

Economically important cephalopods of southern Angola,  
with a focus on the artisanal jig fishery.

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## *Abstract*

The global decline in marine finfish stocks has been met with a concomitant expansion of fisheries for cephalopods. Despite the increase in the exploitation and commercialization of cephalopods, there is a dearth of scientific information for over 90% of the extant species and this is even more marked in the developing world. Angolan capture fisheries production noted a tenfold increase in cephalopod landings between 1994 and 2003. One of the important fisheries is a cephalopod directed jig fishery that targets the squid *Loligo reynaudii* and the cuttlefish *Sepia vermiculata* in southern Angola, however, there is a complete lack of socio-ecological information available for this fishery. Hence the aim of this thesis was to provide basic biological and demographic information on *L. reynaudii* and *S. vermiculata* distributed off the coast of southern Angola, assess the importance and dependence of local artisanal fishers on these two species and examine the current management strategies and policies in the region

This study found that the artisanal cephalopod jig fishery is critical for the livelihoods of the coastal communities of southern Angola, particularly due to the limited alternative income generating opportunities available. The cephalopod jig fishery is highly labour intensive, with fishers spending a considerable amount of time per day, drifting over known fishing grounds. Catch composition of the artisanal jig fishery indicated that squid is the dominant species within the fishery, in terms of numerical abundance and weight. The productivity and progression of the fishery is hampered by a number of ecological, socio-economic and governance constraints, as highlighted by socio-economic surveys conducted with local squid fishers. Such constraints include, but are not limited to declining catches, increased negative interactions with seals, increased inter-sector competition, lack of infrastructure, poor quality fishing equipment as well as a lack of communication and support from government officials.

To examine aspects of the biology and demography of *L. reynaudii*, whole specimens were collected monthly, from the two primary fishing areas in southern Angola; Namibe and Tombua, during two main sampling periods, June 2008 – May 2009 (Period 1) and June 2014 – May 2015 (Period 2). Male *L. reynaudii* were found to be significantly larger in size and weight than females, however both the average and maximum dorsal mantle length (DML) decreased between sampling periods. Length-at-50% maturity was larger for male *L.*

*reynaudii* (170.47 mm DML – 1<sup>st</sup> period, 165.44 mm DML – 2<sup>nd</sup> period) than female *L. reynaudii* (114.71 mm DML – 1<sup>st</sup> period, 109.43 mm DML – 2<sup>nd</sup> period). Gonadosomatic indices (GSI) varied significantly during month and season for both sexes. Peak GSI coincided with a low catches in the artisanal jig fishery suggesting that the population may undergo a spawning migration away from fishing grounds, during late spring and summer. The theory of a seasonal spawning migration is further supported in this study by the low abundance of juvenile and sub-adult *L. reynaudii* collected during the study, along with the inability to detect egg beds in known fishing grounds. Stomach content analysis indicated that teleosts were the most important dietary item (66.3% F of the stomach contents). *Trachurus capensis* and *Engraulis encrasicolus* are both highly abundant small pelagic fishes in the cold nutrient rich waters of the Benguela Current and dominated the diet of sampled squid during autumn and winter months. It is likely that the prevalence of large, adult squid off the coast of Angola, as observed within the current study, may be ascribed to the suitable environmental conditions and the abundance of suitable prey. The results from the current study indicate that the southern Angolan subpopulation reveals similarities to that of the West Coast subpopulation of squid in South Africa, with regards to demographics and reproductive characteristics. It is likely that the population in southern Angola is an extension of the South African subpopulation of *L. reynaudii* on the western extremities.

To examine the basic population biology and ecology of *S. vermiculata* off southern Angola whole specimens were collected from the fishery between December 2014 and April 2015. Morphological results indicate clear sexual dimorphism in soft part characteristics, cuttlebone and beak morphometry. Length-at-50% maturity was smaller in male *S. vermiculata* (217.53 mm DML) than female *S. vermiculata* (231.13 mm DML), although these differences were not significant. Stomach content analysis indicated that *S. vermiculata* predominantly fed on teleost species which were found within 64.5% of stomachs. Teleosts were more dominant in the diet of male *S. vermiculata* (78.6% F) than female *S. vermiculata* (53.0% F), which ate a more varied diet including crustaceans (41.2% F) and cephalopods (17.7% F). Availability and abundance of cuttlefish in Namibe indicates that the species may undergo a spatio-temporal shift in distribution, with majority of the artisanal catches of *S. vermiculata* occurring during summer months.

The results from the current study highlights the fisheries potential of *L. reynaudii* and *S. vermiculata* and the dependence of artisanal fishers in southern Angola on cephalopods, and

more specifically squid. The development of sustainable fisheries management strategies for the artisanal cephalopod jig fishery is critical, particularly as the global exploitation of cephalopods continues to increase with declining finfish populations. Failure to implement management strategies may remove this critical economic safety net for vulnerable coastal communities which have little alternative livelihood opportunities. Ongoing ecological research, a co-management approach and an increased consideration of local ecological knowledge will assist in designing appropriate management plans for the southern Angolan cephalopod jig fishery.

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# CHAPTER 1

## GENERAL INTRODUCTION

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The marine ecosystem constitutes one of the most important economic and ecological resources, however human pressures have resulted in the exploitation of this environment at unsustainable levels, resulting in many fisheries being classified as overexploited (Arkhipkin et al. 2015, Selig et al. 2016, Mouritsen & Strybaek 2018, Sauer et al. 2019).

Overexploitation of any species, not only risks species endangerment and extinction, but also plays a significant role in initiating regime shifts which subsequently disrupts marine ecosystem equilibriums (Mullon et al. 2005). World marine capture fisheries contributed 84.4 million tonnes towards the total global capture fisheries production, of 96.4 million tonnes, in 2018 (FAO 2020). The increasing population growth coupled with the rise in demand for marine resources, as illustrated by the increase of marine capture fisheries production by 6.1 million tonnes between 2016 and 2018, with a substantial increase (24.2% from 1974 to 2017) in the percentage of marine stocks which are harvested at biologically unsustainable levels (FAO 2020).

The global decline in marine commercial finfish catches has coincided with an increased expansion of fisheries to lower trophic level species, resulting in the increased exploitation and commercialization of cephalopods as a marine fisheries resource (Piatkowski et al. 2001, Rodhouse 2001, Jereb et al. 2005, Agnew et al. 2005, Hunsicker et al. 2010, Molfese et al. 2014, Arkhipkin et al. 2015, Sauer et al. 2019, FAO 2020, Ospina-Alvarez et al. 2021). The development and expansion of these “unconventional” cephalopod fisheries has subsequently resulted in the exploitation of “new resources” as well as seen a drastic increase in the utilization of traditionally exploited species (Jereb et al. 2005, Hunsicker et al. 2010, Molfese et al. 2014, Xavier et al. 2015, Sauer et al. 2019). Despite the growing interest and demand within this class, the lack of knowledge on cephalopod species biology, ecology and physiology is hampering their management (Boyle 1990, Jereb & Roper 2010, Norman et al. 2016). Of the 800 extant species of cephalopods worldwide, extensive research and literature is only available for approximately 60 species, with 6% of species within the family Sepiidae being sufficiently studied and 20% of species within the family Loliginidae (Rodhouse et al. 2014, O’Brien et al. 2018).

The class Cephalopoda contains two extant subclasses, the Nautiloidea and the Coleoidea. The Nautiloidea, comprises of a single extant genus, *Nautilus*, all of which possess an external shell (Roper 1984, Jereb et al. 2005). The Coleoidea is comprised of the squid (Order Teuthida) and the cuttlefish (Order Sepiida), among others, and are characterised by an internal shell (Boyle 1990). The squid are further subdivided into two suborders; the Myopsida, which are classified as coastal squid, closely associated with the continental shelf, and the oceanic squid, the Oegopsida (Roper 1984, Jereb et al. 2010). Total world catches by major fisheries have highlighted the global importance of squid and cuttlefish resources (FAO 2020). The bulk of squid catches comprises of species from two families, the Ommastrephidae and the Loliginidae, whilst the Sepiidae dominate global catches within the Sepioidea (Boyle 1990, Reid et al 2005, Jereb & Roper 2010, Arkhipkin et al. 2015).

The majority of cephalopod species are characterized by a short lifespan, rapid growth and semelparous reproductive life history (Jackson & O' Dor 2001, Jackson 2004, Guerra et al. 2010, Arkhipkin et al. 2015, Doubleday et al. 2016, Rosa et al. 2019). These life history traits raise the question whether cephalopod species can be considered to be extremely resilient or highly vulnerable to external changes (such as overfishing, climate change, habitat degradation etc.) (Boyle & Boletzky 1996, Guerra et al. 2010, Xavier et al. 2015, Doubleday et al. 2016, Anguilera 2018). Research has suggested a recent proliferation of cephalopod populations as a result of the combination of global climate change, increased fishing pressure on the predators and competitors of cephalopods, as well as their “ecological plasticity/flexibility” (Doubleday et al. 2016, Rosa et al. 2019).

Cephalopods are a vital component in the trophic relations of marine ecosystems, both as prey and predators (Clarke 1996, Rodhouse 2005, Hastie et al. 2009, Guerra et al. 2010, Hunsicker et al. 2010). Cephalopods are generally classified as predatory opportunistic feeders, exploiting a variety of different prey items depending on availability and abundance (Hastie et al. 2009, Jereb & Roper 2010, Hunsicker et al. 2010, Villanueva et al. 2017). Furthermore, cephalopods form an important dietary component for a number of large marine predators, including marine mammals, seabirds and fish (Boyle 1990, Clarke 1996, Hunsicker et al. 2010). Their contribution to the diet of many commercially important finfish stocks has raised concerns as to whether increased exploitation of cephalopods will cause a further imbalance within these exploited marine ecosystems (Hunsicker et al. 2010). Whilst the trophic dynamics between cephalopods and their predators are not particularly well

understood, research has suggested that the decline of predatory finfish (as a result of exploitation) has subsequently resulted in an increase in cephalopod abundance (Boyle & Boletzky 1996, Caddy & Rodhouse 1998, Vecchione et al. 2009, Rodhouse et al. 2014).

### *Cephalopod fisheries*

Cephalopods have been targeted for human consumption for millennia, however commercial cephalopod fisheries were only formally developed during the 1950's, with the FAO first publishing a global cephalopod catch value, of approximately 0.6 million tonnes in 1950 (Lipinski et al. 1998, Mouritsen & Strybaek 2018, Clark 2019). The contribution of cephalopods to world capture fisheries production has subsequently increased substantially over the years, with catches exceeding 3.7 million tonnes by 2010 (Hunsicker et al. 2010, FAO 2012, Molfese et al. 2014, Arkhipkin et al. 2015, Ospina-Alvarez et al. 2021). From the total reported global capture production values, from 2005 to 2014, the squid fisheries dominated cephalopod landings, accounting for approximately 80% of the total, whilst the octopus and cuttlefish fisheries each represented 10% of total cephalopod landings (Sauer et al. 2019). The rise in demand for cephalopods has subsequently resulted in increasing global prices, with squid, cuttlefish and octopus estimated to have contributed 7% towards the total value of internationally traded fish products in 2018, whilst finfish accounted 66% and crustaceans, 22% (FAO 2020).

Cephalopods contribute to three major fishery types: large-scale directed fisheries, by-catch fisheries and small-scale directed fisheries (Rodhouse et al. 2014, Anguilera 2018). The extent of the contribution of cephalopods to each of these fisheries varies. However, the majority of cephalopod species are caught as by-catch or in small-scale fisheries. As a result, many of the targeted species stocks are not adequately defined, have limited monitoring and assessment, as well as few regulations (Lishchenko et al. 2021).

Whilst an observed decline in global cephalopod catches was noted in both 2017 and 2018 (approximately 3.6 million tonnes) from a peak of 4.9 million tonnes in 2014, exploitation levels remain relatively high with an overall steady rate of increase, particularly over the past two decades (Hunsicker et al. 2010, Arkhipkin et al. 2015, FAO 2020). Ospina-Alvarez et al. (2021), noted a six-fold increase in volume caught in terms of the commercialisation of cephalopods since the onset of formal fisheries in 1950. Similarly, Angelini & Velho (2011)

found that cephalopod catches increased from 0.001 t km<sup>-2</sup> in 1986 to 0.004 t km<sup>-2</sup> in 2003. Angolan fisheries capture production indicated a substantial increase in cephalopods catches from 191 tonnes in 1994 to 2500 tonnes in 2002 (Konda 2008). However, despite the volume and increases in cephalopod landings, the dearth of catch and species composition information in the various fisheries is concerning. It is however likely that the increase in cephalopod catches, in Angola, is not purely driven by an increase in artisanal fishing activity but is the accumulative result of increasing industrial fishing activity, and more specifically, trawl fishing activity.

Extensive research on only a few cephalopod species of commercial value has highlighted major issues pertaining to the management of cephalopod directed fisheries. This includes but is not limited to; 1) taxonomic challenges, 2) difficulties in stock identification, 3) difficulties in understanding and forecasting population abundance and distribution, 4) extensive damage to spawning habitat, 5) lack of historical fishing data, and 6) poor capture of fisheries related data and a lack of reporting within fisheries (Boyle 1990, Pierce & Guerra 1994, Boyle & Boletzky 1996, Rodhouse 2005, Jereb & Roper 2010, Rodhouse et al. 2014, Arkhipkin et al. 2015, Mouritsen & Strybaek 2018, Sauer et al. 2019, Arkhipkin et al. 2021).

### *Fisheries in Africa*

Africa has followed the global trend of an increasing demand for fish, of which the majority of the domestic fish supply is dependent on capture fisheries (FAO 2020). The demand for fish is not only linked to an increased population growth but also as a result of an increase in the awareness of the health benefits associated with the consumption of fisheries products, particularly when considering the more frequently occurring disease outbreaks within livestock (Sowman & Cardoso 2010, Sauer et al. 2019, FAO 2020). Furthermore, the global demand for seafood has resulted in extensive pressure being placed on developing countries fish stocks, particularly in Africa, by industrial distant water fishing fleets whom are unable to meet the demand within their local waters (Pauly & Zeller 2016).

The African fisheries sector is vital for the socio-economic growth of the continent, in terms of poverty alleviation and food security, at household, community and national levels (du Preez 2009, Sowman & Cardoso 2010). This is particularly true for marginalized coastal communities. Balancing the needs of communities and ecosystems, within the fisheries

context, is of utmost importance. The need for balance within fisheries was initially highlighted in the Food and Agriculture Organization (FAO) Code of Conduct for Responsible Fisheries (FAO 1995), stating that “Fisheries management should promote the maintenance of the quality, diversity and availability of fisheries resources in sufficient quantities for present and future generations in the context of food security, poverty and sustainable development...”. Understanding the dynamics between fisheries, sustaining and developing livelihoods and conserving resources is complex, however it is fundamental in developing conservative, sustainable management practices (du Preez 2009, Sowman & Cardoso 2010, FAO 2020).

Throughout Africa, marine fisheries play a fundamental role as a source of nutrition as well as for providing an important source of micronutrients, vitamins and essential fatty acids (Sowman & Cardoso 2010, Chan et al. 2019, FAO 2020). Fish is estimated to provide 19% of animal protein intake to people living within Africa, however the contribution of fish to animal protein supply was estimated to be greater than 20% for Angola (Chan et al. 2019, FAO 2020). Furthermore, the African marine fisheries sector is considered to play major role in supporting the livelihoods of many coastal communities, by providing income through capture, sales, processing and trading of fisheries resources (du Preez 2009, Sowman & Cardoso 2010, Belhabib & Divovich 2015, FAO 2020). Income generation is critical in sustaining households in terms of; the procurement of alternative foods, shelter, medical care and the development of education and businesses, thereby enhancing the socio-economic profile of these local communities (du Preez 2009, Sowman & Cardoso 2010).

### *Squid fisheries*

The Teuthoidea comprise of approximately 290 extant species, of which approximately 40 species are currently considered to be of substantial commercial importance (Arkhipkin et al. 2015). The majority of global squid catches originate from two families, namely the the Ommastrephidae and Loliginidae (Arkhipkin et al. 2015). The Ommastrephidae and Loliginidae were documented to account for approximately 31% of the total mollusc marine capture production in 2018 (FAO 2020). However, it is important to note that these values may not be an accurate representation of global squid catches due to a lack of catch statistics and a lack of accurate species identification (Arkhipkin et al. 2015). The Ommastrephidae, dominate catch landings in terms of biomass, and are primarily represented by 5 main target

species including *Todarodes pacificus*, *Nototodarus sloanii*, *Illex argentinus*, *Illex illecebrosus* and *Dosidicus gigas* (Arkhipkin et al. 2015, FAO 2020). However, the Loliginidae are typically considered to be of higher commercial value than the Ommastrephidae (Pierce et al. 2010). Of the Loliginidae, a number of species are exploited around the globe including, but not limited to, *Loligo vulgaris*, *Loligo forbesii*, *Doryteuthis pealii*, *Loligo reynaudii* and *Doryteuthis gahi* (Rodhouse 2005, Arkhipkin et al. 2015).

Squid are captured in both directed and bycatch fisheries around the world. These fisheries vary globally in their degree of commercialization, as well as the method or gear used to target the various species (Rodhouse et al. 2014, Arkhipkin et al. 2015, Anguilera 2018). Commercial, directed squid fisheries typically rely upon the exploitation of the concentration of individuals as a result of ecological or behavioural characteristics. Industrial fishing vessels typically makes use of echosounding technologies to locate squid aggregations (Sauer 1995, Sauer et al. 2013, Arkhipkin et al. 2015). A large proportion of the commercial loliginid fisheries primarily rely on bottom trawls to target squid aggregated near the sea bed during the day (Rodhouse 2005, Arkhipkin et al. 2015). Squid caught by trawls is considered to be of inferior quality and subsequently classified as a lower value product. Jigging is a preferred method of fishing in a number of commercial loliginid fisheries, including the *L. reynaudii* fishery off the coast of South Africa (Rodhouse 2005, Sauer et al. 2013). Within commercial fisheries, jigging is typically used in conjunction with lights to attract squid to the surface at night, whilst jigging activity during the day typically targets onshore spawning aggregations (Augustyn et al. 1992, Sauer 1995, Arkhipkin et al. 2015, Sauer et al. 2013). Furthermore, jigging is considered to be one of the primary fishing methods of small-scale and artisanal directed squid fisheries, globally (Rodhouse 2005, Arkhipkin et al. 2015).

Present day artisanal and small-scale inshore squid fisheries occurring throughout the Mediterranean, Europe, South America, the far east and west Africa make use of a variety of different fishing gears including drift nets, seine nets and traps however hand-jigging is generally regarded as the preferred method of capture (Jereb et al. 2015, Postuma & Gasalla 2010, Arkhipkin et al. 2015). Artisanal squid fisheries play a major role in providing income and livelihood security for vulnerable coastal communities, however in many regions around the globe these fisheries typically remain relatively unmanaged with a large proportion of catches unreported despite the economic importance of the resource (Arkhipkin et al. 2015, Anguilera 2018).

### *Cuttlefish fisheries*

Whilst the FAO (2020) estimated cuttlefish to have only contributed 6% towards the total global marine mollusc capture production for 2018, approximately 50 species of cuttlefish have been identified as of interest to fisheries or of value to fisheries around the globe (Jereb 2005). Whilst cuttlefish fisheries are unevenly distributed globally, throughout their distribution they are targeted by either commercial or artisanal fisheries, or a combination of both (Sasikumar et al. 2015, Davies & Nelson 2018, Lishchenko et al. 2021). Cuttlefish is considered primarily as a bycatch species within commercial trawl fisheries, however, artisanal fisheries make use of highly selective gear along with knowledge on the behavior and biology to actively target cuttlefish (Jereb 2005, Reid et al. 2005, Hastie et al. 2009 Sasikumar et al. 2015). Small-scale cuttlefish fisheries contribute greatly toward total cephalopod catches within European waters, off the northwest coast of Africa and within the Mediterranean Sea (Pierce et al. 2010). In Greece, the small-scale fishery was estimated to account for on average 80% of the total cuttlefish landings within local fishing areas, thereby highlighting the potential importance of cuttlefish species for local livelihoods (Ganias et al. 2021).

Artisanal cuttlefish fisheries are often described as multi-gear fisheries, as they are known to make use of a variety of fishing equipment, including; jigs, traps, spears, gillnets and trammel nets, as well as fish aggregating devices (FADs) (Belcari et al. 2002, Royer et al. 2006, Lefkadiou et al. 2007, Pierce et al. 2010, Jereb et al 2015).

Artisanal cuttlefish fishing, around the globe, generally targets mature individuals which have aggregated in shallow coastal waters for spawning (Le Goff & Daguzan 1991, Belcalari et al. 2002, Royer et al. 2006, Bloor et al. 2013, Sasikumar et al. 2015). This is concerning as catchability is high during these periods and thereby highlights the need for sustainable harvesting procedures and management measures within artisanal cuttlefish fisheries. This is particularly within fisheries, such as trap fisheries, which exploit the attraction of spawning individuals to suitable egg deposition substrates and subsequently result in high levels of egg destruction and low levels of recruitment (Watanuki & Kawamura 1999, Belcari et al. 2002, Bloor et al. 2013, Melli et al. 2014).

In the northeast Atlantic, cuttlefish represent the most commercially important cephalopod, in terms of both yield and economic value (Pierce et al. 2010, Jereb et al. 2015, Davies & Nelson 2018). During the period of 2000-2018, cuttlefish accounted for, on average, 41% of annual landings within north-east Atlantic waters, in comparison to the Octopodidae (31%) and the Loliginidae (21%) (ICES 2020). Furthermore, the market value of cuttlefish increased by approximately £2.00/kg between 2008 and 2017 (Davies & Nelson 2018). This increase has been attributed to the increased global demand, coupled with the underperformance of existing cuttlefish fisheries (Davies & Nelson 2018, FAO 2020).

### *The fishery importance of *Loligo reynaudii**

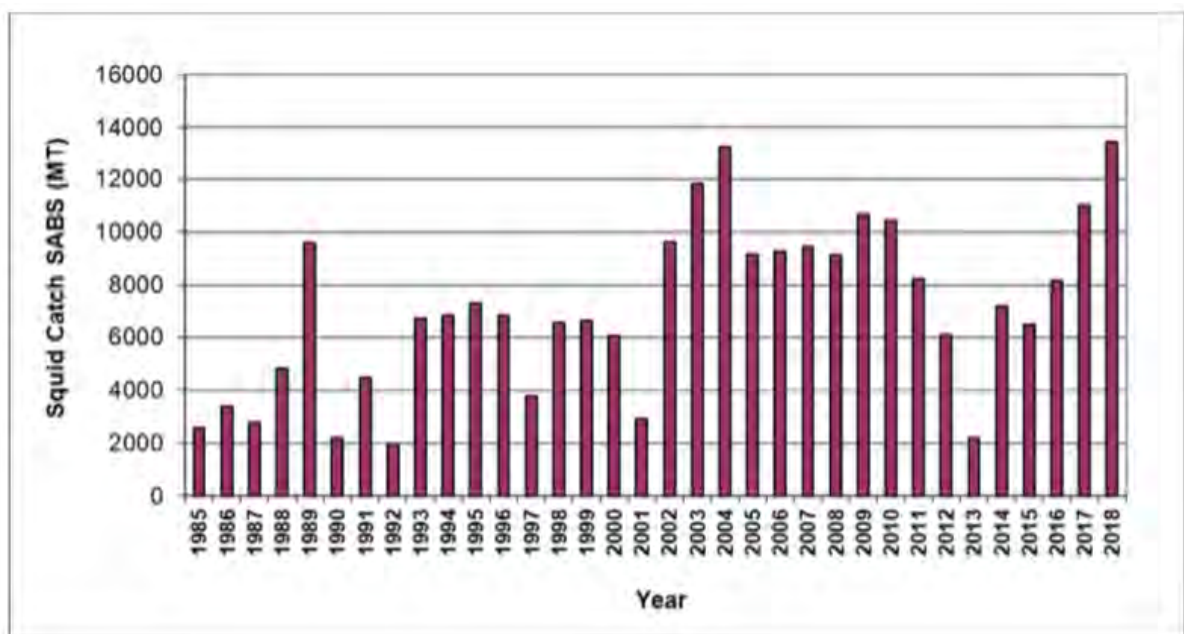
*Loligo reynaudii*, commonly known as the chokka squid in South Africa, is the most commercially exploited cephalopod in South African waters (Augustyn 1990). Until the 1980's the South African chokka squid fishery was a minor component of the multi-species trawl fishery, however, in 1984 a species-specific hand-line jig fishery was established (Sauer et al. 1992, Augustyn & Roel 1998). The chokka squid fishery has since expanded dramatically and thus so have catches, ranging between 6000 – 13 000 t caught annually (Augustyn & Roel 1998, Arkhipkin et al. 2015) (Figure 1.1). Furthermore, it is estimated that approximately 200 – 500 t is caught annually as by-catch in the demersal trawl fishery (Augustyn & Roel 1998, Arkhipkin et al. 2015). The jig-fishery is estimated at providing employment for over 3 000 people locally and during periods of good catches has been known to generate in excess of 480 million ZAR annually (DAFF 2016).

The current jig-fishery fleet is comprised of large-decked vessels with a fisher capacity of between 12 and 32 crew, onboard freezing facilities which enable vessels to remain at sea for weeks at a time, and numerous strong incandescent lights (1-2kw) which attract feeding squid to aggregate around the boat during the night allowing for fishing to continue (Augustyn et al. 1992, Arkhipkin et al. 2015, DAFF 2016, Sauer et al. 2013). The jig fishery is considered to be the one of the most valuable fisheries within South Africa and as such is of major social and economic importance, particularly within the Eastern Cape (Mather et al. 2003, Arkhipkin et al. 2015, Glazer & Butterworth 2006).

The South African chokka jig-fishery is restricted in terms of the number of crew and as such the number of fishers on each vessel is fixed (Augustyn & Roel 1998, Mather et al. 2003,

Burg 2019). Currently, effort levels within the jig-fishery is capped at 136 vessels and 2422 crew (Sauer et al. 2013, Burg 2019). At present, the jig-fishing industry experiences two closed seasons (April -June as well as a 5-week closure during Oct/Nov) as well as a ban of fishing within the various Marine Protected Areas along the coast of South Africa (Burg 2019). The combination of effort based management practices as well as the implementation of closed seasons and areas plays a major role in ensuring that the species is harvested at a sustainable level (Augustyn et al. 1992).

The South African squid fishery has been documented to experience drastic fluctuations in catches, as can be seen in Figure 1.1 (Sauer et al. 2013, Glazer and Butterworth 2016, Burg 2019). Periods of low catches, which are most often associated with environmental conditions, have the potential to result in devastating social and economic effects on the industry and its' participants (Schon et al. 2002, Sauer et al. 2013). During these periods of low yield, many vessels often undergo exploratory trips out of preferred fishing grounds in an attempt to locate an alternative biomass.

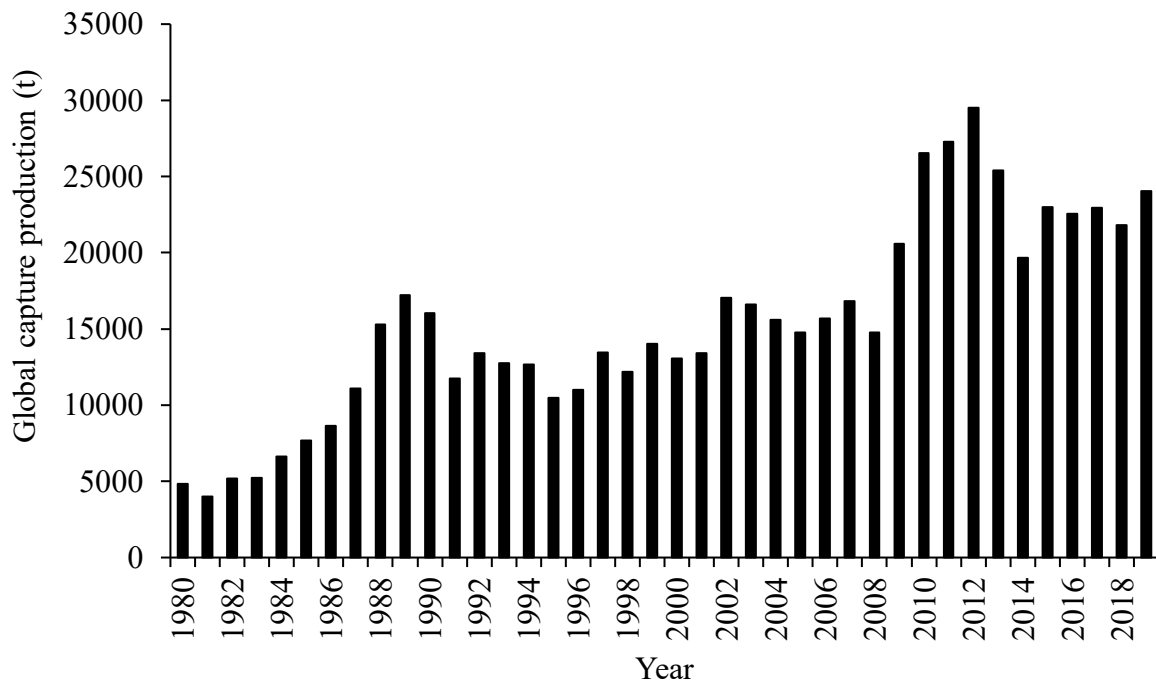


**Figure 1.1:** Catches in the South African squid jigging fishery from 1985 – 2018, taken from Burg (2019).

Currently, the species is only exploited at industrial levels within South African waters despite its occurrence off the southern coast of Angola. However, the potential expansion of the industrial South African chokka jig fishery, coupled with increasing occurrence of foreign vessels in Angolan waters and the increasing local demand for this species in Angola, has highlighted the need for information on the species, in this region.

#### *The fishery importance of the Sepia officinalis species complex*

The *Sepia officinalis* species complex comprises of three sister species including *Sepia officinalis*, *Sepia hierredda*, and *Sepia vermiculata* (Khromov et al. 1998). Of these, *S. officinalis* is the most exploited species (Belcari et al. 2002, Hastie et al. 2009, Pierce et al. 2010, FAO 2012, Jereb et al. 2015). Global capture production indicates an overall increase in *S. officinalis* catches from 1980 to 2019 (Figure 1.2), however it is likely that catches are underrepresented as the species is known to contribute towards “cuttlefish and bobtail squid nei” (Jereb & Roper 2005). *Sepia officinalis* is an important fisheries resource in France, the UK, Spain, Portugal and Greece where it supports both commercial and artisanal fisheries (Denis & Robin 2001, Belcari et al. 2002, Hastie et al. 2009, FAO 2012, Jereb et al. 2015, ICES 2020). Within the north East Atlantic, the English Channel represents the major fishing area for *S. officinalis*, with the species primarily being targeted by otter and beam trawlers, or as bycatch within demersal finfish trawls (Pierce et al. 2010, Jereb et al. 2015, ICES 2020). Catch statistics in the English Channel, over the past 15 years, indicate a decline in landings within the French fishery and an increase in UK landings (ICES 2020). The observed changes in catch landings within the English Channel has however primarily been attributed to a northerly distributional shift of the species (ICES 2020).



**Figure 1.2:** Global capture production (tonnes) for *Sepia officinalis* from 1980 – 2019 (Data source: <https://www.fao.org/fishery/en/aqspecies/2711>).

Small-scale *S. officinalis* fisheries primarily make use of gillnets, trammel nets and traps to target cuttlefish during onshore spawning migrations (Pierce et al. 2010). Small-scale fisheries, targeting *S. officinalis*, are generally considered to be highly sustainable as they have very little by-catch and have reduced impacts on the seabed. Artisanal *S. officinalis* fisheries are typically considered to be seasonal, with fishers primarily target spawning adults (Pierce et al. 2010). The contribution of small-scale *S. officinalis* fisheries to global marine capture production is not well documented despite being of high socio-economic importance, as a large proportion of catches is sold through unmonitored markets.

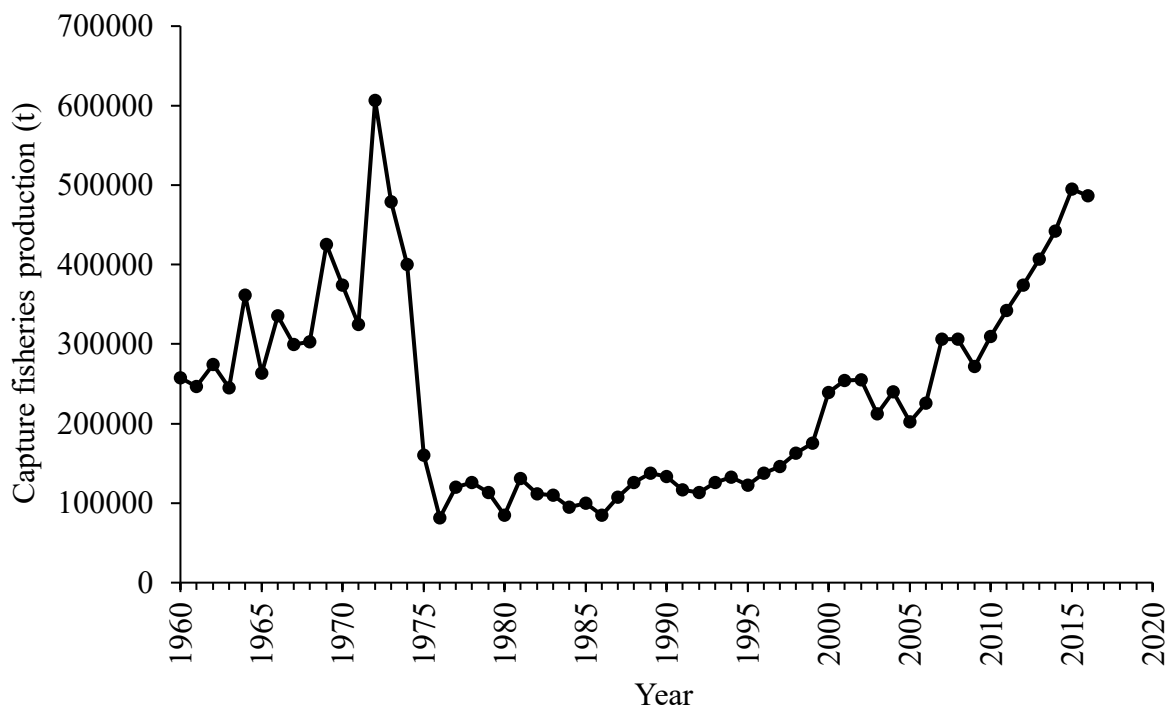
Whilst limited catch statistics are available for *S. hierredda*, the species is considered to be the most commercially important cuttlefish species within the east central Atlantic (Jereb & Roper 2005). *Sepia hierredda* targeted off Western Sahara and in Mauritania waters, by Spanish trawlers, represented 90% and 65% of the cuttlefish caught within the two regions, respectively (Jereb & Roper 2005). In Ghana, *S. hierredda* accounts for 90% of the cephalopod catch where it is targeted by commercial trawlers (FAO CECAF-SC 2008). The species is targeted by artisanal fisheries throughout North West Africa, however catch landings are not well managed and reported and as such in many instances are grouped as

“cephalopods” or not reported (Belhabib et al. 2012, Belhabib et al. 2014, Rodhouse et al. 2014).

*Sepia vermiculata* is currently not exploited by industrial or artisanal directed fisheries, however it is recognised as a species of fisheries potential (Roeleveld 1998). Furthermore, the species has been identified as a bycatch species in the Kwazulu-Natal prawn trawl fishery, contributing 20% of the total species composition by mass of the landed bycatch of the fishery in 2018 (DEFF 2020).

### *Angola*

Angola is the seventh largest country on the African continent. Located on the west coast of sub-Saharan Africa, the country is situated within the Benguela Large Marine Ecosystem (BCLME) (Cochrane et al. 2009, Sowman & Cardoso 2010, Huntley et al. 2019). The BCLME is considered to be one of the most productive large marine ecosystems boasting high levels of productivity in terms of fisheries (Duarte et al. 2005, Cochrane et al. 2009). Angolan capture fisheries production exhibits an increasing trend (Figure 1.3). Whilst fisheries contributed less than 3.7% of the country’s GDP during 2017 this was a significant increase from the 1.7% reported for 2012, and is above the global average of 0.5 – 2.5% (Sowman & Cardoso 2010). Despite the low contribution of fisheries to the country’s GDP in comparison to many other sectors, marine fisheries are still considered to be of great importance to the national economy as it sustains a large proportion of the population in terms of a source of livelihood and nutrition (Konda 2008, du Preez 2009, Sowman & Cardoso 2010, Paterson et al. 2014). The importance of fisheries resources to the domestic market is highlighted by the low contribution of exports to international markets, which has been estimated to be approximately 5% of the total catches (Konda 2008, du Preez 2009, Sowman & Cardoso 2010, de Young et al. 2012, Paterson et al. 2014).



**Figure 1.3:** Angolan capture fisheries production (metric tons) from 1960-2017 (Data source: <https://data.worldbank.org/>).

*The socio-political history of Angola, with a focus on the fisheries sector.*

Angola experienced 14 years of anti-colonial war, resulting in the country gaining independence from Portugal in 1975 (The World Bank 2019). This was followed by approximately three decades of civil war which continued, with interludes, until 2002 (The World Bank 2019). The declaration of independence coincided with the mass exodus of European nationals, subsequently resulting in the abandonment of productive infrastructure and institutions as well as a large-scale loss of human capital (Duarte et al. 2005, Belhabib & Divovich 2015). The situation worsened with the onset of the civil war, which resulted in the collapse of the formal economy (du Preez 2009).

The socio-political history of Angola had major implications on the various sectors of the country’s fisheries (Agostinho et al. 2005, Duarte et al. 2005, Belhabib & Divovich 2015). The combination of the anti-colonial and civil war resulted in the departure of foreign fleets, the crippling of fisheries related infrastructure and the collapse of the domestic industrial sector, as represented by the drastic reduction in the countries’ marine capture fisheries production values (Figure 1.1) (du Preez 2009, Belhabib & Divovich 2015).

The occurrence of the war played a significant role in conserving Angola's fish stocks (Duarte et al. 2005). It is, however, important to note that there was a lack of monitoring, control and surveillance during this period (du Preez 2009, Belhabib & Divovich 2015). This not only could have resulted in an underreporting of local capture information but coincided with an increase in illegal catches by foreign industrial fishing fleets (du Preez 2009, Belhabib & Divovich 2015). Furthermore, the war led to the displacement of local communities, towards the coast, in search of refuge and livelihoods (Agostinho et al. 2005, du Preez 2009). As such considerable growth of coastal subsistence and artisanal fisheries occurred during this period (du Preez 2009, Belhabib & Divovich 2015). The development, transformation and implementation of governmental policies, beginning in the mid-1980's, with the aim of promoting the domestic industrial and artisanal fisheries sectors, saw a gradual increase in the capture fisheries (Figure 1.3) (Agostinho et al. 2005, Duarte et al. 2005, Sowman & Cardoso 2010, Belhabib & Divovich 2015). During the 1990's, further efforts were made to develop the fisheries sector, including implementing strategies to attract private investors to rehabilitate and recover industrial production units, by promoting and supporting fundamental partnerships and furthermore by enhancing conditions to promote growth within the artisanal sector (Duarte et al. 2005, Konda 2008).

The end of the civil war in 2002 resulted in substantial economic growth for the country (The World Bank 2019). The potential of fisheries to contribute towards poverty alleviation, food security and enhancing the sustainability of livelihoods was recognized and prioritized (Agostinho et al. 2005, du Preez 2009, Sowman & Cardoso 2010). However, the development and expansion of fisheries as a result of the combination of the anti-colonial and civil war, large scale population displacement of communities to coastal towns, poor economic conditions, limited alternative livelihood opportunities and the promotion of fisheries related governmental policies have subsequently placed the regions fish stocks at an increasing risk of overexploitation (Agostinho et al. 2005, Sowman & Cardoso 2010, Belhabib & Divovich 2015).

Angola recognises the importance of the fisheries sector, this is highlighted within the National Development Plan 2018-2022, with the Angolan government estimating sector growth during this period to range between 4.7% and 8.3% (NDP, Plano de Desenvolvimento Nacional 2018-2022). The NDP focuses on achieving inclusive, sustainable and diversified

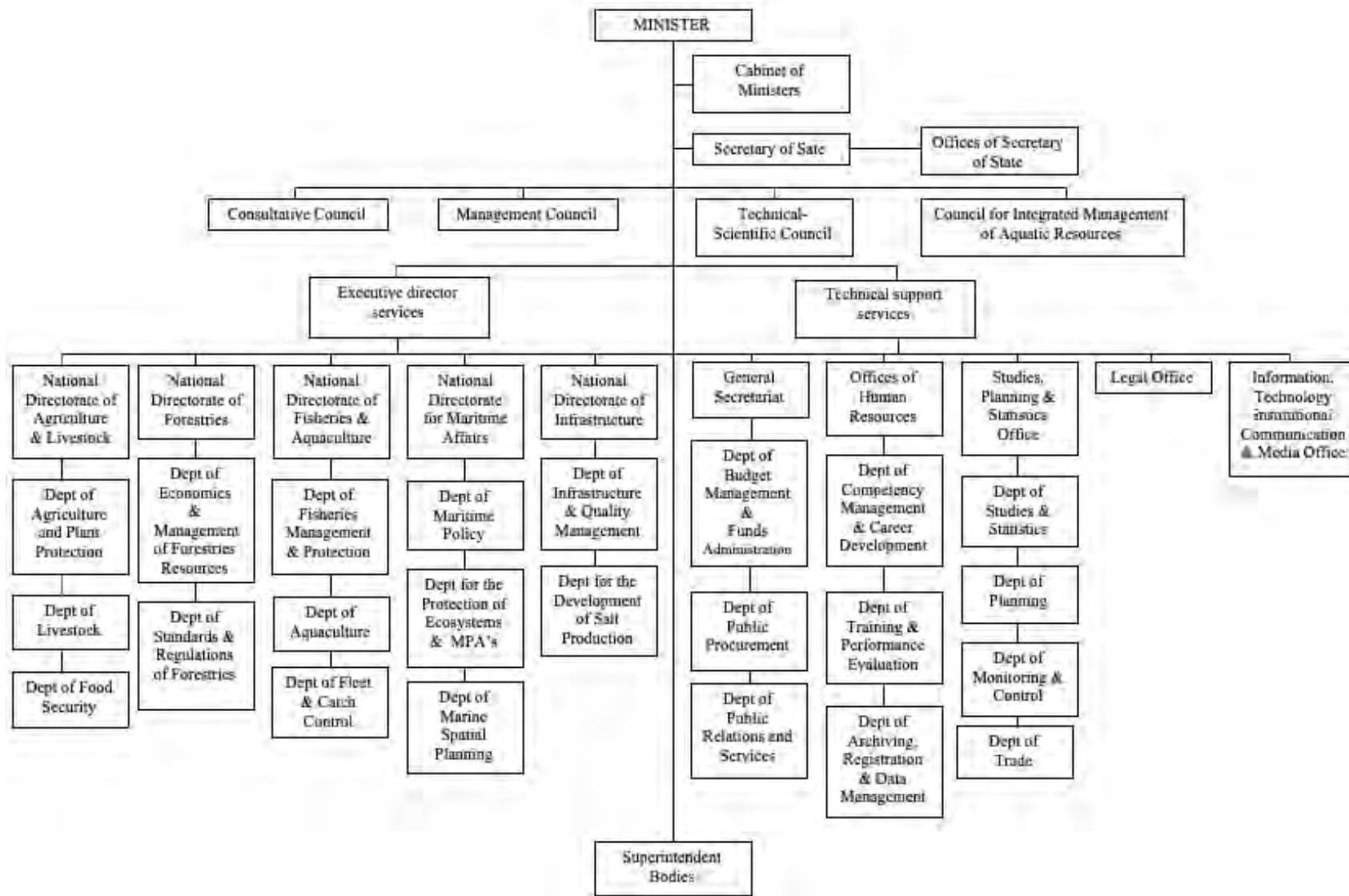
economic growth, human development and welfare, specifically with a focus on non-oil related sectors, such as fisheries, agriculture and construction. With regards to fisheries, the NDP highlights the need for an ecosystem based approach to the management of fisheries resources to maximise benefit without compromising fisheries resources and ecosystem health. Such benefits include social benefits, such as food security, as well as economic benefits, such as job creation, import substitution and the promotion of exports.

### *The Angolan fisheries governing system*

The governing system of Angolan fisheries has undergone several changes over the past few decades, subsequently resulting in changes in the bureaucracy and governance within the fisheries sector (Sowman et al. 2011). Prior to the establishment of the Ministry of Fisheries (MINPESCAS) in 2012, the Ministry of Agriculture, Rural Development and Fisheries (MINADERP) was responsible for the development, implementation, supervision and control of marine capture fisheries. In 2018, the Ministry of Fisheries and the Sea (MINPESMAR) was established by Presidential Decree N°23/18 of 31 January 2018 (Angola 2018). In 2020, the Angolan Government decided that to enhance efficiency and efficacy within the fisheries governing system, the Department of Agriculture and Forestry would merge with MINPESMAR. Currently, and as of the Presidential Decree N°177/20, the institutional framework for Angolan capture fisheries falls within the purview of the Ministry of Agriculture and Fisheries (MINAGRIP) (Figure 1.4) (Angola 2020b).

As stipulated within Article 2 of the Decree, MINAGRIP and more specifically the departments associated with Fisheries, Aquaculture and Salt production, as well as the competent support bodies, are responsible for the below mentioned; 1) propose policy and implement strategy to allow for the development of the fisheries, aquaculture and salt production sectors, 2) design and implement, both regional and national, strategies for marine biodiversity as well as for integrated coastal zone management, 3) promote the sustainable development of the sectors and ensure the implementation of measures for the preservation and sustainable management of aquatic ecosystems and resources; 4) to ensure scientific research and technological development within fisheries and aquaculture, 5) promote international and regional cooperation within the agriculture and fisheries sectors, 6) ensure the control, registration and monitoring of Sector data, 7) coordinate all the inspection activities with regards to fishing, aquaculture and health and ensure the application of the

respective sanctions, 8) to guide and disseminate information about technical and technology transfer in matters of fisheries, aquaculture and salt, processing of fishery products, protection of fishing stocks and aquatic ecosystems (Angola 2020b).



**Figure 1.3:** Organizational structure of the Ministry of Agriculture, Rural Development and Fisheries (MINAGRIP) as outlined in the Presidential Decree N°177/20 (Angola 2020b).

As outlined in Article 18 of the Decree, the National Directorate of Fisheries and Aquaculture (NDFA) is the governmental department responsible for the design, management, implementation and control of fisheries and aquaculture policies, to develop these sectors whilst maintaining sustainable use of resources and the integrity of the ecosystems concerned. The internal structure of the NDFA includes the Department of Fisheries Management and Protection; Department of Aquaculture and the Department of Fleet and Catch Control. Broadly, the NDFA is responsible for the following: a) ensure sustainable management, conservation and protection of aquatic biological resources whilst establishing mechanisms to maximise socio-economic benefits; b) provide technical specifications of fishing vessels and ensure that construction and modification is approved by the Minister, to ensure growth of the fishing sector; c) propose and manage the decentralization of fisheries management, assign and manage licences and rights necessary for fishing/aquaculture in accordance with current legislation; d) propose a species list of specimens for import and export; e) propose regulations related to fishing activities and seasons, with regards to species which require protection or rehabilitation, as well as develop measures to protect and preserve aquatic ecosystems, genetic stocks and biodiversity; f) propose and implement management strategies for fisheries and aquaculture, in collaboration with other institutions, including; community fishing organizations and other interested parties; g) propose strategies for the granting and cancellation of licences and rights, for fisheries and aquaculture, and ensure these are in accordance with current legislation; h) register rights holders, fishing vessels and aquaculture enterprises; i) propose research and evaluation cruises, these may include investigating new, prospective fisheries resources; j) propose bio-economic models that allow for development projections to be determined, for both medium and long term; k) propose and elaborate “planos de ordenamento” for fisheries and aquaculture; l) propose total allowable catches, fishing quotas and effort limits for fisheries; m) manage and control fish husbandry practices as well as regulate chemical and biological product use within aquaculture; n) to practice the following competencies established by law or issues above (Decreto Presidencial n.o 177/20).

### *Angolan fisheries legislation*

The Law of Aquatic Biological Resources (LRBA - Lei dos Recursos Biológicos Aquático) n.º6-A/04 implemented on the 8<sup>th</sup> of October 2004, replaced the previous legislation, the Fisheries Law (Lei das Pescas) (Angola 2004). The LRBA was implemented as it is

considered to be more inclusive and reflective of both international and regional fisheries objectives, policies, legislation and development goals as well as recognise the importance of a more integrated management approach for marine resources (Paterson et al. 2014). The law, often referred to as the “new fisheries law” governs the management and conservation of all aquatic living resources and as such defines the general guidelines and objectives for; 1) the use and exploitation of aquatic biological resources, 2) the fisheries legal system, 3) rules and regulations concerned with the protection and conservation of aquatic resources and ecosystems, 4) the basic regulations with regards to ports and vessels as well as, 5) the rules for scientific research and monitoring (Angola 2004). As stipulated within the Angolan Fisheries Law, the management of Angolan fisheries are primarily based on catch and effort-based regimes, through the implementation of total allowable catches (TAC), quotas, and limited entry into the various sectors or fisheries. In order to ensure that regulatory management measures are relevant and effective, in terms of sustainable and conservative utilization, the management measures are revised annually and include adjusted TAC’s and quotas, as well as revised regulations on gear and area restrictions, closed seasons and licencing.

Article 5 of the Angolan legislation distinguishes between commercial and non-commercial fishing practices, with commercial fishing being defined as a fishing practice which generates profit (Angola 2004). As such, non-commercial fishing is described as subsistence, recreational or research related fishing activities (Angola 2004). Commercial fishing is further categorised as artisanal, semi-industrial and industrial, the defining characteristics of which are outlined in Article 1 and represented in Table 1.1 (Angola 2004).

**Table 1.1:** Characteristics of the different types of commercial fishing, as defined by the Law of Aquatic Biological Resources (Lei dos Recursos Biológicos Aquáticos) N.6-A/04 implemented on the 8<sup>th</sup> of October 2004 (Angola 2004).

	Artisanal	Semi-industrial	Industrial
Size of Vessel	Less than 14m.	Up to or less than 20 m.	Greater than 20 m.
Propulsion System	Oars, sails, outboard or inboard engines.	Inboard engine	Inboard engine.
Fishing Gears	Handlines, gillnets, entangling nets, and seine nets.	Longline, handlines, nets, trawling and other methods.	Mechanical.
On-board refrigeration/preservation	No freezing facilities, rarely make use of ice.	Make use of ice onboard.	Onboard freezing or alternative processing methods.

### *Governing the Angolan artisanal sector*

The Institute for the Development of Artisanal Fisheries and Aquaculture (IPA - Instituto de Desenvolvimento de Pesca Artesanal e da Aquicultura), which was established in the early 1990's, is the primary governing body concerned with the development, monitoring, support, and administration of the artisanal fishing sector within Angola (OCAR 2002, Agostinho et al. 2005, du Preez 2009, Paterson et al. 2014). More specifically the IPA provides technical advice to the sector; designs, implement and promotes projects; manages, organises and coordinates training and workshops; gathers and documents critical information on the sector; produces fiscal measures and policies and proposes rules and regulations for the management of the aforementioned; furthermore the IPA manages and optimises institutional human capacity (OCAR 2002). The IPA currently falls under MINAGRIP, however the institute remains administratively and financially autonomous and as such plays a vital intermediary role between the government and the stakeholders (du Preez 2009). Furthermore, the institute is delegated with the responsibility of the gathering of critical data, extension and the policymaking (OCAR 2002). The IPA, which is based in the capital city of Luanda, has provincial delegations within each of the coastal provinces (OCAR 2002).

### *Management of the artisanal sector*

Within the BCLME, Angola is considered to be the country that makes the most provision for the artisanal sector within their fisheries management framework and legislation (du Preez 2009). Management of the Angolan artisanal fishery sector is undertaken through several measures, these are highlighted within the Law of Aquatic Biological Resources as well as in the annual Presidential Decree which addresses the management measures of the fisheries sector. Currently the artisanal sector is managed accordingly; 1) biennial census, 2) required annual fishing licences, 3) output controls through total allowable catch (TACs) and quotas, 4) fishing restrictions, 5) implementation of legislation and regulations related to fisheries infringements and, 6) the use of fisheries observers and inspectors (Angola 2004, Angola 2020a).

Since 1996, a biennial census has been conducted by IPA officers in their respective provinces, to obtain information on the artisanal sector. This includes but is not limited to, the number and type of operational vessels, the number of fishers, the fishing gear in use, the characteristics of fisheries processing infrastructure and facilities as well as social-economic data (Sowman et al. 2011, Paterson et al. 2014). However, data collected by IPA representatives is considered to not be a true representation of fishing activity, due to a lack of capacity and coverage throughout the sector (du Preez 2009, Paterson et al. 2014).

As per article 31.3 of the LRBA, artisanal fishing rights are only granted to “Angolan persons” which are defined in Article 1.64 as a) an Angolan citizen, as recognised within the Nationality Law; b) an Angolan company, as defined within Article 1.30 of the LRBA; and lastly; c) any collective grouping of individuals which constitutes a single or group of Angolans, who exercise effective control over the collective (Angola 2004). Annual fishing licences are issued by provincial IPA offices, however holders of artisanal fishing rights may be exempt from the annual licence fees, for a period of up to 5 years, if licence holders are currently undertaking investments on land (Article 52 of LRBA, Angola 2004).

TACs are determined for the main target species, which are categorised into three distinct categories: 1) crustaceans and molluscs, 2) demersal species and 3) pelagic species. A total of 30% of the TAC is allocated to the artisanal fishing sector. However, the artisanal sector is not allocated a percentage of pelagic species and as such, any artisanal vessel which lands

large quantities of pelagic species are likely to have their licences revoked. TACs are determined by the executive decree upon scientific and technical information obtained from the Ministry and the Council for Integrated Aquatic Biological Resources (Article 19 of the LRBA, Angola 2004). TACs are published annually within the Presidential Decree and unless altered, TACs from the previous year are maintained (Article 19 of the LRBA, Angola 2004). The TAC allocated for Cephalopods, was maintained at 1400 tons for the year 2020 (Annex I of the Presidential Decree no 130/20). Species or area specific quotas are subsequently determined and allocated as a percentage of the TAC. Such quotas may be reduced as a result of a reduction in the overall TAC.

As stipulated within Article 11 of the Presidential Decree no 130/20, the number of artisanal fishing vessels for 2020 was restricted to 5500 (Angola 2020a). Varying percentages were allocated to the seven coastal provinces, of which three provinces; (Luanda (32.4%), Benguela (23.0%) and Namibe (18.2%) accounted for 73.5% of the allocated vessels (Table 1.2) (Angola 2020a).

**Table 1.2:** Number of vessels allocated per province to the marine artisanal sector, as specified within Article 11 of the Presidential Decree n.o 130/20 (Angola 2020a).

Province	Number of vessels	Percentage (%)
Cabinda	297	5.40
Zaire	605	11.00
Bengo	198	3.60
Luanda	1 782	32.40
Cuanza-Sul	356	6.47
Benguela	1 262	22.95
Namibe	1000	18.18

As outlined within the Fisheries Law (Art 33 of the LRBA), Angola has made special provisions for small-scale fishing activities, which includes artisanal and subsistence fishing, due to the recognition of the important role that these sectors play in reducing poverty and increasing food security (Angola 2004). Such provisions include a complete ban on all semi-industrial and industrial fishing within four nautical miles (nm) of the coast. This area

reserved for non-industrial and artisanal fishing extends to 8nm between Ambriz and Cabinda (Article 13, Presidential Decree no 130/20, Angola 2020a).

### *Project aim*

In 2008, the Angolan Government published the “Angola Visão 2025”, a document outlining the country’s long term aspirations. These aspirations broadly fell under 4 main goals; 1) peace and national reconciliation, 2) development of an integrated, diversified national economy, 3) reduce inequalities and discrimination, 4) ensure that development was achieved in a sustainable manner and prevent further damage to the natural environment.

Historical fishing data and biological information plays a critical role in developing reliable reference points which subsequently allow for long term, sustainable and conservative fisheries management strategies to be developed. The socio-political history of Angola, coupled with the continued expansion of the fisheries sector and the need for improvement in fisheries monitoring, control and surveillance has led to unreliable estimates, high levels of unreported catches and a lack of scientific research (Agostinho et al. 2005, Belhabib & Divovich 2015, Pramöd 2017).

To achieve this vision of economic growth whilst maintaining sustainability, basic biological information gaps need to be addressed. Angola is likely to follow the global trend of declining marine finfish populations, as pressure on African marine capture fisheries increases, from both local and foreign fleets. African marine capture fisheries production has almost doubled over the past two decades (FAO 2020). As pressure on Angolan marine resources increases, it is likely that more emphasis will be placed on cephalopods as a fisheries resource as has been observed globally, particularly as the country aims to increase exports of fisheries products in an attempt to enhance and diversify the economic nature of the country. Cephalopod catches have the ability to fetch high prices on the international market and globally have been documented to exhibit a 14-fold increase in USD in terms of monetary value since the 1950’s (Ospina-Alvarez et al. 2021).

The aim of the study was to provide basic life history information on *Loligo reynaudii* and *Sepia vermiculata* off the coast of southern Angola, assess their importance and dependence of local artisanal fishers on these two species and examine the current management strategies and policies in the region. This information is not currently documented and will contribute

towards making recommendations on the management of artisanal cephalopod fisheries, and non-directed cephalopod fisheries in general, in southern Angola.

To achieve this aim, this thesis is divided into six chapters:

Chapter 1 is the general introduction which defines the scope of the project and outlines the overall aim of the study. Chapter 2 provides information on the study site and the general methods. Chapter 3 provides insight into the artisanal squid jig fishery by exploring the socio-economics of the fishery as well identifying and exploring the observed trends in catch variability within the fishery. Chapter 4 provides a first description of aspects of the biology and demography of the squid *L. reynaudii* off southern Angola and therefore aims to identify the basic biological attributes of squid distributed off the coast of Angola whilst providing a comparative analysis between the two study periods. In Chapter 5, aspects of the biology and demography of the patchwork cuttlefish, *S. vermiculata*, off southern Angola are investigated. Chapter 5 therefore aims to provide the first description of the species population biology for cuttlefish distributed off the coast of southern Angola. Chapter 6 is the general discussion, this chapter discusses the findings of the data orientated chapters in relation to the theoretical body of knowledge, with consideration of their implications for fisheries management, conservation and climate change, at both a regional and global scale. Limitations of the study and areas for potential future research are highlighted.

## CHAPTER 2

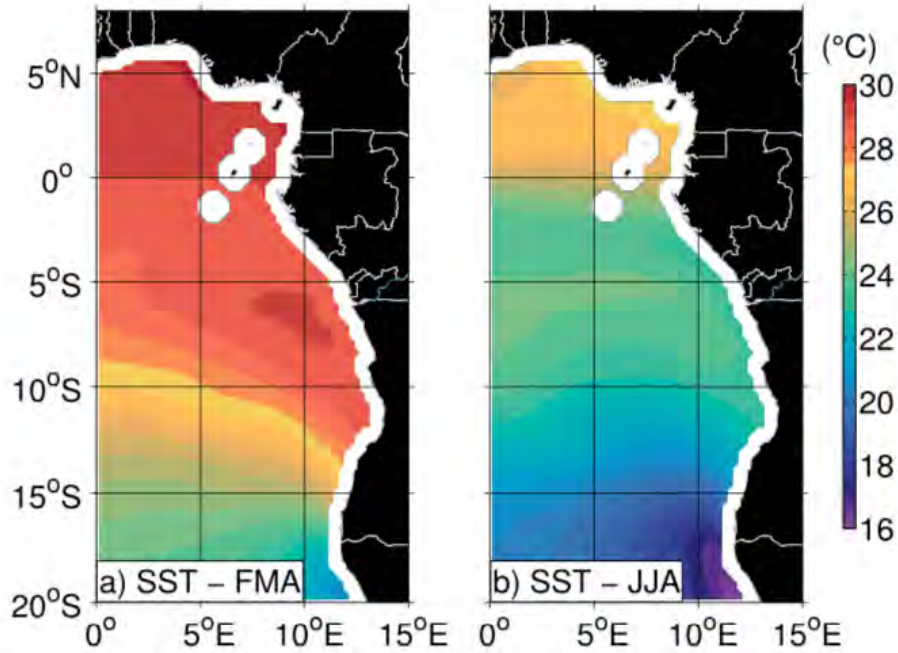
# STUDY SITE AND GENERAL METHEDODOLOGY

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### *Description of the study site*

The sampling region falls within the coastal region of the Namib desert, which extends 450 km north of the Angola-Namibia border. As such, the terrestrial environment is extremely arid because of low levels of annual precipitation (rainfall < 20 mm) within the region (Potts et al. 2015). The marine environment of Angola is a subtropical transitional zone, due to the gradient in mean sea surface temperatures observed throughout the year, across the 1650 km stretch of coastline (Figure 2.1) (Hutchings et al. 2009, Anderson et al. 2012, De Young et al. 2012, Potts et al. 2015, Tchipalanga et al. 2018). Along the coast, the southernmost extremities of the country exhibit a strong temperate element due to the upwelling of the Benguela in the south, whilst the northern extremities are dominated by the Equatorial Atlantic (Anderson et al. 2012, Hutchings et al. 2009, Kirkman & Nsingi 2019).

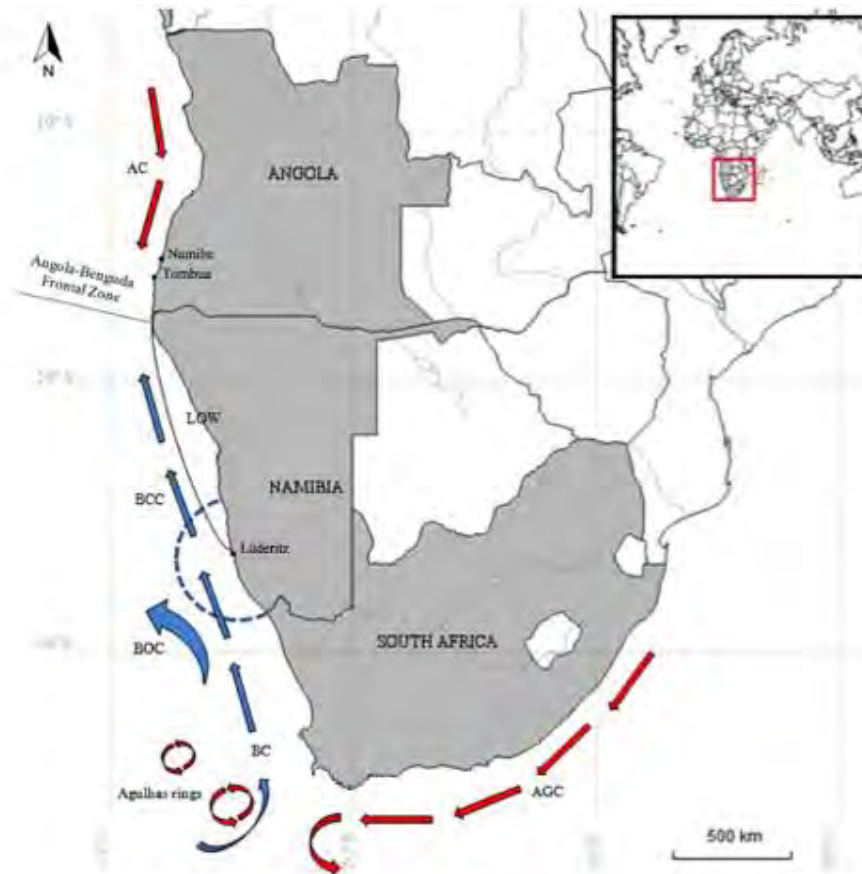
Biogeographic zonation based on SST and the biogeographic distributions of seaweeds identified three zones along the Angolan coastline; warm temperate, sub-tropical and tropical (Anderson et al. 2012, Potts et al. 2015). The study region which extends between Namibe and Tombua, falls into the warm temperate zone. As such, the study region is situated in the Angolan Benguela frontal zone (ABFZ) which separates the two northern subsystems of the Benguela Current Large Marine Ecosystem (BCLME), as identified by Kirkman et al. (2016). Subsystem 1, a subtropical zone extends in a northerly direction from the frontal zone whilst subsystem 2 extends in a southerly direction from the ABFZ to Lüderitz in Namibia (Kirkman et al. 2016).



**Figure 2.1:** Mean sea surface temperatures (SST) for months of; a) February to April and b) June to August, off the 1600km of Angolan coastline (Tchivalanga et al. 2018).

*Oceanographic features of the study region*

The oceanography of the study region is dominated by the convergence of two currents; the warm, saline southward flowing waters of the Angola Current and the cold, northward flowing upwelling waters of the Benguela Current, to form the meridional ABFZ (Meeuwis & Lutjeharms 1990, John et al. 2004, Veicht et al. 2006, Tchivalanga et al. 2018) (Figure 2.2).



**Figure 2.2:** Map illustrating the major oceanographic features, sampling locations and other important features and locations discussed within the text. AC = Angola Current, BCC = Benguela Coastal Current, BOC = Benguela Oceanic Current, AGC = Agulhas Current, LOW = Low Oxygen Area (adapted from Shannon et al. 2006).

The Angolan Current (AC) is a typical tropical eastern boundary current within subsystem 1 of the BCLME, transporting warm, saline, low oxygen South Atlantic Central Water (SACW) in a southerly direction (Kirkman et al. 2016, Tchiplanaga et al. 2018). The Angola Current system is fed by Kelvin waves propagating from multiple eastward equatorial currents including, the Equatorial Undercurrent (EUC), the South Equatorial Undercurrent (SEUC), the South Equatorial Counter Current (SECC) as well as the Gabon Current (GC) (Kirkman et al. 2016, Kopte et al. 2017, Tchiplanaga et al. 2018). Coastal oceanic variability, in terms of sea surface temperatures and biogeochemical characteristics, in the Angolan Current are considered to be controlled by the passage of coastally trapped waves (Bachelery et al. 2015, Kopte et al. 2017).

The Benguela Current (BC) is a cold water, eastern boundary current located off the southwestern coast of Africa (Shannon & O'Toole 1999, Hutchings et al. 2009, De Young et al. 2012). The Benguela Current System is one of four Eastern Boundary Upwelling Systems (EBUS). Combined, these four systems sustain approximately 20% of global fisheries, as such they are therefore one of the most productive oceanic ecosystems types around the globe (Bachèlery et al. 2015). The high level of productivity within EBUS is primarily associated with the upwelling of cold, saline, nutrient rich waters (Bachèlery et al. 2015). The upwelling of the Benguela Current ecosystem extends from the coast of southern Angola, along the coast of Namibia down to the most southern point of the African continent, on the coast of South Africa (Shannon & O'Toole 1999, Lass et al. 2000, Hutchings et al. 2009). Whilst the Benguela system shares many characteristics with other eastern boundary currents, the system is unique, due to the presence of the warm equatorial water regimes, of the Angolan Current and Agulhas Current, on either side of the system (Shannon & O'Toole 1999, Bachèlery et al. 2015).

The establishment of the Benguela upwelling system, approximately 12 million years ago (Mya) and subsequent strengthening of the oceanographic features of the system, approximately 2 Mya, played a major role in isolating warm water, coastal species distributed in the currents bounded on the northern and southern extremities (Krammer et al. 2006). Understanding the presence or absence of genetic diversity of a species across its distribution is critical in understanding stock structure and thereby ensuring sustainable fisheries management throughout a species distribution, particularly when fisheries resources, such as squid and cuttlefish, are shared between neighbouring countries as is seen within the BCLME.

The ABFZ represents the confluence of the AC and the BC and is a key oceanographic feature, situated between 14°S and 18°S in the south eastern Atlantic. The ABFZ is considered to have considerable impact on the regional climate as well as the marine ecosystem in the area (Lass et al. 2000, Colberg & Reason 2006, Veicht et al. 2006, Mohrholz et al. 2008, De Young et al. 2012, Tchipalanaga et al. 2018). Whilst this dynamic thermal frontal zone is a permanent feature, it is however not impermeable (John et al. 2004). The front is characterised by invariably steep sea surface temperature gradients, with across front temperature differences varying between 5° and 8°C (Mohrholz et al. 2008, Tchipalanga et al. 2018).

The geographical positioning and intensity of the front exhibits seasonal, annual and interannual variability resulting in physical and chemical changes (Meeuwis & Lutjeharms 1990, Bianchi 1992, Veicht 2002, De Young et al. 2012, Kirkman et al 2016, Tchupalanga et al. 2018). The midpoint of the ABFZ shifts to its southerly most point during the Austral summer and extends to the northern extremities during the Austral winter (Meeuwis & Lutjeharms 1990, Lass et al. 2000, Veicht et al. 2006). Furthermore, the front extends from 250 km to 700 km south west during the Austral winter and Austral summer, respectively. (Meeuwis & Lutjeharms 1990, Lass et al. 2000, Kirkman et al. 2016, Tchupalanga et al. 2018). These shifts in the position of the front have a major influences on the biochemical properties in the area and subsequently the marine ecosystem. However, this biochemical influence is exaggerated when there is significant southward intrusion of warm, nutrient poor equatorial waters (Hutchings et al 2009, Kirkman et al. 2016, Tchupalanga et al. 2018). These intrusion events have increased in frequency over the past decade and it has been hypothesised, that these intrusions which extend as far as the Namibian shelf, during Benguela Niño events, cause a reduction of biological productivity (Hutchings et al. 2009). However, these large scale intrusions may also allow for connectivity of warm temperate species distributed on either side of the cold water Benguela barrier (Hutchings et al 2009).

The ABFZ has been identified as a global hotspot for climate change (Munnik 2012, Hobday & Pecl 2014, Potts et al. 2014, Potts et al. 2015). Whilst recent studies have revealed that a large proportion (up to 71.6%) of the worlds coastline is warming at a rate of 0.25°C per decade, the ABFZ has experienced a rise of sea surface temperatures at a rate of 0.8°C, which is more than triple that of the global mean (Munnik 2012, Hobday & Pecl 2014, Potts et al. 2014, Potts et al. 2015). Furthermore, the increase in global CO<sub>2</sub> emissions is expected to have a significant impact on the reduction of the average pH of coastal waters, the effects of which are predicted to be highest along the western coast of southern Africa (Potts et al. 2015). Along with other major climatic changes as a result of global climate change, rises in SST and increased levels of ocean acidification, are likely to have major implications for cephalopods, particularly marine calcifying organisms such as cuttlefish, within climate change hotspots (Potts et al. 2015, Seibel 2016, Otjacques et al. 2020). Thus, an understanding of the basic life history and ecology of species within the region is critical in predicting how these organisms may respond to altered regimes, as well as serve as an

indicator for changes in other systems which may be warming at a comparatively slower rate (Potts et al. 2014).

The Angolan coastline is characterised by a relatively narrow continental shelf (Bianchi 1992, Kirkman & Nsingi 2019). This is seen to be exacerbated in the southern extremities of the country between Tombua and Benguela, where it is as little as 6 km wide in certain stretches along the coast (Bianchi 1992). The narrow continental shelf, which extends to depths of approximately 200m, has been identified as a potential barrier to dispersal, between the cold southern waters of the Benguela and the warmer equatorial waters typical of the central and northern regions of the country, for species that are typically associated with “this zone” (Kirkman & Nsingi 2019).

Interestingly, comparative systematic research, on multiple species, has revealed contrasting evolutionary responses across the Benguela system, suggesting that the system may act as a biogeographical barrier (de Beer 2014, Henriques et al. 2014a, b, Richardson 2011).

Interestingly, the two study species, which are distributed along the coast of South Africa and Angola, show different genetic responses across the Benguela Current, these are addressed in greater detail in the respective chapters.

#### *Sample collection and preservation*

To gain a comprehensive understanding of the artisanal jig fishery, trips were undertaken to observe fishing activities, locate and map major fishing areas, as well as to conduct surveys to gain an insight into the socio-economics of the fishery, the methods of which are further outlined in Chapter 3. Preliminary investigations and exploratory trips revealed that squid was the primary target species of the artisanal jig fishery of southern Angola. Whilst fishers in Namibe would actively target cuttlefish, trolling of jigs for cuttlefish was primarily undertaken during trips to, from and between squid fishing grounds and during periods when squid was less abundant. Furthermore, the artisanal jig fishery actively targets squid throughout the year, whilst cuttlefish is only available for a limited period of time. As such, interviews focused on the main component of the fishery. Unfortunately, due to the variability and sporadic nature of the jig fishery coupled with the complex nature of input data required, catch per unit effort (CPUE) could not be accurately determined. As such

indicative catches and species catch compositions were obtained through interviews with fishers and onboard catch inspections at sea.

In order to gain a comprehensive understanding of the importance of the two study species within southern Angola, biological data collection was carried out on samples which were purchased from fish markets in the most southerly ports of the Namibe Province; Namibe and Tombua (Figure 2.3). Due to the paucity of *L. reynaudii* north of Namibe and the remote nature further south of the city of Tombua, sampling efforts were focussed around these two major artisanal fishing areas. Sample collection and methodology of the two study species is further addressed in each of the respective chapters. To the best of our knowledge, all samples were jigged with handlines. Due to the lack of ice and freezing facilities onboard and within local fishing markets, when possible squid and cuttlefish were purchased directly from the fishers at sea to ensure that specimens were of the highest quality.



**Figure 2.3:** Map illustrating important locations within the study region that are discussed within the text.

Biological samples were frozen after collection and thawed prior to analysis. Due to fixation discrepancies associated with freezing, each specimen was defrosted at room temperature and all measurements were taken immediately. No measurements were taken on soft part morphometric variables which exhibited damage or appeared to have previously been damaged, such as missing or regenerating arms. Measurements for regenerating or damaged arms were therefore estimated using the mean arm length for the respective individual.

## CHAPTER 3

# UNDERSTANDING THE ARTISANAL JIG FISHERY FOR *LOLIGO REYNAUDAI*

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Artisanal fisheries, which are often categorised as small-scale fisheries, are diverse and dynamic in nature, as such their definition and characteristics typically vary depending on location (Teh & Sumaila 2011, World Bank 2012, García- Flórez et al. 2014, Basurto et al. 2017, Smith & Basurto 2019). Whilst there is no standard, global definition for artisanal fisheries, this sector is typically characterised by the following; a) fishing technologies which includes; vessel type, capacity and vessel motorization etc, b) fishing technique and capacity including; gear used, fishing effort and areas fished etc, c) socio-cultural dimensions; including ethnic group, class, employment, ownership etc, d) environmental aspects such as species targeted, low catch discards, low energy use and e) disposal of catch whether for household consumption or sale at the various levels (FAO 2008, World Bank 2012, García-Flórez et al. 2014, FAO 2017, Smith & Basurto 2019). As such, artisanal fisheries are generally characterised by smaller vessels with a lower investment in technology and gears (Teh & Sumaila 2011, World Bank 2012, Belhabib et al. 2017). Whilst an increase in motorization has been observed, vessels are typically self-propelled and as such fishing grounds are within close proximity to the shore, with fishers targeting a range of species on a variety of different gears (Belhabib et al. 2017). Fishers are generally considered to undergo daily trips, in either a part time or full time capacity (Belhabib et al. 2017).

Artisanal fisheries are complex to manage because of the large number of external dimensions which influence the dynamics of fisheries management; including poverty alleviation, social justice, economic viability, sustainable development, conservation of resources as well as maintaining ecosystem health (Jentoft 2000, FAO 2008, World Bank 2012, Kolding et al. 2014, Smith & Basurto 2019). These fisheries have exhibited considerable growth globally, in terms of the number of vessels and the size and capacity of these vessels (Kolding et al. 2014, Pauly & Zeller 2016, Belhabib 2017). This growth has resulted in high catches, with small-scale fisheries accounting for approximately half of the total global fish catches (Bennett et al. 2018, FAO 2020). Despite this, the small-scale

artisanal sector is often regarded as low impact and as such is overlooked and overshadowed by industrial fisheries (Basurto 2017, Belhabib 2017, Smith & Basurto 2019, FAO 2020).

Small-scale fisheries are generally data poor and lack reliable information as a result of the multiple challenges concerned with the diversity, locality and abundance of small-scale fisheries (García- Flórez et al. 2014, FAO 2017, Basurto 2017, Bennett et al. 2018, Smith & Basurto 2019). These challenges are further exacerbated by poor institutional capacity and infrastructure as well as the continuous trend of undermining their priority (García- Flórez et al. 2014, Basurto 2017, Bennett et al. 2018, Smith & Basurto 2019). Together, these challenges have resulted in poor management measures, monitoring, control and surveillance in the sector and this has in turn led to a decrease in the potential socio-economic benefits and values of targeted resources (FAO 2020). This is particularly true in Africa, where small-scale fisheries play a fundamental component in providing food security, poverty alleviation and livelihood generation (FAO 2005, Sowman & Cardoso 2010, García- Flórez et al. 2014, BCC 2015, Isaacs & Hara 2015, Golden et al. 2016, Bennett et al. 2018, Smith & Basurto 2019, FAO 2020).

Marine capture fisheries provide a high-quality source of protein, essential fatty acids, vitamins and micronutrients (Golden et al. 2016, Thilsted et al. 2016, Bogard et al. 2017, Teh & Pauly 2018). These fisheries are therefore critical in diversifying and improving diets, subsequently preventing malnutrition and associated diseases, particularly in developing coastal regions where communities are traditionally dependent on these resources (Golden et al. 2016, Teh & Pauly 2018). Cephalopods are high in minerals, omega-3 fatty acids and micronutrients, and as such are considered as a suitable alternative source of protein to dwindling marine finfish stocks (Mouritsen & Styrbaek 2018).

Unlike industrial fisheries, artisanal fisheries are labour intensive and require relatively low levels of capital investment (FAO 2016a, Belhabib 2017). It has been estimated that small-scale fisheries employ up to 90% of the individuals involved in fisheries (Smith & Barusto 2019, FAO 2020). Thus, the marine artisanal sector contributes greatly to employment, particularly within developing coastal communities which may have limited alternative employment opportunities (Richardson Temm et al. 2008, Teh & Sumaila 2011, FAO 2016a, Belhabib 2017, Smith & Barusto 2019). High levels of employment within the small-scale marine fisheries sector therefore contributes considerably to local and national economies

(Teh & Sumaila 2011). Furthermore, research conducted by Belhabib et al. (2015), estimated that the artisanal sector generates approximately \$3.6 billion USD on an annual basis, which subsequently contributes towards the economy within the African continent.

Despite the importance and growth within the marine artisanal sector, globally, there is a lack of information regarding the socio-economic characteristics. This is particularly true for small-scale cephalopod fishing fleets which are considered to significantly contribute towards the local economies, particularly within Asian, African, European and island states (Agostinho 2005, Pierce et al. 2010). This is of major concern as a paucity of information within this critical yet growing artisanal sector undermines and challenges economic and ecological sustainable fisheries management and governance practices.

### *Artisanal fisheries of Angola*

The African Caribbean and Pacific Fish II Programme (ACP Fish II), estimated that the total production of Angolan artisanal fisheries ranged between 60 and 100 thousand tonnes per annum between 2008 and 2012, with approximately 42% of the total fisheries production during 2009 being generated by the artisanal sector (ACP Fish II 2013). However, Belhabib and Divovich (2015) indicated that Angolan fisheries catches reported to the FAO are considered to be highly unreliable, due to increasing underreporting and a lack of monitoring, control and surveillance. At present information regarding the artisanal landings and demographics of the sector has been recorded by the IPA, however this data is yet to be assimilated and published (dos Santos pers comm). Reconstruction of artisanal catches indicate that fishing is likely to have increased from approximately 11 800 t in 1979 to an estimated 158 700 t in 2010 (Belhabib & Divovich 2015). It is important to highlight however, that there is a paucity of information regarding the contribution of the various fisheries towards the total artisanal landings, as well as data pertaining to catch species composition within the respective fisheries (Agostinho 2005, Belhabib & Divovich 2015). Whilst the artisanal sector contributes significantly towards the total fisheries production of the country, it is estimated to contribute greatly towards local fish consumption and livelihood generation (Paterson et al. 2014).

During the Portuguese colonial rule, Angolans were excluded from the marine artisanal fishery (Sowman & Cardoso 2010). The gain of independence, as discussed in Chapter 1, subsequently led to the reclamation of historical fishing rights for local communities during

the post-colonial civil war and this resulted in a considerable increase in participation. Marine artisanal fisheries within Angola play a critical role in providing livelihoods and food security for coastal communities (Agostinho 2005, du Preez 2009, ACP Fish II 2013, de Young et al. 2012, Paterson et al. 2014, BCC 2015, Sowman & Raemaekers 2018). Fish is considered to form an integral part of the diet of Angolan citizens. However, it is estimated that the demand is not being met and therefore the sector is likely to experience increasing levels of exploitation (ACP Fish II 2013). The artisanal sector has been estimated to contribute approximately 35 - 40% of the total catch for the country and a study conducted during 2005 estimated that approximately 20% of households within Angola were directly involved with the fishing industry (Agostinho 2005, ACP Fish II 2013, Benguela Current Commission 2015, Gonçalves et al. 2015). There are approximately 102 coastal fishing communities distributed along the 1650 km coastline (Sowman et al. 2011). Approximately 50 - 66% of fishers fall within the Angolan artisanal fishing fleet which according to the IPA consists of approximately 35 000 fishers and 6600 artisanal fishing vessels (Sowman et al. 2011). However, it is unclear how many fishers partake in artisanal fishing and more specifically the cephalopod jig fishery, within these coastal communities. Efforts to quantify the number of fishers participating in the cephalopod jig fishery could provide critical information for management on the fishery.

Research on artisanal fisheries of Angola, is relatively limited. However, it is estimated that majority of artisanal vessels, approximately 75%, are not motorized (du Preez 2009, Sowman et al. 2011, BCC 2015). Majority of the artisanal catch is sold fresh or on ice for local consumption (Agostinho 2005, Sowman et al. 2011). A small proportion of the total landings undergoes further processing, which mainly involves salting and drying (Sowman et al. 2011, ACP Fish II 2013, Gonçalves et al. 2015). Traditionally, post-harvest activities such as processing, selling and trading is predominately carried out by women, whilst men are primarily involved directly in fishing activities (Agostinho 2005, Du Preez 2009, Sowman et al. 2011, ACP Fish II 2013, Gonçalves et al. 2018, Gonçalves et al. 2020).

The aim of the present chapter is therefore to provide an overview of the artisanal jig fishery for squid, in southern Angola to provide a baseline for future socio-economic and management assessments and policies. This includes:

- 1) Gaining an understanding of the spatial characteristics of important fishing grounds for the artisanal squid jig fishery,
- 2) Providing insight into the catch composition of the fishery,
- 3) Gaining an understanding of the socio-economic aspects of the artisanal jig fishery by analyzing; i) the demographics of participants within sector; ii) the characteristics of fishing operations; iii) determining the importance of the fishery in terms of livelihood and employment to local coastal communities; iv) understanding factors which may be hindering the progression and development of the fishery and the participants within the sector; v) gaining an understanding of spatio-temporal changes in the fishery and the drivers behind these changes.

## *Methods and Materials*

### *Data collection*

To determine the spatial characteristics of the southern Angola squid fishery, trips to sea were conducted monthly, between June 2014 and May 2015, to map fishing activity, gain an understanding of species composition as well as conduct interviews with local squid fishers. When possible, this was carried out bimonthly, however due to the remoteness of the location as well as the weather conditions this was not always possible.

### *Mapping the main *Loligo reynaudii* fishery areas*

GPS coordinates of aggregated fishers actively targeting squid were recorded to allow for major fishing areas in which the artisanal jig fishery operates to be mapped. As fishers fish within proximity of one another (within 5m of each other), a single coordinate was taken per aggregation of fishers during each trip. Coordinates of fishing areas were plotted using TimeZero Professional v4.1.

### *Catch composition of the artisanal jig fishery*

In order to gain an understanding of the species composition of the jig fishery, catch composition was recorded for the artisanal jig fishery by conducting onboard inspections, for 61 fishers at sea. Catch was taxonomically identified to genus, and where possible species, and grouped accordingly. The species catch composition was calculated determining the relative abundance of each taxonomic group (%N) and the corresponding percentage

composition by weight (%W). The frequency of occurrence (%F) of each species was also determined. The weight of each taxonomic group was determined to the nearest 0.1g using a Rapala digital hanging scale. To assess the importance of the species within the artisanal jig fishery, the index of relative importance (IRI) was determined as;

$$IRI = (%N + \%W) \times \%F$$

*Survey to understand the socio-economic aspects of the squid jig fishery*

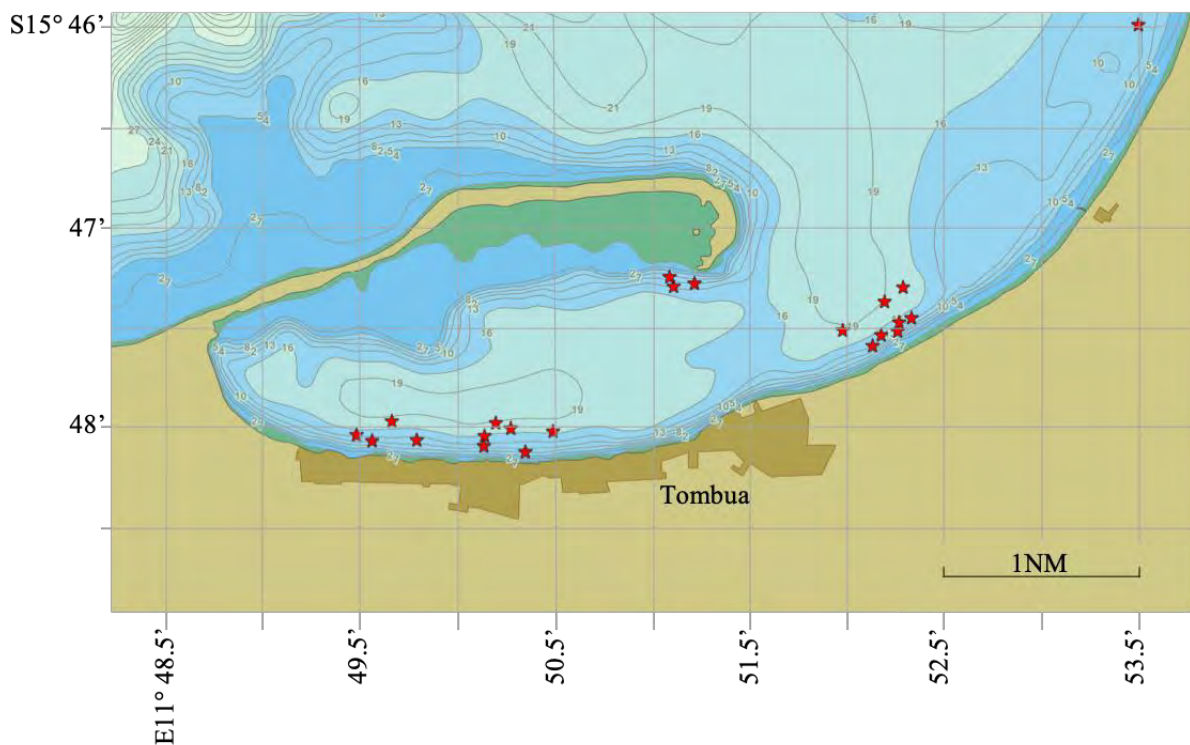
Data on the social and economic aspects of the artisanal jig fishery was obtained by in-person surveys, during 2015 with 44 local fishers, based within Namibe and Tombua. All interviews were conducted in Portuguese and translated to English. Prior to each interview, the purpose of the project was explained, and each individual was asked whether they would like to partake in the study. An experienced squid fisher with knowledge of the local areas assisted with all interviews. A semi-structured questionnaire (Appendix 1) was utilised to gather the necessary information whilst allowing participants to provide insight and address other issues which may emerge during the interview process. As such, a set of questions were followed, to standardize the process, however by engaging in conversation with participants further aspects and concerns could be raised and addressed further.

The questionnaire was divided into five sections. Section 1 focussed on the demographics of the fishers within the artisanal cephalopod fishery. Section 2 addressed the methods of fishing, characteristics of the vessel as well as methods for the preservation of catch. Section 3 aimed to explore the income and expenditure of artisanal fishers, with regards to fishing related expenses. Section 4 of the questionnaire assessed the importance of fishing as a source of livelihood and employment. The final section of the questionnaire, Section 5, consisted of questions which aimed to quantify catch and effort within the fishery, assess whether changes in catch have been noticed as well as address any concerns regarding the fishery which may have been raised.

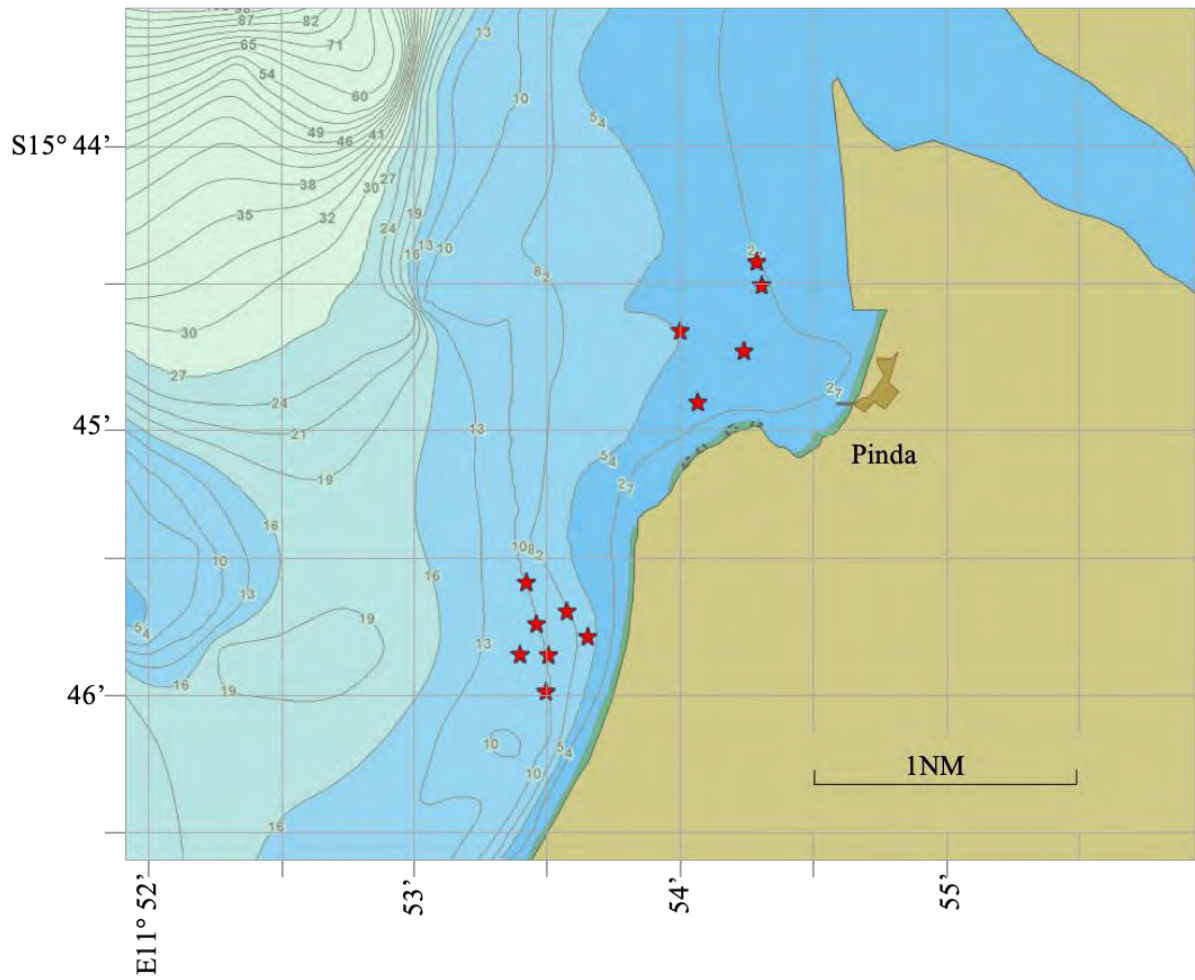
## Results

### Mapping the main *Loligo reynaudii* fishery areas

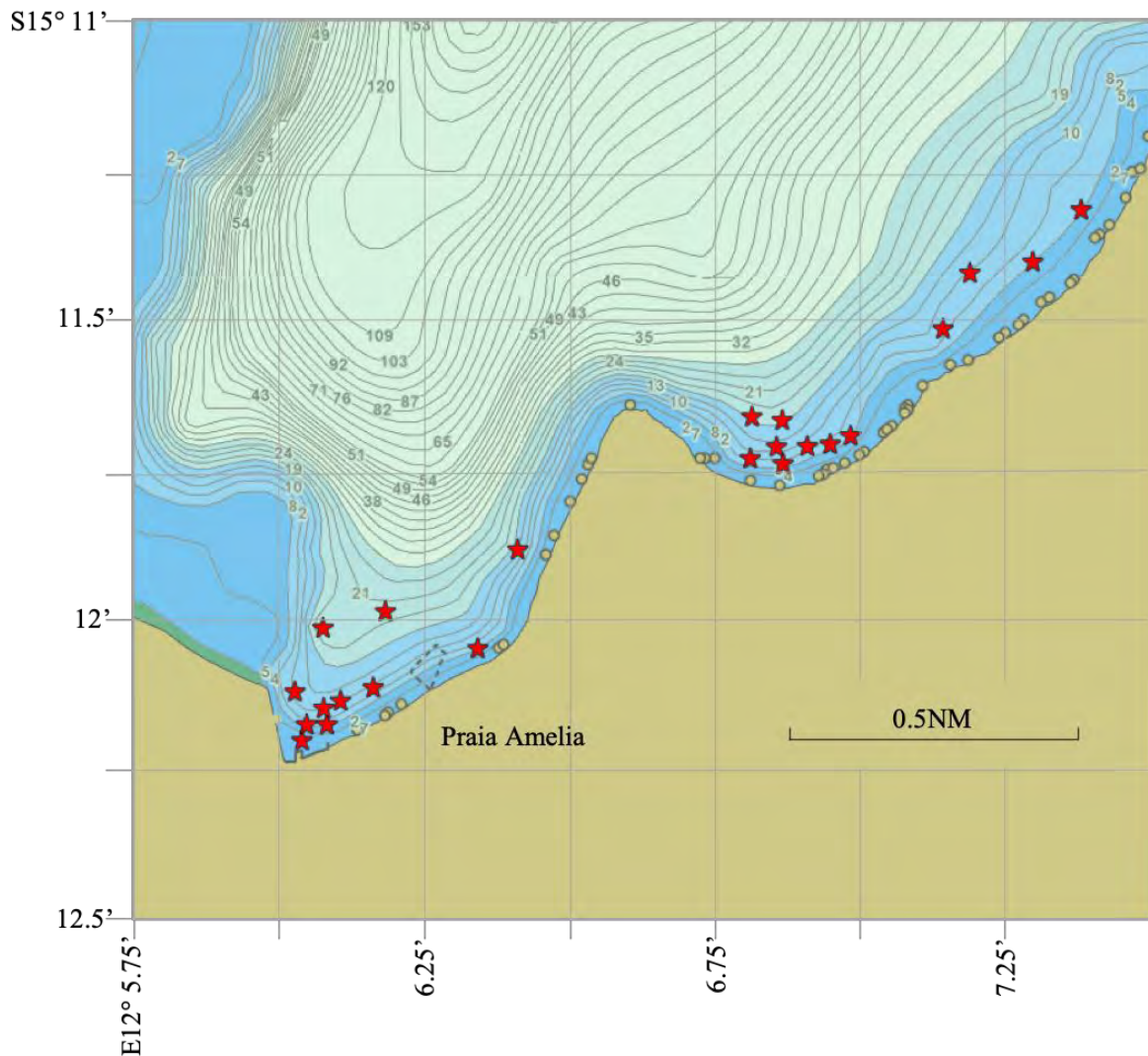
*Loligo reynaudii* is targeted by the artisanal jig fishery in three major areas in southern Angola; 1) Tombua Bay and surrounds, 2) Pinda and 3) Praia Amelia (Figure 3.1, 3.2 & 3.3). Fishing in Tombua Bay generally occurred in close proximity to shore, with majority of observations situated within 0.1nm offshore (Figure 3.1). Fishing areas off Pinda were generally further offshore, fishing activity observed up to 0.43nm from the shoreline (Figure 3.2). However, fishing activities within Praia Amelia were all observed within 0.15nm of the shore (Figure 3.3). The majority of the squid is sold through the two larger fish markets in the towns of Namibe and Tombua.



**Figure 3.1:** Contour map (depth in meters) illustrating the main fishery areas, within Tombua, for the artisanal *L. reynaudii* jig fishery.



**Figure 3.2:** Contour map (depth in meters) illustrating the main fishery areas, within Pinda, for the artisanal *L. reynaudii* jig fishery.



**Figure 3.3:** Contour map (depth in meters) illustrating the main fishery areas, off Praia Amelia, for the artisanal *L. reynaudii* jig fishery.

#### *Catch composition of the artisanal jig fishery*

Whilst the artisanal jig fishery actively targets *L. reynaudii* and *S. vermiculata*, squid is the primary target species, in terms of percentage by number (74.0%), percentage by weight (58.2%), frequency of occurrence (98.4%) and IRI (83.7%) (Table 3.1). *S. vermiculata* contributed to 7.8% of the catch in terms of weight, however due to the high seasonality, fishers in Namibe typically targeted the species when moving to or between squid fishing grounds, during periods when cuttlefish was more readily available or when squid was less abundant. Teleost catches contributed towards 24.4%, in terms of abundance, contributing 33.7% of the total weight (Table 3.1). The two most important fish species within the catch

composition in terms of abundance, weight and based on the IRI were *Dentex* sp. and *D. capensis*.

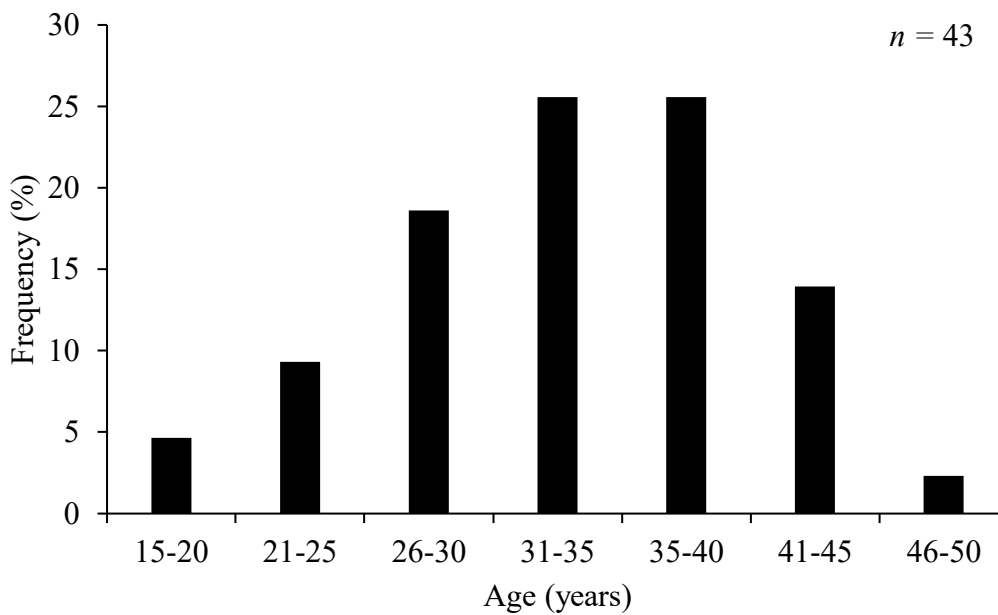
**Table 3.1:** Species catch composition percentages by number (%N), percentage by weight (%W), frequency of occurrence (%F) and index of relative importance (IRI) for the artisanal jig fishery of southern Angola.

Taxon	Angolan name	% N	% W	% FO	IRI	%IRI
<i>L. reynaudii</i>	Lula	74.0	58.2	98.4	13 005.00	83.7
<i>O. vulgaris</i>	Polvo	0.1	0.3	1.6	0.58	< 0.1
<i>S. vermiculata</i>	Choco	1.5	7.8	29.5	275.16	1.8
<i>Atractoscion aequidens</i>	Corvina	1.6	5.7	16.4	120.89	0.8
<i>Cheimerius nufar</i>	Quissanga	0.2	0.2	3.3	1.19	< 0.1
<i>Dentex</i> sp.	Cachucho	10.8	12.5	45.9	1 069.00	6.9
<i>Diplodus capensis</i>	Mariquita	9.3	9.2	49.2	910.04	5.9
<i>Mycteroperca rubra</i>	Garoupa	0.4	1.1	9.8	15.27	0.1
<i>Plectorhinchus mediterraneus</i>	Peixe burro	0.2	0.3	4.9	2.14	< 0.1
<i>Pomatomus saltatrix</i>	Anchova	1.7	4.4	21.3	129.61	0.8
<i>Pseudupeneus prayensis</i>	Salmonete- barbudo	0.2	0.2	4.9	1.77	< 0.1
<i>Sphyraena sphyraena</i>	Barracuda	0.1	0.1	1.6	0.24	< 0.1
Total cephalopods		75.6	66.3	100	14 190.00	74.1
Total fish		24.4	33.7	85.2	4 952.90	25.9

*Survey to understand the socio-economic aspects of the squid jig fishery*

*Section 1: Demographics of fishers*

The age of the respondents ranged between 18 and 48, with a mean age of  $33.42 \pm 7.22$  years and most between 31 and 45 years of age (Figure 3.4). All participating artisanal fishers were male. Of the individuals interviewed, 29.6% lived in Namibe, 27.3% in Pinda and 43.2% in Tombua



**Figure 3.4:** Age (years) distribution of respondents from the artisanal squid jig fishery survey, within southern Angola.

*Section 2: Characteristics of the vessel, methods of fishing and preservation*

All participants identified themselves as artisanal fishers, who fished from self-propelled polystyrene rafts, locally known as *bimbas* (Figure 3.5). Fishers are not equipped with any form of navigational systems, fish detecting devices or any form of safety equipment. In the event of any mishap, fishers are entirely dependent upon their swimming abilities.

When fishing for squid all participants preferred to drift, rather than lay on anchor, however, those fishing for cuttlefish in Namibe indicated that greater success in catches were because of trolling jigs on or around reef. Fishers made use of handlines (*pesca ligna*) with handmade jigs (*xangarillo's*), of varied colours and sizes, when targeting cephalopods (Figure 3.5). However, 79.5% of individuals indicated that they would simultaneously make use of a handline line with small baited hooks to target small reef fish while drifting and actively targeting squid. Baited handlines typically consisted of a multiple hooks baited with squid tentacles or mussel. Hook sizes ranged from no6 to 1/O. Teleost bycatch was identified as a source of nutrition for local fishers and in many instances is sold at the local fish markets to supplement income from cephalopod catches. Of the fishers interviewed, 79.5% said they made use of 2-3 lines during any fishing outing, of these 65.9% indicated that they preferred

to fish with two lines rigged with jigs and one line with baited hooks. Furthermore, only 25.0% of individuals exclusively fished with jigs whilst undergoing fishing trips to target squid. None of the participants made use of any form of ice or preservation methods and all catch lay loosely on the deck of their rafts. Fishers identified that quality of cephalopods due to lack of preservation was an issue however maintained that there was little options available for them to resolve this issue.



**Figure 3.5:** Angolan artisanal lula fishers (left) and their handmade jigs and handlines (right).

### *Section 3: Income and expenditure*

Fishers had difficulties quantifying income and expenditure, as well as average monthly salary, as fishing related income and expenses were primarily described as being highly variable. Average monthly salary was stated to range from between 3000 – 25 000 AKZ (approximately 23.08 - 192.31 USD, with an exchange rate of 130 AKZ to 1 USD), with participants indicating that fishing related expenses could range between 0 – 500AKZ (approximately 0 – 3.85 USD) per trip. Most fishers identified two primary fishing related expenses; 1) tackle and vessel maintenance and, 2) transport to fishing grounds. Tackle expenses were classified as being highly variable, dependent on sea conditions, area of fishing as well as the presence of seals within the area. However, due to the nature of the vessels, vessel maintenance and expenditure was generally described as being minimal. Of the interviewed fishers who were able to quantify tackle expenses (52.3%), expenses were considered to range between 100 – 500 AKZ (0.77 – 3.85 USD) per fishing trip. Whilst

fishers from Tombua primarily paddled out into the bay, those in Namibe and Pinda primarily made use of chatas (motorised wooden vessels) to reach fishing locations, as such one of the primary expenses for these individuals was the fee charged by the chata owner which transported fishers and their bimbos between fishing grounds and the mainland. Whilst the cost of the chata was dependent on distance travelled, of the fishers who relied on these vessels to reach fishing grounds, average expense per fishing trip was 340.00 AKZ (2.62 USD) for fishers in Tombua, 496.15AKZ (3.82 USD) for fishers in Namibe and 575.50 AKZ (4.43 USD) for fishers in Pinda.

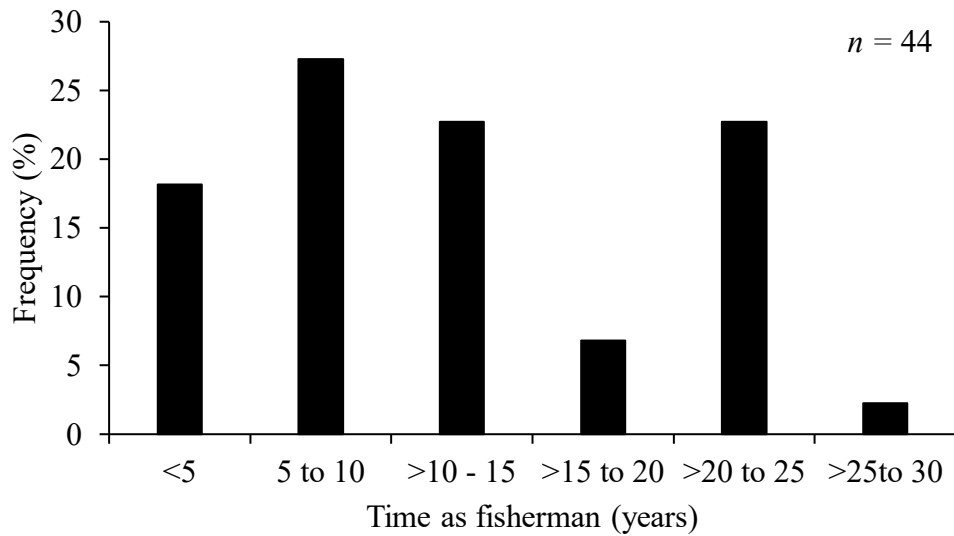
All participants indicated that they preferred to sell the cephalopod catch, than to exchange it or to use it as bait. All fishers indicated that they primarily sold their catch directly to female vendors in the local fish market. Almost a fifth (16.7%) of interviewed fishers indicated that they generally sold their catch to a female relative. Participants indicated that whilst this had remained relatively static for the past five years, there had been an increase in “out of town” buyers purchasing larger quantities from female vendors within the local markets. Furthermore, 18.8% indicated that they did occasionally sell directly to “out of town buyers” or local restaurants.

Fishers were unable to quantify the price per kg. Due to a lack of scales, catch was generally valued according to size. This was particularly the case for squid which was broadly classified as small or large specimens and priced and sold as bundles accordingly. Participants indicated that small squid were generally sold as a bundle of six, ranging between 350 – 400 AKZ (2.69 – 3.08 USD) per bundle, whilst larger squid were sold in bundles of three for 500 – 550 AKZ (3.85 – 4.23 USD). All participants indicated that the price did occasionally fluctuate due to availability, with price increasing when the catch is scarce and decreasing when it is readily available. Furthermore, 91.7% of individuals stated that the price of cephalopods had increased since they began fishing.

#### *Section 4: Importance of fishing as a source of livelihood and employment.*

Most participants (84.1%) had engaged in fishing activities for more than five years, with the highest proportion (29.6%) of individuals having engaged in fishing related activities for > 5 to 10 years, 22.7% for > 10 to 15 years and 22.7% for > 20 to 25 years (Figure 3.6). Of the

participants, only 2.3% of individuals had been involved within the fisheries sector for more than 25 years (Figure 3.6).



**Figure 3.6:** Approximate amount of time (years) that respondents from the artisanal cephalopod jig fishery survey have relied upon fishing activities as a primary source of employment.

Participants were largely reliant on fishing as a source of income and livelihood, with 86.1% of individuals indicating that they did not have alternative livelihood or employment opportunities. Of the 13.9% of participants which indicated an alternative source of income, all identified agricultural activities as a secondary occupation. However, all 13.9% indicated that fishing still provided majority of their monthly income. Of the individuals which were not reliant solely upon fishing, two thirds indicated that they farmed during summer months and engaged in fishing activities during winter when catches were perceived to be higher.

The majority of fishers (77.7%) indicated that whilst they were the primary provider within the household, there were other family members and dependents who contributed towards the total household income. However, the contribution from other members of the family and dependents was generally small ( $\leq 25.0\%$  of the total household income). The remaining participants (27.3%) indicated that they were the sole provider within their households. Of the fishers who took part in the survey on average, participants had six dependents, with a minimum of 0 and a maximum of 15.

All participants identified squid as an important resource on which they were largely dependent as a source of income, particularly during the months in which it was readily available for harvest.

*Section 5: Quantify catch and effort within the fishery, assess whether changes in catch have been noticed as well as address any concerns regarding the fishery which may have been raised.*

Of the fishers who resided within Namibe, 69.2% of individuals stated that they fished between the Port of Namibe and Praia Amelia, whilst the remaining individuals fished closer to port. Those which lived in Pinda, all stated that they fished between Pinda and Tombua, whilst those which lived within Tombua, only fished within the Bay of Tombua and its surrounds.

All participants indicated that the days of fishing per week was highly variable, depending on weather. However, of the participants, 13.6% of individuals stated they only fished five days of the week, as they did not fish over weekends. Of the remaining individuals, 70.5% stated that they generally fished between four and six days a week, depending on weather but did not fish on a Sunday regardless of sea state, weather conditions or catches. The remaining 18.2% of fishers indicated that when fishing was good, that they would fish seven days a week, weather permitting. Fishing activities typically commenced between 06:00 and 07:00am, depending on sunrise. Fishers indicated that they typically fished between seven to nine hours per day and would return to shore between 13:00 and 15:00, depending on catch, weather etc. All participants emphasized that they did not partake in night time fishing activities as it was regarded as extremely dangerous, particularly due to the characteristics of the vessel.

All fishers interviewed emphasised that daily catch varied considerably and was highly dependent on sea state and weather conditions, with catches on good days resulting in an estimated 20kg per person. Whilst individuals were unable to identify which size category the majority of the catch fell into, a large proportion (88.6%) of individuals indicated that squid less than 16cm in dorsal mantle length was not frequent within landings. Most (90.7%) respondents felt there had been an increase in fishing pressure since they began fishing or

activities related to the fishing sector. Of those which were unable to identify changes in fishing pressure, all individuals had less than five years of experience within the fishing sector. Whilst a large proportion (32.6%) of individuals were unable to identify when the observed increase in fishing pressure began, 34.9% mentioned that a drastic increase had occurred during the last five years, whilst 4.7% identified a substantial increase within the last ten years and 27.9% stated that the increase had gradually occurred over the years.

Substantial changes in catches within the past five years were identified by 88.4% of individuals. When asked to identify how catch had changed over time, a number of factors were raised. The majority of fishers felt that there was a decline in catches over time. Of the fishers who were able to identify a change over time, 77.5% stated that they now had to expand fishing area and duration of trips to catch the same quantity or less. Many respondents attributed the change in catches to increased fishing activity within the region, such activity included all sectors. Furthermore, many fishers, particularly those within Tombua, expressed that declined catches were as a result of an increase in the number of seals and subsequently interactions with seals during fishing trips.

There was a large discrepancy in the number of months participants actively targeted squid, ranging from three to 12 months of the year. Less than one third (27.3%) of the respondents stated that they fished almost exclusively for squid for up to four months of the year, however the majority (61.4%) of the participants targeted squid for between four to six months of the year. Interestingly, all participants from Namibe cited that squid were only targeted for three months of the year.

When questioned with regards to the availability of cephalopods throughout the year, most fishers (65.9%) broadly classified winter as yielding the highest catches of squid, with May to August being identified by several individuals as the preferred squid season. Whilst there was a general perception amongst fishers that there was a shift in cephalopod biomass, with squid being more abundant in winter, a large proportion of individuals were unable to suggest as to why this shift occurs and to where they may migrate. Several participants suggested that the squid follow the cold water and as such there is a shift in biomass in either a southerly direction or, alternatively, offshore.

When asked to identify concerns within the artisanal cephalopod fishery, several ecological, socio-economic and governance issues were raised by fishers (Table 3.2). Whilst the majority of the concerns raised appeared to be of a socio-economic nature, the main issue that was raised by fishers was a notable decline in catch or increase in effort to obtain the same catch. The decline in catches was attributed to one or a combination of the following factors i) an increase in competition, within and between fisheries and sectors was raised by 65.0% of respondents; ii) an increase in seal interactions was highlighted by 45.0% of respondents. These interactions resulted in a decrease in catches, either due to predation or alternatively to squid dispersing when seals entered an area but also resulted in a higher loss of gear and iii) a decline in weather conditions and sea state making a higher proportion of days unfishable, was discussed by 27.5% of fishers.

**Table 3.2:** Ecological, socio-economic and governance related stressors identified by artisanal cephalopod fishers.

Ecological	Socio-economic	Governance
Declining catch	Lack of infrastructure	Conflict with other sectors
Weather increasingly unpredictable	Lack of appropriate fishing equipment	Rules and regulations not negotiated with fishers
Increase in seal predation	Lack of employment and alternative income opportunities	Lack of communication and support from officials
	Lack of finances or access thereof	
	Lack of health services	
	The need for better market conditions	
	No access to ice or refrigeration	

### *Discussion*

The artisanal squid jig fishery of southern Angola is critical for the livelihoods of people in traditional coastal communities, particularly as fishers within the region have very few viable alternative livelihood opportunities. The vessels and gear are rudimentary, consisting of self-propelled polystyrene rafts, hand-lines and hand-made jigs (a crown of hooks mounted on a lead filled polyvinyl chloride (PVC) cylinder). Fishing unsurprisingly, takes place in the

nearshore region and while the cephalopod catch is sold, fish are simultaneously targeted with hook and line gears for personal consumption. Fishers highlighted temporal changes in the squid jig fishery, with perceived declines in catches being attributed to an increase in collective effort, among other factors. However, many fishers indicated that the progression of the fishery is hindered by various social, ecological and governance related issues which if addressed by the relevant authorities, could have positive ramifications for fishers within the region.

Of the interviewed fishers, 14.0% were below the age of 25 years, whilst 16.3% of participants were over the age of 40. The lack of representation of older individuals may be due to the highly labour-intensive nature of the fishery and the harsh fishing conditions which fishers are exposed to. Fishers paddle out individually, with hand paddles, on partially submerged polystyrene rafts to actively jig for cephalopods. Due to the characteristics of the vessels and the paddles, fishers spend a considerable amount of time during colder winter months when squid are more abundant within the region, partially soaked in water, with their feet submerged whilst actively fishing. Furthermore, the under-representation of fishers below 25 years of age was unexpected due to the low population median age of 16.4 years documented for 2015 (Worldometer 2021). The lack of individuals participating in the artisanal cephalopod fishery may be reflective of younger individuals working within other more lucrative fisheries sectors or alternatively migrating to urban areas to source alternative livelihoods. Rural-urban migration of younger generations is common within Africa, and in many regions the populations within urban areas has been noted to have increased drastically (Angola 2016, Wegner & Abulfotuh 2019). Migration of youth to urban areas, which is primarily considered to be driven by economic incentives such as increased salaries or opportunities, can have major negative consequences for small, rural communities (Angola 2016, Wegner & Abulfotuh 2019, Amare et al. 2021). Consequences, include but are not limited to, a decline in labour availability, a decline in local knowledge and experience within sectors such as the artisanal fishing as well as negative implications on the social cohesion and family structures of these communities (Angola 2016, Wegner & Abulfotuh 2019).

Whilst women play prominent roles within the artisanal fishery, fishers were exclusively male. Females associated with the cephalopod jig fishery, were found only being involved in post-harvest related activities. This is generally characteristic of artisanal and small-scale fisheries globally and has been previously observed within Angolan artisanal fisheries, with

women dominating the post-harvest “sector” (Agostinho 2005, Du Preez 2009, Sowman et al. 2011, ACP Fish II 2013, Paterson et al. 2014, Gonçalves et al. 2018, Gonçalves et al. 2020, Smith & Basurto 2019). Female vendors predominantly obtained squid and cuttlefish from husbands or other relatives to sell within local fishing markets. Unlike many other fisheries resources, cephalopods within the local markets, are not processed or transformed and are sold in size “bundles” by female vendors.

One of the major concerns highlighted by fishers impeding the development of the sector was the inaccessibility to fishing tackle, technology and equipment. Fishers indicated that whilst fishing tackle such as jigs had become more readily available in Namibe, these were too expensive for artisanal fishers. The lack of access to credit, volatility in the price and fluctuations in catches (Lankester 2002, OCAR 2002, Agostinho et al. 2005, Sowman et al 2010, Raemakers & Sowman 2015) reduces the likelihood of fishers ever improving their current tackle and equipment. The OCAR (2002) reported that artisanal fishers in the region typically rely on informal financial loans, such as those from relatives or shop keepers, when capital is needed to maintain vessels or purchase new fishing equipment, as well as to subsidise households during periods of low catches. However, this is not always available and only available to some fishers. A lack of financial credit is considered to be a major constraint to the development of artisanal fisheries worldwide (Lankester 2002, OCAR 2002, Agostinho et al. 2005, Sowman et al 2010). An increase in accessibility to low interest micro-credit and loans, or alternatively conditional grants, may be a key strategy for improving the returns from the artisanal squid fishery in southern Angola and will be necessary for improving the socio-economic status of the communities reliant upon these volatile resources.

The complete lack of safety equipment or personal protective equipment (PPE) and training makes the cephalopod fishers extremely vulnerable, particularly during harsh, cold winter months. The issue of a lack of safety regulations and procedures, within the fishery, is further exacerbated by the poor quality of health care available within these communities (Paterson et al. 2014). Fishers safety should be an integral part of fisheries management regulations, policies and strategies (FAO 2010a) and collaboration between government organisations, relevant stakeholders and communities, at both a national and regional scale, is necessary to improve i) safety guidelines and standards, ii) the channels used to report accidents at sea and the provision of emergency response services, iii) availability of sea safety training and

awareness, iv) availability of low-cost safety equipment (FAO 2010a). This becomes even more important due to the declining catches, which require fishers to travel further and fish for longer during the harsh winter months.

It was clear throughout the current study that alternative or supplementary livelihood opportunities were limited, with most indicating that they were entirely dependent on fishing related activities as a source of income and livelihood. The majority of fishers, particularly those living in Tombua, highlighted how important squid were towards their total household income. Whilst the majority of fishers were not sole providers within households, they were in most instances the primary providers with a high number of dependents. The high dependence upon cephalopods, particularly squid, as a source of income and livelihood, highlights the need for appropriate management regimes so as to ensure sustainable harvesting, particularly as a high proportion of interviewed fishers expressed that they had observed negative changes within the fishery over time. As highlighted by Jentoft (2000), in order for fishing communities to be viable, viable stocks are required and vice versa.

The major constraints faced by artisanal fishers in southern Angola were highlighted throughout the study by interviewed fishers, as well as through observations made during the study of the entire squid supply chain. Major factors limiting the productivity and progression of the artisanal jig fishery could be broadly categorised as a result of the following; i) lack of resources to enable for productivity and work conditions to be improved, ii) inadequate capture and postharvest conditions, iii) a lack of infrastructure at both national and regional levels. Such constraints need to be addressed by local government to improve the livelihoods of local fishing communities dependent upon fisheries as a means of survival.

Improving onboard and post harvesting conditions by reducing transport times and improving methods of preservation will result in a higher quality product, thereby reducing post-harvest losses, reducing market storage time and increasing quality and subsequently price along the value chain. However, it is important that the restoration and improvement of fisheries related infrastructure is aligned with appropriate management measures as increased sales and prices due to higher quality is likely to result in increasing pressure on declining local resources (Agostinho 2005). Whilst Angola has invested substantial amount of funds towards the development of roads and prioritized the development of roads within the National Development Plan, the poor state of access routes to many coastal towns remains a major

concern. Jensen (2018) suggested that relatively low levels of road construction, despite this being recognised as an important aspect in improving national cohesion, infrastructure and product distribution, was a result of unrealistic planning, overambitious targets and the challenging construction environment. Poor road infrastructure is often considered to play a considerable role in hampering market access as well as hindering the distribution of required inputs, particularly to rural coastal fishing towns such as Pinda (OCAR 2002, Paterson et al. 2014).

Whilst fishers were concerned about the lack of ice onboard, the general perception seemed to be that post-harvest fish losses (PHFL) were higher due to degradation within local fish markets which subsequently resulted in an increased product price volatility. It is well known that squid jigging produces a high quality product, in comparison to other fishing methods (Arkhipkin et al. 2015). However, the product quality within the Angolan artisanal squid jigging fishery was severely compromised by both capture and post-harvest conditions. One of the major challenges faced by fishers and vendors within the artisanal sector, which was observed and furthermore raised by fishers throughout the study, was the lack of preservation which resulted in reduced quality and spoilage. PHFL is a common issue within artisanal fisheries globally and occurs as a result of both physical and quality losses which subsequently result in an economic loss as well as a loss in the nutritional contribution of fish to communities which may be heavily dependent on marine resources for food security (FAO 2010b, Ward & Signa 2017).

Landing sites in Angola are generally characterised by a lack of running water, with catches being handled, distributed and marketed in unhygienic conditions (OCAR 2002, Paterson et al. 2014, Raemaekers & Sowman 2015). Local markets lacked cold-storage facilities as well as ice and insulated containers, which often resulted in catches being exposed to elements such as high temperatures and insect infestations. The lack of appropriate catch and post-harvest conditions and the consequent deterioration of product quality is a major constraint for the development of the artisanal cephalopod jigging fishery as it not only effects the livelihood of the fishers, the vendors and the stakeholders, but directly results in a loss of nutritional contribution at a local level as a result of discarded fish due to quality deterioration (OCAR 2002, FAO 2010b, Getu et al. 2015, Ward & Signa 2017).

It has been estimated globally, that approximately 10% of the total global fish production is lost due to spoilage (Getu et al. 2015). From the current study it is evident that there is a high need for loss reduction initiatives within the southern Angola cephalopod fishery. Such initiatives will not only result in a direct increase of income to fishers and vendors but could subsequently result in increased employment opportunities for local communities, as well as potentially increase both local and foreign market demand (FAO 2010b). However, it is vital that initiatives to improve squid quality make use of low-cost technology so as to not escalate prices excessively for domestic consumers (FAO 2010b). Capture and post-harvest losses, along with product quality, therefore need to be assessed and incorporated into fisheries assessments in order for the issue to be conclusively addressed within fisheries policy and subsequently monitored.

Lack of infrastructure, with regards to basic and fisheries related infrastructure, was identified as one of the major socio-economic constraints for artisanal cephalopod fishers within the southern region of Angola. These deficiencies have been identified throughout the BCLME region (OCAR 2002, Agostinho et al. 2005, ACP Fish II. 2013, Raemaekers & Sowman 2015). As highlighted in Chapter 1, the extended civil war within Angola resulted in the degradation of many of the existing roads, community centres etc. Whilst the Angolan Government and the IPA has prioritised the repair, expansion and modernization of national infrastructure over the past decade, efforts are considered to be undermined by a decline in international oil prices as the country was considered to be highly dependent on the supply of capital generated from oil revenues (Jensen 2018). The decline in oil related capital subsequently led to a decrease in both foreign and public investments, the mismanagements of resources, a decline in the levels of skilled labour and a and a lack of capacity (Jensen 2018). In order for artisanal fisheries to contribute to social development in the small coastal towns of Angola, initiatives to improve existing and the development of new infrastructure is necessary (OCAR 2002, Agostinho et al. 2015, ACP Fish II 2013, Paterson et al. 2014).

It was clear throughout the current study that alternative or supplementary livelihood opportunities were limited, with most indicating that they were entirely dependent on fishing related activities as a source of income and livelihood. The majority of fishers, particularly those living in Tombua, highlighted how important squid were towards their total household income. Whilst the majority of fishers were not sole providers within households, they were in most instances the primary providers with a high number of dependents. The high

dependence upon cephalopods, particularly squid, as a source of income and livelihood, highlights the need for appropriate management regimes so as to ensure sustainable harvesting, particularly as a high proportion of interviewed fishers expressed that they had observed negative changes within the fishery over time. As highlighted by Jentoft (2000), in order for fishing communities to be viable, viable stocks are required and vice versa.

Due to the nature of the fishery, many fishers indicated that there were periods of low catches, which subsequently lead to a decline in income. Variability in squid catches is known to be influenced by a several factors such as seasonal changes in biomass, presence of aggregations as a result of spawning activity and environmental conditions (Roberts 1998). As highlighted in Chapter 4 and 5, both cuttlefish and squid exhibit strong seasonal temporal and spatial fluctuations in abundance within the region of southern Angola. Periods of low income as a result of low catches, is further exacerbated by high price volatility, which represents a major concern raised by fishers. Many fishers stated that the price of cephalopods, in local markets, fluctuated drastically due to a combination of issues such as the inability to preserve the quality of catches, increased capacity within the fishery, and the variability and uncertainty of the market. Price volatility is a global concern for artisanal fisheries (Richardson Temm et al. 2008) and is likely to continue to have major implications on the socio-economic viability of the southern Angolan jig fishery without some kind of government intervention. Periods of low catches coupled with volatile prices and fluctuations in demand, increases the vulnerability of fishers dependent on the resource as a source of income and highlights the need for stability within the market force or alternative sources of livelihoods. An understanding of the pricing mechanisms and market forces coupled with regimes to increase product quality and market stability may prove to be critical in reducing price volatility and subsequently socio-economic vulnerability (FAO 2016b).

Fishers raised concerns with regards to declining catches, with many expressing that fishing range, in both time and space, had drastically increased in comparison to historical fishing trips. This is a concern that has been raised within many artisanal fisheries (Raemaekers & Sowman 2015, Belhabib et al. 2017). Many participants attributed the decline in catches to increased levels of participation within the artisanal squid fishery, increased competition between sectors, as well as a drastic increase in seal predation and/or interactions. Whilst there is a paucity of information regarding catch and effort information within the artisanal cephalopod fishery, the observed decline in catches is of concern and may be a result of one,

or a combination of the following factors; i) increased exploitation levels throughout the fisheries sector; ii) increased predation, particularly by seals, iii) a result of climate-induced changes in cephalopod populations.

Belhabib et al. (2017), suggests that artisanal fishing effort within West African fisheries has increased 10-fold between 1950 and 2010. Resource depletion within West African countries was therefore largely attributed to an increase in the number of artisanal boats and subsequent increase in their collective effort (Belhabib et al. 2017). This highlights the need of effective management strategies within artisanal fisheries, as the collective effort of this sector and subsequent environmental and socio-economic consequences, are often overlooked (Belhabib et al. 2017, Teh & Pauly 2018). Increased levels of fishing effort as a result of overcapacity needs to be addressed as it will result in the decline of exploited stocks. Furthermore, whilst competition within the sector has increased due to growing participation and effort, many interviewed artisanal fishers attributed the decline in catches to an increase in semi-industrial and industrial vessels within the area. Conflict between fishing sectors was increasingly evident within Angolan coastal waters (Lankester 2002, OCAR 2002, Belhabib et al. 2015, Belhabib et al. 2017). Whilst the government has reserved the first 4nm of the coastline for artisanal fishers along with recreational fishing activities and research related practices, semi-industrial and industrial fishing vessels are known to violate these measures (Lankester 2002, OCAR 2002). Based on the distribution of the squid fishers observed in this study, there should be limited operational conflict between them and the industrial/semi-industrial vessels. However, in order to evaluate whether there is a resources conflict, it is necessary to monitor the proportion and biomass of cephalopod bycatch in these sectors. In addition, an increase in surveillance to improve the compliance of the industrial and semi-industrial sectors is required. Importantly, illegal, unreported and unregulated (IUU) fishing must be addressed.

IUU fishing occurs in all fishery sectors and is a global phenomenon (Agnew et al. 2009, Martini 2013). This issue of IUU fishing, within Angolan waters, has been previously been acknowledged, however additional efforts and management measures are required to combat IUU fishing within these coastal zones (Martini 2013, Belhabib & Divovich 2015, Pramůd 2017). The occurrence of IUU fishing, can be attributed to a number of factors, including but not limited to, inadequate surveillance infrastructure, lack of trained compliance officers and fisheries observers, inadequate finance for training, inspections and surveillance, inadequate

management regimes and conflicts of interest (Lankester 2002, Martini 2013, Paterson et al. 2014, Belhabib & Divovich 2015, Pramöd 2017). The growing importance of the artisanal sector, globally, and more specifically the high dependence on coastal communities of Angola on marine resources as a source of livelihood and poverty alleviation, highlights the need for effective and efficient monitoring, control and surveillance (MCS) to enforce and support management regimes and objectives (FAO 2002, Agnew et al. 2009, du Preez 2009, Belhabib & Divovich 2015). However, MCS requires capital, as well as recurrent and operational investments which are likely to be costly. Currently, MCS within Angolan waters is not perceived to be reaching annual benchmarks and efforts are considered to primarily focus on oil related sectors in tracing maritime offences and infringements rather than those related to the fishing sector (Pramöd 2017). As such community-based initiatives or participatory management strategies may offer a more cost-efficient approach as well as increase incentives for voluntary compliance within the artisanal fisheries sector (Bergh & Davies 2002, FAO 2002).

Conflict between seals and fisheries is not a new issue and is a problem which has been identified within fisheries around the globe (Wickens et al. 1992, Stewardson 2001, Harwood and Walton 2002, Sauer et al. 2013). Operational or direct conflict between seals and fishers can be a result of a number of factors; 1) operational consumption: seals directly removing and consuming catch from fishers, 2) operational disturbance: disruption of fishing operations due to dispersal of squid when seals are present within an area, 3) operational damage: which results from a direct loss or damage of fishing equipment/gear due to seals (Wickens et al. 1992, Harwood and Walton 2002).

The population of Cape fur seals, *Arctocephalus pusillus pusillus*, within the Benguela represents the top marine predator biomass within the BCLME (BCLME 2007, Ministry of Environment 2014, Kirkman et al. 2019). Furthermore, Cape fur seals have previously been identified as a conflict species within Angolan waters (Ministry of Environment 2014). During the current study, all three operational conflicts were identified by fishers within Tombua as a major issue within the fishery. Whilst research on the Angolan seal population is relatively scarce, research on *A. pusillus pusillus* has highlighted a range expansion of these populations. The northern breeding limit was initially described by Wickens et al. (1991), as Cape Cross in central Namibia. The recent expansion of the population has resulted in a shift of the northern breeding limit to Ilha dos Tigres in southern Angola

(Winkler et al. 2019). In this region, Winkler et al. (2019) found that the contribution of cephalopods to the diet of Cape fur seals was higher than elsewhere in their distribution. Assessments on the interaction and conflict between seals and the artisanal cephalopod jig fishery, as well as research on the population dynamics of the Ilha dos Tigres breeding colony, is required to understand and predict the interactions, particularly as many fishers identified the need to cull as the only solution to reduce the conflict with the growing seal population. Furthermore, the increase in fishing pressure as a result of increased population growth and increased demand for cephalopods, coupled with the growth of the Angolan seal population is likely to result in increased levels of conflict and interaction. The need to quantify these interactions is therefore required to develop appropriate management strategies. However, it is important that any management strategies which aim to reduce the conflict between fisheries and Cape fur seals is highly adaptive due to the dynamic nature of these interactions.

As highlighted throughout interviews, particularly by fishers who had been involved in the fishery for an extended period of time, catch per unit effort decreased drastically over time. Many fishers mentioned that they now had to fish further, for longer in order to catch similar quantities to what they historically caught. This was primarily attributed to two factors; i) less fish and ii) increase in the occurrence of unfavourable conditions. This is of major concern, as both squid and cuttlefish exhibited seasonal variability within the region, with both species only being captured for limited periods of time, when environmental conditions appeared optimal within fishing areas. Furthermore, the artisanal squid jig fishery which primarily operates out of Tombua, falls within the ABFZ, a zone which is identified as a hotspot for global climate change, due to the significant rises in sea surface temperatures, as highlighted in Chapter 2. Research by Belhabib et al. (2017), suggested that climate change induced migrations may have severe implications on catch per unit effort, particularly for artisanal fishers who operate close to shore, within a relatively limited area due to restrictions such as vessel capacity. The paucity of data on the climate-induced changes on the abundance and distribution of squid in southern Angola is concerning as it undermines adaption efforts.

Whilst the Angolan government recognises the importance of artisanal fisheries and has made provisions to allow for the development of this sector, as highlighted in Chapter 1, the challenges and constraints need to be addressed to enhance productivity, maximise profitability and subsequently contribute towards sustainable livelihoods (Angola 2004, du

Preez 2009). Unfortunately these fishers, like most artisanal fishers in Angola currently find themselves fishing purely for food security rather than to economic development (Agostinho et al. 2005, Ramaekers & Sowman 2015).

The incorporation of fisher ecological knowledge (FEK) into these ecological and stock assessments is critical as the fishers often hold an in-depth understanding of spatio-temporal and biological aspects of populations at a local level (Rodhouse et al. 2014). Furthermore, the incorporation of FEK into the biological and stock assessments is an important step toward co-management, which has been recognised as a critical principle for the management of small-scale fisheries, particularly in data or resource deficient regions (Worm et al 2009). This would include fishers observations as well as contextual and experiential knowledge not only on the target species but on the social, economic and governance aspects of the artisanal jig fishery. And will ultimately contribute greatly towards the development of a more sustainable fishery.

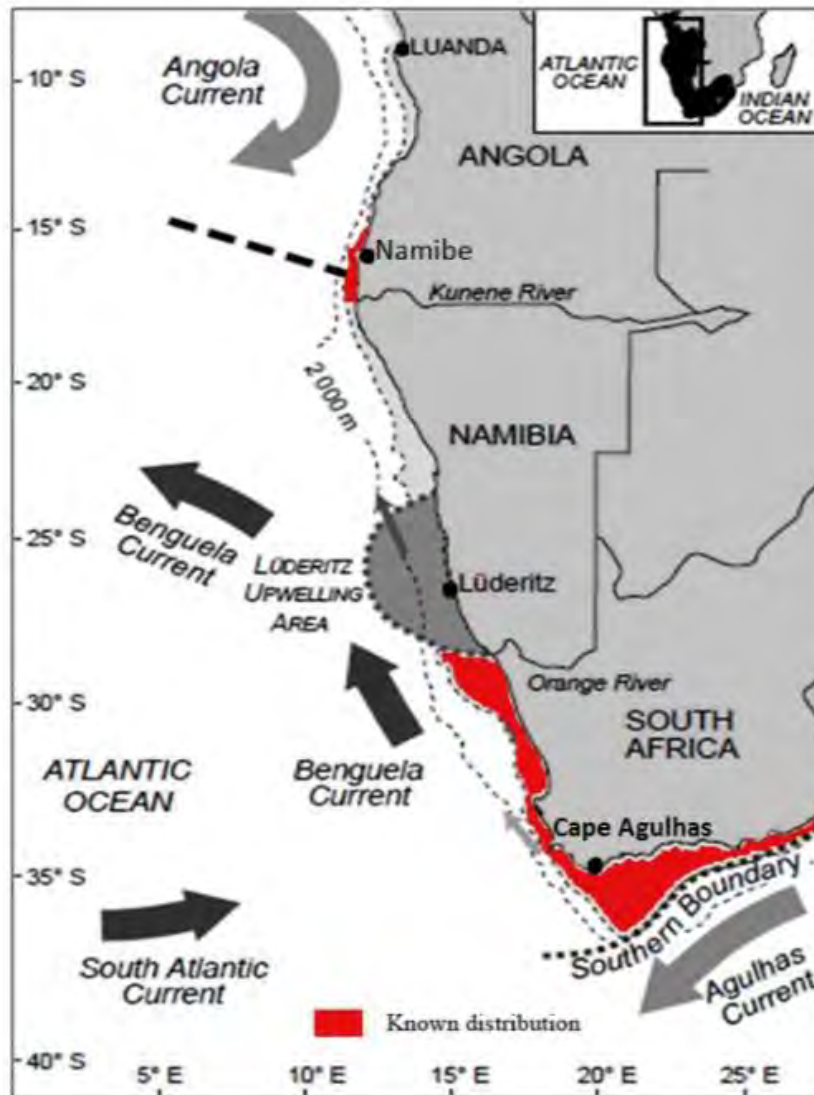
In conclusion, the socio-economic importance of the cephalopod and more specifically squid fisheries in southern Angola highlights the need for improved management of the fishery. For majority of these small coastal communities fishing is enmeshed within their cultural, traditional, and social standards and systems. Such communities are extremely vulnerable due to the increased susceptibility to risks, a high sensitivity to such risks and a limited capacity to adapt. Such risks may be physical risks to fishers (drowning etc), or to catch quantity and quality to weather related risks which may be exacerbated by climate change or resource-related risks, such as changes in biomass due to climate-induced migrations or overfishing (FAO 2021).

## CHAPTER 4

# A FIRST DESCRIPTION OF ASPECTS OF THE DEMOGRAPHY AND BIOLOGY OF THE SQUID, *LOLIGO REYNAUDII* (D'ORBIGNY 1845), OFF SOUTHERN ANGOLA

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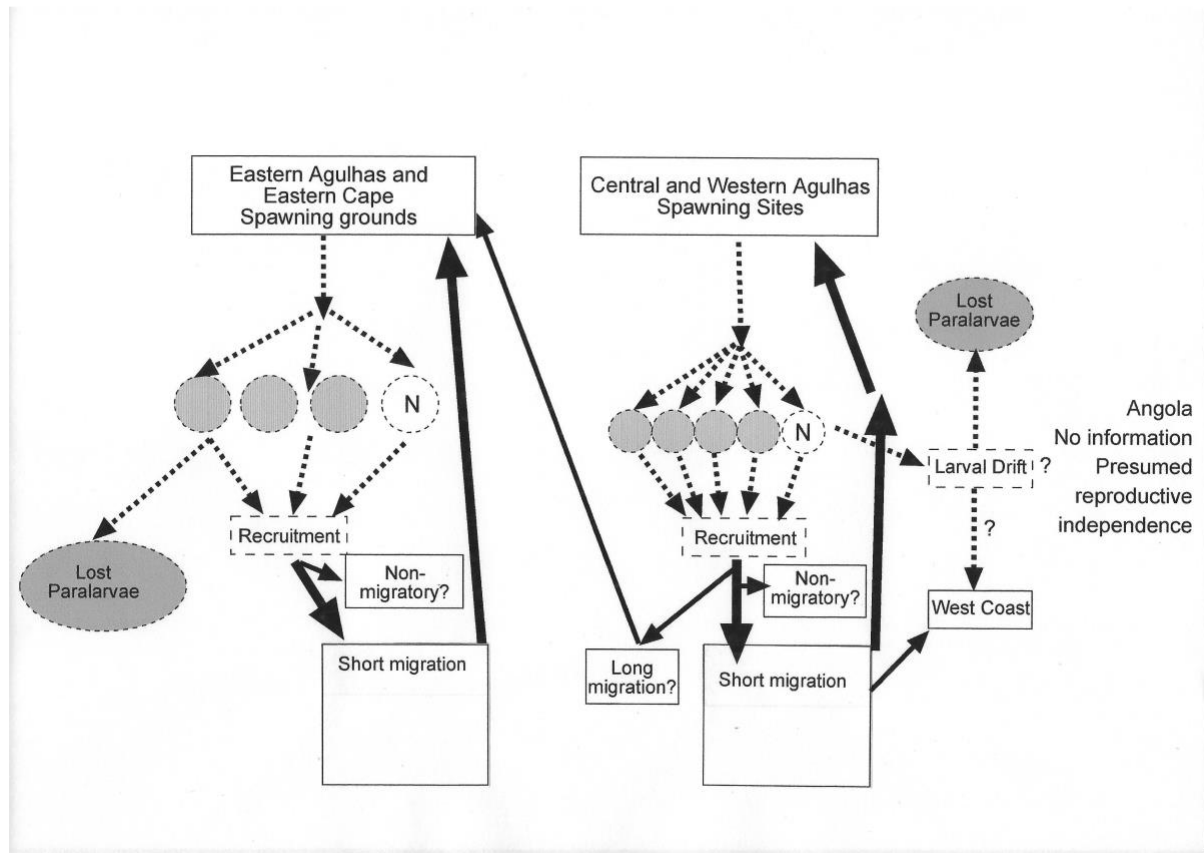
The Cape Hope squid, commonly known as Chokka squid, *L. reynaudii* is a primary target in the coastal fisheries of Southern Africa (Arkipkin et al. 2015). It is distributed from the south east coast of South Africa (RSA) to southern Angola, with the majority of the biomass occurring over the eastern Agulhas Bank (Figure 4.1) (Augustyn 1989, 1991, Augustyn et al. 1993, Roberts 2005). Despite the presence of a large metapopulation, van der Vyver (2015) identified three distinct subpopulations; i) south coast of SA, ii) western Agulhas and west coast of SA, and iii) Angola, based on morphological diversity despite the lack of clear genetic diversity across the region (Shaw et al. 2010). Studies summarized by Lipiński et al. (2016), indicated that the subpopulation of squid off southern Angola may be the result of northerly range expansion and is likely to be characterized by its own breeding and paralarval regime. Research conducted on *L. reynaudii* along the coast of SA, which has primarily been driven by the commercial importance of the resource, has highlighted the differentiation in the abundance, distribution, composition and reproductive characteristics of South African subpopulations.



**Figure 4.1:** Current known distribution of *L. reynaudii*, and major oceanographic features of the region including, the Angola Current, Benguela Current and Lüderitz upwelling area. (Van der Vyver 2014).

Research on *L. reynaudii* along the coast of South Africa has highlighted the variability in the abundance, distribution, composition and reproductive characteristics of the subpopulations. For example, *L. reynaudii* found along the west coast of SA are characterized by slower growth rates, larger sizes at maturity, a narrower size distribution and a less advanced gonadal development, in comparison with those found off the east coast (Olyott et al. 2007). In contrast to *L. reynaudii* off the coast of SA (Augustyn et al. 1992, 1993, 1994; Roberts & Sauer 1994, Sauer et al. 1997, 2013, Augustyn & Roel 1998, Roberts 2005, Olyott et al. 2006, Lipiński et al. 2016), research on the Angolan subpopulation is limited. The observed variability between South African sub-populations coupled with the lack of research on the

northernmost subpopulation, despite its importance in the local squid directed artisanal fishery in that region, highlights an urgent need for research on this subpopulation (Lipiński et al. 2016).



**Figure 4.2:** The lifecycle of *L. reynaudii* as depicted by Lipiński et al. 2016. Thick arrows indicate main circulation within the life cycle scheme; thinner arrows indicate supplementary processes. Broken lines indicate paralarval movements. Size of rectangular boxes represent approximate strength of each migration event. It remains unclear as to whether any paralarvae reach the west coast (marked by question marks).

*Loligo reynaudii* is considered to be neritic as it is typically associated with coastal environments and the continental shelf, occurring to depths of 200m, although they have been observed to depths of 500m (Augustyn 1991, Shaw et al. 2010, Roberts et al. 2012).

Spawning along the coast of South Africa has been documented to take place between False Bay (18°30'E), in the west, and East London (27°52'E) in the east (Roberts et al. 2012).

*Loligo reynaudii* is a uniseasonal-iteroparous species, with females depositing clutches of eggs over a protracted period of time at multiple spawning sites. (Melo & Sauer 1999, Sauer et al. 1992, Sauer et al. 2000). The species is known to form large spawning aggregations, in both sheltered bays as well as along exposed parts off the southern coast of South Africa

(Augustyn 1989). *Loligo reynaudii* spawns at multiple inshore sights off the coast of South Africa, however collection of eggs from demersal trawls as well as the hydroacoustic location of squid beds suggests that offshore spawning is also common (Augustyn et al. 1994, Roberts et al. 2002, Downey et al. 2010). The formation of spawning aggregations is influenced by environmental conditions, with the occurrence of strong upwelling likely resulting in the initiation of spawning events (Sauer et al. 1991, Roberts 2005, Downey et al. 2010, Arkhipkin et al. 2015). Spawning occurs throughout the year, however inshore spawning activity on the Agulhas Bank peaks during summer months with a secondary peak in spawning during winter having been documented to occur during a number of years (Augustyn et al. 1994, Oosthuizen et al. 2002, Olyott et al. 2006). Aggregations of spawning squid are typically easily detected with the use of echosounder techniques and these are typically targeted by commercial jig fishing boats, off the coast of South Africa (Sauer et al. 1992, Sauer 1995). The targeting of spawning aggregations coupled with the management challenges associated with forecasting recruitment in species characterized by short life spans, make the species vulnerable to overexploitation and thus information on the life cycle and the interactions of the species with the environment is critical for the development of effective management criteria (Augustyn et al 1992, Lipiński et al. 1998).

*Loligo reynaudii*, is characterized by a high growth rate, with mantle-length based daily growth rates ranging from 0.75 to 1.02 mm/day for male squid and 0.32 to 0.45 mm/day for females (Mwanangombe et al. 2021). The fast growth rates characteristic of Loliginids therefore requires high feeding rates and efficient digestion and assimilation (Lipiński 1987, Sauer et al. 2013, Arkhipkin et al. 2015). Squid are active predators which feed on a wide variety of prey, including teleosts, crustaceans, cephalopods and polychaetes (Augustyn et al. 1994, Lipiński 1987). Whilst few studies have described the diet and feeding behavior, several important factors can be highlighted (Sauer & Lipiński 1991, Sauer et al. 2013). Firstly, seasonal variability in prey composition and the intensity of feeding has been noted within many of the Loliginid species, including *L. reynaudii* (Augustyn 1991, Sauer & Lipiński 1991, Collins et al. 1994, Rocha et al. 1994). Sauer and Lipiński (1991) suggested that *L. reynaudii*, on the spawning grounds off the coast of SA, exhibited higher levels of feeding intensity during summer in comparison to autumn and winter months. Crustaceans dominated the diet in winter, whilst teleosts were the dominant prey in summer (Sauer and Lipiński 1991). Diet also varies with ontogeny, with smaller juvenile individuals primarily feeding on small pelagic crustaceans, whilst larger mature squid demonstrate a preference

towards teleost species (Lipiński 1987, Sauer & Lipiński 1991). Cannibalism is a common occurrence but is not likely a consequence of the low prey availability, as was previously hypothesized by Mauer and Bowman (1985) (Lipiński 1987, Augustyn 1990, Sauer and Lipiński 1991) but rather a consequence of the vulnerability of partially spent individual squid in spawning concentrations (Sauer pers comm).

Although the life cycle of *L. reynaudii* has been well-described, Lipiński et al. (2016) highlighted the complexity of the *L. reynaudii* life cycle (Figure 4.2). This complexity may be attributed to multiple factors, including but not limited to, the complexity and variability of oceanographic features and conditions throughout the distribution, the varying environmental effects on paralarval survival and distribution, the complex spatial and temporal patterns in squid migration and the presence of multiple subpopulations. However, it is likely that the complexity of the lifecycle enables squid species to be less susceptible to drastic reductions in biomass in the face of environmental fluctuations (Arkhipkin et al. 2015).

Locally known as lula in Angola, *L. reynaudii* is targeted by an artisanal jig fishery off the southern coast. Lula are targeted using handmade jigs and handlines from small polystyrene rafts, known as bimbos within close proximity to shore as highlighted in Chapter 3 (Sauer et al. 2013). To date, very limited research has been carried out on the Angolan squid population.

The aim of the present chapter is therefore to describe the population biology of *L. reynaudii* distributed off southern Angola. This includes:

- 1) Determine the size composition of the Angolan sub-population of *L. reynaudii*,
- 2) Provide insight into the reproductive biology of *L. reynaudii* distributed within southern Angola,
- 3) Provide a description of the diet of the southern Angola *L. reynaudii* sub-population and
- 4) Explore the interannual variability in the population biology of *L. reynaudii* off the coast of southern Angola

## *Method and Materials*

### *Sample collection*

*Loligo reynaudii* samples were collected during two sampling periods. “Period 1” refers to samples collected between June 2008 and May 2009, whilst “Period 2” refers to individuals collected between June 2014 and May 2015. In both cases, monthly samples were obtained from artisanal fishers operating from two fishing villages situated in the southern Angolan region; namely Namibe and Tombua.

### *Biological data collection*

Biological data collection was guided by Olyott et al. 2006. Total body weight (TBW), dorsal mantle length (DML) and mantle width (MW) was collected for all samples. Gonad mass was recorded for both male and female squid; testes weight (TW) ovary weight (OW). Weights were recorded to the nearest 0.01g using an electronic scale. Length and width measurements were obtained using a digital caliper (Insize electronic Caliper Series 1112) to the nearest 0.01mm.

Maturity was categorized using the defined morphological characteristics as outlined by Lipiński & Underhill 1995, described in Table 4.1. However, due to lower sample sizes, particularly during the earlier maturity stages, data was later pooled into simplified maturity and life history stages for the purpose of analysis, as outlined by Olyott et al. (2006) (Table 4.2).

**Table 4.1:** Morphological characteristics of *L. reynaudii* corresponding to maturity scales and life history stages as outlined by Lipiński & Underhill (1995).

Category	Male	Female
(1) juvenile	Spermatophoric complex as a whole unit, “spot”. The rest invisible	Nidamental glands as transparent strips. The rest invisible
(2) immature	Parts of the spermatophoric complex visible	Oviduct meander visible. Ovary still isomorphic (homogenous)
(3) preparatory	White streak on vas deferens (might be quite inconspicuous)	Oviduct meander extended. Immature ova visible
(4) maturing	Vas deferens extended. White particles in the Needham’s sac. Testis structure (fine grooves and ridges visible on surface) present	Nidamental glands large. Some mature (yellow) ova in the ovary. No mature ova in the oviduct
(5) mature	Spermatophores in the Needham’s sac. Testis structure present	Mature ova in the oviduct. Secretion of nidamental glands
(6) spent	Degenerating spermatophores and spermatophoric complex. Testis structure disappears	No definition

**Table 4.2:** Simplified maturity scales and corresponding life history stages used for assessment of maturity in *L. reynaudii*, as outlined by Olyott et al. (2006).

Lipiński (1979) stage	Simplified stage	Life history stage
1	1	Juvenile
2	2	Sub-adult
3	2	Sub-adult
4	3	Adult
5	3	Adult
6	3	Adult

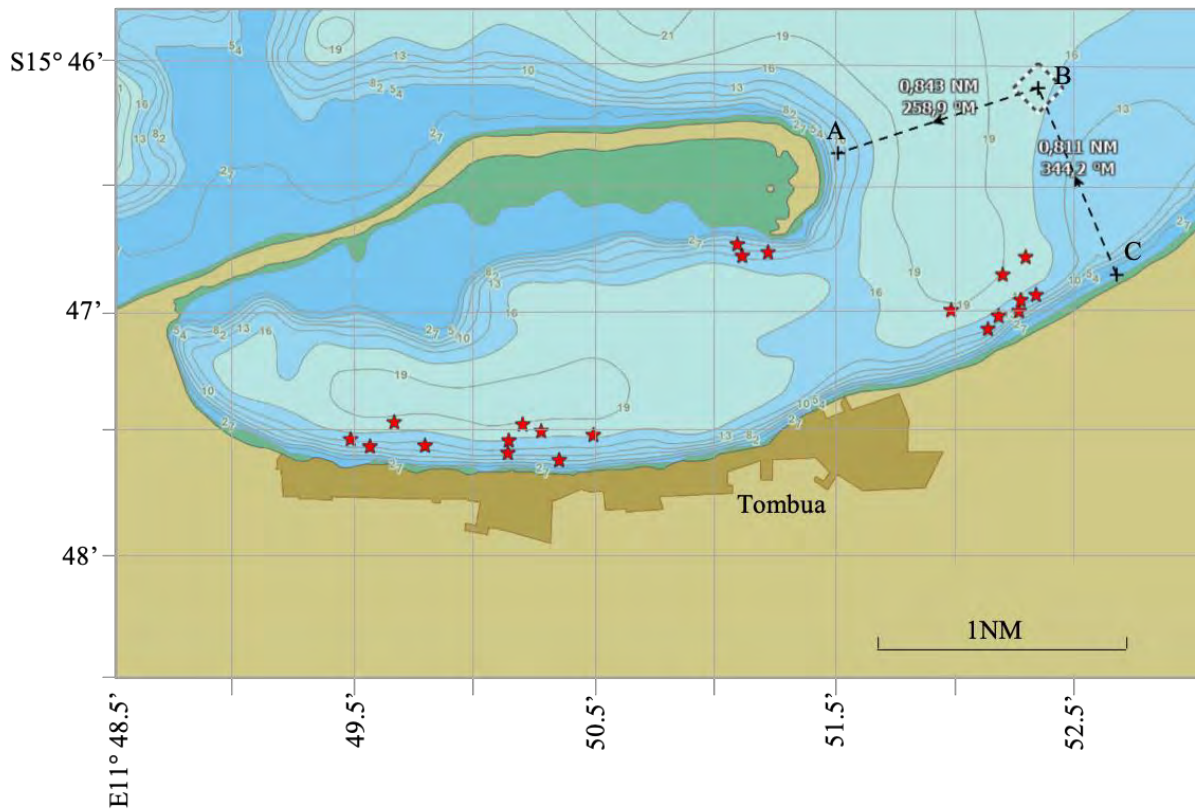
Stomach content analysis was not conducted during the first sampling period. However, during the second sampling period, stomach contents were weighed to the nearest 0.01g and preserved in 10% buffered formalin for 48 hours, after which they were stored in 70%

ethanol. All stomach contents were examined within a week of being stored in ethanol. Upon analysis, stomach contents were classified on the basis of frequency of occurrence (%F) which represented the percentage of *L. reynaudii* that had consumed a particular item of prey. Prey items were classified broadly into categories, such as teleosts, cephalopods or crustaceans, where possible these were later identified to genus and if possible species. Fish were recognized due to the presence of scales, vertebrae, spines, eye lenses and otoliths. The presence of cephalopods within the stomach was recognized by the presence of suckers, tentacles and beaks whilst crustaceans were primarily identified by the occurrence of exoskeletal remains. In many instances, contents were not distinguishable and as such contents were classified as unidentified. Furthermore, due to the macerated nature of the stomach contents, as well as the high levels of digestion and lack of post capture preservation techniques, accurate determination of percentage number and percentage mass of each dietary component was not considered possible.

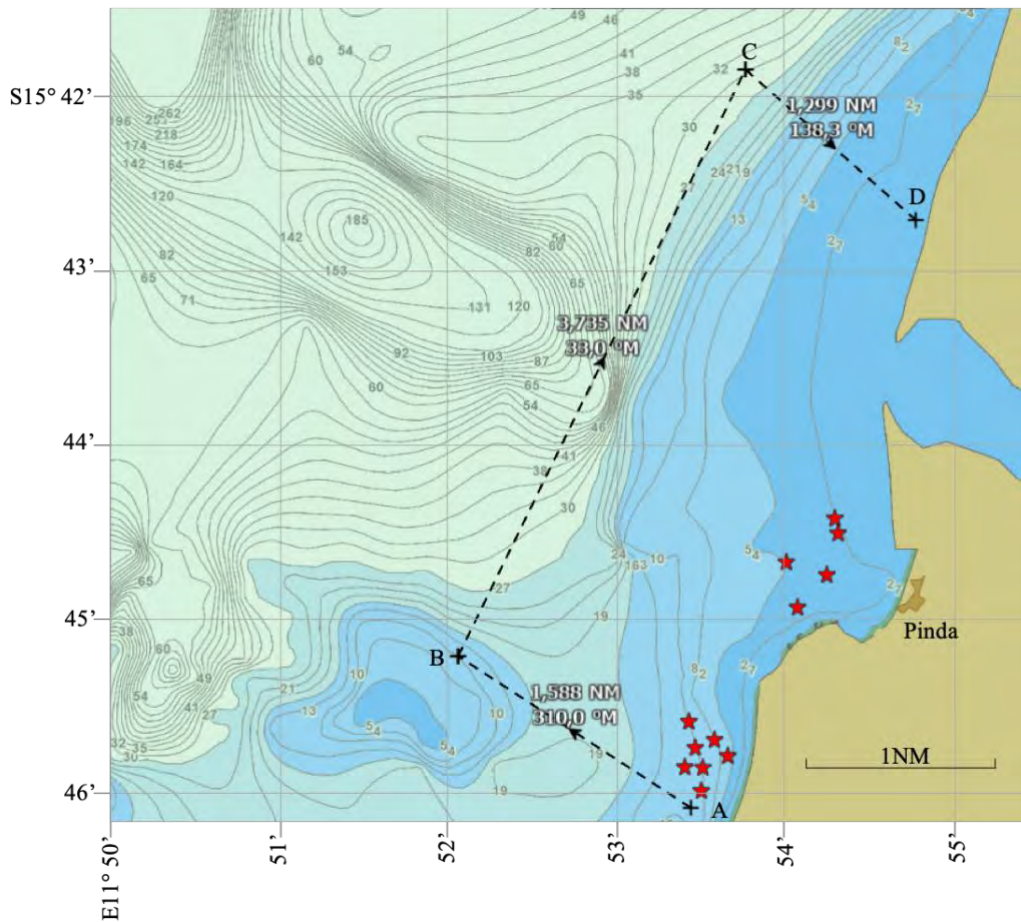
#### *Location of spawning sites*

Attempts to locate and identify egg beds was carried out using three methods:

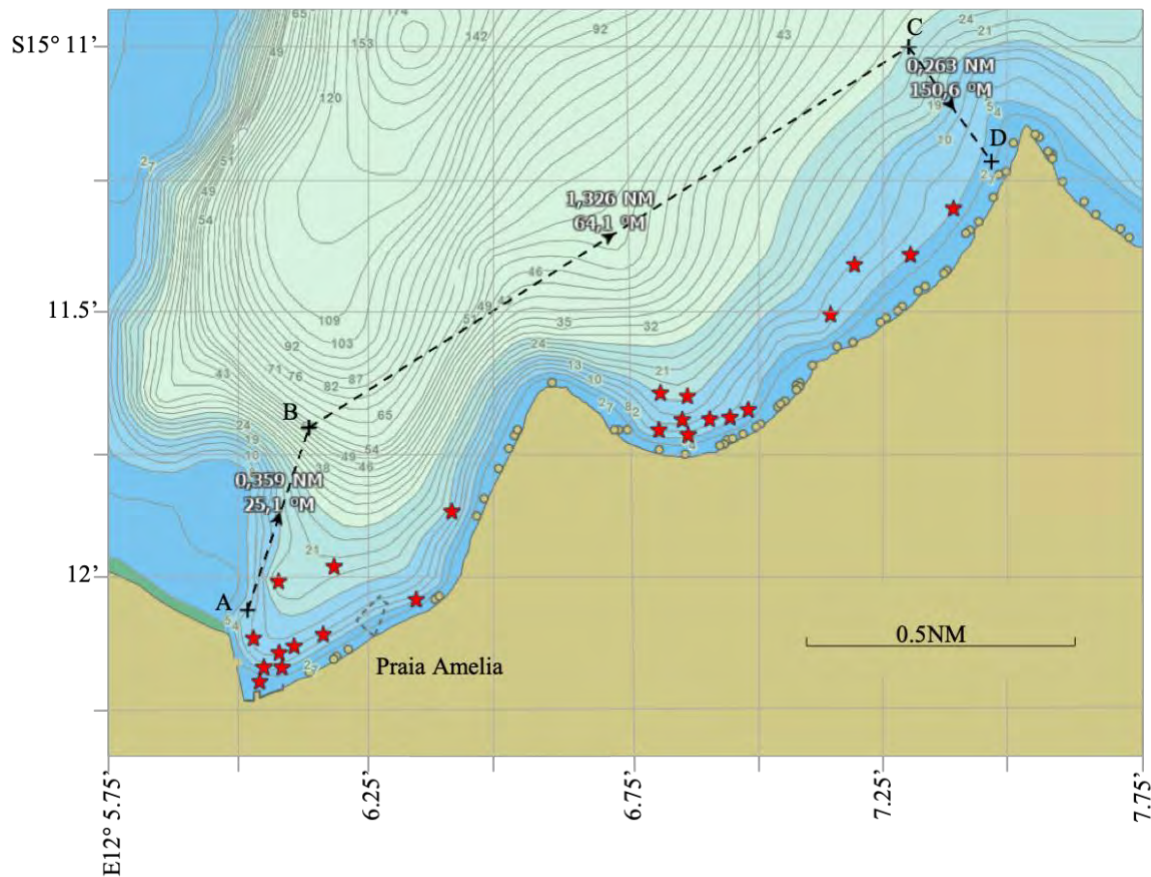
- 1) Grid searches were conducted using a Garmin 7268 Series with a 1kw transducer in the three major fishing areas, as identified in Chapter 3; Tombua, Pinda and Praia Amelia. Surveys were conducted within the designated areas (as indicated in (Figure 4.3, 4.4 & 4.5), across and along isobaths, in waters up to 60m deep. Echosounding was carried out using a dual frequency of 20 kHz and 200 kHz and was performed by a single, experienced South African chokka skipper, throughout the second sampling period, in order to avoid any misinterpretations. When possible, this was carried out twice a month, however due to the remoteness of the location as well as the weather conditions this was not always possible.



**Figure 4.3:** Contour map (depth in meters) illustrating major fishing areas within Tombua (red stars) as well as the designated area and corresponding GPS coordinates (A = S 15° 46,41', E 11° 51,50' B = S 15° 46,16', E 11° 52,34', C = S 15° 46,85', E 11° 52,67') for echosounding surveys in an attempt to locate squid egg beds.



**Figure 4.4:** Contour map (depth in meters) illustrating major fishing areas off of Pinda (red stars) as well as the designated area and corresponding GPS coordinates (A = S 15° 46,07', E 11° 53,42', B = S 15° 45,17', E 11° 52,04', C = S 15° 41,82', E 11° 53,75', D = S 15° 42,68', E 11° 54,76') for echosounding surveys in an attempt to locate squid egg beds.



**Figure 4.5:** Contour map (depth in meters) illustrating major fishing areas off Praia Amelia (red stars) as well as the designated area and corresponding GPS coordinates (A = S 15° 12,06', E 12° 06,05', B = S 15° 11,71', E 12° 06,13', C = S 15° 10,99', E 12° 07,29', D = S 15° 11,21', E 12° 07,45') for echosounding surveys in an attempt to locate squid egg beds.

- 2) When possible a pair of SCUBA divers were deployed when traces on the echogram appeared to be the result of egg masses. Furthermore, during aggregated fishing activities, SCUBA divers were deployed in pairs to assess the presence or absence of eggs on the seabed.
- 3) Communication with local fishers. Fishers were approached at sea. They were shown various images of *L. reynaudii* eggs and asked to identify whether or not eggs had been caught on jigs during fishing.
- 4) Communication with experienced skipper of South African chokka squid vessel during and after an exploratory trip to assess the potential expansion of the commercial jig fishery into southern Angola. Correspondence with the skipper was made in an attempt to determine the area covered during the trip to locate exploitable

biomass, whether there was any sign of squid egg beds or spawning aggregations, as well as to gain an understanding of the catch per vessel and the associated effort.

### *Data analysis*

Data for male and female squid was analyzed separately due to differences in allometric growth. Statistical analysis was guided by the techniques of Olyott et al. (2006). An independent t-test was used to assess the differences in length and weight between male and female squid within each of the sampling periods. An independent t-test was used to examine there were significant temporal differences in the length and weight of squid between the two sampling periods. A Kruskal-Wallis test was to compare the length and weight for male and female *L. reynaudii* between months and seasons. Length-weight relationships were determined, for each sex during each sampling period, by examining the relationship as follows (Bowker 1995):

$$Y = a x^b,$$

where  $Y$  = total body weight in grams,  $x$  = dorsal mantle length in mm,  $a$  and  $b$  are constants.

Length-at-50% maturity ( $L_{50}$ ), for males and females during each sampling period, was established by grouping *L. reynaudii* into 10 mm size classes. The frequency of mature squid per size class was then determined. The data was then fitted using a two-parameter logistic ogive described as:

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

where  $P(L)$  is the proportion of mature squid within each size class  $DML$ ,  $DML_{50}$  is the dorsal mantle length at which 50% of *L. reynaudii* were mature and  $\delta$  is the width or steepness of the logistic ogive. In order to assess the differences in maturity patterns ( $DML_{50}$  and  $\delta$ ), both between sexes within periods as well as within sexes between periods, a likelihood ratio test was conducted.

Gonadosomatic indices (GSI) was determined for each of the sexes as follows:

$$GSI = \frac{GW \times 100}{TBW - GW},$$

where  $GW$  was represented by the weight of the testes in males and the ovary in females, and TBW the total body weight (Pierce et al. 1994). A Kruskal-Wallis test was conducted, in R, in order to assess the difference in GSI between months as well as season, within each of the sampling periods, for both sexes. Monthly and seasonal sex ratios were calculated for both sampling periods. To examine statistical significance of the observed sex ratio's a chi-squared ( $\chi^2$ ) test was performed in R (Zar 1984).

A feeding index was determined as the weight of the food within the stomach as a percentage of the total body weight. In order to assess the influence of seasonality on the dietary composition and feeding index a two-way ANOVA was conducted. An independent t-test was used to establish differences in the dietary composition and feeding index between male and female squid.

### *Results*

A total of 508 individuals (226 from Tombua and 282 from Namibe) were collected during period 1 (June 2008 – May 2009), while 576 (117 from Tombua and 459 from Namibe) were collected during Period 2 (June 2014 – May 2015). Fewer squid were available between Spring and Autumn and this was reflected in the monthly sample sizes (see Table 4.3). The low sample size in July during Period 2 was due to a loss of samples as a result of freezer failure and was not reflective of available specimens.

**Table 4.3:** Monthly sample sizes of *L. reynaudii* collected during the two sampling periods (Period 1 = June 2008 – May 2009,  $n = 508$  and period 2 = June 2014 – May 2015,  $n = 576$ ) in southern Angola.

Month	Period 1			Period 2		
	Male	Female	Total	Male	Female	Total
June	20	28	48	36	58	94
July	22	18	40	9	12	21
August	10	32	42	59	40	99
September	17	20	37	24	25	49
October	19	25	44	25	42	67
November	6	13	19	19	16	35
December	12	15	27	8	12	20
January	16	8	24	10	22	32
February	20	28	48	8	12	20
March	11	3	14	14	22	36
April	16	9	25	11	19	30
May	86	54	140	34	39	73

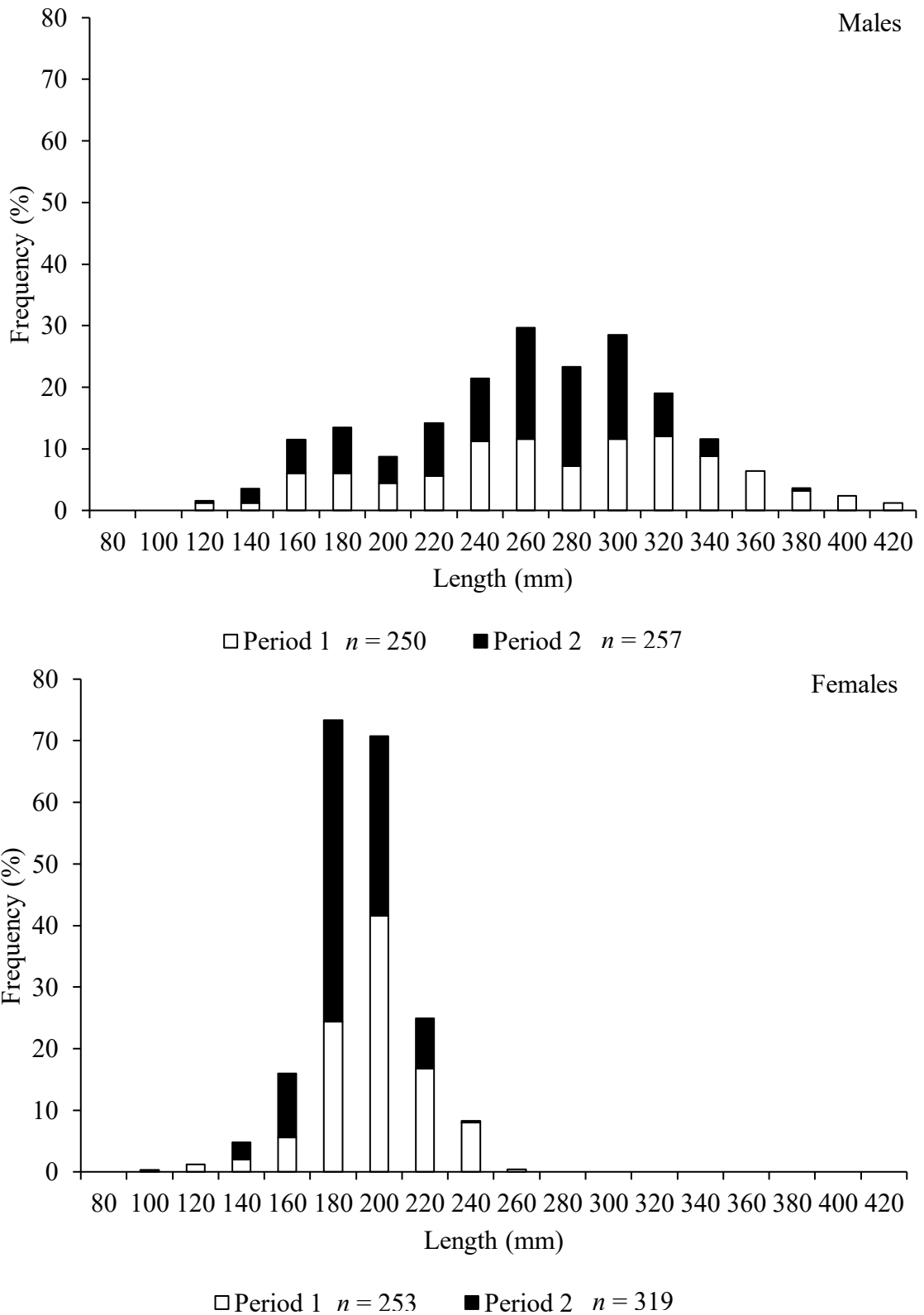
#### *Size composition*

Males were on average significantly larger in length ( $p < 0.01$ ) than females (Table 4.4) during both periods. Males exhibited a considerably higher level of variation in length in comparison to females during both sampling periods (Table 4.4). Comparison of dorsal mantle length of mature individuals revealed the same trend, with mature males being significantly ( $<0.01$ ) larger than their mature female counterparts, during both sampling periods. The average length of males (263.15 mm DML) and females (187.44 mm DML) during period 1 was higher than the average length of males (244.38 mm DML) and females (176.18 mm DML) during period 2 (Table 4.4). Males and females were significantly ( $p < 0.01$ ) larger during period 1.

**Table 4.4:** Minimum, maximum and average ( $\pm$  SD, standard deviation) dorsal mantle length (mm) of *L. reynaudii* collected within southern Angola over two sampling periods (Period 1 = June 2008 – May 2009,  $n = 508$  and period 2 = June 2014 – May 2015,  $n = 576$ ).

	Period 1		Period 2	
	Male	Female	Male	Female
Mean $\pm$ SD	263.15 $\pm$ 68.78	187.44 $\pm$ 23.79	244.38 $\pm$ 50.50	176.18 $\pm$ 17.62
Min	106.00	108.00	114.90	81.60
Max	408.00	260.00	360.45	234.00

Overall, male length class distribution was considerably wider than that of female squid, for both sampling periods (Figure 4.6). Male length distribution was wider during the first sampling period (16 classes) than that of male squid sampled during the second period (13 classes) (Figure 4.6). Female length class distribution for female *L. reynaudii* were similar, with majority of individuals falling within 180-220 mm size class (Figure 4.6).



**Figure 4.6:** Length-frequency histograms of male and female *L. reynaudii* collected during the two sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015).

When compared by life stage (Table 4.5), size variability was generally highest in males, however males and particularly the adults exhibited increased levels of variability during period 1. Female squid exhibited similar patterns in variability between periods, however, higher variability was observed in females during period 1.

**Table 4.5:** Size ranges and sample sizes of *L. reynaudii*, collected in southern Angola during the two sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015) at the various life history stages.

		Period 1		Period 2	
		Male	Female	Male	Female
Juvenile	<i>n</i>	5	4	2	2
	Mean ± SD	132.20 ± 25.46	115.00 ± 6.68	153.04 ± 5.90	128.23 ± 5.64
	Min	106.00	111.00	148.86	124.24
	Max	161.00	116.00	157.21	132.22
Sub-adult	<i>n</i>	15	5	16	10
	Mean ± SD	165.00 ± 34.73	135 ± 19.30	154.16 ± 21.25	162.82 ± 21.91
	Min	120.00	111.00	123.88	126.10
	Max	232.00	162.00	205.70	187.15
Adult	<i>n</i>	235	244	239	307
	Mean ± SD	235.00 ± 63.03	189.70 ± 20.79	251.18 ± 45.36	176.93 ± 16.94
	Min	112.00	108.00	114.90	81.60
	Max	408.00	260.00	360.45	234.00

Average weight of male *L. reynaudii* was found to be highly significantly different to that of female squid ( $p < 0.001$ ). During both sampling periods, average weight was considerably higher for male *L. reynaudii* in comparison to female squid (Table 4.6). The average weight of male and female *L. reynaudii* was significantly different between sampling events ( $p < 0.001$ ), with the observed average weight decreasing from period 1 (301.3g and 164.2g, respectively) to period 2 (252.1g and 148.0g, respectively) (Table 4.6). Intrasexual comparisons of weight of mature squid between sampling periods, resulted in highly significant differences ( $p < 0.001$ ). In both cases, the weight of mature individuals revealed a decrease in body weight, for male and female squid, between the first and second sampling period.

**Table 4.6:** Minimum, maximum and average weight of male and female *L. reynaudii* collected in southern Angola, during the two sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015).

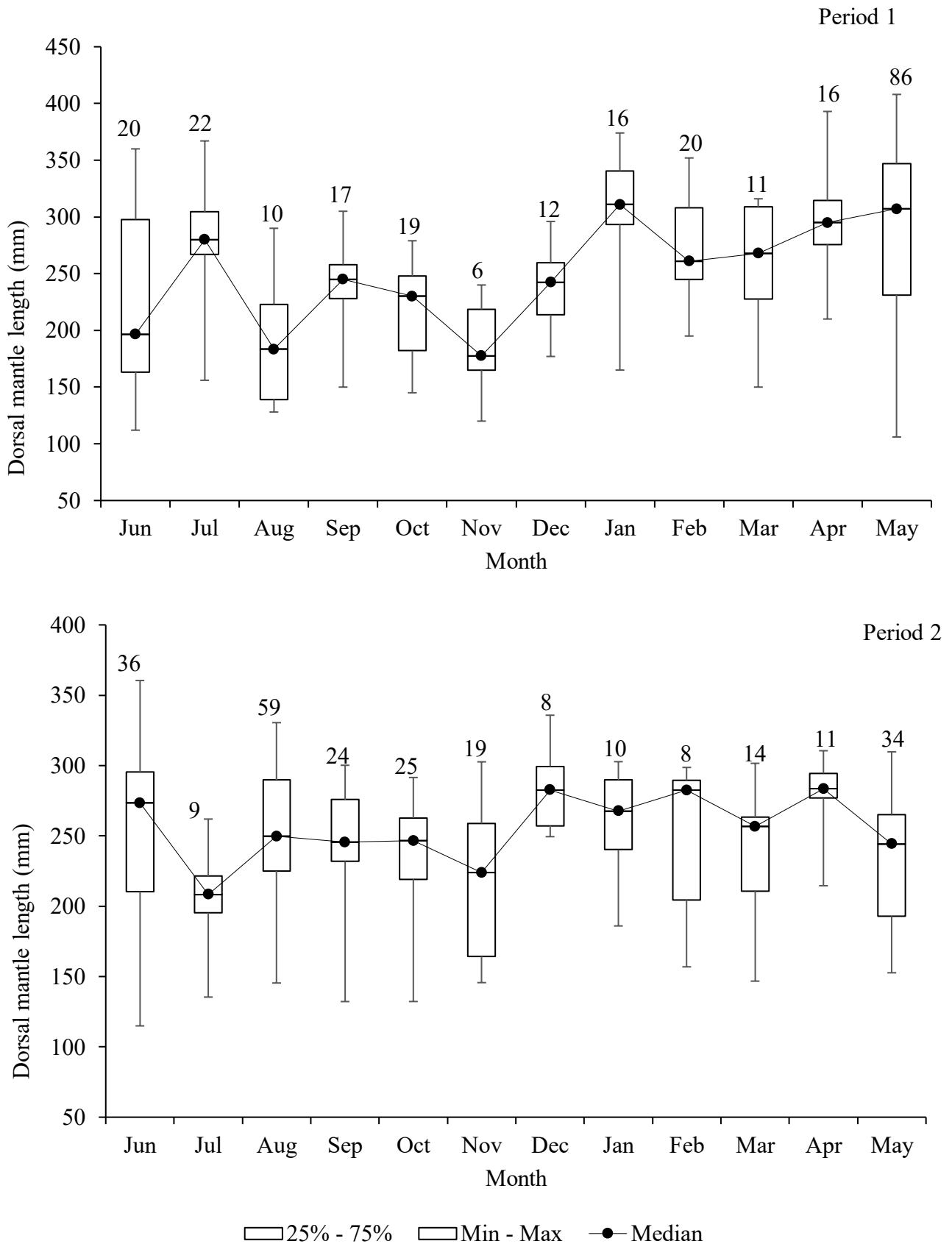
	Period 1		Period 2	
	Male	Female	Male	Female
Mean	301.3	164.2	252.1	148.0
Min	30.9	42.9	45.0	54.4
Max	758.1	374.1	652.7	278.4

*Monthly and seasonal comparisons of Loligo reynaudii size composition*

The median length of male squid exhibited peaks in July, January and May during period 1, while the smallest average lengths observed in August and November (Figure 4.7). The results from the Kruskal-Wallis indicated significant differences in the monthly mean sizes for male squid during period 1 ( $H = 57.93$ , d.f. = 11,  $p < 0.001$ ) (Table 4.7). Whilst median length for males from the second sampling period exhibited less variation across the months, length was seen to peak during February, April, June and December, whilst two distinct dips were observed during the months of July and November (Figure 4.8). Results from the Kruskal-Wallis indicated significant differences in the monthly mean sizes for male squid during period 2 ( $H = 28.58$ , d.f. = 11,  $p < 0.01$ ). Monthly results should however be interpreted with caution due to low sample sizes, as a result of low biomass, during particular months.

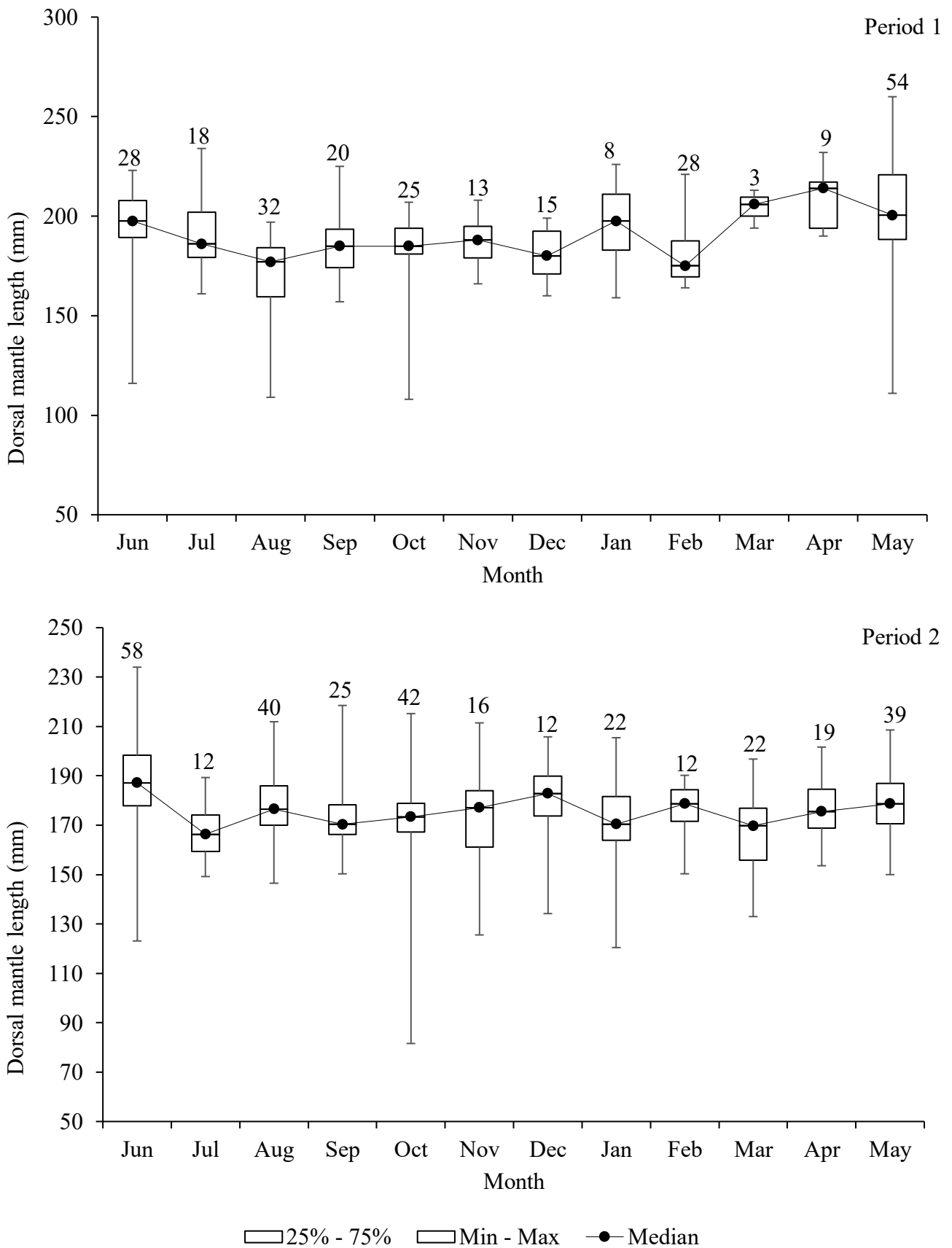
**Table 4.7:** Results from the Kruskal-Wallis test for differences in length of male and female *L. reynaudii* between month for two different sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015), where  $n$  refers to the number of individuals sampled,  $H$  is the Kruskal-Wallis test statistic and d.f. refers to the number of degrees of freedom. Values in bold indicate significant differences.

	Period 1		Period 2	
	Male	Female	Male	Female
$n$	255	253	257	319
H	57.93	63.27	28.58	42.31
d.f.	11	11	11	11
$P$	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.01</b>	<b>&lt; 0.001</b>



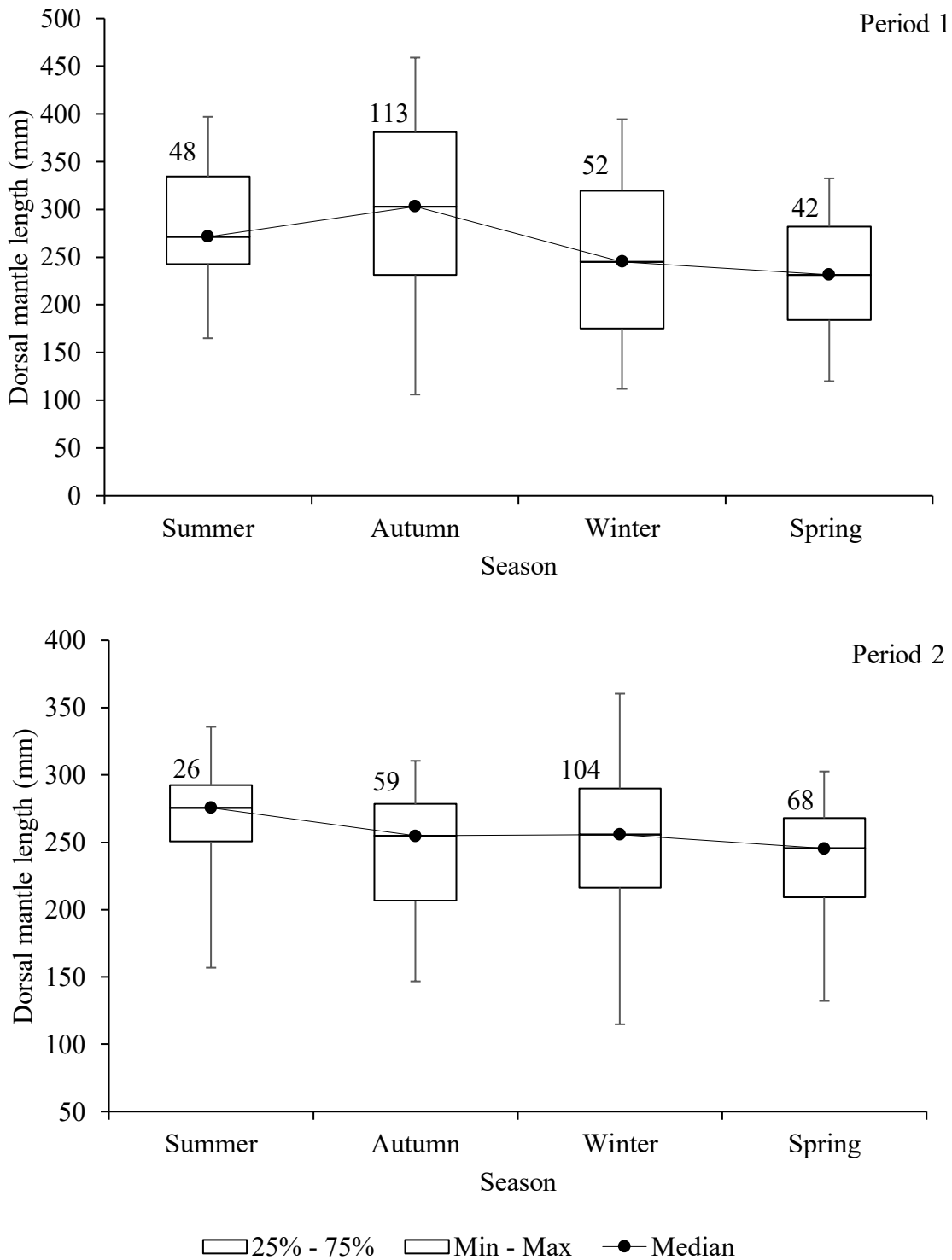
**Figure 4.7:** Median monthly dorsal mantle lengths of male *L. reynaudii* collected during the two sampling periods (Period 1= June 2008 – May 2009 and period 2 = June 2014 – May 2015).

The median length of female squid exhibited peaks in January and April, with the smallest average length in August, December and February (Figure 4.8). The results from the Kruskal-Wallis indicated significant differences in the monthly mean sizes for female squid during period 1 ( $H = 63.27$ , d.f. = 11,  $p < 0.001$ ) (Table 4.7). Average mantle length for females during the second period exhibited a distinct peak in June, followed by the lowest median length in July (Figure 4.10). The results from the Kruskal-Wallis indicated significant differences in the monthly mean sizes for female squid during period 2 ( $H = 42.31$ , d.f. = 11,  $p < 0.001$ ) (Table 4.6).



**Figure 4.8:** Median monthly dorsal mantle lengths for female *L. reynaudii* collected during two sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015).

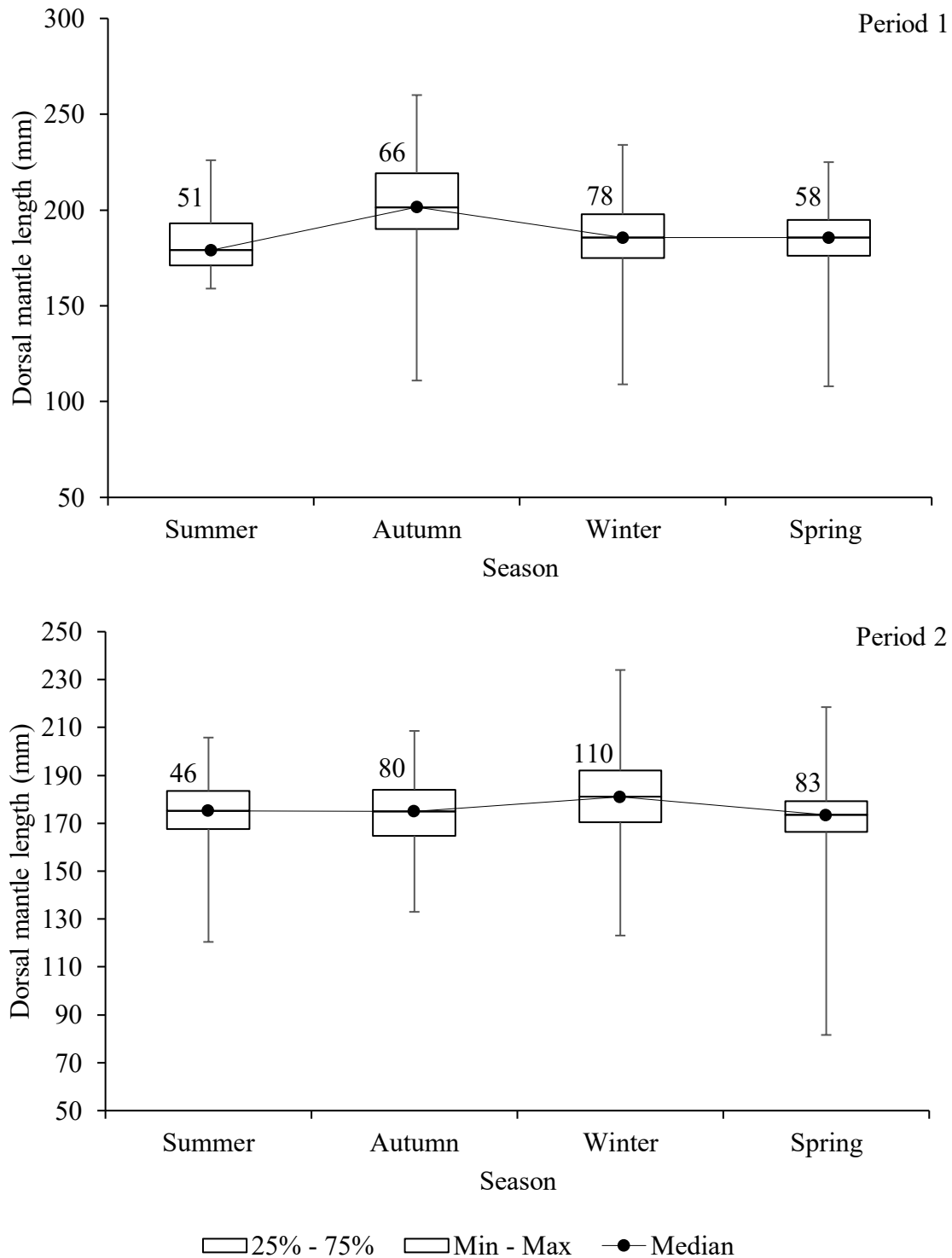
Median length of male squid exhibited a clear peak in autumn during period 1, for male and female squid (Figure 4.9 & Figure 4.10). On average autumn yielded the largest squid during the first sampling period, whilst during the second period male length peaked in summer, whilst female length peaked in winter. There were significant differences in the length of male *L. reynaudii* between seasons during period 1 (Kruskal- Wallis test,  $H = 34.74$ , d.f. = 3,  $p < 0.001$ ) and period 2 (Kruskal- Wallis test,  $H = 9.76$ , d.f. = 3,  $p = 0.02$ ) (Table 4.8).



**Figure 4.9:** Seasonal variation in median dorsal mantle lengths of male *L. reynaudii*, collected during two sampling periods (Period 1= June 2008 – May 2009 and period 2 = June 2014 – May 2015).

Median length of female *L. reynaudii* was found to peak during autumn and steadily decline into summer during period 1 (Figure 4.10). The results from the Kruskal-Wallis indicated significant differences in mean sizes for female squid during period 1 ( $H = 36.10$ , d.f. = 3,  $p < 0.001$ ) (Table 4.8). Median length of females collected during the second sampling period

revealed little variability during summer, autumn and spring with a slight increase being noted during winter, however the Kruskal-Wallis indicated significant differences in monthly mean length ( $H = 14.55$ , d.f. = 3,  $p = 0.002$ ) (Figure 4.10, Table 4.8).



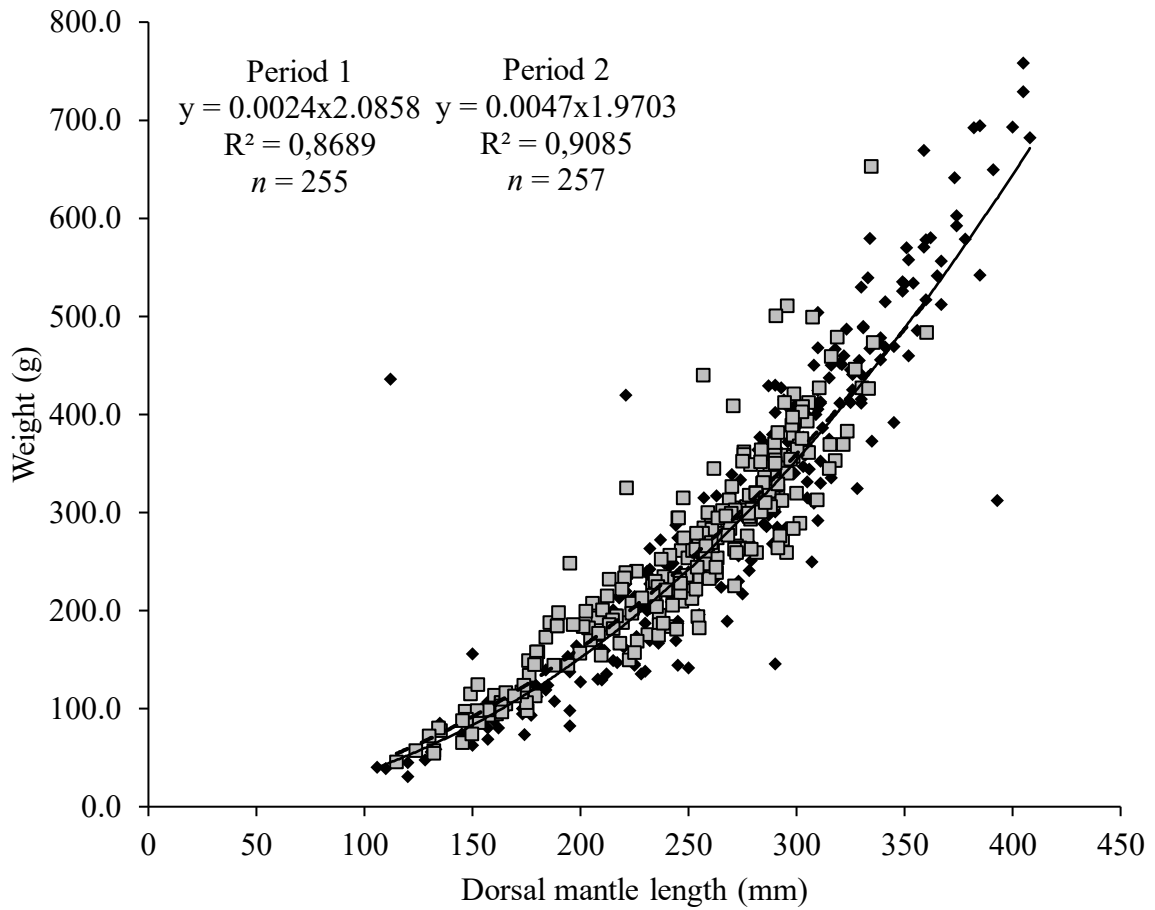
**Figure 4.10:** Seasonal variation in median dorsal mantle lengths of female *L. reynaudii*, collected during two sampling periods (Period 1= June 2008 – May 2009 and period 2 = June 2014 – May 2015).

**Table 4.8:** Results from the Kruskal-Wallis test for differences in length of *L. reynaudii* between seasons for two different sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015), where *n* refers to the number of individuals sampled, *H* is the Kruskal-Wallis test statistic and d.f. refers to the number of degrees of freedom. Values in bold indicate significant differences.

	Period 1		Period 2	
	Male	Female	Male	Female
<i>n</i>	255	253	257	319
H	38.37	36.09	9.762	14.55
d.f.	3	3	3	3
<i>P</i>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>0.02</b>	<b>&lt; 0.01</b>

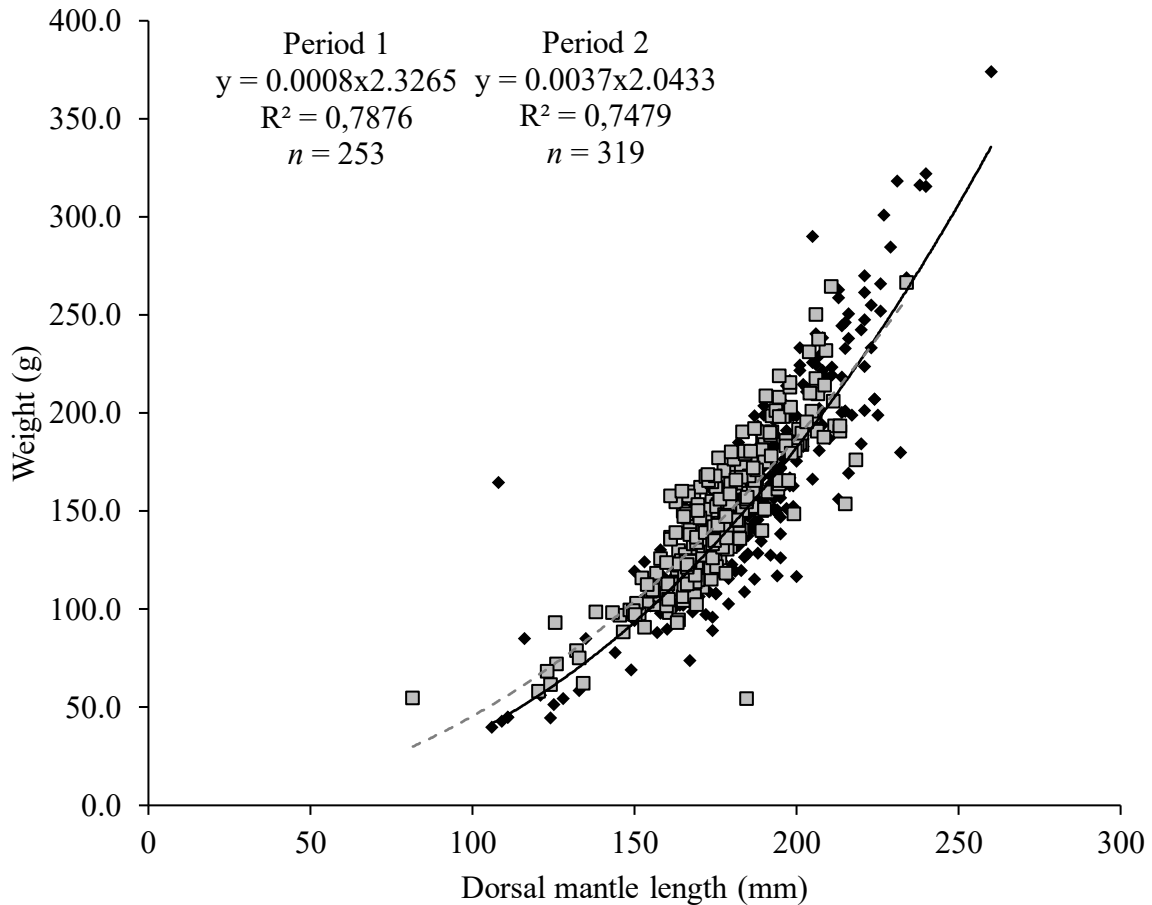
### *Morphometrics*

The length-weight relationships were best described by a power curve. Male squid collected during the first sampling period was described as  $TBW = 0.0024(TL)^{2.0858}$  ( $R^2 = 0.87$ ,  $n = 255$ ) whilst males collected during the second period was described as  $TBW = 0.0047(TL)^{1.9703}$  ( $R^2 = 0.91$ ,  $n = 257$ ) (Figure 4.11).



**Figure 4.11:** Dorsal mantle length to weight relationships for male *L. reynaudii* during sampling period 1 (June 2008 – May 2009, solid black circles and solid trendline) and sampling period 2 (June 2014 – May 2015, grey squares and dashed trendline).

The length-weight relationship for female *L. reynaudii* from the first period was best described as  $TBW = 0.0008(TL)^{2.3265}$  ( $R^2 = 0.79$ ,  $n = 253$ ) and in the second period as  $TBW = 0.0037(TL)^{2.0433}$  ( $R^2 = 0.75$ ,  $n = 319$ ) (Figure 4.12).



**Figure 4.12:** Dorsal mantle length to weight relationships for female *L. reynaudii* during sampling period 1 (June 2008 – May 2009, solid black circles and solid trendline) and sampling period 2 (June 2014 – May 2015, grey squares and dashed trendline).

#### *Sex ratio*

Male biased sex ratios were observed for 5 of the 12 months; July, January, March, April and May during period 1, however these were only significantly biased in March (M:F = 3.67:1,  $p = 0.03$ ) and May (M:F = 1.65:1,  $p < 0.01$ ), with the highest disparity between sexes occurring during the month of March (Table 4.9). No significant male-biased sex ratios were observed during the period 2, despite male-biased ratios being observed, during August (M:F = 1.44:1) and December (M:F = 1.14:1). Females outnumbered males for 7 of the 12 months during

period 1 and 10 of the 12 months during period 2. Results from the chi-squared indicated that these findings were significant during June (M:F = 0.63:1,  $p = 0.04$ ), August (M:F = 0.14:1,  $p < 0.001$ ) and November (M:F = 0.31:1,  $p = 0.03$ ) during period 1. During period 2, female biased sex ratios exhibited significant differences in the months of June (M:F = 0.63:1,  $p = 0.04$ ), October (M:F = 0.55:1,  $p = 0.02$ ) and January (M:F = 0.45:1,  $p = 0.03$ ). Overall during period 1, no significant difference was observed in sex ratio, the sample exhibited a 0.96:1 ratio ( $p = 0.68$ ) however, a significant female biased ratio was observed for period 2 (M:F = 0.78:1,  $p < 0.01$ ) (Table 4.9).

**Table 4.9:** Monthly sex ratios of mature *L. reynaudii* collected during the two sampling periods (Period 1= June 2008 – May 2009 and period 2= June 2014 – May 2015). Values in bold indicate significant differences.

Sampling period	Month	Frequencies		Sex ratio	Chi-squared	p-value
		Male	Female	M:F		
1	June	10	25	0.43:1	5.12	<b>0.02</b>
	July	21	18	1.17:1	0.23	0.63
	August	4	28	0.14:1	18.00	<b>&lt; 0.001</b>
	September	16	19	0.84:1	0.26	0.61
	October	18	25	0.72:1	1.14	0.29
	November	4	13	0.31:1	4.77	<b>0.03</b>
	December	9	15	0.60:1	1.50	0.22
	January	14	8	1.75:1	1.64	0.20
	February	20	28	0.71:1	1.33	0.25
	March	11	3	3.67:1	4.57	<b>0.03</b>
	April	16	9	1.96:1	1.96	0.16
	May	86	52	1.65:1	8.38	<b>&lt; 0.01</b>
	Overall	223	244	0.963:1	0.169	0.681
2	June	33	52	0.63:1	4.24	<b>0.04</b>
	July	7	12	0.58:1	1.32	0.25
	August	56	39	1.44:1	3.04	0.08
	September	21	25	0.84:1	0.35	0.56
	October	23	42	0.55:1	5.554	<b>0.02</b>
	November	14	16	0.88:1	0.13	0.72
	December	8	7	1.14:1	0.07	0.80
	January	10	22	0.45:1	4.500	<b>0.03</b>
	February	8	12	0.67:1	0.80	0.37
	March	14	22	0.64:1	1.78	0.18
	April	11	19	0.58:1	2.13	0.14
	May	34	39	0.87:1	0.34	0.56
	Overall	239	307	0.78:1	8.47	<b>&lt; 0.01</b>

Sex ratios were female biased, although there was a significant male biased sex ratio observed during autumn (M:F = 1.72:1,  $p < 0.001$ ) in period one (Table 4.10). Females were observed to significantly outnumber males during winter (M:F = 0.54:1,  $p < 0.01$ ). During

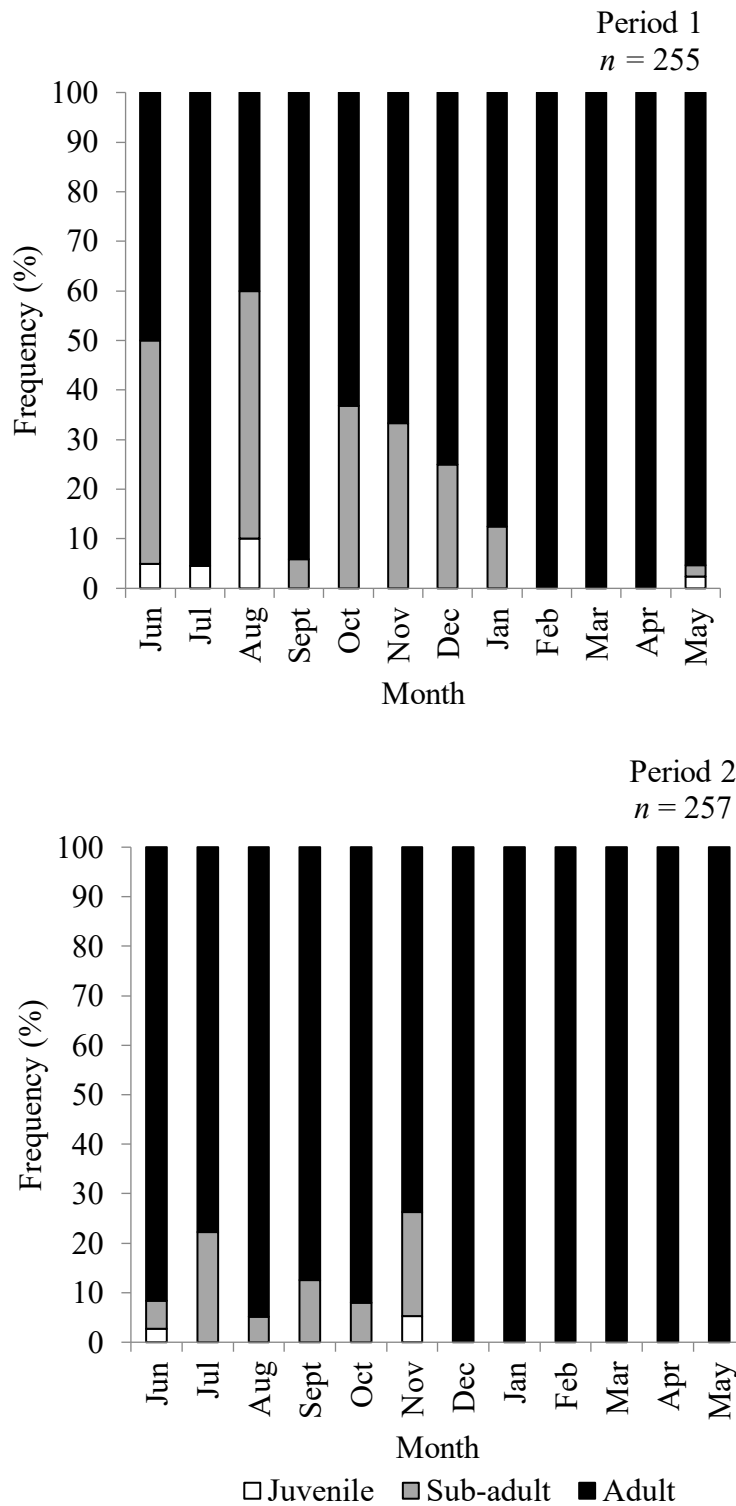
period 2, there was significant female bias in Autumn (M:F = 0.74:1,  $p = 0.02$ ) and Spring (M:F = 0.70:1,  $p = 0.04$ ) (Table 4.10).

**Table 4.10:** Seasonal sex ratios of mature *L. reynaudii* collected during the two sampling periods (Period 1= June 2008 – May 2009 and period 2= June 2014 – May 2015). Values in bold indicate significant differences.

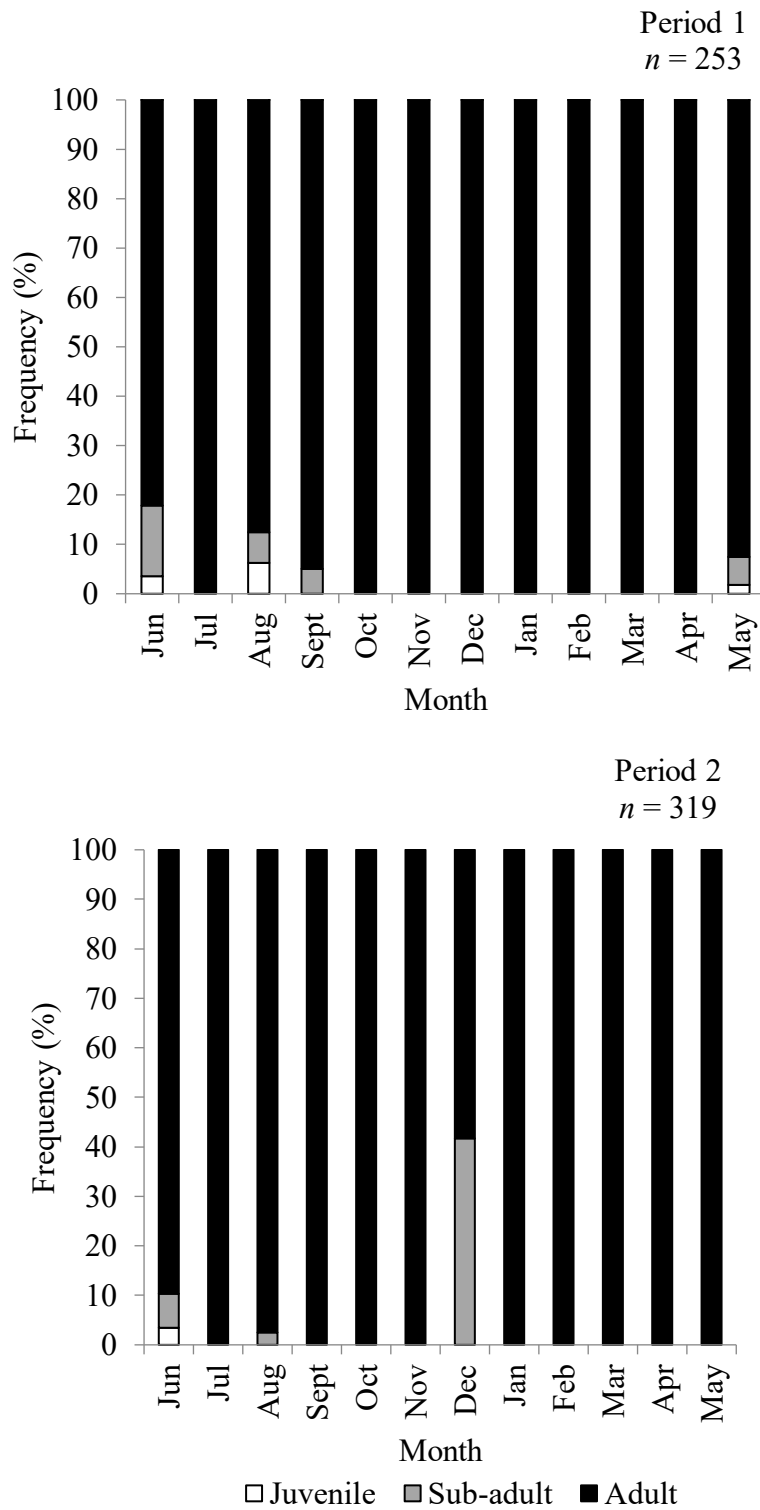
Sampling period	Season	Frequencies		Sex ratio	Chi-squared	p-value
		Male	Female	M:F		
1	Summer	48	51	0.94:1	0.09	0.76
	Autumn	110	64	1.72:1	12.16	< <b>0.001</b>
	Winter	38	71	0.54:1	9.99	< <b>0.01</b>
	Spring	39	58	0.67:1	3.72	0.05
2	Summer	26	41	0.63:1	3.36	0.07
	Autumn	59	80	0.74:1	5.76	<b>0.02</b>
	Winter	96	103	0.93:1	0.25	0.62
	Spring	58	83	0.70:1	4.43	<b>0.04</b>

### *Maturity*

Adult squid dominated the samples of both sexes during both sampling periods (Figure 4.13 & 4.14). A total of 85.9% and 93.0% percent of the males were adults during period 1 and 2, respectively. Similarly, 94.5% and 96.3% of the females were adults during period 1 and 2, respectively. In all cases; the months of February, March and April consisted solely of adult *L. reynaudii* (Figure 4.13 & 4.14). Male sub-adults were present throughout period 1 except during February, March and April whilst they only occurred during June to November in period 2 (Figure 4.14). Female subadults occurred from June to November in period 1 and June, August and December in period 2 (Figure 4.14). Juvenile males were observed from May through to August during period 1 and in period 2, only occurred during June and August. Juvenile females were only observed in June, August and May during period 1 (Figure 4.15). In contrast, during period 2 female juveniles were only observed in June (Figure 4.16).



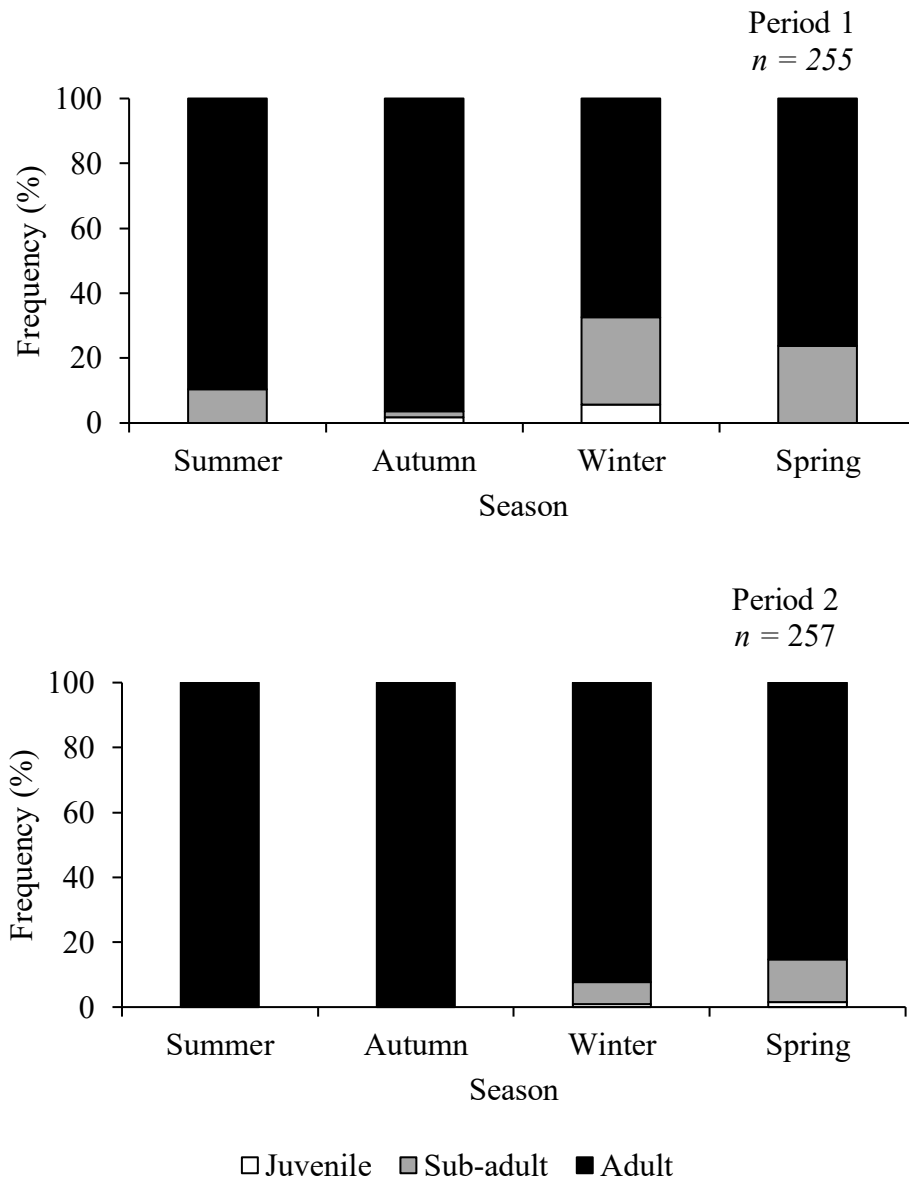
**Figure 4.13:** Monthly percentages of each life history stage of male *L. reynaudii* collected during the two sampling periods (Period 1= June 2008 – May 2009 and period 2 = June 2014 – May 2015).



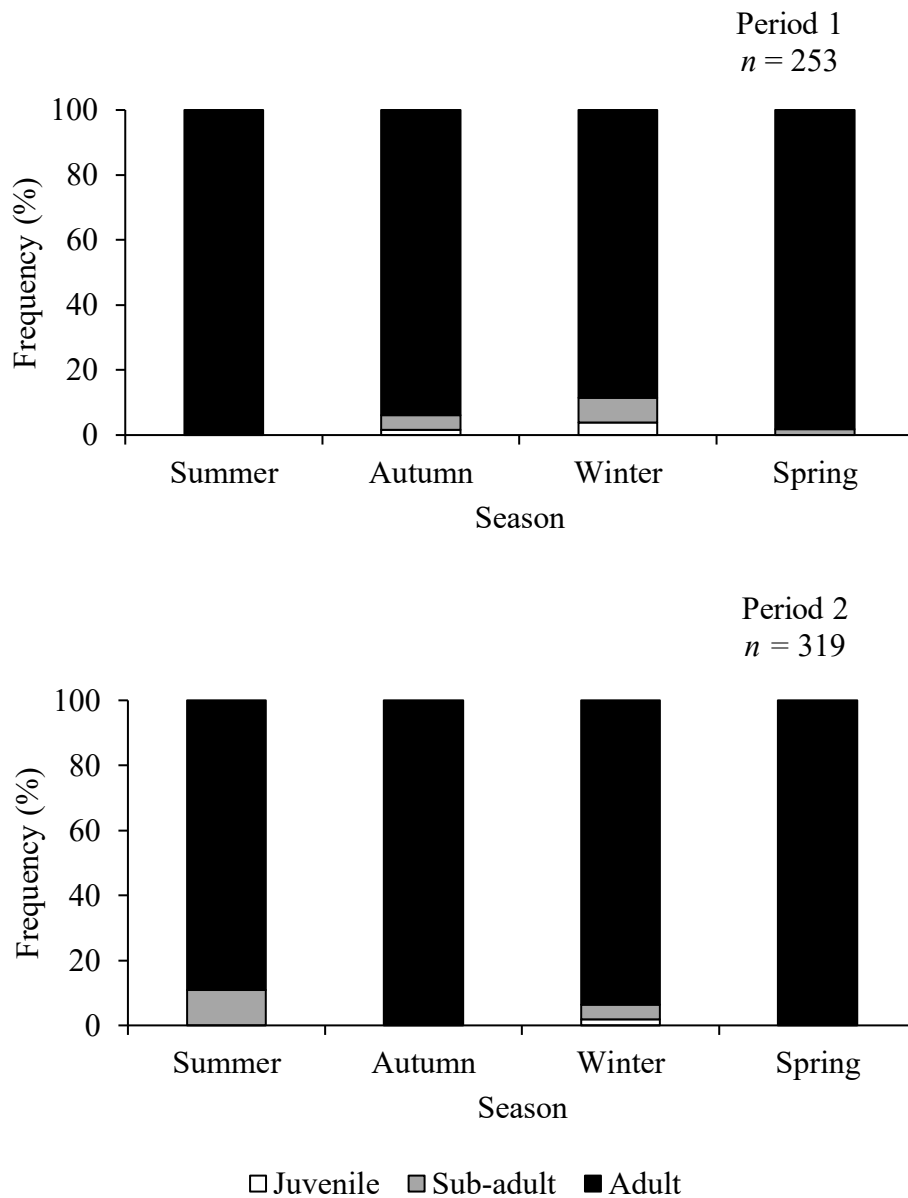
**Figure 4.14:** Monthly percentages of each life history stage of female *L. reynaudii* collected during the two sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015).

Seasonal maturation states highlight the presence of adult squid throughout the year. During the first sampling period, male juveniles were detected during winter months and females

during winter and autumn (Figure 4.15 & Figure 4.16). Whilst during the second sampling period juvenile males were detected during winter and spring and juvenile females only in winter (Figure 4.15 & Figure 4.16). The proportions at each life history stage throughout the seasons was seen to exhibit considerable similarities between female squid collected during the two sampling periods (Figure 4.17).



**Figure 4.15:** Seasonal percentages of each life history stage of male *L. reynaudii* collected during two sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015).



**Figure 4.16:** Seasonal percentages of each life history stage of female *L. reynaudii* collected during the two sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015).

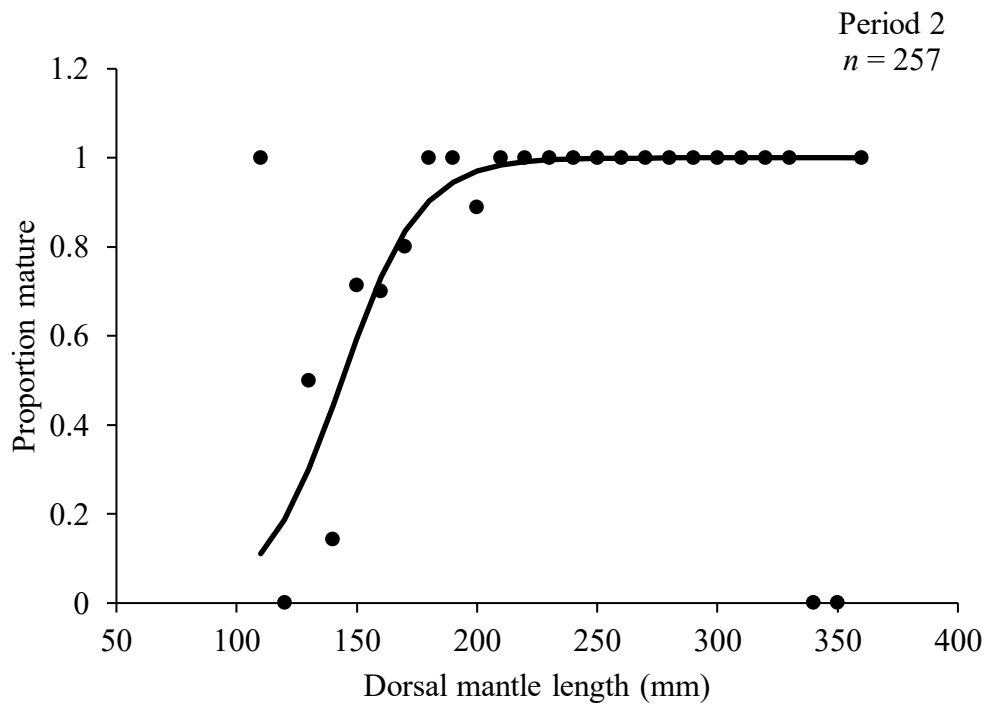
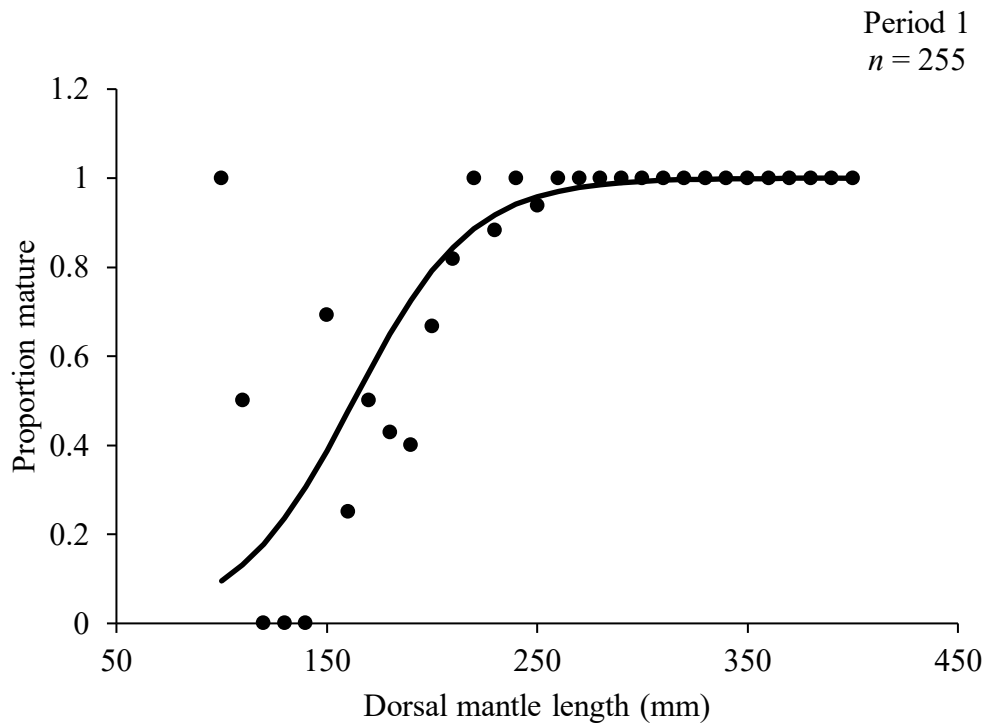
*Length at 50% maturity*

The 50% maturity estimate for males was 112.42 mm during period 1 and 143.72 mm during period 2 (Table 4.11 & Figure 4.17). There was a significant difference in the length-at-50% maturity ( $\lambda = 4.63$ ,  $p = 0.03$ ) between male squid collected during period 1 and 2. However no significant difference was observed in the steepness of the ogive,  $\delta$ , of male squid between the two sampling periods. The 50% maturity estimate for females was 127.17 mm during period 1 and 95.74 during period 2 (Figure 4.18). There was no significant differences

in length-at-50% maturity ( $\lambda = 2.21$ ,  $p = 0.14$ ), or the steepness of the ogive ( $\lambda = 0.64$ ,  $p = 0.42$ ) between the two periods for female *L. reynaudii*.

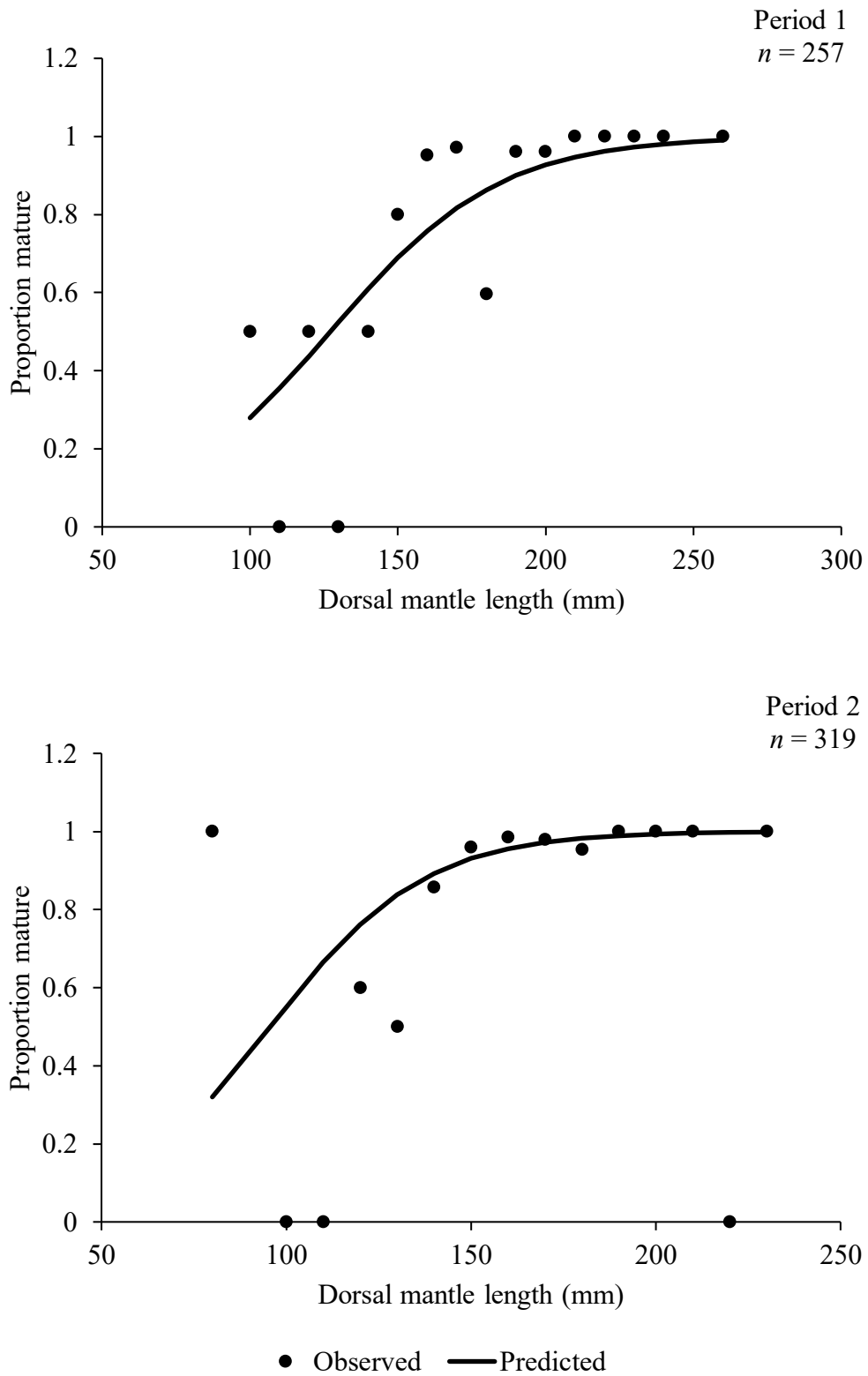
**Table 4.11:** Maturity parameters for male and female *L. reynaudii* collected during two sampling periods (Period 1 = June 2008 – May 2009 and period 2= June 2014 – May 2015).

	Period 1		Period 2	
	Males	Females	Males	Females
$L_{50}$	112.42	127.17	143.72	95.74
$\delta$	27.89	28.64	16.20	20.88



● Observed — Predicted

**Figure 4.17:** Logistic ogives for male *L. reynaudii* collected during two sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015).

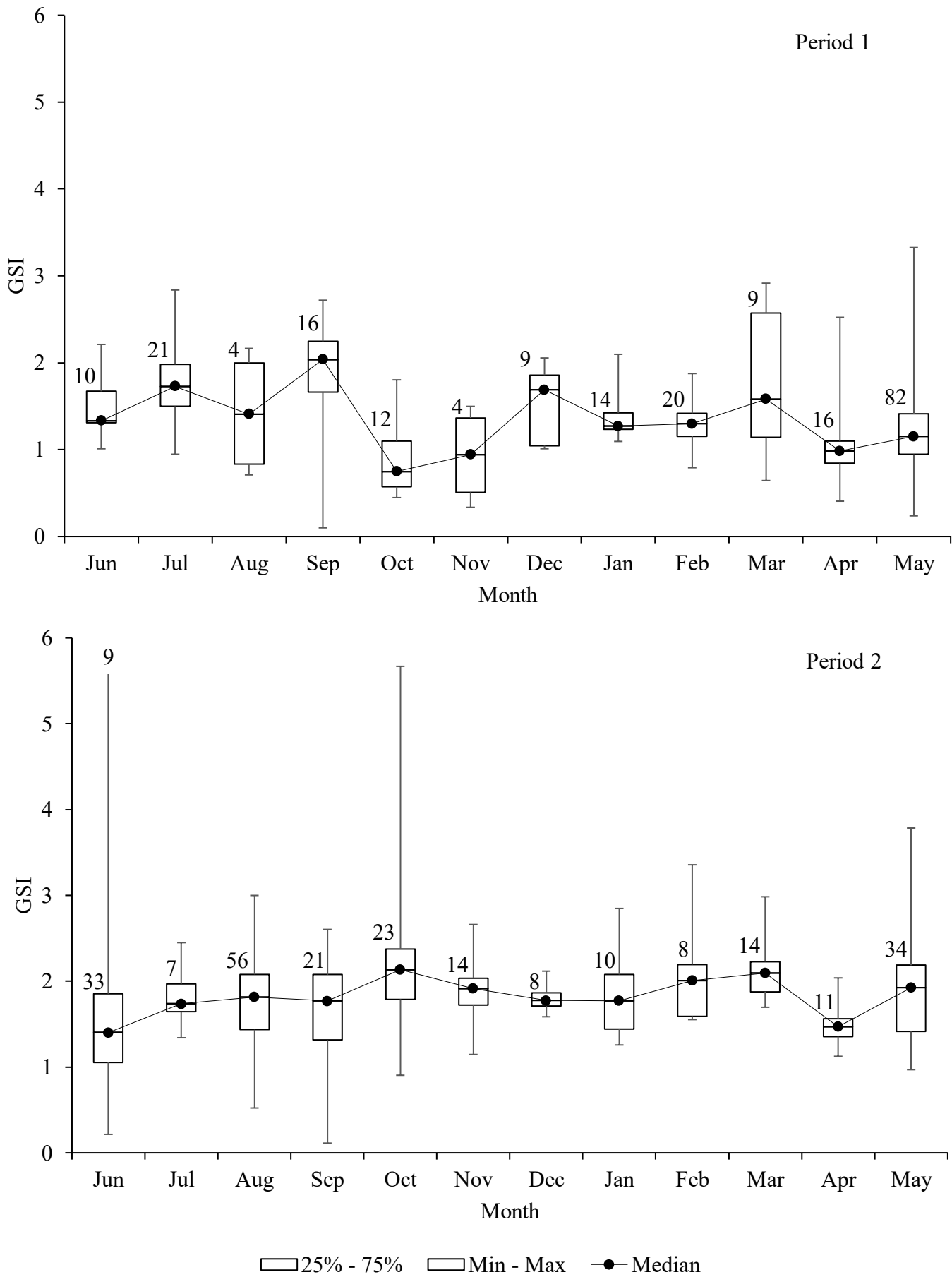


**Figure 4.18:** Logistic ogives for female *L. reynaudii* collected during two sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015).

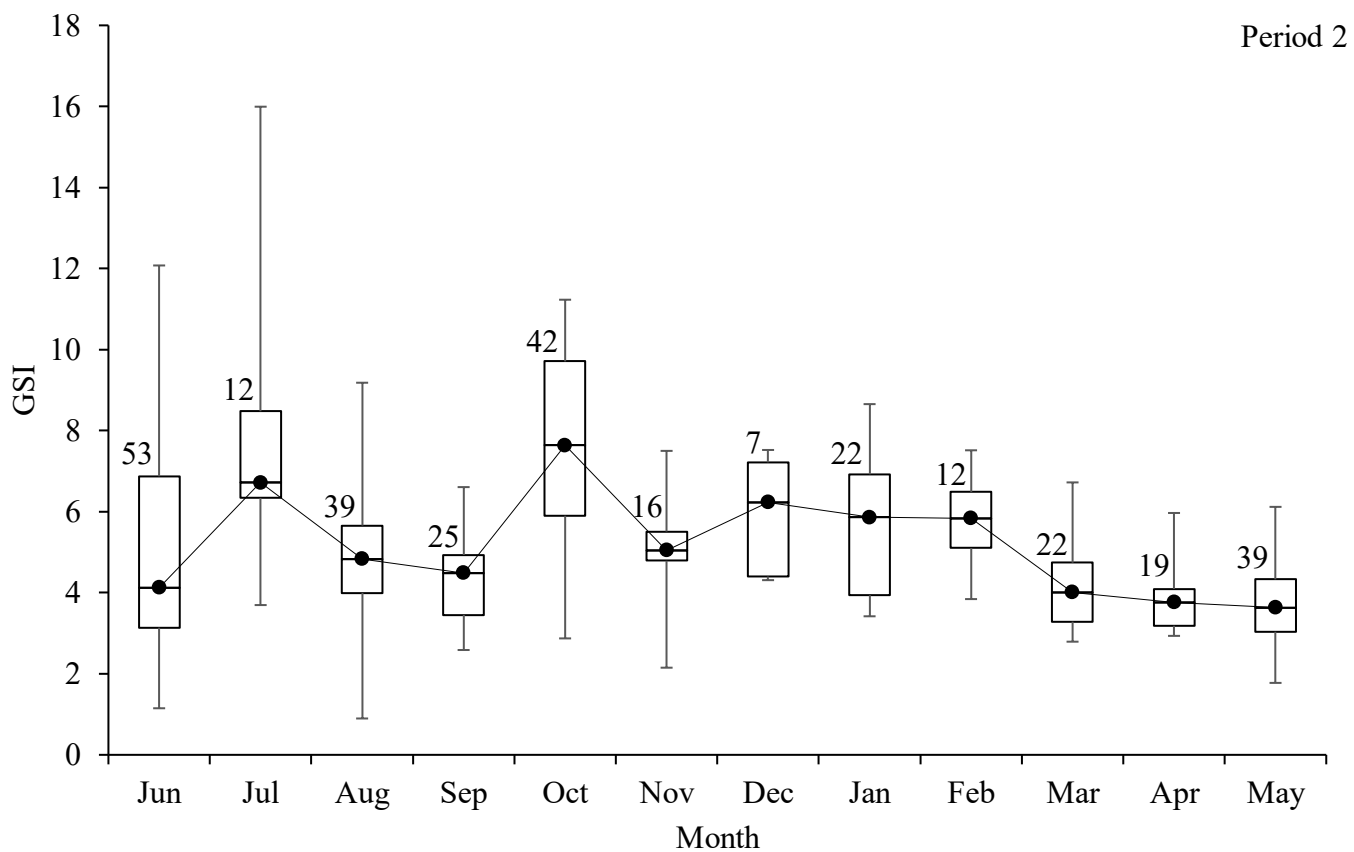
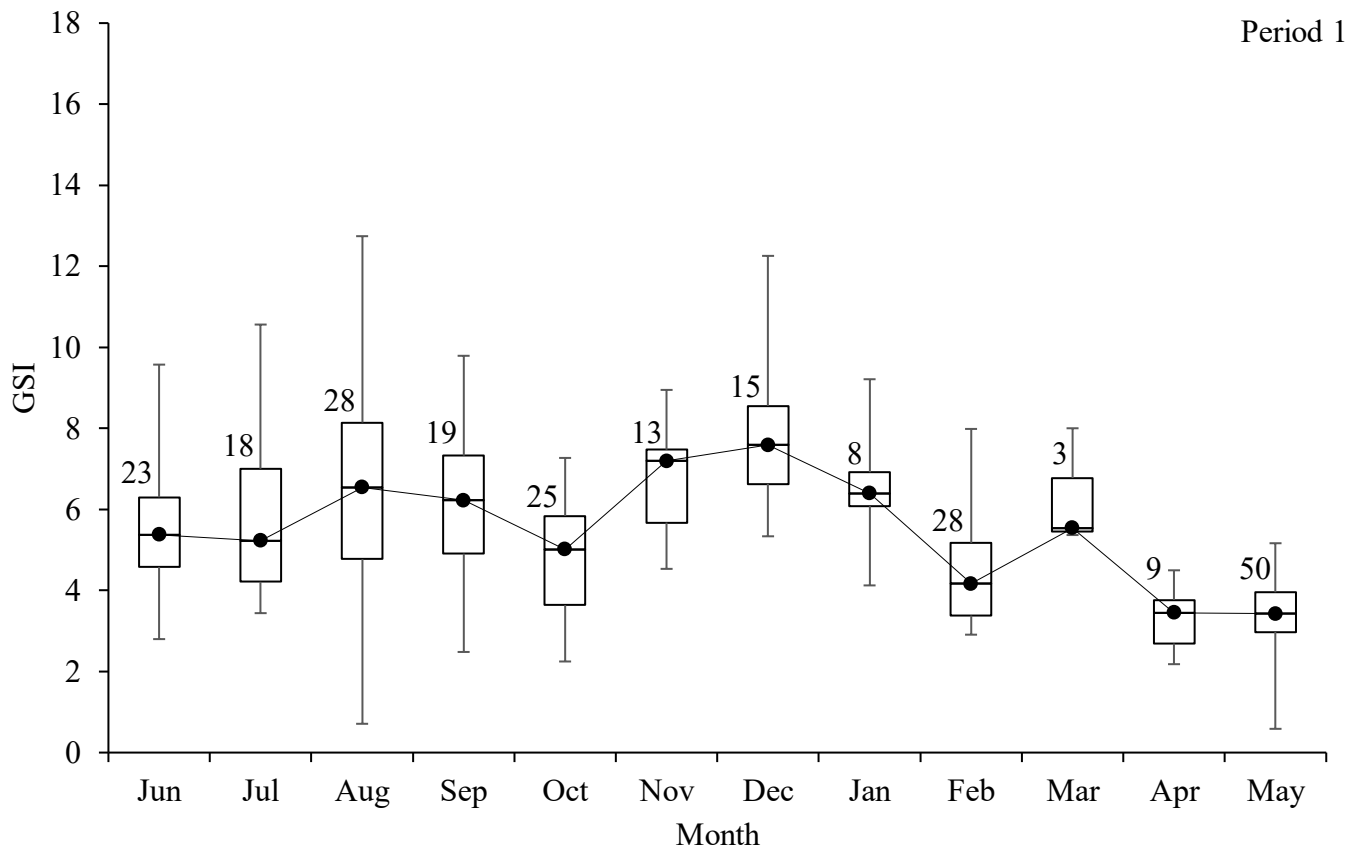
Females matured at a significantly greater length-at-maturity than males in Period 1 ( $\lambda = 7.67$ ,  $p < 0.01$ ), however no significant difference was observed in the steepness of the ogive ( $\lambda = 0.01$ ,  $p = 0.92$ ). During period 2, males matured at a significantly greater length-at-maturity than females ( $\lambda = 10.63$ ,  $p < 0.01$ ), however no significant difference was observed for  $\delta$  ( $\lambda = 0.51$ ,  $p = 0.48$ )

#### *Monthly and seasonal comparisons in Gonadosomatic indices*

GSI was observed to fluctuate throughout the year, during both periods. Similarities in monthly GSI trends were noted within sexes, between sampling periods in GSI peaks (Fig 4.19 & 4.20). During period 1, both male and female squid exhibited peaks in GSI during December and March, whilst during period 2 GSI peaked during October for both sexes. Males exhibited an all-time high in GSI during September in period 1 and October during period 2, whilst GSI was observed to be at the lowest in October during period 1. During period 2, GSI was observed to be at the lowest in male squid during June and April. Monthly GSI trends for females exhibited very little similarity in trends between periods, with GSI peaking in December during period 1 and October in period 2. However, GSI was generally observed to be the lowest during the months of April and May for female squid. Results of the Kruskal-Wallis tests for differences in monthly GSI of mature squid indicated that GSI was significantly different between months for both male and female squid during both sampling periods (Table 4.12). Furthermore, low number of samples during several months during each of the sampling periods may result in the observed trends. Seasonal comparisons are therefore more likely to exhibit reliable trends in GSI.



**Figure 4.19:** Monthly gonadosomatic indices (GSI) for mature male *L. reynaudii* collected during the two sampling periods (1 = June 2008 – May 2009 and 2 = June 2014 – May 2015).



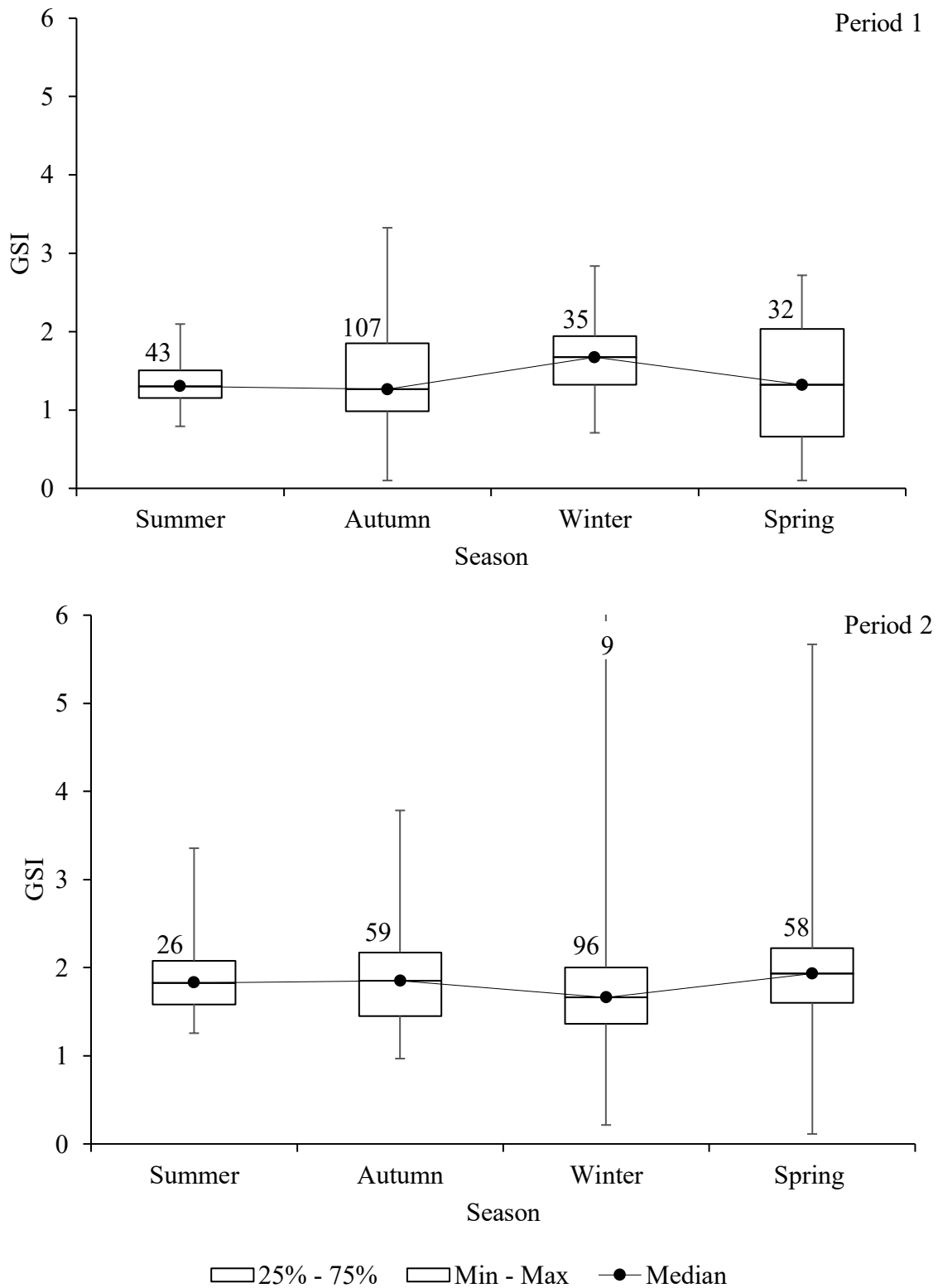
25% - 75%   
  Min - Max   
  Median

**Figure 4.20:** Monthly gonadosomatic indices (GSI) for mature female *L. reynaudii* collected during the two sampling periods (1 = June 2008 – May 2009 and 2 = June 2014 – May 2015).

**Table 4.12:** Results from the Kruskal-Wallis test for differences in GSI of mature *L. reynaudii* between months for two different sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015), where *n* refers to the number of individuals sampled, *H* is the Kruskal-Wallis test statistic and d.f. refers to the number of degrees of freedom. Values in bold indicate significant differences.

	Period 1		Period 2	
	Male	Female	Male	Female
<i>n</i>	223	241	239	307
<i>H</i>	53.84	113.18	40.93	102.35
d.f.	11	11	11	11
<i>P</i>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>

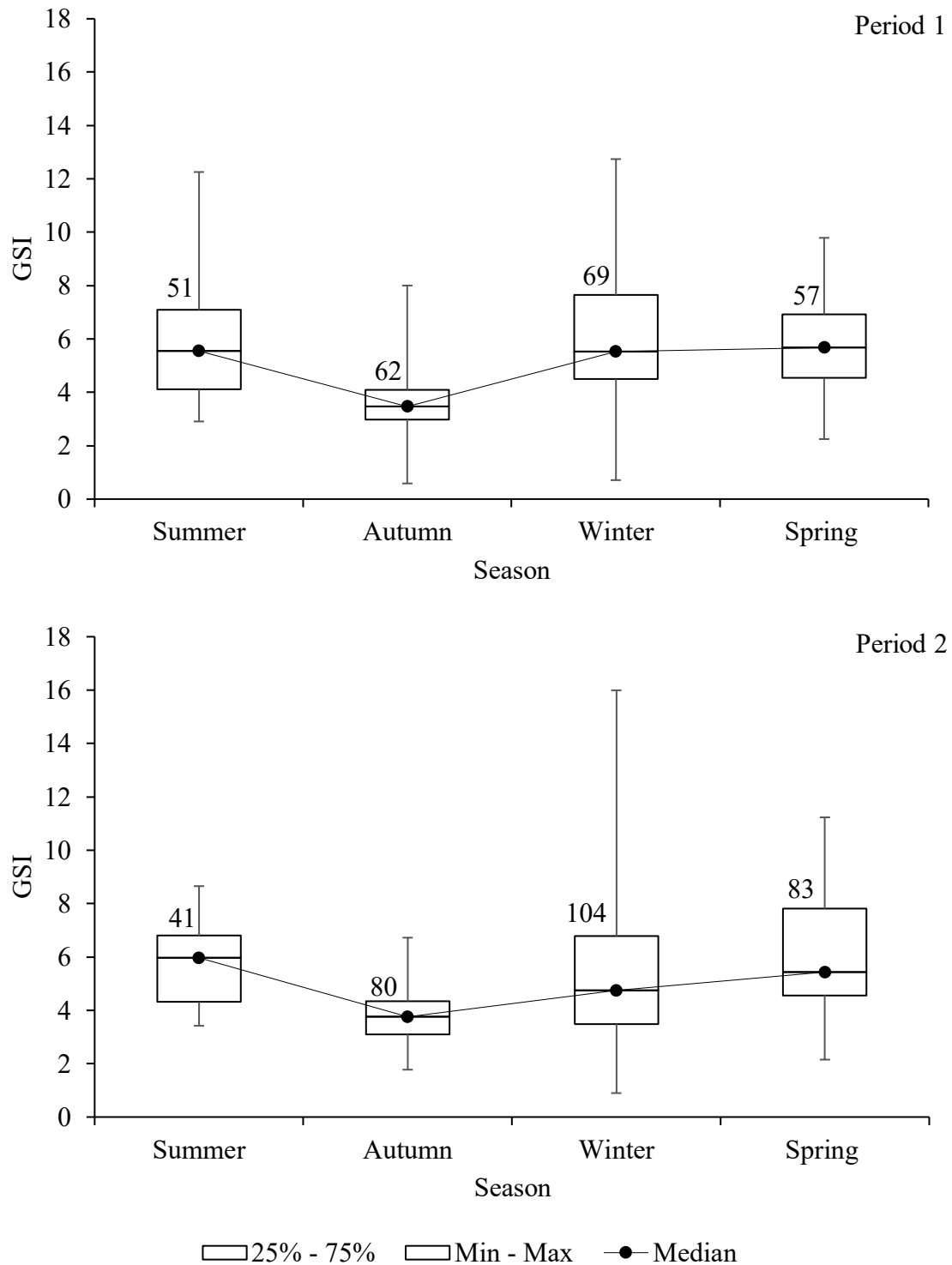
Seasonal comparisons of GSI for mature male *L. reynaudii* indicated very little difference in median GSI between spring, summer and autumn (Figure 4.21). However, during period 1 GSI peaked during winter, whilst it exhibited a slight decline during period 2. Whilst highly significant differences in GSI between season were noted during period 1 ( $H = 19.29$ ,  $p < 0.001$ ), slight significant differences in the seasonality of GSI was observed in period 2 ( $H = 9.42$ ,  $p = 0.02$ ) (Table 4.13). Variability in GSI was observed to be the highest in autumn during period 1, and winter during period 2.



**Figure 4.21:** Seasonal gonadosomatic indices (GSI) for mature male *L. reynaudii* collected during two sampling periods (1 = June 2008 – May 2009 and 2 = June 2014 – May 2015).

Seasonal comparisons of GSI for females revealed similar trends between the two sampling periods with a decline in GSI observed in autumn (Figure 4.22). Furthermore, trends in GSI variability were similar for female squid, during both periods, with winter exhibiting the

highest levels of variability. Results from the the Kruskal-Wallis indicate highly significant differences in GSI for female squid during period 1 ( $H = 69.46$ ,  $p < 0.001$ ) and period 2 ( $H = 58.56$ ,  $p < 0.001$ ) (Table 4.13).



**Figure 4.22:** Seasonal gonadosomatic indices (GSI) for mature female *L. reynaudii* collected during two sampling periods (1 = June 2008 – May 2009 and 2 = June 2014 – May 2015).

**Table 4.13:** Results from the Kruskal-Wallis test for differences in GSI of mature *L. reynaudii* between seasons for two different sampling periods (Period 1 = June 2008 – May 2009 and period 2 = June 2014 – May 2015), where *n* refers to the number of individuals sampled, *H* is the Kruskal-Wallis test statistic and d.f. refers to the number of degrees of freedom. Values in bold indicate significant differences.

	Period 1		Period 2	
	Male	Female	Male	Female
<i>n</i>	239	219	239	307
H	19.29	69.46	9.42	58.56
d.f.	3	3	3	3
<i>P</i>	<b>&lt;0.001</b>	<b>&lt; 0.001</b>	<b>0.02</b>	<b>&lt; 0.001</b>

#### *Location of spawning sites*

No spawning grounds or egg beds were detected by use of the echo sounder or by undergoing dives under artisanal fishers actively targeting squid. Of all the local fishers, whom were shown images of squid eggs, none of them had noted their presence within waters during the time that they had been fishing.

Furthermore, during the course of the study, two commercial squid vessels from the South African squid jig fleet undertook an exploratory trip, within Angolan waters, during June 2014. Communication with, Steve Benade, the skipper of FV Sea Lion confirmed that both vessels were manned with 24 crew and fished in Angolan waters for a total of 20 days within Angolan waters, during their trip. Further communication with S. Benade confirmed that fishing was restricted to south of Namibe, due to high water temperatures (25-26 degrees Celsius) further north. As per conversation with S. Benade, the two vessels worked in tandem conducting grid searches between waters of 15 and 60m of depth. Efforts were focused on the region between Baía dos Tigres and Namibe. Of the two vessels, FV Sea Lion had a total catch of 2.5 tons for the 20 days of fishing, of which all of the squid was caught within close proximity to shore, in 9-15m of water. Furthermore, no egg beds were detected on the echosounder or were collected on the jigs by the crew of either of the two vessels.

## Diet

Of the 572 individuals collected during period, a total of 92 (16.1%) (54 males, 38 females) individuals contained food within their stomachs. Stomach content analysis highlighted the importance of teleosts (66.3%) in the diet of *L. reynaudii* (Table 4.14).

**Table 4.14:** Percentage frequency of occurrence (% F) values for stomach content analysis of *L. reynaudii* ( $n = 92$ ) off southern Angola, during period 2.

Group	Species	%F
Teleosts	<i>Trachurus capensis</i>	14.1
	<i>Engraulis encrasicolus</i>	10.9
	<i>Sardinella aurita</i>	10.9
	<i>Merluccius</i> sp.	2.2
	Unidentified fish	28.3
Cephalopods	<i>Loligo reynaudii</i>	9.9
	<i>Octopus vulgaris</i>	3.3
	Unidentified cephalopod	3.3
Crustaceans	Caridea	1.1
	Unidentified crustacean	4.4
Unidentified		12.0

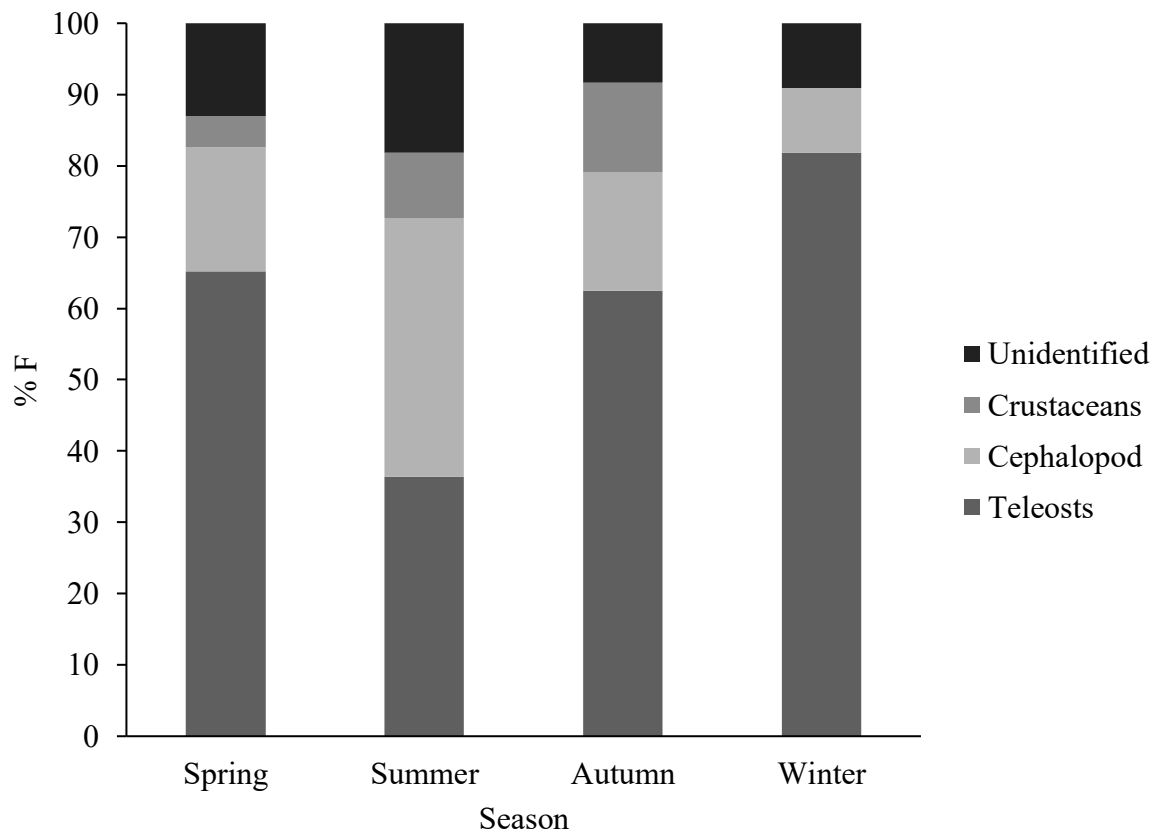
### Seasonal comparison of diet

On average, the feeding index was highest during autumn (1.05), followed by summer (0.97), winter (0.81) and spring (0.84). However, there was no significant differences in the feeding index between seasons ( $p > 0.05$ ). The results from the two-way ANOVA indicated significant differences ( $p < 0.05$ ) in the composition of the diet of *L. reynaudii* between seasons.

The stomach contents of *L. reynaudii* was dominated by teleosts in autumn, winter and spring (Table 4.15, Figure 4.23). In summer, teleosts contributed substantially less to the diet (36.4%), however cephalopods accounted for 36.4% of the diet. Cannibalism was highest in summer with *L. reynaudii* representing 27.3% of the stomach contents (Table 4.15, Figure 4.23). Crustaceans were absent in the stomach contents during the winter months (Table 4.15, Figure 4.23).

**Table 4.15:** Seasonal comparison of the percentage frequency of occurrence (% F) values for stomach content analysis of *L. reynaudii* ( $n = 92$ ) off southern Angola, during period 2.

Group	Species	%F			
		Summer	Autumn	Winter	Spring
Teleosts	<i>Trachurus capensis</i>	-	12.5	27.3	13.0
	<i>Engraulis encrasicolus</i>	-	20.8	12.1	4.4
	<i>Sardinella aurita</i>	-	8.3	12.1	8.7
	<i>Merluccius</i> sp.	-	0	3.0	4.4
	Unidentified fish	36.4	20.8	27.3	34.8
Cephalopods	<i>Loligo reynaudii</i>	27.3	4.2	6.1	13.0
	<i>Octopus vulgaris</i>	-	8.3	3.0	-
	Unidentified cephalopod	9.1	4.2	-	4.4
Crustaceans	Caridea	-	4.2	-	-
	Unidentified crustacean	9.1	8.3	-	4.4
Unidentified		18.2	8.3	9.1	13.0



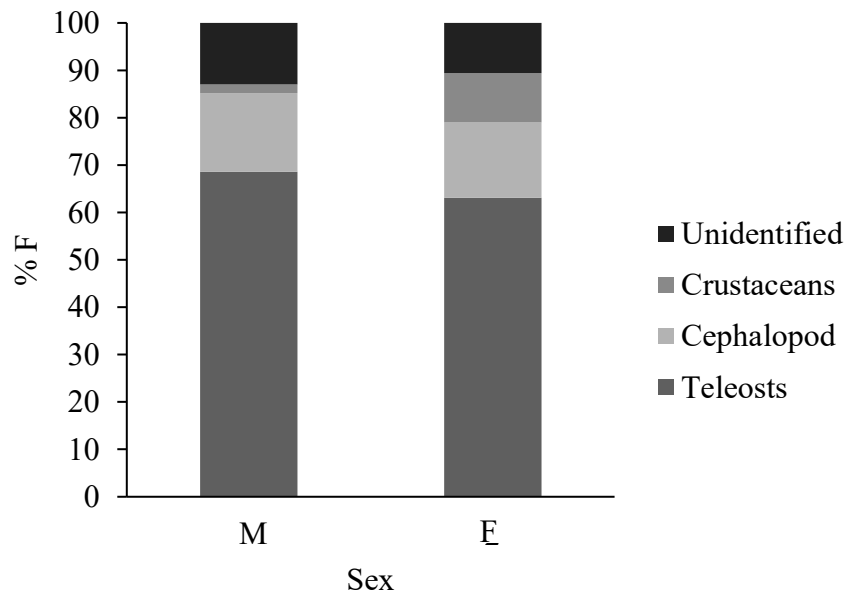
**Figure 4.23:** Seasonal percentage frequency of occurrence (% F) of broad dietary categories values for stomach content analysis of *L. reynaudii* ( $n = 92$ ) off southern Angola, during period 2.

*Intersexual comparison of diet*

There were no significant difference in the feeding index of males (0.92) and female (0.88) squid. Whilst the contribution of crustaceans was higher in female squid (10.5%) when compared to that of males (1.9%), overall no significant differences in the dietary composition of *L. reynaudii* was observed between sexes ( $p > 0.05$ ) (Table 4.16, Figure 4.24).

**Table 4.16:** Intersexual comparison of the percentage frequency of occurrence (% F) values for stomach content analysis of *L. reynaudii* ( $n= 92$ ) off southern Angola, during period 2.

Group	Species	% F	
		Male	Female
Teleosts	<i>Trachurus capensis</i>	18.51	7.89
	<i>Engraulis encrasicolus</i>	7.41	15.79
	<i>Sardinella aurita</i>	5.56	18.42
	<i>Merluccius</i> sp.	3.7	-
	Unidentified fish	33.33	21.05
Cephalopods	<i>Loligo reynaudii</i>	9.26	10.53
	<i>Octopus vulgaris</i>	3.70	2.63
	Unidentified cephalopod	3.70	2.63
Crustaceans	Caridea	-	2.63
	Unidentified crustacean	1.85	7.89
Unidentified		12.96	10.53



**Figure 4.24:** Comparison of the diet of male and female *L. reynaudii* ( $n = 92$ ) off southern Angola, during period 2.

### Discussion

The findings of this study highlights the variability in population characteristics of the species in southern Angola. Interannual variation is common within the *Loliginidae* and has been observed within the South African population of *L. reynaudii* (Roberts 2005, Sauer et al. 2013, Jereb et al. 2015). These high levels of temporal variability are thought to be highly associated with the variable life history traits of the species and the influence of their surrounding environmental conditions (Roberts 2005, Sauer et al. 2013, Jereb et al. 2015). Due to their relatively short and adaptive life history traits, *L. reynaudii* along with many other cephalopod species, are often considered as “ecological opportunists”, taking advantage of favorable conditions when they are presented (Sauer et al. 2013, Arkhipkin et al. 2015). However, it is important to note that these same biological traits may put them at high-risk during periods of unfavorable conditions which are often observed to have major effects on the abundance and recruitment of a population (Sauer et al. 2013, Arkhipkin et al. 2015, Glazer and Butterworth 2016, Burg 2019). This is concerning as interannual fluctuations can have major socio-economic consequences, as highlighted within the commercial squid jig fishery off the coast of South Africa.

**Table 4.17:** Life history characteristics of *Loligo reynaudii*, *Loligo vulgaris* and *Loligo forbesii*.

Species (Common name)	Main areas of exploitation	Life span	Max size (ML, weight)	Size at maturity (mm)	Spawning season	Habitat	Ref
<i>L. reynaudii</i> (current study)	Southern Angola		M: 408.00 mm, 758.0 g F: 260.00 mm, 374.1 g	M: 112.42 mm (1), 143.72 mm (2) F: 127.17 mm (1), 95.74 mm (2)	Spawning activity not documented.	Fishing activity predominantly occurred within waters less than 20m deep.	
<i>L. reynaudii</i> (Cape Hope squid)	South Africa		400mm, >1 kg	East: M = 132.6 mm, F = 145.4 mm Central: M = 182.3 mm F = 168.7 mm West: M = 217.5mm, F = 181.1mm (Varies according geographic location and time of year)	Spawns throughout year, two major peaks per year (Summer & winter)	Mainly associated with shallow waters and the continental shelf, offshore distribution up to 350m.	1, 4, 8, 10, 11
<i>L. vulgaris</i> (European squid)	Northeast Atlantic, Mediterrane an	up to 15 months	M: 640 mm F: 485 mm	M: 80 mm F: 119 mm (High variability depending on geographic location)	Spawns throughout year, two major peaks (varies across distribution)	Mainly associated with shallow waters and the continental shelf, found up to depths of 500m.	3, 4, 5, 6, 9

Species (Common name)	Main areas of exploitation	Life span	Max size (ML, weight)	Size at maturity (mm)	Spawning season	Habitat	Ref
<i>L. forbesii</i> ( <i>Veined squid</i> )	Northeast Atlantic	15 - 16 months	M: 937 mm, 8.3 kg F: 462 mm, 2,2 kg. Smaller sizes (200 – 300 mm) common in Mediterranean and NE Atlantic	M: 150 mm -240 mm F: 170 mm – 200 mm Varies across distribution	Timing of peak spawning varies across distribution	Continental shelf in temperate regions and in deeper waters within subtropical areas. Recorded to depths greater than 1000m in Azores.	2, 3, 4, 5, 6, 7

1. Augustyn et al. 1992; 2. Boyle et al. 1995; 3. Guerra & Rocha 1994; 4. Jereb & Roper 2010; 5. Jereb et al. 2015; 6. Hastie et al. 2009, 7. Martins 1982; 8. Olyott et al. 2006; 9. Perales Raya 2001; 10. Sauer 1991; 11. Sauer et al. 2013

Male squid, in southern Angola, were found to be much larger, as well as represent a much broader range in length and weight, than their female counterparts. This is not unusual as male loliginids are generally seen to obtain larger sizes than females of the same species (Table 4.17). Based on these findings, it therefore appears unlikely that the variability in male length is a result of multiple cohorts and more likely to be the result of the alternative reproductive tactics and quicker growth rates characteristics of male *L. reynaudii*. However, females tended to be heavier than males of equivalent lengths and this was a consequence of the higher slope in the length weight relationship. This is typical for the species with Augustyn (1990) and Lipiński (1994) finding similar trends for the species in South Africa. Furthermore, comparisons between reported slope parameters for the species (Augustyn 1990, Lipiński 1994) and those from the current study may be indicative of a decrease in weight with any given size as one moves from the east to the west of the distribution of *L. reynaudii*, with Angolan squid exhibiting similar length-weight relationships to squid distributed off the western region of the Agulhas Bank in comparison to those on the central and eastern portion of the Agulhas Bank.

Size-based sexual dimorphism is common in the *Loliginidae* (Coelho et al. 1994, Raya et al. 1999, Jones et al. 2019) and has been observed in *L. reynaudii* from South Africa (Augustyn 1990, Olyott et al. 2006) (Table 4.18). The high variation in the size composition of male squid, particularly in adults can either be attributed to the complex mating behavior of the species or perhaps the result of the presence of multiple cohorts of male squid, or a combination of both. As within most squid species, larger males generally have a competitive advantage for mating opportunities (Hanlon 1998, Hanlon et al. 2002). This may explain the significantly larger maximum length and weight that was exhibited by male squid during the present study. However, within the species, smaller males, particularly those of a similar size to females, are known to make use of sneaking behavior to increase their likelihood of reproductive success (Hanlon & Messenger 1996, Hanlon et al. 2002). Alternatively, the larger variation in size range observed for male sub-adult and adult squid, may be attributed to differential growth patterns as a result of different environmental conditions. This trend of potential population overlap, which was observed during both sampling periods, was however only observed for male squid. This is not unlike the South African population of *L. reynaudii* and may be describe a higher longevity in males, which would allow them to participate in more than one spawning season (Augustyn 1990, O' Dor 1998). However,

since Lipiński et al. (2020) estimated the mean age of male and female *L. reynaudii* to be 323 days and 316 days, respectively, this is unlikely.

From the current study it is apparent that the population of squid off southern Angola is dominated by mature, adult *L. reynaudii*. The presence of adult squid throughout the year was initially considered to be indicative of year-round spawning, as has been found for *L. reynaudii* off the coast of South Africa (Olyott et al. 2006). However, it is important to highlight that the presence of mature or spent squid was not determined due to the simplified maturity scale. It is important to take into consideration, that all attempts to locate spawning grounds or *L. reynaudii* eggs during the current study were unsuccessful.

The feasibility of locating egg beds with the use of echo sounding technologies has been investigated for *L. reynaudii* within the waters of South Africa and has been demonstrated to be a highly effective method to locate the presence of eggs on the sea floor (Sauer et al. 1993, Lipiński et al. 1998, Sauer et al. 2013). The importance of these technologies is highlighted by the reliance of the commercial squid jig fishery of South Africa on echosounding technology to locate squid aggregated during spawning events to optimize catches. Furthermore, eggs are frequently retrieved during jigging operations in South African waters. Ultimately, the inability to locate spawning beds or eggs during the current study coupled with the lack of eggs found by local artisanal vessels as well as the two industrial vessels investigating the potential of the local squid stock, may suggest that i) spawning is taking place further offshore along the Angolan coastline, or further south in Namibian waters and has not been detected, ii) *L. reynaudii* make use of the rich waters of Angola as a feeding ground, and subsequently return to more suitable spawning areas during warmer summer months, iii) squid distributed off the coast of southern Angola is a small stock of migrants, which do not spawn due to unsuitable environmental conditions. Whilst, industrial fishing does not occur within the identified artisanal squid fishing grounds due to the four nautical mile exclusion, further efforts to detect the presence of eggs in the region, and understand the reproductive behavior of *L. reynaudii*, may be undertaken through determining whether egg recovery occurs within the demersal trawl fishery, operating offshore of the identified fishing areas.

Adult squid were found to dominate monthly samples, throughout the study, and were present throughout the year. Whilst this may support the hypothesis that spawning occurs outside of

the artisanal fishing grounds, it is possible that juveniles and sub-adults were poorly represented as a result of gear selectivity bias. Lipiński (1994) suggested that jigging can result in a mis-representation of a population due to the dynamics of squid aggregations of *L. reynaudii*.

Studies by Tinbergen and Verwey (1945) indicated that catches of *Loligo vulgaris* were often biased towards a particular sex. During both sampling periods, female biased sex ratios were predominant throughout the year, with male biased sex ratios only occurring during a limited number of months. The female biased sex ratio is therefore either a true representation of the population of squid occurring off southern Angola or a mis-representation due to a sampling bias that can be attributed to the complex and dynamic nature of squid aggregations.

Koronkiewicz (1995) attributed female biased ratios in *I. argentinus* jig catches to the more active nature of female squid during feeding activity.

In South Africa, male-biased sex ratios have been more common for *L. reynaudii* (Augustyn 1994, Lipiński 1994, Hanlon 1998, Hanlon et al. 2002, Olyott et al. 2006) and these have generally been associated with peak spawning periods and spawning aggregations (Hanlon et al. 2002, Olyott et al. 2006, Augustyn 1989, Augustyn 1991). However, female-biased sex ratios have been observed predominantly on offshore spawning grounds and these were attributed to the higher abundance of males in the inshore spawning aggregations (Augustyn 1990). The male-biased ratios observed for limited months of the year during both sampling periods were ubiquitous in both periods however they did not coincide directly with observed GSI trends. This may suggest that unlike *L. reynaudii* off South Africa (Sauer et al. 1992, Lipiński 1994, Olyott et al. 2006) where aggressive males dominate the catch in spawning aggregations (Lipiński 1994), the aggregation and capture of squid off southern Angola may not be associated with spawning. However, jigging may also be selective for sex and the use of this gear may therefore influence the estimates of sex ratio and maturity schedules of squid (Lipiński 1994, Koronkiewicz 1995, Rodhouse et al. 2014). A lack of smaller squid within sampling efforts is a common issue within squid fisheries, particularly within jig fisheries (Lipiński 1994, Martins & Perez 2007). This is of concern as it undermines efforts to determine recruitment to the fishery and subsequently inhibits the ability to forecast stock recruitment.

There was a high variability (between sexes and sampling periods) in monthly GSI in the current study. Lipiński & Underhill (1995) note that the interpretation of squid dynamics, based on GSI, should be done with caution. In this study, squid was more readily available from May through to October in both sampling periods and the higher abundance during this time was supported by information collected during fisher interviews.

Variability in GSI may highlight changes in the reproductive potential of these species throughout the different seasons. With the end of spring and the beginning of summer, squid became apparently less available, however the reproductive potential of the squid within the region remained relatively stable. The observed trends in declined availability, may therefore be indicative of mature adults undergoing a late migration to more suitable spawning grounds, during late spring and summer, this would coincide with the peak spawning of *L. reynaudii* off the coast of South Africa (Roberts et al. 2012). Spawning and feeding migrations have been documented within a number of loliginid species (Mangold 1987). More specifically, *L. reynaudii* have been documented to have very preferential conditions for spawning and are known to undergo extensive spawning migrations to optimize reproductive success (Sauer et al. 1992, Sauer et al. 2000).

Based on the findings of this study it is possible that adult squid in southern Angola may undergo a northerly feeding migration, to the southern coast of Angola with the strengthening of the Benguela current. The dietary composition of the sampled squid, during the second period, highlighted the importance of teleosts off the Angolan coast. . Studies conducted by Augustyn (1989) indicated an ontogenetic shift in the dietary requirements of *L. reynaudii*, with larger squid (over 150mm) showing a preference for fish whilst smaller, juvenile squid were considered to be more dependent on crustaceans (Lipiński 1987). It is therefore possible that the prevalence of large, adult squid off the coast of Angola, particularly during austral winter which typically coincided with the lowest reproductive potential, may be a result of a high abundance of suitable prey within the region. Loliginid squid are known to undergo spawning and feeding migrations, however the temporal and spatial nature of these migrations remains relatively unknown for *L. reynaudii* (Sauer et al. 2013). Sauer et al. (2013) highlighted that within a single year it is possible for an individual to remain within a relatively small area or undergo migrations of up to 1000km, whilst Olyott et al. (2006) indicated that squid may travel distances of up to 2000km.

*Trachurus capensis* and *E. encrasicolus* which were the dominant prey items in this study during autumn and winter months are both abundant within the region and supported by cold nutrient rich waters of the Benguela Current. The seasonal upwelling that occurs during the austral winter along the coast of Angola, during which productivity is considered to be highest within inshore waters (Ostrowski et al. 2009, Tchikalanga et al. 2018) most likely further supports these prey items through the associated increase in primary productivity.

Regardless of the spawning location, the findings of this study suggest that the presence of *L. reynaudii* along the southern coast of Angola, may be attributed to the abundance of suitable prey within the region. Studies within Loliginid squid, and more specifically *L. reynaudii* within South African waters, have highlighted the complex nature of the interactions of these species and their environment. The dynamic nature of squid populations and the complex interactions between individuals and their environment over a relatively short life period highlights the importance of research for sustainable management practices. Furthermore, understanding the migratory patterns of the population of squid off southern Angola has major implications for the artisanal jig fishery within the region, whom are heavily on the resource as a source of livelihood.

Spatial and temporal variability in the biomass of squid as a result of foraging displacement has been observed in a number of loliginid species (Martins et al. 2004, Arkhipkin et al. 2015). For example, catches of *D. plei* are known to exhibit high levels of seasonality and spatio-temporal variability. Increased catches by artisanal jiggers in coastal bays, was attributed to the onset of upwelling events which consequently resulted in the onshore aggregation of species of Clupeidae, on which *D. plei* is known to prey (Martins et al. 2004, Arkhipkin et al. 2015). The aggregation of *L. reynaudii* and subsequent increased availability of squid to the artisanal fishers therefore may be modulated by upwelling events occurring along the coast of southern Angola. A better understanding of these oceanographic processes and their subsequent effects may be critical in developing management strategies, particularly for coastal communities heavily dependent on the resource.

Spawning activity within South African *L. reynaudii* occurs within discrete geographical locations and is considered to be the result of favorable environmental conditions for the development of eggs as well as the survival of *L. reynaudii* hatchlings (Augustyn 1991, Roberts 2005, Roberts and Sauer 1994). It is important to note that despite the presence of

mature adult squid on the West Coast of South Africa, no trace of egg beds or spawning has been detected within this region, as was observed for squid in southern Angola (Roberts and Sauer 1994, Roberts et al. 2012). Studies by Roberts (2005), indicated that temperature and bottom dissolved oxygen levels were consistently lower on the West Coast than those within the preferred spawning environment on the Agulhas Bank. Furthermore, environmental conditions on the eastern extremities of spawning distribution are characterized by bottom temperatures which are too high for hatching (Roberts 2005). Understanding the influence of the environmental conditions and oceanographic features, in the complex ABFZ is critical in understanding the reproductive behavior and observed lack of spawning for *L. reynaudii* in Angolan waters.

Whilst inshore spawning is a common characteristic of loliginids, with spawning typically occurring in waters less than 60m deep, deepwater spawning has been documented in a number of species, including *L. pealei*, *L. forbesi* and *L. reynaudii* (Roberts et al. 2012). Studies by Oosthuizen & Roberts (2009) triggered by the location of deep-water spawning sites, revealed that despite delayed development, low rates of egg mortality were documented for eggs exposed to temperatures of 8.2 to 13.7 °C, at depths of 112-116m for periods of 6-8 weeks. However, these areas of deep-water spawning are typically thought to be associated with downwelling regimes within the area, resulting in temporary intrusions of warm water, and subsequently water temperatures greater than 10 °C (Oosthuizen & Roberts 2009). The possibility of offshore spawning activity for the southern Angolan squid cannot be excluded and requires further investigation in order to gain an understanding of recruitment in the region.

The results from the current study indicate that the southern Angolan subpopulation is similar to the West Coast subpopulation with regards to demographics and reproductive characteristics. It is therefore possible that the population in southern Angola is an extension of the West Coast subpopulation of *L. reynaudii*, albeit an entirely separate stock (van der Vyver et al. 2014). This hypothesis is further supported by the lack of observed genetic differentiation throughout the known distribution of *L. reynaudii* (Shaw et al. 2010). Within any species, the range margins are generally associated with less favorable conditions and subsequently a lower biomass of any particular species, whilst conditions near the center of the distribution are generally associated with the most favorable conditions and subsequently higher levels of biomass (Mott 2010). Physiological stresses associated with peripheral

populations are known to result in differences in the morphology and life history characteristics when compared to individuals within the core of the distribution (Mott 2010). Furthermore, as highlighted by *L. reynaudii* off the coast of South Africa, an environmental niche for spawning is evident within the species and as such results in large aggregations of squid within the region. In contrast, the lack of evidence of spawning for the southern Angolan subpopulation may be a consequence of smaller, isolated spawning events that may occur along the distributional margin of this species. However, the possibility of spawning aggregations occurring further south and in the waters of Namibia, or offshore, cannot be excluded. Whilst the presence of *L. reynaudii* off the coast of Namibia is considered to be scarce, understanding the abundance and biology of the species along the coast is critical.

Studies of *Loliginids* around the globe have highlighted the variability of life history traits of many commercially important species as well as the complex nature of the interaction between these characteristics, their environment and the fisheries dependent upon them (Table 4.18) (Augustyn et al. 1992, Moreno et al. 2002, Moreno et al. 2005, Olyott et al. 2006, Rodhouse et al. 2014, van der Vyver et al. 2014, Arkhipkin et al. 2015, Sauer et al. 2019). As outlined in Chapter 1, research plays a fundamental role in ensuring that appropriate, species specific management strategies are developed in order to ensure sustainable harvesting of a fishery, particularly when the fishery is dependent upon a species characterized by a short lifecycle, high interannual variability, and as such a lack of a buffer to the effects of overfishing and poor environmental conditions (Augustyn et al. 1992, Lipiński 1998, Olyott et al. 2006, Rodhouse et al. 2014). More specifically, despite *L. reynaudii* distributed off the coast of South Africa being extensively studied, high variability has been noted with regards to the structure of spawning populations, the biological attributes of squid throughout the distribution on the South African coast and more specifically on the spawning grounds, as well as the positioning of preferred spawning grounds (Olyott et al. 2006, Sauer et al. 2013, Arkhipkin et al 2015, Lipiński et al. 2016). The challenge of stock identification, variability within and between the stocks as well as the mechanisms driving these changes are continuously highlighted throughout the literature (Augustyn & Grant 1988, Augustyn et al. 1992, Olyott et al. 2006, Shaw et al. 2010, Sauer et al. 2013, Van der Vyver et al. 2015). The current study highlights the uncertainty regarding whether the southern Angolan stock has the biomass to continue to provide for these communities and whether there is room for expansion within the fishery, particularly as the method of recruitment and lifecycle of the Angolan stock remains relatively unknown.

Finally, whilst the lifecycle of squid distributed off the coast of southern Angola remains relatively unknown, results from the current study indicate that it is likely that the stock represents migrants which do not spawn within the region but make use of the abundant food resources. However, the lack of artisanal jig fishing activity south of Tombua due to the lack of infrastructure beyond the city, the lack of access to Baía dos Tigres and the preclusion of commercial vessels within 4nm of the coast precludes the exploration of this subpopulation further. As highlighted within Chapter 3 majority of cephalopod fishing activity occurs within close proximity to shore or in sheltered bays, the lack of access to areas south of Tombua may therefore be providing a refuge for spawning individuals on this isolated stretch of coast. Future studies should aim to understand the shift in the biomass and distribution of squid within the region.

## CHAPTER 5

# ASPECTS OF THE BIOLOGY AND DEMOGRAPHY OF THE PATCHWORK, CUTTLEFISH *SEPIA* *VERMICULATA* (QUOY & GAIMARD 1832), OFF SOUTHERN ANGOLA

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*Sepia vermiculata* (Quoy & Gaimard 1832), the patchwork cuttlefish, falls within the *Sepia officinalis* species complex which is comprised of two other species; *Sepia officinalis* (Linnaeus 1758) and *Sepia hierredda* (Rang 1837) (Guerra et al. 2001). All three species of the *S. officinalis* complex are distributed off the coast of West Africa (Guerra et al. 2001). The common cuttlefish, *S. officinalis*, is the most extensively studied of the species complex and is distributed in the eastern Atlantic and Mediterranean Sea (Beclari 1999, Reid et al. 2005). The distribution of *S. officinalis* off the coast of Africa is thought to extend as far south as 16°N, on the border of Mauritania and Senegal, where it occurs sympatrically with *S. hierredda* (Reid et al. 2005). *S. hierredda* commonly known as the giant African cuttlefish, and while it occurs as far north as Cape Blanc (21°N), its southernmost distribution has not yet been defined. Up to now, research suggests that *S. hierredda* occurs throughout the tropics and subtropics reaching as far south as Baía dos Tigres, in southern Angola (Hatanaka 1979, Roeleveld 1998, Reid et al. 2005). Until recently the distribution of *S. vermiculata*, was thought to be from the southern coast of South Africa, into central Mozambique, as well as the Saya-de-Malha Bank and Mascarene Ridge (Reid et al. 2005). However, Healey et al. (2017) using genetic techniques found that all *Sepia* samples collected from southern Angola belonged to *S. vermiculata*, thereby suggesting that the species also has a West coast distribution.

Research on *Sepia* sp. off the Angolan coast is limited and the findings are contradictory. Bianchi (1986) identified only two species of *Sepia* within Angolan waters; *S. officinalis* subspecies and *S. orbignyana*, but later broadly classified all *Sepia* sp. within the demersal trawls off the coast of Angola as *S. officinalis*, despite research suggesting that the species does not extend as far south as Angola. As Healey et al. (2017) only found *S. vermiculata* in southern Angola, it is likely that this species forms a considerable proportion of cuttlefish bycatch in the demersal trawl fishery (FAO CECAF-SC 2011). Up until now, there is limited

information on *S. vermiculata* and this undermines the development and implementation of appropriate fisheries management and conservation strategies. This is particularly concerning due to the dependence of the local people on the resource in southern Angola, the growing global demand for cuttlefish and subsequent increasing exploitation coupled with the known inter and intra-specific variability of life-history characteristics of its conspecifics.

Cuttlefish are characterised by high inter- and intraspecific variability in their life-history traits (see Table 5.1). The variability in the life-history characteristics of cuttlefish is considered to be critical for the survival of these short-lived cephalopods as they rely on an adaptable, opportunistic life strategy to optimise reproductive success and survival (Hall & Fowler 2003, Jereb & Roper 2005, Pecl & Moltschanowskyj 2006).

Despite the high level of life history plasticity, a number of characteristics are similar between congeners (Hall & Fowler 2003, Jereb & Roper 2005). The lifespan of Sepiids ranges between 18 months and 2 years, however research suggests that male cuttlefish may live longer than their female counterparts (Reid et al. 2005). Interestingly, two alternative lifecycle patterns have been proposed for both *S. officinalis* (Mangold-Wirz 1963) in the Mediterranean Sea and *S. apama* in South Australia, with a proportion of individuals attaining sexual maturity at smaller sizes within 1 year and others attaining sexual maturation at a larger size within the second year (Mangold-Wirz 1963, Hall & Fowler 2003). This plasticity is considered to play an integral role in buffering the effects of poor recruitment that may have severe consequences for populations that have an annual cycle (Hall & Fowler 2003). However, this alternative life cycle has to date not been reported in other areas where these two species are distributed (Hall & Fowler 2003). The short lifespan of Sepiids suggests a rapid turnover with little generational overlap. This is considered to provide these species with an improved ability to adapt to environmental and climatic variability (Guerra 2006, Jereb et al. 2015). However, this characteristic may make these species highly vulnerable to overexploitation in areas lacking routine stock assessment and regular amendments to fisheries regulations (Boyle & Boletzky 1996, Jereb et al. 2015).

Majority of the Sepiidae are considered to be nektonic or demersal species as they are primarily associated with the bottom, occurring over a variety of substrate types, including sandy and muddy bottoms, rocky and coral reefs as well as extensive seagrass beds (Bloor et al. 2013, Carpeneter et al. 2014, Sasikumar et al. 2015, Reid et al. 2005, Xavier et al. 2016, Guerra 2006, Hall & Fowler 2003). The Sepiidae are predominantly found within shallow

coastal waters, however the influence of depth on the distribution is not well understood (Reid et al. 2005). Research conducted by Ward and Boletzky (1984) suggested that *S. officinalis* were unlikely to occur below depths of 200m due to elevated levels of hydrostatic pressure on the internal cuttlebone. However, further research has indicated ontogenetic shifts within the depth tolerance of the species, with larger adult cuttlefish having a considerably higher tolerance than those that may be newly hatched or within the early developmental stages (Guerra 2006). *Sepia vermiculata* is primarily a shallow waters species, distributed from only a few meters deep to depths of 290m (Carpenter et al. 2014). Whilst the species is generally associated with shallower waters, depth is not considered to act as a biogeographical barrier, as is evident by the known distribution in southern Africa and Mauritius (Reid et al. 2005). In southern Africa, *S. vermiculata* is the only *Sepia* species that occurs in lagoons and permanently open estuaries, as such it is tolerant of variations in salinity (Roeleveld 1998, Carpenter et al. 2014).

Many *Sepia* species are thought to undertake feeding and spawning (Roper et al. 1984, Wang et al. 2003, Guerra 2006, Jereb & Roper 2005, Sasikumar et al. 2013, Jereb et al. 2015). Migratory behaviour, although poorly understood, is considered to be driven by variability in environmental conditions such as temperature, salinity and photoperiod (Lloret et al. 2001, Wang et al. 2003, Hall & Fowler 2013, Sasikumar et al. 2015). Cuttlefish, such as *S. officinalis* found inhabiting temperate waters generally undergo a migration from colder, deeper overwintering grounds found offshore to shallower, coastal spawning and nursery grounds during spring and summer (Guerra 2001, Pecl et al. 2010, Hall & Fowler 2013). Cuttlefish distributed within sub-tropical and tropical water have been reported to migrate offshore to colder, deeper waters during the warmer summer months and return to shallower coastal waters, to spawn, during autumn and spring (Bakhayokho 1983, Hall & Fowler 2013). Whilst localised aggregations associated with spawning are common within a number of *Sepia* species, it is not uncommon for a proportion of mature individuals to occur within a population at any given time throughout the year (Hall & Fowler 2013).

Although research on the reproductive biology of *S. vermiculata* is extremely limited (Carpenter et al. 2014), investigations on the congeners, *S. officinalis* and *S. apama*, have suggested that *Sepia* may exhibit a terminal intermittent spawning pattern (Rocha et al. 2001, Hall & Fowler 2003, Guerra 2006, Piece et al. 2010, Bloor et al. 2013). Terminal intermittent spawning is defined by monocyclic spawning in which cuttlefish lay multiple batches of eggs

throughout the spawning period, however no somatic growth is considered to occur between these spawning events (Rocha et al. 2001, Jereb et al. 2005, Guerra 2006). This reproductive pattern is considered to be an adaptive strategy to overcome unfavourable or unstable environmental conditions and subsequently increase recruitment success within species characterised by a relatively short lifespan (Rocha et al. 2001).

**Table 5.1:** Life history traits of cuttlefish species within the genus *Sepia*.

Species (Common name)	Main areas of exploitation	Life span	Max size (ML, weight)	Size at maturity (mm)	Spawning season	Habitat	References
<i>S. officinalis</i> (Common cuttlefish)	English Channel, European Atlantic, Mediterranean, NW Africa	Alternating 1 - 2 years	450 mm, 4 kg (temperate); 300mm, 2kg (subtropical)	M: 60 – 110 mm F: 80 – 250 mm	all year, peak in spring-summer	Sandy, muddy bottoms. Shore to 200m. Inshore spawning, migration to hard bottom	2, 5, 6, 9
<i>S. hierredda</i> (Giant African cuttlefish)	NW Africa	1 - 2 years	M: 440 mm F: 370 mm	M: 120 – 140 mm F: 130 mm	spring & autumn	Sandy, muddy bottoms. Shore to 120m. Inshore spawning migration to shallower waters (<16m)	1, 2, 5
<i>S. orbignyana</i> (Pink cuttlefish)	Mediterranean, NW Africa		100 mm	M: 40 – 50 mm F: 70 – 80 mm	all year, peak in summer - autumn	Sandy-muddy bottoms, shelf to slope up to 450m deep	2, 4
<i>S. elegans</i> (Elegant cuttlefish)	European Atlantic, Mediterranean, NW Africa	1.5 years	M: 65 mm F: 80 mm	M: 20 – 50 mm F: 30 – 60 mm	all year, peak in spring-summer	Muddy bottoms up to depths of 430m. Inshore spawning migration to shallower waters (40 - 70m)	2, 3

Species (Common name)	Main areas of exploitation	Life span	Max size (ML, weight)	Size at maturity (mm)	Spawning season	Habitat	References
<i>S. bertheloti</i> (African cuttlefish)	Mediterranean, NW Africa	1 - 2 years	M: 175 mm F: 130 mm		summer-autumn	Open bottom habitats, up to 160m deep	5
<i>S. pharaonis</i> (Pharoah cuttlefish)	India, P.D.R. Yemen, Phillipines, Hong Kong, SE Asia, Northern Australia	2 - 3 years, males longer than females	M: 430 mm F: 350 mm Smaller in subtropics	M: 110 – 150 mm F: 120 – 170 mm	all year, peak in spring & autumn	Shore to 110m, inshore spawning migration	5, 11, 12
<i>S. australis</i> (Southern cuttlefish)	Southern Africa		M: 62mm F: 85mm			Depths of 45 - 345m, West coast spawns in deeper waters, south coast spawns in shallower waters	5, 6, 7, 8, 10
<i>S. apama</i> (Australian Giant cuttlefish)	South Australia	1 - 3 years	500 mm, 10.5 kg		peak spawning during winter	Inshore spawning migration, form localised dense spawning aggregations, associated with hard substrate	4, 5

1. Bakhayokho 1983; 2. Guerra et al. 2001; 3. Guerra & Castro 1989; 4. Hall & Fowler 2003; 5. Jereb & Roper 2005; 6. Jereb et al. 2015; 7. Lipiński et al. 1992; 8. Mqoqi et al. 2007; 9. Önsoy & Salman 2005; 10. Roeleveld et al. 1993; 11. Tahnifard & Dastan 2011; 12. Watanuki et al. 1993.

Sepiids are opportunist active predators feeding on a range of prey from crustaceans, molluscs, gastropods, teleosts, cephalopods etc (Castro & Guerra 1990, Guerra 2006, Mqoqi et al. 2007, Hastie et al. 2009, Billard et al. 2010). Studies on the diet of *S. officinalis* have highlighted that dietary composition is highly dependent on the availability of prey species across the geographic distribution. Furthermore, cannibalism has been reported in a number of sepriids, with larger individuals preying on smaller cuttlefish (Roper et al. 1984, Castro & Guerra 1990, Mqoqi et al. 2007, Hastie et al. 2009, Ibáñez & Keyl 2010). Despite a broad trophic scope, ontogenetic shifts in the diet have been observed (Hall & Fowler 2003, Guerra 2006, Mqoqi et al. 2007, Billard et al. 2010). For example, research on the diet of *S. officinalis* found a shift in prey size and composition with increasing body size, with smaller individuals feeding primarily on crustaceans and an increase in the abundance of teleosts in the diet with increasing size (Guerra 2006, Pierce et al. 2010). These ontogenetic shifts in diet have been attributed to the increase in the gape size and sensory capabilities of cuttlefish (Mqoqi et al. 2007, Jereb et al. 2015). As such, larger cuttlefish consume larger and more diverse prey than their smaller congeners (Mqoqi et al. 2007, Jereb et al. 2015).

As highlighted in Chapter 1, there is a complete lack of knowledge on the biology, ecology, physiology and life history of many species of cephalopods, with extensive research only having been carried out on approximately 8% of all known extant cephalopod species (O'Brien 2018). The Sepiidae, in particular are not only the most diverse, but also the least studied with research primarily conducted on commercial species such as *S. officinalis* (Boyle 1990, Hall & Fowler 2003, Jereb et al. 2015). As such, a large proportion of species are classified as data deficient with little to no information currently available. This is concerning, particularly for species which are harvested by fisheries around the globe (Jereb & Roper 2005).

The aim of the present chapter is therefore to describe the basic population biology and ecology of *Sepia vermiculata* distributed off southern Angola. This includes:

- 4) a description of the size composition, morphometrics, demographics and growth rates of *S. vermiculata* distributed in southern Angola,
- 5) the provision of insights into the reproductive biology of *S. vermiculata* distributed within southern Angola,
- 6) a description of the diet of *S. vermiculata* distributed within southern Angola,

- 7) a comparison of the life-history characteristics and morphometrics with those of other *Sepia* sp.

### *Materials and methods*

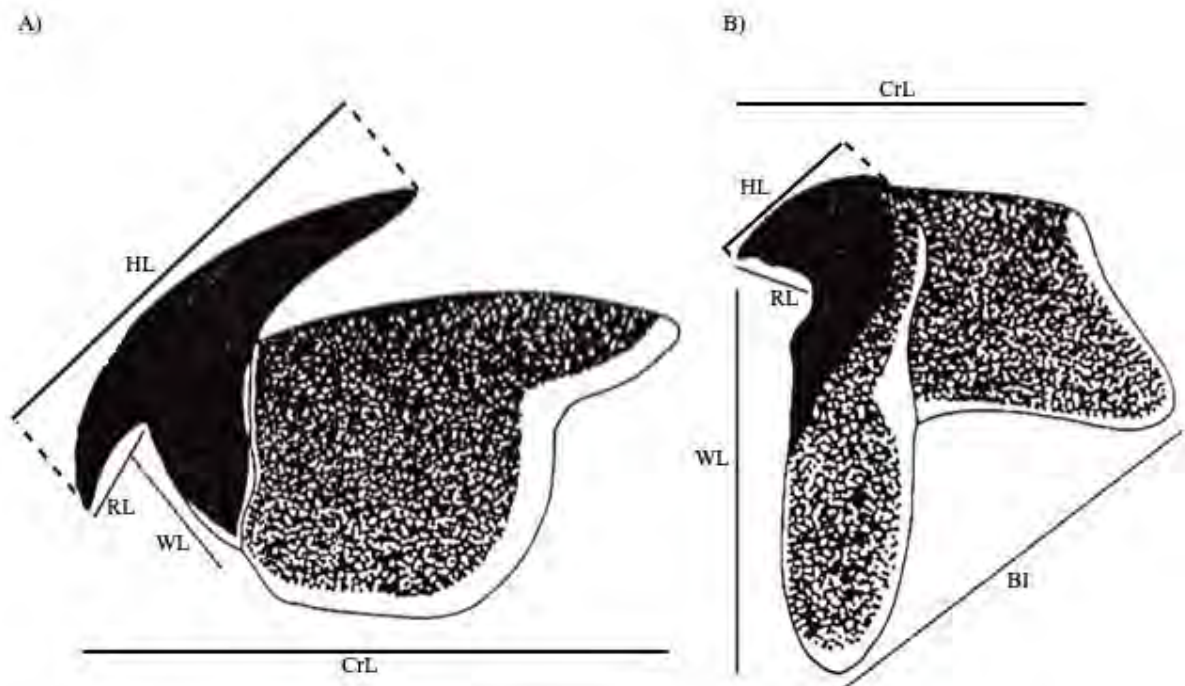
#### *Sample collection*

*Sepia vermiculata* samples were collected from artisanal fishing markets in Namibe, when available (Figure 2.1). Specimens were not obtained from Tombua, due to the low availability and abundance of the species in the market.

#### *Morphological data collection*

The following soft-body part measurements were recorded: dorsal mantle length (DML), total body weight (TBW), mantle width (MW), fin length (FW), fin width (FW), head length (HL), eye diameter (ED), length of right arms (AL I, AL II, AL III, AL IV) and tentacle club length (CL) (Table 5.2). Character choice and measurement description were guided by Guerra et al. 2001. It is important to note that numerous cuttlefish were missing both tentacles and as such club length could not be determined for those specimens. Patterns and sizes of suckers on tentacular clubs were not included in morphometric analysis as these morphometric characteristics are considered to exhibit high intrinsic variation which undermines the accuracy and subsequently the reliability of these characters in resolving systematics (Guerra et al. 2001). Cuttlebones were removed and the following measurements were recorded: cuttlebone length (CBL), cuttlebone width (CBWi), last locus length (LoL), outer cone width (OCW), inner cone width (ICW) and the striated zone length (SZ) (Table 4.2). All beaks were removed and stored in 70% ethanol, to allow for hard part morphometry. Prior to analysis beaks were rehydrated in distilled water. The following measurements were taken on the upper mandible: hood length (UHL), crest length (UCrL), wing length (UWL) and rostral length (URL) whilst the following were recorded for the lower mandible: hood length (LHL), crest length (LCrL), wing length (LWL) rostral length (LRL) as well as the baseline (BI) of the lower beak (Figure 5.1). Hard part morphometric character choice and measurement description were guided by Guerra et al. 2001 and Giordano et al. 2005. Length and width measurements were obtained using a digital caliper (Insize electronic Caliper Series 1112) to the nearest 0.01mm. Arm measurements and all measurements which

exceeded 300 mm were measured to the nearest 0.1 cm using a tape measure. Weights were recorded to the nearest 0.01 g using an electronic scale.



**Figure 5.1:** Upper (A) and lower (B) beak morphometry: hood length (LHL), crest length (CrL), wing length (WL) rostral length (RL) and the baseline (BI) (adapted from Giordano *et al.* 2005).

**Table 5.2:** Definition of soft body and cuttlebone measurements recorded for *Sepia vermiculata*.

Character	Abbreviation	Definition
Dorsal mantle length	DML	Length of the mantle from the posterior tip to the anterior tip, along the dorsal midpoint of the cuttlefish
Total body weight	TBW	Total wet body weight of cuttlefish
Mantle width	MW	Width of the mantle at the greatest point
Head length	HL	Length from the origin of the mantle to the origin of the tentacle
Eye diameter	ED	Diameter of eye across the bulbous
Fin width	FW	Greatest width of the fins between their lateral margins, measured on the ventral surface
Fin length	FL	Length from the anterior margin of the fin to the posterior extreme of the mantle
Arm length	AL I-IV	Length from the beak to the tip of the arm
Club length	CL	Length between the proximal most carpal sucker to the distal tip of the club.
Cuttlebone length	CBL	Length of cuttlebone from anterior of the cuttlebone to tip of the spine
Cuttlebone width	CBWi	Width of cuttlebone at widest point
Last locus length	LoL	Length of smooth zone from the last lamella of the striated zone to the anterior tip of the cuttlebone
Outer cone width	OCW	Width of the outer cone, at widest point
Inner cone width	ICW	Width of inner cone, at widest point
Striated zone length	SZL	Length of the striated zone from the first lamella to the last, on ventral surface of the cuttlebone

*Biological data collection*

Maturity was categorized using the defined morphological characteristics, as outlined by Gabr et al. 1998 (Table 5.3). Maturity was classified into four stages for each sex: females, I- immature, II – maturing, III - prespawning and IV – spawning; males, I – immature, II – maturing, III – fully mature and IV – spawning (Gabr et al. 1998).

**Table 5.3:** Maturity scales for *S. vermiculata* based on morphological characteristics proposed by Gabr et al. 1998.

Category	Male	Female
1) immature	Testis is small, the spermatophoric organ has formed. Hectocotylus is poorly developed.	Nidamental glands (NG) thin and transparent. Ovary very small, no ova apparent.
2) maturing	Testis has enlarged considerably. Needham's sac often contains some spermatophores, most of them poorly developed. This stage can be distinguished from Stage I males because the separate parts of the spermatophoric organ are clearly visible (vas deferens, spermatophoric complex glands and Needham's sac) and a few spermatophores are present in the Needham's sac.	NG are clearly visible, thicker and transparent. The colour of the accessory NG ranges from creamy white to beige. Ovary granular with small ova, clearly visible medium-sized uniformly whitish ova, but very few of them reticulated.
3) fully mature (males)/ prespawning (females)	Needham's sac is completely full of tightly packed spermatophores, which are well developed with a distinct spiral filament, cement body and sperm mass.	NG are white. The colour of the accessory NG ranges from yellow to orange. Ovary has small ova, medium-sized ova and large yellow round reticulated ova.
4) spawning	Up to 70% of spermatophores inside Needham's sac degenerating and appear as white mass.	NG swollen and white in colour, the accessory NG are pink or coral colour. Ovary has small ova, medium ova,

large yellow reticulated ova and large smooth transparent ova. Proximal oviduct is filled with mature eggs from the ovary to the oviducts (proximal and distal oviducts).

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Stomach contents were weighed to the nearest 0.01g and preserved in 10% buffered formalin for 48 hours, after which they were stored in 70% ethanol. Prey items were classified broadly into categories, such as teleosts, cephalopods or crustaceans, where possible these were later identified to genus and if possible species. Fish were recognized due to the presence of scales, vertebrae, spines, eye lenses and otoliths. The presence of cephalopods within the stomach was recognized by the presence of suckers, tentacles and beaks whilst crustaceans were primarily identified by the occurrence of exoskeletal remains. In many instances, contents were not distinguishable and as such contents were classified as unidentified. Furthermore, due to the macerated nature of the stomach contents, as well as the high levels of digestion and lack of post capture preservation techniques, the accurate determination of percentage number and percentage mass of each dietary component was not possible.

#### *Data analysis*

##### *Morphometrics*

The mean, standard deviation and range of variation was determined for each morphometric variable, for male and female *S. vermiculata*. An independent t-test was carried out to assess for significant differences in variable means between male and female cuttlefish. Linear regression analysis between soft part variables and the dorsal mantle length, cuttlebone measurements and cuttlebone length as well as beak measurements and dorsal mantle length were conducted in order to estimate regression coefficients (Guerra et al. 2001). A Student's *t*-test (Zar 1984) was carried out to allow for slope comparison between male and female cuttlefish for the various morphometric characteristics. Log-transformation of morphometric variables was conducted in order to improve the normality and homoscedasticity of the data. In order to investigate sexual dimorphism within *S. vermiculata* an ANOVA was carried out on log-transformed morphometric measurements

Length-weight relationships were determined, for each sex during each sampling period, by examining the relationship as follows (Bowker 1995):

$$Y = a x^b,$$

where  $Y$  = total body weight in grams,  $x$  = dorsal mantle length in mm,  $a$  and  $b$  are constants.

### *Maturity*

Length-at-50% maturity ( $L_{50}$ ), for males and female cuttlefish was determined by grouping *S. vermiculata* specimens into 20 mm dorsal mantle length size class ranges. The frequency of mature cuttlefish per size class was then determined. The data was then fitted using a two-parameter logistic ogive described as:

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

where  $P(L)$  is the proportion of mature cuttlefish within each size class  $DML$ ,  $DML_{50}$  is the dorsal mantle length at which 50% of *S. vermiculata* were mature and  $\delta$  is the width or steepness of the logistic ogive. In order to assess the differences in maturity patterns ( $DML_{50}$  and  $\delta$ ) between sexes, a likelihood ratio test was conducted.

### *Diet*

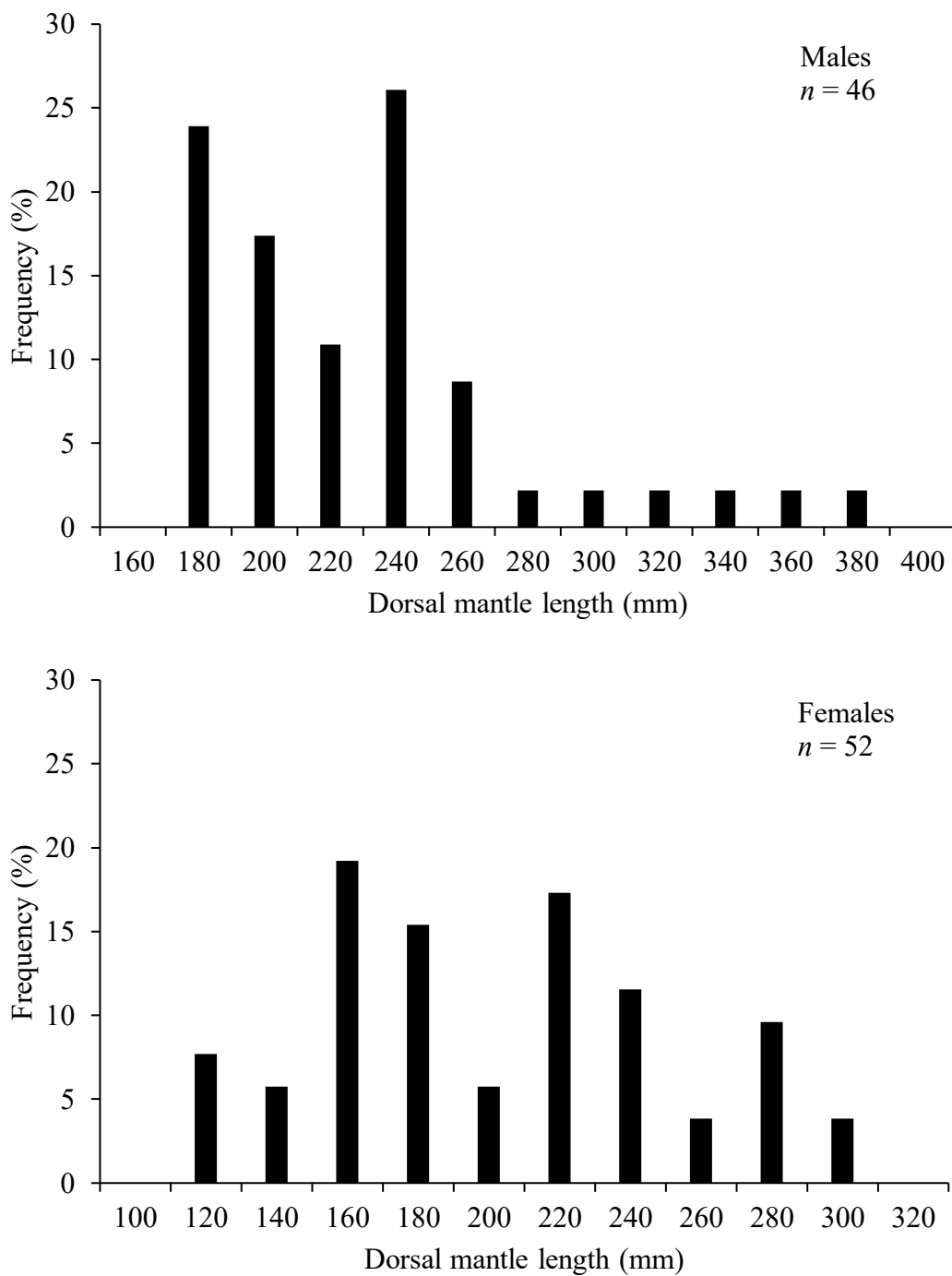
Stomach contents were quantified on the basis of frequency of occurrence (%F) which represented the percentage of *S. vermiculata* that had consumed a particular item of prey. Frequency of occurrence for each prey items was determined for males and females, to allow for comparison of diet between sexes, however due to low sample sizes, %F was pooled.

### *Results*

A total of 98 cuttlefish were obtained, consisting of 46 males and 52 females. Cuttlefish was not always readily available, in Namibe, as discussed in Chapter 3. All specimens were collected between December 2015 and April 2016, with majority of samples (79.6%) of samples being obtained during the months of December, January and February.

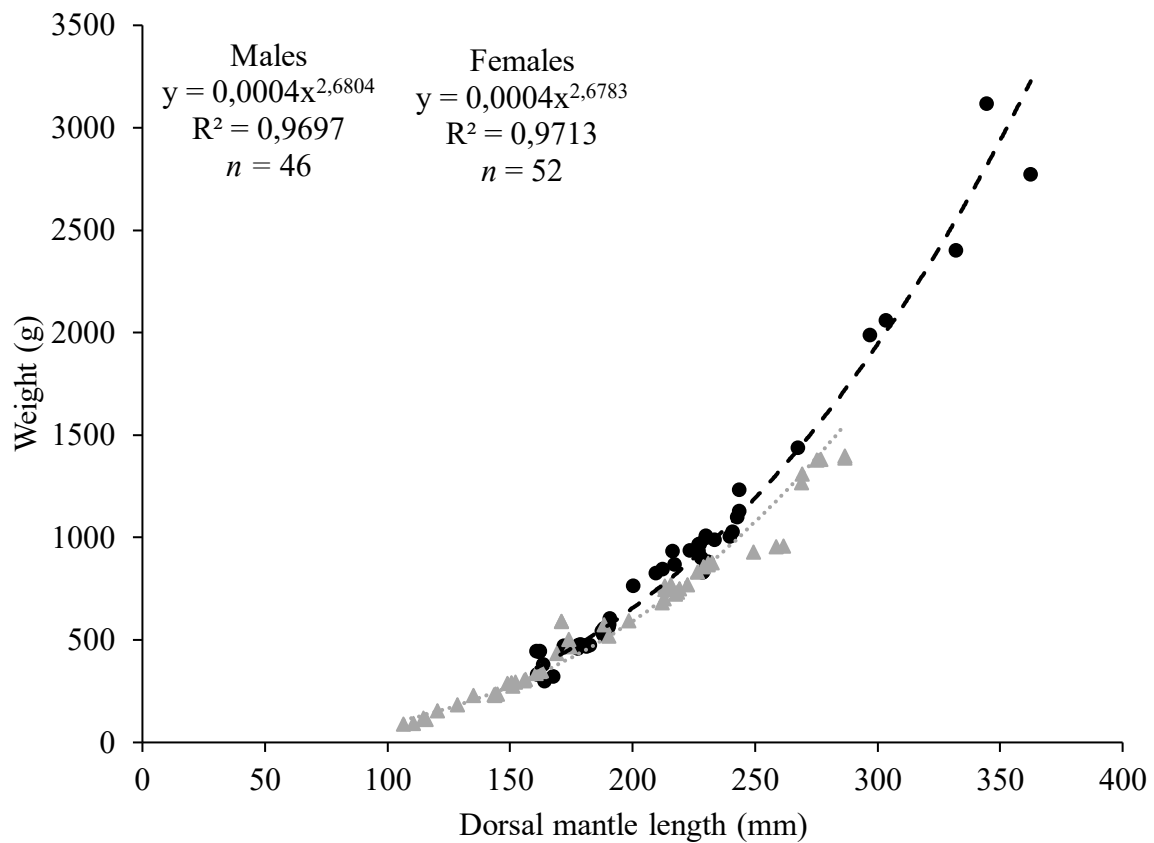
### *Size composition and morphometrics*

Male DML was significantly ( $F = 2.22$ ,  $p < 0.01$ ) larger (160.81 – 362.50 mm) than female DML (106.5 – 286.64 mm) (Table 4.4). Male *S. vermiculata* were also significantly heavier (298.4 – 3116.0g) than females (89.7 – 1397.7g).



**Figure 5.2:** Length-frequency histograms for male and female *S. vermiculata* collected in southern Angola, between December 2015 and April 2016.

The relationship between DML and TBW for *S. vermiculata* was best described by a power curve. The relationship between length and weight for male cuttlefish was expressed as  $TBW = 0.0004(DML)^{2.6804}$  ( $R^2 = 0.9697$ ,  $n = 46$ ) and for female cuttlefish as  $TBW = 0.0004(TL)^{2.6783}$  ( $R^2 = 0.9713$ ,  $n = 54$ ) (Figure 5.3).



**Figure 5.3:** The dorsal mantle length and total body weight relationship for male (black circles and dashed trendline) and female (grey triangles and solid trendline) *S. vermiculata* off the coast of southern Angola, collected between December 2015 and April 2016.

There was evidence for sexual dimorphism when comparing soft part morphometrics between sexes (Table 5.4). Significant intersexual differentiation was observed for the following variables; DML ( $F = 8.21$ ,  $p < 0.01$ ), TBW ( $F = 12.87$ ,  $p < 0.01$ ), ED ( $F = 19.01$ ,  $p < 0.001$ ), FW ( $F = 7.69$ ,  $p = 0.005$ ), FL ( $F = 8.39$ ,  $p = 0.009$ ), as well as the lengths of all four arms ( $p = 0.02$ ,  $< 0.01$ ,  $< 0.01$ ,  $0.04$ , respectively) (Table 5.4).

**Table 5.4:** Descriptive statistics of soft part morphometric measurements conducted on male ( $n = 46$  and female ( $n = 52$ ) *S. vermiculata* (SD, standard deviation and % DML which represents the mean of ((variable/DML)\*100). See Table 5.2 for variable abbreviations and definitions. Values in bold indicate significant differences.

Variable	Male		Female		<i>p</i>
	Mean $\pm$ SD Range (mm/g)	% DML	Mean $\pm$ SD Range (mm/g)	% DML	
DML	218.25 $\pm$ 48.55 (160.81 – 362.50)		192.10 $\pm$ 50.71 (106.5 – 286.64)		<b>&lt; 0.01</b>
TBW	924.5 $\pm$ 623.4 (298.4 – 3116.0)		607.8 $\pm$ 375.6 (89.7 – 1397.7)		<b>&lt; 0.01</b>
MW	126.10 $\pm$ 27.00 (88.66 – 189.42)	57.8	118.41 $\pm$ 24.88 (77.38 – 163.24)	61.6	0.14
HL	67.28 $\pm$ 22.62 (41.23 – 132.50)	30.8	65.00 $\pm$ 11.46 (38.81 – 88.61)	33.8	0.95
ED	23.49 $\pm$ 2.12 (20.16 – 30.09)	10.8	20.09 $\pm$ 5.80 (10.85 – 37.23)	10.5	<b>&lt; 0.001</b>
FW	164.90 $\pm$ 54.50 (108.60 – 281.40)	75.6	139.54 $\pm$ 31.26 (88.22 – 223.43)	72.6	<b>&lt; 0.01</b>
FL	202.41 $\pm$ 50.24 (140.89 – 335.20)	92.7	175.68 $\pm$ 48.20 (99.37 – 281.29)	91.5	<b>&lt; 0.01</b>
AL I	114.5 $\pm$ 41.7 (39.0 – 241.6)	52.5	97.67 $\pm$ 27.46 (57.2 – 155.2)	50.8	<b>0.02</b>
AL II	115.1 $\pm$ 41.8 (65.8 – 232.4)	52.8	96.39 $\pm$ 24.34 (52.5 – 152.5)	50.2	<b>&lt; 0.01</b>
AL III	117.2 $\pm$ 40.8 (70.3 – 237.8)	53.7	98.02 $\pm$ 26.18 (58.5 – 158.3)	51/0	<b>&lt; 0.01</b>
AL IV	117.9 $\pm$ 43.5 (23.8 – 243.2)	54.0	99.92 $\pm$ 25.90 (60.9 – 156.6)	52.0	<b>0.04</b>
CL	80.06 $\pm$ 21.04 (50.39 – 139.44)	36.7	72.50 $\pm$ 21.34 (37.20 – 118.28)	37.7	0.06

CBL as a percentage of the DML was found to be significantly ( $p < 0.001$ ) higher in male (95.23%) than female *S. vermiculata* (89.05%) (Table 5.5). Significant differences between male and female cuttlefish was observed for the six cuttlebone variables; CBL ( $F = 19.12$ ,  $p < 0.001$ ), CBWi ( $F = 8.76$ ,  $p < 0.01$ ), LoL ( $F = 23.93$ ,  $p < 0.001$ ), SZ ( $F = 8.75$ ,  $p < 0.01$ ), ICW ( $F = 5.13$ ,  $p = 0.03$ ) and OCW ( $F = 15.96$ ,  $p < 0.001$ ). When expressed as a percentage of the CBL, the mean width of the cuttlebone (37.7% vs 35.1%), ICW (2.9% vs 2.6%) and SZ (51.9% vs 49.2%) were found to be higher in female *S. vermiculata* whilst the length of

the last locus was higher in males (Table 5.5). Male cuttlefish were therefore characterised by a longer, narrower cuttlebone than females of the same size.

**Table 5.5:** Descriptive statistics of cuttlebone morphometric measurements conducted on male ( $n = 46$ ) and female ( $n = 52$ ) *S. vermiculata* (SD, standard deviation, % DML which represents the mean of  $((\text{variable}/\text{DML}) * 100)$  and % CBL which represents the mean of  $((\text{variable}/\text{CL}) * 100)$ ). Values in bold indicate significant differences. See Table 5.2 for variable abbreviations and definitions.

Variable	Male			Female			<i>p</i>
	Mean $\pm$ SD Range (mm)	% DML	% CBL	Mean $\pm$ SD Range (mm)	% DML	% CBL	
CBL	207.83 $\pm$ 42.62 (145.62 – 332.54)	95.2		171.06 $\pm$ 45.24 (39.67 – 94.35)	89.05		<b>&lt; 0.001</b>
CBWi	72.86 $\pm$ 14.84 (53.90 – 109.41)		35.1	64.44 $\pm$ 14.53 (39.67 – 94.35)		37.67	<b>&lt; 0.01</b>
LoL	95.26 $\pm$ 16.89 (58.18 – 155.86)		45.8	77.47 $\pm$ 20.21 (45.34 – 123.71)		45.30	<b>&lt; 0.001</b>
OCW	15.58 $\pm$ 3.65 (10.20 – 26.73)		7.5	12.68 $\pm$ 3.96 (6.23 – 19.71)		7.41	<b>&lt; 0.001</b>
ICW	5.31 $\pm$ 0.75 (4.02 – 7.47)		2.6	4.92 $\pm$ 1.40 (2.55 – 7.84)		2.88	<b>0.03</b>
SZ	102.25 $\pm$ 24.89 (74.32 – 185.62)		49.2	88.75 $\pm$ 26.95 (43.98 – 142.58)		51.88	<b>&lt; 0.01</b>

Sexual dimorphism was observed in the beak of cuttlefish with significant differentiation ( $p < 0.05$ ) observed for all nine beak morphometric variables for *S. vermiculata*. When expressed as a proportion of the dorsal mantle length, female cuttlefish were characterised by a higher UHL (9.8% vs 9.6%), UCrL (12.8% vs 12.4%), URL (2.3% vs 2.2%) and LCrL (8.1% vs 8.1%) (Table 5.6).

**Table 5.6:** Descriptive statistics of beak morphometric measurements for male ( $n = 46$ ) and female ( $n = 52$ ) *S. vermiculata* (SD, standard deviation, % DML which represents the mean of  $((\text{variable}/\text{DML}) * 100)$ ). Values in bold indicate significant differences. See Figure 5.1 for variable abbreviations and description.

Variable	Male		Female		<i>p</i>
	Mean $\pm$ SD Range (mm)	% DML	Mean $\pm$ SD Range (mm)	% DML	
UHL	20.99 $\pm$ 4.35 (15.01 – 34.34)	9.62	18.84 $\pm$ 4.43 (11.30 – 27.91)	9.8	<b>&lt; 0.01</b>
UCrL	27.12 $\pm$ 5.26 (20.45 – 44.52)	12.4	24.53 $\pm$ 6.18 (14.78 – 37.40)	12.8	<b>0.01</b>
UWL	9.26 $\pm$ 1.18 (6.91 – 12.47)	4.2	7.62 $\pm$ 1.93 (4.34 – 12.21)	4.0	<b>&lt; 0.001</b>
URL	4.85 $\pm$ 0.85 (2.42 – 7.07)	2.2	4.42 $\pm$ 0.95 (2.76 – 6.59)	2.3	<b>0.02</b>
LHL	9.28 $\pm$ 2.17 (5.99 – 16.85)	4.3	7.84 $\pm$ 2.17 (4.21 – 12.26)	4.1	<b>&lt; 0.001</b>
LCrL	17.66 $\pm$ 3.54 (13.16 – 28.93)	8.1	15.62 $\pm$ 4.21 (8.98 – 22.87)	8.1	<b>&lt; 0.01</b>
LWL	16.98 $\pm$ 3.20 (12.82 – 26.13)	7.8	14.81 $\pm$ 3.35 (8.43 – 21.58)	7.7	<b>&lt; 0.001</b>
LRL	4.15 $\pm$ 0.84 (2.98 – 7.22)	1.9	3.06 $\pm$ 0.81 (1.48 – 4.96)	1.6	<b>&lt; 0.001</b>
BI	20.49 $\pm$ 4.14 (13.92 – 34.44)	9.4	17.78 $\pm$ 4.91 (10.10 – 28.50)	9.3	<b>&lt; 0.01</b>

When investigating the relationship between soft part variables and dorsal mantle length significant differences were observed in the HL ( $t = 6.67$ ,  $p = 0.03$ ), FW ( $t = 10.54$ ,  $p < 0.001$ ) and the lengths of AI ( $t = 5.88$ ,  $p < 0.001$ ), AII ( $t = 4.74$ ,  $p < 0.001$ ), AIII ( $t = 7.39$ ,  $p < 0.001$ ) and AIV ( $t = 8.33$ ,  $p < 0.001$ ) of males and females (Table 5.7). There was also significant differences in the relationship between cuttlebone variables and the length of the cuttlebone were only found for LoL ( $t = 2.38$ ,  $p = 0.01$ ) (Table 5.7). Females were found to exhibit a greater LoL than male cuttlefish (Table 4.7). The relationship between beak variables and DML exhibited similar trends for male and female cuttlefish (Table 5.7).

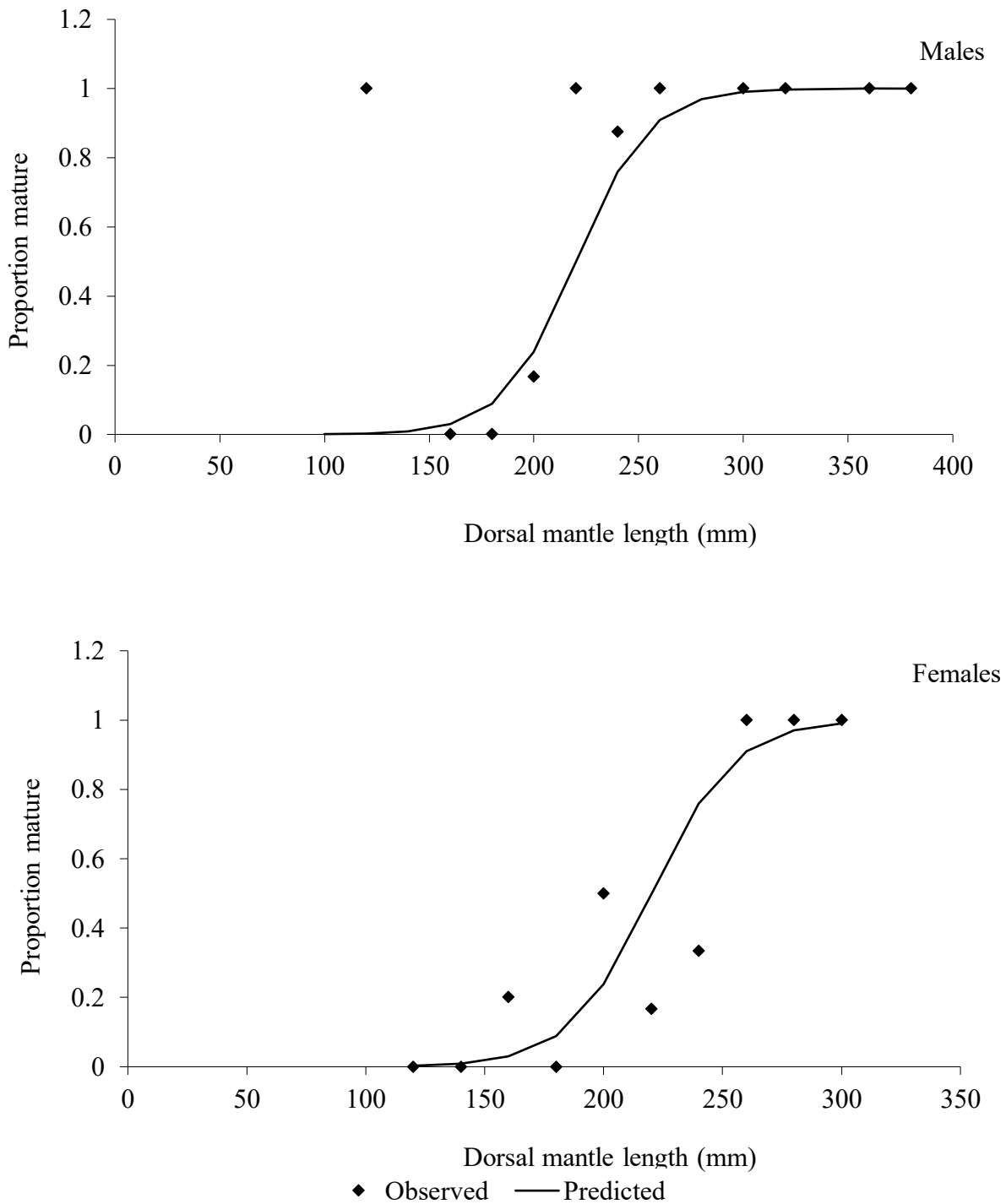
**Table 5.7:** Regression values and results of slope comparisons of the morphological variables between male (n = 46) and female (n = 52) *S. vermiculata*. Linear equation:  $y = b(x) + a$  ( $a$  – intercept,  $b$  – slope,  $r^2$  – regression coefficient). \*  $p < 0.05$ , \*\*  $p < 0.01$ .

	Variable	Males			Females			Slope comparison
		$a$	$b$	$r^2$	$a$	$b$	$r^2$	$t$
DML vs	MW	13.66	0.52	0.86	26.64	0.48	0.95	1.13
	HL	-23.99	0.42	0.81	27.44	0.20	0.75	6.67**
	FW	-51.79	0.99	0.78	25.77	0.59	0.92	10.54**
	FL	-11.67	0.98	0.90	-3.16	0.93	0.96	1.25
	ED	18.13	0.03	0.32	0.67	0.10	0.78	2.53*
	AI	-49.23	0.48	0.79	5.35	0.48	0.76	5.88**
	AII	-50.86	0.78	0.68	11.87	0.46	0.53	4.74**
	AIII	-52.71	0.78	0.86	6.92	0.47	0.84	7.39**
	AIV	-62.07	0.83	0.85	13.34	0.45	0.780	8.33**
	CL	-6.56	0.40	0.95	-2.89	0.40	0.92	0.11
CBL vs	CBWi	3.12	0.34	0.93	10.19	0.32	0.98	0.54
	LoL	20.87	0.36	0.82	2.03	0.44	0.97	2.38*
	OCW	-1.94	0.08	0.97	-1.94	0.09	0.95	0.04
	ICW	1.99	0.02	0.82	-0.17	0.03	0.93	0.41
	SZ	-14.14	0.56	0.92	-12.18	0.59	0.98	0.85
DML vs	UHL	1.6	0.09	0.95	2.33	0.08	0.93	0.10
	UcrL	3.95	0.11	0.96	1.52	0.11	0.97	0.46
	UWL	4.39	0.02	0.85	0.60	0.04	0.93	0.49
	URL	1.94	0.01	0.58	1.10	0.02	0.85	0.14
	LHL	-0.11	0.04	0.93	-0.08	0.04	0.93	0.06
	LCRL	2.15	0.07	0.95	0.04	0.08	0.95	0.34
	LWL	3.02	0.06	0.94	3.42	0.06	0.81	0.16
	LRL	0.762	0.015	0.815	0.500	0.013	0.69	0.01
	BI	2.425	0.083	0.940	-0.516	0.095	0.96	0.43

### *Maturity*

The first fully mature males (stage 3) were observed to occur within the 200 mm DML size class, with 100% maturity observed in the 260 mm DML size class. A small percentage (10%) of females in the 160 mm DML size class were classified into the pre-spawning stage (stage 3). In contrast, all females in the 260 mm size class were classified as belonging to the pre-spawning stage. The length-at-50% maturity was smaller for male (217.53 mm DML) than female (231.13 mm DML) *S. vermiculata* (Figure 5.4). However, the length-at-50%

maturity ( $\lambda = 1.46$ ,  $p = 0.23$ ) and the steepness of the ogive ( $\lambda = 2.46$ ,  $p = 0.12$ ) were not significantly different between sexes.



**Figure 5.4:** Logistic ogives, for male and female *S. vermiculata* collected from Namibe, in southern Angola, between December 2015 and April 2016.

## Diet

Of the 98 stomachs that were examined, a total of 31 (31.6%) (14 males; 17 females) contained food, of which 7 (22.6%) contained more than one prey item (Table 5.8). *Sepia vermiculata* predominantly fed on teleost species which were found within 64.5% of stomachs. Crustaceans and cephalopods were found within 32.3% and 25.8% of stomachs, respectively. Whilst the diet of male cuttlefish was dominated by teleosts (78.6%), the dietary composition of females consisted of 52.9% teleost, 41.2% crustacean and 17.65% cephalopod. Males had a broader dietary composition than female cuttlefish (Table 5.8).

**Table 5.8:** Dietary composition of *S. vermiculata* collected in southern Angola, between December 2015 and April 2016.

Group	Species	%F Male	%F Female	% F Pooled
Teleosts	<i>Cynoglossus capensis</i>	21.4	0.00	9.7
	<i>Sardinella aurita</i>	14.3	11.8	12.9
	<i>Gymnamodytes</i> sp.	7.1	0.0	3.2
	Gobiidae sp.	0.0	11.8	6.5
	<i>Merluccius</i> sp	7.1	0.00	3.2
	Unidentified fish	28.6	29.4	29.0
Cephalopods	<i>Sepia vermiculata</i>	0.00	5.9	3.2
	<i>Octopus vulgaris</i>	14.3	0.0	6.5
	Unidentified cephalopod	21.4	11.8	16.1
Crustaceans	Mysidacea sp.	7.14	29.4	19.4
	Unidentified crustacean	14.3	11.8	12.9

## Discussion

The current study highlights the variability in the biology and demography of *S. vermiculata*. Male cuttlefish obtained significantly larger sizes, yet had a smaller length-at-maturity (albeit not significant) and a broader diet than females. There was also evidence for sexual dimorphism in both morphometric and reproductive characteristics. The significantly larger size of *S. vermiculata* in Angola, when compared to other commercially exploited sepiids, may increase the appeal and market value of the species as a fisheries resource commodity, particularly for the export market, if targeted by the means of jigging and preserved appropriately in order to reduce biochemical spoilage. Knowledge on the of basic life history

characteristics of the species, as discussed within this chapter, therefore provides a starting point on which local management and conservation frameworks can be developed, as well as provide a reference point for future stock assessments.

Male cuttlefish obtained significantly larger lengths and weights (362.50 mm DML, 3116.0g TBW) than their female (286.64 mm DML, 1397.7 g TBW) conspecifics. Larger males have been documented in a number of *Sepia* sp including *S. bertheloti*, *S. latimans*, *S. hierreda*, *S. officinalis*, *S. pharonis* (Table 5.1) (Hall & Fowler 2003, Jereb & Roper 2005, Guerra-Marrero et al. 2019). This sexual dimorphism may be attributed to: 1) greater longevity in males or 2) reduced female growth due to the higher energetic cost associated with reproduction (Dan et al. 2012).

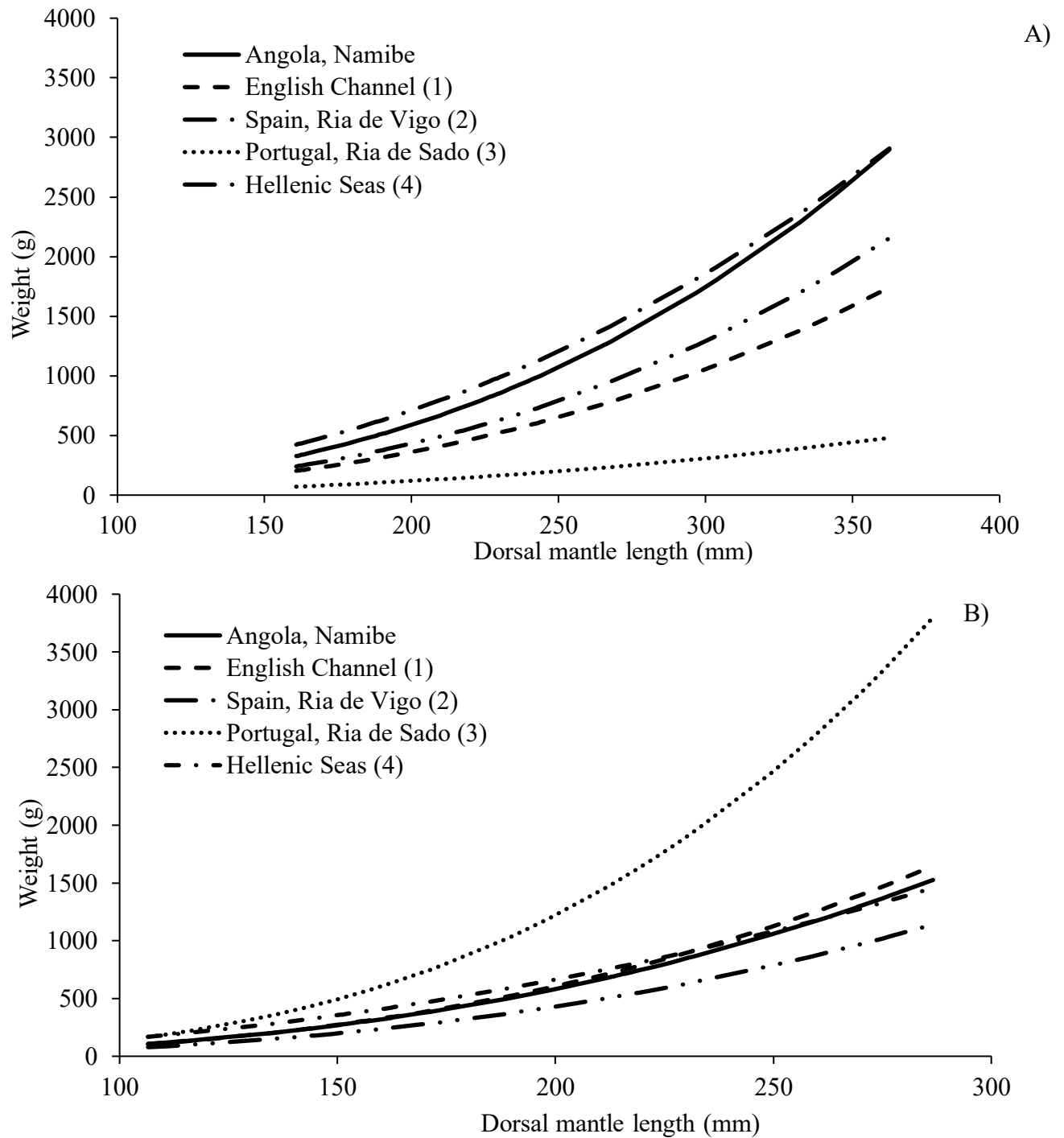
The observed maximum DML of male and female *S. vermiculata* in Namibe, were found to exceed size values reported for the species distributed in South Africa, as well as recently reported values for *S. officinalis* and *S. hierredda* distributed throughout the Northeast Atlantic and the Mediterranean Sea (Table 5.9). According to the systematic key developed by Khromov et al. (1998) adult *S. vermiculata* are small (maximum ML of 150 mm) in comparison to *S. officinalis* (maximum ML of 250 mm) and *S. hierredda* (maximum ML of 450 mm). This contradicts ML measurements reported by Guerra et al. (2001) who observed a larger maximum mantle length of 228.0 mm for *S. officinalis* and a maximum ML of 99.3 mm for *S. hierredda*, as well as the results from the current study which observed a maximum ML of 362.50 mm. Morphological research on *Sepia* (Jereb et al. 2015, Neige 2021), particularly those which are exploited commercially has since indicated that high levels of intraspecific variation in body size between regions (see Table 5.9). Intraspecific variability in morphometric characteristics is often considered to be a result of either phylogenetics, ecological conditions or a combination of both processes. As such, intraspecific variability in morphometrics and more specifically body size, is generally considered to arise within species distributed across heterogeneous environments, such as the Benguela upwelling system (Neige 2021). Understanding intraspecific morphometric variability is therefore critical in resolving taxonomic issues, identifying diagnostic features and understanding the mechanisms driving the observed evolutionary change and plasticity, both within and between species. Whilst comparisons of DML of *S. vermiculata* from the current study with numerous studies on *S. officinalis* and *S. hierredda* indicate that *S. vermiculata* may attain a larger maximum size and on average have a larger DML, it is

important to take into consideration that the morphometrics across the entire distribution of *S. vermiculata* is not well documented (Table 5.9). Understanding variability across the distribution of any species is therefore likely to identify intraspecific inter-population morphological variation and subsequently provide a more holistic understanding of interspecific morphological variability.

**Table 5.9:** Maximum mantle lengths (mm) for male and female *Sepia* sp in different geographical areas.

Species	Region	M	F	Reference
<i>S. vermiculata</i>	Southern Angola	362.50	286.64	Current study
<i>S. officinalis</i>	Bay of Biscay	350	290	Le Goff & Daguzan 1991
	Thracian Sea	320	264	Lefkadiou et al. 2007
	Izmir Bay	324	241	Onsoy & Salman 2005
	Senegal	228.0	95.5	Guerra et al. 2001
	Ría de Vigo	205	235	Guerra & Castro 1988
	Karataş Coast	152.0	155.5	Yesilyurt et al. 2019
<i>S. hierredda</i>	Senegal	74.8	67.4	Guerra et al. 2001

Male and female cuttlefish exhibited no significant differences in the length-weight relationship, with both sexes being characterised by negative allometric growth, which, is indicative of a decreasing weight in proportion to size as growth occurs. Negative allometric growth has been identified within a number of cuttlefish species (Dunning et al. 1994, Reid et al. 2005, Sasikumar et al. 2013, Kennouche & Nouar 2016, Vasconcelos et al. 2018). The length-weight relationship of male *S. vermiculata* from this study was similar to that of *S. officinalis* from Ría de Vigo, Spain (Figure 5.5) (Guerra & Castro 1988). However, comparisons of length-weight relationships of female *S. vermiculata* exhibited similar patterns to *S. officinalis* distributed in the Hellenic Seas, Ría de Vigo and the English Channel (Figure 4.6) (Guerra & Castro 1988, Dunn 1999, Lefkadiou et al. 2007). Together, these findings suggest that there are high levels of variability in the length-weight relationships between sexes as well as within species occurring across different geographic locations. The extensive literature on *S. officinalis* highlights this variability in length-weight relationships, with some populations exhibiting a larger weight in females at any given length, some exhibiting no intersexual variability and others being characterised by a larger weight in males at any given length (Guerra & Castro 1988, Dunn 1999, Neves et al. 2009, Lefkadiou et al. 2007, Sasikumar et al. 2013, Neige 2021).



**Figure 5.5:** Length-weight relationships for male (A) and female (B) *S. vermiculata* in Namibe, southern Angola, in comparison to *S. officinalis* from populations distributed within the eastern Atlantic and Mediterranean Sea. Where necessary, original equations converted to  $W = aML^b$ , where  $W$  is the mass (g), and  $ML$  is the mantle length (mm). References: 1 = Dunn 1999, 2 = Guerra & Castro 1988, 3 = Neves et al. 2009, 4 = Lefkaditou et al. 2007.

Morphometric analysis indicated sexual dimorphism within *S. vermiculata*. This is a common trait among the Sepiidae and is often a result of differential patterns of somatic growth, as a result of varying reproductive demands between males and females (Almonacido-Rioseco et al. 2009, Guerra-Marrero et al. 2019). Interestingly, the results from the current study exhibited significant differences in cuttlebone width between male and female *S. vermiculata*, as has been found in a number of species, including but not limited to; *S. officinalis*, *S. bertheloti* and *S. apama* (Hall & Fowler 2003, Jereb & Roper 2005, Almonacido-Rioseco et al. 2009, Guerra-Marrero et al. 2019). The observed sexual dimorphism of the cuttlebone has previously been hypothesised to represent a reproductive adaptation in females, by which a larger cuttlebone width allows for increased support and volume for a larger pallial cavity and subsequently an increased volume of oocytes (Guerra-Marrero et al. 2019).

The cuttlebone is an important structure in distinguishing taxonomically between *Sepia* species (Guerra et al. 2001, Jereb et al. 2015, Khromov 1998). Interspecific comparison of the 5 cuttlebone morphometric characteristics indicated that CBL (as a % of DML) and ICW (as a % of CBL) for male and female *S. vermiculata* was lower than both *S. officinalis* and *S. hierredda* (Table 5.10). Results from the current study indicate that *S. vermiculata* has a shorter cuttlebone with a narrower ICW than the other two species in the species complex. However, CBWi and OCW were narrower than values from *S. officinalis*, yet wider than those observed within *S. hierredda* (Table 5.10). The striated zone of both male (49.20% of CBL) and female (51.88% of CBL) *S. vermiculata* was higher than in *S. hierredda* and *S. officinalis* (Table 5.10). Furthermore, unlike the present study, CBL for male *S. officinalis* and *S. hierredda* distributed off Galician and Senegalese waters did not exhibit a higher percentage of the DML (Table 5.10). Whilst the results from the current study indicate morphological differences between species within the *Sepia officinalis* complex, there is a need for a comprehensive morphometric analysis of *S. vermiculata* across the known distribution as subtle genetic differences have been noted to occur between specimens occurring across the Benguela upwelling region. Phylogenetic differences may drive intraspecific morphometric variability (Healey et al. 2017, Neige 2021).

**Table 5.10:** Comparison of variable measurements, expressed as a % of DML and CBL between *S. vermiculata* from the current study and *S. officinalis* and *S. hierredda* from Guerra et al. 2001.

Sex	Variable	% DML			
		<i>S. vermiculata</i>	<i>S. officinalis</i>	<i>S. hierredda</i>	
Male	MW	57.78	59.8	54.5	
	AL I	52.47	61.8	45.0	
	AL II	52.74	61.6	47.0	
	AL III	53.70	64.2	47.4	
	AL IV	54.02	67.2	53.5	
	CBL	95.23	96.6	100.6	
Female			% CBL		
	CBWi	35.06	37.2	34.7	
	OCW	7.50	9.3	6.6	
	ICW	2.55	4.4	4.3	
	SZ	49.20	41.8	46.1	
	MW	61.64	61.8	54.7	
	AL I	50.84	55.3	46.6	
	AL II	50.18	56.0	47.3	
	AL III	51.03	57.2	48.2	
	AL IV	52.01	62.8	55.3	
	CBL	89.05	97.8	101.1	
				% CBL	
	CBWi	37.67	38.9	35.7	
	OCW	7.41	9.7	6.8	
ICW	2.88	4.2	4.5		
SZ	51.88	40.7	47.8		

Male cuttlefish generally attain sexual maturity at smaller sizes than females (Boletzky 1982, Gabr et al. 1998, Guerra & Castro 1988, Dunn 1999, Önsöy & Salman 2005, Mqoqi et al. 2007, Jereb et al. 2015). This was also documented with the present study, with dorsal mantle length-at-50% maturity ( $L_{50}$ ), as well as 100% maturity smaller for males. Understanding the growth and reproduction of any species is critical in developing suitable harvest size restrictions (Pierce & Guerra 1994). Minimum landing size restrictions are currently used as a management tool for *S. officinalis* fisheries in Galicia as well as within Portugal and France (Jereb et al. 2015, Pierce et al. 2010). Harvest restrictions are considered to be one of the most common management tools in fisheries, with restrictions on minimum sizes being set to

ensure that species are able to obtain maturity and subsequently spawn prior to harvest thereby reducing the effects of fishing on stock recruitment success. Length at maturity trends can be used as indicators of fishery-induced changes, particularly within stocks which may be characterised as data deficient.

Earlier maturation of males, as observed within the current study, may allow for an increase in the duration of spawning activity and subsequently result in increased rates of genetic exchange within any population (Mqoqi et al. 2007). Various factors, such as environmental conditions, locality, food availability and age are considered to play a major role in determining cuttlefish size at maturation (Duysak et al. 2014). Research has highlighted the effects of external environmental conditions, such as temperature and light in influencing maturation within cuttlefish (Boletzky 1983, Jereb et al. 2015). Cuttlefish in warmer waters, are generally considered to attain sexual maturity earlier than those found to be distributed in colder temperatures, whilst higher light intensities have been documented to result in delayed onset of maturation (Boletzky 1983, Jereb et al. 2015). As such the length at maturity has been observed to exhibit high levels of spatio-temporal variability for a number of species, and should therefore be assessed regularly (Guerra 2006, Jereb et al. 2015). In order for effective size restrictions to be implemented, long-term assessments of the stock is critical in understanding the spatio-temporal variability of maturity within the species, at a local scale. Furthermore, and of particular importance for transboundary stocks, and understanding interpopulation variability across the known geographical distribution is necessary.

In the current study, only 31.6% of sampled individuals had the remains of food in their stomachs. Due to these relatively low samples sizes, the results should therefore be interpreted with caution. Furthermore, whilst stomach contents are thought to be indicative of the last meal, this is not necessarily the case due to differential digestive rates (Ibáñez et al 2008, Mqoqi 2007). Hard structures such as beaks and otoliths have been documented to accumulate within the stomach (Ibáñez et al 2008, Mqoqi 2007). As such the use of hard structures to identify prey may result in the overestimation of the importance of certain prey items whilst prey items characterised by faster digestive rates may be underestimated (Ibáñez et al 2008, Mqoqi 2007). Due to differential digestive rates, the presence-absence methodology is recommended for the estimation of diet within cephalopod species (Ibáñez et al 2008). The current study did not make use of prey weights estimates, as stomachs contents were well digested and subsequently primarily in liquid form, throughout the study. This may

have been exacerbated by post capture digestion, which was facilitated by the poor preservation methods after capture.

Regardless of the post capture digestion the frequency highlighted the importance of crustaceans and teleosts within the diet of *S. vermiculata*. Similar findings have been made for other *Sepia* (Castro & Guerra 1990, Alves et al. 2006, Mqoqi et al. 2007, Jereb et al. 2015, Pal et al. 2020). In this study, the diet of *S. vermiculata* was comprised of eight identified species, of which seven *Cynoglossus capensis*, *Gymnamodytes* sp, *Gobiidae* sp, *Merluccius* sp, *S. vermiculata*, *Octopus vulgaris* and *Mysidacea* sp are associated with the benthic environment. The importance of demersal species in the diet is not surprising due to the benthic nature of *S. vermiculata*. However, the variability observed within the diet, highlights the opportunistic predatory behaviour of the species, as has been described for many cuttlefish species (Alves et al. 2006, Villanueva et al. 2017). Furthermore, cephalopods were an important component of the diet and were identified in the stomachs of both males and females. Unlike female *S. vermiculata*, male cuttlefish did not exhibit cannibalistic behaviour, however this may have been confounded by the higher proportion (21.4%) of unidentified cephalopod within male stomachs. Cannibalism is common within cephalopods and has been reported to occur within *S. australis*, *S. pharonis* and *S. hierreda*. and is often thought to intensify during reproductive events due to aggression and behaviour associated with spawning activities however, sexual cannibalism has not been previously documented to occur within the genus *Sepia* (Roper 1984, Castro & Guerra 1990, Mqoqi et al. 2007, Ibáñez & Keyl 2010, Rodhouse et al. 2014, Villanueva et al. 2017).

Whilst crustaceans appeared to be of higher importance for females, this may be attributed to sampling bias and in particular the low sample size. Alternatively, it is possible that the relative importance of crustaceans in the diet of females may be attributed to; 1) the smaller sizes of the females or, 2) a result of the observed intersexual differences in beak morphometry. Ontogenetic variation in the diet has been observed in numerous cephalopods, and more specifically *Sepia* species, with the occurrence of teleosts and cephalopods in the diet typically increasing with cuttlefish length (Mangold 1987, Alves et al. 2006, Villanueva et al. 2017, Pal et al. 2020). This ontogenetic shift in diet has been attributed to a number of factors, including but not limited to, 1) smaller benthic crustaceans being more readily abundant and easier to catch, 2) a higher energy demand with an increase in size, 3) an increase in hunting area with growth and 4) the development of prey capture and handling

skills with age (Guerra & Castro 1990, Alves et al. 2006, Villanueva et al. 2017, Pal et al. 2020). Further studies may be carried out to identify the relative importance of the identified prey items as well as whether ontogenetic and intersexual differences in dietary composition and whether these result in differential feeding niches between sexes.

*Sepia vermiculata* was readily available within Namibe during December through to April, with catches peaking during the summer months; December, January and February. Namibe is located within the region of the Angola Benguela Frontal Zone (ABFZ), with the midpoint of the front being documented to occur between 14°S and 16°S (John et al. 2001, Lass et al. 2000, Veitch et al. 2006). As outlined in Chapter 2, this area experiences seasonal latitudinal shifts. The presence of cuttlefish, and commencement of catches within the artisanal cuttlefish jig fishery, during the warmer months is therefore likely to be the result of either an onshore migration to shallower, coastal waters or alternatively a shift of biomass in a southerly direction with warming sea surface temperatures as a result of the annual variability in the geographical positioning of the ABFZ, as highlighted in Chapter 2. The observed high proportion of maturing and fully mature individuals in this study may suggest that the species undergoes a spawning migration to the region, this can be further supported by fishers reporting the presence of cuttlefish eggs during periods of high catches. The lower proportion of immature, juvenile individuals may therefore indicate a migration to mature, as has been found within a number of *Sepia* sp, or alternatively, may be a result of gear selectivity as discussed, in Chapter 4 (Sasikumar et al. 2013). The seasonal displacement of the ABFZ, may result in the observed seasonal variations in cuttlefish abundance within the region, as is considered to be the case for *S. officinalis* within the waters of the English Channel (Wang et al. 2003). Wang et al. (2003), in their study in the English Channel concluded that spatio-temporal changes in the abundance of cuttlefish may therefore be closely related with the positioning of frontal zones due to a high dependency upon these bio aggregating oceanographic features and their subsequent increased levels of food availability.

Marine environmental conditions play a vital role in the distribution of *Sepia* sp (Augustyn et al. 1995, Guerra 2006, Wang et al. 2003, Rodhouse et al. 2014). For example, spatio-temporal shifts in *S. officinalis* distribution have been documented to occur with the strengthening of the Atlantic Current into the English Channel and southern regions of the Celtic Seas, subsequently resulting in the annual migration of cuttlefish into these areas (Wang et al. 2003). Furthermore, the migration of *S. officinalis*, into the English Channel and

southern Celtic Sea, was positively correlated with a rise of sea surface temperatures in the area. The southerly distributional shift theory for *S. vermiculata* off the coast of southern Angola, as a result of thermal preference may further be supported by the lack of cuttlefish further south, in Tombua. It is therefore possible that Namibe forms the southern boundary of the distribution of *S. vermiculata*, with an influx of cuttlefish into the area as SST's increase (Figure 2.2). This may be further corroborated by the observed phylogenetic divergence between South African and Angolan *S. vermiculata*, as identified by Healey et al (2017) indicative of the presence of a biogeographical barrier in the distribution across the cold, nutrient rich waters of the Benguela current. Understanding these biomass displacements is critical for the management of cuttlefish populations, particularly in areas such as southern Angola which have been identified as a global hotspot, with sea surface temperatures rising at a rate of 0.8C faster than the global mean (Munnik 2012, Hobday & Pecl 2014, Potts et al. 2014).

As with all studies, there may have been caveats in the data collection. Increased sample sizes, particularly for the dietary composition, may provide better insight into the observed trends. Furthermore, it is unclear whether the lack of juvenile cuttlefish is a result of size selectivity due to the method of capture (jig). *Sepia* sp. have been documented as a bycatch for the demersal trawl fishery. Future research therefore may aim to include samples from this sector, in order to assess the size composition of *S. vermiculata* in southern Angola. The lack of juveniles, raises concerns regarding the recruitment and the life history strategies of the species within Angolan waters.

*Sepia vermiculata* exhibits similar life history characteristics with other extensively studied *Sepia* sp. The short lifespan, early maturation and rapid turnover of populations common to these species pose major difficulties to fisheries managers, particularly in areas where little to no reliable historical/current catch data is available. A lack of fisheries information not only undermines current management strategies but has the ability to compromise future management and conservation efforts. Sustainable management of short-lived species such as *S. vermiculata* requires regular biological assessments to understand their dynamic variability in the demographics of the stock and the drivers of this variability.



# CHAPTER 6

## GENERAL DISCUSSION

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Cephalopods of southern Angola are exposed to increasing anthropogenic pressures and a rapidly changing environment, as is observed globally (Doubleday et al. 2006, Pierce et al. 2010). These factors, when combined with a complete lack of biological data, make it difficult to predict and determine the population dynamics of *L. reynaudii* and *S. vermiculata* within the region. Whilst the results from the current study provide valuable information on the biology and demography of *L. reynaudii* and *S. vermiculata* in southern Angola, it is clear that both species exhibit strong seasonal patterns which are likely to be exacerbated by the high levels of changes in environmental conditions as a result of the convergence of the two opposing currents in the region. Fishers in this area rely heavily on the seasonal squid fishery as a source of livelihood, however it is likely that climate change, as well as seasonal variability, have the potential to have major implications for communities which are currently characterised by limited alternative livelihood opportunities and poor adaptive capacity.

Interestingly, fishers interviewed were able to identify patterns and spatio-temporal changes in the abundance and biogeographic distribution and available biomass, which aligned well with results from Chapter 4 and 5, as well as corresponding scientific knowledge on the climate-induced changes within the region (Shannon et al. 2006, Potts et al. 2014). This strongly suggests that both species undergo extensive ontogenetic migrations, with changes in biomass reflecting favourable conditions within an unstable environment and consequently resulting in a seasonal variability. Ontogenetic migrations and subsequently changes in spatio-temporal distributions of populations, has been documented for *L. reynaudii* off the coast of South Africa and many targeted loliginid and sepiid species around the globe (Arkhipkin et al. 2015). Changes in spatio-temporal abundance and distribution of these species is often primarily attributed to the presence of differential spawning and feeding grounds (Arkhipkin et al. 2015, Boyle & Rodhouse 2005, Rodhouse et al. 2014).

Understanding these migrations and the forces driving the observed patterns is important in developing sound management policies as well as for understanding and predicting future responses, particularly in communities which are highly dependent on the fishery for poverty

alleviation and food security. The Academy of Fishery and Marine Sciences, in Namibe, is well placed to initiate further studies on these species, incorporating both local knowledge and the changing oceanographic features of this region

### *Biological challenges of managing cephalopod fisheries*

Cephalopods are generally characterised by a “live fast, grow smart, die young” life history strategy (O’Dor & Webber 1991, O’ Dor 1998, Jackson & O’ Dor 2001, Doubleday et al. 2016, Amodio et al. 2018, Arkhipkin et al. 2021). This characteristic is often considered to play a major role in enhancing the adaptive capacity and phenotypic flexibility of these species to changing, and emerging, environmental and anthropogenic pressures (Amodio et al. 2018, Arkhipkin et al. 2021). However, research has also suggested that the short life cycle of cephalopods may make these marine invertebrates more vulnerable to short term changes, such as climate change and increased localised fishing pressures (Pierce et al. 2010, Rodhouse et al. 2014). The cephalopod populations occurring in southern Angola, are distributed in a known climate change hotspot, as such these species may be of increasing importance as biological indicators in the response of cephalopods to changes in anthropogenic and climatic pressures.

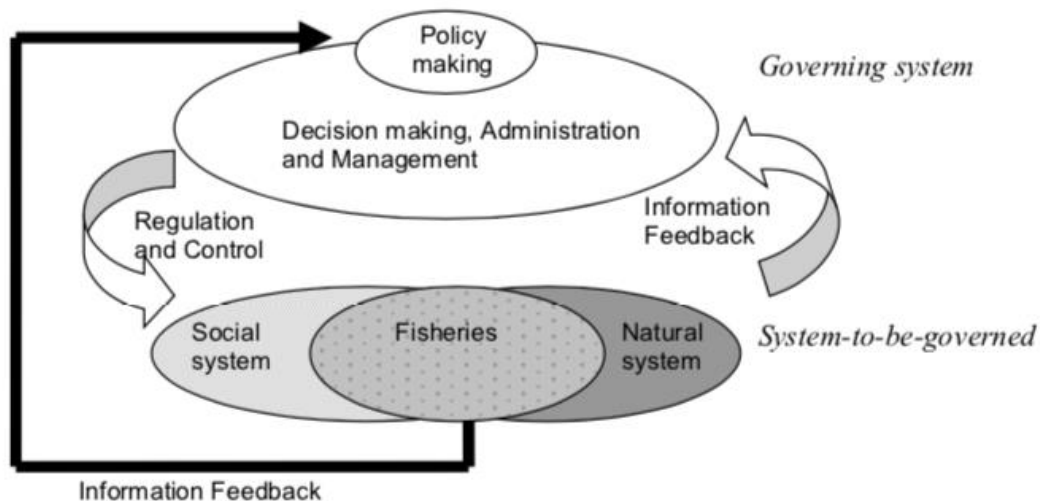
Their rapid growth rates, short lifespans and high levels of life history plasticity often result in biological and ecological challenges for the management of cephalopod fisheries due to the high levels of variability observed within species, and furthermore within stocks (Lipiński 1998, Arkhipkin et al. 2021). High levels of interannual variability, as well as differences in biological characteristics between *L. reynaudii*, were highlighted in Chapter 4. Challenges arising from high levels of plasticity may be further exacerbated within fisheries where landings are either poorly documented, there is a lack of routine stock assessment, and species are misidentified or broadly identified to family level. This is the case in southern Angola, where catches of the artisanal jig fishery are not well documented and industrial cephalopod catches are largely categorised as bycatch or broadly classified into taxonomic groups. As such, the importance of stock assessment and species specific management of cephalopods and the governance of the artisanal jig fishery is not viewed as a priority.

*Angolan fisheries governance, with a focus on the artisanal cephalopod fishery*

Modern fisheries governance is a systemic concept relating to the exercise of social, political, economic and administrative authority concerned with the management of resources (FAO 2016). Governance is characterised by the conceptual and operational guiding principles and goals; the ways and means of organization and coordination; the infrastructure of socio-political, economic and legal institutions and instruments; the nature of the processes and their modus operandi; the various actors and their roles and capacity; the policies, plans and measures that are produced and finally; the outcomes of the governance (FAO 2016). Furthermore, fisheries governance has international, national and regional dimensions (FAO 2016).

Effective fisheries governance aims to establish the overriding principles and goals of the fisheries sector to ensure sustainable practices which maximise socio-economic benefits; develop effective and efficient policy, legislation and regulatory frameworks in order to meet the objectives; minimize conflict at the individual, sectoral and societal level to maximize the productivity of the socio-ecological systems and subsequently maintain societal harmony; legitimize stakeholder interaction and contribution; enforce legislation and regulations whilst maintaining coherence across jurisdictional scales; determine the allocation of power, resources and benefits, all whilst ensuring that the system has the ability to learn and adapt (FAO 2016). As such, fisheries governance can be defined as the complex interaction between the “governing system” and the “system-to-be-governed”, with participation, accountability and transparency, coherence, effectiveness and efficiency being classified as the key principles for good, sound large-scale fisheries management (Figure 6.1) (Johnsen 2014).

The system to be governed further involves the complex interaction between fisheries and the natural ecosystem and social systems on which they depend (du Preez 2009). Understanding these systems and their interactions is the first step towards developing effective governance.



**Figure 6.1:** The fisheries governance model (based on Johnsen et al. 2009 – from Johnsen 2014).

Whilst Angola recognises the importance of artisanal fisheries, and makes provisions for them within policy, to quantify the importance, value and scale of each fishery, in this case the cephalopod jig fishery, there is a strong need for the data, definitions and information about the fishery. Lack of information feedback from the system-to-be-governed severely undermines the governing system and the regulatory and control inputs towards the jig fishery.

Traditionally governance was often regarded as unitary, single minded, top-down and instrumental however more contemporary governance can be considered to be more participatory, devolved and multi-stakeholder driven (Jentoft 2006). Applying a more contemporary style of governance to artisanal fisheries, allows for governing bodies to incorporate and develop community and co-management strategies. Furthermore, in order for artisanal fisheries to contribute towards food security and poverty alleviation it is necessary that collaboration between government, fishing communities, cooperatives and other stakeholders is increased. Globally there has been an increase in cooperatives as governance shifts from traditional, hierarchical regimes towards more holistic, interactive regimes which are subsequently more inclusive of non-state participants in the role of sector development and governance and as such allow for more locally accountable management strategies (du Preez 2009). Cooperatives can be defined as ‘autonomous associations of persons united voluntarily to meet their common economic, social and cultural needs and aspirations through

a jointly owned and democratically controlled enterprise' (ICA 1995). Cooperatives are positioned between the government, market and civil society and are therefore often considered to be within the ideal position to promote socioeconomic development and environmentally sustainable practices (du Preez 2009).

The IPA, since 1998, has recognised the importance of such institutional instruments and as such fishing cooperatives are found to occur within many of the coastal fishing communities of Angola. The Angolan Government and more specifically, the IPA recognises the importance of fisheries cooperatives as a structural instrument for enhancing the implementation of social, economic and sectoral development policies and programs, providing incentives and input as well as financial and technical support. As such, MINAGRIP and the IPA encourage the formation and registration of artisanal fisheries cooperatives (Sowman et al. 2011, Duarte et al. 2005). Typically cooperatives are formed on the basis of geographical location. Whilst it is clear that the government recognises the importance of stakeholder participation and the benefits of cooperatives, further consultation and assistance is required to strengthen and develop existing and new management methods. Of primary concern, and as highlighted in Chapter 3, there is a strong need for infrastructure development and an increase in institutional capacity within existing organizations in order for artisanal fisheries management and productivity to be improved. Strengthening capacity within existing organizations, as well as improving infrastructure, could allow for more efficient monitoring systems within the fishery thereby allowing for increased feedback and subsequently more appropriate, flexible management strategies. Currently artisanal fisheries within southern Angola are relatively data deficient. Information such as daily landings and catch compositions, postharvest losses, socio-economic characteristics, responses to climate changes as well as feedback from the market, is fundamental for fisheries development and sustainability.

#### *Managing the artisanal cephalopod jig fishery of southern Angola*

Management strategies for fisheries can typically be divided into short-term and long-term measures (Pierce & Guerra 1994). Within fisheries that may be data deficient or lack well-developed management strategies and frameworks, management policies should emphasize long-term measures. Long-term management options could include restrictions on tackle, area or season closures, size limits or effort limitations. As highlighted by Rodhouse et al.

(2014), there are a number of precautionary principles which may be applied to data deficient, unmanaged fisheries, such as the southern Angola artisanal jig fishery; including; 1) restricting access to the fishery, 2) limiting effort or TAC, through the implantation of more conservative input controls until enough data is available to ensure the fishery is operating at socio-ecological sustainable capacity, 3) reduce incentives to encourage new investments or entrants into the fishery, 4) implement closed seasons, 5) make use of precautionary biological reference points, 6) make use of co-management regimes, or alternative measures which are likely to promote user accountability and responsibility, 7) develop systems to enhance data collection such as catch landings etc.

As highlighted in Chapter 1, the artisanal cephalopod fishery of Angola is managed through a mixed-species TAC of 1400t, with no species specific quotas being outlined for the group. Furthermore, it is unclear as to what extent *L. reynaudii* and *S. officinalis* are exploited by semi-industrial and industrial vessels. Whilst TACs have traditionally been considered as an appropriate management option within cephalopod fisheries globally, these are typically used in conjunction with other measures and should be developed and adapted annually by the scientific technical committee, in response to feedback from stock assessments (Baudron et al. 2010, Arkhipkin et al. 2021). TAC's can likely result in the following; 1) overfishing, the effects of which could be exacerbated should environmental conditions not be ideal for successive years; 2) recruitment overfishing, and lastly, 3) a conservative TAC may result in the under exploitation of the resource (Augustyn & Roel 1998). The lack of species-specific and sector-specific catch information within Angola, on both *L. reynaudii* and *S. vermiculata*, and the multi-species TAC approach is of major concern as it undermines the effectiveness of management and conservation strategies as well as compromises future efforts. The life history characteristics of the species coupled with the lack of comprehensive, routine, real time stock and recruitment assessments as well as the monitoring and capturing of cephalopod landings, along with the characteristics of the fishery undermines catch-based management efforts within the artisanal cephalopod fishery of southern Angola. Management by total allowable effort (TAE), which is currently used in conjunction with an annual closed season within the South African *L. reynaudii* jig fishery, has been argued to be a more effective management strategy for cephalopod fisheries and as such is more commonly used within cephalopod fisheries globally (Caddy 1983, Rosenberg et al. 1990, Augustyn et al. 1992, Sauer et al. 2013). Effort based management, typically relies on restricting effort within the fishery to maximise the percentage of biomass available for harvest (Arkhipkin et al.

2021). Unlike the TAC, a fixed TAE would therefore ensure that the same proportion of biomass be harvested per year, allowing for the fishery to maximise catches during years of high abundance whilst providing a buffer and protecting the resource during years of decreased biomass.

The introduction of territorial use rights (TURFs) may be an applicable management regime for the cephalopod jig fishery of southern Angola, especially if the current TAC is to remain unchanged and the ban on all semi-industrial and industrial fishing within four nautical miles of the coast continues. TURFs, are currently used as an effective management regime in numerous small-scale cephalopod fisheries around the globe (Rodhouse et al. 2014). As outlined in Chapter 4, the artisanal jig fishery can be clearly defined into distinct zones, namely Namibe and Tombua, thereby granting fishers from different fishing communities access and harvest rights within a specified geographic area. At present, the lack of infrastructure and the remote nature of these two fishing communities, is likely to strengthen the adherence to such a management regime, whilst providing incentives for a co-management approach.

At present, the artisanal cephalopod jig fishery requires little investment, as such it is often viewed as a viable alternative or supplementary source of income for the household, particularly during periods of higher catches. This, combined with the lack of enforcement, is likely to undermine compliance to licencing schemes. As mentioned in Chapter 3, a co-management, participatory approach, particularly when combined with the implementation of TURFs, is not only likely to provide a means of collecting valuable fishers knowledge, which is critical for management in a fishery which experiences high levels of interannual variability, but is likely to hold fishers more accountable to the regulations and subsequently increase monitoring, control and surveillance;

Closed areas and seasons and the introduction of marine protected areas are considered to be an effective strategy to reduce fishing capacity on cephalopod stocks. However, for these measures to be effective, fishers need to be accountable for the resource, and a high level of monitoring and policing needs to be carried out. The complete lack of infrastructure and restricted accessibility due to the remote nature along the coast south of Tombua, and to some extent between Namibe and Tombua, plays a major role in limiting artisanal fishing activity

within this region and therefore to some extent provides protection for the proportion of the stock distributed within the region.

It is important to note that for the artisanal cephalopod fishery of southern Angola to be managed effectively the following is required; 1) identification of cephalopod stocks; 2) a comprehensive understanding of the life cycle; 3) routine, real-time assessment in order to allow for the collection of statistical data regarding to all aspects of the fishery; 4) development and implementation of appropriate recruitment indices 5) an understanding of the emigration/immigration patterns within the fishery 6) an in depth understanding of the role of *L. reynaudii* and *S. vermiculata* within coastal fishing communities (fishers) as well as the ecosystems in which these resources occur; 7) an understanding of environmental parameters of the region, how these are changing with time and their subsequent effects (Pierce & Guerra 1994).

Currently, the distributional limits of both species remain relatively unclear; however it is likely that both species have populations which extend across maritime boundaries.

Transboundary management of such populations is vital in increasing the sustainability of the stocks and the future profitability of the fisheries, however this relies on cooperation between neighbouring countries. It is therefore pivotal that in such instances where transboundary stocks do occur that neighbouring countries ensure that the tenure rights of artisanal fishing communities are highlighted and protected. As outlined in Chapter 1, Angola falls within the Benguela Current Large Marine Ecosystem (BCLME) and as such shares a number of transboundary stocks, with Namibia and South Africa. In January 2007, the three states signed an interim agreement to establish the Benguela Current Commission (BCC), this was strengthened by the signing of the Benguela Current Convention (BCC) in 2013 and ratified in July 2014 (Benguela Current Commission 2013, Hamukuaya et al. 2016). This formal treaty recognises the complexity and significance of the system and outlines the need for the states involved to conserve, protect, enhance and sustainably make use of the marine ecosystem to maximise economic, environmental and social benefits (Benguela Current Commission 2013, Hamukuaya et al. 2016). Interestingly, this is the first formal inter-governmental, multi-sectoral Large Marine Ecosystem framework to be developed for ocean governance (Hamukuaya et al. 2016).

### *Adaptability to climate change*

Climate change is a global phenomenon which is becoming increasingly prominent (FAO 2018). Within the marine environment, impacts of climate change include ocean warming and subsequently sea level rise and changes in oxygen concentrations, changes in ocean acidification, stratification and circulatory patterns as well as the intensification of extreme weather events (de Young et al. 2012, O'Brien et al. 2018, Gissi et al. 2020, Schickele et al. 2021). As such, it is fundamental that fisheries, and the communities dependent upon them, are able to increase their adaptive capacity to the impending effects of climate change and subsequently increase climate resilience (FAO 2018). Forecasting and understanding the effects of climate change on fisheries is a vital component in the development of adaptive, sustainable management and conservation strategies (Schickele et al. 2021).

Research conducted by Allison et al. (2009) assessed the vulnerability of 132 countries to climate change. Vulnerability was considered to be a result of a combined effect of the sensitivity to the physical and biological effects of climate change, the relative importance of fisheries to GDP and food security, as well as the limited adaptive societal capacity to respond to impacts and opportunities (Allison et al. 2009, van der Lingen & Hampton 2018). The study revealed Angola's national economy as the most vulnerable to climate-induced changes as far as fisheries are concerned (Allison et al. 2009). As highlighted in Chapter 1 and Chapter 3, despite the relatively low contribution of fisheries to the country's GDP, marine capture fisheries are a vital component to Angola's national economy due to the important role it plays in reducing poverty and increasing food security (du Preez 2009, Sowman & Cardoso 2010, Paterson et al. 2014). Within the Angolan fisheries sector, the semi-industrial and artisanal sub-sectors have been identified as being the most vulnerable to climate-induced changes due to the high number of coastal communities dependent on the fisheries as a nutritional source as well as a livelihood, combined with the sectors limited adaptive capacity (de Young et al. 2012, FAO 2018, Cochrane et al. 2020). The lack in adaptive capacity within the artisanal sector is primarily due to financial restrictions, lack of alternative livelihood opportunities and limited government support, as addressed in Chapter 3. As highlighted in Chapter 3, majority of interviewed fishers noted that changes in climate conditions over the decade were considerable, with many stating that the occurrence of extreme or unfavourable weather had increased substantially.

As highlighted in Chapter 2, southern Angola has been recognised as a hotspot for global climate change with evidence of an average annual increase of SST by 0.23°C to 0.8°C, depending on the satellite-data source, over the past three decades (Hobday and Pecl 2014, Potts et al. 2014, Jarre et al. 2015). This is above the global average and raises major concerns as to the vulnerability of the country to climate-induced changes, particularly for fisheries, which are reliant on seasonal resources, as a means of livelihood and nutrition (Hobday and Pecl 2014), as observed within the current study.

Ocean warming is likely to have major implications on cephalopod fisheries, as temperature is often regarded as one of the major environmental parameters determining distributional patterns due to its effect on the biological processes of marine organisms (Pierce et al. 2010, de Young et al. 2012, Rodhouse et al. 2014, Xavier et al. 2014, O'Brien et al. 2018). However, research has attributed a global proliferation in cephalopods to climate change, with temperature being considered the most plausible driver for this observed change in population dynamics (Pecl & Jackson 2008, Rodhouse et al. 2014, Doubleday et al. 2016). Cephalopods are considered to be highly adaptable, e.g. increasing SST has been suggested to increase growth rates, subsequently increasing the rate of the lifecycle resulting in an increase in population turnover (Pecl & Jackson 2008, Doubleday et al. 2016, Seibel 2016). However, should temperatures exceed optimal thermal limits, negative changes in population dynamics are likely to be observed.

The population of *L. reynaudii* off southern Angola exhibits high levels of seasonality, with the biomass available to fishers being higher during cooler winter months, when the southerly Angolan current is at its weakest and the ABFZ has shifted to its northern boundary. It has been suggested that increased SST may not only result in distributional shifts which may have negative implications for resource dependent coastal communities but may also have negative ramifications on the recruitment of cephalopod populations (Pierce et al. 2008, Rodhouse et al. 2014, Schickele et al. 2021). Reproductive success of cephalopods and the survival of juveniles is likely to decline with increasing sea surface temperatures (Repolho et al. 2014, Rosa et al. 2012). Higher temperatures are expected to result in accelerated embryonic development which could result in premature hatching and subsequently have detrimental consequences for survival during the early life history (Forsythe 1993, Steer et al. 2003, Oosthuizen & Roberts 2009, Repolho et al. 2014, Rosa et al. 2012). Uncertainty in recruitment success may increase challenges already faced in forecasting cephalopod

recruitment and therefore undermine efforts to ensure sustainable management practices (Rodhouse et al. 2014, Schickele et al. 2021). It is therefore vital that an in depth understanding of the thermal sensitivities and thermal windows at the different life stages are determined for species specific responses to changes in SST to be forecasted, particularly for populations which are distributed at geographical range limits, as may be the case for the population of *L. reynaudii* off the coast of southern Angola (O'Brien et al. 2018). Increased SST beyond optimal conditions may therefore result in increased physiological stressors. This may therefore result in a decline in the biomass of the population within the region, resulting in a decline in the stability and profitability of the fishery or alternatively result in a southerly distributional shift for *L. reynaudii*. This is of major concern due to the high dependency of coastal communities in southern Angola, on *L. reynaudii*, and the lack of alternative livelihood opportunities. However, the increasing SST and the southerly shift of the ABFZ may coincide with the extension of the *S. vermiculata* distribution further south. Research has suggested that several species will expand their biogeographic distribution as a response to climate induced changes, with poleward shifts as a result of climate having been observed in a number of cephalopod species across the group (Golikov et al. 2013, Doubleday et al. 2016, Xavier et al. 2016). Should this be the case, *S. vermiculata* may become more readily available to coastal communities south of Namibe and may therefore offer an alternative to the squid directed fisheries in Pinda and Tombua.

The absorption of increasing amount of anthropogenic CO<sub>2</sub> has resulted in the changes in the marine carbon chemistry of the oceans, resulting in an increase in the acidity of marine waters (Seibel et al. 2003, FAO 2018, NOAA, Otjacques et al. 2020). Whilst the direct effects of ocean acidification on cephalopods remains relatively uncertain, research has suggested that the reduction in pH could have detrimental effects on these invertebrates who possess structures formed of aragonite such as cuttlebones and statoliths (Gutowska et al. 2009, Kaplan et al. 2013, Rosa et al. 2013). Furthermore, research on *S. officinalis* suggests that acidification of marine waters may not only have an effect on the structure and development of the hard anatomy but could have implications on the embryonic development which ultimately result in poor development and survival during early ontogenetic stages (Kaplan et al. 2013, Rodhouse et al. 2014, Xavier et al. 2014, Seibel 2016, Otjacques et al. 2020). Whilst the impacts of ocean acidification on cephalopods in the region remain relatively uncertain, future research is required to understand the response of these marine invertebrates to acidification.

Global oceanic circulation patterns have been documented to have undergone considerable changes. However, forecasting and understanding these changes is challenging due to the timescale and spatial extent over which these patterns exist. Circulation patterns play a major role in cephalopod biogeographic distribution, not only by regulating climatic conditions within a region but through enabling or restricting population connectivity, particularly for planktonic paralarvae (Xavier et al. 2015, O'Brien et al. 2018). Research has suggested an intensification of the ABFZ, along with a southward shift in the positioning of the frontal zone (Vizy et al. 2018). These changes have primarily been attributed to a poleward shift in the South Atlantic subtropical anticyclone (Vizy et al. 2018). The southerly shift in the ABFZ is likely to have alternative ramifications on the distribution of *S. vermiculata* and *L. reynaudii*. Unlike *L. reynaudii*, the population of *S. vermiculata* in southern Angola is therefore likely to exhibit a poleward expansion of the known distribution in the region. The shift and intensification of the warm, saline waters in a southerly direction is likely to make conditions unfavourable for the population of *L. reynaudii* distributed locally and as such have major implications on the artisanal squid jig fishery based in Tombua.

The characteristic plasticity in the life-history and biology coupled with the high mobility of cephalopods, has been suggested to allow these species to adapt more rapidly to changing environmental conditions (Doubleday 2016, O'Brien et al. 2018). The interaction of the effects of climate change and the adaptive nature of cephalopods is ultimately likely to result in changes in the distribution and abundance of cephalopods (Pierce et al. 2010, Xavier et al. 2014, Doubleday 2016, O'Brien et al. 2018). Such changes are likely to have implications for coastal communities dependent upon these resources. Uncertainties highlight the need for flexible, adaptive management strategies, particularly within data deficient fisheries in order to increase the adaptive capacity of vulnerable communities (Xavier et al. 2014, FAO 2018). Cephalopods within the region of southern Angola, within the region of the ABFZ, a global climate change hotspot, provide a unique opportunity to investigate potential changes in the population dynamics of *L. reynaudii* and *S. vermiculata*, and the fisheries which are dependent upon them. Such research may be critical in developing adaptive management strategies for cephalopod species, within changing environmental conditions, both locally and globally.

### *Concluding remarks and future research considerations*

The results from the current study provide a first insight into the population characteristics of *L. reynaudii* and *S. vermiculata* off the coast of southern Angola, where the two species are an essential resource to the artisanal cephalopod jig fishery. Additional research on the following may provide further knowledge on the study species, as well as provide insight into the management and development of the fishery, whilst investigating the response of these two species to changing environments within a global hotspot:

1. An in depth understanding of the movement and migration of the two species, at the various life history stages which *inter alia*, would provide insight into demographic population connectivity.
2. Extensive research on the physiological limitations, such as thermal tolerances, of these species at all life history stages may provide valuable information into the consequences of climatic changes.
3. Vulnerability assessments which focus on the exposure to climate change within the global hotspot and the sensitivity and adaptive capacity of local, artisanal fishing communities can provide a basis for adaptive policies as well as highlight the risks and opportunities for those dependent on the resource.
4. Investigate, as a precautionary approach with the current limited data, the effects of the introduction of effort control in the short to medium term to allow for the appropriate management measures to be adopted so as to ensure the sustainable use of fisheries resources.

*References:*

- ACP Fish II. 2013. Estudo da Cadeia de Abastecimento das Pesca Artesanaus e Mercados na Região de Luanda – Angola. Technical Report. Projecto ref. N° SA-4.3-B23
- Agnew DJ, Pearce J, Pramod G, Peatman T, Watson R, Beddington JR, Pitcher TJ. 2009. Estimating the Worldwide Extent of Illegal Fishing. *PLoS ONE* **4**: e4570. <https://doi.org/10.1371/journal.pone.0004570>
- Agnew DJ, Hill SL, Beddington JR, Purchase LV, Wakeford RC. 2005. Sustainability and management of southwest Atlantic squid fisheries. *Bulletin of Marine Science* **76**: 579 – 593. <https://doi.org/10.1071/MF12085>
- Agostinho D, Fielding P, Sowman M, & Bergh M. 2005. *Overview and analysis of socio-economic and fisheries information to promote the management of Artisanal Fisheries in the BCLME region - Angola. Final Report and Recommendations. Evaluation.*
- Allison EH, Perry AL, Badjeck MC, Adger WN, Brown K, Conway D, Halls AS, Graham MP, Reynolds JD, Andrew NL, Dulvy NK. 2009. Vulnerability of national economies to the impacts of climate change on fisheries. *Fish and Fisheries* **10**: 173–196. <https://doi.org/10.1111/j.1467-2979.2008.00310.x>
- Almonacido-Rioseco E, Hernandez-Garcia V, Solari AP, del Pino, AS, Castro JJ. 2009. Sex identification and biomass reconstruction from the cuttlebone of *Sepia officinalis*. *Marine Biodiversity Records*. **2**: E7 <https://doi.org/10.1017/S1755267208000079>
- Alves DM, Cristo M, Sendão J, Borges TC. 2006. Diet of the cuttlefish *Sepia officinalis* (Cephalopoda: Sepiidae) off the south coast of Portugal (eastern Algarve). *Journal of the Marine Biological Association of the United Kingdom* **86**: 429-436. <http://dx.doi.org/10.1017/S0025315406013312>
- Amare, Mulubrhan & Abay, Kibrom & Arndt, Channing & Shiferaw, Bekele. 2021. Youth Migration Decisions in Sub-Saharan Africa: Satellite-Based Empirical Evidence from Nigeria. *Population and Development Review* **47**. <https://doi.org/10.1111/padr.12383>

- Amodio P, Boeckle M, Schnell A, Ostojic L, Fiorito G, Clayton N. 2018. Grow Smart and Die Young: Why Did Cephalopods Evolve Intelligence? *Trends in Ecology & Evolution* **34**. <http://dx.doi.org/10.1016/j.tree.2018.10.010>
- Anderson RJ, Bolton JJ, Smit AJ, da Silva Neto D. 2012. The Seaweeds of Angola: The Transition Between Tropical and Temperate Marine Floras on the West Coast of Southern Africa. *African Journal of Marine Science* **34**: 1-13.  
<https://doi.org/10.2989/1814232X.2012.673267>
- Angola. 2004. Lei dos Recursos Biológicos Aquático n.º6-A/04, 8<sup>th</sup> of October 2004).
- Angola. 2016. Angola National Report for Habitat III. Natitional Habitat Committee Presidential Decree no. 18/24. Luanda, Angola. 133pp
- Angola. 2018. Decreto Presidencial n.o 23/18:Aprova o Estatuto Orgânico do Ministério das Pescas e do Mar. Luanda. 31 January 2018.
- Angola. 2020a. Decreto Presidencial n.o 130/20: Medida de Gestão das Pescarias Marinhas, da Pesca Continental, da Aquicultura e do Sal par o Ano de 2020. Luanda. 11 May 2020.
- Angola. 2020b. Decreto Presidencial n.o 177/20: Estatuto Orgânico do Ministério da Agricultura e Pescas. Luanda. 23 June 2020.
- Anguilera SE. 2018. Measuring squid fishery governance efficacy: A social-ecological system analysis. *International Journal of the Commons* **12**: 21-57.  
<http://doi.org/10.18352/ijc.821>
- Arkhipkin AI, Rodhouse PGK, Pierce GJ, Sauer W, Sakai M, Allcock L, Arguelles J, Bower JR, Castillo G, Ceriola L, Chen CS, Chen X, Diaz-Santana M, Downey N, González AF, Granados Amores J, Green CP, Guerra A, Hendrickson LC, Ibáñez C, Ito K, Jereb P, Kato Y, Katugin ON, Kawano M, Kidokoro H, Kulik VV, Laptikhovsky VV, Lipiński MR, Liu B, Mariátegui L, Marin W, Medina A, Miki K, Miyahara K, Moltschaniwskyj N, Moustahfid H, Nabhitabhata J, Nanjo N, Nigmatullin CM, Ohtani T, Pecl G, Perez JAA, Piatkowski U, Saikliang P, Salinas-Zavala CA, Steer

- M, Tian Y, Ueta Y, Vijai D, Wakabayashi T, Yamaguchi T, Yamashiro C, Yamashita N, Zeidberg, LD. 2015. 'World squid fisheries', *Reviews in Fisheries Science and Aquaculture* **23**: 92-252. <https://doi.org/10.1080/23308249.2015.1026226>
- Arkhipkin A, Hendrickson L, Payá, I, Pierce G, Roa-Ureta R, Robin JP & Winter, A. 2021. Stock assessment and management of cephalopods: advances and challenges for short-lived fishery resources. *ICES Journal of Marine Science* **78**: 1-17. <https://doi.org.10.1093/icesjms/fsaa038>
- Augustyn C.J. 1989. Systematics, life cycle and resource potential of the chokker squid *Loligo vulgaris reynaudii*. Ph.D. thesis, University of Port Elizabeth. 378pp
- Augustyn CJ. 1990. Biological studies on the chokker squid *Loligo vulgaris reynaudii* (Cephalopoda; Myopsida) on spawning grounds off the south-east coast of South Africa. *South African Journal of Marine Science* **9**: 11-26. <https://doi.org/10.2989/025776190784378736>
- Augustyn CJ. 1991. The biomass and ecology of the chokka squid, *Loligo vulgaris reynaudii* off the West Coast of South Africa. *South African Journal of Zoology* **26**: 164 – 181. <https://doi.org/10.1080/02541858.1991.11448245>
- Augustyn CJ, Grant WS. 1988. Biochemical and morphological systematics of *Loligo vulgaris vulgaris* Lamarck and *Loligo vulgaris reynaudii* d'Orbigny nov.comb. (Cephalopoda: Myopsida). *Malacologia*. 29:215-233.
- Augustyn CJ, Lipiński MR, Sauer WHH. 1992. Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. *South African Journal of Marine Science* **12**: 903 – 918. <https://doi.org/10.2989/02577619209504751>
- Augustyn CJ, B. Roel A, Cochrane KL. 1993. Stock assessment in the chokka squid *Loligo vulgaris reynaudii* fishery off the coast of South Africa. In: Okutani T, O'Dor RK, Kubodera T (eds) *Recent Advances in Fisheries Biology*, Tokyo: Tokai University Press. pp 3–14.

- Augustyn CJ, Lipiński MR, Sauer WHH, Roberts MJ, Mitchell-Ines BA. 1994. Chokka squid on the Agulhas Bank: life history and ecology. *South African Journal of Science* **90**: 143-154. [https://hdl.handle.net/10520/AJA00382353\\_4623](https://hdl.handle.net/10520/AJA00382353_4623)
- Augustyn CJ, Lipiński MR, Roeleveld MAC. 1995. Distribution and abundance of Sepioidea off South Africa. *South African Journal of Marine Science* **16**: 69-83. <https://doi.org/10.2989/025776195784156593>
- Augustyn CJ, Roel BA. 1998. Fisheries Biology, stock assessment and management of the chokka squid (*Loligo vulgaris reynaudii*) in South African waters: An overview. *California Cooperative Oceanic Fisheries Investigations Report* **39**: 71-80
- Bachelery M-L, Illig S, Dadou I. 2015. Interannual variability in the South-East Atlantic Ocean, focusing on the Benguela Upwelling System: Remote versus local forcing. *Journal of Geophysical Research: Oceans* **120**: <https://doi.org/10.1007/s00227-012-2059-6>
- Basurto X, Franz N, Mills D, Viridin J, Westlund L. 2017. *Improving our Knowledge on Small-Scale Fisheries: Data Needs and Methodologies* (Rome). FAO Fisheries and Aquaculture Proceedings (FAO).
- Baudron A, Ulrich C, Nielsen JR, Boje J. 2010. Comparative evaluation of a mixed-fisheries effort-management system based on the Faroe Islands example. *ICES Journal of Marine Science* **67**: 1036–1050.
- BCLME. 2007. The changing state of the Benguela Current Large Marine Ecosystem: Expert workshop on climate change and variability and impacts thereof in the BCLME region.
- Belcari P, Sartor P, Sanchez P, Demestre M, Tsangrdis A, Leondarakis P, Lefkaditou E, Papaconstantinou C. 2002. Exploitation patterns of the cuttlefish, *Sepia officinalis* (Cephalopoda, Sepiidae), in the Mediterranean Sea. *Bulletin of Marine Science* **71**: 187-196.

- Belhabib D, Harper S, Zeller D. and Pauly D. 2012. Reconstruction of marine fisheries catches from Morocco (north, central and south), 1950-2010. In: Belhabib D, Zeller D, Harper S, Pauly D (eds.) *Marine fisheries catches in West Africa, 1950-2010, part I*. Fisheries Centre Research Reports 20 (3). Fisheries Centre, University of British Columbia, Canada.
- Belhabib D, Koutab V, Sall A, Lam VWY, Pauly D. 2014. Fisheries catch misreporting and its implications: The case of Senegal. *Fisheries Research*. **151**: 1-11.  
<https://doi.org/10.1016/j.fishres.2013.12.006>.
- Belhabib D, Divovich E. 2015. Rich fisheries and poor data: a catch reconstruction for Angola, 1950 – 2010, an update of Belhabib and Divovich (2014). Pp 115-128. In: Belhabib, D, Pauly D (eds). *Fisheries catch reconstructions: West Africa, Part II*. Fisheries Centre Research Reports. 23. Fisheries Center, University of British Columbia.
- Belhabib D, Greer K & Pauly D. 2017. Trends in Industrial and Artisanal Catch Per Effort in West African Fisheries. *Conservation Letters* **11**: 1-10.  
<https://doi.org/10.1111/conl.12360>
- Belhabib D, Sumaila UR, Pauly D. 2015. Feeding the poor: contribution of West African fisheries to employment and food security. *Ocean Coastal Management* **111**: 72-81.  
<http://dx.doi.org/10.1016/j.ocecoaman.2015.04.010>
- Benguela Current Commission. 2015. Evidence based management recommendations for the Angolan Horse Mackerel and Sardinella Fishery with special emphasis on use value and employment. Specific objective 3 SoV 1 Case Study Angola.
- Bennett, A, Patil P, Kleisner K, Rader D, Virdin J, Basurto X. 2018. *Contribution of Fisheries to Food and Nutrition Security: Current Knowledge, Policy, and Research*. NI Report.
- Bergh PE, Davies S. 2002. Fishing monitoring, control and surveillance. Pages 373–403 in K. L. Cochrane and S. M. Garcia, editors. *A fishery manager's guidebook: management measures and their application*. Food and Agriculture Organization, Rome.

- Bianchi G. 1986. Guia de campo espécies comerciais marinhas e de águas salobres de Angola. Fichas FAO de identificação de espécies para popósitos comerciais. Roma, FAO, 184 p.
- Bianchi G. 1992. Demersal assemblages of the continental shelf and upper slope of Angola. *Marine Ecology Progress Series* **81**: 101-120.
- Billard P, Schnell AK, Clayton NS, Jozet-Alves C. 2020. Cuttlefish show flexible and future-dependent foraging cognition. *Biology Letters* **16**: 20190743.  
<https://doi.org/10.1098/rsbl.2019.0743>
- Bloor I, Attrill M, Jackson E. 2013. A Review of the Factors Influencing Spawning, Early Life Stage Survival and Recruitment Variability in the Common Cuttlefish (*Sepia officinalis*). *Advances in Marine Biology* **65**: 1-65. <http://dx.doi.org/10.1016/B978-0-12-410498-3.00001-X>
- Bogard J, Farook SC, Marks G, Waid J, Belton B, Ali M, Toufique K, Mamun A, Thilsted SH. 2017. Higher fish but lower micronutrient intakes: temporal changes in fish consumption from capture fisheries and aquaculture in Bangladesh. *PLoS ONE* **12**: e0175098. <https://doi.org/10.1371/journal.pone.0175098>
- Boletzky SV. 1993. Development and reproduction in the evolutionary biology of Cephalopoda. *Gebios* **26**: 33-38. [https://doi.org/10.1016/S0016-6995\(06\)80358-X](https://doi.org/10.1016/S0016-6995(06)80358-X).
- Bowker DW. 1995. Modelling the patterns of dispersion of length at age in teleost fishes. *Journal of Fish Biology* **3**: 469-484. <http://dx.doi.org/10.1111/j.1095-8649.1995.tb05988.x>
- Boyle PR. 1990. Cephalopod Biology in the Fisheries Context. *Fisheries Research* **8**: 303-321. [https://doi.org/10.1016/0165-7836\(90\)90001-C](https://doi.org/10.1016/0165-7836(90)90001-C)
- Boyle P, Rodhouse P. 2005. Cephalopods: Ecology and Fisheries. Blackwell Science, Oxford. <http://dx.doi.org/10.1002/9780470995310>

- Boyle PR, Pierce GJ, Hastie LC. 1995. Flexible reproductive strategies in the squid *Loligo forbesii*. *Marine Biology* **121**: 501–508. <https://doi.org/10.1007/BF00349459>
- Boyle PR & Boletzky S. 1996. Cephalopod populations: definitions and dynamics. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **351**: 985-1002. <https://doi.org/10.1098/rstb.1996.0089>
- Burg M. 2019. Status and management of the South African Squid and West Coast Rock Lobster- 2017. Oceana Group, Cape Town.
- Caddy JF. 1983. The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. In: Caddy JF (eds) *Advances in Assessment of World Cephalopod Resources*. Fisheries Technical Paper 231, FAO, Rome, pp 416-499.
- Caddy JF, Rodhouse PG. 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? *Reviews in Fish Biology and Fisheries* **8**: 431-444
- Carpenter KE, De Angelis N. eds. 2014. The living marine resources of the Eastern Central Atlantic. Volume 1: Introduction, crustaceans, chitons, and cephalopods. FAO Species Identification Guide for Fishery Purposes, Rome, FAO. 663 pp
- Castro BG, Guerra A 1990. The diet of *Sepia officinalis* (L., 1758) and *Sepia elegans* (Blainville, 1827) (Mollusca, Cephalopoda) from the Ría de Vigo (NW Spain). *Scientia Marina* **54**: 375-388.
- Chan CY, Tran N, Pethiyagoda S, Crissman CC, Sulser TB, Phillips MJ. 2019. Prospects and challenges of fish for food security in Africa. *Global Food Security* **20**: 17-25. <https://doi.org/10.1016/j.gfs.2018.12.002>.
- Clarke MR. 1996. The Role of Cephalopods in the World's Oceans: An Introduction. *Philosophical Transactions: Biological Sciences* **351**: 979-983.
- Cochrane KL, Augustyn CJ, Fairweather T, Japp D, Kilongo K, Iitembu J, Moroff N, Roux JP, Shannon L, van Zyl B, van Velho F. 2009. Benguela Current Large Marine Ecosystem – Governance and Management for an Ecosystem Approach to Fisheries

in the Region. *Coastal Management* **37**: 235 – 254.

<https://doi.org/10.1080/08920750902851187>

Cochrane KL, Ortega-Cisneros K, Iitembu JA, dos Santos CI, Sauer

WHH. 2020. Application of a general methodology to understand vulnerability and adaptability of the fisheries for small pelagic species in the Benguela countries: Angola, Namibia and South Africa. *African Journal of Marine Science* **42**: 473-493. <https://doi.org/10.2989/1814232X.2020.1844798>

Coelho ML, Quintela J, Bettencourt V, Olavo G, Villa H. 1994. Population structure, maturation patterns and fecundity of the squid *Loligo vulgaris* from southern Portugal. *Fisheries Research* **21**:87–102. [https://doi.org/10.1016/0165-7836\(94\)90097-3](https://doi.org/10.1016/0165-7836(94)90097-3)

Colberg F, Reason C. 2006. A model study of the Angola Benguela Frontal Zone: Sensitivity to atmospheric forcing. *Geophysical Research Letters* **331**.  
<http://dx.doi.org/10.1029/2006GL027463>

Collins MA, De Grave S, Lordan C, Burnell GM, Rodhouse PG. 1994. Diet of the squid *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Irish waters. *ICES Journal of Marine Science* **51**: 337-344. <https://doi.org/10.1006/jmsc.1994.1034>

DAFF (Department of Agriculture, Forestry and Fisheries). 2016. *Status of the South African marine fishery resources 2016*. Cape Town: DAFF

Dan S, Hamasaki K, Yamashita T, Oka M, Kitada S. 2012. Age-based life cycle traits of the broadclub cuttlefish *Sepia latimanus* confirmed through release-recapture experiments. *Aquatic Biology* **17**: 181-195. <https://doi.org/10.3354/ab00474>

Davies D, Nelson K. 2018. Supporting Sustainable *Sepia* stocks. Report 2: the English Channel Fishery for Common Cuttlefish (*Sepia officinalis*) IFCA, Sussex. 29pp

De Beer CL. 2014. Genetic and morphometric variation of *Octopus vulgaris* in the Benguela Current Region. MSc Thesis, Rhodes University.

- DEFF (Department of Environment, Forestry and Fisheries) 2020. Status of the South African marine fishery resources 2020. Cape Town: DEFF. 112pp.
- De Young C, Hjort A, Sheridan S, Davies S. *Climate change implications for fisheries of the Benguela Current region – Making the best of change*. FAO/Benguela Current Commission Workshop, 1–3 November 2011, Windhoek, Namibia. FAO Fisheries and Aquaculture Proceedings. No. 27. Rome, FAO. 2012. 125 pp.
- Denis V, Robin J-P. 2001. Present status of French Atlantic fishery for cuttlefish (*Sepia officinalis*). *Fisheries Research* **182**: 1–12.
- Doubleday ZA, Prowse TAA, Arkhipkin A, Pierce GJ, Semmens J, Steer M, Leporati SC, Lourenço S, Quetglas A, Sauer W, Gillanders BM. 2016. Global proliferation of cephalopods. *Current Biology* **25**: 406-407. <https://doi.org/10.1016/j.cub.2016.04.002>
- Downey NJ, Roberts MJ, Baird D. 2010. An investigation of the spawning behaviour of the chokka squid *Loligo reynaudii* and the potential effects of temperature using acoustic telemetry. *ICES Journal of Marine Science* **67**: 231-243. <https://doi.org/10.1093/icesjms/fsp237>
- Du Preez M. 2009. Fishing for sustainable livelihoods in Angola: The cooperative approach. South African Institute of International Affairs, Johannesburg.
- Duarte A, Fielding P, Sowman M, Bergh M. 2005. Overview and analysis of socio-economic and fisheries information to promote the management of artisanal fisheries in the Benguela Current Large Marine Ecosystem (BCLME) region (Angola). Unpublished Final Report. Rep. No. LMRAFSE0301B. Cape Town Environmental Evaluation Unit, University of Cape Town, Cape Town.
- Dunn MR 1999. Aspects of the stock dynamics and exploitation of cuttlefish, *Sepia officinalis* (Linnaeus, 1758) in the English Channel. *Fisheries Research* **40**: 277–293. [http://dx.doi.org/10.1016/S0165-7836\(98\)00223-9](http://dx.doi.org/10.1016/S0165-7836(98)00223-9)
- Dunning M, McKinnon S, Lu C, Yeatman J, Cameron D. 1994. Demersal cephalopods of the Gulf of Carpentaria, Australia. *Australian Journal of Marine and Freshwater Research* **45**: 351–374.

- Duysak O, Özcan G, Çek S, Tureli C. 2014. Reproductive Biology of the common cuttlefish (*Sepia officinalis* Linnaeus 1758) in Iskenderun Bay (Northeastern Mediterranean). *Indian Journal of Geo-Marine Sciences* **43**: 1689-1694.
- Ekau W, Verheye H. 2005. Influence of oceanographic fronts and low oxygen on the distribution of ichthyoplankton in the Benguela and southern Angola currents. *African Journal of Marine Science* **27**: 629-639.  
<http://dx.doi.org/10.2989/18142320509504123>
- Emam WH, Saad AA, Riad R, Alweraly HA. 2014. Morphometric study and length-weight relationship on the squid *Loligo forbesi* (Cephalopoda: Loliginidae) from the Egyptian Mediterranean Waters. *International Journal of Environmental Science and Engineering* **5**: 1-13
- FAO CECAF Scientific Committee. *Report of the FAO/CECAF Working Group on the Assessment of Demersal Resources –Subgroup South Freetown, Sierra Leone, 9–18 October 2008*. CECAF/ECAF Series/ COPACE/PACE Series No. 11/73. Rome, FAO.
- FAO CECAF Scientific Committee (FAO CECAF-SC). CECAF Fisheries Reports 2011. Angola Trawl demersal fish fishery – Angolan waters. FIRMS Reports. In: *Fisheries and Resources Monitoring System*. Rome.
- FAO. 1995. Code of Conduct for Responsible Fisheries. FAO, Rome, Italy. In: <http://www.fao.org/docrep/005/v9878e/v9878e00.HTM>.
- FAO. 2002. The costs of monitoring, control and surveillance of fisheries in developing countries. FAO Fisheries Circular No 976. Rome. 47pp
- FAO. 2005. Increasing the contribution of small-scale fisheries to poverty alleviation and food security. FAO Technical Guidelines for Responsible Fisheries. No. 10. Rome. 79 pp
- FAO. 2008. Towards integrated assessment and advice in small-scale fisheries: principles and processes. FAO Fisheries and Aquaculture Technical Paper 515. Rome.

- FAO 2010a. Safety at sea for small-scale fisheries in developing countries. Field Document No. 10. Rome. 83pp
- FAO. 2010b. Post-harvest losses in small-scale fisheries: Case studies in five sub-Saharan African countries. *FAO Fisheries and Aquaculture Technical Paper*. No. 550. Rome. 72pp
- FAO. 2012. The state of world fisheries and aquaculture 2012. Rome, Italy: FAO Fisheries Department. 209 pp.
- FAO 2016a. Technical and socio-economic characteristics of small-scale coastal fishing communities, and opportunities for poverty alleviation and empowerment. FAO Fisheries and Aquaculture Circular No.1111. Rome. 123pp
- FAO. 2016b. The State of World Fisheries and Aquaculture 2016. Contributing to food security and nutrition for all. Rome. 200pp.
- FAO. 2017. Workshop on improving our knowledge on small-scale fisheries: data needs and methodologies. Workshop proceedings, 27–29 June 2017, Rome, Italy. FAO Fisheries and Aquaculture Proceedings No. 55. Rome. 87pp
- FAO. 2018. Impacts of climate change on fisheries and aquaculture. Synthesis of current knowledge, adaptation and mitigation options. FAO Fisheries and Aquaculture Technical Paper 627. Rome. 628pp
- FAO. 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in action. Rome. <https://doi.org/10.4060/ca9229en>
- Forsythe JW. 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In Okutani T, O’Dor RK, Kubodera T (eds) *Recent Advances in Cephalopod Fisheries Biology*. Tokai University Press, Tokyo, Japan, pp133-143.
- Gabr HR, Hanlon RT, Hanafy MH, El-Etreby SG. 1998. Maturation, fecundity and seasonality of two commercially valuable cuttlefish, *S. paraonis* and *S. dollfusi*, in Suez Canal. *Fisheries Research* **39**: 99-115.

- Ganias K, Christidis G, Kompogianni I-F, Simeonidou X, Voultziadou E, Antoniadou C. 2021. Fishing for cuttlefish with traps and trammel nets: A comparative study in Thermaikos Gulf, Aegean Sea. *Fisheries Research* **234**: 105783. <https://doi.org/10.1016/j.fishres.2020.105783>.
- García-Flórez L, Morales J, Gaspar M, Castilla-Espino D, Mugerza E, BerthouP, Fuente L, Oliveira MM, Moreno O, García del Hoyo J, Arregi L, Vignot C, Chapela R, Murillas A. 2014. A novel and simple approach to define artisanal fisheries in Europe. *Marine Policy* **44**: 152–159. [10.1016/j.marpol.2013.08.021](https://doi.org/10.1016/j.marpol.2013.08.021).
- Getu A, Misganaw K, Bazezew M. 2015. Post-harvesting and Major Related Problems of Fish Production. *Fisheries and Aquaculture Journal*. **6**: 154. <https://doi.org/10.4172/2150-3508.1000154>
- Giordano D, Bottari T, Busalacchi B, Jereb P, Ragonese S, Rinelli P. 2005. On the relationship between beaks and body size in *Sepia officinalis* from the southern Tyrrhenian Sea (Central Mediterranean). *Cahiers de Biologie Marine* **46**: 35-41.
- Gissi E, Manea E, Mazaris AD, Frascchetti S, Almpnidou V, Bevilacqua S, Coll M, Guarnieri G, Lloret-Lloret E, Pascual M, Petza D, Rilov G, Schonwald M, Stelzenmüller V, Katsanevakis, S. 2020. A review of the combined effects of climate change and other local human stressors on the marine environment. *Science of The Total Environment* **755**: 142564. <https://doi.org/10.1016/j.scitotenv.2020.142564>.
- Glazer JP, Butterworth DSA 2016 updated assessment of the squid resource, *Loligo reynaudii*. DAFF Branch Fisheries document. FISHERIES/2016/OCT/SWG-SQ/25: 19pp.
- Golden C, Allison EH, Cheung WW, Dey MM, Halpern, BS, McCauley DJ, Smith M, Bapu V, Dirk Z, Myers SS. 2016. Fall in fish catch threatens human health. *Nature* **534**: 317–320. <https://doi.org/10.1038/534317a>
- Golikov AV, Sabirov RM, Lubin PA, Jørgensen LL. 2013. Changes in distribution and range structure of Arctic cephalopods due to climatic changes of the last decades. *Biodiversity* **14**: 28–35.

- Gonçalves HJB, Queda O, Ribeiro ML. Pescadores Artesanais na Comunidade Pesqueira do Nzeto-Angola , Anais do VIII Simpósio Sobre Reforma Agrária e Questões Rurais Terra, Trabalho e Lutas No Século XXI: Projetos Em Disputa. UNIARA 2018.
- Gonçalves HJB, Ribeiro ML, Ferrante VLSBB, Queda O, Sossae FC. 2018. Women in fishing activity: a study in the Nzeto-Angola fishing community. *Reviste Brasileira Multidisciplinar* **23**: 68-75. <https://doi.org/10.25061/2527-2675/ReBraM/2020.v23i3.1126>
- Guerra Á. 2006. Ecology of *Sepia officinalis*. In *The Cuttlefish Sepia officinalis*, 56, pp. 970107. Ed. By N. Koueta, JP Andrade and S von Boletzky. *Vie et Milieu*. **56**
- Guerra Á, Castro BG. 1988. On the life cycle of *Sepia officinalis* (Cephalopoda, Sepioidea) in the ria de Vigo (NW Spain). *Cahiers de Biologie* **29**: 395-405
- Guerra Á, Castro BG. 1989. Some aspects of the biology of *Sepia elegans* (Cephalopoda, Sepioidea) from Ria de Vigo, NW Spain. *Vie Milieu* **39**: 213-218
- Guerra Á, Rocha F. 1994. The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). *Fisheries Research* **21**: 43–69. [https://doi.org/10.1016/0165-7836\(94\)90095-7](https://doi.org/10.1016/0165-7836(94)90095-7)
- Guerra Á, Perez-Losada M, Rocha F, Sanjuan A. 2001. Species differentiation of *Sepia officinalis* and *Sepia hierredda* (Cephalopoda: Sepiidae) based on morphological and allozyme analyses. *Journal of the Marine Biological Association of the United Kingdom*. **81**: 271-281. <http://dx.doi.org/10.1017/S0025315401003745>
- Guerra Á, Allcock L, Pereira J. 2010. Cephalopod life history, ecology and fisheries: An introduction. *Fisheries Research* **106**: 117-124. <http://dx.doi.org/10.1016/j.fishres.2010.09.002>
- Guerra-Marrero Á, Jiménez-Alvarado D, Hernández-García V, Curbelo-Muñoz L, Castro-Hernández JJ. 2019. Cuttlebone morphometrics and sex identification of *Sepia bertheloti* (d'Orbigny, 1835) from the central-east Atlantic. *Helgoland Marine Research* **73**:10. <https://doi.org/10.1186/s10152-019-0531-0>

- Gutowska MA, Melzner F, Pörtner HO, Meier S. 2010. Cuttlebone calcification increases during exposure to elevated seawater pCO<sub>2</sub> in the cephalopod *Sepia officinalis*. *Marine Biology* **157**: 1653–1663. <https://doi.org/10.1007/s00227-010-1438-0>
- Hall KC & Fowler AJ (eds.) 2003. The fisheries biology of the cuttlefish *Sepia apama* Gray, in South Australian waters. Final Report to FRDC (Project No. 98/151). SARDI Aquatic Sciences, Adelaide, 289pp
- Hanlon, R.T. 1998. Mating systems and sexual selection in the squid *Loligo*: How might commercial fishing on spawning grounds affect them? *California Cooperative Oceanic Fisheries Report* **39**: 92 – 100.
- Hanlon RT, Messenger JB. 1996. Cephalopod Behaviour. Cambridge University Press, Cambridge.
- Hanlon RT, Smale MJ, Sauer WHH. 2002. The mating system of the squid *Loligo vulgaris reynaudii* (Cephalopoda, Mollusca) off South Africa: Fighting, guarding, sneaking, mating and egg laying behavior. *Bulletin of Marine Science* **71**: 331-345.
- Harwood J, Walton M. 2002. Interactions between seals and commercial fisheries in the north-east Atlantic. Fisheries Series FISH 110 EN. Working paper to the European Parliament's Committee on Fisheries European Parliament, Luxembourg.
- Hastie L, Pierce G, Wang J, Bruno I, Moreno A, Piatkowski U, Robin JP. 2009. Cephalopods In The North-eastern Atlantic: Species, Biogeography, Ecology, Exploitation And Conservation. *Oceanography and Marine Biology* **47**: 111-190. <http://dx.doi.org/10.1201/9781420094220.ch3>
- Hatanaka H. 1979. Spawning season of cuttlefish, *Sepia officinalis* Linne, off the northwestern coast of Africa. In Report of the ad hoc Working Group on the Assessment of Cephalopod stocks, Appendix 5, 7pp. Fishery Committee for the Eastern Central Atlantic CECAF/ECAF Series 78/11.

- Healey AJE, McKeown NJ, Potts WM, De Beer CL, Sauer W, Shaw PW. 2017. Phylogeny of the *Sepia officinalis* species complex in the eastern Atlantic extends the known distribution of *Sepia vermiculata* across the Benguela upwelling region. *African Journal of Marine Science* **39**: 307-313.  
<https://doi.org/10.2989/1814232X.2017.1371076>
- Henriques R, Potts WM, Sauer WHH, Shaw PW. 2014a. Incipient genetic isolation of a temperate migratory coastal sciaenid fish (*Argyrosomus inodorus*) within the Benguela Cold Current system. *Marine Biological Research* **11**: 423-429
- Henriques R, Potts WM, Santos CV, Sauer WHH, Shaw PW. 2014b. Population connectivity and Phylogeography of a Coastal Fish, *Atractoscion aequidens* (Sciaenidae), across the Benguela Current Region: Evidence of an Ancient Vicariant Event. *PLoS ONE* **9**: 1-11.
- Hobday AJ, Pecl GT. 2014. Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. *Review in Fish Biology and Fisheries* **24**: 415-425.  
<https://doi.org/10.1007/s11160-013-9326-6>
- Hunsicker ME, Essington TW, Watson R, Sumaila UR. 2010. The contribution of cephalopods to global marine fisheries: can we have our squid and eat them too? *Fish and Fisheries* **11**: 421-438. <http://dx.doi.org/10.1111/j.1467-2979.2010.00369.x>
- Huntley B. 2019. Huntley et al. (eds) Biodiversity of Angola.  
[https://doi.org/10.1007/978-3-030-03083-4\\_2](https://doi.org/10.1007/978-3-030-03083-4_2)
- Hutchings L, van der Lingden CD, Shannon LJ, Crawford RJM, Verheyen HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS. 2009. The Benguela Current: An ecosystem of four components. *Progress in Oceanography* **83**: 15-32
- Ibáñez CM, Arancibia, Cubillos LA. 2008. Biases in determining the diet of jumbo squid *Dosidicus gigas* (D'Orbigny 1835) (Cephalopoda: Ommastrephidae) off southern

- central Chile (34°S - 40°S) *Helgoland Marine Research* **62**: 331.  
<https://doi.org/10.1007/s10152-008-0120-0>
- Ibáñez CM, Keyl F. 2010. Cannibalism in cephalopods. *Reviews in Fish Biology and Fisheries* **20**: 123-136. <http://dx.doi.org/10.1007/s11160-009-9129-y>
- ICES. 2020. Working Group on Cephalopod Fisheries and Life History (WGCEPH; outputs from 2019 meeting). *ICES Scientific Reports* **2**: 46. 121pp.  
<https://doi.org/10.17895/ices.pub.6032>
- Isaacs M & Hara M. 2015. Backing Small-Scale Fisheries: Opportunities and Challenges in Transforming the Fish Sector. Institute for Poverty, Land and Agrarian Studies, Cape Town, South Africa. 22pp. <https://doi.org/10.13140/RG.2.1.2240.0720>.
- Jackson GD, O’Dor R. 2001. Time, space and the ecophysiology of squid growth, life in the fast lane. *Vie et Milieu* **51**: 205-215.
- Jackson GD. 2004. Advances in defining the life histories of myopsid squid. *Marine and Freshwater Research* **55**: 357–365. <https://doi.org/10.1071/MF03152>.
- Jarre A, Hutchings L, Kirkman SP, Kreiner A, Tchivalango PCM, Kainge P, Uanivi U, van der Plas AK, Blamey LK, Coetzee JC, Lamont T, Samaai T, Verheye HM, Yemane DG, Axelson BE, Ostrowski M, Stenevik EK, Loeng H. 2015. Synthesis: climate effects on biodiversity, abundance, and distribution of marine organisms in the Benguela. *Fisheries Oceanography* **24**: 122–149. <https://doi.org/10.1111/fog.12086>
- Jensen SK. 2018. Angola’s Infrastructure Ambitions Through Booms and Busts. Policy, Governance and Reform. Chatham House, London. 38pp.
- Jentoft, S. 2000. The community: A missing link of fisheries management. *Marine Policy*. **24**: 53-59. [https://doi.org/10.1016/S0308-597X\(99\)00009-3](https://doi.org/10.1016/S0308-597X(99)00009-3).
- Jentoft S. 2006. Beyond fisheries management: The Phronetic dimension. *Marine Policy*. **30**: 671-680.

- Jereb P, Roper CFE. 2005. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 1. Chambered nautilus and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae). FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 1. Rome, FAO. 2005. 262p. 9 colour plates.
- Jereb P, Roper CFE. 2010. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 2. Myopsid and Oegopsid Squids. FAO Species Catalogue for Fishery Purposes. No 4, Vol 2. Rome, FAO 2010, 605p.
- Jereb P, Allcock AL, Lefkaditou E, Piatkowski U, Hastie LC, Pierce GJ. 2015. Cephalopod biology and fisheries in Europe: II. Species Accounts. ICES Cooperative Research Report No. 325. 360 pp. <https://doi.org/10.17895/ices.pub.5493>
- John H-C, Mohrholz V, Lutjeharms J. 2001. Cross front hydrography and fish larval distribution at the Angola-Benguela Frontal Zone. *Journal of Marine Systems* **28**: 91-111. [https://doi.org/10.1016/S0924-7963\(00\)00085-3](https://doi.org/10.1016/S0924-7963(00)00085-3)
- John H-C, Mohrholz V, Lutjeharms J, Weeks S, Cloete R, Kreiner A, da Silva Neto D. 2004. Oceanographic and faunistic structures across an Angola current intrusion into northern Namibian waters. *Journal of Marine Systems* **46**: 1-22.
- Johnsen JP. 2014. Is fisheries governance possible? *Fish and Fisheries* **15**: 428–444. [10.1111/faf.12024](https://doi.org/10.1111/faf.12024)
- Johnsen JP, Holm P, Sinclair PS, Bavington D. 2009. The cyborgization of the fisheries. On attempts to make fisheries management possible. *Maritime Studies* **7**: 9–34.
- Jones JB, Pierce GJ, Saborido-Rey F, Brickle P, Kuepper FC, Shcherbich ZN, Arkhipkin AI. 2019. Size-dependent change in body shape and its possible ecological role in the Patagonian squid (*Doryteuthis gahi*) in the Southwest Atlantic. *Marine Biology* **166**: 54 [10.1007/s00227-019-3501-9](https://doi.org/10.1007/s00227-019-3501-9)

- Kaplan MB, Mooney TA, McCorkle DC, Cohen AL (2013) Adverse Effects of Ocean Acidification on Early Development of Squid (*Doryteuthis pealeii*). *PLoS ONE* **8**: e63714. <https://doi.org/10.1371/journal.pone.0063714>
- Kassahn KS, Donnellan SC, Fowler AJ, Hall KC, Adams M, Shaw PW. 2003. Molecular and morphological analyses of the cuttlefish *Sepia apama* indicate a complex population structure. *Molecular Biology* **143**: 947-962. <http://dx.doi.org/10.1007/s00227-003-1141-5>
- Kennouche H, Nouar A. 2016. Growth and spawning period of *Sepia officinalis* (Lineaus, 1758) in the Algiers region (centre of Algeria). *Iranian Journal of Fisheries Sciences* **15**: 1500-1510
- Khromov DN, Lu CC, Guerra A, Dong Z, Boletzky SV. 1998. A synopsis of Sepiidae outside Australian waters (*Cephalopoda*: Sepioidea). *Smithsonian Contribution to Zoology* **586**: 77–157.
- Kirkman SP, Blamey L, Lamont T, Field JG, Bianchi G, Huggett JA, Hutchings L, Jackson-Weicht J, Jarre A, Lett C, Lipiński MR, Mafwila SW, Pfaff MC, Samaai T, Shannon LJ, Shin Y-J, van der Lingen CD, Yemane D. 2016. Spatial characterisation of the Benguela ecosystem for ecosystem-based management. *African Journal of Marine Science* **38**: 7-22.
- Kirkman SP, Nsingi KK. 2019. Marine Biodiversity of Angola: Biogeography and Conservation. In: Huntley B, Russo V, Lages F, Ferrand N. (eds) Biodiversity of Angola. Springer. Cham, Switzerland. <https://doi.org/10.1007/978-3-030-03083-4>
- Kirkman SP, Costa DP, Harrison A-L, Kotze PGH, Oosthuizen WH, Weise M, Botha JA, Arnould JPY. 2019. Dive behavior and foraging effort of female Cape seals *Arctocephalus pusillus pusillus*. *The Royal Society of Publishing* **6**: 191369. <https://doi.org/10.1098/rsos.191369>
- Kolding J, Béné C, Bavinck M. 2014. Small-scale fisheries: Importance, vulnerability and deficient knowledge. In: Garcia S, Rice J, Charles A (eds) *Governance of Marine*

*Fisheries and Biodiversity Conservation: Interaction and Co-evolution*. Wiley Blackwell, pp 317-331. <https://doi.org/10.1002/9781118392607.ch22>.

Konda FDM. 2008. Present Status of Fisheries Wealth in Angola. *Journal of Marine Bioscience and Biotechnology* **3**: 1-6

Kopte R, Brandt P, Dengler M, Tchivalanga PCM, Macuéria M, Ostrowski M. 2017. The Angola Current: Flow and hydrographic characteristics as observed at 11°S. *Journal of Geophysical Research: Oceans*. **122**: 1177-1189. <https://doi.org/10.1002/2016JC012374>

Koronkiewicz, A. 1995. Size and maturity differences between trawl and jigger caught short-finned squid *Illex argentinus* (Cephalopoda: Ommastrephidae). *Acta Ichthyologica et Piscatoria* **25**: 97-112.

Krammer R, Baumann K, Heinrich, R. 2006. Middle to late Miocene fluctuations in the incipient Benguela Upwelling System revealed by calcareous nanofossil assemblages (ODP Site 1085A). *Paleogeography, Paleoclimatology, Paleoecology* **230**: 319-334. <http://dx.doi.org/10.1016/j.palaeo.2005.07.022>

Lankester K. 2002. The EU-Angola Agreement and Fisheries in Angola. [http://www.panda.org/downloads/marine/angola\\_fishing\\_brief.doc](http://www.panda.org/downloads/marine/angola_fishing_brief.doc). Accessed: 25/05/2020.

Lass H, Schmidt M, Mohrholz V, Naush G. 2000. Hydrographic and Current Measurements in the area of the Angola-Benguela Front. *Journal of Physiological Oceanography* **30**: 2589 – 2609. [http://dx.doi.org/10.1175/1520-0485\(2000\)030%3c2589:HACMIT%3e2.0.CO;2](http://dx.doi.org/10.1175/1520-0485(2000)030%3c2589:HACMIT%3e2.0.CO;2)

Le Goff R, Daguzan J. 1991. Growth and life cycles of the cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda) in South Brittany (France). *Bulletin of Marine Science*. **49**: 341–348.

Lefkadiou E, Verriopoulos G, Valavanis V. 2007. VII.9. Research on Cephalopod Resources in Hellas. In Papaconstatinou C, Zenetos A, Vassilopoulou V, Tserpes G (eds) *State of Hellenic Fisheries*, pp. 440–451. HCMR Publications, Athens. 466 pp.

- Lipiński, M.R. 1979. Universal maturity scale for the commercially-important squids (Cephalopoda: Teuthoidea). The results of maturity classification of the *Illex illecebrosus* (LeSeur, 1821) populations for the years 1973-1977. International Commission for the Northwest Atlantic Fisheries. 79/II/38:40pp.
- Lipiński MR. 1987. Food and the feeding of *Loligo vulgaris reynaudii* from St Francis Bay, South Africa. In *The Benguela and Comparable Ecosystems*. Payne AIL, Gulland, JA and Brink KH (Eds). *South African Journal of Marine Science* **5**: 557-564.  
<https://doi.org/10.2989/025776187784522513>
- Lipiński MR. 1994. Differences among basic biological parameters in a population of chokka squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) sampled by three methods. *South African Journal of Marine Science* **14**: 281-286.  
<https://doi.org/10.2989/025776194784287021>
- Lipiński MR. 1998. Cephalopod life cycles: Patterns and Exceptions. *South African Journal of Marine Science* **20**: 439 -447. <https://doi.org/10.2989/025776198784126205>
- Lipiński MR, Underhill LG. 1995. Sexual maturation in squid: quantum or continuum? *South African Journal of Marine Science* **15**: 207-223
- Lipiński MR, Roeleveld MAC, Augustyn CJ. 1992. First study on the ecology of *Sepia australis* in the southern Benguela ecosystem. *Veliger* **35**: 384-395.
- Lipiński MR, Butterworth DS, Augustyn CJ, Brodziak JKT, Chrsty G, Des Clers S, Jackson GD, O'Dor RK, Pauly D, Purchase LV, Roberts MJ, Roel BA, Sakurai Y, Sauer WHH. 1998. Cephalopod fisheries: a future global upside to past overexploitation of living marine resources? Results of an international workshop, 31 August – 2 September 1997, Cape Town, South Africa, *South African Journal of Marine Science* **20**: 463-469. <https://doi.org/10.2989/025776198784126557>
- Lipiński MR, van der Vyver F, Shaw PW, Sauer WHH. 2016. Life cycle of Chokka squid *Loligo reynaudii* in South African waters. *African Journal of Marine Science* **38**: 589 – 593. <https://doi.org/10.2989/1814232X.2016.1230074>

- Lipiński MR, Mwanangombe CH, Durholtz D, Yemane D, Githaiga-Mwicigi J, Sauer WHH. 2020. Age estimates of chokka squid *Loligo reynaudii* off South Africa and their use to test the effectiveness of a closed season for conserving this resource, *African Journal of Marine Science* 42: 461-471.
- Lishchenko F, Perales-Raya C, Barrett C, Oesterwind D, Power A, Larivain A, Laptikhovsky V, Karatza A, Badouvas N, Lishchenko A, Pierce G. 2021. A review of recent studies on the life history and ecology of European cephalopods with emphasis on species with the greatest commercial fishery and culture potential. *Fisheries Research* 236. <https://doi.org/10.1016/j.fishres.2020.105847>
- Lloret, Josep & Lleonart, Jordi & Solé, Ignasi & Fromentin, Jean-Marc. 2001. Fluctuations of landings and environmental conditions in the North-Western Mediterranean Sea. *Fisheries Oceanography*. 10: 33-50. 10. <http://dx.doi.org/10.1046/j.1365-2419.2001.00151.x>
- Mangold, K. 1987. Reproduction. In Boyle PR (eds) *Cephalopod Life Cycles*, Academic Press, London, pp.157–200.
- Mangold KM, Young RE, Nixon M. 1993. Growth versus maturation in cephalopods. In: Okutani T, O'Dor RK, Kubodera T (eds) *Recent Advances in Fisheries Biology*. Tokai University Press, Tokyo, Japan, pp. 697-703.
- Mangold-Wirz K. 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie Milieu* 13: 1-285
- Martini M. 2013. Illegal, unreported and unregulated fishing and corruption. *U4 Expert Answer* 392: 1-9.
- Martins HR. 1982. Biological studies of the exploited stock of *Loligo forbesii* (Cephalopoda) in the Azores. *Journal of the Marine Biological Association of the United Kingdom* 62: 799–808. <https://doi.org/10.1017/S002531540007034X>
- Martins RS, Perez JAA, Schetini CAF. 2004. The squid *Loligo plei* around Santa Catarina Island, Southern Brazil: Ecology and Interactions with Coastal Oceanographic environment. *Journal of Coastal Research* 38: 1285–1290.

- Mather D, Britz PJ, Hecht PJ, Sauer WHH. 2003. An Economic and Sectoral Study of the South African Fishing Industry. Volume 1. Economic and regulatory principles, survey results, transformation and socio-economic impact. Report prepared for Marine and Coastal Management, Department of Environmental Affairs and Tourism, by Rhodes University.
- Meeuwis JM, Lutjeharms JRE. 1990. Surface thermal characteristics of the Angola-Benguela Front. *South African Journal of Marine Science* **9**: 261-279.  
<https://doi.org/10.2989/025776190784378772>
- Melli V, Riginella E, Nalon M, Mazzoldi . 2014. From Trap to Nursery. Mitigating the Impact of an Artisanal Fishery on Cuttlefish Offspring. *PLoS ONE* **9**: e90542.  
<https://doi.org/10.1371/journal.pone.0090542>
- Melo YC, Sauer WHH. 1999. Confirmation of serial spawning in the chokka squid *Loligo vulgaris reynaudii* off the coast of South Africa. *Marine Biology* **135**: 207-313.
- Ministry of Environment. 2014. 5<sup>th</sup> National Report on Biodiversity in Angola 2007-2012. 54pg
- Mohrholz V, Bartholomae CH, van der Plas AK, Lass HU. 2008. The seasonal variability of the northern Benguela undercurrent and its relation to oxygen budget on the shelf. *Continental Shelf Research* **28**: 424-441.  
<http://dx.doi.org/10.1016%2Fj.csr.2007.10.001>
- Molfese, C, Beare D, Hall-Spencer J. 2014. Overfishing and the replacement of demersal finfish by shellfish: an example from the English Channel. *PLoS ONE* **9**.  
<https://doi.org/10.1371/journal.pone.0101506>
- Moreno A, Pereira JMF, Arvanitidis C, Robin JP, Koutsoubas D, Raya CP, Cunha MM, Balguerias E, Denis V. 2002. Biological variation of *Loligo vulgaris* (Cephalopoda: Loliginidae) in the eastern Atlantic and Mediterranean. *Bulletin of Marine Science* **71**: 515-534

- Moreno A, Pereira J, Cunha M. 2005. Environmental influences on age and size at maturity of *Loligo vulgaris*. *Aquatic Living Resources* **18**: 377-384
- Mott, CL. 2010. Environmental Constraints to the Geographic Expansion of Plant and Animal Species. *Nature Education Knowledge* **3**: 1-72
- Mouritsen OG, Styrbaek K. 2018. Cephalopod Gastronomy – A Promise for the Future. *Frontiers in Communication* **3**. <https://doi.org/10.2289/fcomm.2018.00038>
- Mqoqi M, Lipiński MR, Salvanes AGV. 2007. The ecology of *Sepia australis* (Cephalopoda: Sepiidae) along the south coast of South Africa. *ICES Journal of Marine Science*.**64**: 945–955.
- Mullon C, Fréon P, Cury P. 2005. The dynamics of collapse in world fisheries. *Fish and Fisheries* **6**: 111-120.  
<https://doi.org/10.1111/j.1467-2979.2005.00181.x>
- Munnik KC. 2012. The relationship between coastal oceanographic variability and the spatial distribution of *Argyrosomus coronus* on the west coast of southern Africa. MSc thesis, University of Cape Town, South Africa.
- Mwanangombe CH, Durholtz D, Yemane D, Githaiga-Mwicigi J, Sauer WHH, Lipiński MR. 2021. Growth rates of the chokka squid *Loligo reynaudii* d'Orbigny, 1845 (Cephalopoda: Myopsida: Loliginidae) off South Africa, investigated over two years. *Folia Malacologia*. 29: 153-162.
- Nalwa MK, Kumar R, Jaiswar AK, Swamy RP. 2005. Morphometry, length-weight relationship and biology of *Sepia aculeata* (d'ORBIGNY, 1848) from Mumbai Coast, India. *Journal of Indian Fisheries Association* **32**: 19-27.
- Neige P. 2021. The geography of body size in cuttlefishes (Cephalopoda, Sepiidae). *Swiss Journal of Palaeontology* **140**: 17. <https://doi.org/10.1186/s13358-021-00231-1>
- Neves A, Cabral H, Segueira V, Figueiredo I, Moura T, Gordo LS. 2009. Distribution patterns and reproduction of the cuttlefish *Sepia officinalis* in the Sado estuary

(Portugal). *Journal of the Marine Biological Association of the United Kingdom* **89**: 579–584. <https://doi.org/10.1017/S0025315409002677>

NOAA. Trends in Atmospheric Carbon Dioxide. Earth System Research Laboratory Global Monitoring Division. Available online: <https://www.esrl.noaa.gov/gmd/ccgg/trends/> (accessed on 17 July 2020).

Norman MD, Nabhitabhata J, Lu CC. 2016. An updated checklist of the cephalopods of the South China Sea. *Raffles Bulletin of Zoology Supplement* **34**: 566-592.

O'Brien CE, Roubledakis K, Winkelman IE. 2018. The Current State of Cephalopod Science and Perspectives on the Most Critical Challenges Ahead from Three Early-Career Researchers. *Frontiers in Physiology* **9**.  
<https://doi.org/10.3389/fphys.2018.00700>

OCAR 2002. Appraisal Report, Artisanal Fisheries Development Project, Republic of Angola. African Development Fund ANG/PAAF/2002/01. Luanda, Angola. 58pp

O'Dor RK. 1998. Can understanding squid life-history strategies and recruitment improve management? *South African Journal of Marine Science* **20**: 193-206.  
<https://doi.org/10.2989/025776198784126188>

O'Dor RK, Webber DM. 1991. The constraints on cephalopods: why squid aren't fish. *Canadian Journal of Zoology* **64**: 1591-1605.

Olyott LJH, Sauer WHH, Booth AJ. 2006. Spatio-temporal patterns in maturation of the chokka squid (*Loligo vulgaris reynaudii*) off the coast of South Africa. *ICES Journal of Marine Science* **63**: 1649-1664. <https://doi.org/10.1016/j.icesjms.2006.06.011>

Olyott LJH, Sauer WHH, Booth AJ. 2007. Spatial patterns in the biology of the chokka squid, *Loligo reynaudii* on the Agulhas Bank, South Africa. *Reviews in Fish Biology and Fisheries* **17**: 159-172.

- Önsoy B, Salman A. 2005. Reproductive biology of the common cuttlefish *Sepia officinalis* (Sepiida: Cephalopoda) in the Aegan Sea. *Turkish Journal of Veterinary Science* **29**: 613-619.
- Oosthuizen A, Roberts M. 2009. Bottom temperature and in situ development of chokka squid eggs (*Loligo vulgaris reynaudii*) on mid-shelf spawning grounds, South Africa. *ICES Journal of Marine Science* **66**: 1967-1971.
- Ostrowski M, da Silva JCB, Bazik-Sangolay B. 2009: The response of sound scatterers to El Niño– and La Niña–like oceanographic regimes in the southeastern Atlantic. *ICES Journal of Marine Science* **66**: 1063–1072. [https:// doi.org/10.1093/icesjms/fsp102](https://doi.org/10.1093/icesjms/fsp102)
- Ospina-Alvarez A, Juan SdJ, Pablo P, Ainsworth G, Matos F, Pita C, Villasante S. 2021. Main actors in the Cephalopod Global Trade Network: a graph theory analysis. [10.21203/rs.3.rs-721404/v1](https://doi.org/10.21203/rs.3.rs-721404/v1).
- Otjacques E, Repolho T, Paula JR, Simão S, Baptista M & Rosa R. 2020. Cuttlefish Buoyancy in Response to Food Availability and Ocean Acidification. *Biology* **9**: 147. <https://doi.org/10.3390/biology9070147>
- Pal M, Kardani HK, Kumar V, Sarman V. 2020. Food and feeding habits of pharaoh cuttlefish, *Sepia pharaonic* Ehrenberg, 1831, along the Gujart coast of North-eastern Arabian sea. *Journal of Experimental Zoology India* **2**: 1685-1694
- Paterson B, Sowman M, Raemaekers S, Russel D, Nkosi L, Draper K, Willemse N (eds). 2014. Strengthening the Human Dimension of an Ecosystem Approach to Fisheries Management in the BCC region. FINAL REPORT of FAO-BCC Project EAF 09/12. Windhoek. Benguela Current Commission. 93 pp
- Pauly D & Zeller D. 2016. Catch reconstructions reveal that global marine fisheries are higher than reported and declining. *Nature Communications* **7**: 10244. <https://doi.org/10.1038/ncomms10244>
- Pecl GT, Moltshaniwskyj NA. 2006. Life history of a short-lived squid (*Sepioteuthis australis*) resource allocation as a function of size, growth, maturation and hatching season.

*ICES Journal of Marine Science* **63**: 995-

1004. <https://doi.org/10.1016/j.icesjms.2006.04.007>

Pecl GT, Jackson GD. 2008. The potential impacts of climate change on inshore squid: biology, ecology and fisheries. *Review in Fish Biology and Fisheries* **18**: 373–385.

Perales Raya C. 2001. Determinación de la edad y estudio del crecimiento del choco (*Sepia hierredda* Rang, 1837), el calamar (*Loligo vulgaris* Lamarck, 1798) y el pulpo (*Octopus vulgaris* Cuvier, 1797) de la costa noroccidental africana. PhD thesis, University of La Laguna, Spain. 192 pp.

Piatkowski U, Pierce GJ, Morais de Cunha M. 2001. Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. *Fisheries Research* **52**: 5-10.

Pierce GJ, Guerra A. 1994. Stock assessment methods used for cephalopod fisheries. *Fisheries Research* **21**: 255-285.

Pierce GJ, Boyle PR, Hastie LC, Key LN. 1994. The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Fisheries Research* **21**: 17 – 41. [https://doi.org/10.1016/0165-7836\(94\)90095-7](https://doi.org/10.1016/0165-7836(94)90095-7)

Pierce GJ, Valavanis VD, Guerra A, Jereb P, Orsi-Relini L, Bellido JM, Katara I, Piatowski U, Pereira J, Balguerías E, Sobrino I, Lefkaditou E, Wang J, Santurtun I, Boyle PR, Hastie LC, MacLeod CD, Smith JM, Viana M, González Á, Zuur AF. 2008. A review of cephalopod-environment interactions in European Seas. *Hydrobiologia* **612**: 49-70.

Pierce GJ, Allcock L, Bruno I, Bustamante P, González Á, Guerra, Á, Jereb P, 2010. Cephalopod Biology and Fisheries in Europe: ICES Cooperative Research Report. No. 303.

Pierce G, Belcari P, Challier L, Cherel Y, González Á, Guerra A, Jereb P, Kouéta N, Lefkaditou E, Moreno A, Pereira J, Piatkowski U, Pita C, Robin, JP, Roel B, Santos M, Santurtún M, Seixas S, Zumholz K. 2010. The future of cephalopod populations, fisheries, culture, and research in Europe. ICES Cooperative Research Report. 30. <https://doi.org/10.17895/ices.pub.5414>

- Pinczon Du Sel G, Blanc A, Daguzan J. 2000. The diet of the cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda) during its life cycle in the Northern Bay of Biscay (France). *Aquatic Sciences* **62**: 167-178. <https://doi.org/10.1007/PL00001329>
- Postuma FA, Gasalla MA. 2010. On the relationship between squid and the environment: artisanal jigging for *Loligo plei* at São Sebastião Island (24°S), southeastern Brazil. *ICES Journal of Marine Science* **67**: 1353–1362. <https://doi.org/10.1093/icesjms/fsq105>
- Potts WM, Henriques R, Santos CV, Munnik K, Ansorge I, Dufois F, Booth AJ, Kirchner C, Sauer WH, Shaw PW. 2014. Ocean warming, a rapid distributional shift, and the hybridization of a coastal fish species. *Global Change Biology* **20**: 2765-2777. <https://doi.org/10.1111/gcb.12612>
- Potts WM, Götz A, James N. 2015. Review of the projected impacts of climate change on coastal fishes in southern Africa. *Reviews in Fish Biology and Fisheries*. <https://link.springer.com/article/10.1007/s11160-015-9399-5>
- Pramöd G. 2017. Angola – Country Report, 8 pages, In: Policing the Open Seas: Global Assessment of Fisheries Monitoring Control and Surveillance in 84 countries, IUU Risk Intelligence - Policy Report No. 1, Canada, 814 pages.
- Raemaekers S, Sowman M. 2015. Community-level socio-ecological vulnerability assessments in the Benguela Current Large Marine Ecosystem. Report prepared for the Food and Agricultural Organisation (FAO) and the Benguela Current Commission (BCC). University of Cape Town, South Africa. 140pp.
- Raya CP, Balguerías E, Fernández-Núñez MM, Pierce GJ. 1999. On reproduction and age of the squid *Loligo vulgaris* from the Saharan bank (north-west African coast). *Journal of the Marine Biological Association of the United Kingdom* **79**:111–120. <https://doi.org/10.1017/S002531549700012X>
- Reid A, Jereb P, Roper CFE. 2005. Family Sepiidae: In: Jereb P, Roper CFE (eds). *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Vol 1. Chambered nautilus and sepioids (Nautilidae, Sepiidae, Sepiolidae,*

*Sepiadariidae, Idiosepiidae and Spirulidae*). FAO Species Catalogue for Fisheries Purposes No. 4. Vol. 1. Rome: FAO, pp 57-152.

- Repolho T, Baptista M, Pimentel MS, Dionísio G, Trübenbach K, Lopes VM, Calado R, Diniz M, Rosa R. 2014. Developmental and physiological challenges of octopus (*Octopus vulgaris*) early life stages under ocean warming. *Journal of Comparative Physiology B* **184**: 55–64. <https://doi.org/10.1007/s00360-013-0783-y>
- Richardson T. 2011. The Taxonomy, Life History and Population Dynamics of Blacktail, *Diplodus capensis* (Perciformes: Sparidae), in southern Angola. MSc Thesis, Rhodes University.
- Richardson Temm G, Marshood R, Stedman-Edwards P. 2008. The Global Fisheries Crisis, Poverty and Coastal Small-Scale Fishers.
- Ricker WE, Carter NM. 1958. Handbook of computations for biological statistics of fish populations. No 119. The Fisheries Research Board of Canada. Queen's printer and controller of stationary, Ottawa.
- Roberts MJ. 1998. The influence of the environment on chokka squid *Loligo vulgaris reynaudii* spawning aggregations: steps towards a quantified model. *South African Journal of Marine Science* **20**: 267- 284.
- Roberts M. 2005. Chokka squid (*Loligo vulgaris reynaudii*) abundance linked to changes in South Africa's Agulhas Bank ecosystem during spawning and the early life cycle. *ICES Journal of Marine Science* **62**: 33-35. <https://doi.org/10.1016/j.icesjms.2004.10.002>
- Roberts M, Sauer WHH. 1994. The environment, the key to understanding the chokka squid *Loligo vulgaris reynaudii* life cycle and fishery? *Antarctic Science* **6**: 249-258.
- Roberts MJ, Barange M, Lipiński MR, Prowse MR. 2002. Direct hydroacoustic observations of chokka squid *Loligo vulgaris reynaudii* spawning activity in deep water. *South Africa Journal of Marine Science* **24**: 387-393.

- Roberts MJ, Downey NJ, Sauer WH. 2012. The relative importance of shallow and deep shelf spawning habitats for the South African chokka squid (*Loligo reynaudii*). *ICES Journal of Marine Science* **69**: 563 – 571. <https://doi.org/10.1093/icesjms/fss023>.
- Rocha F, Castro BG, Gil MS, Guerra A. 1994. The diets of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Northwestern Spanish Atlantic waters. *Sarsia* **79**: 119-126. <https://doi.org/10.1080/00364827.1994.10413552>
- Rocha F, Guerra A, Gonzalez AF. 2001. A review of reproductive strategies in cephalopods. *Biological Reviews* **76**: 291-304. <https://doi.org/10.1017/s1464793101005681>
- Rodhouse PG. 2001. Managing and forecasting squid fisheries in variable environments. *Fisheries Research* **54**: 3-8. [http://dx.doi.org/10.1016/S0165-7836\(01\)00370-8](http://dx.doi.org/10.1016/S0165-7836(01)00370-8)
- Rodhouse PG. 2005 World squid resources. In: *Review of the state of world marine fishery resources*. Rome, Food and Agriculture Organization, 175-187. FAO fisheries technical paper, 457.
- Rodhouse PGK, Pierce GJ, Nichols OC, Sauer WHH, Arkhipkin AI, Laptikhovskiy VV, Lipiński ML, Ramos J, Gras M, Kidokoro H, Sadayasu K, Pereira J, Lefkaditou E, Pita C, Gasalla M, Haimovici M, Sakai M, Downey N. 2014. Environmental effects on cephalopod population dynamics: implications for management of fisheries. *Advances in Marine Biology* **67**: 99–233.
- Roeleveld MAC, Lipiński MR, van der Merwe MG. 1993. Biological and ecological aspects of the distribution of *Sepia australis* (Cephalopoda: Sepiidae) off the south coast of southern Africa. *South African Journal of Zoology* **28**: 99 – 106. <https://doi.org/10.1080/02541858.1993.11448301>
- Roeleveld MAC. 1998. The status and importance of cephalopod systematics in southern Africa. *South African Journal of Marine Science* **20**: 1-16. <https://doi.org/10.2989/025776198784126296>
- Roper C, Sweeney J, Nauen C. 1984. Cephalopods of the world, an annotated and illustrated catalogue of species of interest to fisheries. *FAO Fisheries Synopsis* **3**: 1-127.

- Rosa R, Trübenbach K, Repolho T, Pimentel M, Faleiro F, Boavida-Portugal JMB, Dionlsio G, Leal M, Calado R, Pörtner HO. 2013. Lower hypoxia thresholds of cuttlefish life stages living in a warm acidified ocean. *Proceedings of the Royal Society, B* **280**. <https://doi.org/10.1098/rspb.2013.1695>
- Rosa R, Trübenbach K, Pimentel M.S, Boavida-Portugal J, Faleiro F, Baptista M, Dionlsio G, Calado R, Pörtner HO, Repolho T. 2014. Differential impacts of ocean acidification and warming on winter and summer progeny of a coastal squid (*Loligo vulgaris*). *Journal of Experimental Biology* **217**: 518–525. <https://doi.org/10.1242/jeb.096081>
- Rosa R, Pissarra V, Borges FO, Xavier J, Gleadall IG, Golikov A, Bello G, Morais L, Lishchenko F, Roura A, Judkins H, Ibáñez CM, Piatkowski U, Vecchione M, Villanueva R. 2019. Global Patterns of Species Richness in Coastal Cephalopods. *Frontiers in Marine Science* **6**: 469. <https://doi.org/10.3389/fmars.2019.00469>
- Rosenberg AA, Kirkwood GP, Crombie JA, Beddington JR. 1990. The assessment of stocks of annual squid species. *Fisheries Research* **8**: 335-350.
- Royer J, Pierce GJ, Foucher E, Robin JP. 2006. The English Channel stock of *Sepia officinalis*: Modelling variability in abundance and impact of the fishery. *Fisheries Research* **78**: 96–106. <https://doi.org/10.1016/j.fishres.2005.12.004>
- Sasikumar G, Mohamed KS, Bhat US. 2013. Inter-cohort growth patterns of pharaoh cuttlefish *Sepia pharaonis* (Sepioidea: Sepiidae) in Eastern Arabian Sea. *Revista de Biología Tropical* **61**: 1-14.
- Sasikumar, G, Mohamed, K., Rohit, P. and Sampathkumar, G. 2015. Policy guidance on cuttlefish fishery using Fish Aggregating Devices 2015. *CMFRI Marine Fisheries Policy Series* **1**: 1-56.
- Sauer, WHH. 1991. Population characteristics of the choker squid, *Loligo vulgaris reynaudii*, and it's distribution in the Algoa Bay-St Francis Bay area in relation to environmental conditions. MSc thesis, University of Port Elizabeth. 87pp.
- Sauer, WHH. 1995. The impact of fishing on chokka squid *Loligo vulgaris reynaudii* concentrations on inshore spawning grounds in the South-Eastern Cape, South Africa.

*South African Journal of Marine Science* **16**: 185-193.

<https://doi.org/10.2989/025776195784156502>

- Sauer, WHH. & Smale MJ. 1993. Spawning behaviour of *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) in shallow coastal waters of the south-eastern Cape, South Africa. In Okutani T, O'Dor RK, Kubodera T (eds) *Recent Advances in Fisheries Biology*. Tokai University Press, Tokyo. pp 489-498.
- Sauer WHH, Lipiński MR. 1991. Food of squid *Loligo vulgaris reynaudii* D'Orb. (Cephalopoda: Loliginidae) on their spawning grounds in Eastern Cape, South Africa. *South African Journal of Marine Science* **10**: 193-201.
- Sauer WHH, Smale MJ, Lipiński MR. 1992. The location of spawning grounds, spawning and schooling behaviour of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) off the Eastern Cape Coast, South Africa. *Marine Biology* **114**: 97-107. <https://doi.org/10.1007/BF00350859>
- Sauer WHH, McCarthy C, Smale MJ, Koorts AS. 1993. An investigation of the egg distribution of the chokka squid, *Loligo vulgaris reynaudii*, in Krom Bay, South Africa. *Marine Science* **53**: 1066-1077.
- Sauer WHH, Lipiński MR, Augustyn CJ. 2000. Tag recapture of the chokka squid *Loligo vulgaris reynaudii* d'Orbigny, 1845 on inshore spawning grounds on the south-east coast of South Africa. *Fisheries Research* **45**: 283-289. [http://dx.doi.org/10.1016/S0165-7836\(99\)00118-6](http://dx.doi.org/10.1016/S0165-7836(99)00118-6)
- Sauer WHH, Downey NJ, Lipiński MR, Roberts MJ, Smale MJ, Glazer J, Melo Y. 2013. *Loligo reynaudii*, Chokka Squid. In: Rosa R, Pierce G, O'Dor R (eds) *Advances in Squid Biology, Ecology and Fisheries* Nova Science Publishers Inc, New York. pp. 33–72
- Sauer WHH, Gleadall IG, Downey-Breedy N, Doubleday Z, Gillespie G, Haimovici M, Ibáñez CM, Katugin ON, Leporati S, Lipiński MR, Markaida U, Ramos JE, Rosa R, Villanueva R, Arguelles J, Briceño FA, Carrasco SA, Che LJ, Chen C, Cisneros R, Connors E, Crespi-Abril AC, Kulik VV, Drobyazin EN, Emery T, Fernández-Álvarez FA, Furuya H, González LW, Gough C, Krishnan P, Kumar B, Leite T, Lu C,

- Mohamed KS, Nabhitabhata J, Noro K, Petchkamnerd J, Putra D, Rocliffe S, Sajikumar KK, Sakaguch H, Samuel D, Sasikumar G, Wada T, Zheng X, Tian Y, Pang Y, Yamrungrueng A, Pecl G. 2019. World Octopus Fisheries, *Reviews in Fisheries Science & Aquaculture* **29**: 279-429.  
<https://doi.org/10.1080/23308249.2019.1680603>
- Scales KL, Miller PI, Hawkes LA, Ingram SN, Sims DW, Votier SC. 2014. Review: on the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology* **51**: 1575-1583. <https://doi.org/10.1111/1365-2664.12330>
- Schickele A, Francour P, Raybaud V. 2021. European cephalopods distribution under climate-change scenarios. *Scientific Reports* **11**: 3930.  
<https://doi.org/10.1038/s41598-021-83457-w>
- Schön P-J, Sauer WHH, Roberts, MJ. 2002. Environmental influences on spawning aggregations and jig catches of chokka squid, *Loligo vulgaris reynaudii*: A ‘black box’ approach. *Bulletin of Marine Science* **71**: 782-800.
- Seibel BA. 2016. Cephalopod Susceptibility to Asphyxiation via Ocean Incalescence, Deoxygenation, and Acidification. *Physiology (Bethesda)* **31**: 418-429.  
<https://doi.org/10.1152/physiol.00061>
- Selig ER, Kleisner KM, Ahoobim O, Arocha F, Cruz-Trinidad A, Fujita R, Hara M, Katz L, McConney P, Ratner BD, Saavedra-Díaz LM, Schwarz A-M, Thiao D, Torell E, Troëng S, Villasante S. 2016. A typology of fisheries management tools: using experience to catalyse greater success. *Fish and Fisheries* **18**: 543-570.  
<https://doi.org/10.1111/faf.12192>
- Shannon V, O’Toole M. 1999. Integrated Overview of the Oceanography and Environmental Variability of the Benguela Current Region: Thematic Report 2, Synthesis and Assessment of Information on BCLME: October 1998, UNDP, Windhoek, Namibia.
- Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney C, Woods J. 2006. Benguela: Predicting a Large Marine Ecosystem. Elsevier, Amsterdam, 438pp

- Shaw PW, Hendrickson L, McKeown NJ, Stonier T, Naud M-J, Sauer WHH. 2010. Discrete spawning aggregations of loliginid squid do not present genetically distinct populations. *Marine Ecology Progress Series* **408**: 117-127.  
<http://dx.doi.org/10.3354/meps08593>
- Sifner SK, Vrgoč N. 2004. Population structure, maturation and reproduction of the European squid, *Loligo vulgaris*, in the central Adriatic Sea. *Fisheries Research* **69**: 239– 249.  
<https://doi.org/10.1016/j.fishres.2004.04.011>
- Smith H & Basurto X. 2019. Defining Small-Scale Fisheries and Examining the Role of Science in Shaping Perceptions of Who and What Counts: A Systematic Review. *Frontiers in Marine Science* **6**: 236. <https://doi.org/10.3389/fmars.2019.00236>
- Sowman M & Cardoso P. 2010. Small-scale fisheries and food security in countries in the Benguela Current Large Marine Ecosystem (BCLME) region: Angola, Namibia and South Africa. *Marine Policy* **34**: 1163-1170.  
<https://doi.org/10.1016/j.marpol.2010.03.016>.
- Sowman M, Raemaekers S. 2018. Socio-ecological vulnerability assessment in coastal communities in the BCLME region. *Journal of Marine Systems*.  
<https://doi.org/10.1016/j.jmarsys.2018.01.013>.
- Sowman M, Cardoso P, Fielding P, Hauck M, Raemaekers S, Sunde J, Schultz O. 2011. Human dimensions of small-scale fisheries in the BCLME region: An overview. *Prepared for Benguela Current Commission (BCC) and Food and Agricultural Organisation (FAO)*; Food and Agricultural Organisation of the United Nations: Rome, 2011.
- Steer MA, Pecl GT, Moltschaniwskyj NA. 2003. Are bigger calamary *Sepioteuthis australis* hatchlings more likely to survive? A study based on statolith dimensions. *Marine Ecology Progress Series* **261**: 175–182. <http://dx.doi.org/10.3354/meps261175>

- Stewardson CL. 2001. Biology and conservation of the Cape (South African) fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae) from the Eastern Cape Coast of South Africa. PhD Thesis. The Australian National University. 172pp
- Tchupalanga P, Dengler M, Bradt P, Kopte R, Macuéria M, Coelho P, Ostrowski M, Keenlyside NS. 2018. Eastern Boundary Circulation and Hydrography off Angola: Building Angolan Oceanographic Capacities. *Bulletin of the American Meteorological Society* **99**: 1589-1605. <https://doi.org/10.1175/BAMS-D-17-0197.1>
- Teh LCL, Sumaila UR. 2013. Contribution of marine fisheries to worldwide employment. *Fish and Fisheries* **14**: 77-88. <https://doi.org/10.1111/j.1467-2979.2011.00450.x>
- Teh LCL, Pauly D. 2018. Who Brings in the Fish? The Relative Contribution of Small-Scale and Industrial Fisheries to Food Security in Southeast Asia. *Frontiers in Marine Science* **5**: 44. <https://doi.org/10.3389/fmars.2018.00044>
- Tehranifard A, Dastan K. 2011. General morphological characteristics of the *Sepia pharaonic* (cephalopoda) from Persian gulf, Bushehr region. *International Proceedings of Chemical, Biological and Environmental Engineering* **11**: 120-126.
- Thilsted S, Thorne-Lyman A, Webb P, Bogard J, Subasinghe R, Phillips MJ, Allison EH. 2016. Sustaining healthy diets: the role of capture fisheries and aquaculture for improving nutrition in the post-2015 era. *Food Policy* **61**: 126–131. <https://doi.org/10.1016/j.foodpol.2016.02.005>
- Tinbergen, L. & Verwey, J. 1945. Zur biologie von *Loligo vulgaris* Lam. *Arch. Neeri. Zool.* **7**: 213-286.
- Van der Lingen C, Hampton I. 2018. “Climate change impacts, vulnerabilities and adaptations: Southeast Atlantic and Southwest Indian Ocean marine fisheries,” in Barange, M., Bahri, T., Beveridge, M.C.M., Cochrane, K.L., Funge-Smith, S. and Poulain, F eds *Impacts of climate change on fisheries and aquaculture. Synthesis of current knowledge, adaptation and mitigation options* (Rome: FAO). 219–250pp.

- Van der Vyver, J.S.F. 2014. The geographic stock structure of chokka squid *Loligo reynaudii*, and its implications for management of the fishery. MSc thesis, Rhodes University. 128pp
- Van der Vyver JSF, Sauer WHH, McKeown NJ, Yemane D, Shaw PW, Lipiński MR. 2015. Phenotypic divergence despite high gene flow in chokka squid *Loligo reynaudii* (Cephalopoda: Loliginidae): implications for fishery management. *Journal of Marine Biological Association of the United Kingdom* **96**: 1507-1525. <https://doi.org/10.1017/S0025315415001794>
- Vasconcelos P, Pereira F, Carvalho AN, Gaspar MB. 2018. Weight-length Relationships and Relative Growth of the Cuttlefish (*Sepia officinalis*): Causes and Effects of Hypoallemetry. *Thalassas: An International Journal of Marine Sciences* **34**: 323-331. <https://doi.org/10.1007/s41207-018-0067-0>
- Vecchione M, Allcock L, Piatkowski U, Jorgensen E, Barratt I. 2009. Persistent elevated abundance of octopods in an overfished Antarctic area. *Smithsonian at the Poles: Contributions to International Polar Year Science*, Smithsonian Institution Scholarly Press. Washington, DC. pp. 197-203
- Veicht JA. 2002. Surface thermal characteristics of the Angola-Benguela front (ABFZ) from analysis of 18 years of satellite data. Hons Thesis, University of Cape Town, South Africa, 48pp
- Veicht JA, Florenchie P, Schillington FA. 2006. Seasonal and interannual fluctuations of the Angola-Benguela Frontal Zone (SBFZ) using 4.5km resolution satellite imagery from 1982 to 1999. *International Journal of Remote Sensing* **27**: 989-1000
- Villanueva R, Perricone V, Fiorito G. 2017. Cephalopods as Predators: A Short Journey among Behavioural Flexibilities, Adaptations, and Feeding Habits. *Frontiers in Physiology* **8**: 598. <https://doi.org/10.3389/fphys.2017.00598>

- Vizy EK, Cook KH, Sun X. 2018. Decadal change of the south Atlantic ocean Angola–Benguela frontal zone since 1980. *Climate Dynamics* **51**: 3251–3273.  
<https://doi.org/10.1007/s00382-018-4077-7>
- Wang J, Pierce GJ, Boyle PR, Denis V, Robin JP, Bellido JM. 2003. Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences – a case study using trawl fishery data in French Atlantic coastal, English Channel, and adjacent waters, *ICES Journal of Marine Science*. **60**: 1149-1158. [https://doi.org/10.1016/S1054-3139\(03\)00118-8](https://doi.org/10.1016/S1054-3139(03)00118-8)
- Ward P, Boletzky S. 1984. Shell implosion depth and implosion morphologies in three species of *Sepia* (Cephalopoda) from the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* **64**: 955-966.
- Ward A, Signa D. 2017. Reducing post-harvest fish losses for improved food security, SMARTFISH Programme.
- Watanuki N, Rodriguez E, Blanco R, Badan R. 1993. Introduction of cuttlefish basket traps in Palawan, Philippines. pp. 627-631. In: Okutani T, O'Dor RK, Kubodera T (eds) *Recent Advances in Fisheries Biology*. Tokai University Press, Tokyo, Japan, pp. 627-631.
- Watanuki N, Kawamura G. 1999. A review of cuttlefish basket trap fishery. *South Pacific Study* **19**: 31–48.
- Wenger, C. and Abulfotuh, D. 2019. *Rural Migration in the Near East and North Africa – Regional trends*. Cairo, FAO. 80 pp.
- Wickens PA, David JHM, Shelton PA, Field JG. 1991. Trends in harvests and pup numbers of the South African fur seal: implications for management. *South African Journal of Marine Science* **11**: 307-326.
- Wickens PA, Japp DW, Shelton PA, Kriel F, Goosen PC, Rose B, Augustyn CJ, Bross CAR, Penney AJ, Krohn RG. 1992. Seals and fisheries in South Africa — competition and conflict. *South African Journal of Marine Science* **12**: 773-789.  
<https://doi.org/10.2989/02577619209504741>

- Winkler et al. 2019. A snapshot assessment of the diet of Cape fur seals *Arctocephalus pusillus pusillus* at Ilha dos Tigres, Angola. *African Journal of Marine Science* **41**: 443-447. <https://doi.org/10.2989/1814232X.2019.1683069>
- Woodson CB, Litvin SY. 2015. Ocean fronts drive marine fishery production and biogeochemical cycling. *PNAS* **112**: 1710-1715. <https://dx.doi.org/10.1073%2Fpnas.1417143112>
- World Bank 2012. The Hidden Harvest. The global contribution of capture fisheries. World Bank. Washington DC. 69pp
- World Bank. 2019. Climate Change and Marine Fisheries in Africa: Assessing Vulnerability and Strengthening Adaption Capacity. World Bank. Washington DC. 68pp
- Worldometer. 2021. Population of Angola (2020 and historical). Retrieved August 15, 2021. <https://www.worldometers.info/world-population/angola-population/>
- Xavier JC, Walker K, Elliot G, Cherel Y, Thompson D. 2014. Cephalopod fauna of South Pacific waters: new information from breeding New Zealand wandering albatrosses. *Marine Ecology Progress Series* **513**: 131-142.
- Xavier J, Allcock A, Cherel Y, Lipiński M, Pierce G, Rodhouse P, Rosa R, Shea E, Strugnell JM, Vidal E, Villanueva R, Ziegler A. 2015. Future challenges in cephalopod research. *Journal of the Marine Biological Association of the United Kingdom* **95**: 999-1015. <https://doi.org/10.1017/S0025315414000782>
- Xavier JC, Peck LS, Fretwell P, Turn. 2016. Climate change and polar range expansions: could cuttlefish cross the Arctic? *Marine Biology* **163**. <https://doi.org/10.1007/s00227-016-2850-x>
- Yesilyurt IN, Türeli C, Duysak Ö. Growth Parameters of the Cuttlefish, *Sepia officinalis* Linnaeus, 1758 from the Karataş Coasts of the Mediterranean Sea, Turkey. 3<sup>rd</sup> International Congress on Advances in Bioscience and Biotechnology (ICABB), July 10-14, 2019 Kiev, Ukraine. 25-36.

*Appendix 1*

*LULA QUESTIONNAIRE*

Locality: \_\_\_\_\_ Date \_\_\_/\_\_\_/\_\_\_ Time \_\_\_:\_\_\_

*Section 1: Demographics of the fishers*

- 1.1. Name of Skipper/Fisherman:
- 1.2. Age:
- 1.3. Sex:
- 1.4. Where do you live?

*Section 2: Characteristics of the vessel, methods of fishing and preservation*

- 2.1. Type of boat:
- 2.2. Category: Semi commercial / Artisanal / Subsistence / Other
- 2.3. Percentage of time spent drifting and/or anchored
- 2.4. Method: hand lines/beach seine/trammel nets/pots/other
- 2.5. Handlines: number used
- 2.6. Ice/No Ice?

*Section 3: Income and expenditure*

- 3.1. How far did you travel to come fishing today? (kilometres one way)
- 3.2. What method of transport did you use and what is the cost?
- 3.3. If using own vehicle, please specify the number of passengers. How many of the passengers are fishing?
- 3.4. How much do you spend on fishing tackle per trip? Boat fuel?

- 3.5. How much was spent on fishing gear in the past month and the past 12 months?
- 3.6. Is the boat your own? YES / NO / SHARED. If no, who owns it?
- 3.7. Do you get a salary or a percentage of the catch?
- 3.8. How much do you earn on average each month?
- 3.9. Do you pay the crew? YES / NO
- 3.10. Do you pay per kg of lula caught or per day?
- 3.11. Are you paid per day or per kg? How much do you earn?
- 3.12. How much do you spend on boat maintenance (repair, license) per year?
- 3.13. What happens to your catch?
  - Eat it
  - Sell it
  - Exchange it
- 3.14. Where do you sell your catch? Has this changed over the last 5 years?
- 3.15. What price so you get for your catch? Has this changed over the last 5 years?

*Section 4: Importance of fishing as a source of livelihood and employment.*

- 4.1. How many years have you been fishing?
- 4.2. Do you have other work as well as fishing?
- 4.3. What percentage of your income is from fishing?
- 4.5. Are you the only breadwinner? If not percentage contributions from other members?
- 4.5. How important is fishing to your family income? How many dependants do you have?
- 4.6. How important is Lula in terms of your income from fishing?

*Section 5: Quantify catch and effort within the fishery, assess whether changes in catch have been noticed as well as address any concerns regarding the fishery which may have been raised.*

- 5.1. How many times have you fished in the past week? Past month? Past 12 months?
- 5.2. Do you ever fish at night? YES / NO. How often in the last 12 months?
- 5.3. What day and time did you start fishing on this trip? When did you stop?
- 5.4. Have you caught anything? Yes/ No **Indicate catch below.**
- 5.5. What size lula do you generally catch?
  - Small (<16cm)
  - Medium (16-20cm)

- Large (20-24cm)
- Extra Large (>24cm)

5.6. Has fishing effort in this area increased or decreased in the last 5 years?

5.7. When did this start happening?

5.8. Has your catch changed in the last five years?

5.9. In which ways is your current catch in this area different from that in the past?

- More lula
- Fewer lula
- Bigger lula
- Smaller lula
- No difference
- I don't know

5.10. For how many months of the year do you catch lula?

5.11. What is the best time of the year to catch lula?

5.12. Is there a shift in the biomass over the year? If so, please describe the movement?

5.13. Where do the lula go when you are not catching?