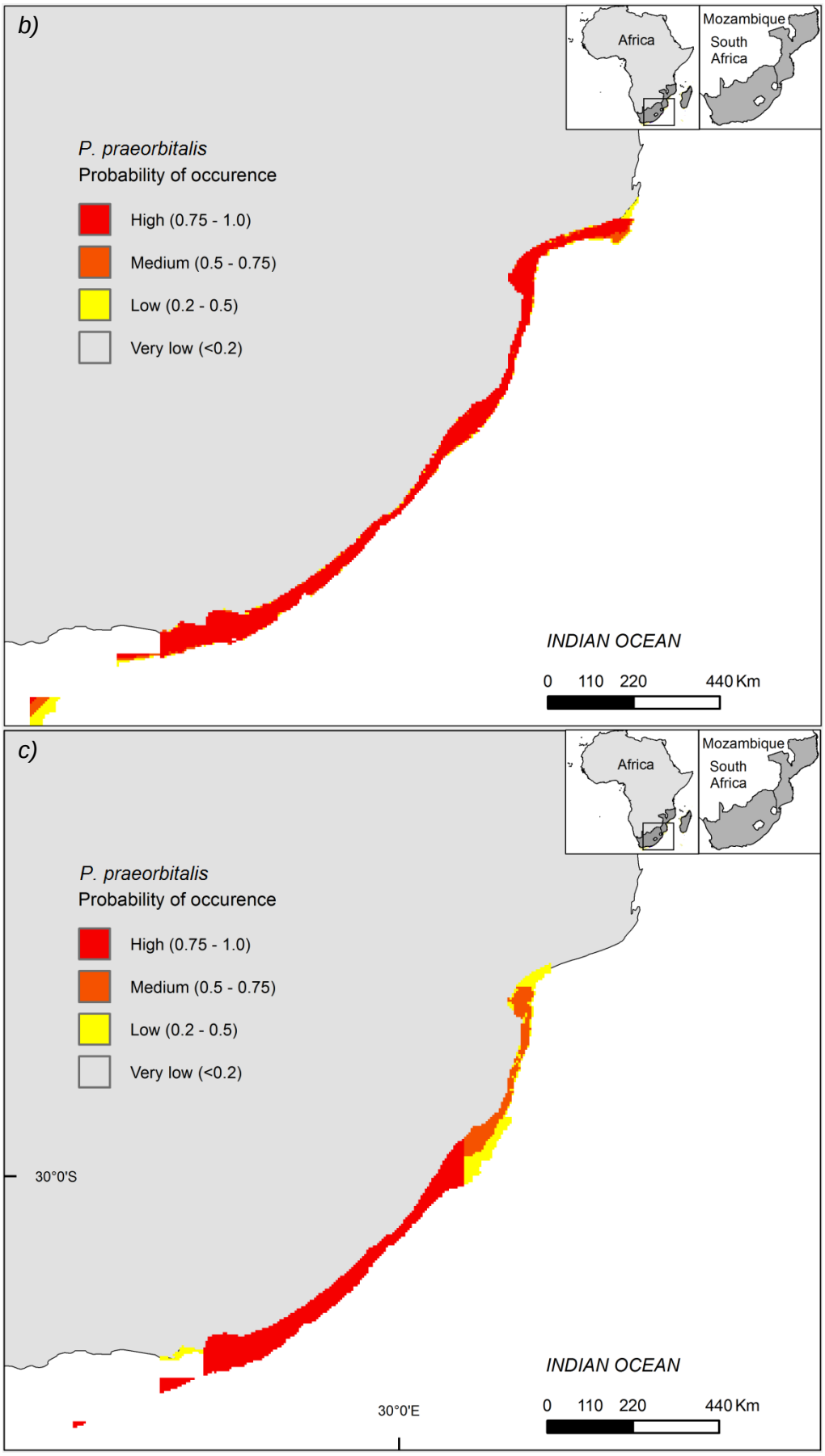

d)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km
e)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km

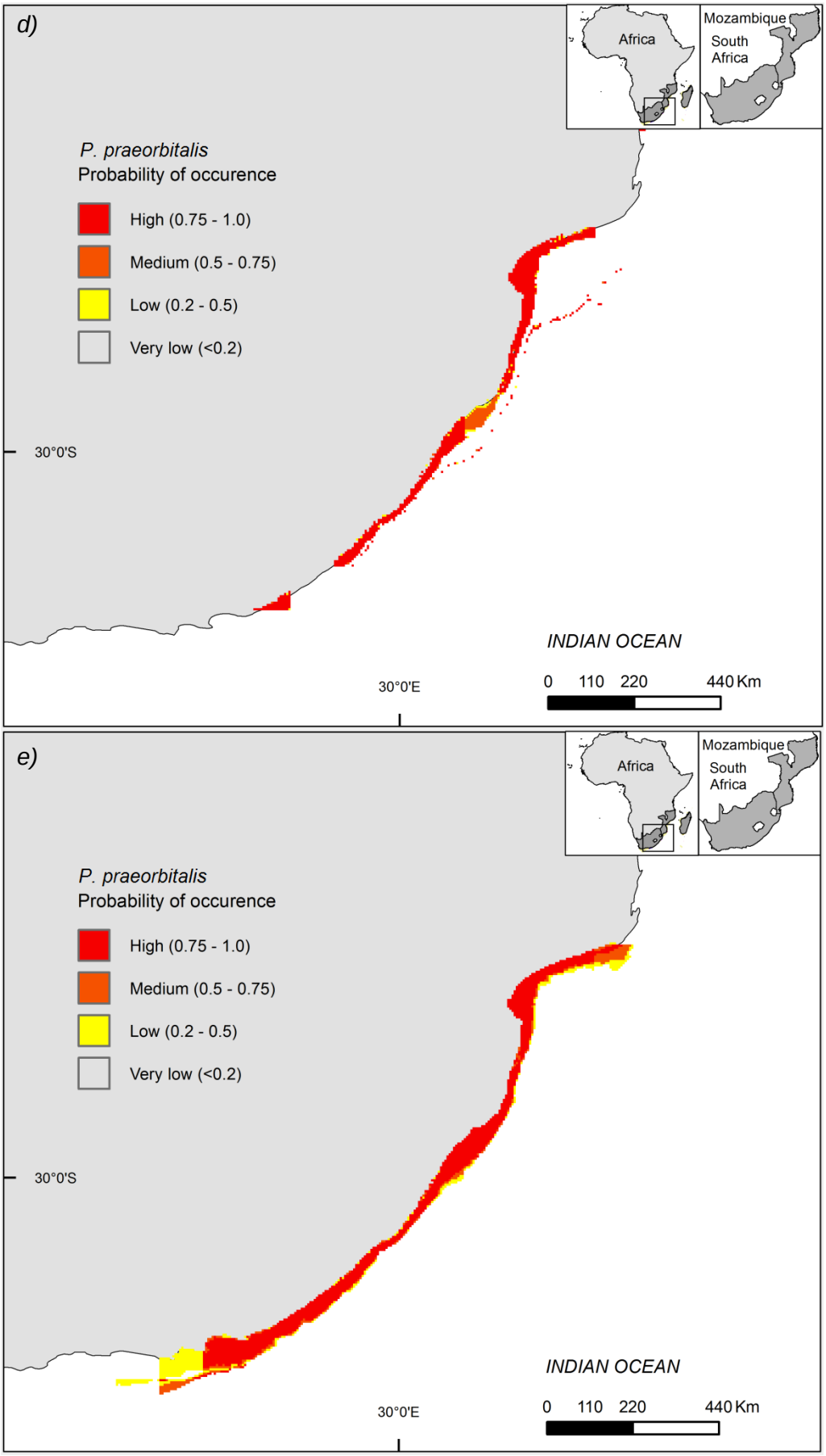

f)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
INDIAN OCEAN
0 110 220 440 Km
g)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km

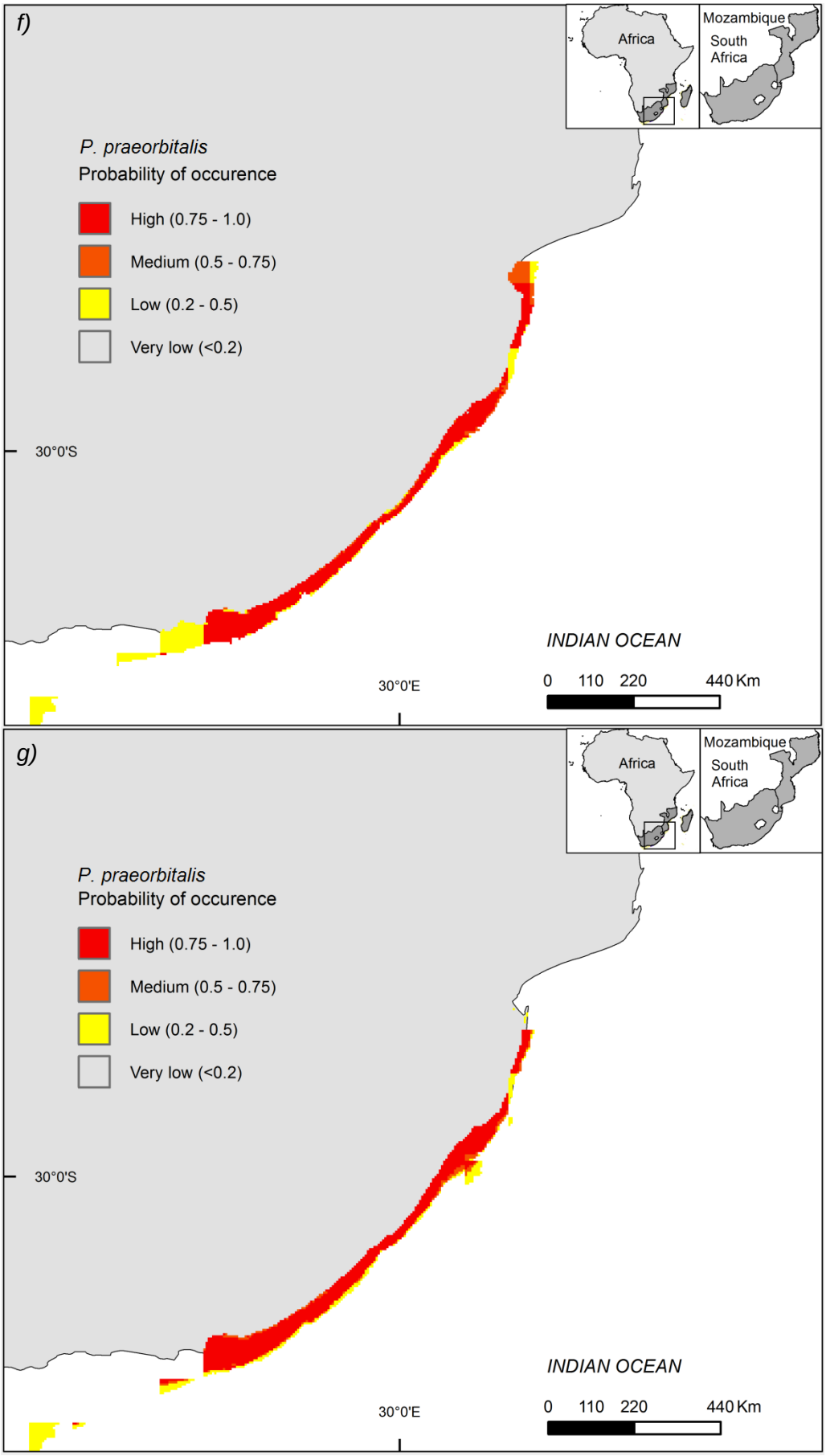
Appendix 3

Probability of occurrence maps of model projections for *P. praeorbitalis* showing 30-year future distribution as predicted by seven different models. Models shown are: a) CTA, b) GAM, c) GBM, d) GLM, e) MARS, f) Maxent, and g) RF.




b)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
INDIAN OCEAN
0 110 220 440 Km
c)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km


d)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km
e)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km


f)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km
g)
Africa
Mozambique
South Africa
P. praeorbitalis
Probability of occurence
High (0.75 - 1.0)
Medium (0.5 - 0.75)
Low (0.2 - 0.5)
Very low (<0.2)
30°0'S
INDIAN OCEAN
30°0'E
0 110 220 440 Km