

**SHORT-TERM CHANGES TO THE LIFE HISTORY OF
SHAD, *POMATOMUS SALTATRIX* (PERCIFORMES:
POMATOMIDAE), IN SOUTHERN ANGOLA**

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Roy Steven John Bealey

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ABSTRACT

A general lack of biological information is hampering the effective management of Angola's fisheries. While this lack of information is largely a result of the country's extended civil war that ended in 2002, the subsequent rapid expansion of fisheries is most likely impacting fish abundance and influencing the biology of this regions fishes. Besides the influence of fisheries, the southern Angolan coastal region is considered to be a climate change "hotspot" due to rapidly ($>0.8^{\circ}\text{C}/\text{decade}$) increasing water temperatures. These changes are thought to drive further changes to the biology of fishes. It is therefore critical to provide baseline biological information and to identify the impacts of exploitation and warming on the biology of southern Angolan fishes.

Pomatomus saltatrix is a warm-temperate marine fish species that forms an important component of fisheries throughout its broad distribution. *P. saltatrix* is a migratory predator that displays variable growth and maturity schedules. Typically it is heavily targeted in a range of coastal fisheries of Angola and is therefore an ideal candidate to study the biological impacts of exploitation and climate change. The aim of this study was to provide the first description of *P. saltatrix* biology in Angola and examine recent changes of the species biological parameters in an attempt to uncouple fishery driven from climate driven changes.

Samples of *P. saltatrix* were collected monthly using standardised biological methods from June 2005 to December 2006 (period 1) and from June 2012 to February 2013 (period 2). The average (508mm – 1st period, 462mm – 2nd period) and maximum (760mm – 1st period, 746mm – 2nd period) size of *P. saltatrix* was smaller during the second period to suggest selective overharvesting of large individuals by developing fisheries.

Angolan *P. saltatrix* grew very rapidly in their first year and thereafter, relatively slowly when compared to other populations globally. However, fish grew faster ($\omega = 103$ – 1st period, $\omega = 124$ – 2nd period), matured at a larger size (303mm - 1st period, 336mm - 2nd period) and younger age (0.83 years - 1st period, 0.67 years – 2nd period) during the second period. Peaks in reproductive activity remained similar (November) during both periods but a

temperature anomaly appears to have influenced spawning during period 2. *Sardinella aurita* was the dominant prey during both periods but a greater dependence upon *mugilids* was observed during the second period.

Although the changes in life history were not statistically significant, the faster growth observed during period two could be attributed to both increasing temperature and/or exploitation. Fishes generally grow faster, mature smaller and attain a smaller maximum size in warmer temperatures. Fisheries targeting small and large specimens of a species (as observed in this study) largely have the same impacts as ocean warming. With rapidly increasing water temperatures and exploitation rates, faster growth and earlier maturation of *P. saltatrix* populations will mitigate the impacts of exploitation in the short-term. However, the sustainability of Angola's *P. saltatrix* stock is questionable as phenotypic adaptation will have a limited thermal scope and overexploitation will, like in all fisheries, negatively influence recruitment. Ultimately, strict monitoring, regulation and control will be necessary to ensure the sustainability of the *P. saltatrix* resource in Angola as it continues to face increasing anthropogenic and environmental pressures. Management guidelines and future research suggestions are therefore outlined with reference to the results of analyses conducted during this study.

Key words: *P. saltatrix*; marine fisheries management; climate change, ecology

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CHAPTER 1

Introduction

More than one billion people survive on less than US\$1 per day and 840 million people are classified as undernourished (FAO 2005). The caloric intake of many of these is met through the consumption of fish, which provides an important source of dietary protein, micro-nutrients and essential fatty acids in their diets (FAO 2005). In 1990 over 120 million people, 95% of whom were from developing countries, were involved in activities that are directly related to the capture, processing and sale of fish (Allison and Ellis 2001). The coastal oceans (areas shallower than 200m) generate biological production that supports over 90% of global fish catches (Pauly et al. 2002) and are estimated to provide over US\$12.5 trillion worth of ecosystem services annually, which is more than average estimated services provided per hectare by the terrestrial biome (Costanza et al. 1997). Although coastal marine regions are among the most ecologically and socio-economically important ecosystems on earth they are heavily exploited by competing subsistence, small-scale, artisanal, recreational and commercial fisheries and are significant for the livelihoods of coastal communities (Béné 2003, Neiland and Béné 2004, Duarte et al. 2005, FAO 2005, Stobutzki et al. 2006, Harley et al. 2006, Andrew et al. 2007, Glavovic and Boonzaier 2007, Cinner et al. 2008, Sowman and Cardoso 2010). With continued human population expansion in coastal areas, there is an increased demand for fish resources while the sustainability of these resources is questionable. This trend has been recognised in West Africa and has prompted the development of a Sustainable Fisheries Livelihood Programme (SFLP), which prioritizes sustainable fisheries development as a modern poverty alleviation tool (Neiland and Béné 2004, FAO 2005).

Although legal and institutional mechanisms recognise and protect small-scale fishers in Angola (Sowman and Cardoso 2010), fishers from poorer households are more likely to be retained in “poverty traps”, as they lack the resource capacity to overcome the impacts of declining catches by pursuing alternative livelihoods (Cinner et al. 2008). Therefore, stock

restoration is widely regarded as a requirement to regain the sustainability of fisheries that support poor coastal dwellers. However, a prerequisite for this is an understanding of the composition and abundance of unexploited fish stocks relative to contemporary ones (Myers and Worm 2003). A lack of knowledge about pristine stocks and their biological parameters is referred to as the “missing baseline” and the restoration of fish stocks is frequently complicated by this lack of information (Myers and Worm 2003).

The biology of a species determines its vulnerability to changes in its environment (within which fisheries are included), the productivity of its populations and the resultant socio-economic benefits that may be accrued from its harvest. While an understanding of the biological parameters of pristine stocks is important to examine how species are reacting to exploitation, fisheries management strategies should largely be based on information of the present and not historical biological characteristics of the species (Trippel 1993, Smith et al. 1999, Berkes et al. 2001, Gerber et al. 2002, Potts et al. 2008, 2010a, King 2013, Smallwood et al. 2013). Furthermore, consistent monitoring of abundance and biological parameters to analyse trends can also reflect the effectiveness of management methods (Trippel 1995).

Angola is a large West African country with approximately 1650 km of coastline which supports a dynamic and highly productive marine ecosystem (John et al. 2001, Duarte et al. 2005, Veitch et al. 2006). Although the fishery sector only contributes 3% to the Angolan GDP and employs only 4% of the labour force, it provides an important share of the staple protein sold in the country and contributes significantly to the livelihoods of thousands of coastal dwellers (Duarte et al. 2005). Angolan artisanal fisheries contribute approximately 20% of captured fish by mass, with a value of approximately US\$70 million per annum (Duarte et al. 2005). Subsistence fishing and the trade of dried fish began as early as 1884 in Angola, with subsistence fishers being legally recognised and defined as those fishers that generally capture fishes for consumption by their families, but may occasionally sell surplus catches (Duarte et al. 2005). As in many developing nations subsistence fishing provides a vital source of nutrition and livelihood security in Angola and the reliance upon coastal fisheries is exacerbated by the limited agricultural opportunities in the coastal desert of southern Angola. With continued population expansion in the coastal regions of Angola, the

demand for fish continues to increase, promoting the expansion of fisheries in both the artisanal and subsistence sectors.

The recreational fishery sector is also expanding in southern Angola (Potts et al. 2009). This fishery and the activities associated with it provide employment opportunities and contribute to Angola's economy. For example, a relatively small recreational fishery in southern Angola contributed US\$ 344 364 to the national economy annually with US\$ 1007 and US\$ 243 spent per harvested fish and kilogram respectively (Potts et al. 2009). The contribution to the local economy of US\$ 151 685 was particularly significant when considering the lack of alternative formal employment opportunities available in this desert region (Potts et al. 2009). There are at least three tourist-based recreational fishing lodges in Angola and the popularity of recreational fishing amongst locals is also increasing (Potts et al. 2009, Chapter 3).

The socio-political history of Angola includes a 14 year anti-colonial war, which ended in 1975. This was followed by a 27 year long civil war that ravaged the nations' infrastructure, agricultural and human capital (Duarte et al. 2005). Following independence, most Europeans fled the country abandoning productive infrastructure and fishing fleets, with their exodus representing a loss of skilled labour that previously dominated the fishing industry and provided much needed technical expertise (Duarte et al. 2005). A rehabilitation of the fishing industry occurred following changes to economic policy in the mid-1980s. These new policies spurred the departure of opportunistic foreign fleets from the region in the beginning of the 1990s and allowed the Angolan government to begin actively stimulating the local fishing sector (Duarte et al. 2005). As with many wars, the protracted period of socio-economic instability in southern Angola had the ironic effect of protecting the regions' fish stocks (Duarte et al. 2005). However, with the recent expansion of fisheries, which is in part aided by governmental policies, the anthropogenic threat to the regions' fish stocks is rapidly increasing.

Because fisheries provide such vital nutritional and financial support to Angola's coastal communities that lack alternative sources of livelihood security, the regions' fish stocks require effective protection so that they may continue to provide future benefits despite the

increasing exploitation pressures arising from competition between the various expanding fishery sectors. With continued population expansion in coastal areas and post war development focussed in major cities, the demand for fish in this country is set to continue increasing for the foreseeable future. Angola's artisanal fisheries capture a variety of fish species and are dominated by a hook and line sector but beach and pelagic seine nets, gill nets, lift nets and pole fishing methods are also used. The greatest catches are obtained in southern provinces and anecdotal evidence suggests that fishing effort is rapidly increasing in both legal and illegal fishing sectors (Duarte et al. 2005). Total catches in the province of Namibe increased from 3 512 to 27 364 tons from 1996 to 2004 (Duarte et al. 2005) and with ever increasing fishing effort, this region provides an ideal location to investigate and monitor the impacts of exploitation on fish populations.

Besides depleting fish stocks, fisheries also induce a variety of biological adaptations in fishes (Trippel 1995, Rochet 1998, Lorenzen and Enberg 2002, Lorenzen 2008, Eikeset et al. 2013). Reductions in fish abundance generally promote growth and survival rates through reducing intraspecific competition for food, through a phenomenon known as "density-dependent growth" (Trippel 1995, Lorenzen and Enberg 2002, Lorenzen 2008). In addition to indirectly influencing growth rates, fisheries have multiple influences upon other life history parameters, including those related to maturation rates, and the direction of biological trends can reverse over short- and long-term exploitation to have a variety of either beneficial or detrimental influences upon a stock's productivity and future evolutionary fitness (Trippel 1995, Jennings et al. 1998, Rochet 1998, Eikeset et al. 2013).

Expanding fisheries are not the only factor potentially influencing fish stocks in southern Angola. The impact of climate change on fish and fisheries is set to become one of Africa's greatest challenges. Allison et al. (2009) in their global review suggested that Angola's economy was the most vulnerable to the impacts of climate change on fisheries. The study suggested that vulnerable countries will suffer increased economic hardship and missed opportunities for development if they do not implement adaptive fishery strategies (Allison et al. 2009).

Climate change driven biological alterations to fish species life histories remain largely uncertain due to the complexity of marine environments (Allison et al. 2009), but they may either improve or reduce a stock's capacity to support fisheries. As ectotherms, changing temperature regimes are likely to have great impacts upon fishes; besides influencing physiological aspects such as metabolism and respiration, changing temperatures will influence all aspects of the life history of fishes, including growth (Trippel 1995, Angilletta et al. 2004), longevity (Angilletta et al. 2004) and reproduction (Trippel 1993, 1995, Angilletta et al. 2004, Potts et al. in press). Thermal reaction norms for ectothermic organisms include faster growth rates and maturity schedules in warmer temperatures (Angilletta et al. 2004). These impacts will have major consequences for the productivity and sustainability of fisheries.

Besides the effects of temperature, there will be several other climate driven variable drivers of change in fishes. Ocean acidification will influence the toxicity of various chemicals while current dynamics, metabolic costs associated with salinity, oxygen availability and planktonic productivity are also likely to change in marine environments (Wuenschel et al. 2005). Although the effects of these environmental changes have not yet been fully explored it is possible that these changes may have greater influences upon marine biota than the direct effects of increasing temperatures (Harley et al. 2006, Frusher et al. 2013). For instance the effects of changing ocean circulation may have dramatic impacts on species with pelagic larvae and may alter entire marine community structures (Harley et al. 2006).

In order to effectively conserve marine resources in face of climate change, improvements to existing predictive frameworks are required (McFarlane et al. 2000, Harley et al. 2006, Frusher et al. 2013, Hobday and Pecl in press). To this end, there has been an increase in the number of studies trying to obtain an understanding of the mechanistic links between warming and biological changes (Harley et al. 2006, Frusher et al. 2013). However, because the assessment of climate change impacts and the development of predictive methods are still in their infancy, the identification of "hotspots" where the climate is changing at an above average rate provides an alternative, interim approach as these regions may act as natural laboratories or focal points for expanding our knowledge (Hobday and Pecl in press). Biological responses in these "hotspots" may provide predictive information about the

expected consequences of climate change in regions that are warming at slower rates (Frusher et al. 2013).

Southern Angola has been identified as a global hotspot for climate change with sea temperatures increasing by $0.8^{\circ}\text{C}.\text{decade}^{-1}$ faster than the global mean ($0.07^{\circ}\text{C}.\text{decade}^{-1}$) since 1982, and particularly so in nearshore environments (Munnik 2012, Potts et al. submitted). As such, monitoring the response of marine organisms to climate effects in this region will expand knowledge of the influence of ocean warming on the biology of fishes and may allow inference of expected changes elsewhere. This information will provide opportunities for a precautionary, and scientifically guided fisheries management approach to promote sustainability of the world's fisheries (Frusher et al. 2013).

Pomatomus saltatrix is the only extant species in the family *Pomatomidae* (Deshpande and Dockum 2013). It has a cosmopolitan distribution and is found in all temperate coastal waters, except for those of the Eastern Pacific Ocean (Harding and Mann 2001). It is known by a variety of common names (FAO 2014), including “enchova” in Brazil (Haimovici and Krug 1996) and Angola, “bluefish” in America (Callihan et al. 2008), “shad” or “elf” in South Africa (Govender 1996), and “tailor” in Australia (Smith et al. 2013). *P. saltatrix* is a voracious predator which readily takes baits and artificial lures and its high quality flesh makes it a popular target in recreational, small-scale and artisanal fisheries that use a wide variety of active and passive gears (Wilk 1977, Govender 1996, Ceyhan et al. 2007, Smith et al. 2013, FAO 2014). *P. saltatrix* inhabits depths from 0-200m and is therefore targeted in both shore and vessel-based fisheries (FAO 2014).

Generally, *P. saltatrix* is a fast growing species that has a maximum reported size of 14.4kg (IGFA 2014) and a maximum age of 14 years (Wood 2013). However, the species maximum recorded size and age varies both temporally and regionally (Van der Elst 1976, Govender 1996, Haimovici and Krug 1996, Juanes et al. 1996, Ceyhan et al. 2007, Robillard et al. 2008, Smallwood et al. 2013, Smith et al. 2013). *P. saltatrix* displays considerable plasticity in its life history characteristics with the number of annual reproductive peaks, adult growth

patterns, maximum age and reproductive parameters showing variability between populations (Juanes et al. 1996).

Seasonal migrations of adult *P. saltatrix* are extensive, with tagged individuals having been recorded travelling distances in excess of 1300 km in north America (Lund and Maltezos 1970) and 1760 km in South Africa (Hedger et al. 2010). These return migrations are generally related to spawning events. *P. saltatrix* larvae, that are planktonic for up to 30 days in some regions, rely on cross-shelf transport to nursery areas (Graves 1998, Hare and Cowen 1996, Kendall and Walford 1979). Juvenile *P. saltatrix* overwinter in specific regions and ontogenetic changes in habitat use have been noted in western Australia (Smith et al. 2013) and America (Salerno et al. 2001) with the survival of juveniles in America being dependent on abundance (Wiedenmann and Essington 2006). Predictable spawning migrations increase the susceptibility of adults to fisheries as they are targeted both along their migratory routes, and at spawning sites, with this trend believed to have encouraged hyper stability in some fisheries (Wilk 1977, Govender 1996, Hoyle et al. 2000, Smith et al. 2013).

The nearshore habits, valued flesh and fighting ability of *P. saltatrix* make it an important target in shore-based recreational fisheries. *P. saltatrix* contributed 24.1% of the recreational catch along the east coast of Australia (Gartside et al. 1999) while in the South African shore-angling recreational fishery it was the dominant species caught by mass (Brouwer et al. 1997) and number (Govender 1996). In South Africa's KwaZulu-Natal Province, *P. saltatrix* constituted between 28% and 80% of catches recorded by recreational shore-based anglers (Maggs et al. 2012). *P. saltatrix* was also the dominant species by weight in North American recreational fisheries (Wilk 1977). Between 1981 and 2012 a total of 4700 tons of *P. saltatrix* were captured along the American East coast (Murphy 2013) and recreational anglers were estimated to have captured 81% of the 660 689 kilograms of *P. saltatrix* captured annually (FWRI 2010). In a tagging study along the west coast of Australia conducted by Young et al. (1999), recreational fishers caught 98.9% of recaptured *P. saltatrix*. Similarly in southern Angola *P. saltatrix* is the most frequently captured of three target species in the developing recreational fishery that caught 27 975kg of fish in 2006 (Potts et al. 2009). Unfortunately, the catches of this species have declined in recreational fisheries globally. In Western Australia anecdotal evidence suggests that there was a substantial abundance decline during

the 1980s and 1990s, with an 80% decline in recreational boat catches occurring from 1996/97 to 2005/06 (Smith et al. 2013). Similar declines have been noted in other regions (Wilk 1977, Govender 1996), suggesting that fisheries have already had large impacts on other *P. saltatrix* stocks that now require rebuilding.

Thesis outline

The overall aims of this study were to provide a description of the biology of *P. saltatrix* in southern Angola, to investigate biological changes seen in the stock between two study periods (period 1 = 2005-2006 and period 2 = 2012-2013) and to gain an understanding of the impact of expanding fisheries and ocean warming on the life history of the species. This information was used to make recommendations for the regional management of this species.

To achieve these aims, this thesis is divided into three data oriented chapters:

Chapter two describes the study area and provides a description of the changes observed in both temperature and fisheries pressure in southern Angola since 2005.

Chapter three describes the diet of *P. saltatrix* in southern Angola and investigates dietary shifts between the two study periods. The results are discussed in the context of changing predator and prey interactions driven by both climate variation and the impacts of fisheries.

Chapter four provides a comparative age and growth analysis of *P. saltatrix* during the two experimental periods in southern Angola. This information is compared with global populations to gain an understanding of the effects of temperature and exploitation pressures upon the growth of the species.

Chapter five uses a variety of analyses to provide a detailed description of the reproductive style, gametogenesis and reproductive seasonality of *P. saltatrix* in Angola while investigating how the reproductive cycle relates to environmental cues. The results are

compared with those of other populations to gain an understanding of how climate change and fisheries can affect the patterns of maturation and reproductive seasonality of the species.

This thesis culminates in Chapter six which summarises the findings from previous chapters to describe the life history of Angolan *P. saltatrix*. The observed and expected future impacts of fisheries and climate change on *P. saltatrix* in the region are then discussed with research and monitoring priorities and an appropriate management strategy for southern Angola's *P. saltatrix* stock being described.

CHAPTER 2

Study area and general methods

Study area

This study was conducted along a 23 kilometre stretch of coastline located between the towns of Tombua (15° 48' S, 11° 50' E) and Namibe (15° 11' S, 12° 09' E) in southern Angola (Figure 2.1). The sample region is located in the northern extent of the Namib Desert and due to a general lack of precipitation only contains one functional estuary, the Cunene, which has been categorised as a river mouth type estuary (Simmons et al. 1993). Marine conditions in southern Angola are highly influenced by interactions of the northward flowing Benguela and southward flowing Angola currents (Figure 2.1), with their convergence in this region creating the Angola Benguela Frontal Zone (ABFZ) (Shannon et al. 1987, Meeuwis and Lutjeharms 1990, Veitch et al. 2006).

The ABFZ is a permanent, yet mobile, frontal system with consistently steep sea surface temperature (SST) gradients, that extend up to 250 nautical miles offshore (Meeuwis and Lutjeharms 1990, Veitch et al. 2006, Hutchings et al. 2009). On average the ABFZ is located at around 16°S, but its position oscillates seasonally by approximately three degrees of latitude (Meeuwis and Lutjeharms 1990, Veitch et al. 2006, Von-Bodungen et al. 2008). The ABFZ shifts northwards in autumn and winter with strengthening of the Benguela Current but is located farthest south, extends farthest offshore and is most clearly defined during austral summer months (Meeuwis and Lutjeharms 1990, Veitch et al. 2006). Unsurprisingly the latitudinal fluctuations of the ABFZ are reflected by a seasonal dominance of local currents which in turn, influence the composition, spawning and abundance of species in the study area. Contrasting environmental parameters across the ABFZ are generally considered to act as an environmental barrier because waters of the Benguela and Angola currents support distinct ecosystems (Lass et al. 2000, Postel et al. 2007).

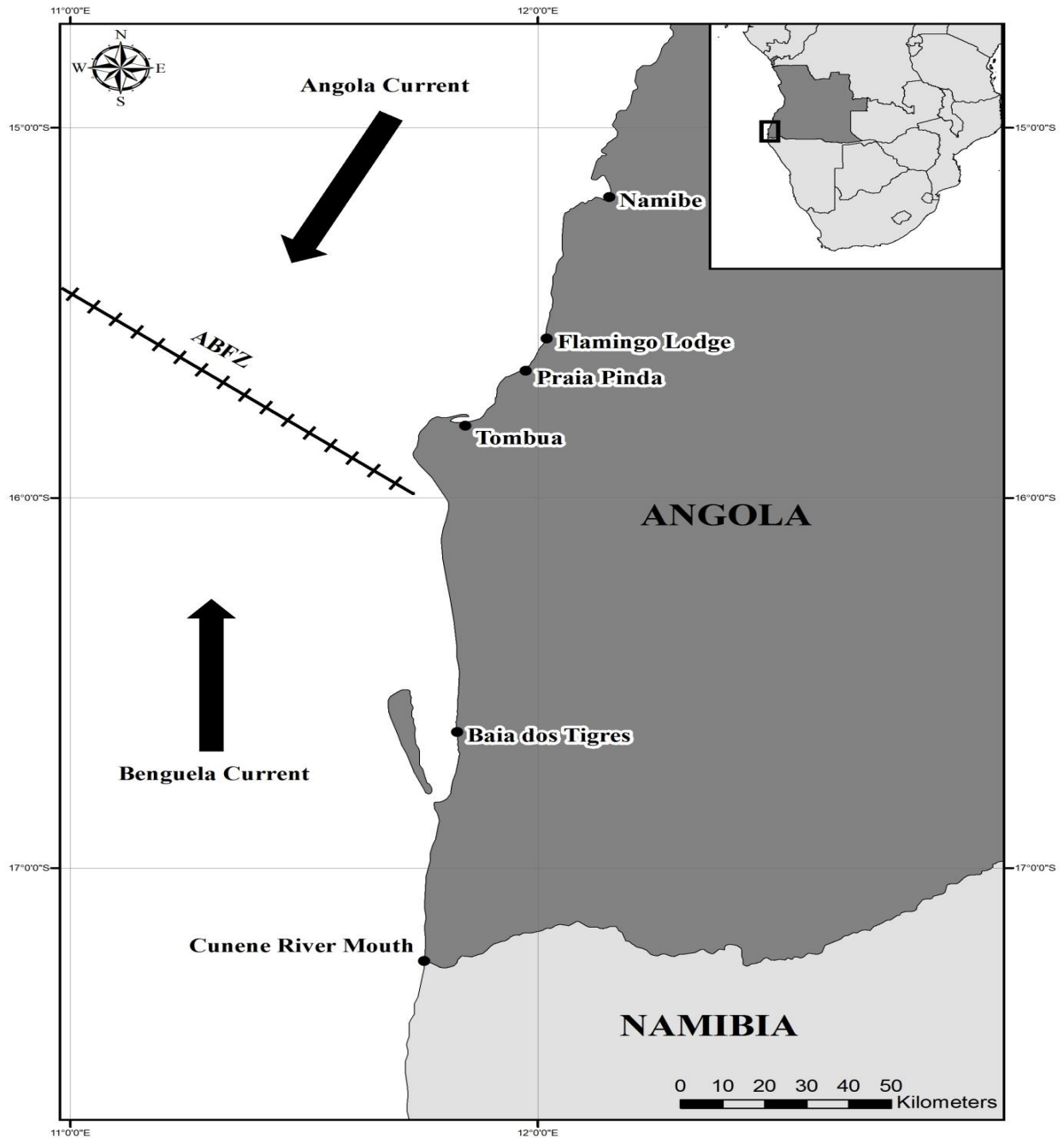


Figure 2.1: Location of the study site, based at Flamingo Lodge in southern Angola and other towns and features mentioned in the text, including the Angola Benguela Frontal Zone (ABFZ).

Benguela Current waters are relatively cold and fertile due to regionally consistent upwelling of nutrients which support high productivity (Summerhayes et al. 1995). Although the Angola Current is warmer and comparatively nutrient and oxygen deprived, when compared with other tropical current systems, it is considered to be relatively productive and nutrient

rich (Lass et al. 2000, John et al. 2004, Colberg and Reason 2006, Veitch et al. 2006). Combined characteristics of the Benguela and Angola currents therefore, support a highly productive marine ecosystem in and around the ABFZ.

Although the region's marine environment is highly productive, the large seasonal fluctuations in environmental parameters require marine species to either undertake seasonal movements such as those of the west coast dusky kob (*Argyrosomus coronus*) (Potts et al. 2010b, submitted), evolve broad environmental tolerances as seen for many of the resident species in the region (Potts et al. in press), or display unusual behavioural adaptations to ensure their survival. For example, the distribution of *Bathylagus argyrogastrus* in unusually shallow waters off Angola is considered a consequence of oxygen deficits originating from the submergence of Angola Current waters at the ABFZ (Von-Bodungen et al. 2008).

An important environmental parameter influenced by the current dynamics off southern Angola is sea surface temperature (SST), which fluctuates both seasonally and annually (Figure 2.2 & 2.3). Water temperature follows typical seasonal trends in southern Angola with lower average temperatures observed during winter and higher temperatures observed during the summer months. In addition to seasonal variation, an anomalous decrease in SST occurs during summer months in many years (Figure 2.2, 2.3). The direct mechanisms that cause the summer drop in SST have not been specifically determined, but the phenomenon has been linked to the movements and reproduction of fish species in the region (Potts et al. 2010b, in press, submitted, Richardson 2010, Richardson et al. 2012, Winkler 2013).

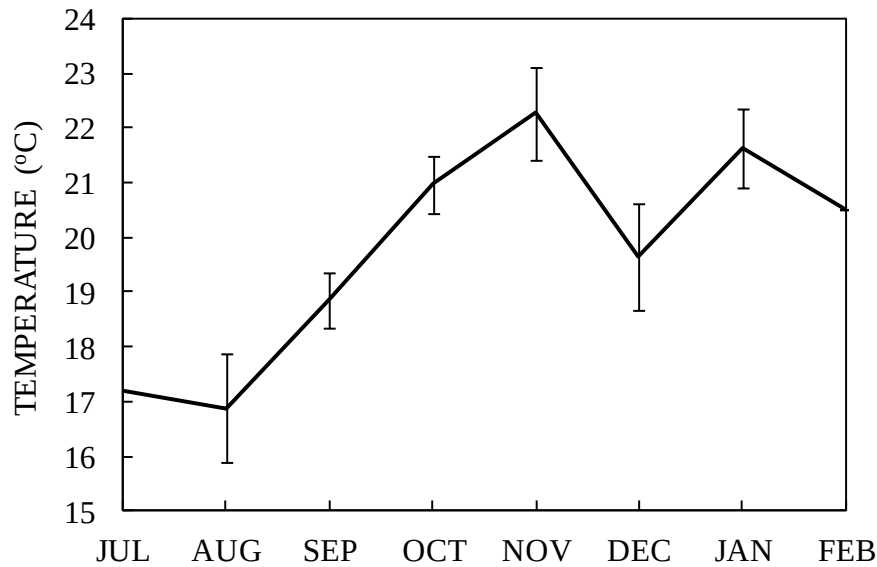


Figure 2.2: Mean monthly temperature measured daily between 07:00 and 08:00 from the inshore zone directly in front of Flamingo Lodge (2012-2013). Error bars represent monthly standard deviations.

Changes in temperature also occur over longer time scales causing southern Angola to be classified as a ‘global climate change hotspot’ due to a long-term warming SST trend of $\sim 0.6\text{--}0.8^{\circ}\text{C}.\text{decade}^{-1}$ being observed in the region between 1985 and 2009, with this rate becoming more than $0.8^{\circ}\text{C}.\text{decade}^{-1}$ between 2002 and 2012 (Munnik 2012, Potts et al. submitted). This warming trend is more than $0.8^{\circ}\text{C}.\text{decade}^{-1}$ faster than the global ocean average ($0.07^{\circ}\text{C}.\text{decade}^{-1}$). Veitch et al. (2006) showed that from 1982 to 1999, mean annual temperature increased by 3°C to the north of, 2.5°C within and 1°C to the south of the ABFZ and suggested the trend was not isolated to coastal areas. During this study, an increase of 0.78°C was seen in monthly average SST between 2006 and 2012 for the comparable months of July to December.

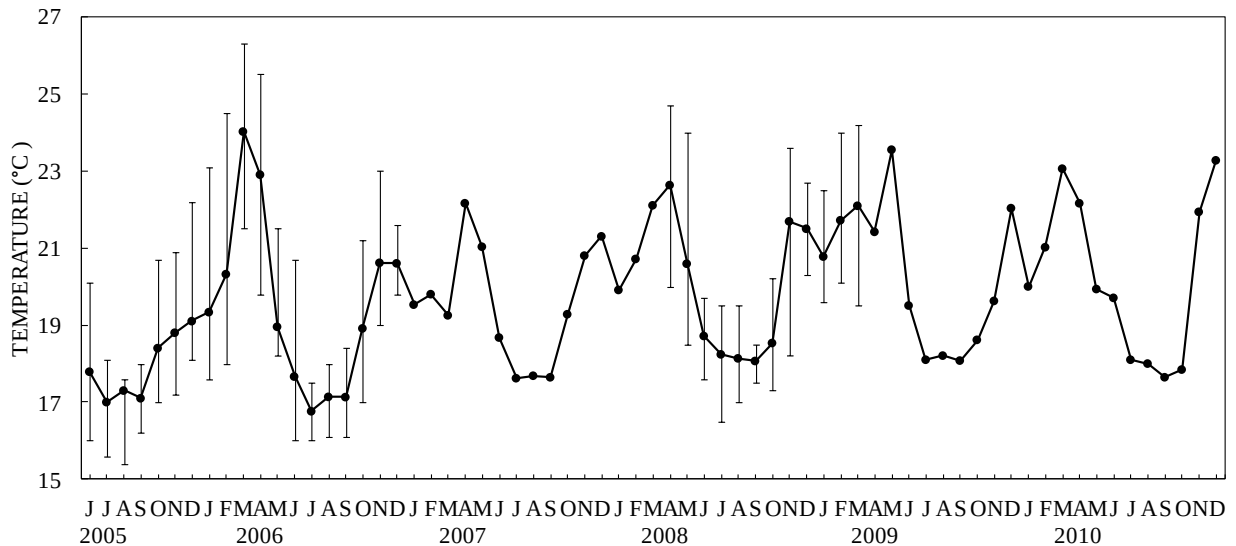


Figure 2.3: Average sea surface temperature of the surf zone at Flamingo Lodge from June 2005 to December 2010. Error bars indicate maximum and minimum SST values obtained from *in situ* data, while data points without error bars were obtained from a remote sensing satellite (Modis Terra) and adjusted using a correction factor to acquire accurate surf zone temperature estimates (Munnik 2012).

Regardless of environmental fluctuations, the protracted period of civil unrest has left southern Angola's *P. saltatrix* population in a relatively pristine condition. While fisheries in the region remain relatively small and underdeveloped, an apparent increase in fishing pressure since 2002 was noted by all Flamingo Lodge researchers, staff and guests between 2005 and 2012. To provide some form of quantification for this, a questionnaire about fishing practices was circulated among researchers that had previously worked in the region and had lived at Flamingo Lodge for a minimum of eight months. Researchers had no knowledge of the responses of their peers to the questions and questions were aimed at investigating observed fishing pressure in the study area (see Appendix 1).

Table 2.1: Selected results of a questionnaire directed at researchers based in southern Angola between 2005 and 2010 to understand changes in the dynamics of the coastal fisheries in southern Angola.

	(2005-2006)	(2009-2010)	(2010-2011)	(2011-2012)	(2012-2013)	(2013)
# Recreational fisher groups	2 groups monthly	1 group monthly but 2 groups per long weekend	At least 2-3 groups	2-3 groups on average but up to 5-10 on long weekends	2-3 on average and often 8 or 10 on long weekends	3 groups every weekend
Recreational equipment	Bait only	Bait only	Generally bait but $\pm$ 2/5 used lures.	Bait and “rudimentary lures”	Bait and lures	Bait and lures
Were fish released?	No	No	No	No	No	No
Commercial fishing gears	Some gill and seine nets	Beach and raft handliners, gillnets became more prevalent during stay	Raft handliners, gill nets	Beach seine nets, traps	Many raft handliners, traps, artisanal beach anglers, beach seine nets, gill nets	About 50 raft handliners operating daily, many traps, beach seine nets, extensive use of gillnets
Commercial Vessels and crew	Motorised artisanal vessels ($\pm$ 8m), and smaller vessels (6m) for gillnet and beach seine fishers	Motorised artisanal vessels ($\pm$ 8m, 4-8 crew). Smaller boats ($\pm$ 6m, 2-3 crew) for gillnets	Motorised artisanal vessels (5-10 crew)	Motorised artisanal vessels ($\pm$ 4m, 4 crew)	Motorised artisanal vessels ($\pm$ 6m, 4-5 crew)	Motorised artisanal vessels ($\pm$ 6m, 4-5 crew) to deploy gill nets, seine nets and drop off raft fishermen. Larger ($\pm$ 8m, 6-7 crew) vessels used to deploy traps

The responses (Table 2.1) suggest that the monthly average number of recreational fishers operating in the region has increased since 2005, and these fishers capacity to efficiently target game fish species such as *P. saltatrix* and *Lichia amia* has improved with the increasing use of imported artificial lures after 2009. While the catch and release policy enforced for fishing guests at Flamingo Lodge is believed to minimise the negative influence of mortalities accrued by recreational fishers, the questionnaire responses indicate a concerning lack of release policy amongst ‘local’ recreational fishers. Question four (Appendix 1) distinguished between edible and non-edible species because it was observed that many of the “non-edible” species (e.g. *Rhinobatidae* and *Tetradontidae*) were frequently left to die on the beach by local recreational anglers rather than being released.

In response to the perception of declining catch rates, the Angolan government has previously assisted artisanal fishers by upgrading their vessels to small-scale commercial vessels (Duarte et al. 2005, Potts et al. 2010a). Technology and effort creep is encouraged by government policies and many fishing co-operatives have now facilitated microcredit capacities that allow fishers to obtain technology upgrades (Potts et al. 2010a). While these factors may increase catch rates in the short-term, the increased fishing capacity on apparently declining stocks has potential long-term consequences, and based on questionnaire responses, the artisanal fisheries have diversified the gears and techniques they use in the study area to maintain or increase their catch rates (Table 2.1).

P. saltatrix are particularly susceptible to hook and line fisheries. Besides the recreational fisheries, the number of hook and line fishers who operate in the nearshore zone (< 200m from the shore) from small rafts (built from any available buoyant material) using hand paddles to transport themselves is increasing. Due to their superior catch rates, these fishers appear to be replacing traditional subsistence beach-based hook and line fishers. In addition the raft hook and line fishers have begun (since 2009) expanding their traditional fishing grounds adjacent to coastal towns by using artisanal fishing vessels for transport. As a result, many nearshore areas that were previously unfished are now exploited by these “raft” fishers.

The widespread use of gill nets is a concern in southern Angola and increasing availability of nets and materials required to repair these gears is believed to have promoted increases in

fishing effort (Duarte et al. 2005). Gill nets have become more frequently utilised by commercial fishermen in the study area (Table 2.1) and fishers began using motorised vessels to chase fish into these gears in the nearshore zone from 2010. Traps that generally capture small *Sparidae* species were first observed in 2011 and their use appears to have increased dramatically with greater numbers of these gears being washed onto beaches in the study area. While catch trends were difficult to ascertain based on answers to questions 3 and 8 (Appendix 1), a decline in the diversity and in the average size of many species was apparent. *P. saltatrix* was regularly captured in all fishery sectors and while technology creep, improved methods and diversification of gears may create the illusion of a stable stock, noted adaptations within fisheries (Table 2.1) are considered to largely reflect compensatory measures in the face of reduced abundances of targeted species.

Sampling procedure

P. saltatrix samples were collected between June 2005 and December 2006 (referred to as “period 1”) and between June 2012 and February 2013 (referred to as “period 2”). The reduced sampling time during period 2 was motivated by the reproductive seasonality of *P. saltatrix*, as these months were thought to adequately cover the species reproductive cycle based on findings from period 1. *P. saltatrix* were captured using rod and line techniques during both sampling periods and a minimum of 30 monthly samples was maintained to ensure statistical relevance of data. Total sample sizes were 614 for period 1 and 324 for period 2. In rare cases where the minimum monthly samples ($n = 30$) could not be attained using rod and line techniques, additional specimens were purchased from fishing communities or markets which received *P. saltatrix* captured locally. Some of these fish were captured by gill nets but with only twelve samples being purchased rather than captured by researchers using rod and line techniques, these gears potential selectivity influence was considered negligible.

Dissection Procedure

Each *P. saltatrix* was measured (TL and FL), weighed (total and eviscerated mass), and sexed with the level of gonad development being noted macroscopically (see Chapter 5). Gonads were also weighed to the nearest 0.01g during period 2. Representative samples of each macroscopic stage were preserved in a seawater buffered 10% formalin solution during period 2 for later histological analysis. Stomach contents were identified to the lowest possible taxon and enumerated during both sample periods. Prey items were additionally weighed wet to the nearest 0.01g during period 2. Both sagittal otoliths from each fish were collected whole and stored dry in Eppendorf tubes. Any additional observations or relevant information about individual fish was also noted during dissections, including the presence and abundance of parasites.

A long-term fish monitoring and tagging project was initiated in 2005 to gain an understanding of the relative abundance and movement patterns of recreationally important species, including *P. saltatrix*, around Flamingo Lodge. The time and location fished, number of anglers, and numbers of *P. saltatrix* captured was noted during all fishing excursions undertaken from the lodge. *P. saltatrix* that were not sacrificed for biological sampling were therefore externally tagged with PDL-type plastic dart tags (Hallprint), and released as continues to be done in the region for *P. saltatrix*, *Argyrosomus coronus* (Potts et al. 2010b) and *Lichia amia* (WM Potts, unpublished data).

CHAPTER 3

The diet composition and feeding habits of *P. saltatrix* in southern Angola

Introduction

The use of stomach content analysis to describe the diet of species has become common practice in fish ecology research (Hyslop 1980, Arrington et al. 2002). Analysis of stomach contents allows fisheries scientists to ascertain what a species is consuming and in what quantity. Diet descriptions provide invaluable information on the nutritional requirements of a species, contextualise its trophic status within ecosystems, and can be used to estimate the pressure that it places on populations of its prey species. Understanding the dietary requirements of *P. saltatrix* in southern Angola, and ranking the importance of different prey species may guide potential ecosystem based management decisions to ensure the future sustainability of fishing practices. Changes in the diet of fishes may also provide an indication of ecosystem changes and comparison of the diet of *P. saltatrix* between the two study periods will aid our understanding of other potential biological changes.

Since resource availability varies in time and space, marine fishes that are able to effectively adapt their feeding activities will consistently meet their nutritional requirements and gain greater levels of evolutionary fitness (Arrington et al. 2002). *P. saltatrix* have rapid evacuation and consumption rates, which support one of the fastest specific growth rates known for temperate fishes (Juanes and Conover 1994a, Buckel et al. 1995). Therefore, the temporal availability and nutritional value of important prey species in southern Angola is critical for the growth and survival of the regions' *P. saltatrix* population. Environmental changes, the value of dominant prey species and the harvests from fisheries targeting prey species may have significant impacts on the abundance and nutritional value of food available to the Angolan *P. saltatrix* population. Since the composition of diet influences the life history of fishes, some of the variability in life history between *P. saltatrix* populations around the world may be attributed to diet and a comparison of the species feeding habits globally is therefore useful.

P. saltatrix is generally considered to be piscivorous although it also feeds on copepods, cladocerans, crustaceans, polychaetes and cephalopods, in different proportions throughout its life history (Kendall and Naplin 1981, Smale 1986, Friedland et al. 1988, Haimovici and Krug 1996, Juanes et al. 1993, 1996, 2001, Buckel et al. 1999a, Scharf et al. 2000, 2004). Crustaceans, crab larvae and polychaetes can form important components of the diet of juvenile *P. saltatrix* (Friedland et al. 1988, Marks and Conover 1993) but the species generally becomes piscivorous at a small size, and displays a concomitant increase in growth rate (Marks and Conover 1993, Juanes and Conover 1994 a,b, Juanes et al. 1994, Buckel et al. 1998). A global comparison conducted by Juanes et al. (1996) showed that pelagic species of the *Atherinidae* and *Engraulidae* families represent important and highly nutritious prey sources for *P. saltatrix* populations throughout their distribution. Adults tend to feed less on invertebrates and more on fish and squid, with cannibalism also being noted and potentially influencing recruitment off the American east coast (McBride and Conover 1991, Haimovici and Krug 1996, Bell et al. 1999).

This chapter aims to:

- 1) provide a description of the diet of *P. saltatrix* in southern Angola,
- 2) compare the diet during two research periods (2005-2006 and 2012-2013) and
- 3) compare the diet composition with that of other *P. saltatrix* populations.

Methods and Materials

General methods and diet description

Fish were captured using the methods described in Chapter 2, weighed (0.01g) and measured (FL) to the nearest millimetre before their stomach contents were identified and enumerated during both periods. During period 2, each dietary item was also weighed wet on an electronic scale (0.01g).

Index measures

Prey diversity and dietary breadth was described and compared using the Shannon-Wiener method (Shannon 1948) as defined by Krebs (1989) of the form:

$$H' = -\sum P_i \ln P_i$$

where P is the proportion of the numerical contribution of each identified prey species i .

A measure of evenness (Zar 1984) was used to compare the dietary breadth:

$$J = \frac{H'}{H'_{max}}$$

where $H'_{max} = \ln(k)$ and is the maximum possible diversity according to the number of prey species (k) in each comparison.

Levins' (1968) measure of niche breadth (B) which was standardised (B_A) as recommended in Marshall and Elliot (1997) was also calculated as:

$$B = \frac{1}{\sum p_j^2}$$

and

$$B_A = \frac{(B - 1)}{(n - 1)}$$

respectively where p_j is the dietary proportion filled by prey species j and n is the number of prey species used to describe dietary breadth.

Relative importance of prey items

Analysis of diet information during the second period included the use of an Index of Relative Importance (IRI) as proposed by Pinkas et al. (1971) of the form:

$$IRI = (\%N + \%W)\%FO$$

where %N is the number of times each prey species was recorded as a percentage of the total number of food items in all stomachs, %W is the gravimetric contribution of each prey category as a percentage of the total mass of food items and %FO is the percentage of stomachs containing each prey category to the total number of non-empty stomachs.

Comparisons according to maturity

An ANOSIM permutation test (Clarke 1993, Clarke and Warwick 1994) using the Bray-Curtis distance measure (Bray and Curtis 1957) was used to compare the diets of juvenile (293 – 495 mm FL) and adult (> 495 mm FL) *P. saltatrix* and a cluster analysis was used to investigate the similarities between these two groups. The ANOSIM results are based on the R statistic, which ranges between zero and one, with a value of one indicating that all replicates within groups are more similar to each other than replicates from compared groups.

Comparisons by season and period

Diet data was separated into winter (June-August), spring (September-November) and summer (December-February). Seasonal differences in the diet of *P. saltatrix* were tested using a Bray-Curtis similarity analysis (Bray and Curtis 1957) in the statistical package PAST Version 2.16 and illustrated using dendograms. Differences between the diets for each season were tested for significance using an analysis of similarity (ANISOM) presumption test (Clarke and Warwick 1994) with differences considered significant at $p < 0.05$.

Feeding intensity

Seasonal differences in feeding intensity were investigated using a stomach fullness index proposed by Man and Hodgkiss (1977) of the form:

$$SFI = \frac{\text{Stomach content mass}}{\text{Eviscerated fish mass}} \times 100$$

Results

A total of 324 of the 415 (78.1%) and 258 of the 325 (79.4%) stomachs examined during the first and second period respectively, were empty. The diet composition during both periods was dominated by various teleost species, associated with either pelagic or inshore habitats, with one cephalopod (period 1) and one crustacean species (period 2) also observed. Seven prey species were recorded during period 1 and six during period 2, with only three common species noted during both periods (Table 3.1). *Sardinella aurita* occurred most frequently and represented the greatest numerical contribution to stomach contents during both periods (Table 3.1). Fishes belonging to the family *Mugilidae* (13.4% in period 2) replaced *Trachurus* species (13.7% in period 1) as the second highest contributors to %FO during period 2 (Table 3.1). Unidentified fish species numerically (%N) contributed 37.4% and 47.8% of stomach contents during period 1 and period 2 respectively.

During period 2 “unidentified fish” had the highest relative dietary importance according to percent Index of Relative Importance (52.7%) followed by *S. aurita* (42.4%), while *Mugilidae* species ranked third (4.5%). Combined relative importance percentages of the other four prey species identified during period 2 contributed only 0.7% to the index (Table 3.1).

Table 3.1: Comparison of the diet composition for *P. saltatrix* in southern Angola between June 2005 and December 2006 (Period 1); June 2012 and February 2013 (Period 2).

	Period 1		Period 2				
	% N	%FO	% N	%W	%FO	IRI	%IRI
Unidentified fish	37.4	38.5	47.8	22.0	50.0	3488.5	52.7
<i>Sardinella aurita</i>	40.7	46.2	31.3	58.4	31.3	2803.2	42.4
<i>Mugilidae</i> sp.	2.2	2.6	13.4	10.5	12.5	299.4	4.5
<i>Trachurus</i> sp.	13.2	5.1	1.5	4.7	1.6	9.7	0.1
<i>Oblada melanura</i>	2.2	2.6	-	-	-	-	-
<i>Dentex barnardi</i>	-	-	1.5	2.0	1.6	5.5	0.2
<i>Lithognathus mormyrus</i>	1.1	1.3	-	-	-	-	-
<i>Sphyræna</i> sp.	1.1	1.3	-	-	-	-	-
<i>Tetradontidae</i> sp.	-	-	3.0	2.1	1.6	7.9	0.3
<i>Loligo reynauldi</i>	2.2	2.6	-	-	-	-	-
Unidentified crustacean	-	-	1.5	0.3	1.6	2.8	0.1

Niche breadth according to the evenness index (J) and Levins' measure (B_A) increased from period 1 to period 2 while the Shannon-Wiener index indicated no change in prey diversity (Table 3.2).

Table 3.2: Values for indices used to describe and compare the dietary breadth of *P. saltatrix* in southern Angola during both study periods.

	Period 1	Period 2	Combined periods
Shannon-Wiener information statistic (H')			
Juveniles	1.22	1.12	1.50
Adults	0.94	0.98	1.06
Overall	1.12	1.12	1.32
Evenness measure (J)			
Juveniles	0.68	0.81	0.72
Adults	0.48	0.71	0.51
Overall	0.58	0.63	0.58
Levins' measure (B_A)			
Juveniles	0.38	0.52	0.33
Adults	0.11	0.39	0.13
Overall	0.20	0.26	0.16

When both periods were combined for an overall analysis, juvenile (293 – 495 mm FL) *P. saltatrix* had a greater dietary breadth than adults (> 495 mm FL) (Table 3.2). Adults fed more frequently on *S. aurita* while the diet of juveniles was dominated by Mugilidae species (Table 3.3). Because of the difficulty with identification of fish in the Mugilidae family and rapid digestion of the smaller prey consumed, the stomach contents of juveniles were also less frequently identified to genus or species level (Table 3.3).

Table 3.3: Combined period average percent dietary contributions for prey species of *P. saltatrix* according to maturity.

	Juvenile		Adult	
	%FO	%N	%FO	%N
<i>Sardinella aurita</i>	13.4	12.4	19.6	19.7
<i>Trachurus sp.</i>	2.1	6.1	1.3	1.8
<i>Mugilidae sp.</i>	15.3	13.1	13.9	14.5
Unidentified fish	15.7	15.2	12.9	11.7

Although ontogeny had a greater influence on the diet of *P. saltatrix* than sampling period (Figure 3.1), the differences between the diets of adults and juveniles were not statistically significant ($p > 0.05$, ANOSIM) (Figure 3.1).

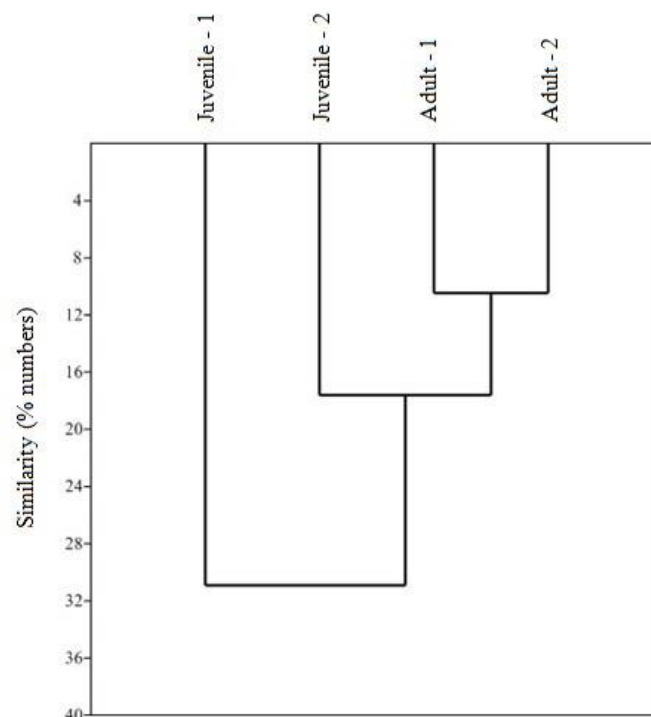


Figure 3.1: Similarity dendrogram from a cluster analysis comparing the diet of juvenile and adult *P. saltatrix* in period 1 and period 2 (numbers indicate period).

There was a general increase in dietary breadth from winter to summer during both periods with *S. aurita* contributing the largest proportion to the diet during spring in period 1 and summer in period 2 (Table 3.4). *Trachurus* species were only observed during summer in both study periods, while *Mugilidae* were only absent in the diets during the winter of period 1 (Table 3.4).

Table 3.4: Seasonal percent numerical contribution (%N) and frequency of occurrence (%FO) values for the stomach content analysis of *P. saltatrix* in southern Angola during period 1 and period 2.

Percent numerical contribution to diet (%N)						
	Winter		Spring		Summer	
	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
Empty	90.6	89.6	72.6	77.9	66.3	71.3
Unidentified fish	4.4	8.5	7.6	11.5	16.8	9.6
<i>Sardinella aurita</i>	4.4	-	17.8	3.8	1.0	14.8
<i>Mugilidae sp.</i>	-	1.9	0.5	4.8	1.0	1.7
<i>Loligo reynauldi</i>	-	-	0.5	-	1.0	-
<i>Oblada melanura</i>	-	-	1.0	-	1.0	-
<i>Trachurus sp.</i>	-	-	-	-	11.9	0.9
<i>Lithognathus mormyrus</i>	-	-	-	-	1.0	-
<i>Sphyraena sp.</i>	0.6	-	-	-	-	-
<i>Dentex Barnardi</i>	-	-	-	-	-	0.9
Unidentified crustacean	-	-	-	-	-	0.9
<i>Lagocephalus sp.</i>	-	-	-	0.9	-	-

Percent Frequency of Occurrence in diet (%FO)						
	Winter		Spring		Summer	
	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
Empty	91.8	89.6	74.5	79.4	72.8	71.9
Unidentified fish	3.2	8.5	6.3	11.8	17.4	9.6
<i>Sardinella aurita</i>	4.4	-	17.2	3.9	1.1	14.0
<i>Mugilidae sp.</i>	-	1.9	0.5	3.9	1.1	1.8
<i>Loligo reynauldi</i>	-	-	0.5	-	1.1	-
<i>Oblada melanura</i>	-	-	1.0	-	1.1	-
<i>Trachurus sp.</i>	-	-	-	-	4.3	0.9
<i>Lithognathus mormyrus</i>	-	-	-	-	1.1	-
<i>Sphyraena sp.</i>	0.6	-	-	-	-	-
<i>Dentex Barnardi</i>	-	-	-	-	-	0.9
Unidentified crustacean	-	-	-	-	-	0.9
<i>Lagocephalus sp.</i>	-	-	-	1.0	-	-

When results from the two periods were combined, the dietary compositions of summer and winter were more similar to one another than to spring (Figure 3.2). An ANOSIM determined a significant difference ($p = 0.01$) between the spring and summer season diet compositions.

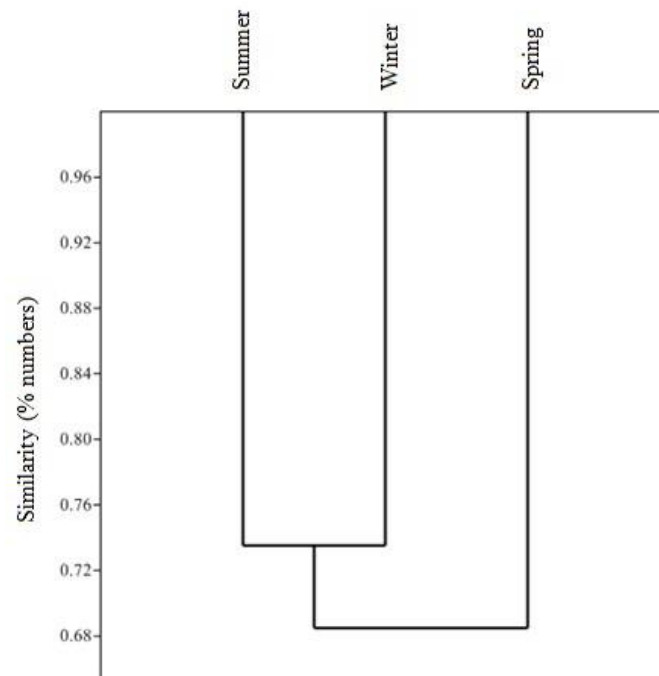


Figure 3.2: Similarity dendrogram displaying relationships of seasonal dietary composition for *P. saltatrix* in southern Angola across both study periods.

Feeding intensity

Feeding intensity increased from winter to summer during period 2, while the opposite trend was observed for the percentage of empty stomachs (Table 3.5).

Table 3.5: Average stomach fullness index (Mean SFI) and percent empty stomachs (% empty) for *P. saltatrix* in southern Angola from June 2012 to February 2013.

	Winter	Spring	Summer
Mean SFI	1.13	1.22	1.88
% empty	89.62	79.41	70.69

Discussion

The diet of *P. saltatrix* in southern Angola comprised 10 species and was dominated in all descriptive analyses by the pelagic, schooling species *Sardinella aurita* (Table 3.1). This was unsurprising as pelagic schooling species dominate the dietary composition of the majority of *P. saltatrix* populations around the world (Table 3.6) (Juanes et al. 1993, 2001, Scharf et al. 1997, 2004, Buckel et al. 1999b, Lucena et al. 2000, Harding and Mann 2001, Gartland et al. 2006). In southern Angola *P. saltatrix* may be considered a generalist piscivore since by percent number, teleosts constituted 97.8% and 98.5% of the diet in periods 1 and 2 respectively (Table 3.1).

The inclusion of gravimetric data in the second sample period allowed calculation of an index of relative importance (%IRI) which further confirmed the importance of small pelagic prey in the diet (Table 3.1). Interestingly, other *P. saltatrix* dietary studies have noted cannibalism (Bell et al. 1999, Buckel et al. 1999a, Juanes 2003, Gartland et al. 2006) but this was not observed during this study. The lack of cannibalism in southern Angola may result from availability of a wide range of alternative prey species. However, and more likely, it suggests that the nursery habitat for juveniles was not located near the study site. The absence of *P. saltatrix* below a length of 293 mm FL in this study suggests that this is most likely to be the case. Early juveniles (< 200 mm FL) have been observed in the catch of fishers that operate on shallow (5-10 m) offshore rocky reefs approximately 40 km south of the study area. Unfortunately, logistics precluded sampling in this area.

Ontogenetic shifts are common in *P. saltatrix*, with juveniles of many populations feeding primarily on Crustaceans while adults prey more intensively upon teleosts (Silvano and Begossi 2005, Table 3.6). The shift to piscivory normally occurs early in the life history and is generally associated with an increase in growth (Juanes and Conover 1994a, b, Buckel et al. 1998). As mentioned above, early juveniles were poorly represented in this study (see length frequency histogram in figure 3.1, Chapter 4), and consequently an ontogenetic dietary shift, if it occurs, was not observed adequately. However, the only crustacean observed in the diet of *P. saltatrix* during this study was found in a juvenile fish, suggesting that an ontogenetic shift is possible. Furthermore, the ANOSIM indicated that the diets of juveniles

between the two sampling periods were more similar to one another than the diets of juveniles and adults during the same period (Figure 3.1). Therefore, although differences between the diets of juvenile and adult *P. saltatrix* were not considered to be statistically significant (ANOSIM, $p = 0.36$), there was still some evidence for an ontogenetic shift in diet. It is likely that more resolution on the dietary shift would be obtained with the inclusion of smaller fish in this study. Future studies should therefore aim to identify and sample the nursery of *P. saltatrix* in southern Angola in order to gain a comprehensive understanding of the species diet.

Table 3.6: Dominant prey items in order of importance for the stomach contents of *P. saltatrix* from around the globe. 1 = Lucena et al. 2000, 2 = Scharf et al. 2004, 3 = Harding and Mann 2001, 4 = Friedland et al. 1988, 5 = Callihan 2005, 6 = Buckel et al. 1999a, 7 = Marks and Conover 1993, 8 = Van der Elst 1976, 9 = Smale 1986, 10 = Sanchez-jerez et al. 2008.

	<i>P. saltatrix</i> size range(mm)	Indices of dietary importance used	Dominant prey (to lowest specified taxa)	Prey habitat classification
Southern Angola	293 – 760 (FL)	%N, %FO, %W, %IRI	Juvenile – <i>Mugilidae</i> spp. Adult - <i>Sardinella aurita</i>	Nearshore Pelagic
Southern Brazil	< 500 ¹ (TL)	%W ¹	<i>Engraulis anchoita</i> ¹	Pelagic
USA (Estuarine)*	100 – 550 ² (TL)	%W, %FO ²	<i>Brevoortia tyrannus</i> ²	Pelagic
USA (Estuarine)	170 – 430 ³ (FL)	%FO, %N ³	<i>Polychaeta</i> ³ <i>Clupeidae</i> ³	Demersal Pelagic
USA (Estuarine)*	60 – 190 ⁴ (TL)	%FO, %N, %W ⁴	<i>Crustacea</i> (%N) ⁴ <i>Anchoa mitchilli</i> (%W) ⁴	Demersal Pelagic
USA (Coastal/bay)*	70 – 360 ⁵ (TL)	%FO, %W ⁵	<i>Anchoa</i> sp. ⁵ <i>Menidia</i> sp. ⁵	Pelagic Pelagic
USA (shelf waters)	250 – 800 ⁶ (FL)	%FO, %N ⁶	<i>Anchoa mitchilli</i> ⁶	Pelagic
USA*	18 – 74 ⁷ (TL)	%FO, %N, %W ⁷	<i>Crustacea</i> ⁷ <i>Teleostei</i> ⁷	Demersal Pelagic
South Africa	> 100 ⁸ (TL)	%N ⁸	<i>Pomadasys ovilaceum</i> ⁸ <i>Ambassis</i> sp. ⁸	Benthopelagic Benthopelagic
South Africa	120-700 ⁹ (TL)	%FO, %N, %W ⁹	<300 mm <i>Loligo reynaudi</i> ⁹ Mysids ⁹	Pelagic Benthopelagic
			>300 mm <i>Sardinops ocellata</i> ⁹ <i>Engraulis capensis</i> ⁹ <i>Etremeus teres</i> ⁹ <i>Loligo reynaudi</i> ⁹	Pelagic Pelagic Pelagic Pelagic
			>500 <i>Pomadasys ovilaceum</i> ⁹ <i>Diplodus sargus</i> ⁹	Benthopelagic Benthopelagic
Mediterranean	310 – 640 ¹⁰ (TL)	%W ¹⁰	<i>Sardinella aurita</i> ¹⁰ <i>Trachurus mediterraneus</i> ¹⁰	Pelagic Pelagic

* indicates studies that specifically analysed juvenile *P. saltatrix* diet

Juveniles also had a broader dietary range than their adult conspecifics. This is unusual as dietary breadth normally increases with size as fish are exposed to additional feeding opportunities and are less restricted by mouth gape (Scharf et al. 2000). The broad dietary breadth of the juveniles in this study may therefore be attributed to the high nutritional demands of their rapid early growth (see Chapter 4) and early maturation during their first year of life (see Chapter 5) (Table 3.2). In addition, the diet of juveniles was dominated by nearshore mugilids instead of the pelagic *S. aurita*, which dominated the diet of the adults (Table 3.3). This suggests that juveniles predominantly fed in the nearshore zone, while adults predominantly fed further offshore. Since the nearshore zone hosts a broad diversity of prey compared with pelagic habitats, it is possible that this may also explain the broader dietary range of juveniles.

The diet of *P. saltatrix* varied between seasons with the diversity of prey species being lowest over the winter during both periods (Table 3.4). Although small pelagic fishes were generally the most nutritionally important (%W) and frequently consumed species (%FO, %N), this was not the case throughout the year. *S. aurita*, was completely absent from stomachs in the winter of period 2 and contributed most to *P. saltatrix* diet during spring and summer in period 1 and period 2 respectively (Table 3.4). Friedland et al. (1988) and Lucena et al. (2000) suggested that the diet of *P. saltatrix* is dependent on the abundance and availability of prey. Therefore, the findings in this study suggest that *S. aurita* were not abundant in the study area during winter months. This conclusion is supported by the findings of Ghéno and Poinard (1968) as well as those of Baptista and Fonseca (1977) who suggested that *S. aurita* appear to undertake a southward movement (into the study area) at the beginning of the warm season (Spring).

Without their primary pelagic food source in winter, one would expect that *P. saltatrix* would shift their feeding habits into the nearshore zone and consume a broader range of prey items. However, as their dietary breadth was lowest in winter, this was not the case. There are two possible explanations for this, both of which are associated with the influence of the Benguela Current. Firstly the water temperature during winter were colder (Chapter 2), suggesting that the metabolism of *P. saltatrix* may have been slower. Secondly the cold Benguela, while extremely productive, generally supports less diversity than the tropical

Angolan Current which dominates the area in summer. The reduced dietary breadth during the winter months may therefore be a consequence of both reduced feeding and the low diversity of potential prey items.

Feeding intensity increased during spring (Table 3.4) which coincided with warmer temperatures, gonad development (Chapter 6) and the return of *S. aurita* into the diet. This is unsurprising as the movement patterns of pelagic prey species have been linked to the reproduction of other populations of *P. saltatrix*. For example, Pradervand and Govender (2003) reported that the spawning migration of *P. saltatrix* was related to the migration patterns of *Sardinops sagax* in South Africa. The highest feeding intensity was observed during summer. This coincided with the highest water temperatures (Chapter 2) and with the peak spawning season of *P. saltatrix* (Chapter 6). The peak in contribution of *S. aurita* to the diet of *P. saltatrix* also coincided with their peak reproductive activity. Similar trends, where spawning coincides with a high abundance of prey in the region have been found for other *P. saltatrix* populations including those from South Africa (Van der Elst 1976, Govender 1996) and Brazil (Lima and Castello 1995, Haimovici and Krug 1996); this suggests that the abundance of small pelagic prey species may be an important determinant of reproductive success in this species. Therefore, the management of these pelagic prey species may have important implications for their predators.

Although piscivorous fishes are a trophic group likely to have high proportions of empty stomachs in diet studies (Pierce et al. 2001, Arrington et al. 2002) the high proportions of empty stomachs in this study, 80.6% and 80.1% for periods 1 and 2 respectively, were believed to at least be partially caused by regurgitation while *P. saltatrix* were being captured. The regurgitation of food items represents a loss of diet information and causes overestimation of stomach vacuity, with consequent underestimations of prey consumption (Vignon and Dierking 2011). Regurgitation was observed in this study during fish capture as it was for the South African *P. saltatrix* population by Smale (1986). However, for the purposes of this study, it is assumed that all prey items had an equal likelihood of being regurgitated and therefore the contents of stomachs were representative of *P. saltatrix* diet.

Although the Shannon-Wiener information statistic suggested that there was no change in overall dietary breadth between the two periods, the Levins' and evenness measures suggested diversification of *P. saltatrix* diet in period 2 (Table 3.2). The greatest change in dietary composition between the two periods was a reduction in the importance of *Trachurus* species (13.2%N) and an increase in the importance of mugilids (Table 3.1). Mugilids are generally associated with the nearshore environment while *Trachurus* species and *S. aurita* are pelagic schooling species (Lloris and Moreno 1995, Ayvazian and Hyndes 1995, Sabatés et al. 2006).

In 2006, the Namibian stock of *Trachurus* was declining, but by 2009 it appeared that the stock was recovering (Smith and Japp 2012); therefore, it is unlikely that overexploitation in Namibia is a reason for the apparent declines of the stock in Angola. However, short lived, pelagic species are also heavily dependent on environmental conditions and two or three years of unfavourable conditions for reproduction can have major implications for their populations. Rosado (1974) demonstrated a clear link between environmental conditions and the abundance of *Trachurus* species and suggested that there was a 6 year cycle of peaks and troughs of abundance in southern Angola. This suggests that unfavourable conditions for reproduction may have occurred just prior to the second period in southern Angola.

Besides cyclical variations, *Trachurus* species are a predominantly warm-temperate fauna, preferring water temperatures between 12 and 14°C (Coombs et al. 2001) with their eggs successfully developing at temperatures from 10.5 to 21.2°C (Pipe and Walker 1987). Alternatively *S. aurita* prefers water temperatures between 25.6 and 25.8°C and has a sub-tropical and tropical distribution (Páramo and Roa 2003). It is therefore possible that the recent warming in southern Angola may have influenced the reproductive success and/or the abundance of these species. The consequences of a reduction in the abundance of *Trachurus* species being driven by climate change will not only have implications for *P. saltatrix* but also for other coastal predatory species, such as *Lichia amia* (Potts et al. 2008) and *Argyrosomus coronus* (Potts et al. 2010b) that also feed on these species.

While there was no doubt that during the first period *P. saltatrix* spent significant amounts of their time feeding in pelagic habitats, the replacement of pelagic *Trachurus* species with

nearshore mugilids, during the second period suggests that they were feeding in the nearshore zone. Temporal changes in feeding habitat have been reported to result from climate change effects in other fish species as was described by Rose (2005) for a variety of North Atlantic fishes. Perhaps the greatest consequence of increased nearshore feeding activity is the different degrees of catchability in the different zones. Accordingly increased feeding in the nearshore zone is likely to result in improved catches in the shore-based recreational and subsistence fisheries.

Conclusion

P. saltatrix can be described as a generalist piscivore that feeds opportunistically on a variety of species in Angola according to their relative abundance. Juvenile *P. saltatrix* had a greater dietary breadth than adults, and overall *S. aurita* represented the most important (%IRI, %FO, %W, %N) prey species. Prey diversity and consumption varied by season, and between study periods. As their most important prey item, the abundance of *S. aurita* appears to be critical for the growth and reproduction of *P. saltatrix* and their management is therefore critical for the wellbeing of this species. Changes in abundance of other important pelagic *Trachurus* species appears to have influenced the feeding habitats of *P. saltatrix* between the two study periods and suggests that an understanding of the environmental drivers influencing their abundance in southern Angola may be necessary. Future research should focus on identifying the nursery habitats of *P. saltatrix* and describing the diet of juveniles. Furthermore, developing a greater understanding of the environmental drivers influencing *Trachurus* species and *S. aurita* would assist in predicting abundance of *P. saltatrix* in Angola.

CHAPTER 4

Recent changes in the demographics and growth of *P. saltatrix* in southern Angola

Introduction

Estimation of age in fishes underpins the calculation of growth and mortality rates as well as the development of productivity estimates, making age one of the most important and influential biological characteristics utilised by fisheries scientists (Campana 2001). Age determination for *P. saltatrix* is a challenging process (Barger 1990, Jenke 2002, Sipe and Chittenden 2002, Brown et al. 2003, Robillard et al. 2009) and several ageing techniques have been used for the species. Sipe and Chittenden (2002) used whole and sectioned otoliths, scales, dorsal spine sections, as well as vertebrae and suggested that sectioned otoliths consistently provided the highest growth zone clarity, confidence scores and the highest between reader agreements to an age of 14 years. Robillard et al. (2009) compared scales and otoliths from 2 652 *P. saltatrix* and suggested that baked, sectioned otoliths provided the most precise age estimates up to age 8. Baking was thought to enhance otolith section microstructure and make growth zone interpretation more precise.

Despite their recommendation to use sectioned otoliths, Sipe and Chittenden (2002) still noted a variety of issues associated with accurately ageing *P. saltatrix* including difficulty identifying the first annulus, relatively long reading times and low reader confidence in growth zone counts. Growth zones were also more difficult to interpret for older fish and this increased the error with age. Brown et al. (2003) concurred and added that high otolith rejection frequencies, difficulty resolving growth ring numbers and false checks were also characteristic difficulties of ageing *P. saltatrix*. Robillard et al. (2009) identified further complications when they noted the infrequent occurrence of “double annuli” between the ages of four and seven.

In spite of problems with the accuracy of ageing, *P. saltatrix* has been described as a moderately long lived species which attains a maximum age of 14 years (Wood 2013). However, the maximum age and growth of this species varies depending on the environmental and fishery characteristics influencing populations throughout its cosmopolitan distribution. *P. saltatrix* are known to have one of the fastest specific growth rates (1-2 mm/day) reported for temperate fishes, particularly when they have a diverse piscivorous diet (Juanes and Conover 1994a,b,c, Buckel et al. 1998). Juanes et al. (1996) noted that growth rate is variable between *P. saltatrix* populations and identified slow (South Africa, the Mediterranean and Australia), medium (Black Sea and Brazil), and fast (Senegal and the United States) growing populations. Goodbred and Graves (1996) concluded that there may be a genetic basis for differential growth rates between populations but differential growth rates may also relate to the metabolic influence of temperature upon fish growth.

Temperature influences biological reaction rates within ectothermic organisms to metabolically regulate achieved growth rates (Neuheimer et al. 2011). The growth rate groupings noted by Juanes et al. (1996) may therefore reflect the influence of regional temperatures on *P. saltatrix* growth. While temperature generally elevates the metabolism of fishes, this only occurs to a species specific critical thermal threshold, where after the metabolic rate falls dramatically (Neuheimer et al. 2011). While Buckel et al. (1995) found that elevated temperatures increased the consumption and growth rates of *P. saltatrix* from the American east coast, and Smith et al. (2013) also linked faster growth rates of *P. saltatrix* in Australia to warmer ambient temperatures, the upper thermal threshold for this species has not been identified. These studies indicate that increasing temperatures in southern Angola may influence the growth rate of *P. saltatrix*.

Metabolic increases in growth rate cannot continue indefinitely due to the energetic demands of increasing metabolic rates (Neuheimer et al. 2011). Furthermore the normal temperature range in which species are found, known as their “thermal window”, influences the extent of the impact changing temperatures will have (Neuheimer et al. 2011). Climate change driven warming is expected to initially promote faster growth rates in temperate fishes to a critical threshold, after which fish will have difficulty in maintaining their metabolic functions leading to rapid decreases in their growth rate (Neuheimer et al. 2011). However, phenotypic

plasticity may play a role in the critical threshold temperature. For example, summer spawned *P. saltatrix* along the east coast of America are thought to have a greater tolerance for cold temperatures than their spring spawned conspecifics. As a result summer spawned fish are thought to be able to survive at cooler temperatures and thus are found at higher latitudes (Slater et al. 2007).

Despite faster growth, fish that are exposed to warmer temperatures tend to attain smaller maximum sizes (Angilletta et al. 2004). This supports the “temperature size rule” which is considered one of the most taxonomically widespread biological trends known to science (Fischer and Fiedler 2002, Angilletta et al. 2004). Temperature has also been shown to influence the natural mortality estimates (M) of fish populations, suggesting higher natural mortality in warmer temperatures (Pauly 1980). This indicates that the M/K ratio, noted by Beverton and Holt (1959) to be relatively constant within taxa, is actually also a function of temperature (Pauly 1980). Temperature is therefore considered to be a major environmental parameter affecting the growth and population structure of *P. saltatrix* populations; however temperature is not the sole environmental determinate of *P. saltatrix* biology and anthropogenic influences (e.g. fishing pressure) can also alter the biological parameters of fish species.

Fishing represents the greatest anthropogenic influence on fish populations and the growth rate of fishes has been closely linked to their level of exploitation (Ward et al. 2006, Akyol and Ceyhan 2007). Fishing practices are generally selective for larger and older fish in a population (Law 2000), and this selectivity typically leads to smaller maximum sizes and younger average ages in harvested populations (Conover and Munch 2002, Berkeley et al. 2004b). Although alterations to population demographics influence a fish stock in many ways, a compensatory increase in growth rate is a common response to fishery harvests (Charnov and Berrigan 1991, Trippel 1995, Conover and Munch 2002, Angilletta et al. 2004, Miethe et al. 2009, Neuheimer and GrønkJær 2012, Eikeset et al. 2013). However, reduced average age and mean length can have a variety of longer-term biological (Jennings et al. 1998) and genetic (Rijnsdorp 1993, Law 2000, Rowe and Hutchings 2003, Hankin et al. 1993) impacts that are difficult or impossible to reverse and will ultimately affect the economics of fisheries targeting the species (Eikeset et al. 2013).

The *P. saltatrix* population in southern Angola has been subject to both the impacts of rapid warming and increasing levels of exploitation over the last decade (see Chapter 2). The similar biological responses of faster growth and reduced maximum size suggests that both increasing temperatures and selective fishing mortality are likely to have combined and complementary influences upon growth in the southern Angolan *P. saltatrix* population. The aim of this chapter was therefore to provide the first scientific description of age and growth for *P. saltatrix* in southern Angola, to compare population demographics and growth rates observed between the two study periods and to evaluate the impact of rising temperatures and increasing levels of exploitation on biological parameters related to growth.

Methods

P. saltatrix were measured (FL and TL) to the nearest millimetre, weighed (total & eviscerated weight) to the nearest gram and both sagittal otoliths were removed and stored dry in Eppendorph containers. In the laboratory, otoliths were prepared following the methods of Robillard et al. (2009). They were set in clear casting resin and transversely sectioned through the nucleus, to a thickness of 0.4 mm using a twin blade diamond edged saw. Sections were then baked in a furnace set to 400°C for at least three minutes (or until golden brown in colour) prior to being placed onto slides with DPX microscopy mountant (Saarchem). A thin layer of DPX mountant was also placed on top of each section to improve its visual clarity.

Otoliths were read at a magnification of 20 X or less under a dissection microscope using transmitted light. Growth zones were counted from the nucleus to the otolith edge, preferably along the sulcus acusticus, or along any axis where growth zones were most visibly distinguishable. The edge of each otolith was also classified as either opaque or translucent.

Three readers analysed all the otolith sections once, while two of the readers conducted multiple readings, with a maximum of five readings being conducted by one reader, including an initial reading to gain familiarity with the structures. Readings by any individual reader were separated by at least two weeks to avoid bias which can arise from readers remembering particular structures (Campana 2001). Growth zone counts were considered valid if the same

value was recorded for a particular otolith by multiple readers in three reading attempts. Alternatively if the results of three readings did not agree but were numerically sequential the median value was chosen as a final estimate. Estimates of age were discarded if there was a lack of fulfilment to either of the above conditions (Campana 2001).

The relationship between fork length (FL) and total length (TL) was described using a linear regression of the form:

$$FL = mTL + c$$

where m represents the slope and c is the slopes intercept.

Length to weight relationship

The relationship between fork length (FL) and total weight (Wt) was assessed using log-transformed length and weight data in the exponential relationship used by Froese (2006) of the form :

$$Wt = \alpha FL^{\beta}$$

where α is the coefficient and β is the exponent of the arithmetic form of the weight-length relationship.

The precision of growth zone counts was estimated using the index of average percent error (IAPE) proposed by Beamish and Fournier (1981) of the form:

$$IAPE_j = \frac{1}{n} \sum_{j=1}^n \left[\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - \bar{X}_j|}{\bar{X}_j} \right] \times 100$$

where n fish are aged, R is the number of times each fish is aged, X_{ij} is the i th age determination for the j th fish and $\bar{X}_j$ is the average age determined for the j th fish. Values were averaged across the range of estimates to obtain a single value that was represented as a percentage.

A coefficient of variation (Chang 1982) was also calculated to investigate the precision of age estimates as:

$$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^R \frac{(X_{ij} - \bar{X}_j)^2}{R-1}}}{\bar{X}_j}$$

where R is the number of times the fish is aged, X_{ij} is the i th age determination of the j th fish and $\bar{X}_j$ is the average age estimate for the j th fish. Values were averaged across the range of estimates to obtain a single value that was represented as a percentage.

Marginal zone analysis

The periodicity of growth zone deposition was validated through a marginal zone analysis with appearance of the growth zone on the marginal edge of each otolith being categorised as either opaque or translucent. Each otolith was assigned to a month (M_i) according to the fishes date of capture and the monthly proportion of otoliths with an opaque edge was then modelled using a periodic regression (Flury and Levri 1999) of the form:

$$\text{logit}(\hat{O}_i) = \beta_0 + \beta_1 \sin\left(2\pi \frac{M_i}{P}\right) + \beta_2 \cos\left(2\pi \frac{M_i}{P}\right)$$

where $\hat{O}_i$ is the expected proportion of otoliths with an opaque growth zone margin during each month (M_i), P is the assumed periodicity of growth zone deposition (12 for annual and 6 for biannual) and β_0 , β_1 and β_2 are regression coefficients.

The estimation of regression parameters was based on non-linear minimisation of a negative log-likelihood function of the form:

$$-LL = -\sum [m_i \ln(\hat{O}_i) + (n_i - m_i) \ln(1 - \hat{O}_i)]$$

where n_i represents the number of otoliths examined in each month and m_i is the number of otoliths that were categorised as having an opaque zone on their margin. The monthly proportions of otoliths with an opaque edge were fitted to the periodic logistic regression using the methods described in Beamish et al. (2005) and a likelihood ratio test (LRT) was used to test the null hypothesis of annual deposition of a single opaque growth zone.

Chemical marking validation

Although marginal zone analysis was conducted, mark recapture studies in natural environments using fluorochrome markers of hard structures are the most widely accepted method of age validation across age classes (Beamish and Mcfarlane 1983, Campana 2001, Potts and Cowley 2005). The validation of otolith growth zone deposition periodicity was

therefore further investigated using the chemical marker oxytetracycline (OTC). This aspect of the study fell within the ongoing fish tagging research being conducted in the Flamingo Lodge region (see Chapter 2) and followed the methods described by Potts and Cowley (2005).

A total of 447 *P. saltatrix* were measured (FL) and intramuscularly injected with High-Tet oxytetracycline (OTC $\pm 0.1\text{ml kg}^{-1}$) between August 2007 and February 2009. These fish were tagged in their dorsal musculature with plastic dart tags (Hallprint; 89 mm long with 1.4 mm diameter) to allow the identification of recaptures. A sharp and disinfected stainless steel applicator was used to insert tags and great care was taken when injecting and tagging fish, with vinyl stretchers and damp cloths being used while minimizing handling times and stress wherever possible.

The sagittal otoliths of chemically marked *P. saltatrix* were stored and processed under dark conditions to minimize the denaturing of OTC that occurs with natural light exposure. The sectioning and processing of these otoliths was otherwise the same as described for other otoliths, but these sections were not baked. The sections were viewed under reflected ultraviolet light, which promoted OTC band luminance. A photograph was taken of the otolith region where the OTC band and other growth zones were clearest.

Length-at-age

Length-at-age was analysed using ages in days, which were calculated based on the date of capture for each *P. saltatrix*, theoretical birth dates and the date of opaque zone formation determined by marginal zone analysis. The theoretical birth date was the 15th of November, as the highest proportion of ripe *P. saltatrix* was noted during November for both study periods (Chapter 5), and opaque zone formation was assumed to occur on the 15th of July as otoliths from this month had the highest proportion of opaque zones on their margin. The calculated ages in days were then divided by 365 to obtain ages in decimal years.

The growth of *P. saltatrix* in southern Angola was modelled using length and age data to develop Von Bertalanffy growth curves (VBGC) as proposed by (Ricker 1975) using the Von Bertalanffy growth function:

$$L(t) = L_{\infty}(1 - e^{-K(t-t_0)})$$

where $L(t)$ is the length of a fish at age (t), L_{∞} is the theoretical maximum length of *P. saltatrix* in the sampled population, K is the Brody growth co-efficient and t_0 is the theoretical age at a length of zero millimetres.

Unfortunately, since there were not enough *P. saltatrix* of less than one year old in the samples, the VBGC and Schnute growth (Schnute 1981) models did not provide an adequate description of early growth of this species and produced unrealistic estimates of t_0 . The rapid growth for young-of-the-year *P. saltatrix* was however assumed to be approximately linear, as it is for estuarine resident *P. saltatrix* on the American east coast (Juanes et al. 1996), and was therefore modelled using the formula:

$$L(t) = mt + t_0$$

where $L(t)$ is the length of a fish at age (t), m represents linear growth and t_0 represents the length at age zero.

The slope intercept was fixed at zero based on the assumption that fish of length zero would also have an age of zero.

A likelihood ratio test was conducted to compare the Von Bertalanffy growth curve parameters between sexes. The variability of parameter estimations was calculated using a parametric bootstrapping procedure with 1000 iterations used to construct 95% confidence intervals through the percentile method outlined in Buckland (1984). The coefficient of variation (CV) from Chang (1982) provided further information on parameter variability and

the model parameters were used to investigate observed changes in the length at age between sexes.

Comparison of the growth rate between periods

A LRT (described above) was also used to compare the VBGC parameters between the two periods. Male and female fish were compared separately. However, since the length frequency of the population has a major impact on the VBGC parameters, a second LRT analysis was conducted. The number of fish in each one cm length class in period 2 was calculated. Fish from period 1 were also divided into one cm size classes and a random sample of the number of fish in each size class in period 2 was selected. This left two datasets comprising periods 1 and 2 with identical length frequencies. The von Bertalanffy growth curve was then re-estimated using the procedure described above and a likelihood ratio test (described above) was conducted to compare the growth curve parameters between periods.

Results

The relationship between fork and total length for *P. saltatrix* in southern Angola (both study periods), was best described as: $TL = 1.1377(FL) - 2.6242$ ($R^2 = 0.97$). The minimum (period 1 = 310 mm, period 2 = 293 mm) and maximum (period 1 = 760 mm, period 2 = 746 mm), fork length decreased between periods (Figure 4.1). The average length also decreased from 507 mm FL during the 1st to 462 mm FL during the 2nd period (Figure 4.1, Table 4.1). Length class distribution breadth was narrower for males (9 size classes) than for females (10 size classes) during both periods (Figure 4.1, Table 4.1). Overall length distribution breadth was equal for both periods (10 size classes) but the distribution shifted to a smaller size class during the second period (Figure 4.1). A students t-test ($p < 0.05$) determined there was a significant difference in the length distribution by sex for period 1 (students t-test, $p = 0.03$) and for combined sexes between periods ($p = 0.04$).

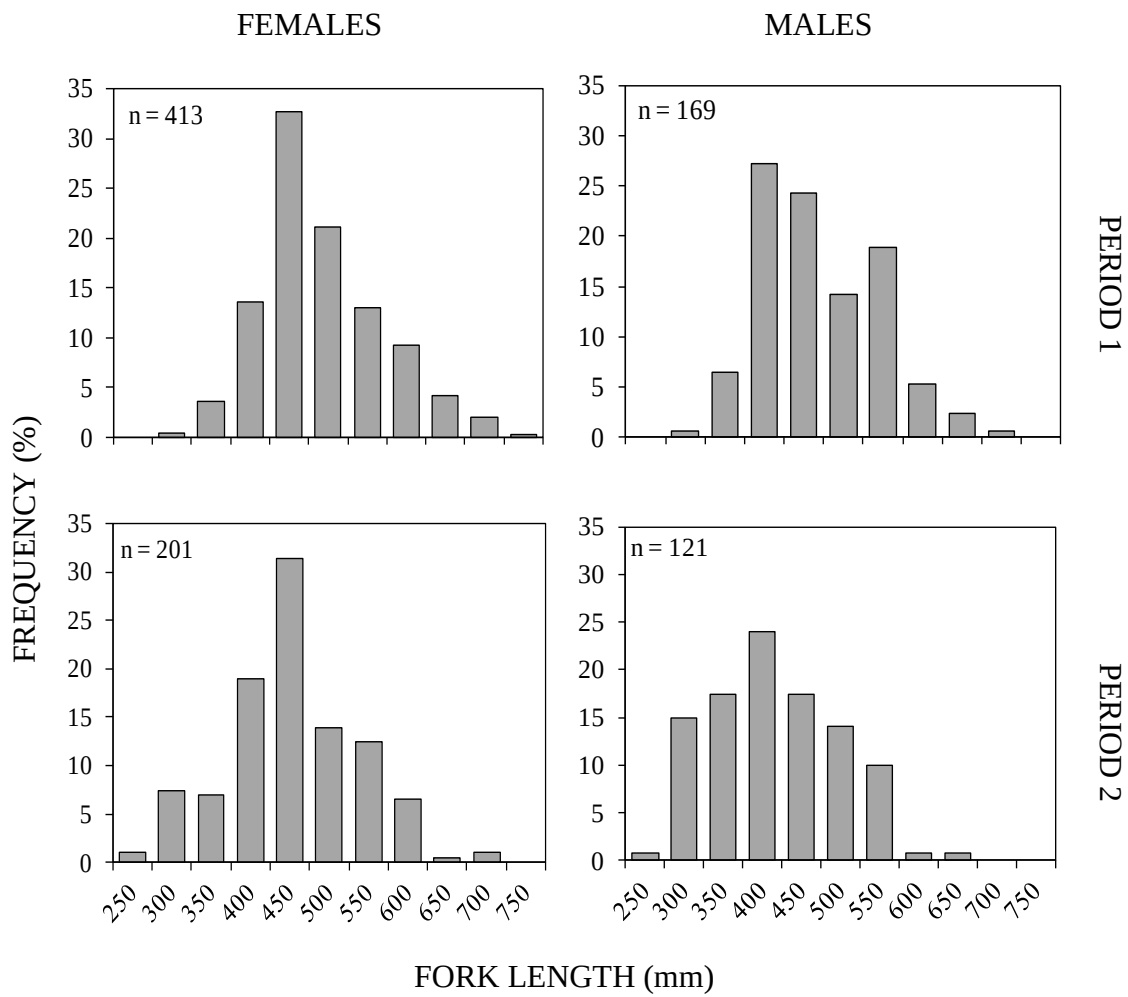


Figure 4.1: Length frequency distributions for male and female *P. saltatrix* sampled during period 1 and period 2 in southern Angola.

Length to weight

The length to weight relationship for the two periods combined was $W = 2E-0.5FL^{2.901}$ and described 91% of the variance. Accurate between periods comparison was not possible due to the difference in the resolution of the weighing scales used but obtained data is displayed in Figure 4.2.

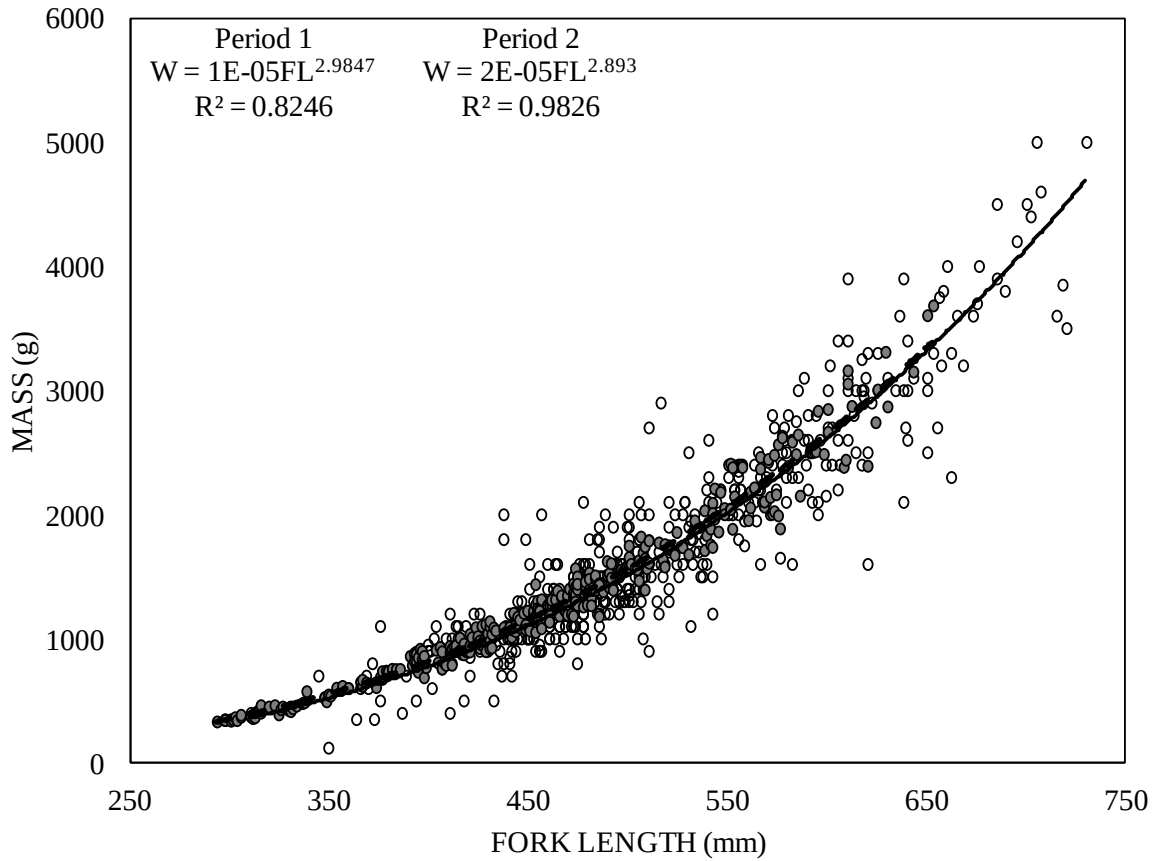


Figure 4.2: Length to weight relationships for *P. saltatrix* in southern Angola during period 1 (circles with no fill and solid black trendline) and period 2 (circles with grey fill and dashed black trendline).

Female *P. saltatrix* were on average heavier during both periods and the average mass of both males and females decreased from period 1 to period 2 (Table 4.1).

Table 4.1: Average mass (g) and fork length (mm) for male and female *P. saltatrix* from southern Angola during both study periods. Brackets display standard error values for each average length but weights were not comparable based on differing mass precision between periods.

	Period 1	Period 2
	Average Fork Length (mm)	
Females	513.70 (3.80)	476.25 (5.82)
Males	491.88 (5.80)	440.44 (7.55)
	Average Mass (g)	
Females	1686.24	1442.13
Males	1439.66	1193.49

Otolith readings

A total of 833 otoliths (period 1 - n=519; period 2 - n=314) were examined. The discard rate was higher during period 1 but this was not reflected in the CV (%) as a result of more reading attempts being conducted on otoliths from this period (Table 4.2).

Table 4.2: Summary results of growth zone counts obtained from sagittal otoliths collected from *P. saltatrix* in southern Angola during period 1 and period 2.

	Period 1	Period 2
IAPE (%)	32.86	31.23
CV (%)	35.53	41.43
Discard rate (%)	64.26	58.64
Reading attempts	4	3
# Readers	3	2

Marginal zone analysis

The highest proportions of otoliths with an opaque margin were observed during the winter months with a peak in July. The full periodic regression model estimated an opaque growth zone deposition periodicity of 12.01 months (Table 4.3). The annual model did not differ significantly from the full model ($p = 0.87$) while the biannual models parameter differences were significant ($p = 0.00$), (Table 4.3). Therefore, the hypothesis that one opaque zone formed annually was accepted and based on the proportion of opaque margins per month (Figure 4.3) this zone generally developed in July.

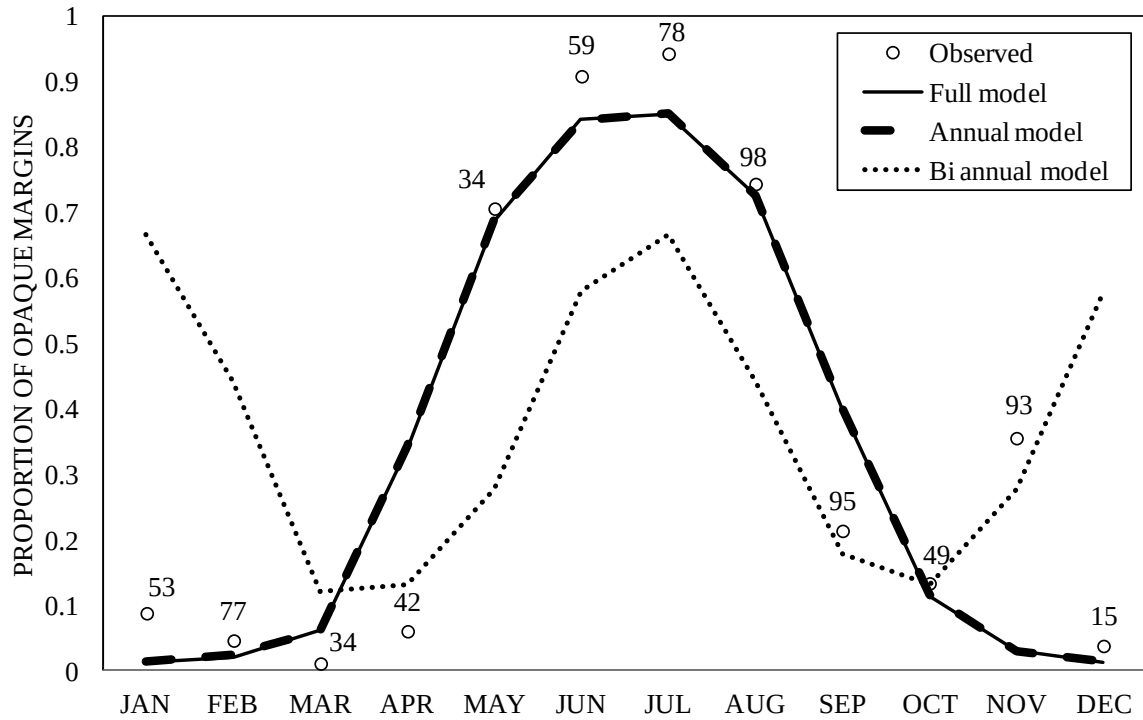


Figure 4.3: Observed monthly proportions of otoliths with opaque margins (clear circles) and the periodic regressions based on the full (solid line), annual (dashed line) and bi annual (dotted line) models used to determine opaque growth zone deposition periodicity.

Table 4.3: Estimated parameters obtained from a logistic periodic regression analysis of opaque growth zone deposition in the saggital otoliths of *P. saltatrix* from southern Angola. Periodicity was fixed for the annual and biannual models but estimated using minimised log likelihood methods for the full model.

Parameter	Periodic regression model		
	Full	Annual	Biannual
β_0	-1.35	-1.35	-0.60
β_1	0.69	-0.69	-0.33
β_2	-3.09	-3.09	1.29
Period	12.01	12.00	6.00
d.f.	4	3	3
LL	281.36	281.38	424.69
P		0.87	0.00

Chemical marking validation

Despite the relatively large number ($n=447$) of chemically marked *P. saltatrix*, only four fish were recaptured. Of these four, the OTC band was only appropriately discernible in one fish, a 489 mm FL individual which was tagged on the 2nd of March 2008 and recaptured after 120 days at liberty on the 9th of July 2008. The OTC band (from the 2nd of March) was visible near the edge of the otolith (Figure 4.4) and there were no opaque bands between it and the edge (representing the 9th of July) of the otolith. The previous opaque zone (indicated by the white dot) was situated far from the edge of the otolith (Figure 4.4). The relative thickness of the hyaline zone in which the chemical band was visible suggests that formation of the next opaque (winter) zone would have begun shortly. Because the fish was recaptured in July this finding provides further evidence for winter opaque zone deposition.

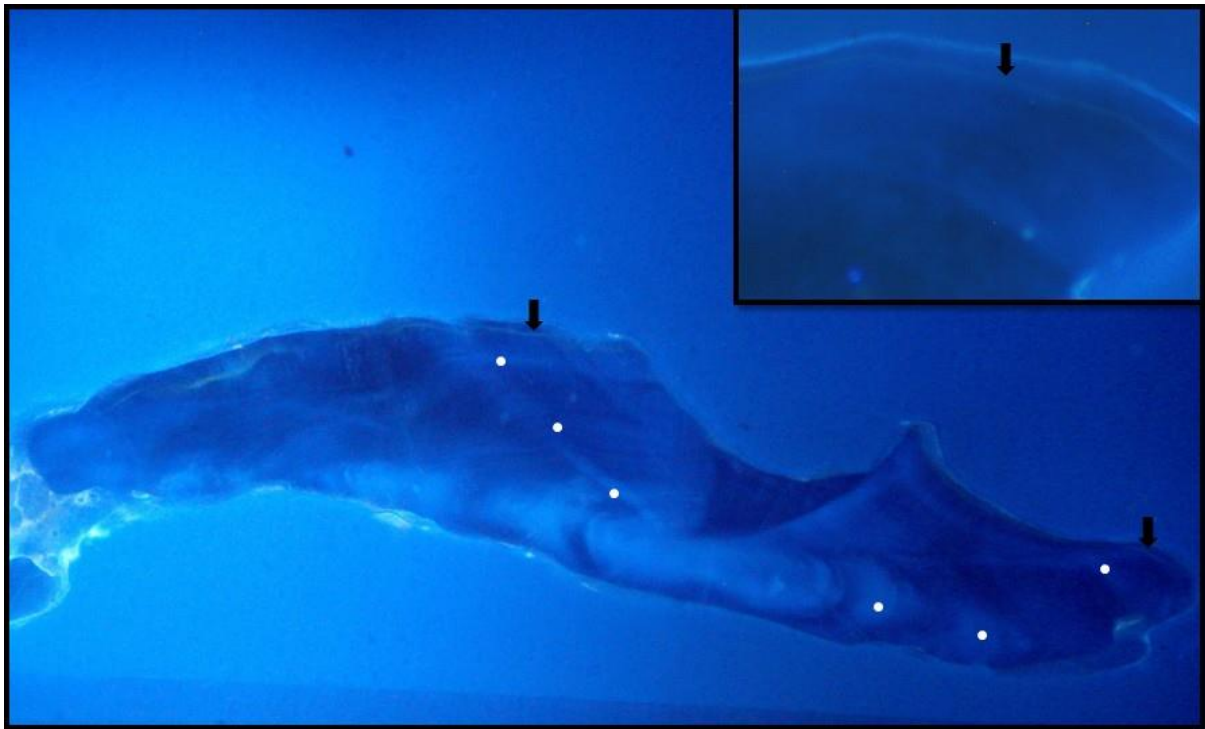


Figure 4.4: Transverse section from the sagittal otolith of a 489 mm FL *P. saltatrix* that was injected with oxytetracycline. White dots represent opaque growth zones and the dull fluorescent OTC band is indicated by the black arrows. Both photographs were taken under reflected UV light and the main photograph was taken at 50X magnification while the inserted photograph was taken at 120X magnification.

Age frequency

There was a decrease in the maximum and median ages of *P. saltatrix* from the first (max. = 13.5, median = 4.1) to the second (max. = 10.0, median = 3.8) period. The modal age for females (period 1 = 4.37; period 2 = 2.65 years) and males (period 1 = 4.41; period 2 = 3.79) also decreased between periods (Figure 4.5). Age truncation was more evident for females in the second period (Figure 4.5).

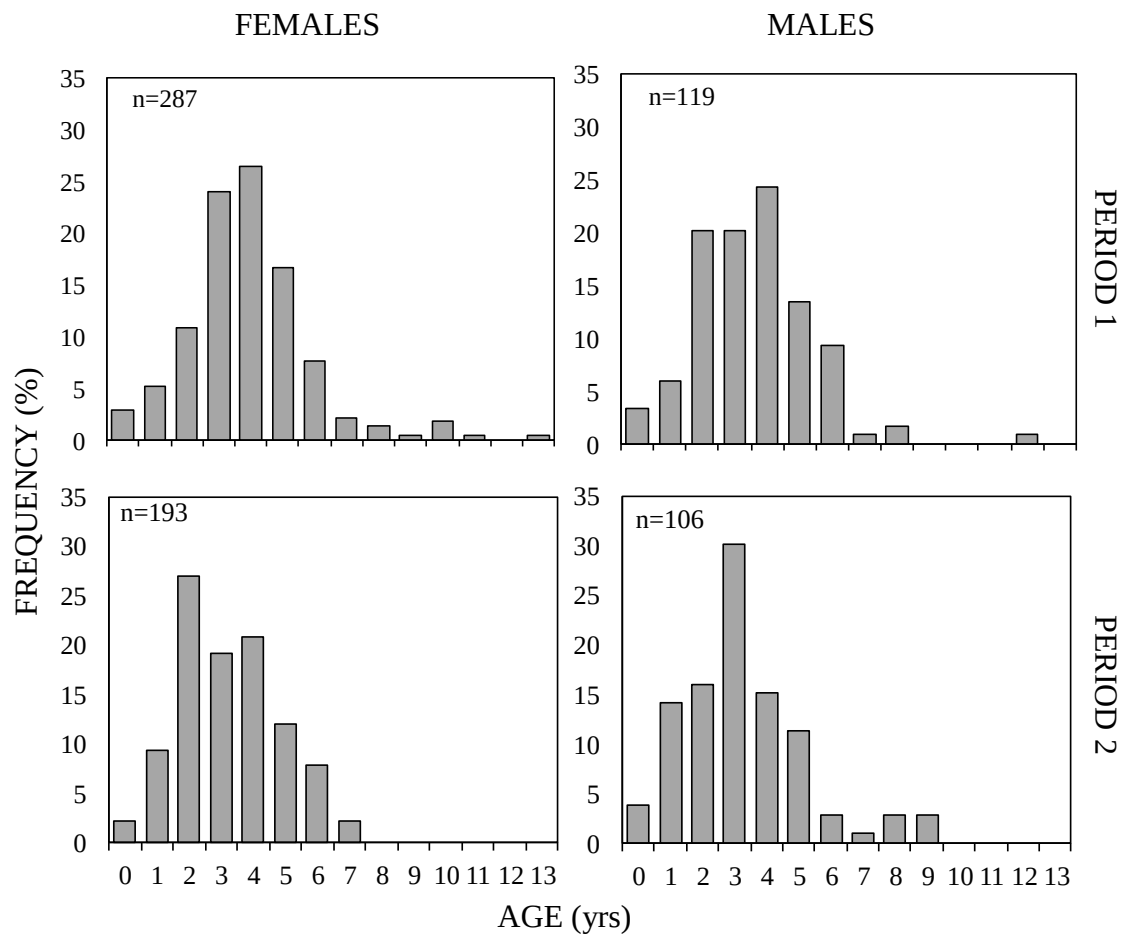


Figure 4.5: Age frequencies for female and male *P. saltatrix* (juveniles represented in both sexes graphs) from southern Angola between June 2005 and December 2006 (period 1) and from June 2012 to February 2013 (period 2).

Von Bertalanffy Growth curves

The first year of linear growth was rapid and the growth from age 1 across both periods was best described by the equation: $L(t) = 684.62(1-e^{-0.162(t-4.22)})$ (Figure 4.6). There was a high level of variability between parameter estimates (Table 4.4). The CV was highest for the Brody growth coefficient (K) (1000 iterations) throughout and the CV was higher for all parameters in period 2 (Table 4.4).

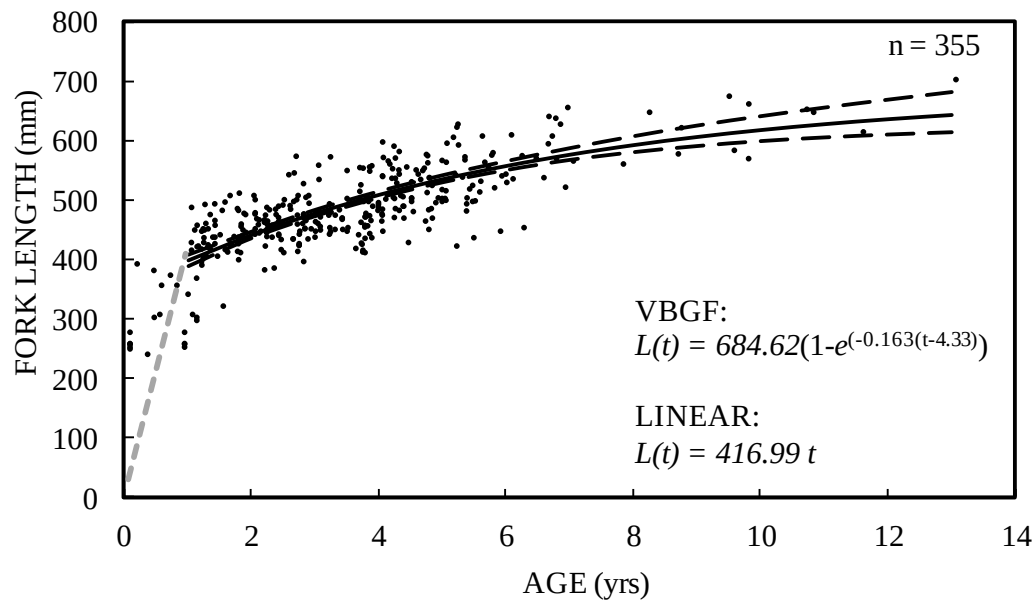


Figure 4.6: Von Bertalanffy growth function plot (for fish over age 1) for *P. saltatrix* across both study periods. Dots represent length at age for individual *P. saltatrix*, solid line represents the Von Bertalanffy growth model while black dashed lines indicate 95% confidence intervals calculated using 1000 bootstrapped iterations. Grey dashed line represents the linear model of growth up to one year of age.

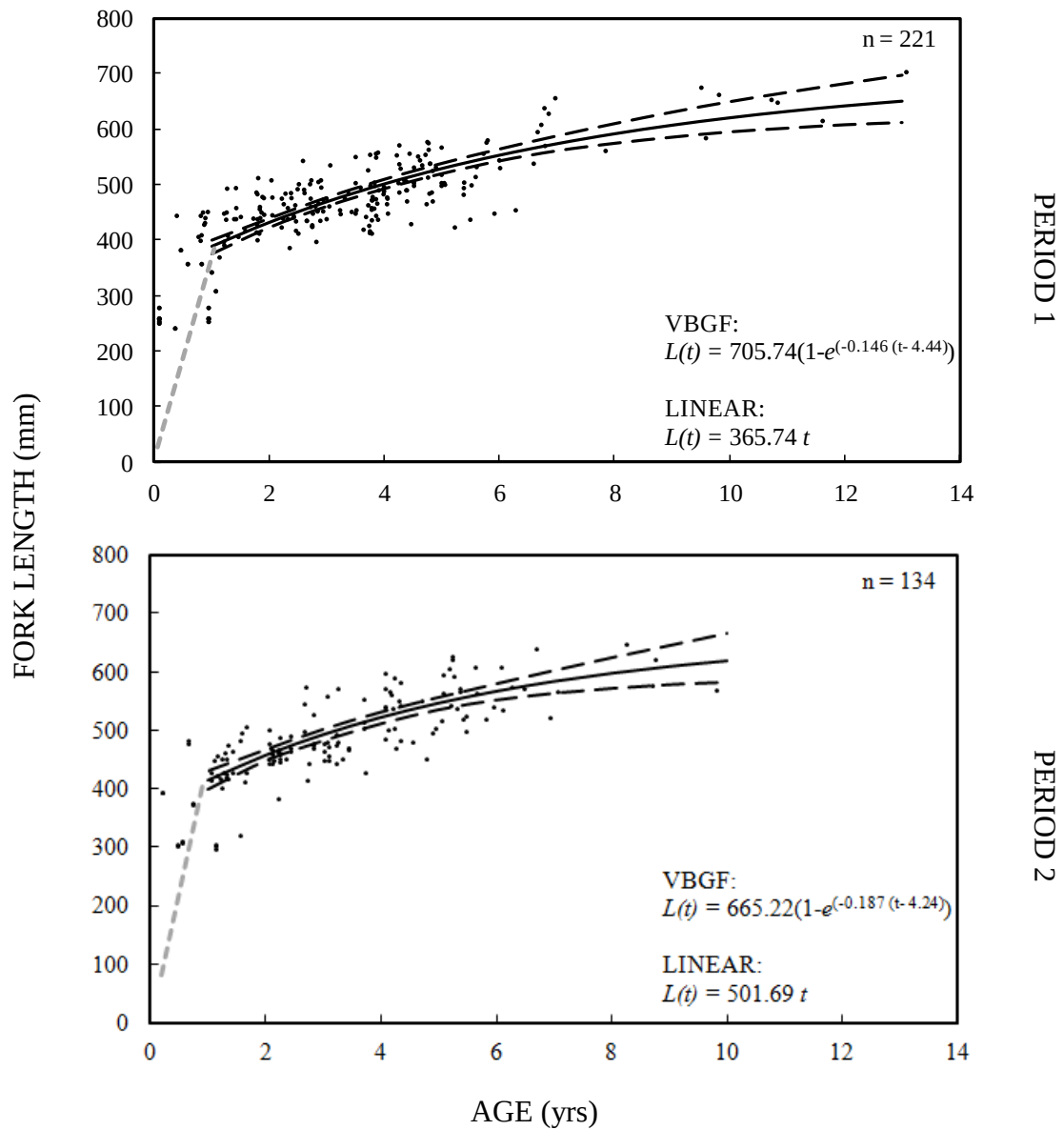


Figure 4.7: Linear model (grey dashed line) for the early growth (up to one year) and the Von Bertalanffy growth curve (solid black line) for *P. saltatrix* in southern Angola during period 1 (June 2005 – December 2006) and period 2 (June 2012 – February 2013). Dots represent observed data for individual fish and dashed black lines are the 95% confidence intervals calculated using 1000 bootstrapped iterations.

Table 4.4: Point estimates and summary statistics obtained for von Bertalanffy growth function parameters using 1000 bootstrapped samples for combined study periods and in period 1 and period 2 separately for *P. saltatrix* in southern Angola.

	Summary Statistics							
	Parameter	Point Estimate	Mean	Coefficient of variation	Standard error	Lower and upper 95% Confidence interval	Min	Max
Combined periods (n = 352)	L_{∞} (mm FL)	684.62	691.66	6.24%	43.15	628.79 – 795.66	610.23	1027.65
	K (year ⁻¹)	0.163	0.164	19.39%	0.03	0.10 – 0.23	0.05	0.28
	t_0 (years)	-4.33	-4.40	16.04%	0.71	-5.92 - -3.25	-8.56	-2.74
	L_{∞} (mm FL)	705.74	715.72	8.73%	62.48	630.45 – 868.69	604.29	1100.00
Period 1 (n = 218)	K (year ⁻¹)	0.15	0.15	24.20%	0.04	0.08 – 0.22	0.05	0.29
	t_0 (years)	-4.44	-4.50	18.92%	0.85	-6.53 - -3.11	-8.53	-2.38
	L_{∞} (mm FL)	665.22	691.82	18.31%	126.68	593.70 – 926.27	545.37	3472.88
Period 2 (n = 134)	K (year ⁻¹)	0.19	0.19	36.66%	0.07	0.07 – 0.33	0.01	0.48
	t_0 (years)	-4.24	4.49	31.77%	1.43	-8.06 - -2.38	-11.79	-1.74

The growth curves of male and female *P. saltatrix* were similar (LRT – full model, d.f. 3, $p = 0.45$) during period 1. However, although females grew significantly faster than males during period 2 (LRT - full model, d.f. 3, $p = 0.01$) there was high variability within the parameter inputs to this analysis (Table 4.4). When the full dataset was used, the VBGC parameters (Linf – LRT, d.f. 2, $p = 0.75$; K – LRT, d.f. 2, $p = 0.66$; t_0 – LRT, d.f. 2, $p = 0.98$) were not significantly different between periods. However, the LRT for the full model indicated that there was a significant difference in the growth curves between period 1 and 2 (LRT, d.f. 3, $p < 0.01$). When the growth curves of the identical length frequency structures (equal Linf and t_0) were compared between the periods, no significant difference was observed for the Brody growth co-efficient (K - LRT, d.f. 2, $p = 0.08$) or for the full models (LRT, d.f. 3, $p = 0.41$).

When growth curves were analysed for each sex separately between periods there was no significant difference observed for males VBGC parameters (Linf – LRT, d.f. 2, $p = 0.98$; K – LRT, d.f. 2, $p = 0.98$; t_0 – LRT, d.f. 2, $p = 0.99$) or the full model (LRT, d.f. 3, $p = 0.31$). For females however, while there was no significant difference for individual VBGC parameters (Linf – LRT, d.f. 2, $p = 0.94$; K – LRT, d.f. 2, $p = 0.99$; t_0 – LRT, d.f. 2, $p = 0.86$), the full model differed significantly between periods (LRT, d.f. 3, $p = 0.01$).

Table 4.5: Von Bertalanffy parameters based on log likelihood minimization of model error, average and maximum ages as well as average and maximum lengths for male and female *P. saltatrix* from which final age estimates were obtained during period 1 and period 2.

	Period 1		Period 2	
	Male	Female	Male	Female
L_{∞}	705.85	705.29	679.83	729.39
K	0.14	0.15	0.16	0.14
t_0	-4.46	-4.54	-4.32	-5.16
# samples	70	151	44	90
Average age	4.08	4.43	4.04	3.89
Max. age	12.20	13.53	9.99	7.88
Average FL	484.27	508.81	455.83	476.01
Max FL	730	722	650	643

Table 4.6: Results from the more comparable between period analysis of growth rate using the Von Bertalanffy growth function after equal length distributions had been attained for each period through random selection within comparable length bins.

	Period 1	Period 2
L_{∞}	684.62	684.62
K	0.16	0.17
t_0	-4.33	-4.33
R^2	0.308	0.452

Discussion

P. saltatrix are characterised by rapid growth during their first year (Juanes et al. 1994a), fish in this study attained 58% (period 1) and 60% (period 2) of their maximum length during their first year. In a South African study, Govender (1996) estimated that *P. saltatrix* attained 44% of their maximum mean length during their first year but other populations globally tend to only attain between 23% and 39% of their maximum length in their first year (Figure 4.9, Table 4.7). Optimal juvenile growth for *P. saltatrix* and other fishes appears to be related to amongst other things, the temperature regime and the quality and quantity of food available (Juanes et al. 2001, Valente et al. 2013).

The optimal temperature for early growth in *P. saltatrix* has not been documented. However, the populations with the fastest early growth rates and nursery areas in the coastal zone had average annual temperatures ranging from 12° to 22° C (Table 4.7). Although the exact location of the southern Angolan nursery area is unknown, the average annual sea surface temperature for both periods (19° C in period 1 and 20° C in period 2) fall within this broad temperature range to suggest that temperature was not a major factor influencing the rapid early growth in southern Angola.

Table 4.7: Environmental and life history parameters for *P. saltatrix* populations in southern Angola and other regions. References indicated by superscript numbers: 1 = Robillard et al. (2009), 2 = Barger (1990), 3 = Smith et al. (2013), 4 = Ceyhan et al. (2007), 5 = Govender (1996), 6 = Salerno et al. (2001), 7 = Haimovici and Krug (1996), 8 = NODC (2013), 9 = METOC (2013), 10 = Dineva (2013), 11 = Smit et al. (2013), 12 = Valentim et al. (2013), 13 = Juanes et al. (1996), 14 = Van der Elst (1976).

	Ageing method	L_{∞}	K	t_0	$\bar{Q}$	Mean temp (range)	Mean age 1 length	Max. age (yrs)	Nursery habitat
Southern Angola Period 1	Otoliths (bake and section)	705.74	0.146	-4.44	103.04	18.4 (16-23)	395	13.53	Unknown
Southern Angola Period 2	Otoliths (bake and section)	665.22	0.187	-4.24	124.39	19.5 (15-24)	420	9.99	Unknown
USA	Otoliths (bake and section) ¹	815.30 ¹	0.311 ¹	-0.301 ¹	253.56	17.04 (1-30) ⁸	270	13 ¹	Estuaries Nearshore ¹³
Gulf of Mexico	Otoliths (whole) ²	944 ²	0.180 ²	-1.033 ²	169.92	24.15 (0-32) ⁸	289	8 ²	Estuaries Coastal ³
Western Australia	Otoliths (whole) ³	592 ³	0.464 ³	-0.096 ³	274.69	21.70 (19-25) ⁹	236 ³	10 ³	Estuaries Coastal environs ^{3, 13}
Turkey	Otoliths (whole/sectioned) ⁴	510 ⁴	0.228 ⁴	-1.260 ⁴	116.28	20.27 (11-25) ¹⁰	195 ⁴	3 ⁴	Inshore environs ^{4, 13}
South Africa	Otoliths (whole) ⁵	552 ⁵	0.43 ⁵	-0.97 ⁵	237.36	17.5 (12-27) ¹¹	315	10 ¹⁴	Sheltered bays ⁵
Southeastern USA	Otoliths (whole) ²	1019 ²	0.096 ²	-2.493 ²	97.82	21.53 (2 -30) ⁸	290	4 ²	Estuaries Nearshore ¹³
Northeastern USA	Scales ⁶	872 ⁶	0.260 ⁶	-0.930 ⁶	226.72	12.62 (1 -26) ⁹	344	12 ⁶	Estuaries Nearshore ³
Southern Brazil	Scales ⁷	662 ⁷	0.387 ⁷	-0.321 ⁷	256.19	24.91 (22-29) ¹²	153	8 ⁷	Estuaries ¹³

Unfortunately, the diet of the early juveniles in southern Angola remains largely undescribed (Chapter 3). However, since the study site is situated in the Benguela Ecosystem, which is considered to be one of the most productive ecosystems in the world and is very rich in fish resources (Olivar and Shelton 1993), it is possible that the quantity and quality of food available may support optimal juvenile growth in this region. However, since the growth in the first year was more than double that generally recorded elsewhere ($\pm 60\%$ vs 23-39% of the maximum size) these results should be questioned further. Possible reasons for the questionable results include inaccuracy in the ageing technique or bias in the sampling.

The structure and preparation method used to age *P. saltatrix* from southern Angola was guided by the comprehensive studies conducted by Robillard et al. (2009) and Sipe and Chittenden (2002). Sipe and Chittenden (2002) identified sectioned sagittal otoliths to be the most suitable calcified structures for ageing this species, while Robillard et al. (2009) refined the technique and suggested that a “bake and thin-section” method of preparation improved the clarity of the otolith for interpretation. Since this preparation method was followed in this study, it is unlikely that this aspect influenced the early growth estimates.

The extensive literature available on the optimal ageing methods suggests that *P. saltatrix* is difficult to age; as such, many authors have struggled with the interpretation of the species sectioned otoliths. For example, the annuli counts of sectioned otoliths varied by up to five years for otoliths from fish with maximum ages of approximately seven years amongst several experienced otolith readers in Australia (Jenke 2002). Despite following the otolith preparation methods and reading techniques outlined by Robillard et al. (2009), there was much variation in annuli counts for some otoliths in this study. This was reflected in the high IAPE and CV values (Table 4.2) and the variation in age estimates for some particularly ambiguous otoliths. For example, the maximum variation between count results for a single, subsequently discarded, otolith was 10 growth zones, with one reader obtaining a count of 13 for an otolith which was considered unreadable by another, and had counts of three and four in other readings. To remove this ambiguity, an experienced otolith reader was used for several readings and the otoliths were subject to a strict rejection policy (see above). As a result, relatively low sample sizes were obtained for fish with accepted ages but accepted estimates were considered to accurately represent the ages of *P. saltatrix* in southern Angola.

Identification of the first opaque zone was challenging for some of the sectioned otoliths analysed in this study, as was the case for the American *P. saltatrix* population (Robillard et al. 2009). If one neglects the first growth zone due to its ambiguity then the age determined from that reading would clearly underestimate age by one year. Therefore, as suggested by Robillard et al. (2009), identification of the first opaque zone in otoliths of this study was aided by careful inspection of first year crenulation and the position of the, often more distinct, second opaque zone relative to the nucleus edge.

Comprehensive life history studies require a representative sample of the species from all life history stages. One of the differences between this and Robillard et al's (2009) comprehensive ageing study was the lack of 0 year old fish captured during this study. This was reflected in the unrealistically low values of t_0 (-4.33 for combined periods) particularly when compared with the other studies. The primary issue was the unknown location of the juvenile nursery area. Possible nursery areas included the Cunene River mouth which is the only functional estuary in the region, the coastal embayment's of Tombua, Baia dos Tigres, Namibe and the shallow (8-20 m) offshore rocky reefs, Banco do Pinda, situated near to Tombua (Figure 2.1, Chapter 2). The Cunene River mouth was sampled regularly during both periods and no juveniles were captured during this time. Baia dos Tigres was sampled with seine nets during three separate field trips but no juvenile *P. saltatrix* were captured. Fishermen's catches in Tombua were also inspected on at least 40 and 10 occasions during the first and second periods respectively and no evidence of juvenile *P. saltatrix* was observed. However, fish between 20 and 30 cm FL were observed in the catches of hook and line fishers operating at Banco do Pinda and were retained for this study. While this may indicate that the nursery area may be on these offshore rocky reefs and hook selectivity may be preventing the capture of the smaller juveniles (<20 cm FL), it is possible that the early juvenile nursery areas are yet to be discovered in southern Angola.

The lack of small (< 20 cm FL) age 0 individuals in this study may be the greatest bias in determining the early growth of this species in southern Angola. Since there is considerable intrapopulation variation of growth and maturity in fishes (Walters and Martell 2004) it is likely that only the fastest growing juveniles left the nursery areas and were captured in the sampling area during this study. Therefore the overrepresentation of fast growing age zero

fish is most likely the primary reason for the extremely rapid early growth observed in this study. Future research on this species should therefore focus on identifying the juvenile nursery area and incorporating smaller fish into the growth estimate.

The rapid early growth was followed by relatively slow growth as the fish reached fork lengths above 400 mm FL. This coincided with the fork lengths over which percent maturity was above 50% and approaching 100% within this population (Chapter 5). This trend of decreasing growth with maturation is evident in the majority of *P. saltatrix* populations (Figure 4.9), but was most similar to the northeast American population (Salerno et al. 2001). These authors identified a significant decrease in the incremental growth of *P. saltatrix* after age two, with maturation occurring between ages one and two. Nevertheless, the adult growth rate of *P. saltatrix* in this study was considerably slower than other global populations. There are a number of potential reasons for this finding including several methodological issues (such as poor validation techniques and the interpretation of the otoliths), environmental factors (such as the thermal regime, food availability and population size and structure) and/or endogenous factors (e.g. genetics).

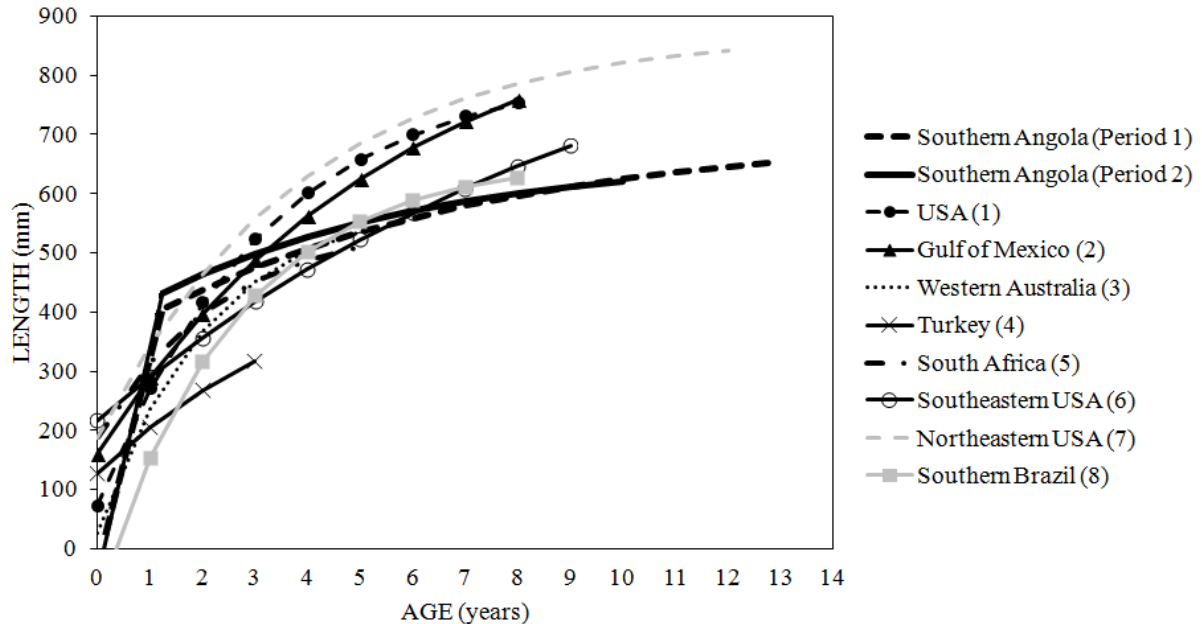


Figure 4.9: Growth curve comparison for *P. saltatrix* populations around the world. References: 1 = Robillard et al. (2009), 2 = Barger (1990), 3 = (Smith et al. 2013), 4 = (Ceyhan et al. 2007), 5 = (Govender 1996), 6 = (Barger 1990), 7 = (Salerno et al. 2001), 8 = (Haimovici and Krug 1996). Black lines indicate studies based on otoliths while grey lines indicate studies based on scales.

Poor age validation techniques can also result in underestimation of age, especially when validation is conducted on young age classes and the results are later applied to older fish (Campana 2001). An example of this was seen for Sablefish (*Anoplooma fimbria*) where scales, that had been validated using marginal increment analysis, were routinely used to age the species, until an OTC validation study determined that scales were underestimating the age of older fish by up to a factor of four (Campana 2001). Despite its limitations, the marginal zone analysis used in this study appeared to provide reasonable evidence for the assumption of annual growth zone deposition across the sampled age classes (Figure 4.3). The information obtained from the OTC validation experiment provided further support for the annual deposition of one opaque zone during the winter season and although the relatively short period at liberty could not confirm an annual growth ring deposition, the position of the OTC band in relation to the increments (Figure 4.4) suggested that this scenario was most likely.

Robillard et al. (2009) also noted annual growth zone deposition for sectioned otoliths from *P. saltatrix* off the American east coast and seasonal temperature fluctuations are often linked to the development and composition of otolith growth zones (Townsend et al. 1992, Wright 2001, Elsdon and Gillanders 2002). Considering that the formation of opaque zones is considered representative of slower winter growth (Anderson et al. 1992), opaque zone deposition during the historically coldest month of July in southern Angola was unsurprising (Figure 2.3, Chapter 2). Furthermore, the lack of pelagic fish in the diet of *P. saltatrix* during that time (Chapter 3) provides further evidence to suggest that this would coincide with the period of slowest growth.

Robillard et al. (2009) identified several “double annuli” in *P. saltatrix* otoliths for individuals older than 4 years and although it was not known if these structures represented one or two years of growth they were considered to be one annulus if the opaque zones joined at either the sulcal groove or the outer edge of the otolith. False rings have been attributed to other periods of slow growth, resulting from events such as spawning events, decreased food availability or a temperature anomaly during the year (Anderson et al. 1992, Colloca et al. 2003) and may significantly alter the estimates of age and growth. To eliminate the problems associated with false rings, Robillard et al.’s (2009) protocol for their identification was used.

However, the sulcal groove or outer edge of the otolith was not always clear and it is therefore possible that in some cases, false rings may have been considered to be annuli. Although the otoliths were read by at least one experienced reader, this potential bias may have, to some degree, contributed to the apparent slow growth rate of adult *P. saltatrix* in this study.

Despite potential methodological problems, if one accepts that the validation and ageing techniques used in this study are robust, then the slow adult growth rates may be attributed to environmental or endogenous factors. While environmental effects upon fish growth are generally difficult to quantify in wild stocks, the growth rate of fish has been related to water temperature in several studies. For example, the growth rate of several stocks of the cod species *Gadus morhua* increased by up to 30% for every 1°C increase in ambient temperature (Brander 1995). Temperature has also been found to influence the food consumption and digestion rate of *P. saltatrix* (Olla and Studholme 1971, Buckel et al. 1995), both of which may support faster growth. Warmer temperatures had a significant effect of increasing the growth of *P. saltatrix* from North America up to a maximum temperature of 24°C for small individuals (mean weight of 2.6 g) and to the maximum temperature of 30°C for ‘medium’ (mean weight of 10.6 g) and ‘large’ (mean weight of 24.12 g) individuals (Buckel et al. 1995). In western Australia summer spawned juvenile *P. saltatrix* grew faster than those spawned in winter and juveniles also grew faster in 2009-10 than during 1991-99 with warming being seen between these periods (Smith et al. 2013).

In this study, there was no significant evidence for a change in the growth rate of this species between the two periods (LRT, d.f. 1, $p = 0.088$, see table 3.7), despite a small change (0.78°C for comparable months) in the average annual temperature range. However, information on other global populations may provide information on the optimal average temperature for growth (Figure 4.9). Although there was a slight positive trend between growth rate (ω) and SST ($y = 0.9589x + 181.72$), it explained very little variation ($R^2 < 0.01$) and it was apparent that the mean annual temperature is not an important determinant of growth rate in this species.

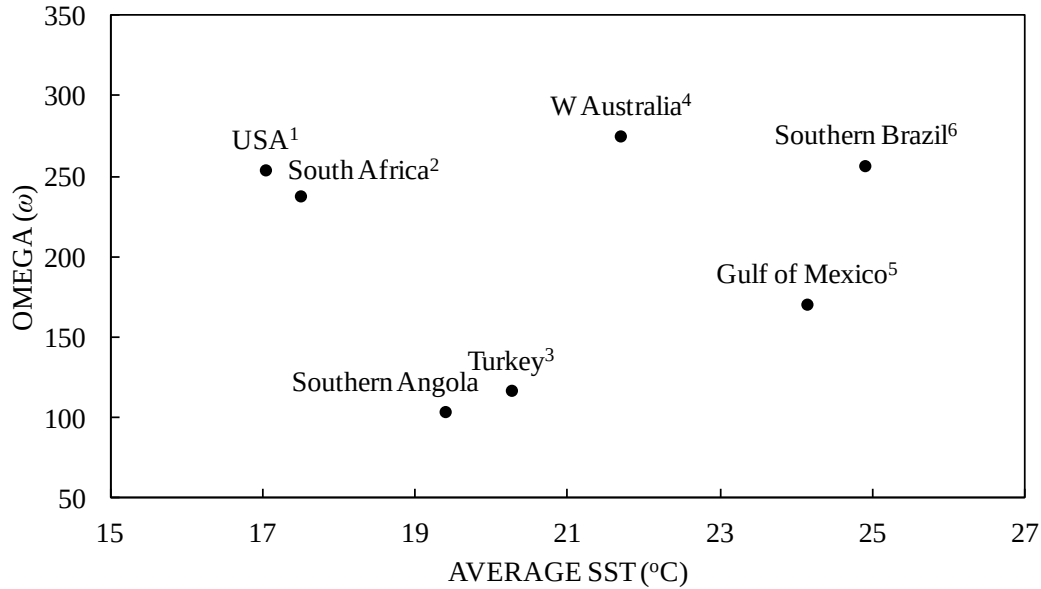


Figure 4.9: Relationship between growth rate (expressed as $\omega = L_{\infty} \times K$) and average annual sea surface temperature for seven global populations of *P. saltatrix*. 1 = Robillard et al. (2009), NODC (2013); 2 = Govender (1996), Smit et al. (2013); 3 = Ceyhan et al. (2007), Dineva (2013); 4 = Smith et al. (2013), METOC (2013); 5 = Barger (1990), NODC (2013); 6 = Haimovici and Krug (1996), Valentim et al. (2013).

The combined influences of food quantity consumed and the nutritional quality of this food can greatly influence the growth rate achieved by fishes. The fast growing *P. saltatrix* populations noted by Juanes et al. (1996) had diets dominated by nutrient rich small pelagic fishes as was the case for the Angolan population (Table 3.6, Chapter 3). The quantification of food availability was, as for most other studies, beyond the scope of this research but a reduced quality or availability of food would negatively influence the condition of *P. saltatrix*. Condition factor increased from winter to summer with greater inclusion of small pelagic fishes to the diet (see Chapter 3) and while comparative values of Fultons condition factor were unavailable for adult *P. saltatrix* in other regions, for fish younger than 1 year of age in southern Angola the average condition factor was lower than that of the comparative studies conducted by Stehlik (2009) or Deshpande and Dockum (2013).

Due to the lack of studies that have calculated Fultons condition factor for adult *P. saltatrix*, a comparison of adult condition was instead conducted using available length to weight relationships. The length to weight relationships in southern Angola were similar to those from other regions (Figure 3.10) and while the exploited American population displayed

greater weights at length, potential differences in the availability or quality of food for compared stocks was not considered to appropriately explain the relatively slow adult growth in the Angolan population based on this analysis.

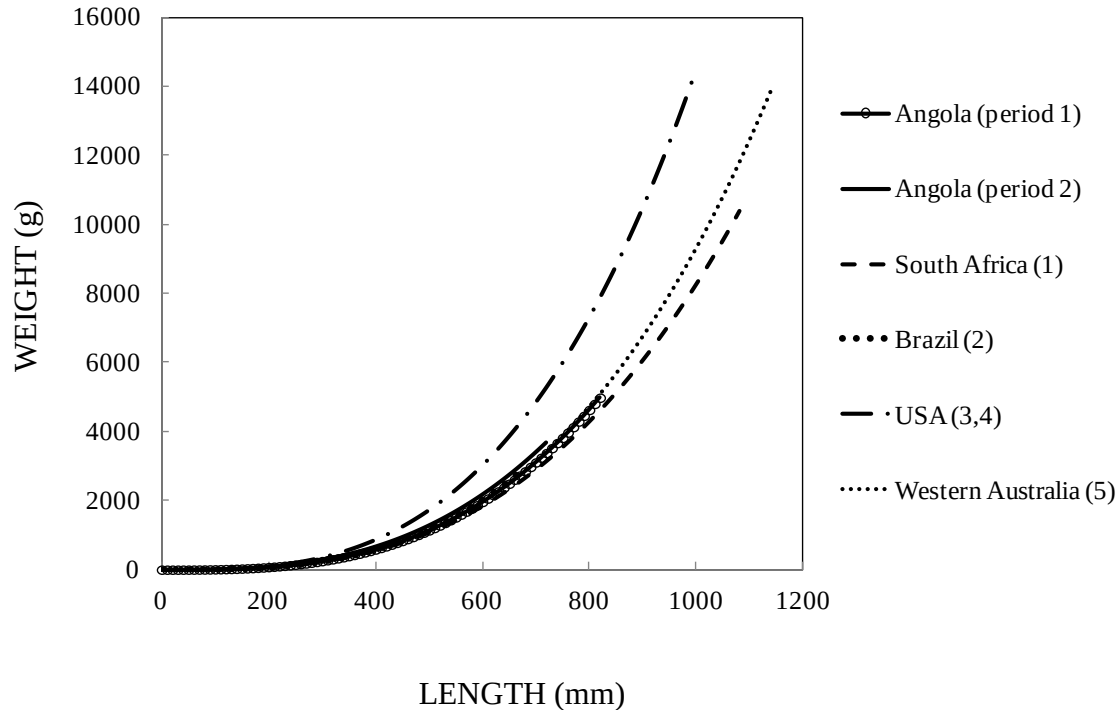


Figure 3.10: Weight at length relationships for *P. saltatrix* in southern Angola and other regions globally. Relationships are continued until they reach the largest mass recorded per region. 1 = Van der Elst (1976), 2 = Haimovici and Velasco (2000), 3 = FWRI (2010), 4 = IGFA (2014), 5 = Smallwood et al. (2013).

The growth rate of fish populations is heritable and this is particularly important when phenotypic changes induced by selective pressures consistently result in greater evolutionary fitness (Law 2000, Wang and Höök 2009, Eikeset et al. 2013). As a result the fast, medium and slow growth groupings noted for *P. saltatrix* by Juanes et al. (1996) may reflect a genetic basis for observed growth variability in this species. While a phylogenetic analysis was beyond the scope of this study, the *P. saltatrix* population in southern Angola constitutes a genetically distinct, recently diverged stock to the South African population (Dos Santos, unpublished data). The South African population is genetically most similar to populations in America and Portugal while these populations are relatively closely related to the genetically distinct stocks of western and eastern Australia (Nurthen et al. 1992, Goodbred and Graves 1996, Graves 1998). The Brazilian population is however somewhat of an outlier that is more divergent from the other population groups (Goodbred and Graves 1996, Graves 1998).

Based on these findings, and on what is known about the growth of these populations, it does not seem likely that there is a relationship between genetic divergence and growth. For example, the growth rate of the South African population, which is considered the least genetically divergent from the southern Angolan population, was one of the fastest of all of the global populations (Table 4.7).

Population size and structure can have a major impact on the growth of fishes (Tomcko and Pierce 2005). Since the level of exploitation significantly influences population size and structure, it can have a major influence on fish growth (Trippel 1995, Jørgensen et al. 2009, Weber et al. 2011). The immediate impact of exploitation is a reduction in population number and the truncation of the average age and length within a fish population (Conover and Munch 2002, Berkeley et al. 2004b). There was significant evidence, including a reduction in average and maximum ages (Figure 4.5, Table 4.5) and sizes (Figure 4.1, Table 4.1) for truncation during the second period of this study. However, when compared with other *P. saltatrix* stocks, exploitation can still be regarded as recent and minimal in Angola. For example, populations have been exploited since at least the 1980s in America (Salerno et al. 2001, Wood 2013) and Australian catch records are available from as early as 1912 with records of commercial effort available from the 1950s onwards (Smith et al. 2013).

When compared with other populations, the maximum age of the relatively small sample ($n = 932$) of fish in this study was high (13.53 years) (Figure 4.9) although a maximum age of 14 years has been recorded for the species off the well-studied American east coast (Sipe and Chittenden 2002, Wood 2013). The 12 year old *P. saltatrix* captured by Salerno et al. (2001) was noted as one of the oldest reported along the northeast coast of America, and Wilk (1977) obtained a maximum age of only nine years within a sample of 25 000 fish in the same region. Govender (1996) captured few fish above the age of three years in South Africa and attributed this to high rates of fishing mortality. The old maximum age of this study is thought to reflect the relatively unexploited nature of the southern Angolan *P. saltatrix* stock during period 1. However, reductions in the maximum age from 13.5 to 10.0 years and the reduction in the median (period 1 = 4.1; period 2 = 3.8) and mean age (period 1 = 3.4; period 2 = 3.3) during the two periods suggests that the increasing level of exploitation (Chapter 2) may be influencing the population dynamics of this stock. The concomitant length truncation during period 2 appears to be further evidence of this.

There are two mechanisms that are thought to promote faster growth in response to exploitation. The first is known as density-dependent growth (Lorenzen 2008), where reduced numbers of fish grow faster because of the reduced competition for food resources; the second is compensatory growth, which is thought to be compensation for the removal of large, highly fecund individuals from a population (Trippel 1995, Miete et al. 2009, Neuheimer and Grønkjær 2012).

When one considers these two mechanisms, one might expect that the growth of *P. saltatrix* may have increased by the second period. However, the similar growth suggests that either the level of exploitation, or the period over which it has been acting upon the stock, was insufficient to have had a major influence on adult growth. When compared with other global populations, the fastest growing, including Brazil, North Eastern USA, South Africa and Western Australia have been heavily exploited for decades and even centuries (Salerno et al. 2001, Smith et al. 2013, Wood 2013). This suggests that the impacts of exploitation may have already had a significant influence upon the growth of *P. saltatrix* populations elsewhere and might help explain the relatively slow growth of the Angolan population.

The relative abundance, measured as catch per unit effort in the shore-based recreational fishery for *P. saltatrix* in Angola (Period 1 – 1.85, Period 2 – 0.56) was high relative to the CPUE calculated for recreational catches from the South African population (Pradervand 2004, Maggs et al. 2012) and the standardised catch rates for the Australian line fishery (Leigh and O'Neill 2004). This suggests a high relative abundance of *P. saltatrix* in Angola and that density-dependent growth mechanisms may be a reason for the faster adult growth in exploited populations elsewhere. In addition CPUE decreased between periods to provide further evidence for fisheries induced decreases in abundance in Angola. While legal size restrictions prohibited accurate comparisons of average catch sizes in other regions, the average size of *P. saltatrix* in Angola (Period 1 – 507 mm FL, Period 2 – 462 mm FL) and the general lack of fish smaller than 300 mm fork length being captured suggests that compensatory growth may also account for faster growth rates in exploited populations. It is therefore likely that the increasing fishing pressure in southern Angola will over time, through the impacts of density-dependent and compensatory growth, illicit a faster adult growth rate in this population.

Conclusion

As noted for other populations, aging the Angolan *P. saltatrix* population was challenging. Using the most contemporary methods and two validation techniques, the first year growth of *P. saltatrix* in southern Angola appeared faster than other global populations. However, a steep decline of growth rate at approximately 100% maturity meant that the adult growth rate was slow relative to other populations globally. Although the rapid juvenile growth could be attributed to optimal environmental conditions, including food availability and temperature, it is most likely that the underrepresentation of smaller, age zero individuals due to spatial sampling selectivity was the overriding reason for this finding. The slower adult growth, when compared to other global populations could most likely be ascribed to the impact of density-dependent growth in this relatively unexploited population. There was no significant evidence to suggest that the increasing levels of exploitation and/or warming has influenced the growth rate of *P. saltatrix* in Angola between the first and second period. However, based on the thermal ranges of other populations, it is likely that further exploitation and warming may result in faster growth rates and lead to higher productivity of the Angolan *P. saltatrix* population in future.

CHAPTER 5

An investigation into the reproductive biology of *P. saltatrix* in southern Angola

Introduction

Successful reproduction and the resultant recruitment of individuals into adult populations is an essential requirement for the perpetuation of species. The spawning success of many fishes has been linked to the presence of optimal environmental windows (Cury and Roy 1989), the location of which varies temporally and geographically according to the reproductive requirements of each species. As a result, fishes have developed a vast array of reproductive strategies and tactics that allow them to reproduce in a wide variety of habitats. An understanding of a species reproductive strategy is not only important from an evolutionary perspective, but it can also guide the methods used to manage fish stocks. This is especially relevant in light of the collapse of one in every four fisheries over the last 50 years (Mullon et al. 2005).

Spatial and temporal closed areas are widely considered to be one of the best tools for conserving fish stocks reproductive capacities (Murawski et al. 2000, Gell and Roberts 2003, Hilborn et al. 2004, Watson et al. 2009). However, the times and location of the protection will only be successful if closed areas or seasons are well informed and designed (Hilborn et al. 2004), and as such, information on fish reproduction has been used to determine optimal locations for, and aid the design of, marine protected areas in many regions (Hutchings et al. 2002, Hannah 2008, Grüss et al. 2011). While typical protected areas are unlikely to be very effective at conserving migratory adult *P. saltatrix* stocks (Grüss et al. 2011), knowledge of the locations and seasons of *P. saltatrix* spawning in Western Australia (Smith et al. 2013) and South Africa (Govender 1996) has been used to impose seasonal area closures to protect the predictable spawning aggregations of adult fish.

Since the timing, location and number of annual reproductive events varies between *P. saltatrix* populations (Juanes et al. 1996), population specific research appears to be a prerequisite to obtain accurate information. Unfortunately, some aspects of the reproduction of *P. saltatrix* have been difficult to determine. For example, specific temporal and spatial information on the spawning of the east coast population of North America has remained elusive, even after 150 years of study (Juanes et al. 1996). This is thought to be largely due to the migratory behaviour of the species, which requires a broad spatial and temporal sampling regime (Robillard et al. 2008). As a result, the spawning location of *P. saltatrix* has often been inferred from the distribution and abundance of eggs and early life history stages. However, the asynchronous development and multiple spawning peaks in some regions, including America, complicate these indirect studies (Norcross et al. 1974, Ditty and Shaw 1995, Miskiewics et al. 1996, Robillard et al. 2008, Smith et al. 2013). In southern Angola, an observation of apparent spawning behaviour (W. M. Potts, pers. obs.) between Flamingo Lodge and Namibe (see Chapter 2) suggests that at least some *P. saltatrix* do spawn within the regions nearshore (< 200m from the shore) environment. During the event, *P. saltatrix* individuals were observed rolling over each other in a condensed shoal of over 1000 similar sized fish. This observation suggests that the study area (Chapter 2) may be a spawning location for the species and is therefore suitable for an investigation of the reproduction of the species in southern Angola.

Although specific locations of the spawning grounds are seldom known, many other aspects of the reproduction of *P. saltatrix* have been described. Studies in America (Shepherd and Packer 2006, Robillard et al. 2008), South Africa (Van der Elst 1976) and Brazil (Haimovici and Krug 1996) have shown that *P. saltatrix* is a batch spawning species with indeterminate fecundity. Although lacking empirical evidence, Smith et al. (2013) assumed that this was also the case for the Western Australian population. Since batch spawning fishes generally have asynchronously developing oocytes, they can continue to spawn at relatively short intervals throughout an extended spawning season (Macchi and Acha 2000). Thus the reproductive output is largely dependent on the duration of the optimal environmental windows available during each spawning season.

Protracted spawning periods have been noted for *P. saltatrix* populations from South Africa (Van der Elst 1976), southern Brazil (Haimovici and Krug 1992), the Australian east coast (Zeller et al. 1996), and off the east coast of North America (Smith et al. 1994, Shepherd and Packer 2006, Robillard et al. 2008, Wuenschel et al. 2012). Within the extended reproductive season, multiple annual peaks in reproductive activity have also been observed around the world. These include the east coast of America (March – May / June – August / September – November), off Western Australia (September – November / January – May) and off the Northwest African coast (May – July / October – November) (Juanes et al. 1996). These extended reproductive seasons, with several peak spawning events suggests that this species employs a bet-hedging reproductive strategy to optimise juvenile recruitment (Stearns 1976).

It is widely assumed that the regulation of fish populations occurs primarily during the juvenile phase of the life cycle (Lorenzen and Enberg 2002), making an understanding of the early development and duration of the juvenile phase an important component of biological knowledge. The size- and age-at-maturity of fishes therefore provide crucial information about their early development and potential fecundity, and as a result, these parameters also influence and reflect a stock's susceptibility to fishing pressures (Jennings et al. 1998).

Knowledge of the length- and age-at-maturity of a species can form the basis of fisheries management strategies. For example, minimum size limits and slot limits are often based on the maturity schedule of fishes. Minimum size limits are often set at the length-at-50% maturity in order to ensure that individuals are given at least one opportunity to reproduce before capture (Vasilakopoulos et al. 2011).

In North America 50% of *P. saltatrix* typically mature at between one and two years of age at sizes from 300 mm FL to 450 mm FL (Wilk 1977, Juanes et al. 1996, Salerno et al. 2001). In a study by Salerno et al. (2001) off the north eastern coast of America, median lengths at maturity of 339 mm (FL) for males and 334 mm (FL) for females were recorded, while median ages were 1.2 and 1.1 years respectively. In Turkey 50% maturity also occurs before individuals reach an age of 2 years and at a minimum size of 254 mm (FL) (Ceyhan et al. 2007), while in South Africa 50% maturity is attained at 203 mm (FL) by males and 213 mm

(FL) by females (Van der Elst 1976). Although maturation generally occurs before the age of two years, there appears to be a great deal of variability in both the size- and age-at-maturity between populations. Juanes et al. (1996) suggested that the size-at-maturity of *P. saltatrix* is related to the growth rate of juveniles with fast growing populations exhibiting greater sizes at maturity.

Exploitation is known to influence demographic parameters in fish populations (Trippel 1995, Rochet 1998, Weber et al. 2011). It is important to understand how fisheries may alter the demographics of fish populations because different species are likely to evolve different plasticity patterns in response to fishing pressures and their adaptability determines their susceptibility to overexploitation (Rochet 1998, Weber et al. 2011).

Changes to a species size- and age-at-maturity can take the form of either a phenotypic response to environmental variation or the evolutionary genetic consequence of longer-term selective pressures upon a population (Barot et al. 2002). In the short-term, high adult mortality brought about by fishing appears to promote, apparently plastic, changes in the size- and age-at-maturity, with exploited populations characteristically displaying earlier ages and larger sizes at maturation (Rochet 1998). However, over the last 30 years many fish stocks have shown a trend of reproducing at younger ages and smaller sizes (Jørgensen 1990, Rochet 1998, Barot et al. 2002, Marshall and Browman 2007). These longer-term reductions in the size of maturation induced by fisheries are believed to reflect the long-term effects of fisheries acting in the same direction as short-term plasticity for age-at-maturity but the opposite being true for length-at-maturity (Rochet 1998). As a result it was believed that that only short-term trends were likely to be reflected in the *P. saltatrix* stock in southern Angola.

Fishing affects populations in a number of ways; firstly, fishing reduces the population density. Reduced densities create an increased availability of food to remaining individuals (Barot et al. 2002) and an associated increase in growth rate through a mechanism known as “density-dependent growth” which influences both juvenile and adult fish (Rochet 1998, Lorenzen and Enberg 2002). These trends are thought to represent the higher food availability at lower densities, nutritionally allowing, or encouraging, earlier maturation with the typical

larger sizes at maturation resulting from increased growth rates as was suggested for *P. saltatrix* by Juanes et al. (1996).

Life history theory predicts that slower growing fish attain larger maximum sizes (see Chapter 4) and because fisheries generally target large fish they often cause fisheries mortality (F) to be greater than natural mortality (M) in adult fish. This may lead to fisheries promoting ‘environmental’ effects on growth and reproduction (Rochet 1998). Through indirectly leading to density-dependent increases in growth rate, typical responses to fisheries effects are considered to mediate the fecundity loss incurred through large adult fish removal (see Chapter 4). Age-at-maturity has been considered to indirectly reflect stock size and therefore, a decrease in age-at-maturity may also represent a reduction in stock size to make this reproductive parameter a potential indicator of fishery effects (Trippel 1995). The size- and age-at-maturity of *P. saltatrix* populations is variable (Juanes et al. 1996) and may, amongst other things, be related to their rate of fishing mortality.

The effects of fishery induced maturity trends are exacerbated by the selective removal of older, larger fish through the population incurring a disproportionate loss in population fecundity due to the high individual fecundity of large individuals. This high relative fecundity relates directly to the Big Old Fat Fecund Female Fish (BOFFFF) hypothesis with maternal effects upon offspring growth and recruitment highlighting the importance of maintaining age and size structures to safeguard reproductive output in exploited stocks (Berkeley et al. 2004a, b, Hsieh et al. 2010, Vasilakopoulos et al. 2011, Hixon et al. in press). In addition BOFFFFs in batch spawning species tend to have earlier and longer spawning seasons, may reproduce in different locations to smaller females, represent a “storage effect” through being able to survive periods of unfavourable conditions and spawn profusely when appropriate conditions return, making them major agents of bet-hedging reproductive strategies (Hixon et al. in press).

An investigation of fish populations under different levels of exploitation by Rochet (1998) determined a positive correlation between their time to 5% survival following maturation and their age at maturation, as well as a negative correlation to their length-at-maturity. The time

to 5% survival also provided the highest contribution to the analysis structure, suggesting that fisheries impacts upon survival had the greatest influence upon reproductive parameters (Rochet 1998). In other studies, faster growth has been found to encourage earlier maturation as a phenotypically plastic response to fishing (Trippel 1995), and this is believed to represent selective fishing mortalities favouring genotypes that code for high fecundity and early maturation (Rijnsdorp 1993).

Rochet (1998) further showed that a population's fecundity-length relationship is positively associated with length-at-maturity and suggested that phenotypic trade-offs between current and future reproduction occur in relation to surplus energy after fulfilment of metabolic demands. Surplus energy was believed to be less available following reproduction at a larger size (i.e. greater initial fecundity). Because following maturation, excess energy must be shared between growth and reproduction, maturation at a larger size as an initial response to fishing therefore has the consequence of reducing the excess energy available for growth following maturation so that adults attain smaller sizes (Rochet 1998). This trend is supported by the findings of Jennings and Beverton (1991) for Atlantic herring and may also link to the rapid reduction in growth following maturation noted in Chapter 4, through a high abundance encouraging the early development of large gonads for individuals to be reproductively competitive in spawning aggregations.

Besides the effects of exploitation, changes in climate can also influence the reproductive characteristics of fishes, including seasonality and the size- and age-at maturity (Rochet 1998, Barot et al. 2002). Temperature is a particularly important environmental variable as it directly influences the metabolic rate of fishes because they are poikilothermic organisms. The minimum spawning temperature of *P. saltatrix* worldwide is 18°C (Wuenschel et al. 2012); therefore, the warming temperatures observed in southern Angola (Chapter 2) may have an impact on the timing and duration of reproduction as well as the size- and age-at-maturity of *P. saltatrix*.

Fishes tend to grow at slower rates and mature at a larger body size in colder environments (Angilletta et al. 2004). While no single theory has the capacity to explain general

temperature-size relationships, adaptive plasticity, resulting from greater benefits, or reduced costs, of delayed maturation in colder environments is thought the most plausible explanation of common trends (Angilletta et al. 2004). As a result, warming temperatures are expected to promote earlier maturation at a smaller size in fishes. In light of global climate change, such trends may explain the discrepancy between short-term plasticity brought about by fishing and the opposite length-at-maturity trends noted for long-term datasets by Rochet (1998). In either case both fisheries and warming temperatures would collectively promote maturation at an earlier age and their relative influences may be represented by observed changes to a species length at maturation.

The aims of this chapter were to determine the reproductive style and compare the spawning seasonality, size-at-maturity and age-at-maturity of *P. saltatrix* during the two sampling periods in southern Angola using a range of standard reproductive biology techniques.

Methods and Materials

P. saltatrix were captured monthly using the methods described in Chapter 2. Fish were measured to the nearest millimetre fork length (FL), weighed to the nearest 100 grams during period 1 and to the nearest 0.01 grams during period 2. Individuals were then dissected, sexed and their gonad development was classified based on the macroscopic criteria described in Table 5.1. At least five representative gonad samples of each macroscopic stage were preserved whole in a sea water buffered 10% formalin solution for later histological analysis. Sea surface temperature (SST) data was measured daily (07:00 - 08:00) at the study site.

Condition factor

Fulton's condition factor (Ricker 1975) was calculated for *P. saltatrix* captured during period 2 using the equation:

$$K = 100000 \frac{W}{L^3}$$

where W is eviscerated mass in grams and L is the fork length in millimetres.

Macroscopic staging & histology

Preserved representative gonads for each macroscopic stage were sectioned transversely (to a thickness of 4-5 microns), stained with Haematoxylin and Eosin (H&E) and mounted onto slides in the laboratory (Bancroft et al. 2001). Histological sections were examined using a dissection microscope at a magnification of between 100X and 400X under transmitted light and representative photographs were taken for analysis. The different maturity stages of cells in the gonad were identified and described. The abundance of each cell type was classified as absent, present or abundant and representative photographs were taken of the cell structure for each macroscopic stage.

Table 5.1: Macroscopic criteria used to describe the gonad development of female and male *P. saltatrix* in southern Angola.

Stage	Macroscopic description
1.Juvenile	Thin flaccid tubes of dark red tissue containing clear fluid. Sex determination only possible towards the end of this stage.
2.Resting	Ovary swollen but retains dark red colouration and sex determined as female through development of oval shape. Testes not swollen like ovaries and colouration changes to a creamy white, but tissue does not release sperm when broken.
3.Developing	Ovary fully attains turgid oval shape and a yellow colouration. Internal structure develops “grainy” texture and more blood vessels clearly visible. Testes expand and thicken to develop gelatinous texture and dorsal ridge. When broken and squeezed, tissue collapses without releasing sperm although sperm is present in main sperm duct.
4.Ripe	Border tissue tensioned and highly vascular. Developed ova visible creating orange colouration. Eggs become clear at end of this stage and can be expelled from rear of gonad with gentle manipulation. Further expansion and thickening of testes exaggerates dorsal ridge to create tension creases in tissue edges. Tissue splits easily when bent and readily exudes sperm that may also be released by the fish during capture.
5.Spent	Gonad appears deflated and has fewer blood vessels. Slight pressure no longer expels eggs and colouration becomes a pale yellow. Testes membranes no longer tensioned and tissue feels softer. Squeezing of tissue still produces sperm but spots of red coloured (haemorrhaged) tissue are visible.

Gonadosomatic index

Because a fine electronic balance was not available during period 1, the gonads were only weighed (to the nearest 0.01g) during period 2. As a result gonadosomatic index (GSI), which was calculated as:

$$GSI = \frac{\text{gonad mass}}{\text{evicerated fish mass}}$$

could only be estimated for period 2.

Reproductive seasonality

The cyclic pattern of reproductive activity was assessed with use of a periodic regression (Flury and Levri 1999) of the form:

$$\text{logit}(\hat{O}_i) = \beta_0 + \beta_1 \sin\left(\frac{2\pi}{P} M_i\right) + \beta_2 \cos\left(\frac{2\pi}{P} M_i\right)$$

Where M_i is the month of the year (numbered sequentially for months included within each comparison), P is the periodicity of spawning activity based on the occurrence of stage 4 gonads (in months) and β_0 , β_1 and β_2 are the regression parameters that were estimated through non-linear minimisation of a negated log-likelihood function (see Chapter 4).

The influence of temperature on the reproductive cycle of *P. saltatrix* was investigated by adding average monthly temperature as a variable of the periodic regression as:

$$\text{logit}(\hat{O}_i) = \beta_0 + \beta_1 \sin\left(\frac{2\pi}{P} M_i\right) + \beta_2 \cos\left(\frac{2\pi}{P} M_i\right) + \beta_3 (TM_i)$$

where β_3 is an additional estimated parameter and T is the average temperature recorded during the month M_i . The same method was used to analyse the effect of photoperiod Ph within each month (M_i) and a likelihood ratio test (LRT) was used to determine each model's variation from the null model (where environmental parameters were not included in the regression).

The model that best described reproductive activity was selected based on results of a likelihood ratio test (LRT) conducted on a log likelihood function and through calculating Akaike's information criterion (AIC). The log likelihood function was calculated as:

$$\ln L = n \ln \sigma$$

where n is the number of months sampled and σ is the model variance.

The LRT p -value was obtained from a chi-square distribution:

$$\chi_k^2 = 2(L_{full} - \ln L_{reduced})$$

where L_{full} is the model for which periodicity was calculated as a parameter, or for which temperature or photoperiod was added as an environmental variable, and $L_{reduced}$ is the model for which periodicity was fixed, or environmental parameters were not added to the regression formula. The full model was considered to adequately describe the reproductive cycle if $p < 0.05$.

The Akaike, information criterion (Akaike 1974) was calculated as:

$$AIC = -2 \times (\ln L) + 2K$$

where K is the number of independently adjusted model parameters. Models with the lowest AIC values had the best fit to observed data. An LRT was conducted, as above, to test if the reproductive cycle followed an annual pattern (i.e. $P = 12$) with the reduced models P parameters being fixed at 12 months. The null hypothesis of an annual cycle was rejected if $p < 0.05$.

Length-at-sexual maturity

P. saltatrix were grouped into 10 mm length classes and a logistic ogive was fitted to the proportion of mature fish within each length class as a means of determining the length-at-50% maturity (L_{50}). A two parameter logistic ogive described as:

$$P(L) = \frac{1}{1 + e^{-(L-L_{50})/\delta}}$$

where $P(L)$ is the proportion of mature *P. saltatrix* (based on the occurrence of reproductively developed gonads) within each length class L , L_{50} is the length at which 50% of the fish were mature and δ is the width of the logistic ogive, was used. Differences in maturity parameters between sexes and periods were tested using a LRT to determine their statistical relevance. Juveniles that could not be distinguished as male or female were included in both ogives.

Results

General

In total 549 and 324 *P. saltatrix* gonads were macroscopically staged during periods 1 and 2 respectively. Population sex ratios were 1.0 M : 2.3 F and 1.0 M : 1.7 F during the first and second sampling periods respectively.

Histological observations

Oogenesis

Five stages of oogenesis were identified in this study and their identification was guided by other histological research conducted on the species (Clarke et al. 2006, Burak 2007, Robillard et al. 2008). The developmental stages noted in this study are illustrated in Figure 5.1 and were identified as:

Perinucleolar stage

The first developmental stage identified in female *P. saltatrix* gonads from southern Angola were perinucleolar oocytes which were relatively small and had highly basophilic ooplasm. They had a high nucleus, cytoplasm ratio and small nucleoli which developed along the nucleus edge and became more prevalent and larger as this stage progressed.

Lipid stage

Oocytes in the lipid stage also displayed relatively strong basophily in the ooplasm. Lipid droplets formed during this stage and the nucleoli converged towards the nucleus centre. An eosinophilic matrix formed between nucleoli which increased the nucleus density and a thin zona radiata formed with progression of this stage.

Early vitellogenesis

The ooplasm of oocytes in the early vitellogenesis stage was only weakly basophilic and there was a marked increase in the size of these cells from that of previous developmental stages. The previous position of the nucleus was visible as an eosinophilic region that appeared to decrease in size with progression of this stage. Cortical alveoli and eosinophilic yolk globules first developed during this stage and these structures became larger and more prevalent while the zona radiata also increased in thickness with progression of this stage.

Late vitellogenesis

During late vitellogenesis, the nucleus became difficult to see due to the development of many cortical alveoli and yolk globules which appeared to increase in number and size during

this developmental stage. The zona radiata thickened further and initial development of the zona granulosa was evident.

Hydrated stage

Hydrated cells were noticeably the largest of all noted cell types and they dominated the surface area of gonad sections when present. Yolk vesicles become prevalent and the zona radiata and zona granulosa became fully developed during this stage. Although hydrated cells dominated the internal structure during this stage, oocytes at the various other levels of development were still present in the ovary (see Figure 5.2).

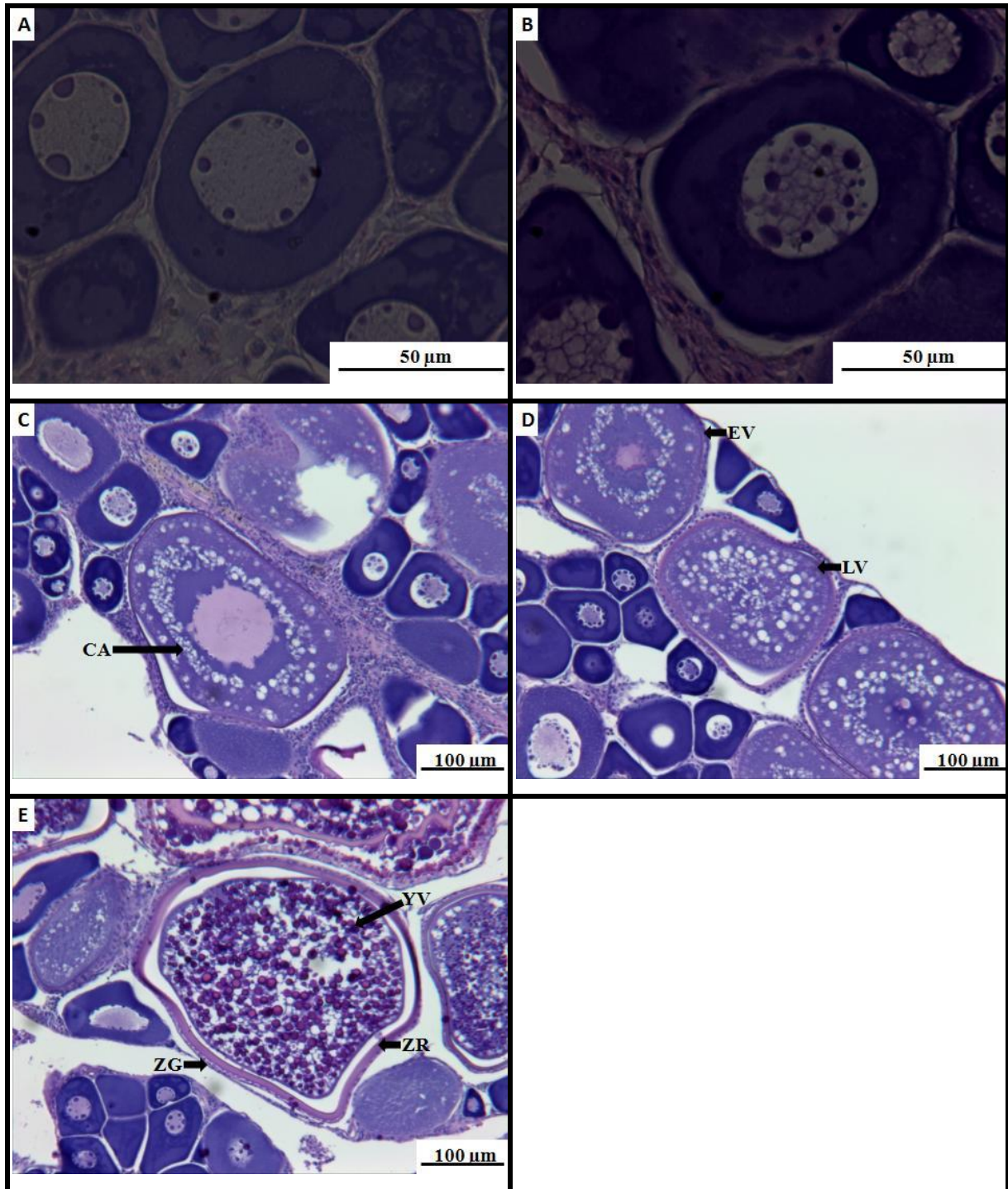


Figure 5.1: Photographs representing each cell developmental stage for female *P. saltatrix* in southern Angola. (A) *Perinucleolar stage* (B) *Lipid stage* (C) *Early vitellogenesis* (note magnification change), (D) *Late vitellogenesis* (E) *Hydrated stage*. Note that photographs (A) and (B) are taken at 400X magnification while the others are taken at 100X magnification and that there was general increases in cell size with development. CA = Cortical alveoli, EV = Early vitellogenesis stage, LV = Late vitellogenesis stage, YV = Yolk vesicles, ZR = Zona radiata, ZG = Zona granulosa.

Spermatogenesis

Spermatogonia were most prevalent in early maturation stages (Figure 5.2) and through mitotic division these cells produced spermatocytes which were highly basophilic and the largest germ cells. Spermatocytes go through two stages of meiosis to produce smaller spermatids which dominated the seminiferous tubules of developing *P. saltatrix* testes (Figure 5.2). In ripe individuals the spermatocytes and spermatids were located on the peripheral margins of the seminiferous tubules while the interior was filled with spermatozoa (Figure 5.2), indicating peak development and the capacity of individuals to successfully spawn given appropriate environmental cues.

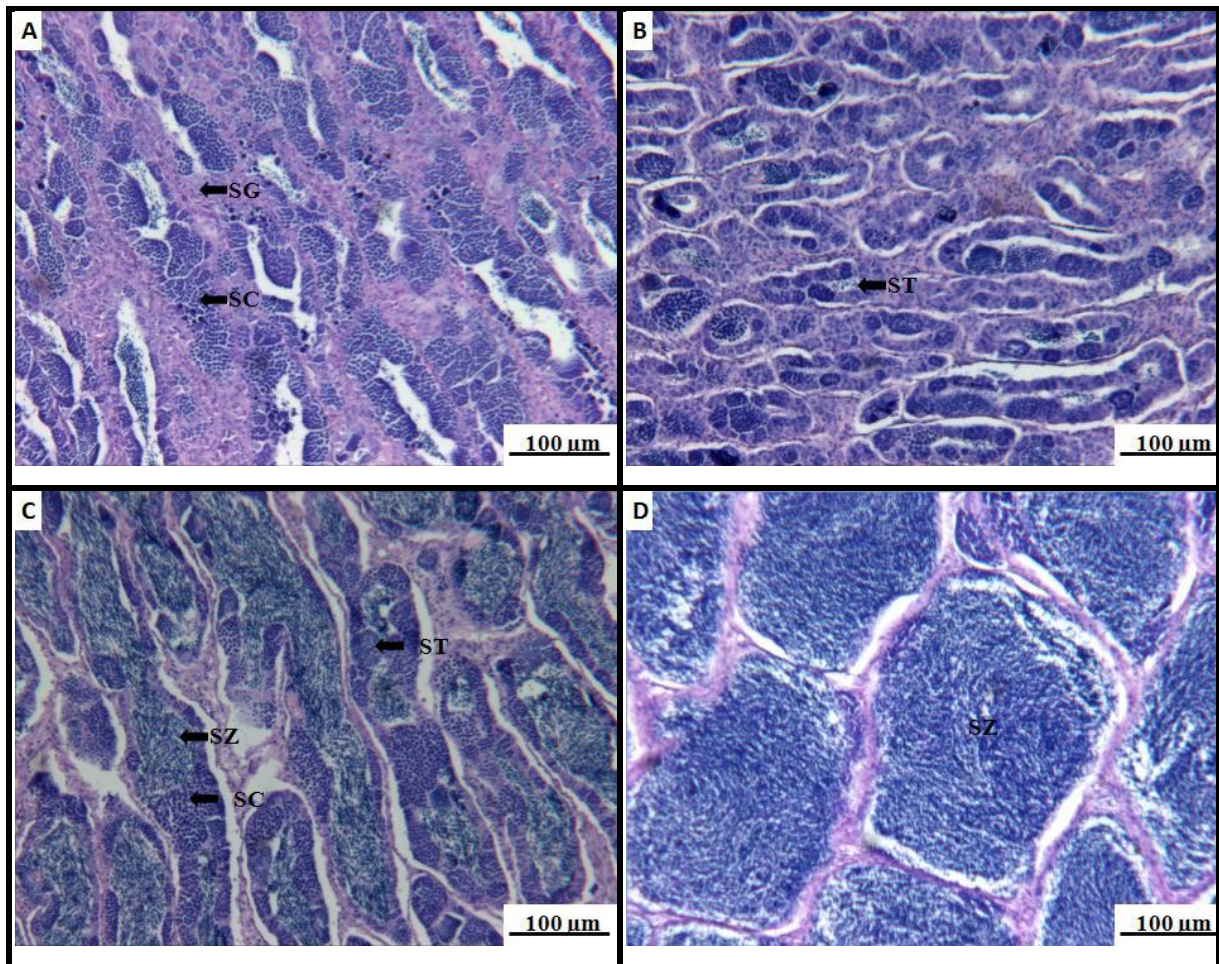


Figure 5.2: Photographs of transverse sections through (A) juvenile, (B) resting, (C) developing and (D) ripe *P. saltatrix* testes to illustrate spermatogenesis in relation to noted macroscopic stages. SG = spermatogonia, ST = spermatids SZ = spermatozoa.

Spawning strategy and histological validation of macroscopic staging

Generally females had several cell types in one gonad (Figure 5.1, Table 5.2) indicating that individuals can spawn multiple times in a season. Histological development trends confirmed the macroscopic sequence of development (Table 5.2, Table 5.4) with juvenile gonads being dominated by perinucleolar cells but also containing some lipid stage cells (Figure 5.1, Table 5.2). Resting ovaries were dominated by lipid stage cells but also contained perinucleolar cells (Figure 5.1, Table 5.2). Developing ovaries contained perinucleolar, lipid, early vitellogenesis and some late vitellogenesis cells but were dominated by lipid and early vitellogenesis cells (Figure 5.1, Table 5.2). The surface area of sections from ripe ovaries was dominated by hydrated cells but late vitellogenesis cells were also common and all previous developmental stages were present (Figure 5.1, Table 5.2). Spent ovaries were the only ones which contained post ovulatory follicles but they were dominated by lipid stage cells and also contained perinucleolar and early vitellogenesis cells (Figure 5.1, Table 5.2).

Males displayed similar trends with several development stages found in a single gonad (Figure 5.2, Table 5.3) and their sequence of development confirming macroscopic stages (Table 5.3, Table 5.4). Juvenile testes were dominated by spermatogonia but also contained sparse clusters of spermatocytes indicating the first stages of spermatogenesis (Figure 5.2, Table 5.3). All other macroscopic stages contained spermatogonia, including resting testes which were dominated by spermatocytes and also showed the first occurrence of spermatids indicating further development (Figure 5.2, Table 5.3). Spermatocytes and spermatids became dominant cell types in developing testes which had larger and denser cell clusters (Figure 5.2, Table 5.3). Ripe testes showed the first occurrence of, and were dominated by spermatozoa while containing all previous developmental cell stages and having the most distinct cell clusters (Figure 5.2, Table 5.3).

Table 5.2: Histological validation of the macroscopic stages noted for female *P. saltatrix* in southern Angola. (+) indicates the presence of a cell type while (+++) represents abundant or spatially dominant cell types.

	Perinucleolar stage	Lipid stage	Early vitellogenesis	Late vitellogenesis	Hydrated stage	Post ovulatory follicles
Juvenile	+++	+				
Resting	+	+++				
Developing	+	+++	+++	+		
Ripe	+	+	+	+++	+++	
Spent	+	+++	+			+

Table 5.3: Histological validation of the macroscopic stages noted for male *P. saltatrix* in southern Angola. (+) indicates the presence of a cell type while (+++) represents abundant or spatially dominant cell types. Histological samples for spent males were unavailable, resulting in this stage being absent from this sexes histological analyses.

	Spermatogonia	Spermatocytes	Spermatids	Spermatozoa
Juvenile	+++	+		
Resting	+	+++	+	
Developing	+	+++	+++	
Ripe	+	+	+	+++

Overall, the histological descriptions and the sequential dominance of the different cell stages (Figure 5.3) suggested that the macroscopic stages provided a valid representation of reproductive development, which is summarised in Table 5.4.

Table 5.4: Results from histological analysis and how histological findings related to described macroscopic stages identified for *P. saltatrix* in southern Angola.

Stage	Macroscopic description	Histological description
1.Juvenile	Thin flaccid tubes of dark red tissue containing clear fluid. Sex determination only possible towards end of this stage.	Ovaries dominated by perinucleolar cells while testes are dominated by spermatogonia.
2.Resting	Ovary swollen but retains dark red colouration and sex determined as female through development of oval shape. Testes not swollen like ovaries and colouration changes to a creamy white, but tissue does not release sperm when broken.	Ovaries dominated by lipid stage cells. Testes dominated by spermatocytes with few spermatids present.
3.Developing	Ovary fully attains "plump" oval shape and a yellow colouration. Internal structure develops "grainy" texture and more blood vessels clearly visible. Testes expand and thicken to develop gelatinous texture and dorsal ridge. When broken and squeezed, tissue collapses without releasing sperm although sperm is present in main sperm duct.	Ovaries develop early and late vitellogenesis stage cells. Testes dominated by spermatids with the development of some spermatozoa.
4.Ripe	Border tissue tensioned and highly vascular. Developed ova visible creating orange colouration. Eggs become clear at end of this stage but remain in gonad and can be expelled from rear of gonad. Further expansion and thickening of testes exaggerates dorsal ridge to create tension creases in tissue edges. Tissue splits easily when bent and readily exudes sperm that may also be released by the fish during capture.	Large hydrated cells develop and spatially dominate the ovary structure. Large and distinct cell clusters develop which are internally dominated by spermatozoa.
5.Spent	Gonad appears deflated and has fewer blood vessels. Slight pressure no longer expels eggs and colouration becomes a pale yellow. Testes membranes no longer tensioned and tissue feels softer. Squeezing of tissue still produces sperm but spots of red coloured (haemorrhaged) tissue are visible.	Ovary similar to developing stage with no hydrated cells remaining and post ovulatory follicles present. Comparative sections from ripe testes not obtained for histological analysis.

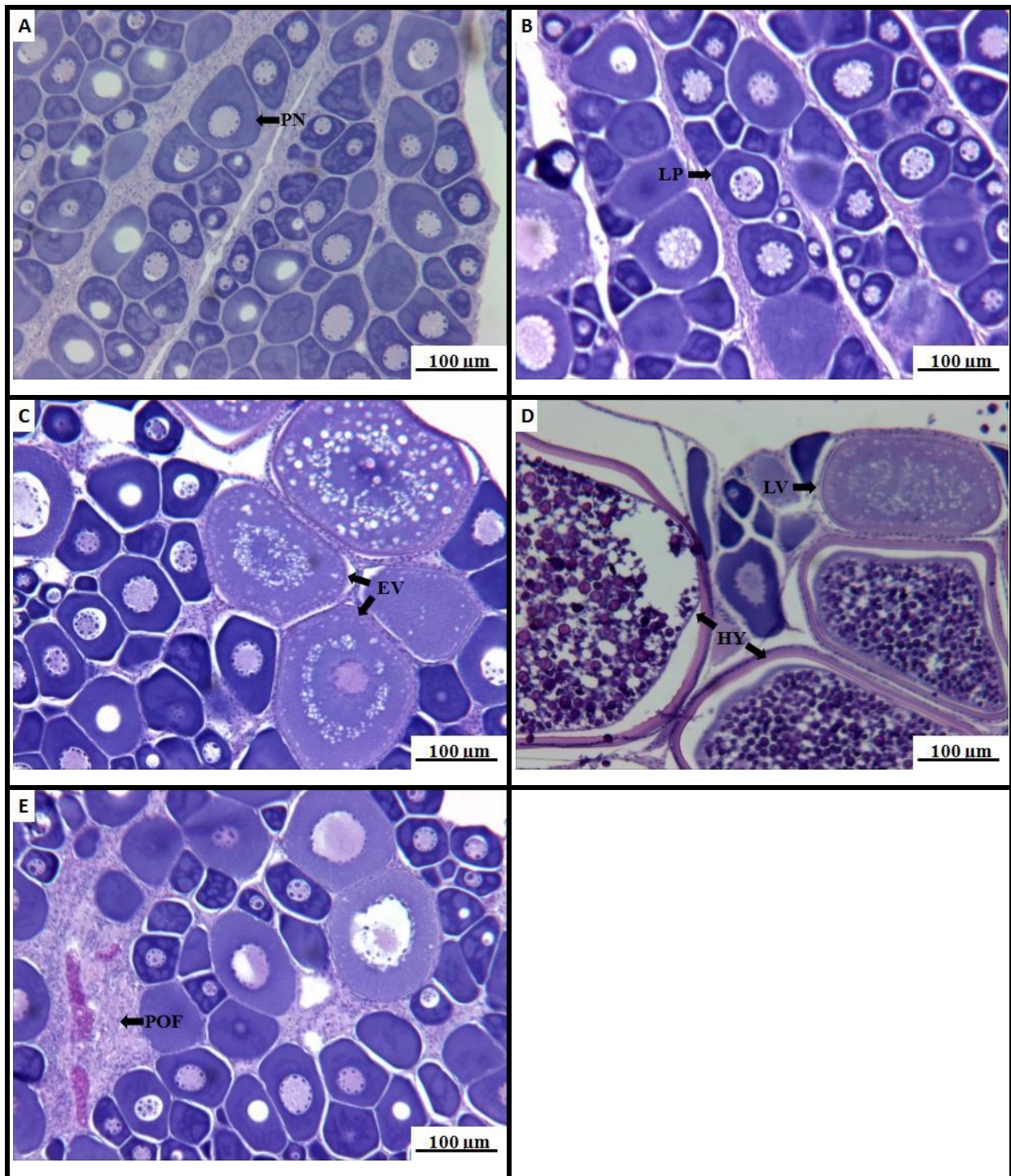


Figure 5.3: Photographs of transverse sections through *P. saltatrix* ovaries to illustrate histology within each macroscopic stage. (A) *Juvenile* ovary illustrating perinucleolar cells (PN), (B) *Resting* ovary illustrating lipid cells (LP), (C) *Developing* ovary showing the first occurrence of early vitellogenesis cells (EV) with the late vitellogenesis stage (LV) also occurring, (D) *Ripe* ovary containing large hydrated cells (HY), (E) *Spent* ovary showing similarity to developing stage and presence of post ovulatory follicles (POF).

Spawning seasonality

Gonad development began in June during period 1 and September in period 2 (Figure 5.4). Ripe gonads were initially recorded in August during period 1 and in October during period 2 and the spawning season was longer during period 1 (Figure 5.4). Spent gonads were only noted during the months of January and February during both periods (Figure 5.4).

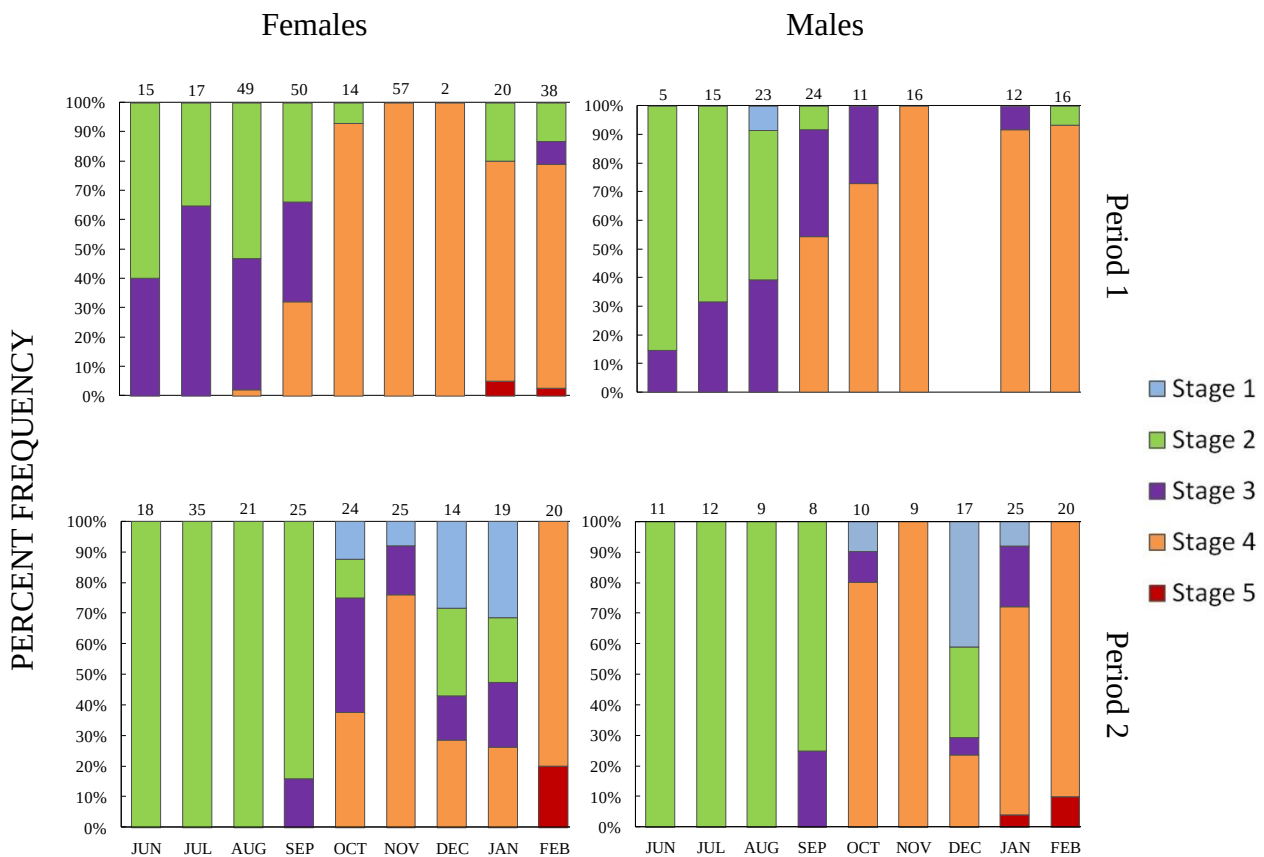


Figure 5.4: Monthly percentage of each macroscopic stage for male and female *P. saltatrix* gonads during period 1 and period 2. Data labels represent the number of *P. saltatrix* examined.

Gonadosomatic index (GSI)

Average GSI was lowest from June to August for both sexes, with little variation between individuals (Figure 5.5). On average, the GSI of females (2.51 ± 2.30) was higher and more variable than for males (2.22 ± 2.18) although average GSI was surprisingly higher for males during October (Figure 5.5). There appeared to be a bimodal distribution in the GSI of both sexes during the spawning season with the highest GSI values and highest variation occurring during the month of October (Figure 5.5). The GSI of males and females was elevated until October and thereafter it reduced until December before increasing again in January and February (Figure 5.5).

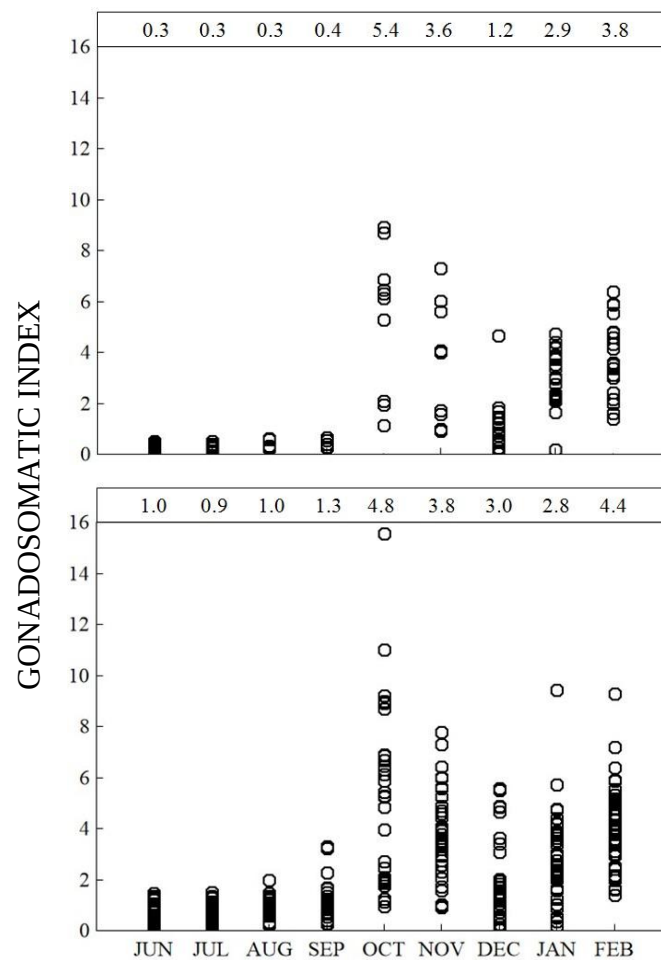


Figure 5.5: Monthly plots of individual GSI values for male (top) and female (bottom) *P. saltatrix* captured in southern Angola from July 2012 to February 2013. Monthly averages are indicated above.

Spawning seasonality

Gonadosomatic index

Neither the annual or biannual models differed significantly from the full model so an annual reproductive cycle could not be definitively confirmed for female *P. saltatrix* in southern Angola during period 2 using GSI data (Table 5.5). Based on Akaikes' information criterion (AIC) the best model fit was obtained for the full model which predicted a periodicity of 19 months, followed by the annual model (Table 5.5).

Table 5.5: Parameter estimates, log likelihood function and likelihood ratio (LRT) results of the periodic regressions fitted to the average monthly GSI.

	β_0	β_1	β_2	P	# parameters	$\ln L$	AIC	Likelihood ratio test*	
								γ	p - value
Full	0.51	-0.79	1.10	19.13	4	7.67	-31.33	-	-
Annual	0.98	-0.93	-0.02	12	3	7.61	-27.22	0.116	0.999
Bi annual	0.64	-0.60	1.10	6	3	5.52	-23.04	4.288	0.232

* LRT results are displayed for each model in comparison to the full model

Macroscopic staging

The best fit for periodic regressions of the proportion of ripe individuals (males and females) during period 1 was for the annual model (AIC = -53.28) (Figure 5.6, Table 5.1). Differences between the full and annual model were not significant while the biannual model differed significantly from the full model (Table 5.6). Therefore, periodic regression analysis using macroscopic staging data confirmed that *P. saltatrix* in southern Angola had an annual reproductive cycle (Table 5.6).

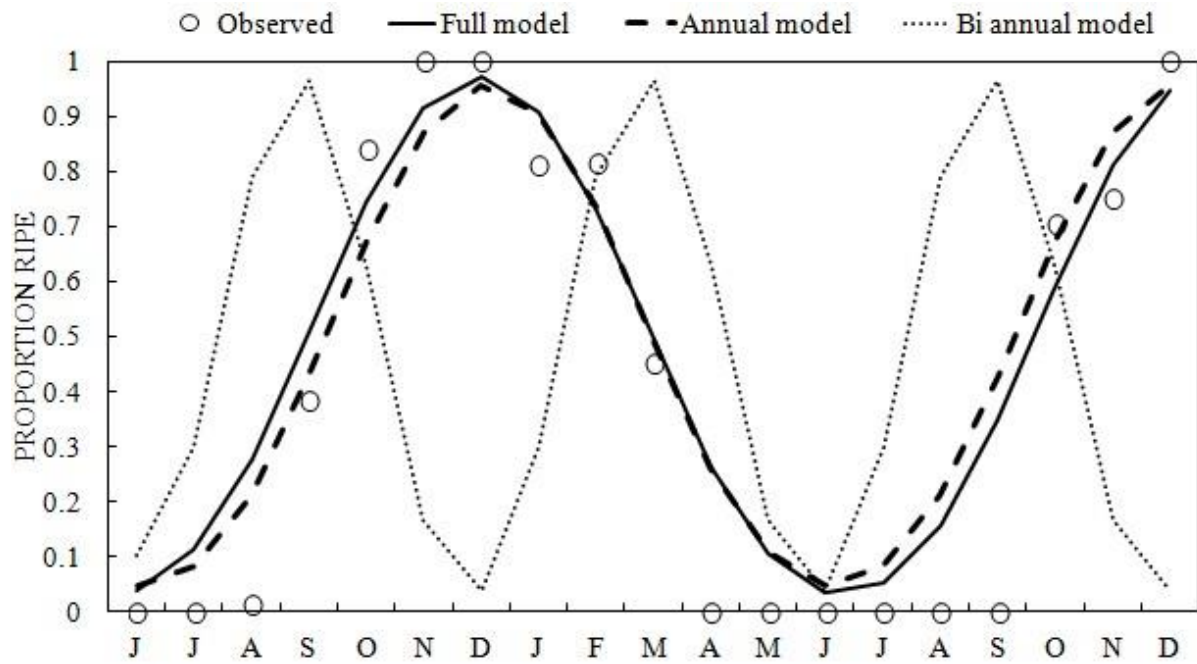


Figure 5.6: Periodic regression curves fitted to the observed proportions of ripe *P. saltatrix* within monthly samples from June 2005 to December 2006.

Table 5.6: Parameter estimates, log likelihood function and likelihood ratio (LRT) results of the periodic regressions fitted to the proportion of ripe individuals within monthly samples.

	β_0	β_1	β_2	P	# parameters	$\ln L$	AIC	Likelihood ratio test*	
								γ	p - value
Full	-0.47	-0.82	0.15	12.67	4	29.49	-50.98	-	
Annual	-0.47	-0.80	-0.06	12	3	29.64	-53.28	0.31	0.959
Bi annual	0.46	-1.61	-1.13	6	3	16.48	-26.96	26.02	9.45×10^{-6}

* LRT results are displayed for each model in comparison to the full model

The relationship between environmental parameters and spawning periodicity

Average sea surface temperatures (SST) below 18°C measured at Flamingo Lodge between June and August of 2005 and between June and September of 2006 coincided with zero *P. saltatrix* gonads being in a ripe state (Figure 5.4). The proportion of ripe gonads (macroscopic stage 4) during both periods increased with increasing SST and photoperiod

until November (Figure 5.7). However, a decline in the percentage of ripe gonads for both sexes coincided with a reduction in the mean SST during December of period 2 (Figure 5.7). During period 1, the first “ripe” individuals were observed when the minimum monthly water temperature was 16.1°C in August. However the peak spawning events (highest proportion of ripe individuals) were only observed when the minimum monthly water temperature was 19.0°C and 19.8°C in November and December, respectively.

Photoperiod increased towards the austral summer solstice before declining as expected (Figure 5.7) but particularly in period 2, variations in temperature appeared to influence gonad development. However, another peak in the percentage of *P. saltatrix* with ripe gonads occurred in February of period 2 while temperatures decreased again to suggest that temperature was not the sole influence of spawning periodicity.

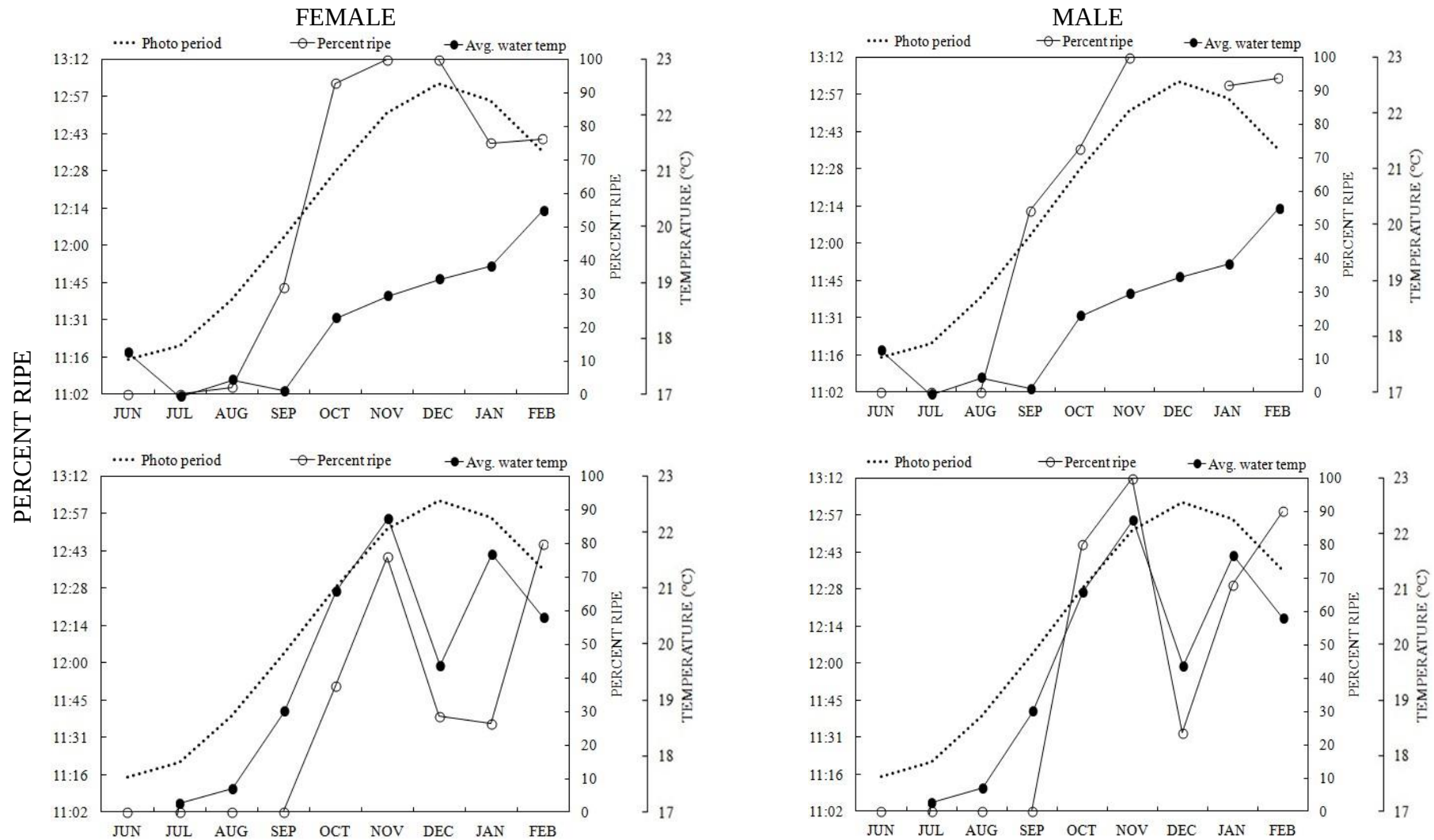


Figure 5.7: The percentage of male and female *P. saltatrix* that were macroscopically staged as ripe (stage 4), mean monthly temperature and mean monthly photoperiod during period 1 (top) and period 2 (bottom) in southern Angola.

Analysis of monthly GSI averages determined relationships to temperature and photoperiod that were similar to those seen for the proportion of ripe individuals. Increases in the average GSI of both sexes co-occurred with increases in both SST and photoperiod until October of period 2 (Figure 5.8). A decline in average GSI (representing the initiation of batch spawning) occurred for both sexes during November to support the theory of this being the peak month of spawning activity, and this decline occurred while temperatures continued to increase until December (Figure 5.8). The declines in GSI led to the lowest spawning season averages for both sexes occurring in December, followed by increases in average GSI that led to secondary peaks occurring in February. The two peaks in average GSI occurred two months either side of the summer solstice but GSI trends also appeared to correlate with average temperatures, especially for males (Figure 5.8).

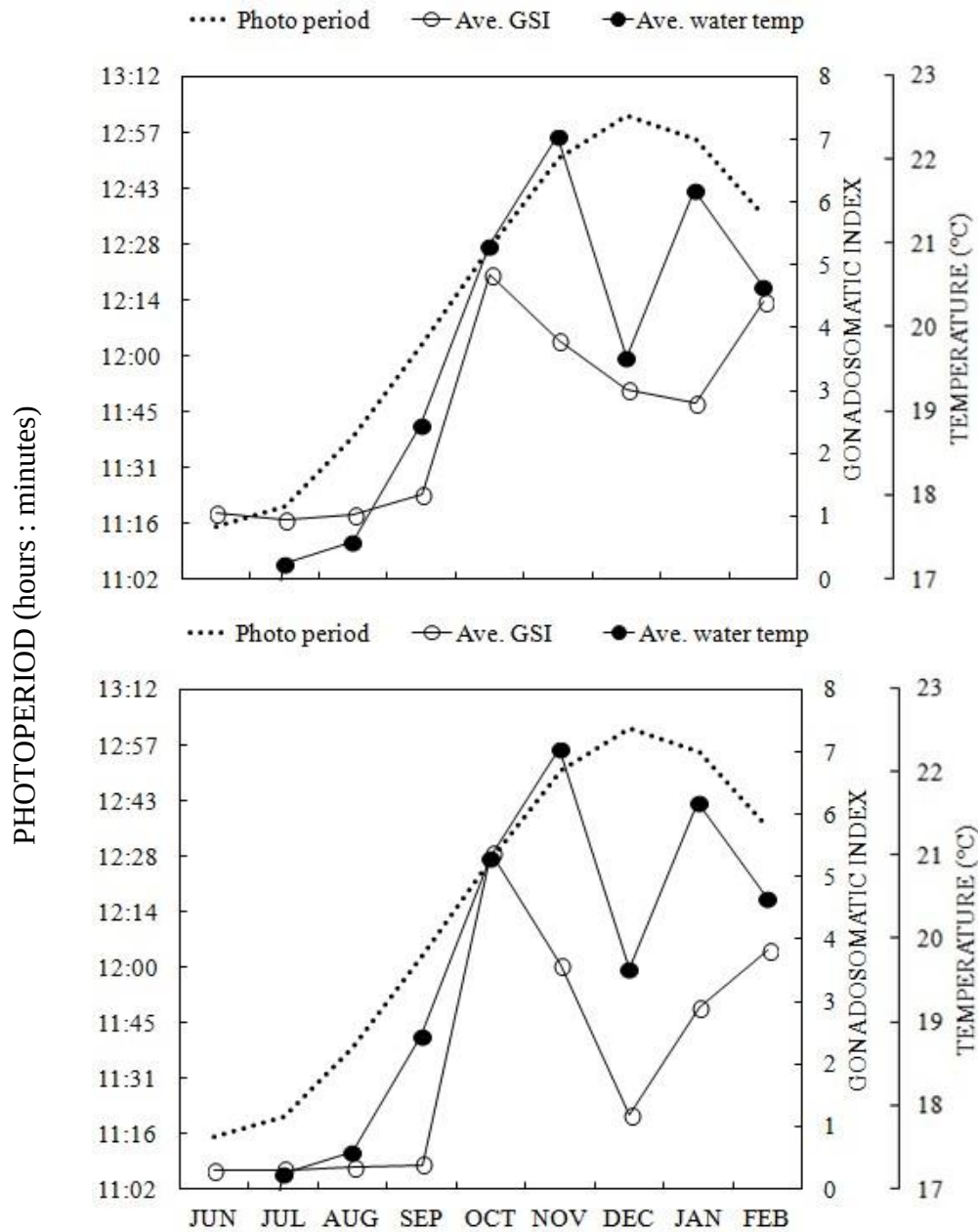


Figure 5.8: Average monthly sea surface temperature, photoperiod and gonadosomatic index (GSI) for female (top) and male (bottom) *P. saltatrix*, from June 2012 to February 2013 in southern Angola.

Both the temperature (PR_{temp}) and photoperiod (PR_{photo}) periodic regressions differed significantly from the full model ($LRT - p = 0.05$) (Table 5.7, Figure 5.9). However, when the model periodicity was fixed at 12 months and the variables were added, the photoperiod model (Figure 5.9) provided the best fit to observed data ($AIC = -61.91$) (Table 5.7).

Table 5.7: Parameter estimates, log likelihood function and likelihood ratio test (LRT) results for the periodic regressions with temperature and photoperiod as additional parameters fitted to the monthly percent of ripe *P. saltatrix* from June 2005 to December 2006 in southern Angola.

	β_0	β_1	β_2	β_3	P	# parameters	$\ln L$	AIC	Likelihood ratio test*	
									γ	p - value
PR _{full}	-0.47	-0.82	0.15		12.67	3	29.49	-50.98	-	
PR _{photo}	-47.70	0.45	-53.47	200.15	12	4	35.96	-61.91	12.94	0.012
PR _{temp}	-19.32	0.45	-19.84	2.14	12	4	7.71	-5.41	43.56	7.9×10^{-9}

* LRT results are displayed for each model in comparison to the full model

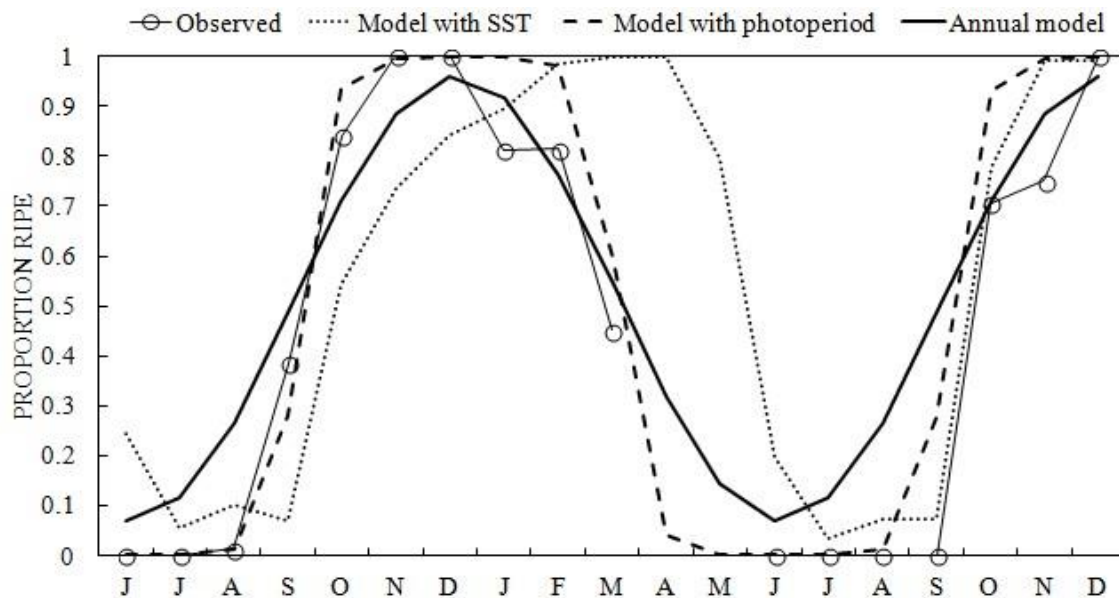


Figure 5.9: Observed proportion of ripe *P. saltatrix*, annual regression model and full regression models with sea surface temperature and photoperiod as additional parameters, between the months of June 2005 and December 2006 in southern Angola.

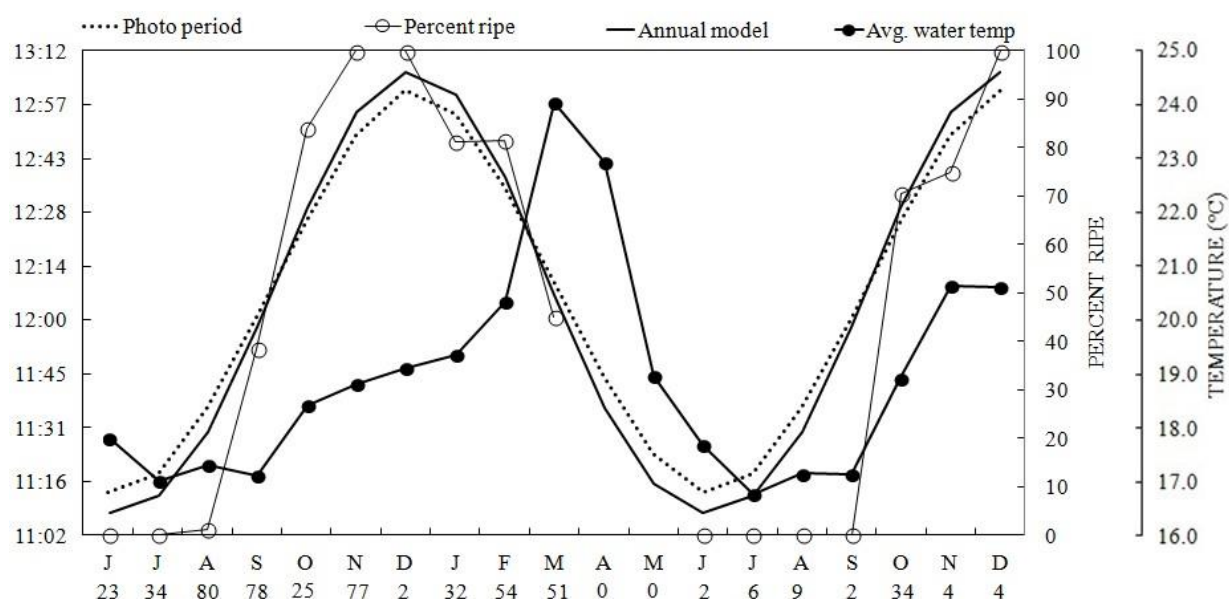


Figure 5.10: Results of the annual (periodicity of 12 months) periodic regression model curve showing the relationship between the percentage of ripe *P. saltatrix* (combined sexes) from June 2005 to December 2006, photoperiod and average temperatures. Note that numbers below month titles represent the number of *P. saltatrix* that were macroscopically staged during the respective month.

Length- and age-at-50% maturity

During both periods females matured at a larger size than males and the size-at-50% maturity was larger for both sexes in period 2 (M = 332 mm, F = 340 mm) than during period 1 (M = 297 mm, F = 306 mm) (Table 5.8). Due to insufficient samples being available for aged juveniles, a logistic ogive could not be fitted to determine the age-at-50% maturity. As a result the age-at-50% maturity was calculated relative to the lengths obtained from the length ogive. Males matured at a younger age than females during both periods and the age at 50% decreased from period 1 (M = 0.81, F = 0.84) to period 2 (M = 0.66, F 0.68) (Table 5.8). While changes to the length-at-50% maturity were not significant (LRT, d.f. 2, $p > 0.05$), the ogive width decreased significantly ($p = 0.004$) between periods (Table 5.8).

Table 5.8: Logistic ogive parameter estimates for length and relative age-at-50% maturity between periods.

	Maturity					
	Period 1			Period 2		
	Overall	M	F	Overall	M	F
L 50% (mm FL)	303.05	296.71	306.18	335.59	331.92	339.58
L 100% (mm FL)	495	495	495	425	425	425
δ_L (mm FL ⁻¹)	*49.31	55.31	45.89	*24.34	26.12	22.58
A 50% (years)	0.83	0.81	0.84	0.67	0.66	0.68
A 100% (years)	1.35	1.35	1.35	0.85	0.85	0.85

*Significant difference ($p < 0.05$)

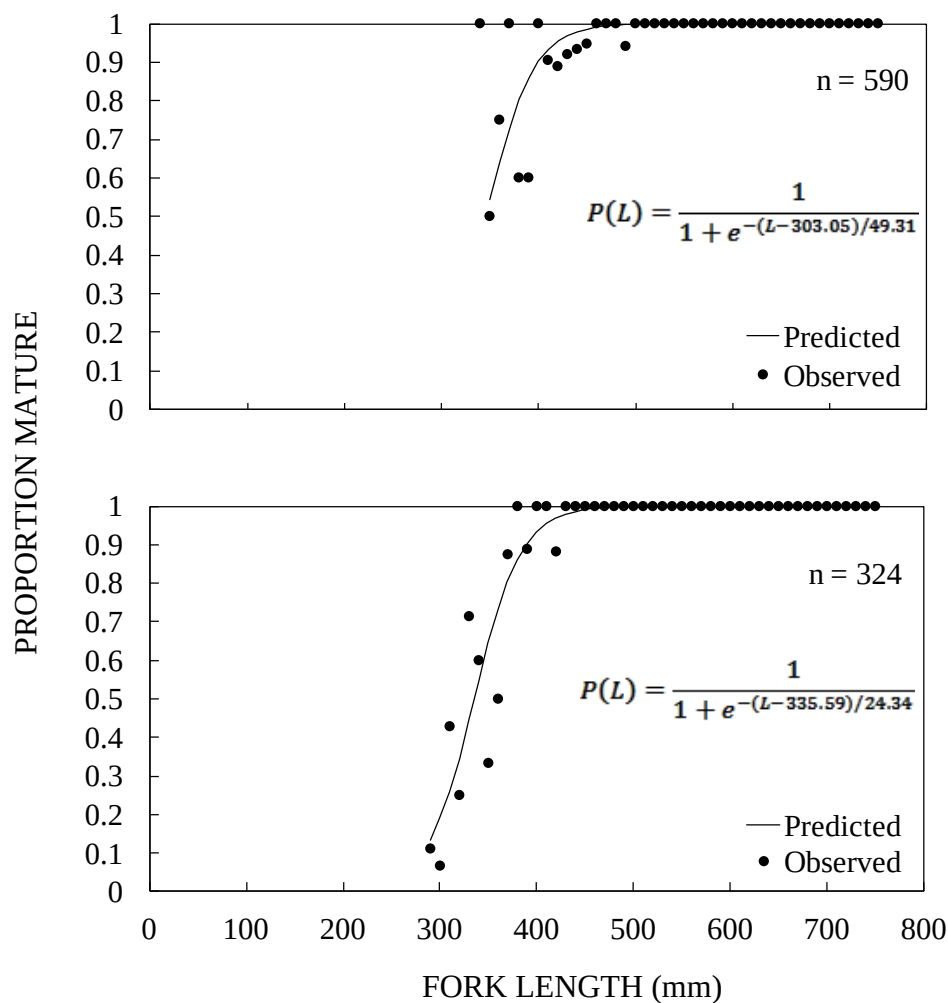


Figure 5.11: Logistic ogives fitted to observed proportions of mature *P. saltatrix* within 10 cm length classes during period 1 (top) and period 2 (bottom) in southern Angola.

Condition factor

The condition factor of *P. saltatrix* was best described by the power equation: $y = 1.00 e^{18} x^{-7.35}$ which described 95% of the variation between individuals and condition decreased steeply in fish smaller than 450 mm FL (Figure 5.12).

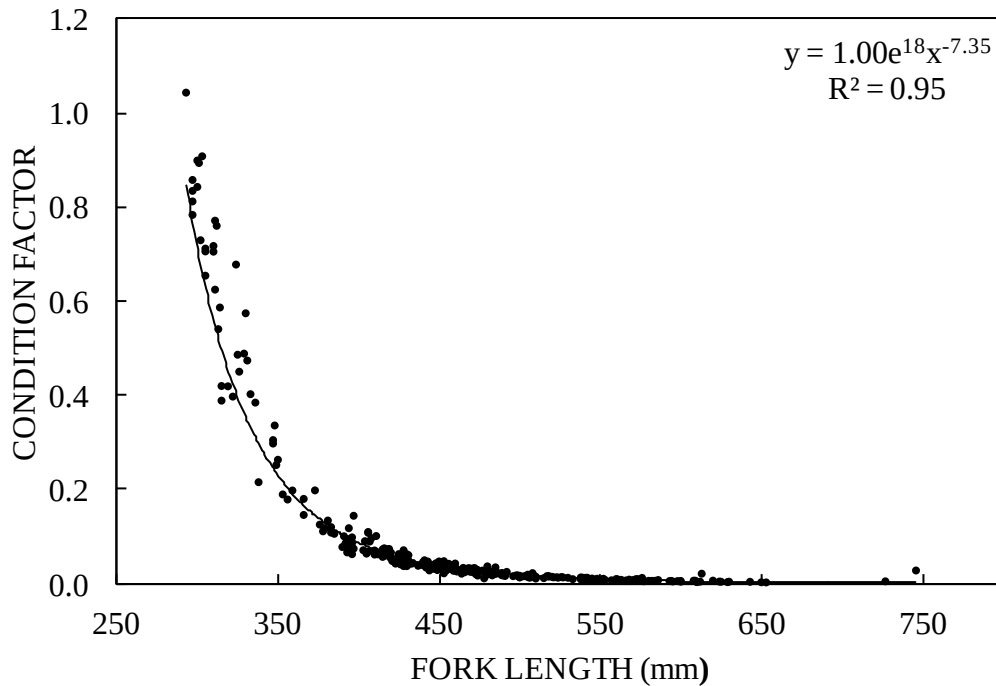


Figure 5.12: Relationship between condition factor and fork length for *P. saltatrix* (combined sexes) in southern Angola.

Parasites

Parasites, identified as the Dracunculoid nematode *Philometra saltatrix* (Clarke et al. 2006, Burak 2007) were observed in ovaries of *P. saltatrix* during both periods. Although the prevalence of these parasites was not quantified, they appeared to be more abundant in fish with well-developed gonads (macroscopic stages 3 and 4).

Discussion

The results of this study confirmed that *P. saltatrix* in southern Angola is an asynchronous spawner (Figures 5.3 and 5.4, Tables 5.2, 5.3 and 5.4). This suggests that each fish may spawn many times during an extended spawning season (August to February in period 1 and

October to February in period 2) (Figure 5.4). Asynchronous gonad development has been observed for other populations of *P. saltatrix* (Clarke et al. 2006, Burak 2007, Robillard et al. 2008) and suggests that this is a common trait for the species. Within the extended spawning season in southern Angola, there appeared to be at least two peak spawning events in period 2 (Figures 5.5, 5.6, 5.9 and 5.10). Bimodal spawning activity is not unusual for this species. For example, a bimodal recruitment pattern has been observed for *P. saltatrix* from North America (Nyman and Conover 1988, Hare and Cowen 1993). Multiple spawning events during an extended spawning season are a common strategy for marine fishes. It is thought that this type of bet-hedging effectively maintains an annual supply of recruits and is particularly successful in unpredictable and environmentally dynamic environments (Berkeley et al. 2004b, Crean and Marshall 2009, Hixon et al. in press, Smith et al. 2013). Since the ABFZ is, like many of the other *P. saltatrix* habitats, hydrogeographically dynamic, it is unsurprising that this mode of reproduction has evolved (Hare and Cowen 1993, 1997, Ditty and Shaw 1995, Smith et al. 2013).

It is interesting to note that had the histological analysis not been done, the conclusions about the reproductive strategy, which would have been based only on macroscopic staging information, may have been different. Robillard et al. (2008) noted considerable overlap in the diameter of the oocytes belonging to different macroscopic stages and it is thus conceivable that researchers, who rely on macroscopic staging alone, may conclude that individuals of this species spawn once during a long reproductive season. This highlights that assumptions of spawning strategy, based on macroscopic analysis alone is inappropriate and that a multi-method approach is necessary for studies of fish and particularly *P. saltatrix* reproduction.

The timing of fish reproduction has evolved to optimise juvenile survival, and fish rely on environmental cues to spawn during periods when larval growth and survival is optimised. These environmental cues can be divided into proximate cues, which trigger gonad development, and ultimate cues, which trigger spawning (Lobel 1989, Munro et al. 1990, Sheaves 2006). The reproductive cycle of *P. saltatrix* in southern Angola was more closely linked to photoperiod than to temperature (Table 5.7 and Figures 5.11, 5.12), suggesting that photoperiod was the primary proximate cue for reproduction in this population. Photoperiod

is considered to be a good proximate cue for many fish species because of its fixed circannual nature. In their global review, Juanes et al. (1996) suggest that photoperiod may be an important seasonal component regulating the spawning of *P. saltatrix* because spawning typically does not occur in winter, despite the winter occurrence of appropriate temperatures in some regions. Photoperiod also influences the seasonal spawning migrations of *P. saltatrix*, their behaviour and responses to changing temperatures elsewhere (Olla et al. 1985, Stehlik 2009).

Temperature can act as a proximate (Olla et al. 1980, López et al. 2006) or ultimate (Mull et al. 2008, Richardson et al. 2012) cue for fish reproduction. While temperature does appear to have a circannual rhythm in southern Angola (see Chapter 2), it is characterised by interannual fluctuations (Chapter 2), driven by the relative strengths of the Angola and Benguela currents. This variability suggests that temperature would be a less reliable proximate cue for *P. saltatrix* in the region and it is therefore unsurprising that the seasonal patterns of reproduction are more aligned with photoperiod.

The correlation between temperature and the proportion of individuals with ripe gonads (Figures 5.9, 5.11, 5.12), especially during period 2, provided some evidence to suggest that temperature may be an ultimate cue for this species in southern Angola. The greatest evidence of spawning from November to December during period 2 coincided with a drop in mean temperature (Figures 5.9, 5.10, 5.11, and 5.12). It is most likely that this drop was triggered by wind driven upwelling, and that the increased nutrients brought from the depths to the surface would increase the food availability for larval fishes. This type of event is common during the summer months in southern Angola and has been linked to the spawning activity of other coastal species including *Dentex barnardi* (Richardson et al. 2012) and *Diplodus capensis* (Richardson 2010). Rapid fluctuations in temperature in the Gulf of Mexico were suggested to initiate *P. saltatrix* spawning (Ditty and Shaw 1995) while temperature fluctuations are also thought to influence the timing of spawning in Australia (Lenanton et al. 1996). These studies support the theory that temperature is an important ultimate cue for this species and that the temperature anomaly of period 2 induced spawning in the Angolan population.

Spawning activity (defined as the period where individuals with ripe gonads were observed) was observed at temperatures between 16°C and 23°C during the first period and between 18°C and 24°C during the second period. Up until this study, the lowest recorded spawning temperature was 18°C (Table 5.9); however the upper spawning temperature (27°C) exceeded the maximum spawning temperature observed in this study. The spawning season during the second period appeared to be shorter (August to February in period 1 and October to February in period 2) and this may have been related to the warming temperatures in the region. However, based on a minimum spawning temperature of 18°C (from the metadata analysis), the peak spawning activity could have begun one month earlier during period 2 (October in period 1 and September period 2) (Figure 5.7). This was not the case and the peak spawning activity was observed in November during both periods (Figures 5.5, 5.6, 5.9, 5.10). This suggests that the small temperature increase (0.78°C) in the region was insufficient to illicit a reproductive response in this species. This is most likely due to the phenotypic plasticity observed with regards to the thermal optima for reproduction in this species (Table 5.9). The impacts of warming temperatures have been found to influence the reproductive scope (defined as the breadth of opportunity for spawning) of a resident species (*Diplodus capensis*) in southern Angola (Potts et al. in press). Based on a metadata analysis, they showed that, at the current rate of warming, *D. capensis* would no longer spawn successfully by 2090 in southern Angola. However, since *P. saltatrix* appear to have a broad spawning temperature range (Table 5.9) and a high maximum spawning temperature, it is unlikely that similar impacts will be seen in this species.

While photoperiod seems to regulate the annual cycle of gonad development in the Angolan population, the seasonal development of appropriate temperatures, especially when followed by a rapid decrease in temperature, is therefore believed to trigger the actual spawning activities of adults in the study region.

An alternative explanation for the shorter spawning period in 2012/13 (Figure 5.4) may be the influence of exploitation. Hixon et al. (in press) suggested that large female fish tended to initiate spawning activity earlier than their smaller conspecifics. They also suggested that large females tended to have longer spawning seasons than smaller fish. It therefore follows that the removal of the largest and oldest females in a population, something that was

observed during the second period of this study (Tables 4.1, 4.5 in Chapter 4), may have resulted in a shortening of the reproductive season. For asynchronous spawning species, this have may significant consequences for overall population fecundity.

Female fish in particular appeared to be more susceptible to fishing, as suggested by the relative changes in their demographic parameters (Chapter 4), and increased levels of exploitation may further negatively influence recruitment. Large females represent a valuable reproductive component of fish populations (see BOFFFF hypothesis, Hixon et al. in press), and this appears to be especially relevant for batch spawning species (Trippel 1995, Law 2000, 2007, Hixon et al. in press). Ultimately, a shorter spawning season, with smaller females contributing to the spawning events may have significant negative impacts on *P. saltatrix* recruitment.

Table 5.9: Spawning temperature ranges, spawning months and sea surface temperatures for populations of *P. saltatrix* around the world.

	Spawning Temperatures	Months of spawning	Reference
Southern Angola (P1)	16-23	August - February	This study
Southern Angola (P2)	18-24	October - February	This study
Eastern Australia	19-25	May - January	(Zeller et al. 1996)
Black Sea	20-26	June - September	(Gordina and Klimova 1996)
NW Mediterranean	21-27	June - September	(Sabates et al. 2012)
South Africa	-	September - January	(Govender 1996)
Western Australia	20-22	1. July – October	(Ward et al. 2003)
	18-24	2. April – December	(Smith et al. 2013)
American east coast	18-26	1. March – May	(Wuenschel et al. 2012)
		2. June - August	

The length- (L50) and age-at-50% maturity (A50) of fish species are important parameters that are used in stock assessments and to develop fishery management regulations (Walters and Martell 2004). *P. saltatrix* in southern Angola matured at sizes that were comparable to populations in the USA and Western Australia, but at a larger size than those from South Africa and Turkey (Table 5.10). However, due to the rapid early growth observed in this study (Chapter 4), the age-at-maturity was lower than other populations, which all mature within their second year (Table 5.10). There are several factors that may have influenced this

finding. These include bias in the ageing analysis (see Chapter 4), rapid early growth (possibly related to high food availability), the influence of temperature, and the effects of exploitation.

As discussed in Chapter 4, it is possible that only rapidly growing individuals were sampled during this study. This suggests that slower growing, and later maturing individuals were potentially underrepresented or not included in this analysis. Poor representation of smaller and possibly slower growing individuals may therefore have biased the estimation of the maturation parameters, and most likely resulted in an underestimate of the age-at-maturity. Other studies of *P. saltatrix* generally had good representation of the small size classes and therefore it was not possible to comparatively examine the influence of this factor on the size- and age-at-maturity using data from this study. However, since there was better representation of the smaller size classes during the second period, one might assume that this may in part have caused the reduction in the age-at-maturity between periods. However, since the percentage of small fishes (<350 mm FL) remained very low (Period 1 – 1.5%, Period 2 – 4.6%), this impact may have been negligible.

Increasing temperature has also been linked to changes in maturity schedules with maturity usually occurring at smaller sizes and earlier ages in warmer conditions (Barot et al. 2002, Dhillon and Fox 2004). Dhillon and Fox (2004) suggested that these responses occur independently of the growth response. When one compares the size- and age-at-maturity of the southern Angolan population with the other global populations (Table 5.10), there appears to be no relationship between maturity and average temperature. This suggests that other factors were more important in determining the maturation schedule. While the younger age-at-maturity values during the second period may suggest that there is some temperature mediated change, the increasing estimated size-at-maturity does not conform to the predictions by Barot et al. (2002) and Dhillon and Fox (2004). It is therefore most likely that factors, other than warming, are responsible for the changes in the maturity schedules of this population.

Fish maturity schedules are often phenotypically variable and may respond quickly to the effects of exploitation (Tripple 1995, Weber et al. 2011). However, the size selective impact of fishing may also have longer-term genetic consequences (Law 2000). The effects of exploitation on the size- and age-at-maturity are contradictory in the literature. For example, Jennings et al (1998) in their study of 18 intensively exploited stocks in the North-Eastern Atlantic suggested that exploited populations mature at an older age, while Rochet (1998) found that exploited fish populations in the North Sea responded with earlier age- and increased size-at-maturity. Rochet (1998) tried to untangle the short-term plasticity from the long-term genetic effects of fishing using long-term data series. She found that although the trend of decreasing age-at-maturity with exploitation can be attributed to both phenotypic and genetic effects, the trends with regards to size-at-maturity were sometimes contradictory. This may be because size-at-maturity is also influenced by other life history parameters (eg. growth) that are also influenced by exploitation (Weber et al. 2011). For example, the short-term phenotypic response to exploitation is an increase in growth rate, which drives a decrease in the age-at-maturity and an increase in the size-at-maturity (Rochet 1998). Therefore, it is very difficult to uncouple the life history consequences of exploitation from the indirect influences of other life history parameters. However, since some fisheries that target *P. saltatrix* have been operating for many decades, it is possible that phenotypic and genetic effects may both be influencing the size- and age-at-maturity (Table 5.10). While there was no clear relationship between the size-at-maturity and the level of exploitation, the age-at-maturity for heavily exploited populations appeared to be fixed at between 1 and 2 years of age. However, since the age-at-maturity for the light/medium exploited Angolan *P. saltatrix* population fell below one year of age, it is likely that the phenotypic and genetic response of this species to exploitation is to increase their age-at-maturity. These changes in the maturity schedule suggest, as recommended by Rochet (1998), that maturity ogives used in stock assessments and projections should be regularly updated to ensure model accuracy.

The short-term impact and phenotypic response to exploitation can be examined for *P. saltatrix* in southern Angola. Based on the results of this study, it appears that the size-at-maturity has increased and the age-at-maturity has decreased since the first period (Table 5.10). Since it is assumed that the length-at-maturity of *P. saltatrix* is positively related to its growth rate (Juanes et al. 1996, Ceyhan et al. 2007), the increase in the size-at-maturity was

unsurprising (see Chapter 4). Further evidence for a phenotypic response to exploitation was the significant increase in the “steepness” of the maturity ogive during period 2. Devlin and Nagahama (2002) suggested that this pattern represents an adaptation towards an optimal size- and age-at-maturity in exploited populations. While this may indicate that *P. saltatrix* in southern Angola are responding to the impacts of exploitation, it is also possible that the fall in the age-at-maturity may be an effect of sampling, as smaller specimens (<350 mm FL) were better represented during the second period (Figure 3.1).

If *P. saltatrix* in southern Angola are responding to exploitation by decreasing their age-at-maturity this may increase their lifetime fecundity. However, the reduced condition factor of *P. saltatrix* after maturation (Figure 5.12) suggests that the large energetic investment that is dedicated to the growth of juveniles is directed to reproduction after maturity. Based on the sharp decline in the adult growth rate (Chapter 4) it is possible that lifetime fecundity will not increase as fish will take longer to reach large and fecund sizes. Therefore, the consequences of a declining female size-at-maturity may be significant for the productivity of the Angolan population.

Table 5.10: Estimates of regional temperature, length- (L 50) and age-at-maturity (A 50), sex ratio and exploitation level during each reproductive study for global populations of *P. saltatrix*. References: 1= NODC (2013), 2 = Smit et al. (2013), 3 = Dineva (2013), 4 = METOC (2013), 5 = Smallwood et al. (2013), 6 = Salerno et al. (2001), 7 = Boreman (1982), 8 = Van der Elst (1976), 9 = Ceyhan et al. (2007), 10 = Smith et al. (2013).

	Mean temp (range)	L 50 (mm FL)	L 50 M - F	A 50 (years)	A 50 M - F	Sex ratio M : F	Level of exploitation
Southern Angola (P1)	18.4 (16-23)	303	297 - 306	0.83	0.81 – 0.84	1 : 2.3	Light
Southern Angola (P2)	19.5 (15-24)	336	332 - 340	0.67	0.66 – 0.68	1 : 1.7	Medium†
USA	17.04 (1-30) ¹	-	339 – 334 ⁶	-	1.2 – 1.1 ⁶	1 : 1 ⁷	Heavy, samples collected from 1985-1996 surveys during which there was a substantial decrease in abundance, maturity analysed from 1993-1996 ⁶
South Africa	17.5 (12-27) ²	-	215 – 224 ⁸	2 ⁸	-	1 : 1.1 ⁸	Heavy, especially during spawning season and increasing ⁸
Turkey	20.27 (11-25) ³	-	M – *254 ⁹	<2 ⁹	-	1 : 1.4 ⁹	Heavy, constituting 36% of global <i>P. saltatrix</i> catch in 2002 with particular pressure upon juveniles due to minimum landing size of only 140mm (TL) ⁹
Western Australia	21.70 (19-25) ⁴	292 ¹⁰	229 – 322 ¹⁰	-	-	1: 1.5 ¹⁰	Heavy/uncertain but recruitment has increased since 2004 following substantial declines in abundance during 1980s and 1990s ¹⁰

*A lack of mature fish precluded statistical estimation of maturity parameters but they were estimated from data for females (Ceyhan et al. 2007).

† No stock assessment data available, but exploitation level is based on the findings of the exploitation survey (Chapter 2).

One of the biggest changes in the reproductive characteristics between periods 1 and 2 was sex ratio (Table 5.10). While there is a large amount of literature on the impact of exploitation on the sex ratio of hermaphrodite fishes (Adams et al. 2000, Armsworth 2001, Devlin and Nagahama 2002, Platten et al. 2002, Hawkins and Roberts 2004, Hamilton et al. 2007), there is little on gonochorists. In period 1, when there was limited exploitation pressure, the sex ratio of Angolan *P. saltatrix* was the highest of compared studies at 1M : 2.3F and then became less female biased by the second period (Table 5.10). This skewed sex ratio suggests either that females are more susceptible to fishing or that the unexploited demographic tended towards a predominance of females. Smith et al. (2013) suggested that the greater prevalence of females (60%) in their samples from Western Australia may reflect either a natural dominance of females, or indicate that females are at greater risk of capture by line fishing techniques. Females are larger than males at an age of 2 years (375 mm TL – 360 mm TL respectively) in Western Australia, suggesting that they are exploited from an earlier age because of that regions minimum size limit of 300 mm TL (Smallwood et al. 2013). If females are more susceptible to the impacts of exploitation, then it could be possible to assess the exploitation status of *P. saltatrix* populations simply by examining their sex ratio. This seems plausible when one compares the sex ratios of the other populations of *P. saltatrix* with that of southern Angola (Table 5.10). It appears that the sex ratio of the more heavily exploited populations was closer to 1 : 1 (Table 5.10), with the greater female dominance in the apparently recovering Western Australian population lending further support to the argument and suggesting that this may be a promising avenue that could be explored further. Included in this exploration however, should be the effect of environmental parameters on sex determination.

Sex determination is a very flexible process in fishes and as a result there are a variety of evolutionary patterns observed between genera and families, with temperature frequently being considered an important environment influence (Strussmann et al. 1996a,b, 1997, Devlin and Nagahama 2002). Sex ratios differing from 1:1 may implicate polyfactorial or environmental controls upon sex determination with temperature effects upon sex having been observed in at least eight families of jawed fishes (Middaugh and Hemmer 1987, Devlin and Nagahama 2002). Temperature is thought to influence the probability of development

towards either male or female fishes due to the thermal influence on the structure and function of proteins and other macro-molecules (Devlin and Nagahama 2002). Increased temperatures have increased the proportion of males in populations of a variety of fish species (Conover 1984, Wang and Tsai 2000, Baras et al. 2001, Devlin and Nagahama 2002). It is therefore possible that the increased temperature between periods of this study (Chapter 2, Table 5.10) may have caused, or at least promoted, the reduced female dominance in samples. However, given that the mean monthly temperature of spawning in this study fell within the broad spawning temperature range observed for this species (Table 5.9), it is unlikely that this will have a major impact on the sex ratio of this population in the short-term.

Regardless of the driver of changing sex ratios, their impact is important from both an evolutionary and a fisheries perspective. The extent of the negative effects brought about by changes to a species operational sex ratio varies according to population size (Møller and Legendre 2001). Potential declines in physical reproductive efficiency may occur at the site of spawning and the overall reproductive output may be drastically reduced since each male has the potential to fertilise batches of eggs from multiple females but the abundance of females determines the egg quantity available for potential fertilisation. The increased relative paternity afforded to eggs through reduced female dominance has however been suggested to increase each females' potential to generate viable offspring, improve the genetic diversity of resultant generations and therefore potentially promote increased resilience of stocks to future selection pressures (Rowe and Hutchings 2003).

Conclusion

The Angolan *P. saltatrix* population spawns in the austral spring and summer with a peak in November. The development of large gonads in males and females; condition declines related to maturation; asynchronous gonad development, as well as multiple spawning events within the annual spawning season suggests that *P. saltatrix* reproductive activity is energy intensive. The protracted spawning period is likely to be an evolutionary development that ensures some spawning success in this oceanographically dynamic region. Photoperiod seems to be the proximate cue for reproduction, while temperatures above 18°C appear to cue

spawning. The ultimate cue for spawning appears to be an upwelling induced temperature decline. The approximate 1 degree increase in sea temperature between the two study periods did not appear to have a major impact on the timing of spawning. The size-at-maturity fell within the normal range for the species. However, this population of *P. saltatrix* appeared to mature at a younger age (less than one year) than the other global populations and this may be a consequence of the relatively unexploited nature of the Angolan population. While the increase in the size-at-maturity and decrease in age-at-maturity between the periods cannot be explained by the changes in temperature, it is likely that the change in the size-at-maturity can be attributed to the impacts of exploitation, while the age-at-maturity can most likely be attributed to the poor representation of small fish (<350 mm FL) during the first period. The relevance of these findings is discussed from an overall life history perspective and from a management perspective in Chapter 6.

CHAPTER 6

General discussion on the life history, management needs, future research direction and the implications of climate change for *P. saltatrix* in southern Angola

The life history of *P. saltatrix*

The results of this study indicate that the life history and biology of *P. saltatrix* in southern Angola is similar to that of other populations around the world. Juvenile growth was rapid with fish attaining 394 mm FL and 420 mm FL in their first year during period 1 and 2, respectively. Although the size-at-maturity (period 1 = 303 mm FL, period 2 = 336 mm FL) was similar to that of other studies (Table 5.10), the age-at-maturity was younger than in other populations, with fish attaining maturity during their first year of life. The rapid early growth and maturation in this region may however be partly related to sampling bias, with the underrepresentation of small individuals a potential concern in this study (Chapters 2, 4 and 5). This underrepresentation was thought to be a reflection of a lack of small juveniles in the area, rather than a gear selectivity problem because the smallest fish captured in the study decreased in size between the two periods, without a change in the hook size or sampling gear. In other populations, juvenile *P. saltatrix* inhabit estuaries (Munch and Conover 2000, Harding and Mann 2001, Buckel et al. 2004, Woodland and Secor 2011, Smallwood et al. 2013, Smith et al. 2013), coastal embayments (Beckley and Connell 1996, Govender 1996, Woodland and Secor 2011) and other shallow coastal environments (Govender 1996, Hutchings et al. 2002, Smallwood et al. 2013, Smith et al. 2013). However, the best evidence collected in Angola suggests that the juveniles occupy shallow bank habitats offshore and it was not possible to sample these areas due to logistical constraints in this study.

Juveniles of other populations of *P. saltatrix* undergo an ontogenetic dietary shift towards teleost prey during estuarine residency (Juanes and Conover 1994b, Juanes et al. 1994); this shift has also been correlated to an increase in the growth of the species (Juanes and Conover

1994b, Juanes et al. 1994). However, without samples from the nursery habitats, it was not possible to fully examine an ontogenetic dietary shift in the southern Angolan population if it occurs. Nonetheless, there was limited evidence of a non-piscivorous diet in one of the smaller *P. saltatrix* in this study, suggesting that it is possible that small juveniles feed on a range of crustaceans and cephalopods in their nursery habitats.

After leaving their juvenile nursery habitats as late-juveniles, *P. saltatrix* in Angola occupy a coastal niche. Here the late-juveniles and adults like other populations of *P. saltatrix*, fed opportunistically on a range of teleosts (Chapter 3). *Sardinella aurita*, a small pelagic species, was the dominant dietary item during both study periods. This was in line with the findings of other studies, where small pelagic species (including fish from the family *Atherinidae* and *Engraulidae*) dominated the diet of this species (Juanes et al. 1996). *S. aurita* was also the dominant dietary item in two other important coastal predatory species, the leerfish, *Lichia amia* (Potts et al. 2008) and the west coast dusky kob, *Argyrosomus coronus* (Potts et al. 2010b) during the first period, suggesting that it is an important dietary component for a variety of coastal predators.

Small pelagics, including *S. aurita* are known for large inter-annual fluctuations in population size due to their short longevity and dependence on optimal environmental windows for reproduction and recruitment (Geldenhuys 1971, Rosado 1974, Pipe and Walker 1987, Sabatés et al. 2006, Casini et al. 2009). This suggests that the growth rate and spawning success of *P. saltatrix* in southern Angola may follow the recruitment success of small pelagic species. During period 2 it appears that surf zone associated mugilids replaced another pelagic species (*Trachurus trachurus*) as the second most dominant prey item (Chapter 3). Interestingly, this shift also coincided with the closure of the purse seine fishery that targeted *Trachurus* species in Angola after an apparent crash in this stock (Decreto Presidencial 47/11, Governo de Angola 2011). This suggests that *P. saltatrix* has been influenced by fisheries targeting its prey species but is capable of shifting its feeding habitat and diet composition in response to fluctuations in prey abundance.

Interestingly *P. saltatrix* along the Atlantic coast of North America also demonstrated a shift in the diet of late-juveniles and early adults to species of the family Mugilidae (Juanes et al. 2013). The lipid content of targeted mugilids were found to be from five to six times higher than the other 30 prey species in that region (Juanes et al. 2013) and since lipid contents provide a good proxy for nutritional value for teleosts (Njinkoué et al. 2002), the dietary shift towards *Mugilidae* species in period 2 may have influenced the energy budget of *P. saltatrix*. However, it is unclear whether this change will be beneficial to the growth of the species and productivity of the fishery. Nevertheless, the findings of this study and those of Juanes et al. (2013) suggest that pelagic prey abundance may significantly influence the behaviour and feeding habits of this species and that the sustainable management of pelagic fisheries may be important for the productivity of *P. saltatrix* in Angola, as well as for other coastal predatory species.

Adult *P. saltatrix* are known to undertake annual spawning migrations in many regions (Govender 1996, Juanes et al. 1996, Sabates et al. 2012). These migrations appear to culminate in spawning areas that allow the later advection of the pelagic eggs and larvae in prevailing surface currents to suitable nursery habitats (Deuel et al. 1966, Norcross et al. 1974, Juanes et al. 1996, Lenanton et al. 1996). However, the exact spawning grounds for many populations remain unknown (Juanes et al. 1996). Observations by research scientists in November 2007 suggested that spawning takes place in the shallow waters (2 - 5 m depth and approximately 80 – 200 m offshore) of the study area in southern Angola. The eggs of South African *P. saltatrix* were predominantly found in waters up to 75 m depth and 6500 m offshore at Park Rynie, in southern Kwa-Zulu Natal (<http://www.fisheggsandlarvae.com/FIIIA4%20Pomatomus.htm>, 19 March 2014), spawning occurs in coastal waters (20-30 m from shore) of the Black Sea (Gordina and Klimova 1996) and in the inshore waters of eastern Australia (Zeller et al. 1996). These studies, combined with the observations of this study suggest that nearshore spawning may be a common trait for the species.

While it is not known if the spawning activity in southern Angola is localised, understanding the egg and larval transport from this region will play a major role in identifying the potential nursery grounds for fish that are spawned in this area. Eggs of *P. saltatrix* hatched in between 46 and 48 hours at 20°C in captivity (Deuel et al. 1966) and the mean larval-juvenile

transition occurred at 21 days (Hare and Cowen 1997). Based on these findings, information on the nearshore current regime could provide information on the potential nursery grounds of the species. Although there is limited oceanographic information in the study area, the late spring and summertime spawning coincides with eddies off the ABFZ and a notable southward intrusion of Angola Current waters (Meeuwis and Lutjeharms 1990, John et al. 2001, http://oceancurrents.rsmas.miami.edu/atlantic/angola_4.php, 19 March 2014). Moroshkin et al. (1970) examined the average coastal current speed between 9°S and 16°S and found it to be 50 cm s⁻¹. Based on the length of the larval period and the average speed of the coastal current, *P. saltatrix* larvae could be distributed up to 900 km south from the spawning grounds before the larval-juvenile transition. This would mean that larvae could be transported as far as Walvis Bay in Namibia. However, although the Angola Current waters travel as far as 33°S, their route is not exclusively along the surface. At approximately 16°S they either join a poleward undercurrent flowing beneath the Benguela Current or travel around the ABFZ's western extent to later mix into the Benguela system through mesoscale eddies (John et al. 2004). As *P. saltatrix* eggs are highly buoyant (Wilk 1977), it is likely that they will not be transported in undercurrents, but will either be retained within, or transported around, the convergence zone between the northward flowing Benguela and southward flowing Angola Current. This convergence zone is at its widest in and normally lies between 15.5°S and 17.5°S (Veitch et al. 2006) during the spawning period for *P. saltatrix* (August – February). Therefore, based on these findings it is most likely that the nursery grounds for fish spawning in the study area are situated in the coastal zone between Praia Pinda (15.4°S), where some evidence of early juveniles has been found, and just south of the Cunene River Mouth which is located at 17.2°S. Such a poleward larval transport mechanism has also been observed in other *P. saltatrix* populations including those in North America, eastern Australia, eastern South America and southeastern Africa (Juanes et al. 1996).

While results of this study are considered to accurately reflect the biology and life history of *P. saltatrix* in southern Angola, some methodological adjustments could have improved the results. The sample region of this study is relatively small in the context of what is known about the habitat and scale of the movements of *P. saltatrix* in other regions (Govender 1996, Haimovici and Krug 1996, Juanes et al. 1996, Shepherd and Moser 2003). Anecdotal information suggests that this species is found as far north as the city of Benguela, Angola

(12.3°S) in the Austral Winter (R. Sakko, pers. comm) and as far south as the Winston Wreck in Namibia (21.3°S) in the Austral Summer. This means that samples may only have been representative of the *P. saltatrix* population around Flamingo Lodge, and within reasonable fishing vessel travel proximity around and between the ports of Namibe and Tombua for bought samples. In other populations, individuals of this species have showed significant residency for extended periods (Shepherd and Packer 2006, Hedger et al. 2010) as well as extended long-shore migrations of over 1000 km Hedger et al. (2010). Consequently, this study may only represent a sub-population and a limited number of migrant individuals from other sub-populations in southern Angola.

Research of Angola's *P. saltatrix* stock across broader geographic scales with the additional use of acoustic telemetry techniques could provide more information about the regional extent of *P. saltatrix* movements and habitat requirements. Multidisciplinary research between fisheries scientists and oceanographers could also provide insight into the larval transport mechanisms which could be modelled in order to identify nursery habitats.

Temperature was the only environmental parameter for which data was actively collected in an attempt to contextualise and explain biological findings. This was justified through temperature having a large influence upon fish biology and directly influencing the biological characteristics investigated in this study (Fischer and Fiedler 2002, Angilletta et al. 2004). The convenience of temperature data collection promoted its daily measurement but additional data on oceanographic features, including more precise knowledge of the ABFZ position, current speeds, salinities and current dynamics for the duration of this study would have aided further inference and discussion of *P. saltatrix* movements and spawning activities.

This study did not extend into estuaries due to the lack of these habitats in this desert region. The bays of Tombua and Baia dos Tigres were also not sampled regularly due to logistical issues associated with attaining *P. saltatrix* from these environments. Therefore, future research should specifically aim to collect samples from these environments to a) effectively determine the nursery habitat of the species in southern Angola and to b) provide better

resolution on the early life history of the species. Future sampling techniques investigating juvenile *P. saltatrix* should also use seine netting, small mesh gill netting and trapping methods in an attempt to remove the selectivity effects of hook and line sampling methods.

Impacts of fishing on the life history of *P. saltatrix* and the consequences for fisheries management

Fisheries management requires scientific knowledge of how stocks react to fishing pressure, and to be effective, the performance of a fishery system should be gauged in relation to reference points (Beddington et al. 2007). In this study, the findings of period 1 provide biological reference points that are believed to appropriately represent the Angolan *P. saltatrix* stock in a healthy state.

The changes to biological parameters between periods of this study suggest that the regions *P. saltatrix* population is adapting to selective pressures and many of the observed changes are typical responses to exploitation (Hutchings 1993, Trippel 1995, Rochet 1998, Worm et al. 2009, Weber et al. 2011). The coastal fisheries of Angola comprise industrial, artisanal, subsistence and recreational sectors which have diversified and expanded their capacity and with improved vessels, motors and equipment available (Chapter 2) appear to have had negative impacts upon the region's marine resources (Potts et al. 2010a) including *P. saltatrix* in recent years.

The most obvious change to the population's demographics, that is likely to relate directly to the fishery expansion noted in Chapter 2, is the truncation of age and length in the samples of period 2 (Chapter 4). Length and age truncation is characteristic of fish stocks selectively harvested for larger, older individuals, and the maintenance of length and age structure is important to maintain spawner biomass levels for the long-term sustainability of stocks (Hutchings 1993, Trippel 1995, Rochet 1998, Berkeley et al. 2004b). There was an 11.0% reduction in the maximum length and a 26.2% reduction in the maximum age of sampled *P. saltatrix* between the two study periods. This reflects the selective removal of large/old *P. saltatrix* which is likely to have negative consequences for the population's reproduction and productivity (see Chapter 4 and 5). While faster growth rates observed during period 2 may

increase the productivity of fisheries (see Chapter 4), the reproductive cost incurred through removing large adult fish is likely to counteract this by decreasing offspring quantity and increasing recruitment variability (BOFFF hypothesis, Hixon et al. in press), especially in years of a summer temperature anomaly (Chapter 5). This is particularly relevant when one considers that warm pulses of water into the northern Benguela that promote rapid temperature changes are increasing in frequency (Munnik, 2012, Shannon et al. 2008).

P. saltatrix is generally priced either per kilogram in the formal markets or by size class in the informal sector, but size truncation will likely reduce the average value per fish captured. Fishers will either respond to this by increasing their fishing effort or the price may increase to meet the demand and negatively influence the nutritional value of purchases.

Besides size truncation, the sex ratio also changed between periods with a reduced female dominance in the population observed during period 2 suggesting that fisheries are having a greater influence on the larger female *P. saltatrix* (Chapters 4 & 5). This finding further suggests that the fisheries are having an impact on the recruitment and productivity of the Angolan *P. saltatrix* population (see Chapter 5).

With clear signals of the effects of exploitation, it is apparent that a policy shift is required to prevent the depletion of the *P. saltatrix* stock as is most likely the case for many coastal fishes in southern Angola. At present, the governmental policies that promote local fishery development aim to increase socioeconomic benefits (Chapter 1), but they are likely to further compound the negative biological effects of fishing. The actual management of fisheries in Angola is in line with the policy goal of fisheries development. With a large multispecies total allowable catch (TAC) of 560 000 tons, that is distributed between all fishery sectors and little accuracy in the fisheries monitoring, it is unlikely that managers will ever notice if the TAC has been exceeded. If this did happen, it is also unlikely that any steps will be taken to close the fisheries. In addition, by operating with a multi species TAC in this manner, this strategies integrity is flawed anyway and ultimately meaningless. To be truly effective, a TAC should be species/stock specific and designed to restrict catches from individual stocks to a level which has been calculated to be sustainable through accurate,

consistent and progressive monitoring. Other controls that are imposed on fishers include the size of their vessels, areas fished and mesh size limits for gill nets (Duarte et al. 2005). However, while the Ministry of Fisheries actively and rightly targets illegal, foreign vessels, little or no action is taken with local transgressors. This epitomises the term “convenience overfishing”, described by Froese (2004) to be “deliberate overfishing sanctioned by official bodies who find it more convenient to risk eventual collapse of fish stocks than risk social and political conflicts”. Therefore, the policy stance which emphasizes fishery development should be reviewed with sustainable utilization as a core value. This kind of review will require the implementation of a different suite of management strategies. However, these will only be useful if based on sound, regional biological information which, for *P. saltatrix* is now available.

Management of P. saltatrix stocks in other regions

Before making recommendations on potential management strategies for *P. saltatrix* in Angola, it would be useful to review those in other parts of the world. The biology of *P. saltatrix* makes it moderately vulnerable to fisheries pressures (Smallwood et al. 2013) and there are a variety of contemporary fisheries management strategy options being used to maintain the sustainability of *P. saltatrix* stocks throughout their cosmopolitan distribution (Govender 1996, Zeller et al. 1996, Lucena and Obrien 2005). In South Africa the capture of *P. saltatrix* is restricted for recreational fishers and the species cannot be sold in KwaZulu-Natal, which is considered to be the primary spawning area (Govender 1996). Additionally there is a daily bag limit of 4 *P. saltatrix* per person per day, a minimum size limit of 30 cm (TL) and a closed season from the 1st of October to the 30th of November, with these restrictions being based on the estimated size-at-maturity and reproductive seasonality of the population (Govender 1996, Maggs et al. 2012, Mann 2013).

Stock management of *P. saltatrix* in Australia includes a minimum size limit of 30 cm (TL), a bag limit of 8 fish per person per day, an annual fishing closure within an identified spawning area and input controls upon commercial and ocean-beach net fishers (Zeller et al. 1996, Ayvazian et al. 2002). In Turkey, a minimum landing size of 140 mm (TL) is enforced for *P. saltatrix* (Ceyhan et al. 2007), but as this is well below the size-at-50% maturity (>254 mm

TL), the stock is subject to growth overfishing and there is a resultant general lack of large *P. saltatrix* in that region for which Ceyhan et al. (2007) provides some evidence. The population in North America is protected based on annual quotas, of which 83% is allocated to recreational fishers and a harvest limit of 4.76 million kilograms is maintained for commercial fisheries (Murdy 2013). The commercial quota along the North American east coast is divided into individual state quotas that are based on landings obtained between 1981 and 1989.

Predictable congregations of spawning and post-spawning adults has increased the susceptibility of some *P. saltatrix* stocks to fishing (Govender 1996, Hoyle et al. 2000, Maggs et al. 2012, Smith et al. 2013). A study by Hoyle et al. (2000) determined an alarmingly high instantaneous mortality rate ($Z = 2.03$) for *P. saltatrix* off the eastern Australian coast and suggested that the *P. saltatrix* fishery in this region may be subject to hyperstability as a result of the targeting of spawning aggregations (Brown et al. 2003). It is difficult to identify stock contractions within such fisheries (Brown et al. 2003) and the use of seasonal area closures in South Africa (Govender 1996, Maggs et al. 2012) and Australia (Zeller et al. 1996, Ward et al. 2003) is thought to protect spawning adult *P. saltatrix* from such selective pressures.

Proposed management of the P. saltatrix stock in Angola

The results of this study have indicated that biological adaptations occurred between the two sampling periods. This suggests that additional mortality pressures have caused reactions among the regions stock which should now be acknowledged and considered by fisheries management. Whether adaptations resulted from environmental (climate change), anthropogenic (fisheries) or a combination of these influences, such adaptations should be incorporated into future stock management strategies to ensure sustainable use. While increasing growth rates and earlier maturation may initially be considered beneficial to stock productivity, the decreased average sizes noted in the population suggest the contrary and that the relevant fisheries practices are currently unsustainable.

Data collected during this study can also be used to further assess Angola's *P. saltatrix* stock through analyses including spawner biomass per recruit (SBR) modelling. With further monitoring of catch data from all fishing sectors, suggested negative trends in Angola's *P. saltatrix* stock could be definitively identified and various interventions should then be considered to effectively manage fisheries which have direct or indirect influences on the studied *P. saltatrix* stock.

Since the Angolan stock is targeted by a number of different fishery sectors (subsistence, artisanal, local recreational and foreign recreational), certain regulations may be unsuitable for certain sectors. For example, a TAC is not appropriate for a broadly dispersed subsistence or recreational fishery. Recreational fisheries are generally managed using appropriate bag and size limit controls, while subsistence fishers are generally managed by a permitting system which ensures that they do not develop their fishing gear sufficiently to commercialise their operation. Artisanal fisheries can be managed using a variety of measures; however, since the multispecies TAC which is currently in place, is ineffective, it appears that this measure would be unsuitable. More appropriate measures would be input controls, including a permitting system and technical measures, such as enforced gear restrictions. Management strategies that would be suitable for all sectors would be closed seasons and Marine Protected Areas.

The size limit recommendations for recreational fisheries should be designed to prevent growth overfishing. Size limits are normally based on maturity schedules, with the size-at-50% maturity normally a good guideline for the minimum size limit. Consequences of not following this guideline for *P. saltatrix* are displayed by the inappropriate size limit, far smaller than the size-at-maturity (see above) being blamed for the growth overfishing in Turkey (Ceyhan et al. 2007). Therefore, a size-at-50% maturity of approximately 33.5 cm FL for combined sexes during period 2 (Chapter 5) suggests that this length may be suitable for a size restriction in Angola. However, as a precautionary measure, a minimum size limit closer to the length-at-100% maturity (42.5 cm FL) could also be considered.

The determination of daily bag limits for recreational fisheries should take into consideration their effectiveness in reducing fishing mortality as this is dependent upon the target species density and resultant daily catch rates (Attwood and Bennett 1995). This suggests that historical catch records for the recreational fishery at Flamingo Lodge, with effective monitoring of effort increases in the region and analyses of bag limit options, corresponding to catch size analyses to determine reductions in fishing effort, could be used to refine a proposed recreational bag limit in Angola. However, in the interim, a recreational bag limit of 5 fish per person per day in southern Angola will promote catch and release, or reduce fishing effort among local recreational fishers. To promote stock sustainability, it may also be appropriate to split the different recreational fishing groups. The participants in the Angolan recreational fishery include local and foreign anglers. The improving economy in Angola has provided many local people with expendable income and an increasing number are taking up recreational angling as a pastime. The relatively unexploited fish stocks in Angola have also supported an important and growing foreign recreational fishery (Potts et al. 2009). These include individuals that fly in from other countries and stay in resort accommodation. These tourists play an important role in supporting local economies and the estimated value per harvested fish was US\$1007 at US\$243 per kilogram. Since anglers that are accommodated in resorts are bound by their conservation policies, it may be more appropriate to regulate the resorts themselves.

Considering the average size of *P. saltatrix* captured by recreational anglers in Angola a restriction of one *P. saltatrix* per angler per day would be a reasonable limit that would allow adequate fish to be retained by these anglers for their own consumption. Adherence to such a limitation would mean that the temptation to overharvest, stockpile and potentially sell excess catches may be eliminated and, especially if a slot limit is adhered to (see above), adequate protection may be afforded to the stock of *P. saltatrix* which, with *P. saltatrix* being the most frequently captured species in this fishery (Potts et al. 2009), is so important to the future existence of the fishing resorts. In addition, the use of treble hooks should be banned in recreational fisheries in line with the significantly higher post release mortality this hook type causes for this species (Ayvazian et al. 2002). The use of slings and other appropriate handling techniques should also be encouraged within resorts to minimise the considerable post release mortality (38.8%) noted for *P. saltatrix* by Fabrizio et al. (2008) that would

undermine the effectiveness of other conservative measures (Coggins et al. 2007, Isermann et al. 2007) .

With knowledge of the high post release mortality rates suggested for this species, a full retention policy, irrespective of size, until a “bag limit” has been reached may be considered the most appropriate intervention. The general absence of juvenile *P. saltatrix* in catches further promotes this suggestion but such a policy would need to enforce that fishing ceases once the bag limit has been captured as all gears used to target other native game fish species also effectively capture *P. saltatrix*. With *P. saltatrix* being the most frequently captured species in Angolan sport fisheries bag limits could also be reached in minutes, especially during the peak fishing season. Such an intervention would therefore negatively influence sport fishing tourism while also reducing resorts capacities to effectively collect catch data for later management use.

Besides tourists that fly in to Angola and are accommodated at resorts, an increasing number of foreign anglers from South Africa and Namibia are driving into Angola on fishing tours. They transport freezers which allow them to depart with frozen fillets of the fish that they have captured and contribute little to the local economy as they bring their supplies with them. The recreational fishery as a whole would therefore benefit from a strict bag limit of 1 fish per person per day and recreational fishers should not be allowed to transport fish around or out of Angola.

A TAC system may be appropriate to control artisanal and commercial fisheries targeting *P. saltatrix* in future but given the currently failing TAC system, an improvement of catch monitoring specifically for *P. saltatrix* would be a prerequisite to its success and as such this may only be an appropriate management measure in the long-term. As monitoring improves, more complex stock modelling techniques including determinations of maximum sustainable yields could allow refinement of management strategies. However, until the more comprehensive data required is available, use of available data in standard spawner per recruit (SPR) analyses, with an emphasis on conservative use of produced stock parameters is encouraged.

With development of appropriate and consistent monitoring of *P. saltatrix* catches, the proposed future TAC system could further be refined to be composed of Individual Transferable Quotas (ITQs) which would further control effort within the fisheries and reduce promotion of a “race to fish” (Hannesson 1996, Sutinen 1999, Kearney 2001, Emery et al. 2014). Again this is a long term management option and effective determination of annual quotas will require consistent monitoring of *P. saltatrix* abundance. Allocations of individual quotas will also be a delicate process requiring a historical study of fishery stakeholders. In the interim while species specific monitoring of catches is being developed, enforcement of a ban on seine and gill net fishing within a mile of the shoreline, with effective enforcement of minimum mesh size limits, or enforced input controls upon nearshore fishers like those used in eastern Australia (Zeller et al. 1996), may prove to be an effective and relatively simple means of protecting *P. saltatrix* throughout the year in southern Angola.

Since *P. saltatrix* are most susceptible when they form spawning aggregations, area and seasonal closures may be appropriate management measures and are appropriate for all of the different fishery sectors. However, in order for this to be successful an understanding of the timing and location of spawning is critical. Based on the timing of spawning noted in this study, a closed season during November may be appropriate. This will protect the species during the most important spawning period of the protracted reproductive season (Chapter 5). Based on the scale of this study, the area between the port towns of Namibe and Tombua should certainly be considered for this seasonal closure and preferably a closure across a broader scale should be considered until further knowledge of the timing of potential spawning in other locations is obtained.

Although spawning activity was observed in the study site, it is possible that this species has other spawning habitats throughout southern Angola. Therefore, until there is more clarity on the location of other spawning sites, closed seasons alone may be inadequate for protecting the species. However, the proposed extension of the Iona National Park (situated between Tombua and the Cunene River mouth, see Chapter 2) to incorporate the marine environment, could protect adults and potentially the juveniles if they use the large coastal embayment, Baia dos Tigres or the Cunene river estuary as nursery or foraging habitats.

Buckel et al. (1999a) showed how the high consumption rates of the *P. saltatrix* population off the east American coast highlights the requirement for multi-species assessments and management for this species. Multi-species management is encouraged in modern fisheries as single-species management methods appear to have outlived their usefulness with further knowledge being gained of marine ecosystem dynamics and population reactions to fisheries and climate change (McFarlane et al. 2000, Smith et al. 2007, Morishita 2008). In Angola the dietary importance of *S. aurita* suggests that this prey species should be a priority for the development of sustainable management practices. Therefore, research on this species is paramount in order to manage this fishery and support a host of coastal predatory fisheries species (Chapter 3). With this consideration, species specific TACs should be developed for *S. aurita*, *Trachurus* and *Mugilidae* species in Angola and their determinations should consider allocating a proportion of these species TACs' to their native predators which include the valuable piscivorous fishes *P. saltatrix*, *L. amia*, *A. coronus* and various marine mammals.

Impacts of climate change and implications for the future of the *P. saltatrix* fishery

While it is now commonly accepted that climate change will have major influences upon marine environments and their biota, a paucity of predictive information about how these may impact fishes remains (Angilletta et al. 2004, Sabatés et al. 2006, Rijnsdorp et al. 2009, Pörtner and Peck 2010, Potts et al. in press). One expected impact of warming coastal oceans is changes to the distribution and abundance of many species targeted by fisheries (Harley et al. 2006). However, the speed and extent of these changes is largely dependent on the thermal tolerance of a species and its ability to adapt to a changing thermal regime (Harley et al. 2006). For example, a temperature sensitive, migratory coastal species *Argyrosomus coronus* has undergone a recent southerly distributional shift from southern Angola into northern Namibia (Potts et al. submitted). In this study *P. saltatrix* were captured in water temperatures ranging from 15.8°C to 26.3°C, indicating the relatively broad thermal tolerance of this species. Adult *P. saltatrix* have been recorded to tolerate temperatures from as low as 11.9°C to as high as 30.4°C (Olla and Studholme 1971). The broad thermal tolerance of adult *P. saltatrix* suggests that between periods, changes in temperature are unlikely to have greatly influenced their distribution but their spawning success may be altered if earlier life history

phases are more thermally sensitive. While ocean warming may not influence *P. saltatrix* directly in the short-term, the reduction in other fisheries species' abundances will place further pressure on the population as fishers will adapt their fishing methods to capture species that are available.

Ocean warming may have an impact on the temperature sensitive prey species consumed by *P. saltatrix*. Warm-water intolerant species such as the temperate members of the *Trachurus* genus may respond to ocean warming by moving southward and this will influence the diet and feeding habits of *P. saltatrix*. Although fishing pressure and fluctuations in suitable environmental conditions for recruitment may have influenced their abundance and distribution, the reduction in the proportion of these species in the diet of *P. saltatrix* may in part be attributed to warming. The loss of temperate species to an area of warming may be mitigated by the arrival of tropical species. *Sardinella aurita*, the most important dietary item of *P. saltatrix* (Chapter 3), has a sub-tropical and tropical distribution. The range of this species has expanded in the Mediterranean as a result of ocean warming (Sabatés et al. 2006), as has the range of *P. saltatrix* (Sabatés et al. 2012), and it is likely that ocean warming in southern Angola may drive an increase in the abundance of this prey species and possibly reduced seasonality in its availability (Chapter 3) which may encourage a northward range expansion for the Angolan *P. saltatrix* population. Ultimately, due to their broad thermal tolerance, ocean warming may have more of an impact on the distribution of prey and competitor species which will have an indirect impact on *P. saltatrix*.

Warming driven distributional shifts are mainly a concern for thermally restricted migratory species; however thermally tolerant species may be influenced by the impact of warming on their reproductive activity. For example, the warming SST in southern Angola has influenced the reproductive scope of the resident sparid *Diplodus sargus capensis*. This asynchronous batch spawning species only reproduces at temperatures below 20°C, regardless of its ambient temperature regime and based on the warming trend, the area suitable for spawning was shown to be shrinking by 7% per decade in southern Angola and expanding by 6% per decade in Namibia (Potts et al. in press). The length of the potential spawning season

declined by 20% per decade in southern Angola, suggesting that reproduction in this region would cease within 60 years.

Although *P. saltatrix* is largely considered migratory, its migrations tend to culminate in spawning within a specific area (Govender 1996, Haimovici and Krug 1996, Juanes et al. 1996, Smith et al. 2013). Therefore, its reproductive scope may be affected in a similar manner to *D.s. capensis*. Along the North American east coast the highest larval abundance was observed during years where the temperature ranged between 22°C and 26°C (Ditty and Shaw 1995), (Chapter 5). In other regions, the preferential surface temperature range for spawning appears to be between 20°C and 26°C (Haimovici and Krug 1996, Sabates et al. 2012). Temperatures during the spawning season of *P. saltatrix* in southern Angola ranged from 16°C to 23°C in period 1 and from 18°C to 24°C in period 2 (Chapter 5). While there was an increase in spawning season temperature between periods, the maximum of 24°C observed during the second period fell within the preferred temperature ranges noted for other populations. However, if temperatures continue to rise at the current rate (0.8°C.decade⁻¹), summer temperatures may exceed 26°C during the species spawning season to potentially influence spawning success from the year 2038. As an asynchronous spawning species, this may have significant consequences for recruitment in this species.

This study focussed on late-juvenile and adult *P. saltatrix*. However, studies have demonstrated that the thermal preference of many species changes with ontogeny and that juveniles generally prefer warmer temperatures than adults in relation to their differential optimal temperatures for growth (McCauley and Huggins 1979, Shrode et al. 1983, Lafrance et al. 2005, Rijnsdorp et al. 2009, Morita et al. 2010, Pörtner and Peck 2010). While the late-juveniles and adults of *P. saltatrix* appear to have a broad temperature tolerance, there is relatively little information for eggs, larvae and early-juveniles. Ditty and Shaw (1995) collected eggs and larvae at temperatures between 22°C and 25°C in the northern Gulf of Mexico while larval *P. saltatrix* densities were highest in the shelf waters of Queensland at temperatures between 19.5°C and 22.4°C (Ward et al. 2003), suggesting that these are favourable thermal ranges for these life history stages. Juvenile *P. saltatrix* appeared to lose equilibrium faster than adults when water temperatures were dropped from 14°C to 5°C in a

study by Olla et al. (1985), suggesting that adults have a greater temperature tolerance than juveniles. However, since juveniles in many populations live in estuaries (Juanes et al. 1996), they may be tolerant of both rapid temperature fluctuations and high temperatures. Therefore, it is unlikely that juvenile *P. saltatrix* will be more sensitive to higher temperatures than adults. However, respirometry experiments on all life history stages may be the most appropriate method to understand the relationship between thermal limits and the life history of this species.

Besides distributional shifts and changes to the reproductive activity, ocean warming can also influence the growth rate and maturity schedules of fishes. Generally, increasing temperatures are expected to cause fishes to grow faster and mature earlier at smaller sizes (Angilletta et al. 2004). However, this will likely only happen up to a tipping point, after which the growth rate will decrease rapidly (Neuheimer et al. 2011). While it appeared that the early growth was faster during period 2, the overall growth rate did not differ significantly between periods. In addition, there appeared to be no relationship between the average water temperature and the growth rate of *P. saltatrix* populations worldwide (Tables 4.9 and 5.10). This may be explained by the migratory habits of this species (Juanes et al. 1996). Migratory species generally maintain their position within their preferred temperature range and therefore, warming is less likely to influence their growth rates than for resident species.

Increasing fishing effort and ocean warming are likely to have a range of influences on the life history and productivity of the southern Angolan *P. saltatrix* population. Changes in these parameters will complicate the management of this important resource and potentially influence the livelihoods of coastal communities in Angola. The typical cycle of fishery collapse and required enforcement of stricter controls to initiate stock rebuilding that has been observed for this species in other regions (Smith et al. 2013, Govender 1996, Murdy 2013), should be avoided in Angola by timeously implementing appropriate management measures. To ensure that management measures are appropriate in this changing environment, consistent monitoring of the population and biological parameters such as growth and age-at-maturation (Trippel 1995) will be necessary. Changes in these parameters should be recognised and appropriate amendments to management strategies should be made as quickly as possible. At present, the most likely response of the Angolan government to a

stock collapse would be to increase fishing effort or improve technology. This will most likely only exacerbate the situation and unless there is a distinct policy shift towards sustainability management, with flexible management strategies that allow rapid responses to change, economic hardship is the most likely future for Angola's coastal communities.

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APPENDIX 1

Questions posed to previous Flamingo Lodge researchers in fishery questionnaire

The questions inquired about recreational and commercial fisheries separately with subsistence and artisanal fishers being considered commercial through their activities being conducted for financial or nutritional gain. The questions posed to researchers were as follows:

1. How many groups of 'local' recreational fishers were in the region on an average weekend?
2. Were those that you did see (if any) generally fishing with bait or using artificial lures?
3. If you saw any of their catches, what species comprised the bulk of their catch, how much did they catch and approximately what size fish (per species) were captured on average?
4. Did you see recreational fishers releasing any edible or non-edible species?
5. What types of commercial fishing gears did you see being used in the region?
6. What size vessels were used, were they motorised and how many fishers were on each on average?
7. Were any additional methods being used to promote capture efficiency?
8. At the town markets what was the general species composition, which species were dominant and what sizes were being captured?